Patterns and Disturbance-Induced Drivers of Plant Diversity and Endemism on High Elevation Islands

Dissertation

zur

Erlangung des akademischen Grades

Doctor rerum naturalium (Dr. rer. nat.)

an der Fakultät für Biologie, Chemie und Geowissenschaften

der

Universität Bayreuth

vorgelegt von

Severin David Howard Irl

geboren am 06.06.1983 in Vilshofen, Deutschland

Bayreuth, im Oktober 2014

Die vorliegende Arbeit wurde im Zeitraum von August 2010 bis Dezember 2014 in Bayreuth an der Professur für Störungsökologie unter Betreuung von Frau Professor Dr. Anke Jentsch angefertigt.

Vollständiger Abdruck der von der Fakultät für Biologie, Chemie und Geowissenschaften der Unicersität Bayreuth genehmigten Dissertation zur Erlangung des akademischen Grades eines Doktors der Naturwissenschaften (Dr. rer. nat.).

Dissertation eingereicht: 29.10.2014

Zulassung durch die Promotionskommission: 05.11.2014

Wissenschaftliches Kolloquium: 16.12.2014

Amtierender Dekan: Prof. Dr. Rhett Kempe

Prüfungsausschuss:

Prof. Dr. Anke Jentsch	(Erstgutachterin)
PD Dr. Gregor Aas	(Zweitgutachter)
Prof. Dr. Thomas Köllner	(Vorsitz)
Prof. Dr. Cyrus Samimi	

„In the case of […] islands we see the importance of taking account of past conditions of sea and land and past changes of climate, in order to explain the relations of the peculiar or endemic species of their fauna and flora; and we may even see an indication of the effects of climatal changes in the northern hemisphere, in the north temperate or alpine affinities of many of the plants, [...]"

Alfred Russel Wallace (1895) Island life. 2nd Edition. Macmillan, London.

„In the north-east part of La Palma, inland, is a spacious high mountain, steep on all sides, called la Caldera, i.e. the Cauldron. [...] All inside the cauldron abounds with herbage, and is covered with laurels, te-a or pitch-pine, palms, lignum Rhodium, and retamas, [...]"

Juan de Abreu y Galindo (1764) The history of the discovery and conquest of the Canary Islands. Translated into English by George Glas. Dodsley, London.

Contents

1. Introduction

1.1 Why high elevation island science?

My personal motivation for this dissertation aims at better understanding the processes and mechanisms, either natural or human-induced, which shape patterns in nature such as species diversity, endemism and speciation. I contribute to improve the knowledge in different scientific sub-disciplines by addressing research questions originating from very different topics, such as treeline science, theoretical ecology, road ecology, invasion and conservation ecology, biogeography, and climate change ecology, and combining all these subjects in an island ecological framework. In my opinion, to achieve such an interdisciplinary goal, no better research object exists than islands, in particular high elevation islands.

High elevation islands or *HEIs* are fascinating research objects for ecologists, biogeographers and evolutionary biologists. Like all islands, HEIs are definite entities with clear boundaries (i.e. surrounded by the ocean) but also possess strong elevational and other environmental gradients leading to relatively high species richness and endemism (Whittaker & Fernández-Palacios 2007). Consequently, HEIs are hotspots of diversity, and thus, among other things, contributing significantly to global biodiversity (Kreft et al. 2008). Due to the dynamic nature of speciation on islands, HEIs are particularly well suited to study 'evolution in the making', emphasizing the excellent suitability of HEIs as natural evolutionary laboratories (Losos & Ricklefs 2009). Many island species, especially island endemics, are highly range-restricted and deserve a particular conservation focus as their regional extinction within the HEI – which may be driven by direct human actions such as land use change and habitat destruction or by indirect human effects such as climate change - will lead automatically to their global extinction. Last but not least, diversity itself is a fascinating topic in its own right, and HEIs harbor an incredible variety of unique species, life forms and habitats.

This dissertation aims at contributing to bridge the gap between island biogeography (i.e. the study of patterns and processes *between* islands) and island ecology (i.e. the study of patterns and processes *within* a single island) using the example of HEIs. These two different scales are therefore represented in the following summary of manuscripts: **Manuscripts 3, 4, 5** and **6** address island ecological topics, while **Manuscripts 1, 2** and **7** focus on large-scale island biogeographical patterns. Besides having a strong focus on empirical and experimental research, this thesis also addresses several important theoretical issues in ecology and biogeography. Table 1 gives a short summary of the manuscripts used in this dissertation.

1

Table 1. Short summary of the manuscripts presented in this dissertation, indicating authorship, topic and the major findings.

	First author	Topic	Major finding(s) and interpretation
Manuscript 1	Yes	Global analysis of the drivers of island treeline elevation	- Island maximum elevation and not latitude is the main driver of island treeline elevation - Treeline elevation decreases from the mainland through continental to oceanic islands
Manuscript 2	No	Introduction of the elevation-driven ecological isolation hypothesis	- Elevation-driven ecological isolation drives speciation on islands - Proposed mechanism: Increase of geographic and ecological isolation with elevation
Manuscript 3	Yes	Impact of introduced herbivores on shrub diversity in the summit scrub of La Palma	- *A. viscosus* subsp. *spartioides* is mono-dominant - Climatically better-adapted shrub species are present but introduced herbivores have driven some to the brink of extinction
Manuscript 4	Yes	Impact of introduced herbivores and fire on plant diversity and seedling recruitment in the summit scrub of La Palma	- Introduced herbivores decrease, fire increases plant diversity and seedling establishment - Possible regime shift induced by introduced herbivores through preferential browsing of endangered species
Manuscript 5	Yes	Influence of roads on endemic plant species on La Palma	- Surprisingly, roads have a positive effect on endemic richness and endemicity - Roadside cliffs act as 'safe sites' by protecting the endemics from introduced herbivores and fire - Many endemics are adapted to rupicolous conditions
Manuscript 6	Yes	Environmental determinants of species richness, endemic richness and endemictiy on La Palma	- Climate (i.e. precipitation seasonality and climatic rarity) and topography are important drivers for island-scale plant diversity and endemism - Spatially decoupled hotspots of species richness, endemic richness and endemicity have strong implications for conservation management
Manuscript 7	No	Review on the impact of global climate change on oceanic island floras	- Climate change will have far-reaching impact on oceanic island floras (esp. the interacting effects of climate change with land use changes) - Particularly threatened systems: Stability-dependent cloud and laurel forests and alpine ecosystems - Research gap: So far most climate change research has focused on continental systems. More and more specific island research needed.

1.2 High elevation islands – A global perspective

1.2.1 Global distribution and characterization of high elevation islands

In this dissertation I define islands as geographical entities that are completely surrounded by oceanic waters (Whittaker & Fernández-Palacios 2007). Islands of varying size, origin, age and elevation can be found throughout all oceans of the world. Besides being natural evolutionary experiments or so-called 'nature's test tubes' (Losos & Ricklefs 2009), islands possess 25% of global biodiversity but only cover 3% of the land surface area. Thus, islands contribute disproportionally to global biodiversity (Kreft et al. 2008). In general, islands possess relatively low total species richness but exhibit high degrees of endemism (Kier et al. 2009). In particular, this holds true for mountainous and high elevation islands because these islands are usually large in area and display high topographic complexity. Often they can be considered climatic mini-continents with a high diversity of vegetation units tracking the elevational changes in climatic conditions and the (often) anisotropic differentiation due to prevailing wind systems such as trade winds (Giambelluca et al. 1986, Irl & Beierkuhnlein 2011, Garzón-Machado et al. 2013) or monsoonal wind systems (Scholte & De Geest 2010). In consequence, islands are highly valuable objects for ecological, evolutionary and biogeographic research questions (Losos & Ricklefs 2009) but also important for nature conservation where multiple threats have emerged (e.g. climate change, introduced species, human-induced disturbances, etc.; Courchamp et al. 2003, Caujapé-Castells et al. 2010, Kueffer et al. 2010, Courchamp et al. 2014, **Manuscript 3, 4, 5, 7**).

In the context of this dissertation I would like to present the concept of high elevation islands (HEIs). I define HEIs as islands that reach from coastal to at least alpine habitats, hence covering a complete altitudinal ecosystem gradient. Additionally, HEIs must reach a minimum elevation of at least 1000 m in order to possess gradients strong enough for a differentiation of ecosystems and sufficient species turnover. I focus on low to mid latitude islands (i.e. roughly <55°N and <50°S). Even though high latitude islands can reach considerably higher elevations than 1000 m, they are excluded for the following reasons: First, the treeline on high latitude islands (as the lower elevational limit of the alpine zone) is generally quite low (for a more detailed description see **Manuscript 1**), resulting in only short gradients of the zone of ecological activity (i.e. the terrestrial areas on HEIs in which life and most biological processes occur) and low overall ecological niche space (i.e. the total niche space provided by a given area for species to occupy; Janzen 1967, Brown 2014 and references therein). Second, most high latitude islands were completely covered by glaciers during the last glacial maximum (LGM; Egholm et al. 2009), leaving only little time for processes such as speciation and the evolution of endemic species, which are a key issue in this thesis.

HEIs are not randomly distributed throughout the world's oceans (Fig. 1). Most islands in general but also most HEIs in particular are found within the tropics. Weigelt et al. (2013) estimated that 65% of the world's islands are found between the Tropic of Cancer and the Tropic of Capricorn. In addition, island elevation follows a latitudinal gradient. Parallel to the latitude-elevation relationship on the continent, island elevation displays a hump-shaped distribution with the highest island peaks found in

the tropics (**Manuscript 1**). This phenomenon has been largely related to the efficient erosive effect of large glaciers at high latitudes during the LGM, referred to as the *glacial buzzsaw* (Egholm et al. 2009). New Guinea (4884 m a.s.l.), Big Island (Hawaii; 4205 m a.s.l.), Borneo (4095 m a.s.l.), Taiwan (3952 m a.s.l.) and Sumatra (3805 m a.s.l.) are positioned between 23°N and 4°S and constitute the five highest islands in the world (Gillespie & Clague 2009).

1.2.2 Oceanic vs. continental islands

HEIs can be distinguished into two main types. On the one hand, we find *oceanic* islands of volcanic origin (e.g. hotspot or rift volcanism), on the other, *continental* islands (Whittaker & Fernández-Palacios 2007). Oceanic islands, per definition, have never had contact with other landmasses during their island *life cycle* (Whittaker et al. 2008, Fernández-Palacios et al. 2011). This *life cycle* begins with the initial volcanic activity, the emergence of the island from the sea and the subsequent strong ontogeny leading to the maximum elevation of the island due to high volcanic activity. After the cessation of volcanic activity erosive processes take over, first leading to high topographic complexity, then to a flat and homogenous island. The *life cycle* ends with the submergence of the island under the sea level, where these former islands remain as so-called *guyots* or seamounts (Fernández-Palacios et al. 2011). Oceanic islands are especially characterized by low species richness, high endemism, relatively young geologic age and relatively small area (Whittaker & Fernández-Palacios 2007). Famous volcanic archipelagos featuring HEIs such as Hawaii, Macaronesia (Azores, Madeira, Canary Islands, Cape Verdes), the Mascarenes (La Réunion, Mauritius), Tristan da Cunha or the Galápagos belong to this group (Fig. 1).

Continental HEIs, however, have a complex history of connection and isolation from the continent either due to plate tectonics or sea level changes induced by glacial-interglacial fluctuations (Whittaker & Fernández-Palacios 2007). Continental HEIs can be constituted of a variety of different bedrock (i.e. sedimentary formations, intrusive bedrock but also volcanic material; Weigelt et al. 2013). This type of HEI is usually larger in area, geologically older and reaches higher elevations but is also often more similar to the mainland in terms of species taxonomy. Seven out of the ten highest islands are continental HEIs (**Manuscript 1**). Typical continental HEIs are, for example, New Guinea, the Greater Sunda Islands (e.g. Borneo, Java, Sumatra, Sulawesi), North and South Islands of New Zealand, the main Japanese islands, Madagascar, Newfoundland, Sicily, Corsica or Britain (Fig. 1).
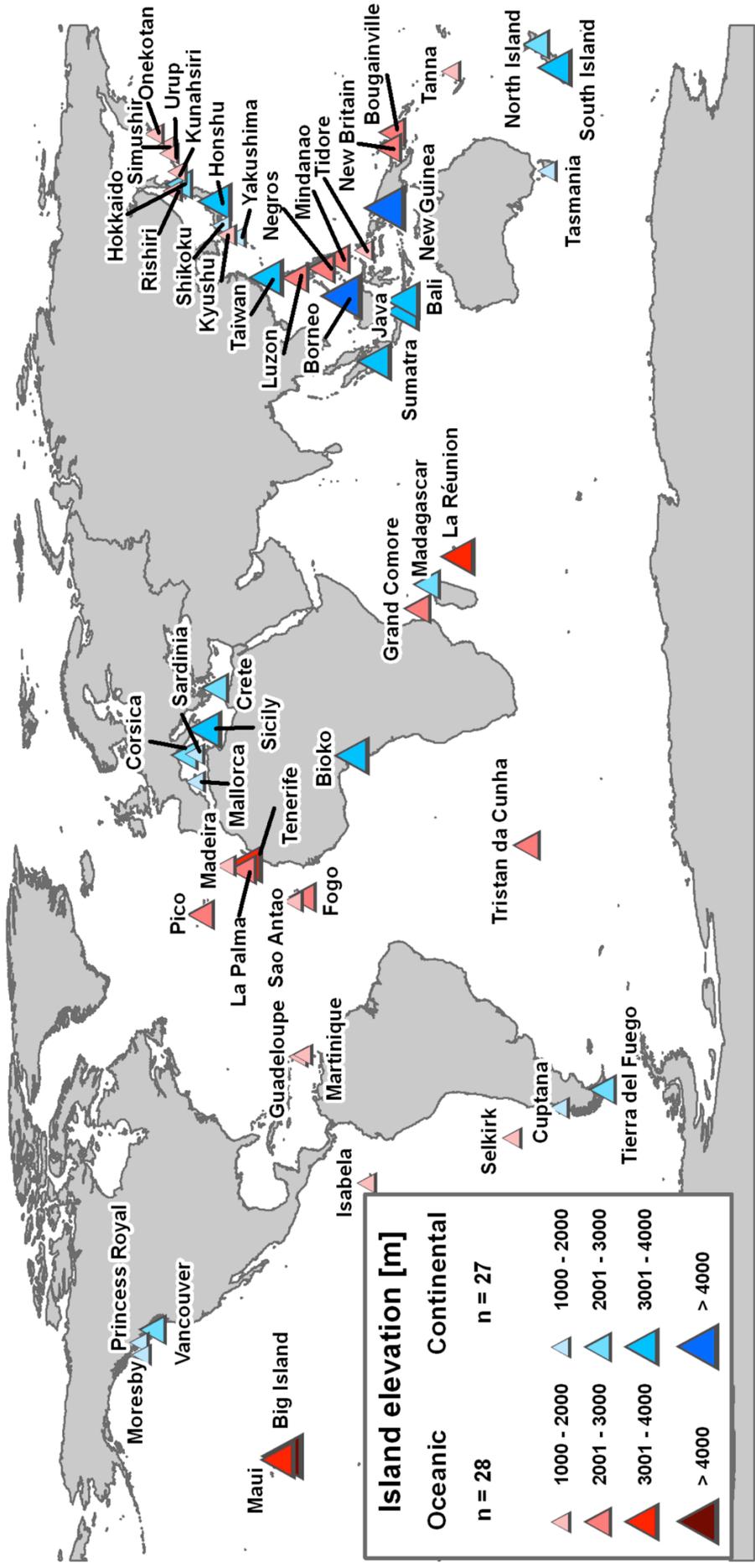
High Elevation Islands of the World

Figure 1. Map of high elevation islands (HEIs), as defined in this dissertation using data acquired for Manuscript 1. HEIs are divided into oceanic (red) and continental (blue) islands (see definition in chapter 1.2.1). Triangles are scaled according to island elevation. Map produced in ArcMap 10 (ESRI Inc., 2010).

5

1.2.3 Latitude-dependent classification of high elevation islands

The definition of HEIs covers a latitudinal range of more than 100°, thus covering several major ecozones (Schultz 2005). Therefore, it is justified to separate three major HEI types, which mainly depend on their latitudinal position and the presence of warm or cool oceanic currents (Kuttler 2013): HEIs dominated by westerlies, HEIs dominated by trade winds and HEIs in equatorial climate conditions (Fig. 2). Several climatic features influence many HEIs, e.g. the Galapagos are subject to trade wind influence only during part of the year. In this classification the most influential climatic feature was selected.

Westerlies high elevation islands

In high to mid latitudes, westerly winds (i.e. the so-called *westerlies*) characterize the major atmospheric wind pattern (Kuttler 2013), also influencing the vegetation types and their elevational distribution on HEIs. However, within this zone two subtypes can be identified: Temperate westerlies HEIs that are in general characterized by overall high precipitation and drier Mediterranean-type HEIs all found within the Mediterranean basin (Fig. 2). For both subtypes, precipitation generally increases with elevation (Lionello et al. 2012). Temperate westerlies HEIs are exposed to frequent westerlies all year round but intensity and frequency depend on the season (Kuttler 2013). Their natural vegetation is generally forested, reaching from mesic lowland forests to humid montane forest and bogs, both possessing broadleaved and/or coniferous tree species (Tutin 1953, Haberle 2003). The alpine vegetation expresses very humid conditions, including bogs and fens (Tutin 1953, Wace & Holdgate 1958). Typical examples are Pico (Azores), coastal islands of NW North America, the northern Japanese Islands, New Zealand, Tristan da Cunha or Selkirk (Juan Fernández Islands; Fig. 2).

The Mediterranean-type HEIs are also influenced by westerlies (esp. in winter), while summers are drier because the Mediterranean basin is influenced by the subtropical high-pressure system during this period (Lionello et al. 2012). Again, we find a clear elevational vegetation zonation ranging from lowland scrub and sclerophyllous forests (or so-called *macchia* or *garrigue*) to mesic mid elevation forests dominated by both deciduous and coniferous tree species (Schönfelder & Schönfelder 2008). Their Alpine vegetation is generally humid but more mesic than for the temperate westerlies HEIs (Vogiatzakis et al 2003). Typical examples are Crete, Corsica, Sardinia, Mallorca and Sicily (Fig. 2).

Trade wind high elevation islands

Trade wind HEIs are, as the name indicates, dominated by the influence of trade winds, although HEIs exist where trade wind influence is only seasonal, e.g. Isabela (Galápagos Islands; Fitter et al. 2007). In the Northern Hemisphere, trade winds come from the Northeast, in the Southern Hemisphere from the Southeast due to the Coriolis effect, which redirects low latitude winds flowing in equatorial direction to the west (Kuttler 2013). The trade wind influence creates an asymmetry of spatial precipitation pattern

and subsequent vegetation units (Ripperton & Hosaka 1942, Pott et al. 2003, Fernández-Palacios et al. 1995, Strasberg et al. 2005). The windward side receives constant year-round precipitation resulting in cloud and laurel forests at mid elevation, the leeward side is drier and with more variable precipitation events, creating dry forests and shrub lands (Fernández-Palacios et al. 1995, Strasberg et al. 2005). On the windward side of trade wind, HEIs precipitation influx is relatively constant and peaks at mid elevations, while on the leeward side precipitation increases with elevation (Giambelluca et al. 1986, Pott et al. 2003, Garzón-Machado et al. 2013). Above the trade wind clouds, the trade wind inversion caps the maximum cloud altitude creating dry climatic conditions with high solar radiation and high diurnal temperature amplitude (Leuschner 2000, Krishnamurti et al. 2013). Characteristic vegetation zones are described in Chapter 1.3.1 for La Palma, Canary Islands – a good example of a trade wind HEI and one of the main focuses in this dissertation. Typical examples are Tenerife and La Palma (both Canary Islands), Maui and Big Island (both Hawaii), Isabela (Galápagos), Fogo and São Antão (both Cape Verdes) and Taiwan (Fig. 2).

Equatorial high elevation islands

The equatorial HEIs are, again as their name suggests, situated in equatorial regions of the tropics and are therefore outside of the trade wind influence (Krishnamurti et al. 2013). This type of HEI is dominated by diurnal convective cloud formation, showing little or no island orientation dependent precipitation pattern and no temperature seasonality. However, seasonal changes in precipitation patterns can occur (Hope 1976, Krishnamurti et al. 2013). Due to the tropical position of these HEIs the zone of biological activity (i.e. from the coast to the upper limit of the alpine zone) is very large and spans a wide temperature and subsequent ecological gradient (*sensu* Janzen 1967). Owing to warm sea temperatures, mangroves and beach strand vegetation characterize coastal ecosystems (Gillespie et al. 2008). With increasing elevation (and precipitation) lowland rainforest is replaced by montane forest, which is followed by hyperhumid cloud forest (Hope 1976, Gillespie et al. 2008). Treeline species are mainly broadleaved tropical taxa (Hope 1976, Ohsawa 1993). As no inversion limiting cloud formation at high altitudes exists, alpine ecosystems are very humid and possess, besides grass- and dwarf shrub species, also bog ecosystems (Hope 1976). Characteristic examples are New Guinea, Bali, Sumatra, Java, Borneo, Bioko or Guadeloupe (Fig. 2).
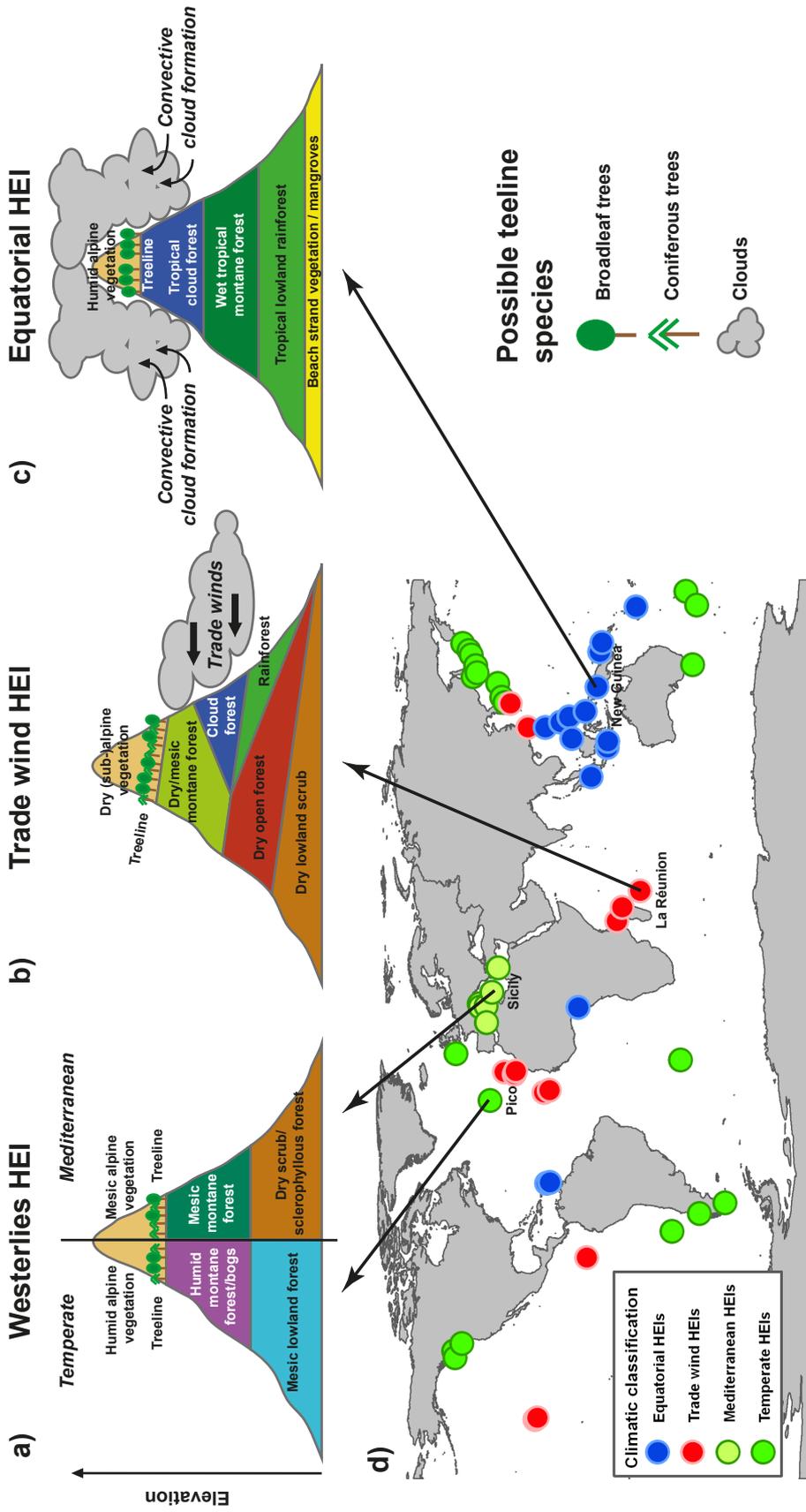
Figure 2. Thematic illustration of the three main climatic types of high elevation islands (HEIs): (a) Westerlies, which are divided into two subtypes: Temperate and Mediterranean (using a simplified vegetation zonation of Pico, Azores taken from Marler & Boatman (1952) and Schönfelder & Schönfelder (2008) for Sicily, respectively), (b) trade wind influenced using the example of La Réunion (simplified from Strasberg et al. 2005) and (c) equatorial HEIs (example redrawn from Gillespie et al. 2008 for tropical Pacific islands). Panel d) displays a global distribution map of the three main HEI types (and the two westerlies subtypes). The separation into the three main types is based on a climatological characterization given in Kuttler (2013) and Krishnamurti et al. (2013). Vegetation zonation for each HEI type shown in this figure is exemplary and can vary within each HEI type. Map produced in ArcMap 10 (ESRI Inc., 2010).

8

1.2.4 Climate on high elevation islands: from stability to variability?

Islands are generally acknowledged for their relative long-term but also short-term climatic stability (Cronk 1997, Whittaker & Fernández-Palacios 2007). However, climatic stability on islands is traditionally based on temperature (Cronk 1997), whereas island precipitation can range from stable to highly variable on a single island (Giambelluca et al. 1986, Dewar & Richard 2007). For example, on subtropical and tropical HEIs within the influence of the trade winds, the areas found within the trade wind cloud layer are characterized by high year-round precipitation, which is directly reflected in the present ecosystems, i.e. cloud forest (Strasberg et al. 2005) or laurel forest (Fernández-Palacios et al. 2011). At the same time, leeward coastal regions as well as high elevation ecosystems situated above the trade wind inversion are highly susceptible to variable and unpredictable precipitation regimes (Giambelluca et al. 1986, García Herrera et al. 2001).

Nevertheless, islands and their ecosystems will face significant changes of climatic conditions in the face of ongoing anthropogenic climate change (IPCC 2014, **Manuscript 7**). Temperature increases and extended droughts have been projected to be nearly certain, while the projections vary greatly with regard to the direction of change (increase or decrease) as well as with regard to spatial and temporal distribution of precipitation. Depending on size, elevation, isolation, latitudinal position of islands or the local human influence, climate change will affect oceanic island floras and their respective ecosystems differently (Please see Fig. 2 and 3 in **Manuscript 7** for details).

1.2.5 Biodiversity and endemism: The 'elevation-driven ecological isolation' hypothesis

Three fundamental processes regulate species diversity on islands: colonization, extinction and speciation (MacArthur & Wilson 1967, Whittaker et al. 2007, 2008). According to the Theory of Island Biogeography postulated by MacArthur and Wilson (1963, 1967), these processes depend on different island characteristics such as isolation and area. In this model isolation reduces species richness and colonization but increases speciation, whereas area increases species richness, colonization and speciation. In their General Dynamic Model (GDM) Whittaker et al. (2007, 2008) introduced another dimension into this model: time, and the subsequent dependency of species richness, endemism and speciation on the ontogeny of oceanic islands. Species richness peaks relatively early in the island *life cycle* because immediate initiation of immigration of new species after the islands emergence from the ocean. However, speciation rates are highest with a certain lag compared to species richness because speciation and the local geographic isolation of topographic complex islands due to erosion take more time than immigration (Steinbauer et al. 2013).

Recently, the importance of elevation for speciation and, consequently, endemism has been identified (Steinbauer & Beierkuhnlein 2010, Kallimanis et al. 2011, Steinbauer et al. 2012), resulting in the *elevation-driven ecological isolation* hypothesis (**Manuscript 2**). This hypothesis postulates that speciation (measured as the percentage of endemics; Emerson & Kolm 2005) increases with elevation due to increasing environmental and geographical isolation. Environmental isolation increases with

elevation because most species colonizing an island are adapted to coastal or lowland conditions, while only few species are pre-adapted to tolerate harsh high elevation conditions (Wilson 1961). Geographical isolation increases with elevation owing to the fact that climatic conditions comparable to high elevation climatic conditions found on an island are substantially farther separated than island and mainland coastal systems, thus reducing species immigration and genetic exchange and giving opportunity for speciation. For example, the nearest coastal region in Morocco from the Canary Islands (Fuerteventura) is found at a distance of about 95 km, while comparable elevations as reached at the treeline on the slopes of Pico del Teide (~2000 m a.s.l.) are located more than 700 km away in the Lower Atlas. I propose that this isolation-induced speciation has substantially contributed to global biodiversity and helps explain the latitudinal diversity gradient.

1.3 Current research on the ecology and plant diversity of high elevation islands

After concentrating on the global perspective, the second part of the introduction will focus on the *within-island* or *landscape* scale, where the importance of certain environmental drivers decreases or other drivers become particularly relevant (Karger et al. 2014). All island ecological case studies of this dissertation are based on La Palma, Canary Islands (**Manuscript 3, 4, 5** and **6**); therefore I will describe the environmental settings of this HEI before presenting several key drivers of species richness, endemism and endemicity on HEI in general and discuss some major disturbances found on La Palma and other HEI.

1.3.1 La isla bonita – a climatic 'mini-continent'

La Palma constitutes a typical HEI of volcanic-oceanic origin of medium age. In the following, I will give an overview of the geological, climatic, floristic and human-mediated features found on this island. Due to its high degree of naturalness, relatively low human population but good infrastructure and its own set of La Palma endemic species, I consider La Palma an ideal island for studying island ecological research questions. In addition, the strong environmental gradients allow testing hypothesis focusing on continental-scale gradients in the spatial context of relatively small oceanic islands.
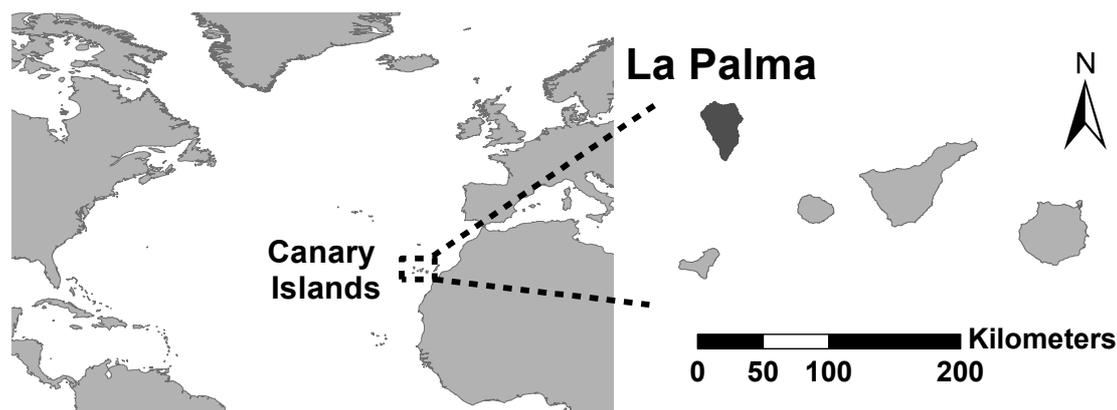
Figure 3. The Canary Islands are situated in the Atlantic Ocean off the northwestern coast of Africa. La Palma is the northwestern-most island of the archipelago. Map was generated in ArcMap 10 (ESRI Inc., 2010).

Geography and geology

La Palma – also called *la isla bonita* ("the pretty island") or *la isla verde* ("the green island") – is a volcanic-oceanic island belonging to the archipelago of the Canary Islands (Spain). The Canary Islands are situated off the coast of northwestern Africa (Morocco) in the Atlantic Ocean (Fig. 3). La Palma is the northwestern-most island of the archipelago (Santa Cruz de La Palma: 28° 41′ N, 17° 46′ W), reaching a maximum elevation of 2426 m a.s.l. at the Roque de los Muchachos. The island is about 45 km long, 27 km wide and measures 706 km^2. With a maximum age of 1.7 Ma, La Palma is the second youngest island of the archipelago after El Hierro (Carracedo et al. 2002). However, geologically, La Palma can be divided into two distinct parts: a northern and a southern part. The northern part of La Palma ('Palaeo-La Palma') is the older half where volcanic activity has already ceased and which is dominated by erosive valley structures (*barrancos*), steep coastal cliffs and the Caldera de Taburiente complex, a large volcanic collapse structure (Fig. 4; Carracedo et al. 2002). The southern part ('Neo-La Palma') consists of younger volcanic material and displays softer geomorphological features. Petrified lava flows, volcanic cones and eruptive ash fields give evidence of recent geological activity (Fig. 3). The most recent volcanic eruption occurred in 1971 at the southern tip of the island, creating the volcanic cone *Teneguía* (Carracedo et al. 2002). The geomorphological features of La Palma also bear witness to several catastrophic mega-landslides throughout its geological history (Carracedo et al. 1999) and discussions exist if another such event might be possibly imminent (Ward & Day 2001, Pararas-Carayannis 2002, Løvholt et al. 2008).

Figure 4. The foreground of this picture shows the gentler slopes of geologically younger Neo-La Palma, while the Caldera de Taburiente complex of older Palaeo-La Palma can be seen in the background. The highest point of the island (Roque de los Muchachos) is located slightly to the left of the central caldera ridge. The trade winds bring clouds from the northeast (right side); however, the inversion caps the cloud layer at around 1700 a.s.l. This picture was taken on the southern ridge (*Cumbre vieja*) facing north at an elevation of about 2000 m. Picture taken in March 2011 by Philipp Gnyoke.

Climatic characteristics

La Palma is characterized by a subtropical-Mediterranean climate with mild temperatures all year round and low annual temperature amplitude (Whittaker & Fernández-Palacios 2007). However, climatic gradients are strong, making La Palma a so-called climatic 'mini-continent': Mean annual temperature ranges from about 22°C at the leeward coast to around 9°C at the highest point (**Manuscript 6**). The Canary Islands are situated within the influence zone of the trade winds, which leads to a strong climatic divide on La Palma, making La Palma a typical trade wind HEI as defined in Chapter 1.2.3. The highest mean annual precipitation has been measured at around 1400 mm on the windward side in the areas of the trade wind clouds (**Manuscript 6**), even though fog drip, which is difficult to measure with traditional rain gauges, can increase the mean annual precipitation by a factor of three or more (Marzol et al. 2011). The leeward side of the island is drier and receives more solar radiation. The lowest mean annual precipitation is found on the leeward coast at around 170 mm (**Manuscript 6**). Due to the subtropical high-pressure system, a trade wind inversion exists roughly above about 1800 m (Fernández-Palacios et al. 1992). This creates relatively harsh conditions with high diurnal temperature amplitude, high solar radiation, and low and variable mean annual precipitation. Infrequent winter low-pressure systems can bring frost, ice and snow (Irl & Beierkuhnlein 2011). In general, the windward side of La

Palma receives the most precipitation of all islands of the archipelago making the vegetation particularly lush and green, hence its nickname 'la isla verde'.

Distribution of zonal vegetation units

The zonal vegetation of La Palma tracks the climatic gradients found on the island (Fig. 4, Irl & Beierkuhnlein 2011, Garzón-Machado et al. 2013). All following vegetation units are based on del Arco-Aguilar et al. (2010); the species names are according to Acebe Ginovés et al. (2010). Halophytic and coastal scrub communities containing species such as *Astydamia latifolia*, *Euphorbia balsamifera*, the archipelago endemic *Euphorbia canariensis*, *Euphorbia lamarckii, Limonium pectinatum* or the La Palma endemic *Sonchus bornmuelleri* characterize the coastal regions. Above, species-rich thermo-sclerophyllous woodlands and lowland scrub exist, characterized by tree species such as *Dracaena draco*, *Juniperus turbinata* subsp. *canariensis*, *Phoenix canariensis* and shrubs such as *Retama rhodorhizoides*, *Kleinia neriifolia*, *Globularia salicifolia*, *Salvia canariensis*, or the La Palma endemics *Aeonium nobile*, *Aeonium davidbramwellii*, *Argyranthemum haouarytheum* and *Echium brevirame*. As this is the main zone of settlement and agriculture, only remnants of the natural vegetation remain. With increasing elevation, the lowland communities are substituted by the drought-prone and fire-adapted Canary Pine forest, which almost exclusively consists of *Pinus canariensis*. The undergrowth is relatively species poor because of introduced herbivore impact (Garzón-Machado et al. 2010), mainly containing species such as *Adenocarpus foliolosus*, *Bystropogon origanifolius*, *Chamaecytisus proliferus* subsp. *proliferus*, *Cistus symphytifolius* or the La Palma endemic *Lotus campylocladus* subsp. *hillebrandii*. The Canary Pine forest ranges from mid elevations to the treeline on the dry leeward side. On the humid windward side a humid evergreen palaeo-endemic laurel forest (or *laurisilva*) substitutes the Canary Pine forest. This laurel forest is a relict of a formerly widespread Tertiary laurel forest, nowadays restricted to the Macaronesian islands (Fernández-Palacios et al. 2011). A high diversity of tree species is found in the laurel forest (e.g. *Laurus novocanariensis*, *Ilex canariensis*, *Persea indica*, *Ocotea foetens*, *Apollonias barbujana* subsp. *barbujana*, *Arbutus canariensis*, *Virburnum rigidum*), although understory species exist as well (e.g. *Crambe santosii*, *Sideritis canariensis*, *Ixanthus viscosus* and the emblematic *Canarina canariensis* or the La Palma endemics *Aeonium goochiae* and *Sonchus palmensis*). Surrounding the laurisilva, the so-called *fayal-brezal* can be found, an evergreen forest containing laurophyllous elements but growing in less humid conditions. Typical tree species of this forest, considered in large parts a human-degraded laurel forest, are *Morella faya* and *Erica arborea* but also shrubs such as *Hypericum grandifolium* or the La Palma endemic *Echium pininana*. Above the treeline at around 2000 m we find a summit scrub or summit broom scrub dominated by the leguminous shrub species *Adenocarpus viscosus* subsp. *spartioides*. However, other shrub and herbaceous species exist as well (e.g. *Genista benehoavensis*, *Spartocytisus supranubius*, *Teline stenopetala* subsp. *sericea*, *Chamaecytisus proliferus* subsp. *proliferus*, *Bencomia exstipulata*, *Echium wildpretii* subsp. *trichosiphon*, *Echium. gentianoides*, *Viola palmensis*) with most being La Palma endemics but severely impacted by introduced herbivores (**Manuscript 3** and **4**). Azonal rupicolous communities exist at all elevations and aspects. As other

volcanic-oceanic islands, La Palma is relatively species poor (658 vascular plant species) but contains its own array of endemics. Of the 193 archipelago endemics, 37 species are single-island endemics (SIEs) globally only distributed on this island (Acebes Ginovés et al. 2010). For a map and pictures of each major vegetation zone, see Fig. 5.

Human settlement and introduced species

Two waves of human settlement have shaped the Canary Islands. The first wave occurred during the settlement of the aboriginal *Guanche* people, presumed to be Berber from North Africa (Moral et al. 1997). Fossil goat bones indicate that humans have inhabited the Canary Islands for at least 2500 years in Fuerteventura (Zöller et al. 2003). It is thought that La Palma was inhabited later because the colonization of Tenerife did not occur until about 2000 years BP as macro-charcoal findings indicate (de Nascimento et al. 2009) and colonization proceeded from east to west. Like on most oceanic islands, no large mammals have ever existed naturally on the Canary Islands; it was the Guanche people who introduced the domestic goat (*Capra hircus*) to the archipelago (Nogales et al. 2006).

The second colonization period is marked by the 'discovery' of the Canary Islands by European conquerors in the XVth century. Ultimately, the Spanish *conquistadores* invaded the Canary Islands and claimed them for the Spanish crown after the submission of the Guanche leaders (González-Reimers et al. 2001). The Spanish – intentionally and unintentionally – introduced a large array of different animals. Most notably are the European rabbit *Oryctolagus cuniculus*, the domestic pig *Sus scrofa domestica*, sheep *Ovis aries*, the muflon *Ovis orientalis orientalis*, different rat species *Rattus* spp. and the feral cat *Felis silvestris catus* (Nogales et al. 2006, Medina & Nogales 2009, Traveset et al. 2009). The last intentional introduction and naturalization of a large mammal is documented from La Palma, where authorities made the rather questionable introduction of the north African Barbary sheep (*Ammotragus lervia*) to the National Park Caldera de Taburiente in order to stimulate big game hunting (**Manuscript 4**). Besides animals, humans introduced many plant species after the Spanish *conquista*. Some have become widespread in natural or semi-natural plant communities (e.g. *Opuntia* spp., *Nicotiana glauca*, *Castanea sativa*, *Vitis vinifera*, *Prunus dulcis*, *Agave* spp. *Ficus carica* and *Pennisetum* spp.; personal observation).

1.3.2 Environmental determinants of species richness, endemic richness and endemicity on HEIs

The major drivers of species richness, endemic richness and endemicity are scale-dependent (Rosenzweig 1995, Crawley & Harral 2001). While at larger scales (e.g. on the inter-island scale) geographic characteristics such as area and isolation are more important, on the landscape or within-island scale of HEIs, environmental conditions are the dominant predictors of species richness and likely also endemic richness and endemicity (Karger et al. 2014).
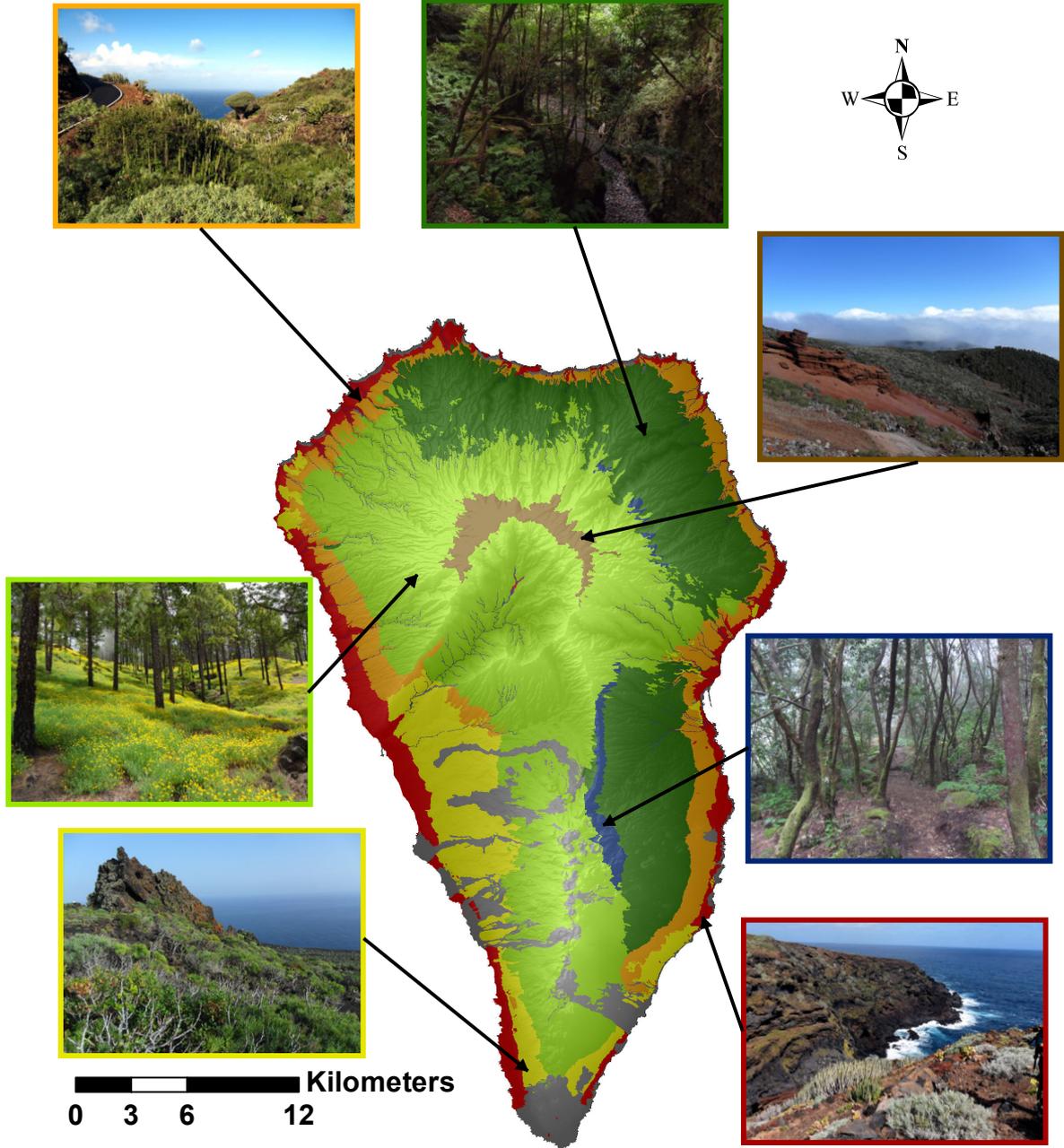
Zonal vegetation units of La Palma

🟥 Halophytic communities / coastal scrub	🟩 Laurel forest
🟨 Lowland scrub	🟦 Fayal-Brezal
🟧 Thermo-sclerophyllous woodland	🟫 Summit scrub
🟩 Canary Pine forest	⬜ no vegtation (lava flows and cones)

Figure 5. Distribution of the main zonal vegetation units of La Palma. The pictures showing typical examples of the respective units illustrate the large diversity of vegetation units, each containing a specific array of plant species. Large parts of the lower elevation communities have been modified due to settlements, agriculture and other human activities. GIS data provided by the Cabildo Insular de La Palma. Map was generated in ArcMap 10 (ESRI Inc., 2010). Pictures taken by Severin D.H. Irl.

Because of the strong climatic gradients, HEIs can be termed *climatic mini-continents*, as they cover climatic gradients (especially regarding temperature and precipitation measures) of approximately continental magnitude on the regional scale of a single island. For example, New Guinea possesses climate conditions ranging from tropical lowland rainforest to (disappearing) glaciated peaks (McAlpine et al. 1983). However, while temperature generally shows little variation within and between years, inter- and intra-annual precipitation distribution can vary quite substantially within a given HEI (e.g. Giambelluca et al. 1986, Dewar & Richard 2007, **Manuscript 6**). This substantially influences the spatial pattern of species richness, endemic richness and endemicity but also leads to specific and sometimes peculiar adaptations in island species (Dewar & Richard 2007). While gigantism and dwarfism are typical for mammals (Lomolino et al. 2013), a characteristic phenomenon for plants is the so-called island woodiness (Carlquist 1974). Island woodiness describes the phenomenon that island plant species of predominantly herbaceous lineages often develop woody life forms such as shrubs and small trees owing to the stable climate conditions and low temperature seasonality of islands.

Strong environmental gradients coupled with the relatively low species richness of insular habitats and the high extinction rates driven by small areas thus offer opportunities for speciation due to the availability of open niche space (Wiens & Graham 2005). As shown in **Manuscript 2** speciation increases, while species richness declines, with elevation on HEIs. However, other environmental drivers besides elevation such as precipitation and topography also influence species richness, endemic richness and speciation (Karger et al. 2014, **Manuscript 6**).

1.3.3 Importance of disturbances on high elevation islands

All HEIs worldwide are – to some degree – influenced by direct and indirect human activities (Sadler 1999). Thus, many HEIs have experienced human-associated disturbances, to which several species might not be adapted regarding their evolutionary history (Bowen & Van Vuren 1997). These disturbances can be considered one of the great unknowns in island ecology, making predictions of future developments of island species and systems highly speculative. Therefore, it is imperative to bridge this knowledge gap, identify patterns and to infer general rules for island ecology. Among other important novel disturbances such as climate change-induced increase of magnitude and frequency of extreme weather events (Loope & Giambelluca 1998, Ross et al. 2008, reviewed in **Manuscript 7**), invasive plant species (reviewed in Kueffer et al. 2010), invasive predators (e.g. Zavaleta et al. 2001, Caujapé-Castells et al. 2010, Nogales et al. 2013), non-native pathogens (Wikelski et al. 2004, Bataille et al. 2009), human degradation of natural island habitat (Brooks et al. 2002, Caujapé-Castells et al. 2010), increasing atmospheric N-deposition (Phoenix et al. 2006), changing hydrology (March et al. 2003) or socio-economic changes of island societies (Reaser et al. 2007, Westphal et al. 2008), this part of my thesis focuses on three major disturbances on islands in general but also HEIs in particular: roads, introduced herbivores and fire.

Roads, endemic plant species and high elevation islands

Roads are among the most widespread human modifications and disturbances of natural ecosystems (Forman & Alexander 1998, Trombulak & Frissel 2000). Besides the direct destruction of natural habitat through road construction, roads fundamentally change the physical environment (e.g. hydrology, light availability, nutrient availability, toxins and heavy metal input, soil material and grain size, etc.) and create edge effects, which have a far-reaching effect into the natural surroundings, especially in forests (Forman & Alexander 1998, Spellerberg 1998, Delgado et al. 2007). Roads also lead to a fragmentation of formerly connected natural habitats and are considered as vectors for the introduction of non-native and invasive species (Spellerberg 1998, Trombulak & Frissel 2000).

Plant species richness has been shown to increase in roadside communities when compared to the surrounding vegetation (Spellerberg 2002). However, this increase is mainly due to the increase of non-native plant species found in roadside communities (Arévalo et al. 2005, Rotholz & Mandelik 2013), even though the impact of non-natives decreases with elevation due to directional ecological filtering (Alexander et al. 2011), bioclimatic origin, and residence time (Haider et al. 2010). Directional ecological filtering reduces non-native richness with increasing elevation, filtering non-natives from the anthropogenic sources in lowlands and the subsequent elimination of small-range specialists (Alexander et al. 2011). This leads to the fact that mainly non-native generalist species with wide ecological amplitude can reach higher elevations, whereas non-native high elevation specialists do not manage to pass through the ecological filter of lowland introduction (Becker et al. 2005, Pauchard et al. 2009, Alexander et al. 2011).

Islands, also HEIs, are susceptible to non-native plant species invasions because of their generally low plant species richness and the often relatively low competitiveness of the endemic flora (Kueffer et al. 2010). Indeed, elevation-dependent trends of non-native plant invasion as in continental systems have been revealed in roadside communities, regarding plant species richness, non-native species (Arévalo et al. 2005, Arteaga et al. 2009, Arévalo et al. 2010), and non-native species composition (Arévalo et al. 2008, Otto et al. 2014) but also for endemics (**Manuscript 5**). Due to their linear structure and movement of vehicles, roads increase the connectivity between many habitats, populations and closely related taxa. This potentially leads to the homogenization of the native and endemic flora (Arévalo et al. 2010) but also to the hybridization of congeners or genetic mixing of populations (van Hengstum et al. 2012), possibly also threatening the genetic integrity of endemics (Francisco-Ortega et al. 2000).

Introduced vertebrate herbivores

On islands, introduced vertebrate herbivores are among the single most destructive agents (Courchamp et al. 2003, Caujapé-Castells et al. 2010), have led to massive degradation of natural island systems (Coblentz 1978, Campbell & Donlan 2005) and possibly also to complete vegetation shifts (Ramirez et al. 2012). Introduced vertebrate herbivores can have severe direct effects on island vegetation (e.g. Coblentz 1978, Courchamp et al. 2003, Garzón-Machado et al. 2010, Ramirez et al.

2012, **Manuscript 3** and **4**) and can also indirectly influence native island systems and species by completely modifying ecosystem properties and functions (e.g. Croll et al. 2005) or by causing extinction of island species, e.g. of endemic prey species via hyperpredation (Courchamp et al. 2001).

Islands are particularly susceptible to introduced vertebrate herbivores because island plant species have developed fewer or no evolutionary traits for herbivore defense (e.g. mechanical, chemical or structural defenses; Bowen & Van Vuren 1997). This makes (poorly defended) endemics more palatable to herbivores and therefore, preferentially consumed (Bowen & Van Vuren 1997). The reason for the poor adaptation of endemics is that most oceanic islands lack large mammals (and thus herbivores). The ocean is a very effective filter for immigration and colonization of large mammals (Paulay 1994), often making the necessity for herbivore defenses in plant evolution obsolete. Recent studies have shown that species-specific evolutionary traits regarding herbivore defense can actually change within decades after herbivore exclusion (Vourc'h et al. 2001, Didiano et al. 2014). The low species richness and functional redundancy of oceanic island floras further increases the susceptibility to disturbances and damage caused by introduced herbivores, potentially leading to co-extinctions (Courchamp et al. 2003).

Two introduced vertebrate herbivores deserve to be highlighted for their impact on island systems: the feral goat (*Capra hircus*) and the European rabbit (*Oryctolagus cuniculus*). These two species have been introduced to virtually every island possessing sufficient vegetation cover and are thus also members of the infamous club of the *world's 100 most invasive species* (Lowe et al. 2000). Feral goat damage has been reported from many major island systems including HEIs around the world, e.g. from the Channel Islands (Coblentz 1978), the Canary Islands (Nogales et al. 2006), the Galapagos Islands (Desender et al. 1999), the Juan Fernández Islands (Haberle 2003) or Hawaii (Spatz & Mueller-Dombois 1973). However, increasingly successful eradication programs have been conducted, which often lead to a fast recuperation of the natural island vegetation (Campbell & Donlan 2005) but also can have unintentional side effects such as the explosive spread of invasive plant species previously kept in check by the herbivore (Zavaleta et al. 2001).

Owing to their high adaptability, large thermal tolerance and high reproduction rates, the European rabbit might be even more widely distributed on the world's islands than the feral goat. The European rabbit can be found from tropical island systems such as Mauritius (North et al. 1994) through subtropical islands (e.g. Canary Islands, Nogales et al. 2006) and temperate islands (e.g. New Zealand, Towns et al. 1997 or the Juan Fernández Islands, Cotinga 2002) to Subantarctic islands such as Macquarie Island (Copson & Whinam 1998). The impact of the European rabbit is twofold: On the one hand, introduced rabbits can directly affect native island vegetation through intense browsing (North et al. 1994, Copson & Whinam 1998, Norbury et al. 2003, **Manuscript 3** and **4**); on the other, introduced rabbits can also alter island food webs and predator-prey interactions (Courchamp et al. 2001). However, many rabbit eradications have been successfully executed on islands, especially using the viral disease *myxomatosis* (North et al. 1994, Priddel et al. 2000, Chapuis et al. 2001).

Human-mediated fires

Globally, natural fires occur at an intermediate position in terms of productivity, i.e. between high productivity forests and low productivity grasslands (Bowman et al. 2014). However, only few island systems are characterized by natural fire regimes, e.g. the Canary Islands (Climent et al. 2004), most Mediterranean islands (Carrión et al. 2010) or Madagascar (Kull 2000), although human interventions have substantially altered the natural fire regimes of these systems (Kull 2000, Carrión et al. 2010). Humans have introduced fire as a major transformatory disturbance to many island systems, e.g. La Réunion (Lagabrielle et al. 2009), New Zealand (McWethy et al. 2010), Hawaii (D'Antonio et al. 2000) or the Channel Islands (Ramirez et al. 2012). A positive feedback cycle between fuel producing invasive plants species (esp. non-native graminoids) and human-induced fire often develops on islands without any natural fire regime. This can lead to massive shifts or even total transformation in vegetation composition, structure and ecosystem functioning of native island systems (Hughes et al. 1991, D'Antonio et al. 2000, Caujapé-Castells et al. 2010). Single fire events have the potential to affect the populations of range restricted native island plant species (esp. endemics) more severely than widespread species (Caujapé-Castells et al. 2010).

On the Canary Islands a natural fire regime was present before human intervention. However, macro-charcoal records indicate that fire frequencies sharply increased after human settlement, (Nogué et al. 2013), potentially even leading to the extinction of certain *Quercus* and *Carpinus* species (de Nascimento et al. 2009). A spatial variation in the distribution of fire occurrence is evident on the Canary Islands. Some ecosystems (e.g. the humid evergreen laurel forest) virtually never burn due to the constant influx of humidity from the trade wind clouds, while others are very fire-prone (e.g. the Canary Pine forest; del Arco-Aguilar et al. 2010). According to Climent et al. (2004) *Pinus canariensis* – the tree species dominating the pine forest – has developed unique adaptation strategies to cope with and even foster fire. First, the Canary Pine is one of the very few representatives of the Pinaceae that has the ability to resprout needles from epicormic shoots from all aboveground organs after the fire event. Second, its several centimeter-thick bark protects it from fire damage (bark thickness of up to 7.2 cm). Third, its long needles (up to 25 cm in length) give the tree the possibility to 'comb out' water from passing clouds, which drips to the ground, enabling it to grow in otherwise low precipitation regions. Fourth, large amounts of highly inflammable needle litter accumulate on the forest floor that increases the probability of fire ignition particularly in dry summer months. Fifth, many cones are serotinous.

On La Palma the Canary Pine forest has a very large distribution (Fig. 4). In general, fire frequency has increased in the last decades owing to man-made fires despite the intense fire management actions that have been undertaken (Garzón-Machado et al. 2012). The increasing fire intensity can severely alter the understory vegetation of the Canary Pine forest (Arévalo et al. 2001).

2. Summarizing discussion and conclusions

In this section I present the major findings identified in my research and discuss their contributions to our current state of knowledge in ecology and biogeography.

2.1 Island treeline elevation – emergence of an unexpected driver

The alpine treeline is an important element defining HEIs, thus a closer characterization of the global pattern of island treeline elevation, as taken in **Manuscript 1**, is necessary. So far, studies on the global treeline pattern have strongly neglected island-specific characteristics such as isolation, small area, young geologic age or low species richness (but see Leuschner 1996). However, island treelines offer the opportunity to study the large-scale drivers of treeline formation without the interacting influences of mass elevation effect (i.e. increasing solar radiation in the interior of large mountain ranges) and continentality (i.e. increasing solar radiation in the interior of continents; Körner 2012).

My research showed that island treeline elevation depends on the position of the island on the latitudinal gradient but, interestingly, more so on maximum island elevation (**Manuscript 1**). In consequence, the highest island treelines are found on high elevation tropical islands. Also, island type (i.e. oceanic or continental island) influences island treeline elevation. Compared to oceanic islands continental islands generally have higher treeline elevations due to their larger area, older age, reduced isolation and higher peaks (**Manuscript 1**). In general, however, I could show that island treeline elevations are lower than on the mainland as postulated by Leuschner (1996) because of the missing mass elevation effect, the negative effect of high cloudiness associated with oceanic climates, the isolation-induced absence of adapted tree species and specific local island climates such as high elevation drought produced by the trade wind inversion (**Manuscript 1**). However, it has been recently shown that although island treelines are generally lower, they still behave in congruence to the lower thermal limit for tree growth, i.e. a minimum root zone temperature during the vegetation period of 7-8°C as proposed by Körner & Paulsen (2004), and are not taxon-specific as previously assumed (Cieraad et al. 2014).

Data for my island treeline study was collected using GoogleEarth (Google Inc. 2013), an innovative sampling method, which is freely available, offers unlimited access and is easy to handle. GoogleEarth combines geo-referenced satellite imagery with a digital elevation model and enables a fairly accurate estimation of position and elevation of treelines. This method allowed me to collect the most extensive dataset on island treeline elevation to my knowledge (n = 85). Although more sophisticated remote sensing methods are available, this sampling method is sufficient to study large-scale biogeographical and macro-ecological patterns, if species identity is not relevant. As a sampling method, GoogleEarth is becoming increasingly important in treeline research as recent publications show, e.g. this is demonstrated by Paulsen & Körner (2014) who applied this method independently of our research approach.

2.2 Going global – explaining global biodiversity with the elevation-driven ecological isolation hypothesis?

Global patterns of biodiversity, especially latitudinal and elevational diversity gradients, are commonly explained by energy availability (i.e. *metabolic theory of ecology*; Brown et al. 2014), biotic interactions (i.e. *diversity begets diversity* hypothesis; Van Valen 1973, Emerson & Kolm 2005) and area (i.e. *species-area relationship*; Losos & Schluter 2000, Kisel & Barraclough 2010). All theories would predict either negative or hump-shaped elevation-speciation relationships owing to the general decrease of temperature, area and species richness with elevation (Rahbek 1995, Körner 2007). However, this does not seem to be the case. As a follow up to **Manuscript 2,** we have collected a dataset of 31 islands and 18 continental mountain systems (with mountains being isolated entities surrounded by a lowland matrix) containing elevation-specific floras and spanning at least a 1000 m elevational gradient. First results find an increase of speciation (measured as the percentage of endemics, Emerson & Kolm 2005) with elevation, which is particularly pronounced in the tropics, for both islands and mountains. The positive elevation-speciation relationship indicates that isolation, as described by the elevation-driven ecological isolation hypothesis (**Manuscript 2**), contributes to global biodiversity and the latitudinal diversity gradient by overriding the other hypothesized drivers of speciation (e.g. temperature, biotic interactions and area) and by acting as so-called *species pumps* during cycles of climate fluctuations (Hughes & Eastwood 2006; Ricklefs & Bermingham 2007).

Janzen (1967) postulated that tropical species occupy smaller elevational ranges than temperate species because temperate species are subject to large seasonal temperature variation while tropical species only experience diurnal temperature variation and little to no seasonal variation. Janzen's influential hypothesis is only based on few examples, but an actual large-scale quantification and validation is still missing (even though attempts have been made to 'revisit' the hypothesis, e.g. by Ghalambor et al. 2006). However, by using our dataset of elevation-specific species ranges spanning from sites in the tropics to temperate regions and referring to Janzen's (1967) seminal paper, we can ask: Are mountain passes really higher in the tropics than in temperate regions and, if yes, can we quantify this effect?

2.3 Regime shift in an alpine ecosystem of a high elevation island? The role of introduced herbivores and fire

The introduced herbivore damage on native island systems has been widely studied due to its importance for ecosystem functioning and species conservation (Courchamp et al. 2003). However, most studies have focused on species-rich lowland scrubs (e.g. Coblentz 1978, Scowcroft & Giffin 1983, Ramirez et al. 2012), low or mid elevation forest (e.g. Wardle et al. 2001, Diet et al. 2004, Garzón-Machado et al. 2012) or subantarctic islands of low richness and low productivity (Leader-Williams et al.

1987, Scott & Kirkpatrick 2008). To my knowledge, the studies presented in this thesis (i.e. **Manuscript 3** and **4**) currently document the only research that has so far been exclusively conducted in the high elevation ecosystem (also known as summit scrub or subalpine vegetation) of an HEI, where the focus is rather on high endemicity than on species richness. Intra-specific herbivore defense capability decreases with elevation (Pellissier et al. 2014), making populations in high elevation ecosystems specifically vulnerable to herbivory.

Although at first glance the summit scrub of La Palma seems relatively natural and undisturbed, our results indicate that introduced herbivores have effectively helped one shrub species to virtual mono-dominance in this system (i.e. *Adenocarpus viscosus* susbp. *spartioides*), indicating a possible herbivore-driven regime shift. However, climatically better-adapted shrub species are actually present as our long-term exclosure experiments reveal (e.g. *Genista benehoavensis*, *Chamaecytisus proliferus* subsp. *proliferus* or *Spartocytisus supranubius*; **Manuscript 3**). In addition, seedling recruitment and seedling richness is severely hindered because introduced herbivores selectively browse rare endemics (**Manuscript 4**). To achieve the long-term conservation of highly endangered species and to realize the full restoration of the natural high elevation ecosystem, massive coordinated eradication programs targeting feral ungulates and rabbits are necessary. However, lacking political will, traditional agricultural practices and a culture of hunting make it highly doubtful that this conservation goal is realistic for La Palma. Also, the high degree of alteration and disturbance in the high elevation ecosystem makes it quite speculative to set scientifically sound restoration goals because we can only imagine what a 'natural' high elevation ecosystem actually looks like.

On La Palma, fires from the Canary Pine forest regularly spread up into the summit scrub, even though many high elevation endemics are considered poorly adapted to fire (Garzón-Machado et al. 2012). The last big fire event in the summit scrub of La Palma occurred in 2005, consuming large parts of the vegetation of the northern and northwestern areas, including some exclosure plots set up by the administration of the Caldera de Taburiente National Park. This natural experiment offered the opportunity to assess the combined impact of introduced herbivores and human-mediated fire on species richness and seedling recruitment of the high elevation ecosystem (**Manuscript 4**). Surprisingly, fire had a positive effect on species richness and seedling establishment, both under herbivore presence and absence when compared to non-fire conditions. To my knowledge this is the first approach specifically targeting a high elevation island system and incorporating the two globally important anthropogenic disturbances: introduced herbivores and fire. So far, other studies on islands, which have targeted this two-factorial combination of disturbances, have only focused on coastal or lowland systems (e.g. Ramirez et al. 2012).

2.4 Are endemics hitchhikers? Novel insights into disturbance-driven road ecology

Although endemics are often an important part of natural island ecosystems (Whittaker & Fernández-Palacios 2007), a focus on the effects of roads on HEIs has been mainly put on non-native species (Arévalo et al. 2005, Arteaga et al. 2009, Arévalo et al. 2010) or native species in general (Otto et

al. 2013). Up to now, only few studies have specifically addressed endemics and endemicity in detail and also only for systems on the continent (e.g. Rotholz & Mandelik 2013). However, endemic plant richness and endemicity in roadside communities are severely affected by roads, but surprisingly not in a negative manner. **Manuscript 5** – to my knowledge the first study specifically targeting the effect of roads on endemic richness and endemicity – describes that endemic richness and endemicity increases in roadside communities when compared to the surrounding vegetation along an elevational and precipitation gradient. I explain this pattern because many rupicolous endemics profit from the newly created roadside cliff habitats and are protected from human-mediated disturbances such as introduced herbivores and fire (Garzón-Machado et al. 2010, del Arco-Aguilar et al. 2010, **Manuscript 3** and **4**). However, these 'safe-sites' are not considered preferential for nature conservation. Rather, the protection of natural habitat of endemics should have top priority due to negative impacts associated with roads and road construction such as destruction of natural habitat (Forman & Alexander 1998), homogenization of island floras (Arévalo et al. 2010), hybridization of closely related taxa (van Hengtsum et al. 2012) threatening the genetic integrity of the Canarian endemics (Francisco-Ortega et al. 2000) and being a vector of non-native plant invasion (Spellerberg 2002).

2.5 Landscape-scale environmental determinants of species richness, endemic richness and endemicity for a climatic mini-continent

For **Manuscript 6** I collected a very extensive dataset of endemic plant species and plant species richness (n = 890 plots / 706 km^2 = 1.26 plots/km^2) to address questions revolving around the landscape-scale relationship of species richness, endemic richness and endemicity with different abiotic factors such as climate and topography. By covering all relevant gradients on a single HEI and by focusing on endemics, which – in the case of SIEs – realize their global niche only on this one HEI, I was able to significantly contribute to our understanding of the processes shaping the distribution of species richness, endemic richness and endemicity in geographical and ecological space. My findings indicate that both climate and topography are of major, but varying importance, depending on the measure in focus. Both eco-evolutionary drivers and human-induced disturbances drive the pattern of species richness, endemic richness and endemicity on the landscape-scale of La Palma.

2.5.1 Spatial patterns

Species richness and endemic richness follow distinct and often diverging patterns in geographical and environmental space (Whittaker & Fernández-Palacios 2007, Lomolino 2010). This is true from a global perspective (Orme et al. 2005) but also for continental (Stohlgren et al. 2005) and island systems (e.g. **Manuscript 6**). On La Palma, this translates to the fact that species richness is highest in the humid mid elevations of the windward side and the steep barrancos of the northern part, whereas the hotspots of endemic richness are found in coastal cliffs, the vertical acclivities in the interior of the Caldera de Taburiente and also in steep barrancos (**Manuscript 6**). The floristic uniqueness, determined by the

percentage of endemic species (i.e. endemicity, Gillespie et al. 2008), shows a very different behavior. It strongly increases with elevation, reaching values of more than 70% for archipelago endemics and up to 100% for single-island endemics at the highest elevations (**Manuscript 6**). This might have major implications for nature conservation because hotspots of species richness, endemic richness and endemicity do not necessarily overlap. In consequence, traditional measures of diversity such as species richness are not able to cover the whole spectrum of biodiversity (Stohlgren et al. 2005). Thus, it is of highest importance that nature conservation and management include a variety of different measures of diversity to be able to achieve overarching conservation goals.

2.5.2 Elevation

Elevation has been long recognized as a fundamental driver in biogeography, ecology and evolution due to its integrating effect of different climatic and other parameters of the physical environment (Körner, 2003). Species richness and elevation can have various relationships, depending on factors like temperature, moisture availability or solar radiation. Some mountainous systems show a monotonic decrease of species richness with elevation (Rahbek 1995, **Manuscript 5, 6**), while others show a moisture-dependent hump-shaped distribution, e.g. in the tropics (Rahbek 1995), the subtropics (Vetaas & Grytnes, 2002) or on HEIs influenced by the trade winds (Steinbauer et al. 2012). A similar importance of elevation, which points in the opposite direction, however, emerges for the endemicity-elevation relationship. As on other islands, elevation increases the specialization and speciation on La Palma due to the increasing harshness of high elevation areas and the increasing geographic distance to climatically similar source regions (**Manuscript 2, 6**). Endemic richness is only poorly connected to elevation because the species set of endemics (as a whole) is adapted to the complete environmental gradient offered by an island where speciation of endemics happened *in situ* (esp. SIEs; Beard et al. 2008, **Manuscript 6**).

2.5.3 Precipitation variability and climatic rarity

Precipitation can display dramatic differences in annual means, seasonality, variability and predictability on a within-island scale, e.g. in Madagascar (Dewar & Richards 2007), La Palma (**Manuscript 6**) and the Canary Islands (García Herrera et al. 2001), Socotra (Scholte & De Geest 2010) or Hawaii (Giambelluca et al. 1986). Dewar & Richards (2007) described how low precipitation predictability has increased the specialization of the fauna of Madagascar, creating a whole array of endemic species. Island floras have undergone similar adaptations. On the Canary Islands several genera representative of the island woodiness phenomenon (Carlquist 1974) can be named, e.g. *Aeonium*, *Argyranthemum*, *Echium*, *Sonchus*, *Plantago* or *Rumex* (Lens et al. 2013). 92% of the endemics of La Palma are actually perennial species, most of them also woody (Shmida & Werger 1992). Although increasing variability and not gradual changes will likely be the major driver of climate change (Jentsch & Beierkuhnlein 2008) and variability has been projected to increase for oceanic systems such as islands

(IPCC 2014), the high tolerance of certain endemics towards short-term climatic variability might actually reduce their extinction risk under current climate change (**Manuscript 6**).

On a within-island scale certain combinations of climatic conditions are more common than others. Based on this finding the concept of climatic rarity was developed by Ohlemüller et al. (2008). The authors could show that on a continental scale, small-ranged species are more likely to be found in rare climatic conditions. In **Manuscript 6** I adapt this concept to endemics, which are generally considered to have relatively small spatial ranges (esp. SIEs; Whittaker & Fernández-Palacios 2007), to the island-scale of La Palma. Here, endemicity, i.e. the degree of specialization of a community, strongly increases with climatic rarity probably because of more available niche space and higher selection pressure due to the increase of climatic harshness with climatic rarity (**Manuscript 6**). All in all, the concept of climatic rarity deserves further attention because it integrates a large variety of different climatic factors, which might affect the distribution of endemic plant species.

2.5.4 Topographic complexity

Topographic complexity, which is connected to the concept of habitat heterogeneity, is positively related to species richness and endemic richness (Hortal et al. 2009). La Palma is a topographically very complex island, possessing steep barrancos, coastal cliffs and very high cliffs in the interior of the caldera (Carracedo et al. 2002). Species richness and endemic richness attain their maxima in these areas (**Manuscript 6**). On the one hand, a complex topography likely renders a large niche space (Whittaker et al. 2008, Steinbauer et al. 2013) as well as an increase in area (Leutner et al. 2011) but is also connected to a high dissimilarity between potential niches. On the other hand, high habitat heterogeneity offers micro-refugia during periods of climatic fluctuation, thus reducing local extinction probabilities (Médail & Diadema 2009). Alternatively, steep and topographically complex areas are likely less strongly impacted by human land use (Niedrist et al. 2009) and the detrimental effects of introduced herbivores (**Manuscript 5**).

2.6 Threats and challenges of climate change for high elevation islands

Climate change is predicted to have major influence on the earth's biota and ecosystems (Parmesan 2006), and HEIs are no exception (**Manuscript 7**). After conducting an extensive literature review, it becomes clear that HEIs are quite vulnerable to global climate change. The current scientific knowledge suggests especially range-restricted endemics generally characterized by small population sizes, small gene pools and poor dispersal abilities to be at risk (Fortini et al. 2013). Also, the combined impact of climate change-induced land use changes and climate change itself are estimated to be of greatest concern for HEI floras. However, large research gaps still exist as climate change science has generally focused on continental systems, while islands are – with few exceptions such as Hawaii (e.g.

Loope & Giambelluca 1998, Benning et al. 2002, Elison Timm et al. 2011, Fortini et al. 2013) – largely underrepresented in assessing the impact of global climate change (**Manuscript 7**).

On HEIs, it is likely that increasing climatic variability and upward range shifts might pose the greatest threat to endemics and other insular species (**Manuscript 7**). Many species and even whole ecosystems on islands are highly specialized to constant and stable climatic conditions. For example, laurel and cloud forests found on HEIs in the tropics and subtropics rely on a constant influx of moisture through trade wind cloud formation (Fernández-Palacios et al. 2011). However, if the intensity or altitude of the trade wind cloud layer changes, this might have the potential to dramatically disrupt these systems (Sperling et al. 2004, Crausbay & Hotchkiss 2010).

Alpine ecosystems on HEIs are probably the ecosystems most threatened by climate change. These systems are often dominated by specialized endemics (e.g. **Manuscript 2**, **3** and **4**) and thus deserve special interest for nature conservation. In addition, these species have small population and range sizes (e.g. **Manuscript 6**). Also, they do not possess the ability to track temperature changes by elevational range shifts because they already occupy the highest elevations (Dullinger et al. 2012). Populations of several iconic alpine endemics have already been shown to decline due to climate change-induced drought, e.g. the Haleakala silversword *Argyroxyphium sandwicense* subsp. *macrocephalum* on Maui, Hawaii (Krushelnycky et al. 2013) or *Helianthemum juliae* on Tenerife, Canary Islands (Marrero-Gómez et al. 2007). Please see **Manuscript 7** and especially Fig. 4 for a more detailed description on the possible effects of changing cloud layer altitude.
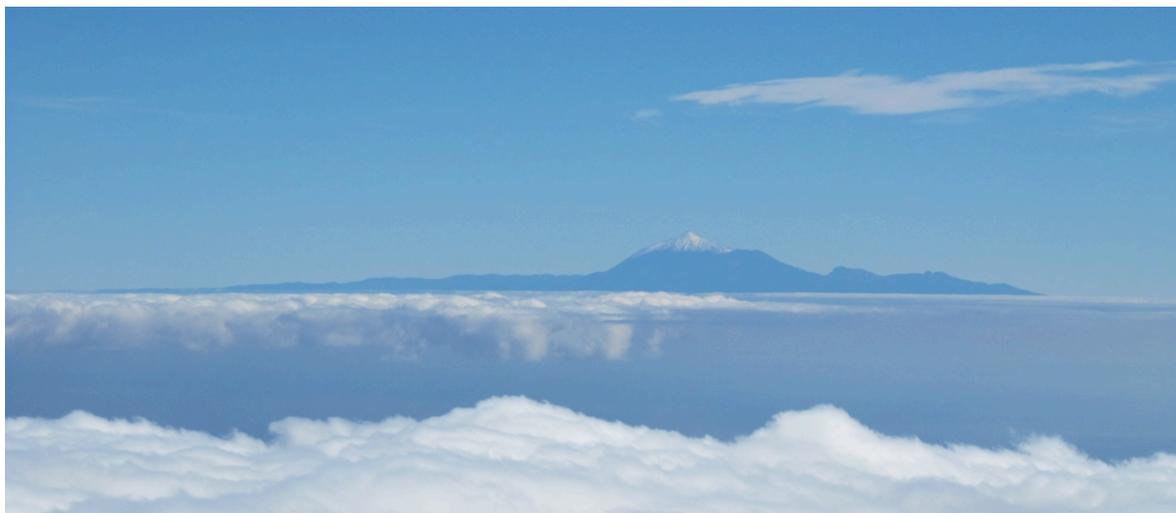
3. Emerging research challenges and frontiers in high elevation island science

In this dissertation I was only able to target certain aspects of research on HEIs and several new and exciting questions have arisen as a result of my research. In the following I would like to present and discuss the eleven most intriguing research questions for future HEI science that reach beyond the issues covered in this thesis. These questions are grouped into three categories: 1) Within-island patterns of species diversity, 2) Disturbance-driven island ecology, and 3) Global patterns.

3.1 Within-island patterns of species diversity

On La Palma, my model HEI, I was able to identify several important environmental drivers of species richness, endemic richness and endemicity using a floristic dataset of unprecedented size (in comparison to the island area) and resolution (100 x 100 m; see **Manuscript 6**). In my opinion, this dataset allows tackling an array of different questions of great interest to the ecology community owing to the spatial nature and the coverage of many different environmental gradients:

1. Recently, ecology has tried to reach beyond the species concept as the basic unit in biodiversity and ecosystem research (Cadotte et al. 2011). A new focus is being put on the functionality of ecosystems and communities, where specific traits or the combination of traits is of major importance (Schleuter et al. 2010). Therefore, it is important to ask how are plant traits such as life form, plant functional type (e.g. N-fixers, succulence, woodiness, flower color), dispersal mode, functional diversity, but also phylogenetic diversity distributed on the within-island scale and are there differences between natives, archipelago endemics and SIEs? Furthermore, I ask what are the major environmental determinants of these different trait-based measures?

2. Species turnover, or β-diversity, has been predicted to change along gradients (e.g. Qian & Ricklefs 2007) but the underlying drivers are still poorly understood, especially for endemic species on HEIs. How is β-diversity distributed within an HEI and what drives these patterns? Are there differences between natives, archipelago endemics and SIEs?

3. How does climate change influence endemic plant species? Does it threaten spatially restricted and poor dispersing SIEs to extinction? Which SIEs are potentially most likely to go extinct? Where would potential conservation areas be most effective and how should conservation programs be designed if considering climate change and future land use change? These questions could be targeted using different species distribution modeling (SDM) techniques such as MaxEnt (Phillips et al. 2006), ensembles (Araújo & New 2007) or n-dimensional hypervolumes (Blonder et al. 2014)

4. Do SIEs really occupy smaller ecological niches than archipelago endemics or natives (Vilenkin et al. 2009), or are they rather (super-)generalists (e.g. Lomolino 2010)? How is a

quantification of their ecological niches possible? Novel methods such as quantifications of n-dimensional hypervolumes (Blonder et al. 2014) might be valuable tools in addressing these questions.

3.2 Disturbance-driven island ecology

Disturbances clearly shape the pattern of species richness and endemism on La Palma. However, our understanding of the disturbance-induced process on HEIs is still in an initial phase, leaving room for further questions. In addition, several follow-up questions arise from the three disturbances studied in this dissertation (roads, introduced herbivores and fire):

5. Roads have been shown to be vectors of non-native plant species in mountainous ecosystems (also HEIs) and non-native plant species richness decreases with elevation according to the directional elevational filtering hypothesis (Alexander et al. 2011). However, a currently unstudied question is how non-native plant species behave along other environmental gradients than elevation such as precipitation, climatic rarity or seasonality and if this behavior differs between islands and archipelagos?

6. Introduced herbivores have been shown to be crucial in shaping ecosystems on the HEIs of the Canary Islands such as pine forests (Garzón-Machado et al. 2010) and the summit scrub (**Manuscript 3** and **4**). However, how do introduced herbivores influence tree rejuvenation in the laurel forest – an iconic ecosystem of the Canaries – and understory diversity? Is it as poor as currently thought or do introduced herbivores depauperate understory diversity, as is the case in the pine forest (Garzón-Machado et al. 2010) and the summit scrub (**Manuscript 4**)?

7. The leguminous shrub *A. viscosus* subsp. *spartioides* is virtually mono-dominant shrub in the summit scrub of La Palma and shows a patchy distribution of living, semi-living, and dead individuals. Do environmental factors such as fire and winter ice storms drive this pattern or are intrinsic drivers responsible, such as cohort dieback?

8. The summit scrub of La Palma has been severely impacted by introduced herbivores, leading to the mono-dominance of *A. viscosus* subsp. *spartioides*. However, why does the floristically very similar summit scrub of Tenerife (del Arco-Aguilar et al. 2010) not show the same dominance of *A. viscosus* subsp. *viscosus* (i.e. a vicariant subspecies), even though the same introduced herbivores and similar environmental conditions are present?

3.3 Global patterns

Explaining large-scale patterns was an integral part of this dissertation, especially in terms of global treeline research, plant diversity and climate change. In particular, the innovative sampling method applied in **Manuscript 1** used to identify island treeline elevations is a promising tool for further treeline research encompassing all landmasses. Climate change is one of the major threats of our times making

estimations of future threats and possible extinctions highly valuable for researchers, decision and policy makers, conservation managers and society in general.

9. Can the island biogeographical determinants of island treeline elevation be transferred to all treelines, also on the mainland? Is it possible to quantify the influence of mass elevation effect and continentality on global treeline elevation?

10. Can we assess the climate change-driven extinction threat of island species on a global scale by combining SDMs with sea level rise models and land use change models?

11. Do tropical species really have smaller elevational ranges than temperate species because of lower temperature seasonality in the tropics? By combining elevation-specific species data from tropical, subtropical and temperate regions, a first global-scale quantification of this hypothesis made by Janzen in 1967 can be achieved, which so far has remained untested but highly cited and influential in ecology (Ghalambor et al 2006).

32

4. Manuscripts presented in this thesis

In the following I will give a short summary of the manuscripts used in this dissertation and present the most important findings of each contribution. Table 2 gives an overview of conference contributions as oral presentations or as posters that I have given at national and international scientific conferences and that deal with the topics and research targeted in this dissertation.

Manuscript 1 is a global study of the latitudinal distribution and other major drivers of island treeline elevation (i.e. an important element in the definition of HEIs) using GoogleEarth as an innovative sampling method. Island treeline elevations are significantly lower and follow a different latitudinal pattern than mainland treelines, mainly owing to the fact that islands lack continental climates and the mass elevation effect, both effective drivers of high treeline elevations. Interestingly, maximum island elevation, and not latitude, is the single best explanatory variable. I argue that maximum island elevation increases island treeline elevation because of increasing cloud layer and the summit syndrome. Island treelines can contribute to the fundamental framework of global treeline distribution because they minimize variation added by mass elevation effect and continentality, which is superimposed onto the global latitude-treeline elevation relationship for mainland treelines.

Manuscript 2 presents the *elevation-driven ecological isolation* hypothesis using the example of two Mediterranean-type HEIs (Crete and Corsica). This hypothesis argues that speciation (measured as the percentage of endemics) increases with elevation on HEIs due to an increasing geographical and ecological isolation with elevation. Geographical isolation indicates that the distance to comparable systems increases with elevation, while ecological isolation deals with the fact that increasing climatic harshness with elevation is an effective filter for species immigration. The paper also argues that *elevation-driven ecological isolation* is not restricted to islands but can be transferred to other terrestrial systems such as continental mountains.

Manuscript 3 focuses on the detrimental effects of introduced herbivores on the endemic flora of the high elevation ecosystem using a 11-yr exclosure experiment in cooperation with the National Park Caldera de Taburiente (La Palma, Canary Islands). Owing to the presence of introduced herbivores, a single shrub species has become mono-dominant in the high elevation ecosystem, even though better-adapted shrub species are present. However, these better-adapted shrub species seem to be preferentially browsed by introduced herbivores, which have even brought some of these shrub species to the brink of extinction.

Manuscript 4 focuses on the combined effects of introduced herbivores and fire on the seedling establishment and species richness of the endemic flora of the high elevation ecosystem of La Palma, Canary Islands using some of the same sites as in **Manuscript 3**. Introduced herbivore presence reduces, while fire increases seedling richness, also in herbivory reference conditions. Introduced herbivores selectively browse on rare endemics, allowing a recuperation of a natural vegetation composition and structure only if introduced herbivores were eradicated from the system.

Manuscript 5 addresses the effect of a man-made disturbance on La Palma, Canary Islands, namely roads, on species richness, endemic richness and the percentage of endemics using a paired approach comparing roadside and surrounding vegetation on an elevational and precipitation gradient. Interestingly, roads have a positive effect on both endemic richness and the percentage of endemics probably because roadside cliffs provide favorable habitat for rupicolous endemics and protect them from other human-mediated disturbances such as introduced herbivores and fire. However, rather than using roadside cliffs for nature conservation, we argue that priority should be given to preserving natural habitat because roads can lead to the homogenization of natural vegetation, hybridization of closely related endemics and act as vectors for invasive plant species.

Manuscript 6 addresses the spatial pattern and environmental drivers of species richness, endemic richness and endemicity on the climatic mini-continent of La Palma using an unprecedented spatial resolution (n = 890; 100 x 100 m resolution), covering the whole island and all relevant environmental gradients. Precipitation variability decreases species richness but increases endemicity because speciation is boosted by variable conditions, to which most incoming species are not pre-adapted. Climatic rarity works in a similar fashion by creating spatially restricted niches for speciation in rare climatic conditions, thus increasing endemicity but decreasing species richness. Topographic complexity increases species richness and endemic richness by providing larger niche space for species to accumulate. Interestingly, hotspots of species richness, endemic richness and endemicity are often spatially decoupled, providing important implications for the conservation of the complete spectrum of biodiversity. All in all, both topography and climate are important drivers of species richness, endemic richness and endemicity on the landscape-scale of La Palma but their influence varies depending on the measure in focus.

Manuscript 7 reviews the existing literature on the potential effects of anthropogenic climate change on oceanic island floras, endemics species and natural island vegetation. Although large research gaps still exist because most climate change-related research has focused on continental systems, the reviewed studies indicate clear threats to oceanic island floras. HEIs containing high degrees of endemism possess systems adapted to stability (e.g. cloud and laurel forests) and high elevation ecosystems. These systems are highly threatened because climate change is projected to increase climatic variability or because high elevation ecosystems cannot shift their ranges farther upward, respectively. Small-ranged endemics might also be threatened because of small population sizes, small gene pool, poor competition and stochastic effects. However, we argue that the most serious threat will likely come from interacting effects of direct climate change impacts and climate change-associated shifts in human activities.

Table 2. Presentation of research at scientific conferences

Date	Organization	Conference and location	Title	Type
07/2014	University of Hawaii at Manoa	Island Biology 2014, Honolulu, Hawaii, USA	Biodiversity and endemism on an environmental mini-continent: effects of climatic variability, climatic rarity and habitat diversity	Oral
03/2014	Ecological Society of Germany, Austria and Switzerland (GfÖ)	8th Annual Meeting of the Specialist Group for Macroecology, Halle, Germany	Global pattern of treeline elevation on islands	Oral
09/2013	Ecological Society of Germany, Austria and Switzerland (GfÖ)	43rd Annual Meeting, Potsdam, Germany	Regional patterns of endemism and diversity on a mountainous oceanic island	Oral
01/2013	International Biogeography Society (IBS)	6th Biennial Meeting, Miami, Florida, USA	Treelines and island biogeography – a global perspective using an innovative research approach	Poster
10/2012	Bayreuth Center of Ecology and Environmental Research (BayCEER)	BayCEER Workshop, Bayreuth, Germany	Burned and devoured - Or how do introduced herbivores and fire influence the endemic high-elevation flora of La Palma, Canary Islands?	Poster
08/2012	University of Hawaii and Office of Mauna Kea Management	Vulnerable islands in the sky: science and management of tropical island alpine & sub-alpine ecosystems, Waimea, Hawaii, USA	Effects of introduced herbivores and fire on diversity, recruitment and vegetation structure in the high-elevation ecosystem of an oceanic island	Oral
02/2012	Association of American Geographers (AAG)	Annual Meeting, New York, USA	Invasion and speciation of vascular plant species on a volcanic oceanic island with steep elevational and environmental gradients	Oral
09/2011	Ecological Society of Germany, Austria and Switzerland (GfÖ)	41th Annual Meeting, Oldenburg, Germany	Dynamics of an island endemic shrub: Herbivores a threat to island biodiversity?	Oral
03/2011	University of Enschede	1st Conference on Spatial Statistics, Enschede, Netherlands	Effects of climate change on endemic plant species of La Palma (Canary Islands) using environmental niche modeling	Poster

5. Declaration of own contribution to each paper

Manuscript 1:
Title: **Patterns of island treeline elevation – a global perspective**
Authors: Irl SDH, Anthelme F, Harter DEV, Jentsch A, Lotter E, Steinbauer MJ, Beierkuhnlein C
Journal: submitted to **Ecography** with major revisions (in review)
Personal contribution: data collection: 80%, data analysis and figures: 70%, writing: 80%, idea and concept: 60%, corresponding author

Manuscript 2:
Title: **Elevation-driven ecological isolation promotes diversification on Mediterranean islands**
Authors: Steinbauer MJ, Irl SDH, Beierkuhnlein C
Journal: **Acta Oecologica** 47 (2013): 52-56
Personal contribution: figure: 75%, writing: 20%, idea and concept: 20%

Manuscript 3:
Title: **An 11-yr exclosure experiment in a high-elevation island ecosystem: introduced herbivore impact on shrub species richness, seedling recruitment and population dynamics**
Authors: Irl SDH, Steinbauer MJ, Babel W, Beierkuhnlein C, Blume-Werry G, Messinger J, Palomares Martínez Á, Strohmeier S, Jentsch A
Journal: **Journal of Vegetation Science** 23 (2012): 1114-1125
Personal contribution: field work: 70%, data analysis and figures: 25%, writing: 75%, idea and concept: 60%, corresponding author

Manuscript 4:
Title: **Burned and devoured – Introduced herbivores, fire and the endemic flora of the high elevation ecosystem on La Palma, Canary Islands**
Authors: Irl SDH, Steinbauer MJ, Messinger J, Blume-Werry G, Palomares Martínez Á, Beierkuhnlein C, Jentsch A
Journal: **Arctic, Antarctic and Alpine Research** 46 (2014), in press, as **invited contribution** to the special issue on tropical alpine ecosystems on islands
Personal contribution: field work: 10%, data analysis and figures: 10%, writing: 90%, idea and concept: 60%, corresponding author

Manuscript 5:
Title: **The Hitchhiker's guide to island endemism - biodiversity and endemic perennial plant species in roadside and surrounding vegetation**
Authors: Irl SDH, Steinbauer MJ, Epperlein L, Harter DEV, Jentsch A, Pätz S, Wohlfahrt C, Beierkuhnlein C
Journal: **Biodiversity and Conservation** 23 (2014): 2273–2287
Personal contribution: field work: 60%, data analysis and figures: 20%, writing: 80%, idea and concept: 50%, corresponding author

Manuscript 6:
Title: **Varying dependencies of species richness, endemic richness and endemicity on climate and topography**
Authors: Irl SDH, Harter DEV, Steinbauer MJ, Gallego Puyol D, Fernández-Palacios JM, Jentsch A, Beierkuhnlein C
Journal: submitted to **Journal of Ecology**
Personal contribution: field work: 70%, data analysis and figures: 90%, writing: 80%, idea and concept: 70%, corresponding author

Manuscript 7:
Title: **Impacts of global climate change on the floras of oceanic islands - projections, implications and current knowledge**
Authors: Harter DEV, Irl SDH, Steinbauer MJ, Triantis KA, Fernández-Palacios JM, Gillespie RG, Beierkuhnlein C
Journal: **Perspectives in Plant Ecology, Evolution and Systematics** (accepted);
DOI: 10.1016/j.ppees.2015.01.003
Personal contribution: literature survey: 20%, data analysis and figures: 0%, writing: 30%, idea and concept: 20%

6. References in introduction and synthesis

Acebes Ginovés JR et al. (2010) Spermatophyta. In: Arechavaleta M, Rodríguez S, Zurita N, García A (eds.) Lista de especies silvestres de Canarias. Hongos, plantas y animales terrestres. Gobierno de Canarias, Tenerife, 122–172.

Alexander JM et al. (2011) Assembly of nonnative floras along elevational gradients explained by directional ecological filtering. Proceedings of the National Academy of Sciences 108: 656-661.

Araújo MB, New M. 2007. Ensemble forecasting of species distributions. Trends Ecol. Evol. 22:42–47

Arévalo JR et al. (2001) The effect of fire intensity on the understorey species composition of two *Pinus canariensis* reforested stands in Tenerife (Canary Islands). Forest Ecology and Management 148: 21-29.

Arévalo JR et al. (2005) Distribution of alien vs. native plants species in roadside communities along an altitudinal gradient in Tenerife and Gran Canaria (Canary Islands). Perspectives in Plant Ecology, Evolution and Systematics 7: 185-202.

Arévalo JR et al (2008) Changes in plant species composition and litter production in response to roads and trails in the laurel forest of Tenerife (Canary Islands). Plant Biosystems-An International Journal Dealing with all Aspects of Plant Biology 142: 614-622.

Arévalo JR et al. (2010). Do anthropogenic corridors homogenize plant communities at a local scale? A case studied in Tenerife (Canary Islands). Plant Ecology 209 23-35.

Arteaga MA et al. (2009). How do alien plants distribute along roads on oceanic islands? A case study in Tenerife, Canary Islands. Biological Invasions 11: 1071-1086.

Bataille et al. (2009) Natural colonization and adaptation of a mosquito species in Galápagos and its implications for disease threats to endemic wildlife. Proceedings of the National Academy of Sciences 106: 10230-10235.

Beard JS et al. (2000) Species richness and endemism in the Western Australian flora. Journal of Biogeography 27: 1257-1268.

Becker T et al. (2005) Altitudinal distribution of alien plant species in the Swiss Alps. Perspectives in Plant Ecology, Evolution and Systematics 7: 173-183.

Benning TL et al. (2002). Interactions of climate change with biological invasions and land use in the Hawaiian Islands: modeling the fate of endemic birds using a geographic information system. Proceedings of the National Academy of Sciences, 99, 14246-14249.

Blonder B et al. (2014). The n-dimensional hypervolume. Global Ecology and Biogeography 23: 595-609.

Brooks TM et al. (2002). Habitat loss and extinction in the hotspots of biodiversity. Conservation biology 16: 909-923.

Brown JH (2014) Why are there some many species in the tropics? Journal of Biogeography 41: 8-22.

Bowen L, Vuren DV (1997) Insular endemic plants lack defenses against herbivores. Conservation Biology 11: 1249-1254.

Bowman MJSD et al. (2014) Pyrogeographic models, feedbacks and the future of global fire regimes. Global Ecology and Biogeogprahy. doi: 10.1111/geb.12180

Cadotte MW et al. (2011) Beyond species: functional diversity and the maintenance of ecological processes and services. Journal of Applied Ecology 48: 1079-1087.

Campbell K, Donlan C (2005) Feral goat eradications on islands. Conservation Biology 19: 1362-1374.

Caujape-Castells J et al. (2010) Conservation of oceanic island floras: present and future global challenges. Perspectives in Plant Ecology, Evolution and Systematics 12: 107-129.

Carlquist S (1974) Island biology. Columbia University Press: New York.

Carracedo JC et al. (2002) Cenozoic volcanism II: the Canary Islands. In: The Geology of Spain. Gibbons W, Moreno T (eds.), pp. 43: 9-472.

Carracedo JC et al. (1999) Giant quaternary landslides in the evolution of La Palma and El Hierro, Canary Islands. Journal of Volcanology and Geothermal Research 94: 169-190.

Carrión JS et al. (2010) Expected trends and surprises in the Lateglacial and Holocene vegetation history of the Iberian Peninsula and Balearic Islands. Review of Palaeobotany and Palynology 162: 458-475.

Chapuis JL et al. (2001) Eradication of rabbits (*Oryctolagus cuniculus*) by poisoning on three islands of the subantarctic Kerguelen Archipelago. Wildlife Research 28: 323-331.

Cieraad E et al. (2014) Southern Hemisphere temperate tree lines are not climatically depressed. Journal of Biogeography.

Climent J et al. (2004) Fire adaptations in the Canary Islands pine (Pinus canariensis). Plant ecology 171: 185-196.

Coblentz BE (1978) The effects of feral goats (*Capra hircus*) on island ecosystems. Biological Conservation 13: 279-286.

Copson G, Whinam J (1998) Response of vegetation on subantarctic Macquarie Island to reduced rabbit grazing. Australian Journal of Botany 46: 15-24.

Cotinga I (2002) Threatened avifauna of the Juan Fernández Archipelago, Chile: the impact of introduced mammals and conservation priorities.

Courchamp F et al. (2000) Rabbits killing birds: modelling the hyperpredation process. Journal of Animal Ecology 69: 154-164.

Courchamp F et al. (2003) Mammal invaders on islands: impact, control and control impact. Biological Reviews 78: 347-383.

Courchamp F et al. (2014) Climate change, sea-level rise, and conservation: keeping island biodiversity afloat. Trends in Ecology & Evolution 29 127-130.

Crausbay SD, Hotchkiss SC (2010) Strong relationships between vegetation and two perpendicular climate gradients high on a tropical mountain in Hawai'i. Journal of Biogeography 37: 1160-1174.

Crawley MJ, Harral JE (2001) Scale dependence in plant biodiversity. Science 291: 864-868.

Croll DA et al. (2005) Introduced predators transform subarctic islands from grassland to tundra. Science 307: 1959-1961.

Cronk QCB (1997) Islands: stability, diversity, conservation. Biodiversity & Conservation 6 477-493.

D'Antonio CM et al. (2000) Variation in the impact of exotic grasses on native plant composition in relation to fire across an elevation gradient in Hawaii. Austral Ecology 25: 507-522.

Delgado JD et al. (2007) Edge effects of roads on temperature, light, canopy cover, and canopy height in laurel and pine forests (Tenerife, Canary Islands). Landscape and Urban Planning 81: 328-340.

Desender K et al. (1999) Conservation on Volcan Alcedo (Galapagos): terrestrial invertebrates and the impact of introduced feral goats. Biological Conservation 87: 303-310.

Dewar RE, Richard AF (2007) Evolution in the hypervariable environment of Madagascar. Proceedings of the National Academy of Sciences 104: 13723-13727.

Didiano TJ et al. (2014) Experimental test of plant defence evolution in four species using long-term rabbit exclosures. Journal of Ecology 102: 584-594.

Dullinger S et al. (2012) Extinction debt of high-mountain plants under twenty-first-century climate change. Nature Climate Change 2: 619-622.

Egholm DL et al. (2009). Glacial effects limiting mountain height. Nature 460: 884-887.

Elison Timm O et al. (2011) Projection of changes in the frequency of heavy rain events over Hawaii based on leading Pacific climate modes. Journal of Geophysical Research: Atmospheres (1984–2012), 116(D4).

Emerson BC, Kolm N (2005) Species diversity can drive speciation. Nature 434: 1015-1017.

Fernández-Palacios JM (1992) Climatic responses of plant species on Tenerife, The Canary Islands. Journal of Vegetation Science 3: 595-603.

Fernández-Palacios JM & Nicolás JP (1995). Altitudinal pattern of vegetation variation on Tenerife. Journal of Vegetation Science 6: 183-190.

Fernández-Palacios JM et al. (2011). A reconstruction of Palaeo-Macaronesia, with particular reference to the long-term biogeography of the Atlantic island laurel forests. Journal of Biogeography 38: 226-246.

Fitter J et al. (2002) Wildlife of the Galapagos. Princeton University Press.

Forman RT, Alexander LE (1998) Roads and their major ecological effects. Annual Review of Ecology and Systematics, 207-C2.

Fortini L, Price J, Jacobi J, Vorsino A, Burgett J, Brinck K, Amidon F, Miller S, 'Ohukani'ohi'a III S, Koob G, Paxton E (2013) A landscape-based assessment of climate change vulnerability for all native Hawaiian plants. Technical Report 044. Hawai'i Cooperative Studies Unit, University of Hawai'i, Hilo, HI.

Francisco-Ortega J et al. (2000) Plant genetic diversity in the Canary Islands: a conservation perspective. American Journal of Botany 87: 909-919.

Ghalambor CK et al. (2006) Are mountain passes higher in the tropics? Janzen's hypothesis revisited. Integrative and Comparative Biology 46: 5-17.

García Herrera R et al. (2001) Influence of the North Atlantic oscillation on the Canary Islands precipitation. Journal of Climate 14: 3889-3903.

Garzón-Machado V et al. (2010) Strong negative effect of alien herbivores on endemic legumes of the Canary pine forest. Biological Conservation 143: 2685-2694.

Garzón-Machado V et al. (2012) Threat or threatened species? A paradox in conservation biology. Journal for Nature Conservation 20: 228-230.

Garzón-Machado V et al. (2013) Bioclimatic and vegetation mapping of a topographically complex oceanic island applying different interpolation techniques. International Journal of Biometeorology, 1-13.

Giambelluca TW et al. (1986) Rainfall atlas of Hawai'i. Hawai'i Division of Water and Land Development, Department of Land and Natural Resources, Honolulu, 267.

Gillespie RG, Clague DA (Eds.). (2009). Encyclopedia of islands (No. 2). Univ of California Press.

Gillespie RG et al. (2008) Biodiversity dynamics in isolated island communities: interaction between natural and human-mediated processes. Molecular Ecology 17: 45-57.

González-Reimers E et al. (2001) Paleonutritional analysis of the pre-Hispanic population from Fuerteventura (Canary Islands). Science of the Total Environment 264: 215-220.

Haberle SG (2003) Late quaternary vegetation dynamics and human impact on Alexander Selkirk Island, Chile. Journal of Biogeography 30: 239-255.

van Hengstum T et al. (2012) Human-induced hybridization among congeneric endemic plants on Tenerife, Canary Islands. Plant Systematics and Evolution 298: 1119-1131.

Hope GS (1976) The vegetational history of Mt Wilhelm, Papua New Guinea. Journal of Ecology 64: 627-663.

Hughes C, Eastwood R (2006). Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. Proceedings of the National Academy of Sciences 103, 10334-10339.

Hughes F et al. (1991) Alien grass invasion and fire in the seasonal submontane zone of Hawai'i. Ecology 72: 743-747.

IPCC Ed. (2014) Climate change 2014: Impacts, adaptation, and vulnerability: Working group II contribution to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Irl SD, Beierkuhnlein C (2011) Distribution of endemic plant species on an oceanic island–a geospatial analysis of La Palma (Canary Islands). Procedia Environmental Sciences 7: 170-175.

Janzen DH (1967) Why mountain passes are higher in the tropics. American Naturalist 101: 233-249.

Jentsch A, Beierkuhnlein C (2008) Research frontiers in climate change: effects of extreme meteorological events on ecosystems. C. R. Geoscience 340: 621-628.

Kallimanis AS et al. (2011) Examining the relationship between total species richness and single island palaeo-and neo-endemics. Acta Oecologica 37: 65-70.

Karger DN et al. (2014) Island biogeography from regional to local scales: evidence for a spatially scaled echo pattern of fern diversity in the Southeast Asian archipelago. Journal of Biogeography 41: 250-260.

Kier G et al. (2009) A global assessment of endemism and species richness across island and mainland regions. Proceedings of the National Academy of Sciences 106: 9322-9327.

Kisel Y, Barraclough TG (2010) Speciation has a spatial scale that depends on levels of gene flow. American Naturalist 175: 316–334.

Kreft H et al. (2008) Global diversity of island floras from a macroecological perspective. Ecology Letters 11: 116-127.

Krishnamurti TN et al. (2013) Tropical meteorology. An introduction. Springer Verlag, New York.

Krushelnycky PD et al. (2013) Climate-associated population declines reverse recovery and threaten future of an iconic high-elevation plant. Global Change Biology 19: 911-922.

Körner C (2003) Alpine plant life: functional plant ecology of high mountain ecosystems. Springer, Basel.

Körner C (2007) The use of 'altitude' in ecological research. Trends in Ecology & Evolution 22: 569-574.

Körner C (2012) Alpine treelines – Functional ecology of the global high elevation tree limits. Springer, Basel.

Körner C, Paulsen J (2004) A world-wide study of high altitude treeline temperatures. Journal of Biogeography 31: 713-732.

Kueffer C et al. (2010) A global comparison of plant invasions on oceanic islands. Perspectives in Plant Ecology, Evolution and Systematics 12: 145-161.

Kull CA (2000) Deforestation, erosion, and fire: degradation myths in the environmental history of Madagascar. Environment and History 6: 423-450.

Kuttler W (2013) Klimatologie. 2nd Edition. Verlag Ferdinand Schöningh, Paderborn.

Lagabrielle E et al. (2009) Identifying and mapping biodiversity processes for conservation planning in islands: A case study in Réunion Island (Western Indian Ocean). Biological Conservation 142: 1523-1535.

Leader-Williams N et al. (1987) Influence of introduced reindeer on the vegetation of South Georgia: results from a long-term exclusion experiment. Journal of Applied Ecology 24: 801-822.

Lens F et al. (2013) Insular woodiness on the Canary Islands: a remarkable case of convergent evolution. International Journal of Plant Science 174: 992-1013.

Leuschner C (1996) Timberline and alpine vegetation on the tropical and warm-temperate oceanic islands of the world: elevation, structure and floristics. Vegetatio 123: 193-206.

Leuschner C (2000) Are high elevations in tropical mountains arid environments for plants? Ecology 81: 1425-1436.

Leutner BF et al. (2012) Mosses like it rough - Growth form specific responses of mosses, herbaceous and woody plants to micro-relief heterogeneity. Diversity 4: 59-73.

Lionello P et al. (2012) Introduction: Mediterranean Climate – Background Information. In: Lionello P (Ed.). The Climate of the Mediterranean Region. From the Past to the Future. Elsevier, London.

Lomolino MV (2010) Four Darwinian themes on the origin, evolution and preservation of island life. Journal of Biogeography 37: 985-994.

Lomolino MV et al. (2013) Of mice and mammoths: generality and antiquity of the island rule. Journal of Biogeography 40: 1427-1439.

Loope LL, Giambelluca TW (1998). Vulnerability of island tropical montane cloud forests to climate change, with special reference to East Maui, Hawaii. Climatic Change 39: 503-517.

Losos JB, Ricklefs RE (2009) Adaptation and diversification on islands. Nature 457: 830-836.

Losos JB, Schluter D (2000) Analysis of an evolutionary species–area relationship. Nature 408: 847–850.

Løvholt F et al. (2008) Oceanic propagation of a potential tsunami from the La Palma Island. Journal of Geophysical Research: Oceans 113: 1-21.

Lowe S et al. (2000) 100 of the world's worst invasive alien species: a selection from the global invasive species database. Invasive Species Specialist Group, Auckland, New Zealand

MacArthur RH, Wilson EO (1963) An equilibrium theory of insular zoogeography. Evolution 17: 373-387.

MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University.

March JG et al. (2003). Damming tropical island streams: problems, solutions, and alternatives. BioScience 53: 1069-1078.

Marrero-Gómez MV et al. (2007) Population viability of the narrow endemic *Helianthemum juliae* (CISTACEAE) in relation to climate variability. Biological Conservation 136: 552-562.

Marzol MV et al. (2011) Meteorological patterns and fog water collection in Morocco and the Canary Islands. Erdkunde 65: 291-303.

McAlpine JR et al. (1983) Climate of Papua New Guinea. CSIRO, Sydney

McWethy DB et al. (2010) Rapid landscape transformation in South Island, New Zealand, following initial Polynesian settlement. Proceedings of the National Academy of Sciences 107: 21343-21348.

Médail F, Diadema K (2009) Glacial refugia influence plant diversity patterns in the Mediterranean Basin. Journal of Biogeography 36: 1333-1345.

Medina FM, Nogales M (2009) A review on the impacts of feral cats (*Felis silvestris catus*) in the Canary Islands: implications for the conservation of its endangered fauna. Biodiversity and Conservation 18: 829-846.

Moral P et al. (1997) Genetic study of the population of Tenerife (Canary Islands, Spain): protein markers and review of classical polymorphisms. American Journal of Physical Anthropology 102 337-349.

de Nascimento L et al. (2009) The long-term ecology of the lost forests of La Laguna, Tenerife (Canary Islands). Journal of Biogeography 36: 499-514.

Niedrist G et al. (2009) Plant diversity declines with recent land use changes in European Alps. Plant Ecology: 202 195-210.

Nogales M et al. (2006) Ecological effects and distribution of invasive non-native mammals on the Canary Islands. Mammal Review 36: 49-65.

Nogales M et al. (2013). Feral cats and biodiversity conservation: the urgent prioritization of island management. BioScience 63: 804-810.

Nogué S et al. (2013) The ancient forests of La Gomera, Canary Islands, and their sensitivity to environmental change. Journal of Ecology 101: 368-377.

Norbury G et al. (2003) Short-term ecological effects of rabbit haemorrhagic disease in the short-tussock grasslands of the South Island, New Zealand. Wildlife Research 29: 599-604.

North SG et al. (1994) Changes in the vegetation and reptile populations on Round Island, Mauritius, following eradication of rabbits. Biological Conservation 67: 21-28.

Orme CDL et al. (2005) Global hotspots of species richness are not congruent with endemism or threat. Nature 436: 1016-1019.

Ohsawa M (1993) Latitudinal pattern of mountain vegetation zonation in southern and eastern Asia. Journal of Vegetation Science 4: 13-18.

Otto R et al. (2014) Road Edge Effect and Elevation Patterns of Native and Alien Plants on an Oceanic Island (Tenerife, Canary Islands). Folia Geobotanica 49: 65-82.

Pauchard A et al. (2009) Ain't no mountain high enough: plant invasions reaching new elevations. Frontiers in Ecology and the Environment 7: 479-486.

Paulay G (1994) Biodiversity on oceanic islands: its origin and extinction. American Zoologist: 34: 134-144.

Paulsen J, Körner C (2014) A climate-based model to predict potential treeline position around the globe. Alpine Botany 124: 1-12.

Pararas-Carayannis G (2002) Evaluation of the threat of mega tsunami generation from postulated massive slope failures of island stratovolcanoes on La Palma, Canary Islands, and on the island of Hawaii. Science of Tsunami Hazards 20: 251-277.

Parmesan C (2006). Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics: 637-669.

Pellissier L et al. (2014) High elevation Plantago lanceolata plants are less resistant to herbivory than their low elevation conspecifics: is it just temperature?. Ecography.

Phillips SJ et al. (2006) Maximum entropy modeling of species geographic distributions. Ecol. Model. 190: 231–59.

Phoenix GK et al. (2006). Atmospheric nitrogen deposition in world biodiversity hotspots: the need for a greater global perspective in assessing N deposition impacts. Global Change Biology 12: 470-476.

Pott R et al. (2003). Die Kanarischen Inseln. Ulmer, Stuttgart.

Priddel D et al. (2000) Eradication of European rabbits (*Oryctolagus cuniculus*) from Cabbage Tree Island, NSW, Australia, to the breeding habitat of Gould's petrel (*Pterodroma leucoptera leucoptera*). Biological Conservation 94: 115-125.

Qian H & Ricklefs RE (2007) A latitudinal gradient in large-scale beta diversity for vascular plants in North America. Ecology Letters 10: 737-744.

Rahbek C (1995) The elevational gradient of species richness: a uniform pattern? Ecography 18: 200-205.

Reaser et al (2007) Ecological and socioeconomic impacts of invasive alien species in island ecosystems. Environmental Conservation 34: 98-111.

Ricklefs RE, Bermingham E (2007) The causes of evolutionary radiations in archipelagoes: Passerine birds in the Lesser Antilles. Am. Nat. 169: 285–297.

Ripperton JC, Hosaka EY (1942) Vegetation zones of Hawaii. Hawaii Agric. Exp. Sta. Bull 89.

Rotholz E, Mandelik Y (2013) Roadside habitats: effects on diversity and composition of plant, arthropod, and small mammal communities. Biodiversity and conservation 22: 1017-1031.

Rosenzweig ML (1995) Species diversity in space and time. Cambridge University Press.

Ross MS et al.(2009) Disturbance and the rising tide: the challenge of biodiversity management on low-island ecosystems. Frontiers in Ecology and the Environment 7: 471–478.

Sadler JP (1999) Biodiversity on oceanic islands: a palaeoecological assessment. Journal of Biogeography 26: 75-87.

Schleuter D et al. (2010) A user's guide to functional diversity indices. Ecological Monographs 80: 469-484.

Scholte P, De Geest P (2010) The climate of Socotra Island (Yemen): a first-time assessment of the timing of the monsoon wind reversal and its influence on precipitation and vegetation patterns. Journal of Arid Environments 74: 1507-1515.

Schönfelder I, Schönfelder P (2008) Die neue Kosmos-Mittelmeerflora. Frankh-Kosmos Verlag, Stuttgart

Schultz J (2005) The Ecozones of the World. The Ecological Divisions of the Geosphere. 2nd Edition. Springer Verlag, Berlin.

Scott JJ, Kirkpatrick JB (2008) Rabbits, landslips and vegetation change on the coastal slopes of subantarctic Macquarie Island, 1980–2007: implications for management. Polar Biology 31: 409-419.

Scowcroft PG, Giffin JG (1983) Feral herbivores suppress mamane and other browse species on Mauna Kea, Hawaii. Journal of Range Management 36: 638-645.

Shmida A, Werger MJA (1992) Growth form diversity on the Canary Islands. Vegetatio 102: 183-199.

Spatz G, Mueller-Dombois D (1973) The influence of feral goats on koa tree reproduction in Hawaii Volcanoes National Park. Ecology 54: 870-876.

Spellerberg IF (1998) Ecological effects of roads and traffic: a literature review. Global Ecology and Biogeography 7: 317-333.

Spellerberg IF (2002) Ecological effects of roads. Science Publish, Enfield.

Sperling FN et al. (2004) Future climate change of the subtropical North Atlantic: implications for the cloud forests of Tenerife. Climatic Change 65: 103-123.

Steinbauer MJ, Beierkuhnlein C (2010) Characteristic pattern of species diversity on the Canary Islands. Erdkunde 64: 57-71.

Steinbauer MJ et al. (2012) Increase of island endemism with altitude–speciation processes on oceanic islands. Ecography 35: 23-32.

Steinbauer et al. (2013) Re-evaluating the general dynamic theory of oceanic island biogeography. Frontiers of Biogeography 5: 185-194.

Strasberg D et al. (2005) An assessment of habitat diversity and transformation on La Réunion Island (Mascarene Islands, Indian Ocean) as a basis for identifying broad-scale conservation priorities. Biodiversity & Conservation 14: 3015-3032.

Stohlgren TJ et al. (2005) Patterns of plant species richness, rarity, endemism, and uniqueness in an arid landscape. Ecological Applications 15: 715-725.

Towns DR et al. (1997) Restoration of New Zealand islands: redressing the effects of introduced species. Pacific Conservation Biology 3: 99.

Traveset A et al. (2009) A review on the effects of alien rodents in the Balearic (Western Mediterranean Sea) and Canary Islands (Eastern Atlantic Ocean). Biological Invasions 11: 1653-1670.

Trombulak SC, Frissell CA (2000) Review of ecological effects of roads on terrestrial and aquatic communities. Conservation Biology 14: 18-30.

Tutin TG (1953) The vegetation of the Azores. The Journal of Ecology 41: 53-61.

Van Valen L (1973) A new evolutionary law. Evolutionary Theory 1: 1–30.

Vetaas OR, Grytnes JA (2002) Distribution of vascular plant species richness and endemic richness along the Himalayan elevation gradient in Nepal. Global Ecology and Biogeography 11: 291-301.

Vilenkin BY et al. (2009) A random process may control the number of endemic species. Biologia 64: 107-112.

Vogiatzakis IN et al. (2003) Environmental factors and vegetation composition, Lefka Ori massif, Crete, S. Aegean. Global Ecology and Biogeography, 12, 131-146.

Vourc'h G et al. (2001) Defensive adaptations of *Thuja plicata* to ungulate browsing: a comparative study between mainland and island populations. Oecologia 126: 84–93.

Wace NM, Holdgate MW (1958) The vegetation of Tristan da Cunha. The Journal of Ecology 46: 593-620.

Ward SN, Day S (2001) Cumbre Vieja volcano - potential collapse and tsunami at La Palma, Canary Islands. Geophysical Research Letters 28: 3397-3400.

Wardle DA et al. (2001). Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. Ecological Monographs 71: 587-614.

Weigelt P et al. (2013) Bioclimatic and physical characterization of the world's islands. Proceedings of the National Academy of Sciences 110: 15307-15312.

Westphal et al. (2008) The Link Between International Trade and the Global Distribution of Invasive Alien Species. Biological Conservation 10: 391-398.

Wiens JJ, Graham CH (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. Annual Reviews in Ecology, Evolution and Systematics 36: 519–539.

Wikelski M et al. (2004) Galápagos birds and diseases: invasive pathogens as threats for island species. Ecology and Society 9: 5.

Wilson EO (1961) The nature of the taxon cycle in the Melanesian ant fauna. American Naturalist 95: 169 –193.

Whittaker RJ, Fernández-Palacios JM (2007) Island biogeography: ecology, evolution, and conservation. Oxford University Press, Oxford.

Whittaker RJ et al. (2007) The island immaturity–speciation pulse model of island evolution: an alternative to the "diversity begets diversity" model. Ecography 30: 321-327.

Whittaker RJ et al. (2008) A general dynamic theory of oceanic island biogeography. Journal of Biogeography 35: 977-994.

Zavaleta ES et al. (2001). Viewing invasive species removal in a whole-ecosystem context. Trends in Ecology & Evolution 16, 454-459.

Zöller L et al. (2003) Geoarchaeological and chronometrical evidence of early human occupation on Lanzarote (Canary Islands). Quaternary Science Reviews 22: 1299-1307.

7. Manuscripts

7.1 Manuscript 1

Patterns of island treeline elevation – a global perspective

Severin D.H. Irl[1],*, Fabien Anthelme[2], David E.V. Harter[1], Anke Jentsch[3], Elisabeth Lotter[1], Manuel J. Steinbauer[1], Carl Beierkuhnlein[1]

[1] *Department of Biogeography, BayCEER, University of Bayreuth, Universitätstraße 30, 95447 Bayreuth, Germany*

[2] *Institut de Recherche pour le Développement (IRD), UMR AMAP, CIRAD, TA A51/PS2, 34398 Montpellier, France*

[3] *Department of Disturbance Ecology, BayCEER, University of Bayreuth, Universitätstraße 30, 95447 Bayreuth, Germany*

*Corresponding author: severin.irl@uni-bayreuth.de; Tel.: +49-921-552299; Fax: +49-921-552315.

ABSTRACT

Treeline research has strongly focused on mountain systems on the mainland. However, island treelines offer the opportunity to contribute to the global framework on treeline elevation due to their island-specific attributes such as isolation, small area, low species richness and relative youth. We hypothesize that similar to the mainland, latitude-driven temperature variation is the most important determinant of island treeline elevation on a global scale. To test this hypothesis, we compared mainland with island treeline elevations, then we focused (1) on the global effects of latitude, (2) on the regional effects of island type (continental vs. oceanic islands) and (3) the local effects of several specific island characteristics (age, area, maximum island elevation, isolation and plant species richness). We collected a global dataset of islands (n = 86) by applying a stratified design using GoogleEarth and the Global Island Database. For each island we extracted data on latitude and local characteristics. Treeline elevation decreased from the mainland through continental to oceanic islands. Island treeline elevation followed a hump-shaped latitudinal distribution, which is fundamentally different from the mainland double-hump. Higher maximum island elevation generated higher treeline elevation and was found the best single predictor of island treeline elevation, even better than latitude. Lower island treeline elevation may be the result of a low mass elevation effect (MEE) influencing island climates and an increasingly impoverished species pool but also trade wind inversion-associated drought. The maximum island elevation effect possibly results from an increasing mass elevation effect (MEE) with increasing island elevation but also range shifts during climatic fluctuations and the summit syndrome (i.e. high wind speeds and poor soils in peak regions). Investigating islands in treeline research has enabled disentangling the global effect of latitude from regional and local effects and, at least for islands, a comprehensive quantification of the MEE.

Keywords: Island biogeography; latitudinal gradient; mountain ecology

INTRODUCTION

The treeline definition and its global distribution have long been the source of various controversial debates among ecologists and biogeographers, particularly when considering the respective influences of local or regional factors (e.g. Hermes 1955, Troll 1973, Jobbágy and Jackson 2000, Smith et al. 2003, Körner and Paulsen 2004). However, recent studies have shown that on large scales thermal limitations determine treeline elevation (Jobbágy and Jackson 2000, Körner and Paulsen 2004, Case and Duncan 2014, Paulsen and Körner 2014).

Mainland treeline elevation reaches its maximum between the southern and northern subtropics/dry tropics and decreases from there towards the poles (Körner 1998, Jobbágy and Jackson 2000). Regions between 25° north and south of the equator have been described by a latitude-

50

independent *plateauing* of treeline elevations due to the low seasonal variation of temperature and the consequential lack of 'summer heat' during the growing season (Ohsawa et al. 1985, Ohsawa 1990, Körner 1998) but also by a subtropical/dry tropical double hump with a tropical depression (Hermes 1955, Troll 1973).

The world's highest treelines are found in subtropical areas of high continentality (i.e. in regions with high diurnal and annual temperature amplitude usually situated in the interior of a continent) and large mass elevation effect (MEE), e.g. in the Himalayas (Miehe et al. 2007) or the Andes (Hoch and Körner 2005, Nagy and Grabherr 2009), both at around 4800-4900 m a.s.l. MEE creates favorable growing conditions by an increased warming of landmasses at high elevations in comparison to surrounding air masses, leading to more sunshine hours and higher temperatures (Körner 2012). From the subtropical/dry tropical maxima, treeline elevation generally decreases towards the poles due to decreasing temperatures and increasing seasonality (Jobbágy & Jackson 2000).

Despite the large number of existing treeline studies, islands are strongly underrepresented in large-scale treeline research. Instead, studies on the distribution of continental treelines have mainly focused on specific regions (e.g. Ohsawa 1990, Holtmeier and Broll 2005, Malanson et al. 2007) and on global treeline distributions at large continental scales (Hermes 1955, Troll 1973, Miehe and Miehe 1994, Körner 1998, Jobbágy and Jackson 2000, Körner and Paulsen 2004, Körner et al. 2012). Leuschner (1996) suggests that treeline elevation may be lower on islands than mainland areas, however no quantitative test was undertaken and the sample size was low (n = 15). The author focused on warm-temperate and tropical islands of volcanic origin, which permitted discussing several potential drivers of lower elevations of treelines on islands: (1) local climatic drought due to trade wind inversion, (2) geographic isolation-induced lack of adapted tree species, which is likely connected to both the distance to the nearest species' source and plant species richness in general, and (3) edaphic conditions (immature volcanic soils). This study demonstrates that by considering local island characteristics islands may offer a unique opportunity to explain the patterns of treeline elevation on the worldwide scale.

MEE likely decreases from large and high mountain ranges on the mainland to smaller and lower islands. However, a comprehensive quantification of MEE is currently lacking in treeline science. Owing to the more or less cone-shaped geometry of islands we propose that MEE on islands is linked to the maximum elevation of an island, as hypothesized by Leuschner (1996). With increasing island elevation, the volume and subsequently also the mass of an island increases, leading to increasingly favorable microclimatic conditions for tree growth. On the mainland, MEE is expected to be highest in large mountain ranges (e.g. Himalayas, Andes, Rocky Mountains, etc.) with maximum MEE found towards the interior of these mountain ranges (Körner 2012).

By using two types of islands – continental and oceanic – and by making a global comparison with data from the mainland, we aimed at refining the current conceptual framework on treeline elevation, which is mainly supported by mainland data. We specifically addressed the following questions: (1) Is treeline elevation significantly lower on islands than on the mainland? (2) How are island treeline elevations influenced by latitude, taken as a global driver of thermal conditions? (3) To what

extent does island type (i.e. continental vs. oceanic islands) as a regional driver influence the global island treeline elevation pattern? (4) How important are local island characteristics such as area, maximum island elevation, distance to the continent, distance to the nearest neighboring island, plant species richness or age as drivers of island treeline elevation when compared to latitude? In line with current literature, our main hypothesis is that latitude (and the associated large-scale thermal variation) is the main driver of the observed global pattern of island treeline elevation.

MATERIAL AND METHODS

Study area

Islands in general possess specific environmental features. These physical features include isolation (MacArthur and Wilson 1967) and, in the case of oceanic islands, an age-dependent island geological 'life cycle' (Fernández-Palacios et al. 2011). Biologically, island-specific floras differ from continents owing to the comparably low total species richness and high degree of endemism (Whittaker and Fernández-Palacios 2007). Here, we define an island as a landmass surrounded by ocean ranging from 50 km^2 to 10^6 km^2. Smaller islands were excluded, as they generally do not reach elevations necessary for treeline formation. A total of 86 island treelines was recorded, covering all oceans. Island treeline locations ranged from 70°N (Sore Kvalo, Norway) to 56°S (Wollaston, Chile; see Fig. 1 and Table A1 in Supplementary Material). Treeline elevations spanned from 110 m a.s.l. on Kodiak Island, Alaska (USA) to 4061 m a.s.l. on New Guinea. Island area ranged from 50 km^2 (Selkirk, Juan Fernández Islands, Chile) to almost 0.8 M km^2 (New Guinea). The most isolated island was observed at a distance of 3682 km from the continent (Big Island, Hawaii, USA) whereas several shelf islands were only separated by 1 km of ocean from the continent.

The sampled islands were divided into two categories: (1) oceanic islands, which are completely of volcanic origin (e.g. hotspot or rift volcanism) and have never had contact with the mainland, and (2) continental islands, which are situated on the continental shelf. Continental islands are characterized by a complex geologic history including continental shelf islands that have had contact with the continent during glacial maxima (e.g. Vancouver Island, Canada, Borneo, or the British Isles), continental fragments or mini-continents (e.g. North and South Island, New Zealand; Neall and Trewick 2008) and volcanic islands, which actually did have contact with the continent during the last glacial maximum (e.g. Bioko, Equatorial Guinea; Jones 1994). Contact during Pleistocene glaciations because of sea level fluctuations allowed continental species to migrate and homogenize the species pool of most of these islands (Weigelt et al. 2013). Among the sampled islands that possess treelines, 29 are of oceanic and 58 of continental origin (see Fig. 1 and Tab. A1 in Supplementary Material). This represents the complete dataset of islands harboring treelines under the constraints of the defined sampling approach. Priority of global coverage was given over equal numbers of replicates per category of oceanic versus continental origin.

The mainland region between 25°N and 25°S has been characterized by a latitude-independent leveling off or *plateau* of treeline elevation (Körner 1998). Adapting this pattern to island treelines, we expected no relationship between latitude and elevation within the same latitudinal range. Thus, by selecting a respective island subset of this geographic sub-region, we test how island characteristics influence treeline elevations independently of latitude. Therefore, a specific focus was put on the subsample of this region in statistical analyses (n = 25). Although not completely accurate we hereafter refer to this region as the *tropics*.
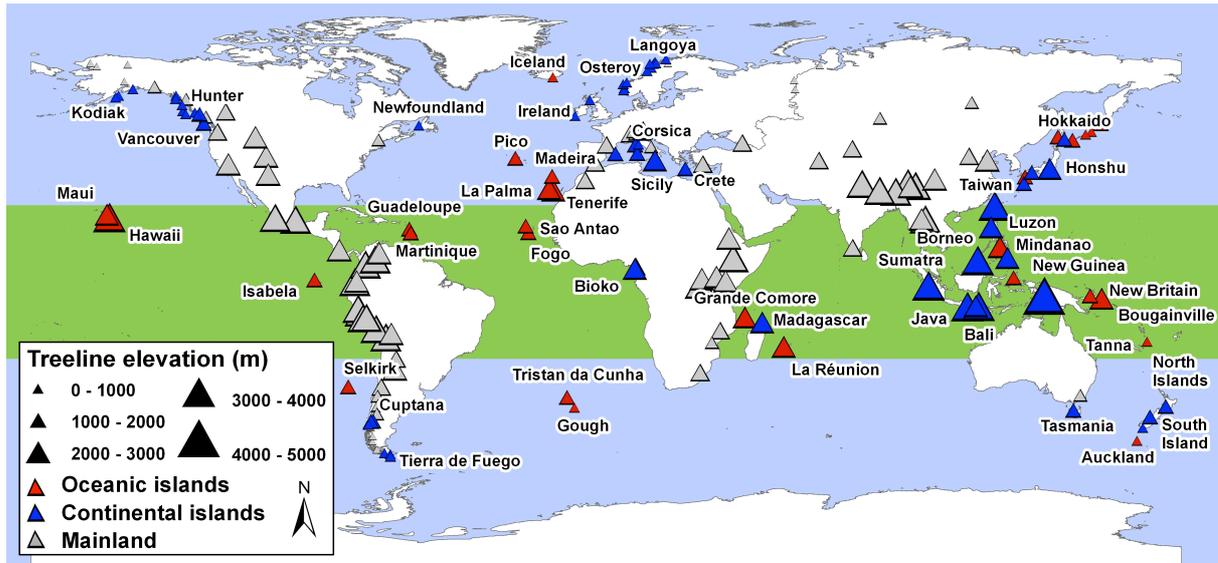

Figure 1. Global distribution of the sampled oceanic islands, continental islands and mainland treelines. Triangle sizes proportionally represent treeline elevation. The green area marks the tropics as defined in this study. For a list of all island data see A1 in Supplementary Material.

Data collection

A global survey identified the location of all island treeline elevations using freely available satellite imagery (i.e. GoogleEarth™, Version 7.1.1.1888, Google Inc. 2013), a novel method, which is gaining importance in global treeline research (Paulsen and Körner 2014). In search of islands, all oceans were systematically sampled, accumulating a comprehensive global dataset. After identifying the highest peak of each island we recorded the elevation and coordinates of the highest tree individuals or forest patch by searching manually in the area around the highest peak. In our study a treeline is defined as the line roughly connecting the highest patches of trees or forest in a certain area (Hermes 1955, Körner 2012). The treeline definition is used in a wide ecological sense, including thermal, moisture, edaphic and other abiotic limitations. The GoogleEarth™ (Google Inc. 2013) image is superimposed onto a digital elevation map using NASA's SRTM data with 90 x 90 m resolution. However, a number of island treelines could not be recorded due to low resolution of satellite imagery or high cloud cover. In these cases, the scientific literature (e.g. Leuschner 1996, Körner and Paulsen 2004) was examined and – if possible – local experts were also contacted (e.g. for Selkirk, Juan Fernández Islands and Bioko,

Equatorial Guinea). Only islands that actually possess treelines were sampled. Treelines were only sampled if the resolution permitted to discern individual trees. Even though it was not possible to identify the exact growth height of tree individuals as defined by literature (Körner 2003), which might constitute a possible source of error, trees were sampled if the resolution allowed morphologically identifying tree individuals (e.g. length and tree-like stature of shadows) in contrast to shrubby *krummholz*. To standardize the sampling approach only the highest treeline encountered per island was recorded.

The GoogleEarth sampling method resulted in treelines, which were significantly higher when compared to treeline data based on a test dataset using 22 mainland treeline elevations from a recent publication on global treeline elevation (Körner & Paulsen 2004) and the currently highest treeline elevations reported in literature (Hoch & Körner 2005, Miehe et al. 2007; Wilcoxon rank sum test p = 0.0003, mean difference ± standard deviation: 99 ± 103 m; see A3 for a list of test dataset treeline elevations taken from literature and GoogleEarth). Although the treelines were significantly higher using the GoogleEarth method, this did not affect the overall pattern. We interpret the GoogleEarth method to be effective in identifying the highest treelines in a certain area. These remote and otherwise inaccessible (remnants of) natural treeline elevations are likely less affected or even unaffected by human-induced treeline modification. All in all, this sampling method is valuable for further macroecological and biogeographic research approaches that do not depend on species identity. It combines the advantages of being freely available and easy to handle with time efficient sampling and virtually unlimited access.

To provide comparisons with island treelines, a representative number of data on mainland treelines enabling global coverage was extracted from literature (n = 22; Körner and Paulsen 2004, Hoch and Körner 2005, Miehe et al. 2007) in combination with the GoogleEarth-method (n = 64). Altogether 86 mainland treeline elevations were applied in this study. Within mountain ranges or areas, the highest peak was chosen to identify and record the highest treeline elevation and coordinates, respectively. Mainland treeline elevation spanned from 83 m to 4900 m a.s.l. and ranged from 69°N to 54°S.

Maximum island elevation, island age and area were extracted from the Global Island Database (UNEP-WCMC 2013), the UNEP Island Directory (Dahl 1991) and other sources such as specific literature (e.g. contributions in Gillespie and Clague 2009) or online databases (Kisel and Barraclough 2010). As suggested by Leuschner (1996), we considered maximum island elevation to be a proxy of MEE. Thus, we expect a positive relationship between maximum island elevation and island treeline elevation. Vascular plant species richness for each island was extracted from various literature sources (see A1). Isolation from the continent and isolation from the nearest island were defined as the distance to the nearest continent and the distance to the nearest neighboring major island, respectively.

Statistical Analysis

To check for significant differences in treeline elevation between mainland, continental islands and oceanic islands, analysis of variance (ANOVA) and a post-hoc Tukey HSD test were used. The significance level was set at α = 0.05. To ensure comparability between treeline elevations of all

latitudes, it was necessary to correct for latitude. Therefore, we fitted a linear model between treeline elevation and latitude and afterwards extracted the residuals, which were implemented into ANOVA and the subsequent post-hoc Tukey HSD test. To fulfill the requirements of the linear model fit we transformed latitude using a hump-shaped term, which is defined as the following: treeline elevation ~ latitude^2 + latitude. ANOVA was also implemented to identify differences between specific characteristics of continental and oceanic islands. Significance levels are given as * for $p < 0.05$, ** for $p < 0.01$ and *** for $p < 0.001$.

We compared maximum island elevation (i.e. our proxy for MEE) of oceanic islands to continental islands. Similar to island treeline elevation, maximum island elevation was corrected for latitude using a hump-shaped transformation for the complete island dataset. The effective glacial erosion process at high latitudes, known as the *glacial buzzsaw* (Egholm et al. 2009), leads to an increasing maximum island elevation towards the equator, making a correction necessary. In addition, a univariate comparison was implemented between island treeline elevation and maximum island elevation for all islands and for the tropics subset using linear regression models.

To investigate the relationships between treeline elevation and island characteristics (latitude, maximum island elevation, island area, geologic age, isolation from the continent, isolation from the nearest neighboring island, plant species richness; Tab. A2), ordinary least squares regression models were applied. In a first step, all variables were checked for collinearity using a bivariate correlation matrix based on Pearson's r. According to Dormann et al (2013) collinearity is reached, if $|r| > 0.7$; however, this was not the case for any variable. Statistical model requirements were checked visually, and if requirements were not met, the best-fitting transformations (logarithmic, square root quadratic and hump-shaped = $x^2 + x$) were applied on predictor variables by accounting for model performance using AICc (i.e. the second-order Akaike Information Criterion; Grueber et al. 2011). To display the latitude-treeline elevation relationship, generalized additive models (GAMs) were implemented using thin plate regression splines to optimize the smoothing term (R-package *mgcv* version 1.7-29; Wood 2006). The level of smoothing is determined by the concept of effective degrees of freedom, which maintains a balance between the total number of observations and total degrees of freedom used when fitting the model (Guisan et al. 2002).

In a second step, the relative importance of each variable in a multiple regression context was assessed in a multi-model inference approach by calculating the R^2 contribution averaged over all possible model combinations (Chevan and Sutherland 1991). We used the R-package *relaimpo* version 2.2-2 (Grömping 2006), which applies a bootstrap approach (n = 1000) to calculate a 95%-confidence interval. Model runs for each dataset were calculated (i.e. all islands, continental islands, oceanic islands plus the same separation for the tropics) with the best-fitting transformation of significant variables from the univariate regression. As plant species richness and island age were only available for 48% of all islands, we undertook two calculation runs per subset: one run using all islands per subset but excluding plant species richness and island age, and one run including plant species richness and island age but only using the islands, where data was available (Tab. 1).

All calculations were conducted in R Statistics (Version 3.0.1, R Core Team 2013). Fig. 1 was built in ArcMap 10 (ESRI Inc. 2010).
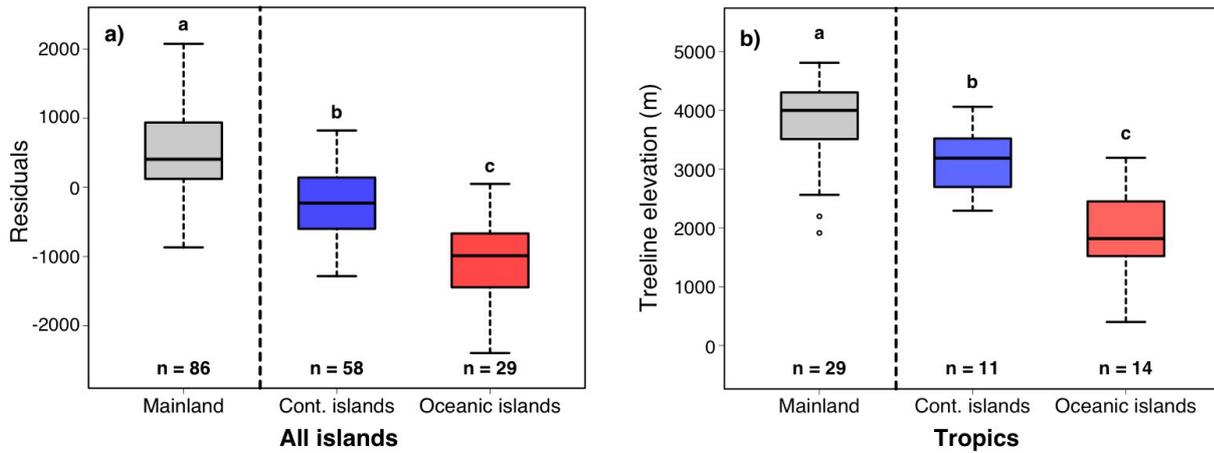
Figure 2. Comparison of treeline elevations between continental mainland, continental island and oceanic islands for a) all islands and b) all islands in the tropics. In figure a) we corrected for the strong latitudinal effect seen in Fig. 3, thus residuals from a model treeline elevation ~ latitude2 + latitude are shown. No correlation between latitude and treeline elevation exists in the tropics, thus no correction was undertaken here. Lowercase letters indicate homogenous groups. Significance level was set at p < 0.05.
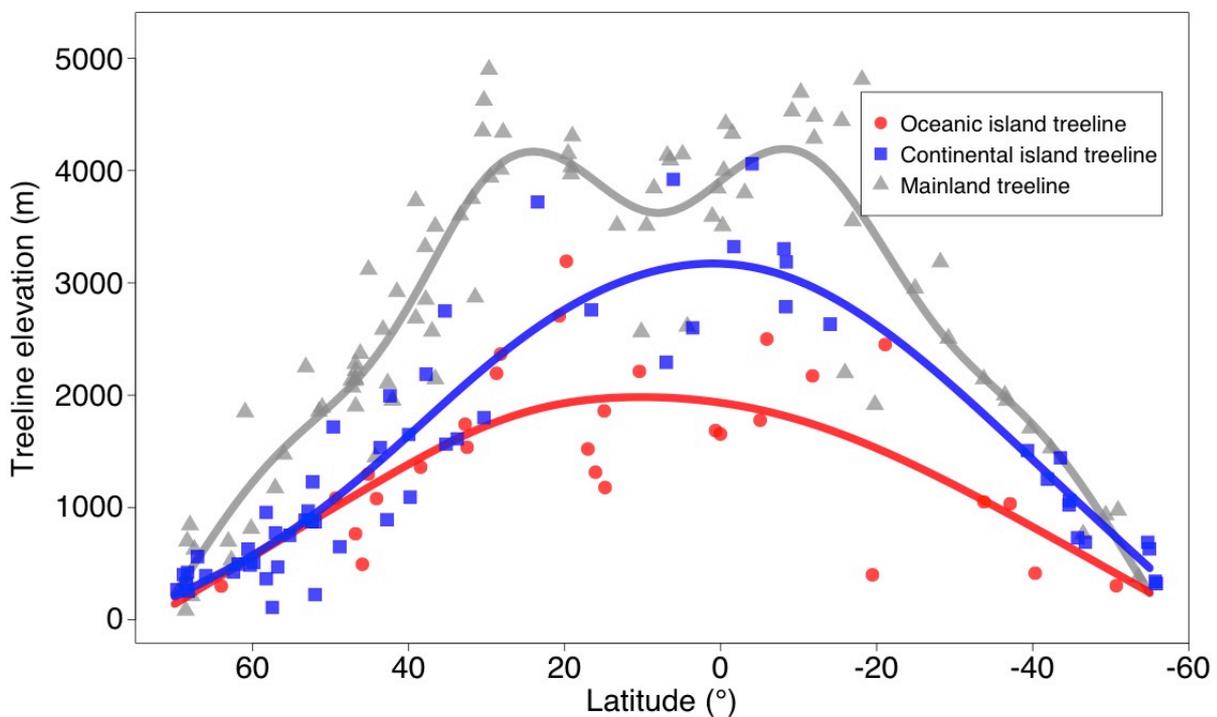
Figure 3. Global latitudinal distribution of oceanic island (circles), continental island treelines (squares) and mainland treeline elevations (triangles). GAM fits are given for the respective category showing significant relationships.

Table 1. Relative importance of each explanatory variable explaining treeline elevation. a) Displays the whole latitudinal gradient with plant species richness and age, b) the whole latitudinal gradient without plant species richness and age, c) the tropics with plant species richness and age, and d) the tropics with plant species richness and age. Plant species richness and island age were only available for 48% of all islands (n = number of islands). Three data (sub-)sets were considered, respectively: all islands, oceanic islands and continental islands. Total explanatory power of a multiple linear regression model is given in brackets for each subset. Transformations (Trans.) used for calculating the relative importance and yielding the highest explanatory power in an a priori univariate test are given as well. Tested transformations were no transformation, logarithmic (log), square root (sq, quadratic and binominal (hump). The direction of relationship (Dir.) is indicated by '+' or '-' or ∩ or ∪ for binominal transformations.

a) All islands with plant species richness and age

	All islands (n = 41, Multiple R² = 0.94)			Oceanic islands (n = 21, Multiple R² = 0.91)			Continental islands (n = 20, Multiple R² = 0.96)		
	R²	Dir.	Transf.	R²	Dir.	Transf.	R²	Dir.	Transf.
Latitude	0.30	-	quad.	0.26	∩	hump	0.39		quad.
Maximum island elevation	0.45	+	none	0.40	+	none	0.43	+	none
Island area	n.s.			0.03	+	none	0.12		quad.
Isolation from continent	n.s.			0.10	+	quad.	n.s.		
Isolation from nearest island	n.s.			0.06	-	none	n.s.		
Island age	n.s.			0.06	-	none	n.s.		
Plant species richness	0.19	+	sqrt	n.s.			0.06.	+	sqrt

b) All islands without plant species richness and age

	All islands (n = 86, Multiple R² = 0.91)			Oceanic islands (n = 29, Multiple R² = 0.87)			Continental islands (n = 57, Multiple R² = 0.94)		
	R²	Dir.	Transf.	R²	Dir.	Transf.	R²	Dir.	Transf.
Latitude	0.31	∩	hump	0.28	∩	hump	0.34	∩	hump
Maximum island elevation	0.44	+	none	0.51	+	none	0.38	+	none
Island area	0.10	+	√	n.s.			0.13	+	√
Isolation from continent	0.06	+	log	n.s.			0.06	+	log
Isolation from nearest island	n.s.			0.08	-	quad.	0.03	-	log

Table 1 continued.

c) *Tropics with plant species richness and age*

	All islands n = 15			Oceanic islands n = 9			Continental islands n = 6		
	R²	Dir.	Transf.	R²	Dir.	Transf.	R²	Dir.	Transf.
Latitude	n.s.			n.s.			n.s.		
Maximum island elevation	0.48	+	none	0.68	+	none	0.45	+	log
Island area	0.22	+	log	n.s.			n.s.		
Isolation from continent	n.s.			n.s.			n.s.		
Isolation from nearest island	n.s.			n.s.			n.s.		
Island age	0.10	+	log	0.25	-	none	0.23	-	log
Plant species richness	0.15	+	√	n.s.			0.29	+	log
	(Multiple R² = 0.96)			(Multiple R² = 0.93)			(Multiple R² = 0.97)		

d) *Tropics without plant species richness and age*

	All islands n = 25			Oceanic islands n = 14			Continental islands n = 11		
	R²	Dir.	Transf.	R²	Dir.	Transf.	R²	Dir.	Transf.
Latitude	n.s.			n.s.			n.s.		
Maximum island elevation	0.67	+	√	0.67	+	log	0.73	+	log
Island area	0.26	+	log	n.s.			0.19	+	qua
Isolation from continent	n.s.			0.24	-	none	n.s.		
Isolation from nearest island	n.s.			n.s.			n.s.		
	(Multiple R² = 0.93)			(Multiple R² = 0.91)			(Multiple R² = 0.91)		

RESULTS

Comparison of treeline elevations

Mainland treelines were significantly higher than continental (p < 0.001) and oceanic island treelines (p < 0.001). Continental island treelines were significantly higher than oceanic island treelines (p < 0.001) if corrected for latitude, respectively (Fig. 2a). Focusing on tropical regions, thus reducing the effects of latitude, treeline elevation followed the same pattern by decreasing significantly from mainland to continental islands (p < 0.05) and from continental islands to oceanic islands (p < 0.001; Fig. 2b). For all (uncorrected) mean values and standard deviation see A2 in Supplemental Material.

Global latitude-treeline elevation relationship

The GAM regression identified a double-hump pattern for mainland treeline elevation with latitude (effective degrees of freedom = 8.03, R^2 = 0.84***; Fig. 3) with two peaks observed at about 23° N and 10° S. Continental islands and oceanic islands followed a hump-shaped relationship with latitude (effective degrees of freedom = 4.13, R^2 = 0.86*** and effective degrees of freedom = 2.69, R^2 = 0.48***, respectively), peaking at about 0° and 12° N, respectively. Within the tropics, treeline elevation was not related to latitude, neither for the mainland nor for continental or oceanic islands (Tab. 1).

Differentiation between continental islands and oceanic islands (regional factor)

Continental islands were significantly larger in area (p < 0.01), less isolated from the continent (p < 0.001), less isolated from the nearest neighboring island (p < 0.01) and possessed more plant species (p < 0.01) than oceanic islands. If corrected for latitude, continental islands were significantly higher than oceanic islands (p < 0.01, Fig. 4a). When compared to oceanic islands, continental islands in the tropics were significantly higher (p < 0.001, Fig. 4b), larger (p < 0.01) and possessed more plant species (p < 0.01). For all mean values and standard deviation see A2 in Supplemental Material.

The effects of local island characteristics compared to global and regional variables

Total explained variation in island treeline elevation data for all islands as well as for the two island types calculated from the pool of local, regional and global variables presented in the methods ranged from R^2 = 0.87 to R^2 = 0.94 (Tab. 1). The most important drivers of island treeline elevation on all islands as well as on continental and oceanic islands were, in decreasing order of relative importance (RI): maximum island elevation (RI between 0.38 and 0.51), latitude (RI between 0.26 and 0.39), island area (RI between 0.03 and 0.13) and plant species richness (RI between 0.06 and 0.19; the latter two not for oceanic islands; Fig. 5a, Tab. 1a and Tab. 1b). Maximum island elevation was significantly correlated with latitude in a hump-shaped relation for all islands (R^2 = 0.46***).
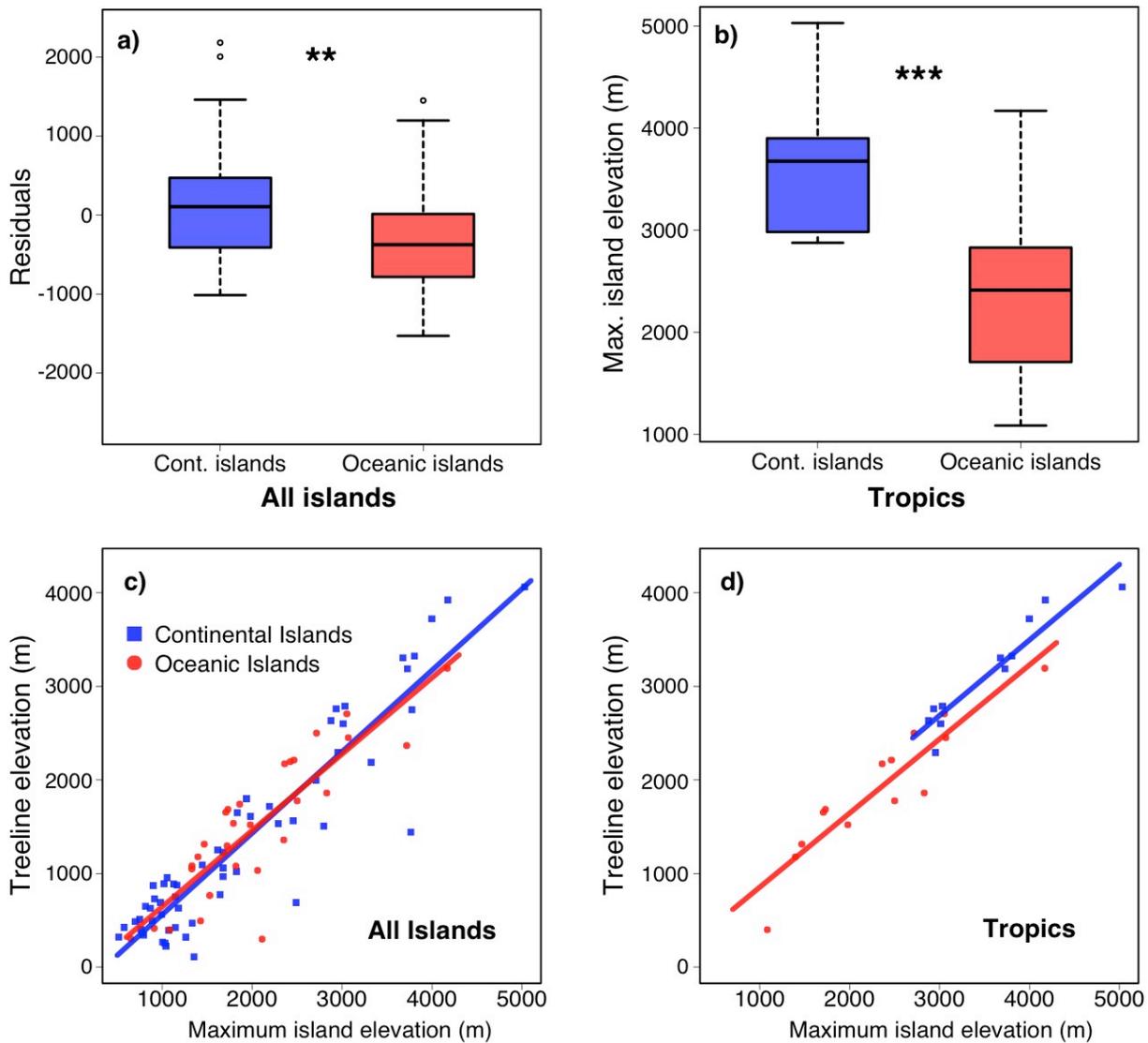
Figure 4. Significant differences in maximum islands elevation between continental and oceanic islands for (a) all islands and (b) the tropics. Note that (a) is corrected for latitude. Linear regressions of treeline elevation and maximum island elevation for continental and oceanic islands using (c) all islands and (d) the tropics. This highlights the strong explanatory power of maximum island elevation, which is used as a proxy of the mass elevation effect.

Total explained variation in island treeline elevation when considering the tropical subset ranged between R^2 = 0.91 and 0.97 (Tab. 1c and Tab. 1d). Again, maximum island elevation had the highest explanatory power (RI between 0.45 and 0.73 Fig. 5b), followed by plant species richness (RI between 0.15 and 0.29), island area (RI between 0.19 and 0.26) and island age (RI between 0.10 and 0.25; Tab. 1c and Tab. 1d, Fig. 5b).

A univariate comparison of island treeline elevation with maximum island elevation, as a proxy for MEE, revealed a strong relationship. For all islands, continental islands and oceanic islands treeline elevation and maximum island elevation were positively correlated with R^2 = 0.93***, R^2 = 0.86*** and R^2 = 0.72***, respectively (Fig. 4c). A similarly strong relationship was found for the tropics subset with

correlations of $R^2 = 0.92^{***}$, $R^2 = 0.88^{***}$ and $R^2 = 0.84^{***}$ for all islands, continental islands and oceanic islands, respectively (Fig. 4d).
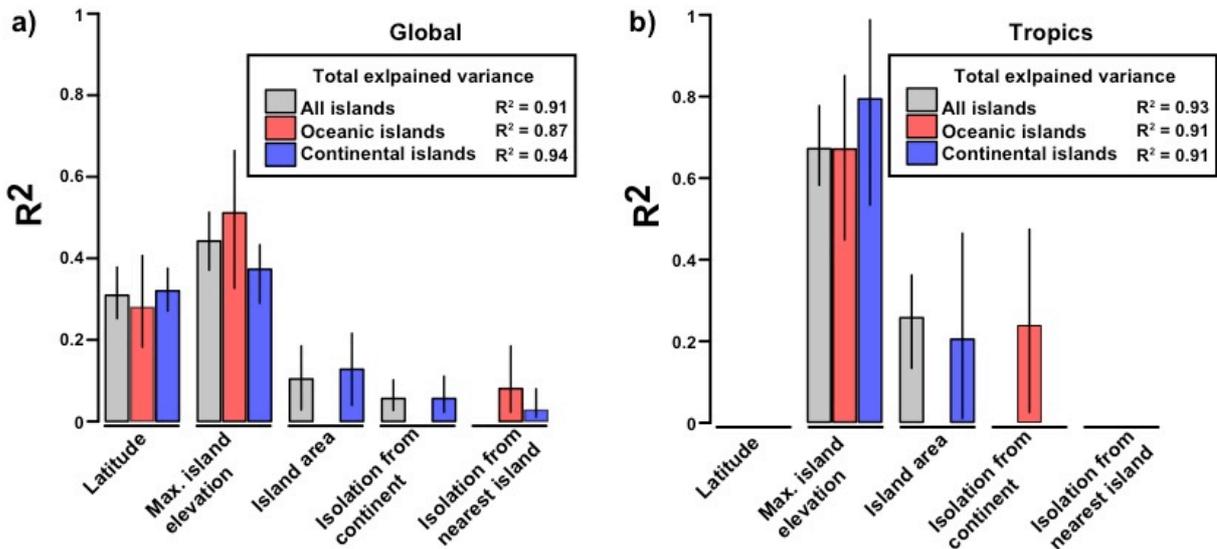

Figure 5. Combined and single explanatory power of independent variables for treeline elevation of the global dataset (a-b) and the tropics (c-d). (a & c) Explanatory power (multiple R2) of a multiple linear regression model combining all variables and (b & d) relative importance per variable displayed as R2 values. Bars indicate mean relative importance, the whiskers upper and lower 0.95-confidence interval per variable for all respective model combinations. Please note that plant species richness and island age are missing because values were only available for 48% of the islands (Tab. A1). Please see Tab. 1 for relative importance values and direction of relationship.

DISCUSSION

Island treelines are lower than mainland treelines

At global scale we comprehensively determine that mean treeline elevation decreases from the mainland through continental islands to oceanic islands, as suggested by Leuschner (1996). This contributes a new background to the fundamental debate on treelines concerning interactions between the physical environment and biodiversity, and might have several possible explanations.

First, lower island treeline elevations may be caused by the specific oceanic climate of high elevation islands. Indeed, because of reduced MEE on islands compared to the continent (Leuschner 1996), this type of climate displays lower diurnal and annual temperature amplitudes, relatively high cloud cover, especially in peak areas, and relatively low daytime solar radiation owing to the small area of islands and the buffering effect of the ocean. All these features of oceanic climates influence treeline elevation and are contrasting to continental climates, which have been argued to increase treeline elevation (Holtmeier 2009, Körner 2012). More specifically, the effect of high cloudiness and high precipitation, especially in peak areas (all islands; Flenley 1995, Paulsen & Körner 2014), and low temperature seasonality (only non-tropical islands) in higher elevations of oceanic islands compared to continental mainland areas of similar latitude has been suggested as a possible cause of reduced tree

growth suitability and thus lower treeline elevations on islands (Körner 1998, Cieraad et al. 2014). High cloudiness and high precipitation are likely to be important on islands of the equatorial tropics (e.g. New Guinea, Sumatra, Java or Borneo; Leuschner 1996) but equally relevant on temperate and high latitude islands. Drought-induced treelines on islands represent an important regional difference to mainland mountain systems as well (Leuschner and Schulte 1991, Leuschner 1996, Gieger and Leuschner 2004, Crausbay et al. 2014). These island treelines are often directly associated with the boundary layer of the trade wind inversion or short-term climatic events such as El Niño (Crausbay et al. 2014), and are not actual thermal treelines. These regional climatic conditions are likely to be very important in shaping island treeline elevation, however it remains unclear how strong they individually contribute.

Second, lower island treeline elevations than on the mainland may be indebted to impoverished species pools on islands (*sensu* MacArthur and Wilson 1967). Indeed, a lower number of species implies that tree species adapted to high-elevation conditions are less likely to be part of the respective island floras (Leuschner 1996). However, our data showed that species richness had a significant positive effect on treeline elevation only on continental islands, but not on oceanic islands. Continental island floras are generally more similar to mainland floras whereas isolated oceanic islands are often characterized by high degrees of neo-endemism (MacArthur and Wilson 1967, Whittaker and Fernández-Palacios 2007, Whittaker et al. 2008). Neo-endemic species, especially on oceanic islands, have evolved via *in situ* speciation from the limited existing island species pool (Whittaker and Fernández-Palacios 2007). The low phylogenetic and low ecological variability of high-elevation floras (Körner 2012) likely leads to a reduced probability of tree species suitable for high-elevation conditions. However, a recent study showed that some treelines on islands are lower due to thermal limitations as suggested by Körner and Paulsen (2004), and not necessarily for taxon-specific reasons (Cieraad et al. 2014).

The global latitude-treeline elevation relationship

Latitude is a strong proxy for temperature availability for plant growth, which increases from high to low latitudes (Körner 2003) and influences treeline formation (Case and Duncan 2014). On islands, latitude can explain the pattern observed in this study, i.e. island treeline elevation increases with decreasing latitude. The simple hump-backed relationship observed in continental and oceanic islands is probably explained by the fact that islands are much less influenced by MEE and continentality in comparison to mainland mountain systems (Körner 2012). Mainland treeline elevation rather displays a more complex pattern. It shows a double-hump pattern with a tropical depression (*sensu* Troll 1973).

A fundamental difference between treeline patterns on islands and the mainland is that maximum treeline elevation is reached within the tropics for islands – regardless of their geological origin – whereas for the mainland it is reached in the subtropics/dry tropics of both hemispheres (see Fig. 3; Hoch and Körner 2005, Miehe et al. 2007). The lower MEE on islands in combination with the overall higher continentality of mainland regions constitute major features differentiating island systems from mainland

mountain systems. Therefore, it is likely that they are crucial drivers for treeline elevation on the global scale.

Most high elevation islands in the subtropics (and many in the tropics) are subject to drought at high elevations due to trade wind inversions (Leuschner 1996), i.e. these treelines are not actual thermal treelines but their maximum elevation is restricted by moisture availability (Crausbay et al. 2014). Thus, island treeline elevation is capped by drought in the subtropics and dry tropics and cannot reach higher elevations, even though tree species might be able to tolerate colder climatic conditions (Holtmeier and Broll 2005). However, one must note that trade wind inversions also occur at high elevation on the mainland (Anthelme and Dangles 2012). In contrast, the areas with the highest treelines on the mainland are usually not limited by humidity but rather by temperature (Körner and Paulsen 2004). This trade wind-effect on islands may increase the elevational gap between treeline elevations on islands and the mainland.

Continental islands vs. oceanic islands: the regional influence of island type on treeline elevation

Continental islands possess higher treelines than oceanic islands. Both island types show specific characteristics that can explain this difference. Continental islands are generally larger in area and higher in elevation because many are continental fragments or mini-continents (e.g. Hokkaido, New Zealand, Tasmania, Borneo, New Guinea, Sumatra, Madagascar, British Isles). In consequence, these islands are not only closer to continents in terms of origin, bedrock and age but also according to the size of mountain ranges. The following five points refer to traits and processes that are related to this intermediate quality: (1) The large size, high elevation and the presence of mountain chains on many continental islands leads to a substantial MEE, increasing treeline elevation; (2) it is plausible that species pools are relatively similar to the mainland (Whittaker and Fernández-Palacios 2007), thus increasing the probability of harboring tree species adapted to high elevation conditions; (3) continental islands exhibit a certain degree of continentality in their interior (Körner 2012), which is likely increased owing to their general proximity to the continent (Hela 1953); (4) continental islands, in contrast to oceanic-volcanic islands, generally do not possess immature soils at high elevations due to their more advanced geological age and setting (Neall and Trewick 2008); and, (5) age also plays a crucial role in producing high elevation tree species via adaptive processes and speciation, thus slowly shifting the treeline upward over (geological) time. It has been shown that speciation increases with elevation on continental and oceanic islands (Steinbauer et al. 2012, 2013), explaining the high proportion of endemism and thus, its importance at high elevations. In conclusion, continental islands behave more similarly to the mainland in terms of treeline elevation, in particular coastal mainland mountain regions.

Due to the generally lower elevation and smaller size of oceanic islands compared to continental islands, the influence of MEE on oceanic islands is – although present – smaller than on continental islands, thus leading to generally lower treeline elevations on oceanic islands. Oceanic islands are also younger than continental islands. Especially, high elevation areas are usually small and exist only for

short geological time periods due to the specific life cycle of volcanic-oceanic islands (Whittaker et al. 2008, Fernández-Palacios et al. 2014). The relative youth and the small area of high elevation systems on oceanic islands compared to continental islands likely leads to a less effective MEE, providing a plausible explanation for finding the lowest treeline elevations on oceanic islands.

The maximum island elevation effect: primary driver of island treeline elevation

Surprisingly and in contrast to our main latitude-dominated hypothesis, maximum island elevation emerged as the best predictor of treeline elevation on islands, i.e. the higher the island, the higher the treeline elevation (Fig. 5a). Although maximum island elevation is correlated with latitude due to the erosive effect of large glaciers during the ice ages (Egholm et al. 2009), the local island characteristic maximum island elevation independently explains most variance in our dataset . This becomes even clearer when looking at the tropical subset, where latitude becomes irrelevant. Here, maximum island elevation clearly dominates (Fig. 5b).

We interpret maximum island elevation as a proxy of MEE following Leuschner (1996). With increasing island elevation the volume (or the mass) and concomitantly the 3D-land area of an island increases owing to the more or less cone-shaped geometry of an island (or any other mountain). Large land areas warm more intensely with solar radiation than surrounding air masses, leading to favorable microclimatic conditions for tree growth at high elevations; a classical MEE (Körner 2012). Thus, our statistical analyses show (Tab. 1, Fig. 5) that the main driver of island treeline elevation on the global scale is the MEE.

The 'summit syndrome' may be a driver of the maximum island elevation effect (Körner 2012), which stands in contrast to the MEE explanation. The summit syndrome describes why trees generally do not grow in exposed summit areas, although the true climatic treeline can be located substantially higher (Holtmeier and Boll 2005). Trees are often not able to colonize summit areas due to wind stress and abrasion as well as poor or non-existent soils. In consequence, the summit syndrome can explain emerging treelines at lower elevations than expected regarding thermal conditions. This might be especially relevant for temperate and high-latitude islands due to their frequent exposition to high wind speeds in association with oceanic low-pressure systems (Archer and Jacobson 2005), while wind speed at high elevation on tropical and subtropical islands has been shown to be relatively low (Leuschner 2000). As the summit syndrome is only active in proximity to the peak of an island (Körner 2012 and references therein), the elevational zone influenced by the summit syndrome is coupled to the summit elevation, probably leading to a positive relationship between treeline elevation and maximum island elevation.

As a possible, complementary explanation, the maximum island elevation effect on island treeline elevation may result in part from the fact that higher islands offer species more opportunities to shift their ranges up and downslope during periods of climatic fluctuations (e.g. during glacial and interglacial periods; Molau 2004), thus acting as climatic refugia for treeline species. This might be especially

relevant for high-elevation tropical islands, which possess more 'environmental space' along the elevational gradient than non-tropical islands, e.g. with vegetation possibly found from 0 to more than 5000 m a.s.l. (Janzen 1967). On low elevation islands pronounced elevational migration for plant species is not possible and the re-colonization of high elevation tree species from the continent is extremely rare (*sensu* MacArthur and Wilson 1967). This leads to a higher extinction probability of tree species that are adapted to high elevation conditions during interglacial periods (Molau 2004). Thus, high elevation islands might have experienced historically reduced extinction probabilities of high elevation tree species in the past, leading to higher island treelines today.

CONCLUSION

We demonstrate that "simple" island biogeographic variables, such as elevation, latitude, plant species richness, area and isolation, can explain almost all variation in the global pattern of treeline elevation on islands. The specific analysis of global island treeline patterns permitted to identify relevant regional features (i.e. island type) and important local island characteristics (especially maximum island elevation) that substantially contribute in explaining large-scale patterns. Our island-based study successfully quantifies MEE, a traditionally descriptive influence factor in treeline science (*sensu* Körner 2012 and references therein), using a comprehensive measure (maximum island elevation). This measure of MEE is likely transferable to mainland treelines, constituting a substantial contribution to our understanding of treeline formation. The high importance of maximum island elevation suggests that the MEE is relevant for treeline formation already on relatively small landmasses such as islands. Interestingly, MEE dominates island treeline formation, whereas latitude, as the globally most important thermal gradient, is only secondary in this respect. A next, stimulating challenge may be to take a closer look at the effects of mass elevation and continentality on treeline elevation for all mountain regions of the world.

ACKNOWLEDGMENTS

REFERENCES

Anthelme, F. and Dangles, O. 2012. Plant–plant interactions in tropical alpine environments. - Perspect. Plant Ecol. 14: 363-372.

Archer, C. L. and Jacobson, M. Z. 2005. Evaluation of global wind power. - J. Geophys. Res-Atmos 110: 1-20.

Case, B. S. and Duncan, R. P. 2014. A novel framework for disentangling the scale-dependent influences of abiotic factors on alpine treeline position. - Ecography 37: 1- 14.

Chevan, A. and Sutherland, M. 1991. Hierarchical partitioning. - Am. Stat. 45: 90–96.

Cieraad, E. et al. 2014. Southern Hemisphere temperate tree lines are not climatically depressed. - J. Biogeogr. 41: 1456-1466.

Crausbay, S. D. et al. 2014. Moisture status during a strong El Niño explains a tropical montane cloud forest's upper limit. - Oecologia 175: 273–284.

Dahl, A. L. 1991. Island directory. - UNEP egional Seas Directories and Bibliographies 35, Nairobi

Dormann, C.F. et al. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. - Ecography 36: 27-46.

Egholm, D. L. et al. 2009. Glacial effects limiting mountain height. - Nature 460: 884-887.

Flenley, J. R. 1995. Cloud forest, the Massenerhebung effect, and ultraviolet insolation. Tropical montane cloud forests. - Ecol. Stu. An. 110: 150-155.

Fernández-Palacios, J. M. et al. 2014. Overview of Habitat History in Subtropical Oceanic Island Summit Ecosystems. – Arct Antarct Alp Res 46: 801-809.

Gieger, T. and Leuschner, C. 2004. Altitudinal change in needle water relations of *Pinus canariensis* and possible evidence of a drought-induced alpine timberline on Mt. Teide, Tenerife. - Flora 199: 100-109.

Gillespie, R. G. and Clague, D. A. 2009. Encyclopedia of the Natural World. Encyclopedia of Islands. - University of California Press, Berkeley

Grömping, U. 2006. Relative importance for linear regression in R: the package relaimpo. - J. Stat. Softw. 17: 1-27.

Grueber, C. E. et al. 2011. Multimodel inference in ecology and evolution: challenges and solutions. J. Evol. Biol. 24: 699-711.

Guisan, A. et al. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. - Ecol. Model. 157: 89-100.

Hela, I. 1953. Regional distribution of the continentality in the climate of the oceans. - Geophysica 4: 41-47.

Hermes, K. 1955. Die Lage der oberen Waldgrenze in den Gebirgen der Erde und ihr Abstand zur Schneegrenze. - Dissertation der Philosophischen Fakultät der Universität Köln.

Hoch, G. and Körner, C. 2005. Growth, demography and carbon relations of *Polylepis* trees at the world's highest treeline. - Funct. Ecol. 19: 941-951.

Holtmeier, F. K. 2009. Mountain timberlines: Ecology, patchiness and dynamics. 2nd Edition. - Springer Verlag, Heidelberg

Holtmeier, F. K. and Broll, G. 2005. Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. - Global Ecol. Biogeogr. 14: 395-410.

Janzen DH 1967. Why mountain passes are higher in the tropics. - Am. Nat. 101: 233-249.

Jobbágy, E. G. and Jackson, R. B. 2000. Global controls of forest line elevation in the northern and southern hemispheres. - Global Ecol. Biogeogr. 9: 253-268.

Jones, P. J. 1994. Biodiversity in the Gulf of Guinea: an overview. - Biodiv. Conser. 3: 772-784.

Kisel, Y. and Barraclough, T. G. 2010. Data from: Speciation has a spatial scale that depends on levels of gene flow. - Dryad Digital Repository. doi:10.5061/dryad.887

Körner, C. 1998. A re-assessment of high elevation treeline positions and their explanation. - Oecologia 115: 445-459

Körner, C. 2003. Alpine plant life: functional plant ecology of high mountain ecosystems, 2nd Ed. - Springer, Berlin.

Körner, C. 2012. Alpine treelines: Functional ecology of the global high elevation tree limits. - Springer Verlag, Basel.

Körner, C. and Paulsen, J. 2004. A world-wide study of high altitude treeline temperatures. - J. Biogeogr. 31: 713-732.

Körner, C. et al. 2012. A definition of mountains and their bioclimatic belts for global comparisons of biodiversity data. - Alp. Bot. 121: 73-78

Leuschner, C., and Schulte, M. 1991. Microclimatological investigations in the tropical alpine scrub of Maui, Hawaii: evidence for a drought-induced alpine timberline. - Pac. Sci. 45: 152-168.

Leuschner, C. 1996. Timberline and alpine vegetation on the tropical and warm-temperate oceanic islands of the world: elevation, structure and floristics. - Vegetatio 123: 193-206

Leuschner, C. 2000. Are high elevations in tropical mountains arid environments for plants? - Ecology 81: 1425-1436.

MacArthur, R. H. and Wilson, E. O. 1967. The theory of island biogeography. Princeton University Press, Princeton

Malanson, G. P. et al. 2007. Alpine treeline of western North America: Linking organism-to-landscape dynamics. - Phys. Geogr. 28: 378-396.

Miehe, G. and Miehe, S. 1994. Zur oberen Waldgrenze in tropischen Gebirgen. - Phytocoenologia 24: 53-110.

Miehe, G. et al. 2007. Highest treeline in the northern hemisphere found in southern Tibet. - Mt. Res. Dev. 27: 169-173.

Molau, U. 2004. Mountain biodiversity patterns at low and high latitudes, - Ambio 13: 24-28.

Nagy, L. and Grabherr, G. 2009. The Biology of Alpine Habitats. - Oxford University Press, Oxford.

Neall, V. E. and Trewick, S. A. 2008. The age and origin of the Pacific Islands: a geological overview. - Philos. T. R. Soc. B 363: 3293-3308.

Ohsawa, M. et al. 1985. Altitudinal zonation of forest vegetation on Mount Kerinci, Sumatra: with comparisons to zonation in the temperate region of east Asia. - J. Trop. Ecol. 1: 193-216.

Ohsawa, M. 1990. An interpretation of latitudinal patterns of forest limits in South- and East-Asian mountains. - J. Ecol. 78: 326-339.

Paulsen, J. and Körner, C. (2014) A climate-based model to predict potential treeline position around the globe. Alp Botany 124: 1-12.

R Core Team 2013. R: A language and environment for statistical computing. - R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Smith, W. K et al. 2003. Another perspective on altitudinal limits of alpine timberlines. - Tree Physiol. 23: 1101-1112.

Steinbauer, M. J. et al. 2012. Increase of island endemism with altitude - speciation processes on oceanic islands. - Ecography 34: 1–10.

Steinbauer, M. J. et al. 2013. Elevation-driven ecological isolation promotes diversification on Mediterranean islands. - Acta Oecol. 47: 52-56.

Troll, C. 1973. The upper timberlines in different climatic zones. - Arctic Alp. Res. 5: A3-A18.

UNEP-WCMC 2013. accessed: 15th of March 2013, Global Islands Database. - UNEP World Conservation Monitoring Centre. Cambridge, UK, www.unep-wcmc.org.

Wood, S. N. 2006. Generalized additive models: An introduction with R. - Chapman and Hall/CRC.

Weigelt, P. et al. 2013 Bioclimatic and physical characterization of the world's islands. - P. Natl. Acad. Sci. USA 110: 15307-15312.

Whittaker, R. J. and Fernández-Palacios, J. M. 2007. Island Biogeography – Ecology, Evolution, and Conservation. 2nd Edition. - Oxford University Press, Oxford.

Whittaker, R. J. et al 2008. A general dynamic theory of oceanic island biogeography. - J. Biogeogr. 35: 977-994.

SUPPORTING INFORMATION IN ELECTRONIC VERSION OF DISSERTATION

Appendix S1 List of all islands including environmental data

Appendix S2 Mean values and standard deviation of all variables and data subsets

Appendix S3 Test dataset treeline elevations used to verify the GoogleEarth method

7.2 Manuscript 2

69

Elevation-driven ecological isolation promotes diversification on Mediterranean islands

Manuel J. Steinbauer, **Severin D. H. Irl** & Carl Beierkuhnlein

ABSTRACT

The percentage of single island neo-endemic species (an indicator for evolutionary diversification) was found to be independent of geographic distance to the continent in the case of the Aegean archipelago. It was concluded that speciation is independent of geographic isolation, while evolutionary processes are rather enhanced by *habitat heterogeneity*. An island's maximum elevation was used as an indicator for *habitat heterogeneity*. In contrast, we argue that *habitat heterogeneity (= habitat diversity, i.e. the richness in different habitats)* may be positively related to biotic richness, but a positive effect on speciation is yet to be proven. For any other type of heterogeneity, we propose a precise wording, especially when assessing its effect on speciation processes.

Alternatively, we propose that *elevation-driven ecological isolation* causes the pattern of endemic species on high-elevation islands. Environmental filtering along an elevational gradient differentiates ecosystems, leading to an increase of isolation with elevation. The reason is that comparable ecosystems are much farther apart than is the case for lowland ecosystems. In addition, ecosystems on neighboring islands or on the continent that may be source regions for colonizing species are small in area in high elevations in comparison with low elevation ecosystems. Consequently, an increased speciation rate resulting in a larger percentage of single island endemic species can be expected for higher elevations on islands and high mountains. Support for this *elevation-driven ecological isolation hypothesis* comes from other islands in the Mediterranean region (e.g. Crete and Corsica), where an increase of the percentage of endemic species with elevation has been observed. Thus, the assessment of (genetic-) isolation should incorporate the distance to similar habitats instead of simple land-to-land connections.

Keywords: island biogeography, Crete, environmental filter, speciation, single island endemic species, neo-endemic, habitat heterogeneity, habitat diversity

Abbreviations: pSIE = percentage of single island endemics

1. Increasing isolation and speciation with elevation

Recently, it was claimed that speciation on continental islands is not directly driven by isolation because no relationship between geographical distance to the mainland and the percentage of neo-endemic species was found (Kallimanis et al., 2011). Instead, it was proposed that *habitat heterogeneity* expressed by an island's maximum elevation drives speciation. A positive effect of *habitat heterogeneity* on speciation has been assumed by several studies (Halas et al., 2005; Stuessy et al., 2006). However, we alternatively suggest that elevation controls speciation rather via the effect of *elevation-driven ecological isolation* (sensu Steinbauer et al., 2012a).

Genetic isolation, as especially provided by islands, is reported to support speciation processes (Heaney, 2000). The degree of genetic isolation is, above all, affected by the number of individuals or propagules that are exchanged among populations. Isolation, however, varies between ecosystems

depending on the location on the island (Steinbauer et al., 2012a). The geographical distance between landmasses, as applied by Kallimanis et al. (2011), is only reasonable for coastal habitats. Especially high-elevation ecosystems (e.g. Mount Psiloritis [2456 m a.s.l.] on Crete or Monte Cinto [2706 m a.s.l.] on Corsica both reaching far into the alpine zone) differ considerably in their environmental setting from the low-elevation regions on the neighboring continent. Here, the distance to comparable continental ecosystems is a better indicator for the degree of isolation (Steinbauer et al., 2012a). This distance increases with elevation, as comparable mainland ecosystems are likely to be located distant from the coast (Fig. 1). In addition, not only focal island ecosystems but also the related continental ecosystems tend to become smaller in area with elevation. A smaller source region is likewise linked to a decline in the number of arriving colonists (i.e. propagule pressure) (MacArthur and Wilson, 1967), leading to an additional increase of isolation - and thus speciation processes - with elevation on islands. This hypothesis of an *elevation-driven ecological isolation* (sensu Steinbauer et al., 2012a) results in an increase of the percentage of single island endemic species (pSIE) with elevation. pSIE is used as an indicator for diversification processes (Emerson and Kolm, 2005) and its increase with elevation was recently proven for oceanic islands (Steinbauer et al., 2012a).

2. The situation on Crete and other continental islands

While oceanic islands generally consist of volcanic bedrock, continental islands may have a more diverse geological history. They often integrate bedrock from the continental plate that is less susceptible to erosion than bedrock of volcanic origin. Continental islands are often geologically older than oceanic ones.

Elevation-specific datasets for islands in general and for continental islands (i.e. true geographical islands surrounded by water but geologically part of the continental plate) in particular are rare. For continental islands the postulated *elevation-driven ecological isolation* hypothesis can be assessed using data for Crete, the highest of the 19 Aegean Islands that actually contain single island endemic species. Kazakis et al. (2007) highlight the richness in endemic species in higher elevations of Crete. They further report that the percentage of Balkan taxa shows an increase with elevation on Crete, while the proportion of Euro-Mediterranean species tends to decrease. Spiders inhabiting high-elevation ecosystems on Crete are mainly reported to be either palearctic or endemic species, while low elevation spiders tend to be xerophilous and are adapted to high temperatures and aridity (Chatzaki et al., 2005). Trigas et al. (2011) identified an increase of pSIE, for vascular plants with elevation, exceeding 40% in the summit region (i.e. ~2400 m a.s.l.).

Comparable conditions are reported from Corsica. Here, the percentage of endemic species reaches up to 50% in the mountainous and alpine vegetation belts but is below 10% in the lowlands (Gamisans, 1991; Thompson, 2005). On Corsica, many mountain species are interpreted to be evolutionary old arctic-alpine species (Contandriopoulous, 1962) with little colonization of newer species (Thompson, 2005). This indicates that high-elevation ecosystems might serve as refugia for old high mountain taxa that were able to withstand climatic fluctuations during the Pleistocene. In general, the ecological isolation of mountain systems does not only reduce gene flow between habitats, but also

prevents the establishment of new (non-native) species (Thompson 2005). This fact supports the remarkable persistence of established species.

On the Mediterranean islands many low-elevation sites were connected during the Pleistocene via land bridges. However, even under continental conditions high-elevation ecosystems remained isolated as distinct ecosystems, even if they were larger in size due to the downward shift during a colder climate. In consequence, we can expect that the populations of Mediterranean high-mountain island endemics were substantially larger during the glaciation periods than they are today.

The observed increase in the percentage of endemic species with elevation is associated with an overall decrease in species richness of high elevation floras, both on Corsica (Thompson, 2005) and Crete (Greuter, 1972). Their relatively low species richness and the associated unoccupied niches are additional evidence for ecological isolation. Indeed, species diversity of island mountain floras was presumably never as high as that of comparable continental high mountains.

The combination of species-poor ecosystems with "empty niche space" and genetic isolation likely drives increased speciation rates at high elevations on islands. Whittaker and Fernández-Palacios (2007) indicated that ancient continental islands host a higher percentage of endemic species than oceanic islands. Values reaching 40-50% of endemic species in high-elevation ecosystems on Mediterranean islands are comparable to the high-elevation ecosystems of oceanic islands like the Canary Islands (Steinbauer et al., 2012a) or La Réunion (Strasberg et al., 2005).
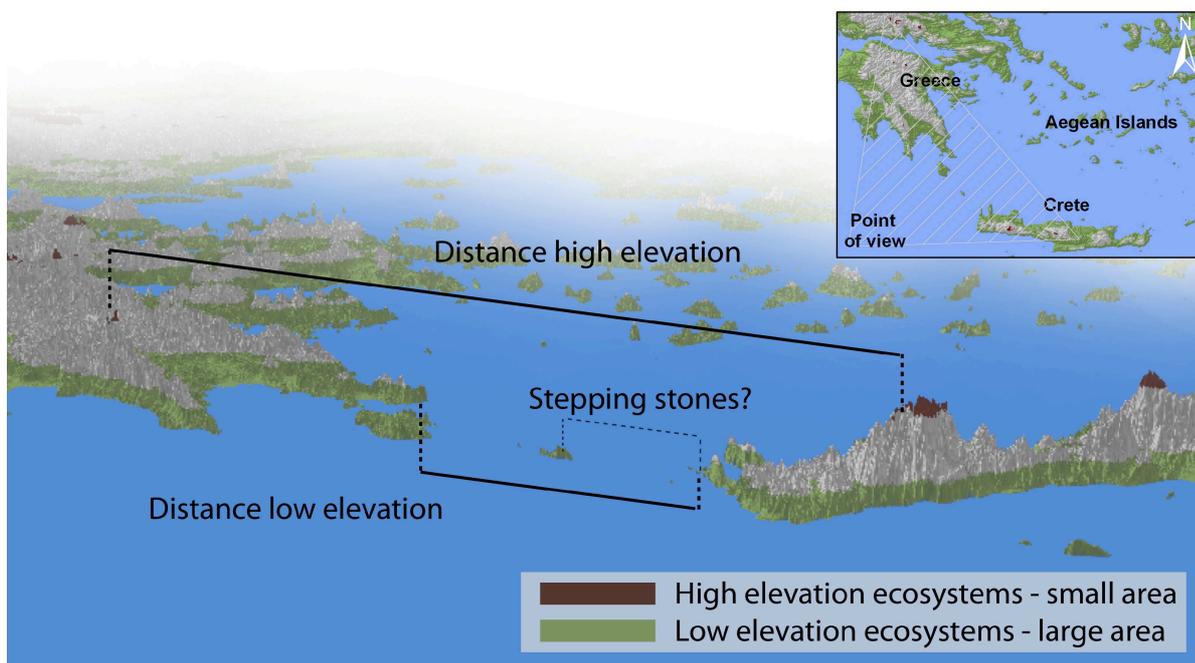

Figure 1. View of Greece (left, with the Peloponnesus in the background), Crete (right foreground) and the Aegaen Islands (center) from the Southwest (inlay). Green areas display the coastal zone (i.e. 0 -500 m a.s.l.), brown the high-elevation ecosystems (2000 – 2500 m a.s.l.). Obvious is the high isolation of high-elevation ecosystems compared to coastal ones and low-elevation stepping stones. As shown, Crete is the only one of the Aegean Islands actually possessing high-elevation ecosystems. Vertical exaggeration: x 10. (SRTM data provided by NASA; image created in ArcScene 10)

72

3. Human influence

An increase of the ratio of endemic species with elevation can be associated with decreasing impact of humans. Endemic species might have gone extinct in low elevations due to the tremendous human pressure on lowland habitats, while endemics could survive in more pristine high-elevation ecosystems (Sarnat and Moreaux, 2010). Losses of endemic species were presumably induced by human overexploitation (Panitsa and Tzanoudakis, 2001). Nevertheless, human influence can hardly explain the increase of pSIE with elevation. The number of endemic species driven to extinction that would be needed in low elevation ecosystems to reach the extraordinary high ratios of high-elevation ecosystems is immense. These hypothetically missing species would need to be new (now unknown) species as community composition differs considerably along elevation due to very strong ecological filters. In fact, the endemic plant species of Greece show narrow geographical and altitudinal distribution ranges (Georghiou and Delipetrou, 2010). Recent studies have emphasized the general tendency to overestimate the magnitude of anthropogenic influence on vegetation composition in the Mediterranean (Collons et al., 2012). Nonetheless, the reported increase of Balkan floral elements on Crete in congruence with a decline in Euro-Mediterranean species along the elevational gradient (Kazakis et al., 2007) can be interpreted in favor for both hypotheses: *human influence* or *elevation-driven ecological isolation.* The higher ratio of Mediterranean species in low elevations on Crete may result from an above-average rate of introduction of Euro-Mediterranean species to low-elevation ecosystems, or from environmental filtering along the elevational gradient favoring mountain species in higher elevations.

4. Isolation via environmental filtering along elevational gradients

Evidence suggests that isolation of continental islands (i.e. located on the shelf close to the continent and consisting of continental parent material) is less effective for inducing speciation than is the case for oceanic islands (volcanic islands on the oceanic crust) (Cody, 2006). This seems to be especially true for the Aegean Islands (Parmakelis et al., 2006; Poulakakis et al., 2008). Yet islands that are located on the shelf of continents are often older than oceanic islands. In addition, the probability for an island to be part of a dense agglomeration of neighboring islands of comparable age is rather high on the shelf. Furthermore, Kallimanis et al. (2011) propose that speciation processes on the Aegean Islands are rather associated to random than to adaptive differentiation (Bittkau and Comes, 2005; Edh et al., 2007; Georghiou and Delipetrou, 2010). Random differentiation is usually induced by very efficient genetic isolation. The distances between coastlines alone can hardly be related to isolation of high-mountain habitats and populations (Fig. 1), owing to the fact that it was likely to be much lower during times of reduced sea level. The strong correlation between maximum island elevation and pSIE on the Aegean Islands identified for neo-endemic species (i.e. in-situ evolution) by Kallimanis et al. (2011) can therefore also hint at *elevation-driven ecological isolation* (senu Steinbauer et al. 2012a) on the archipelago.

However, the phenomenon of elevation-driven isolation is not restricted to island systems. The increase of pSIE with elevation is also reported for continental mountain systems (Kessler et al., 2002; Mallet-Rodrigues et al., 2010) that exhibit strong spatial isolation and genetic distinctness of biota (Mota

et al., 2002). Overall, the highest proportions of endemism in the whole Mediterranean region can be found in high mountains (Médail and Quézel, 1997; Verlaque et al., 1997).

5. The role of heterogeneity for speciation

The understanding and definition of the term *habitat* differs among researchers. Partly it is given a species-specific meaning indicating the living conditions of a species' population (e.g. Tscharnke et al. 2012). However, it is also common to apply habitat in a comprehensive way at the community scale. Then, *habitat diversity* is used synonymously to *habitat heterogeneity* and often quantifies the number of vegetation units (see e.g. Tews et al., 2004; Stuessy et al., 2006; Kallimanis et al., 2011; Triantis et al., 2012) or as the sum of land cover classes (Kisel et al. 2011), which are often correlates of the elevational range. In this case, there is strong evidence that on islands *habitat diversity* (i.e. sum of vegetation units) contributes to both species richness and endemic richness (e.g. Hortal et al., 2009; Kallimanis et al., 2010; Panitsa et al., 2010; Steinbauer and Beierkuhnlein, 2010). Via direct relation high numbers of species are expected to result in a large number of endemic species, if assuming an equal speciation rate for all species.

Here, however, we are interested in how different environmental variables contribute to an increase in speciation rate *per species*, which would be reflected in an increase in the percentage of endemic species per given area. Stuessy et al. (2006) found the proportion of species evolved through adaptive radiation to be positively related to *habitat diversity* (i.e. sum of vegetation units) on islands. Assuming that speciation through adaptive radiation is much faster than random drift, this can be interpreted as an increase of speciation rate *per species* with increasing *habitat diversity*. In consequence there is some evidence that island elevation as a proxy for *habitat diversity* supports diversification processes within islands (Stuessy et al., 2006). Stuessy et al. (2006) identified a strong collinearity between *habitat diversity* and elevation with the latter being the better predictor for the percentage of species evolved through adaptive radiation. Thus we argue that other processes such as the *elevation-driven ecological isolation* are driving adaptive radiation on islands rather then *habitat diversity* per se.

However, the heterogeneity of habitats reflected by differences of environmental properties between and within habitat types may also enhance speciation (Svenning, 2001; Halas et al., 2005). This fact is not covered by the common understanding of *habitat diversity* (i.e. the mere number of habitat types). Environmental micro-heterogeneity may result in genetic differentiation in plants even in very small scales (in some cases even on scales smaller than 1m; Linhart and Grant, 1996; Leimu and Fischer, 2008). The edaphic heterogeneity found within temperate meadows is for instance reported to stimulate within-species differentiation of herbs (Silvertown et al., 1999). Resulting small-scale genetic differentiation facilitates local adaptation by natural selection (Eguiarte et al., 1992). Accordingly, *in situ* speciation should be promoted in "environmentally diverse localities" (Panitsa et al., 2010). Thus we claim that the heterogeneity of the environment is likely to support speciation processes even on very small scales. Approaches towards the quantification of ecological heterogeneity and complexity could address, beside others, microclimatic settings (e.g. Scherrer and Körner, 2011), surface roughness (e.g. Leutner et al., 2012; Steinbauer et al., 2012b), soil types and disturbance regimes (e.g. Buhk et al., 2007).

However, detailed investigations and especially a coherent concept and terminology are still missing (see Palmer 1994). While "heterogeneity" as a vague term is already included in ecological theory (e.g. "habitat complexity" in Whittaker et al. 2007) it is neither precisely defined nor measured in standardized ways. In fact it is likely that pronounced scale effects (grain and extent; in case of topography in three dimensions), methodological problems and missing general concept have hindered a profound examination of heterogeneity effects.

6. Conclusion

Assessing the role of isolation for speciation is not trivial and should at least focus on the distance to environmentally similar habitats rather than to terrestrial surfaces or land-to-land connections. In addition, large islands between the focal one and the coast ecosystems might act as both source systems (Fernández-Palacios et al., 2011) and stepping stones. Climatic fluctuations and the associated elevational shift of vegetation will additionally affect the occurrence of endemic species on islands. Climatic changes are also connected to temporal trends in propagule pressure from the continent. In the past, the probabilities of dispersal and gene flow in the Mediterranean have been substantially different from the present (Thompson, 2005). Thus, distance and/or connectivity to refugia, where species could survive long-term climatic fluctuations, can be another good indication for isolation depending on the timeframe associated with the process under focus (Medail and Diadema, 2009).

While *habitat diversity* is directly linked to the size of regional species pools, local environmental heterogeneity is likely to be positively related to speciation processes. However, this assumption is yet to be proven. An appropriate quantification of spatial heterogeneity and of its reflection in ecological complexity is required. Last but not least, a precise wording for spatial and ecological settings is needed in order to identify generality.

Acknowledgements:

References

Bittkau, C., Comes, H.P., 2005. Evolutionary processes in a continental island system: molecular phylogeography of the Aegean Nigella arvensis alliance (Ranunculaceae) inferred from chloroplast DNA. Mol. Ecol. 14, 4065-4083.

Buhk, C., Retzer, V., Beierkuhnlein, C., Jentsch, A., 2007. Predicting plant species richness and vegetation patterns in cultural landscapes using disturbance parameters, Agricult. Ecosys. Environ. 122, 446-452.

Chatzaki, M., Lymberakis, P., Markakis, G., Mylonas, M., 2005. The distribution of ground spiders (Araneae, Gnaphosidae) along the altitudinal gradient of Crete, Greece: species richness, activity and altitudinal range. J. Biogeogr. 32, 813–831.

Cody, M.L., 2006. Plants on Islands: Diversity and Dynamics on a Continental Archipelago. University of California Press.

Collins, P.M., Davis, B.A.S., Kaplan, J.O., 2012. The mid-Holocene vegetation of the Mediterranean region and southern Europe, and comparison with the present day. J. Biogeogr. doi:10.1111/j.1365-2699.2012.02738.x

Contandriopoulous, J., 1962. Recherches sur la flore endémique de la Corse et sur ses origines, Faculté des Sciences de Montpellier.

Edh, K.A., Widén, B., Ceplitis, A., 2007. Nuclear and chloroplast microsatellites reveal extreme population differentiation and limited gene flow in the Aegean endemic Brassica cretica (Brassicaceae). Mol. Ecol. 16, 4972-4983.

Eguiarte, L.E., Perez-Nasser, N., Piilero, D., 1992. Genetic structure, outcrossing rate and heterosis in Astrocaryum mexicanum (tropical palm): Implications for evolution and conservation. Heredity 69, 217-228.

Emerson, B.C., Kolm, N., 2005. Species diversity can drive speciation. Nature 434, 1015–1017.

Fernández-Palacios, J. M., de Nascimento, L., Otto, R., Delgado J.D., García-del-Rey, E., Arévalo, J.R., Whittaker, R.J., 2011. A reconstruction of Palaeo-Macaronesia, with particular reference to the long-term biogeography of the Atlantic island laurel forests. J. Biogeogr. 38, 226–246.

Gamisans, J., 1991. La vegetation de la Corse. Aix-en-Provence. Edisuid.

Georghiou, K., Delipetrou, P., 2010. Patterns and traits of the endemic plants of Greece. Bot. J. Linn. Soc. 162, 130-422.

Greuter, W., 1972. The relict element of the flora of Crete and its evolutionary significance, in: Valentine, D.H., Taxonomy, phytogeography and evolution, London, Academic Press. 161-177.

Halas, D., Zamparo, D., Brooks, D.R., 2005. A historical biogeographical protocol for studying biotic diversification by taxon pulses. J. Biogeogr. 32, 249–260.

Heaney, L.R., 2000. Dynamic disequilibrium: a long-term, large-scale perspective on the equilibrium model of island biogeography. Global Ecol. Biogeog. 9, 59–74.

Hortal, J., Triantis, K.A., Meiri, S., Thébault, E., Sfenthourakis, S., 2009. Island Species Richness Increases with Habitat Diversity. Am. Nat. 174, 205–217.

Kallimanis, A.S., Bergmeier, E., Panitsa, M., Georghiou, K., Delipetrou, P., Dimopoulos, P., 2010. Biogeographical determinants for total and endemic species richness in a continental archipelago. Biodivers. Conserv. 19, 1225-1235.

Kallimanis, A.S., Panitsa, M., Bergmeier, E., Dimopoulos, P., 2011. Examining the relationship between total species richness and single island palaeo- and neo-endemics. Acta Oecol 37, 65-70.

Kazakis, G., Ghosn, D., Vogiatzakis, I.N., Papanastasis, V.P., 2007. Vascular plant diversity and climate change in the alpine zone of the Lefka Ori, Crete. Biodivers. Conserv. 16, 1603–1615.

Kessler, M., 2002. The elevational gradient of Andean plant endemism: varying influences of taxon- specific traits and topography at different taxonomic levels. J. Biogeogr. 29, 1159–1165.

Kisel, Y., McInnes, L., . Toomey, N.H., Orme, C.D.L. 2011. How diversification rates and diversity limits combine to create large-scale species –area relationships. Phil. Trans. R. Soc. B. 366, 2514-2525

Knope, M.L., Morden, C.W., Funk, V.A., Fukami, T., 2012. Area and the rapid radiation of Hawaiian Bidens (Asteraceae). J. Biogeogr. 39, 1206–1216.

Leimu, R., Fischer, M., 2008. A meta-analysis of local adaptation in plants. PLoS ONE 3, e4010.

Leutner, B., Steinbauer, M.J., Müller, C.M., Früh, A.J., Irl, S., Jentsch, A., Beierkuhnlein, C., 2012. Mosses Like It Rough - Growth Form Specific Responses of Mosses, Herbaceous and Woody Plants to Micro-Relief Heterogeneity, Diversity, 4, 59-73.

Linhart, Y.B., Grant., M.C., 1996. Evolutionary significance of local genetic differentiation in plants. Ann. Rev. Ecol. Syst. 27, 237-277.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, NJ.

Mallet-Rodrigues, F., Parrini, R., Pimentel, L.M.S., Bessa, R. 2010. Altitudinal distribution of birds in a mountainous region in southeastern Brazil. Zoologica 27, 503–522.

Médail, F., Diadema, K., 2009. Glacial refugia influence plant diversity patterns in the Mediterranean Basin. J. Biogeogr. 36, 1333–1345.

Médail, F., Quézel, P., 1997. Hot-spots analysis for conservation of plant biodiversity in the Mediterranean Basin. Ann. Mo. Bot. Gard. 84, 112-127.

Mota, J.F., Pérez-García, F.J., JiMénez, M.L., Amate, J.J., Penãs, J. 2002. Phytogeographical relationships among high mountain areas in the Baetic Ranges (South Spain). Global Ecol. Biogeogr. 11, 497 – 504.

Palmer, M.W. 1994. Variation in species richness: towards a unification of hypotheses. Folia Geobot. Phytotax. 29, 511-530.

Panitsa, M., Tzanoudakis, D., 2001. A floristic investigation of the islat group Sarki and Lipsi (East Aegean Area, Greece). Folia Geobot. 36, 265-279.

Panitsa, M., Trigas, P., Iatrou, G., Sfenthourakis, S., 2010. Factors affecting plant species richness and endemism on land-bridge islands e an example from the East Aegean archipelago. Acta Oecol. 36, 431-437.

Parmakelis, A., Stathi, I., Chatzaki, M., Simaiakis, S., Spanos, L., Louis, C., Mylonas, M., 2006. Evolution of Mesobuthus gibbosus (Brulle, 1832) in the north-eastern Mediterranean region. Mol. Ecol. 15, 2883-2894.

Poulakakis, N., Pakaki, V., Mylonas, M., Lymberakis, P., 2008. Molecular phylogeny of the Greek legless skink Ophiomorus punctactissimus (Squamata: Scincidae): the impact of the Mid-Aegean trench in its phylogeography. Mol. Phylogenet. Evol. 47, 396-402.

Ricklefs, R.E., 2006. Evolutionary diversification and the origin of the diversity-environment relationship. Ecology 87, 3-13.

Sarnat, E.M., Moreaux, C.S., 2010. Biogeography and morphological evolution in a Pacific island ant radiation. Mol. Ecol. 20, 114-130.

Scherrer, D., Körner, C., 2011. Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. J. Biogeogr. 38, 406-416.

Silvertown, J., Dodd, M.E., Gowing, D.J.G., Mountford, J.O., 1999. Hydrologically defined niches reveal a basis for species richness in plant communities. Nature 400, 61-63.

Steinbauer, M.J., Beierkuhnlein, C., 2010. Characteristic pattern of species diversity on the Canary Islands. Erdkunde 64, 57-71.

Steinbauer, M.J., Otto, R., Naranjo-Cigala, A., Beierkuhnlein, C., Fernández-Palacios, J.M., 2012a. Increase of island endemism with altitude – speciation processes on oceanic islands. Ecography 35, 23-32.

Steinbauer, M.J., Gohlke, A., Mahler, C., Schmiedinger, A., Beierkuhnlein, C., 2012b. Quantification of wall surface heterogeneity and its influence on species diversity at medieval castles - implications for the environmentally friendly preservation of cultural heritage, J. Cult. Herit., accepted - doi:10.1016/j.culher.2012.06.003

Strasberg, D., Rouget, M., Richardson, D.M., Baret, S., Dupont, J., Cowling, R.M., 2005. An assessment of habitat diversity and transformation on La Réunion Island (Mascarene Islands, Indian Ocean) as a basis for identifying broad-scale conservation priorities. Biodivers. Conserv. 14, 3015-3032.

Stuessy, T.F., Jakubowsky, G., Salguerò Gómez, R., Pfosser, M., Schlüter, P.M., Fer, T., Sun, B.Y., Kato, H., 2006. Anagenetic evolution in island plants. J. Biogeogr. 33, 1259–1265.

Svenning, J.C., 2001. On the Role of Microenvironmental Heterogeneity in the Ecology and Diversification of Neotropical Rain-Forest Palms (Arecaceae). The Botanical Review 67, 1-53.

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M., Jeltsch, F. (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. J. Biogeogr. 31, 79–92.

Thompson, J.D., 2005. Plant evolution in the Mediterranean, Oxford University Press, New York.

Triantis, K.A., Hortal, J., Amorim, I., Cardoso, P., Santos, A.M.C., Gabriel, R., Borges, P.A.V., 2012. Resolving the Azorean knot: a response to Carine & Schaefer (2010). J. Biogeogr. 39, 1179-1184.

Trigas, P., Panitsa, M., Turland, N., Tsiftsis, S., 2011. Elevational gradient of vascular plant species richness and endemism in Crete. Poster 248 at the Fifth Biennial Conference of the International Biogeography Society, Irakleion, Crete, Greece

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffen-Dewenter, I., Thies, C., van der Putten, W.H., Westphal, C., 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biol. Rev. 87, 661–685.

Whittaker, R.J., Fernández-Palacios, J.M., 2007. Island Biogeography: Ecology, Evolution, and Conservation, 2nd eds. Oxford University Press, Oxford.

Verlaque, R., Aboucaya, A., Cardona, M.A., Contandriopoulos, J., 1997. Quelques exemples de speciation insulaire en Méditerranée occidentale. Botanika Chronika 10, 137-154.

7.3 Manuscript 3

An 11-yr exclosure experiment in a high-elevation island ecosystem: introduced herbivore impact on shrub species richness, seedling recruitment and population dynamics

Severin D. H. Irl, Manuel J. Steinbauer, Wolfgang Babel, Carl Beierkuhnlein, Gesche Blume-Werry, Jana Messinger, Ángel Palomares Martínez, Stefan Strohmeier & Anke Jentsch

ABSTRACT

Questions Do introduced herbivores and fire explain the mono-dominance of one legume shrub (*Adenocarpus viscosus* ssp. *spartioides*) above the tree line on an oceanic island given the fact that a number of other legume shrub species are potentially present? What drives the observed landscape scale life-death pattern within the mono-dominant shrub species population?

Location The subalpine scrub vegetation of La Palma (Canary Islands, Atlantic Ocean).

Methods An eleven-year exclosure experiment with sites distributed along an elevation and orientation gradient was used to identify the influence of introduced herbivore pressure on four endemic shrub species and their seedling recruitment. Further, we assessed the population dynamics and spatial pattern of the dominant shrub species *A. viscosus* ssp. *spartioides*. Habitat and vitality characteristics were investigated assessing spatial topographic features and tree ring based age estimates. Linear mixed models, ANOVA's, linear regression and variation partitioning were used as statistical analysis tools.

Results Outside of the exclosures *A. viscosus* ssp. *spartioides* was virtually mono-dominant in the study area, even though other shrub species seem better suited in the absence of introduced herbivores. The presence of introduced herbivores significantly reduced seedling recruitment within all target species, except for *A. viscosus* ssp. *spartioides*. Mean age of *A. viscosus* ssp. *spartioides* increased with elevation, although vitality analyses indicated that the subalpine scrub is elevated above its growth optimum. Three out of four investigated shrub species showed differences in growth height depending on elevation and island orientation.

Conclusion Introduced herbivores and fire are identified as key disturbances enhancing the occurrence of *A. viscosus* ssp. *spartioides,* a commonly less competitive species. However, *Genista benehoavensis*, a single island endemic shrub species, seems to be better adapted to the harsh climatic conditions of the subalpine scrub in the absence of introduced herbivores than any other shrub species.

Abbreviations: ANOVA = analysis of variance; V_i = vitality index

Nomenclature: Acebes Ginovés et al. (2010)

INTRODUCTION

Island ecosystems rich in endemic species have often evolved under reduced ecological pressures, for example, where the influence of herbivory or competition is low (Bowen & van Vuren, 1997; Nogales et al., 2006). Especially the combination of habitat degradation or change through human disturbances

and the introduction of non-island species have lead to massive problems in isolated island ecosystems (Vitousek et al., 1997; Campbell & Donlan, 2005, Caujapé-Castells et al., 2010). Introduced species generally arrive on islands without their natural array of pests and diseases, which often gives them a competitive advantage over native species (Darwin, 1859; Simberloff, 1995; Courchamp et al., 2003). In particular, introduced herbivores such as feral goats (*Capra hircus*) or rabbits (*Oryctolagus cuniculus*), both among the world's 100 worst invasive species (Lowe et al., 2000), have had detrimental effects on native island biota, degrading complete ecosystems to a state where regeneration without herbivore eradication is (nearly) impossible (e.g. Galapagos (Campbell & Donlan, 2005), Canary Islands (Garzón-Marchado et al., 2010), Hawaii (Mueller-Dombois & Spatz, 1975), Santa Catalina Island (Coblentz, 1978), and New Zealand (Parkes, 1990)).

Introduced herbivores have established themselves, among other ecosystems, in the high-elevation ecosystem of the oceanic island La Palma, Canary Islands (Palomares Martínez et al., 2004; Garzón-Marchado et al., 2010). There, the subalpine scrub has a long legacy of goat grazing. In recent decades rabbits have become the number one herbivore due to the abolition of goat grazing for economic and conservational reasons (Garzón-Marchado et al., 2010). Nevertheless, the vegetation dynamics we witness today are probably still being influenced by the legacy of goat grazing in historic times (see Kyncl et al. (2006) for the subalpine scrub of Tenerife). Additionally, the high-elevation ecosystem of La Palma is an interesting study objects because of its comparatively low species richness, yet high degree of endemism (Steinbauer et al., 2011; Irl & Beierkuhnlein, 2011).

In the transitional zone between tree line and alpine environments, shrubs are the dominant growth form on many oceanic islands including the Canary Islands (Lausi & Nimis, 1986; Kyncl et al., 2006,), the Cape Verde Islands (Leuschner, 1996), La Réunion (Strasberg et al., 2005), Crete (Kazakis et al., 2007) and Hawaii (Leuschner, 1996). Often, subalpine ecosystems are dominated by very few to only one key shrub species.

Shrubs in general have been found to act as ecosystem engineers influencing multiple levels of biological organization (e.g. Cushman et al., 2010). N-fixing legume shrubs are considered to be key pioneer species often dominating primary successional stages (Walker et al., 2003; González et al., 2010) and invading non-native habitats (Shaben & Myers, 2010), but also reaching competitive dominance (MacArthur & Levins, 1967; Callaway & Ridenour, 2004; Hierro et al., 2005).

Although situated off the NW-African coast, the high-elevation scrub of the Canary Islands floristically resembles communities found in comparable elevations of the Mediterranean islands (Brullo et al., 2008). On La Palma *Adenocarpus viscosus* ssp. *spartioides*, a single island endemic legume shrub on the subspecies level, forms an almost mono-dominant cover in the subalpine scrub – sometimes also called the summit broom scrub (Garzón-Machado et al., (2011) –, even though other functionally similar endemic, but highly endangered shrub species are present (del Arco Aguilar et al., 2010). Above the *Pinus canariensis*-forests (called *pinar*) one can observe a distinct pattern in the *A. viscosus* ssp. *spartioides* subalpine scrub (hereafter *codesar*). A high vegetation cover, yet seemingly random distribution of living, half-dead and dead individuals is a common sight on the densely populated outer

flanks of the caldera (Fig. 1), while the almost vertical rocky inner flanks cannot support any type of closed vegetation cover.

We use the example of the *codesar* on La Palma to assess the ecological effect of introduced herbivores on shrub species and their interaction with other key disturbances (i.e. fire, ice storms) and try to gain insights into the mechanisms that control the landscape-scale life-death pattern of *A. viscosus* ssp. *spartioides*. We ask the following research questions: (a) Which factors explain the mono-dominance of one legume shrub above the tree line on an oceanic island best, given the fact that a number of other legume shrub species are potentially present? (b) Which factors drive the observed landscape-scale life-death pattern of living and dead components within the *A. viscosus* ssp. *spartioides* population?

Figure 1. Seemingly random pattern of living, half-dead and dead individuals of Adenocarpus viscosus ssp. spartioides on the densely populated outer NE-flanks of the Caldera de Taburiente at around 2150 m a.s.l. (at Defront and left). The right side shows a NP exclosure site, where the fence has been removed to enable natural regeneration. Here, shrub species diversity is higher, especially well visible are Genista benehoavensis (greyish-green) and Spartocytisus supranubius (dark-green). Unfortunately, Adenocarpus was removed during the deconstruction of the fence, thus this picture does not resemble a true natural stand. The Genista individuals in the foreground on the right-hand side already show browsing marks. The Pinus canariensis-treeline in the background approaches approximately 2000 m a.s.l.. In addition, the clouds of the thermal inversion layer can be seen in the background. (Photo: M.J. Steinbauer, April 2011).

METHODS

Study area

The study took place in the high altitudinal zone of La Palma. The Canary Islands are located near the African coastline between 27° and 29° northern latitude and 14° and 18° western longitude. The archipelago is of volcanic origin and consists of seven main islands larger than 250 km². Covering 708 km² La Palma is the third smallest island (Carracedo et al., 2002) and being around 1.7 Ma old, it is among the youngest islands of the archipelago (maximum age: 20.5 Ma for Fuerteventura; Fernández-Palacios & Whittaker, 2008) expressing steep environmental gradients (Irl & Beierkuhnlein, 2011). The study area is situated on the outer flanks of the rim of the Caldera de Taburiente on the Northern part of La Palma (Fig. 2), ranging from about 1800 m a.s.l. to the top of the rim at around 2400 m a.s.l., and covers 14.3 km². The field survey focusing on the population structure of *Adenocarpus* as well as browsing was conducted in February 2008. Data from the exclosure experiment regarding inter-specific competition and recruitment were collected in April 2011.

The thermal inversion (above 1200 m in summer and 1700 m in winter) created by humid trade winds blowing from the NE against the mountainside effectively impedes the convective and orographic rise of moist air masses towards the summits. Therefore, factors like high solar radiation, extensive arid periods of up to 6 months, high temperature amplitudes and harsh irregular winter conditions in the form of ice and snow influence plant growth strongly (González Henríquez et al., 1986). Furthermore, variation in annual precipitation is very high in the subalpine zone, e.g. ranging from 350 to 2480 mm within one station (Morro de la Cebolla, 2150 m). The mean annual temperature (9.3°C) and precipitation (369 mm/a) of Izaña (2367 m) on the neighbouring island of Tenerife could be attributed to the subalpine scrub of La Palma (González Henríquez et al., 1986), although the measurements conducted by the National Park (NP) Caldera de Taburiente suggest that La Palma receives more precipitation at comparable altitudes. Similar to the subalpine scrub of Tenerife, the legume shrub dominated *codesar* is found on well-developed andosols (Brullo et al., 2008) on the gentle slopes of the outer flanks.

As archaeological findings suggest, the feral goat (*C. hircus*) was introduced more than 2000 years ago by the aboriginal inhabitants (Navarro et al., 1990), while the European rabbit (*O. cuniculus*) was brought to La Palma in the 15th and 16th century by the Castilian conquerors and is now partially controlled by hunting (Cabrera-Rodríguez, 2006). Several other introduced species can be found, such as rats (*Rattus* spp.), also introduced by the conquerors, or the Saharan *arruí* goat (*Ammotragus lervia*; Nogales et al., 2006), deliberately introduced by the National Institute for Environmental Conservation (ICONA) to the National Park in the 1970s to stimulate big game hunting as a new economic field. In general, no native mammalian key herbivore naturally exists or has ever existed in the subalpine scrub of La Palma or on any other island of the Canary archipelago (Traveset et al., 2009).

Fire is another important natural disturbance shaping this ecosystem. In addition to this goat herdsmen regularly burned the *codesar* once it reached an impassable size and density for herding.

Nonetheless, fire frequency (probably less than every 10 years) and intensity has increased in the last decades due to an increase in human-induced fires (Höllermann, 2000; Palomares Martínez et al., 2004). One reason for this is an accumulation of fuel that has been registered due to the ceasing of wood and pine needle extraction. Although fire management is taken seriously by local fire departments, wildfires often spread from the fire-adapted *pinar* up into the treeless subalpine scrub at irregular intervals and intensities.
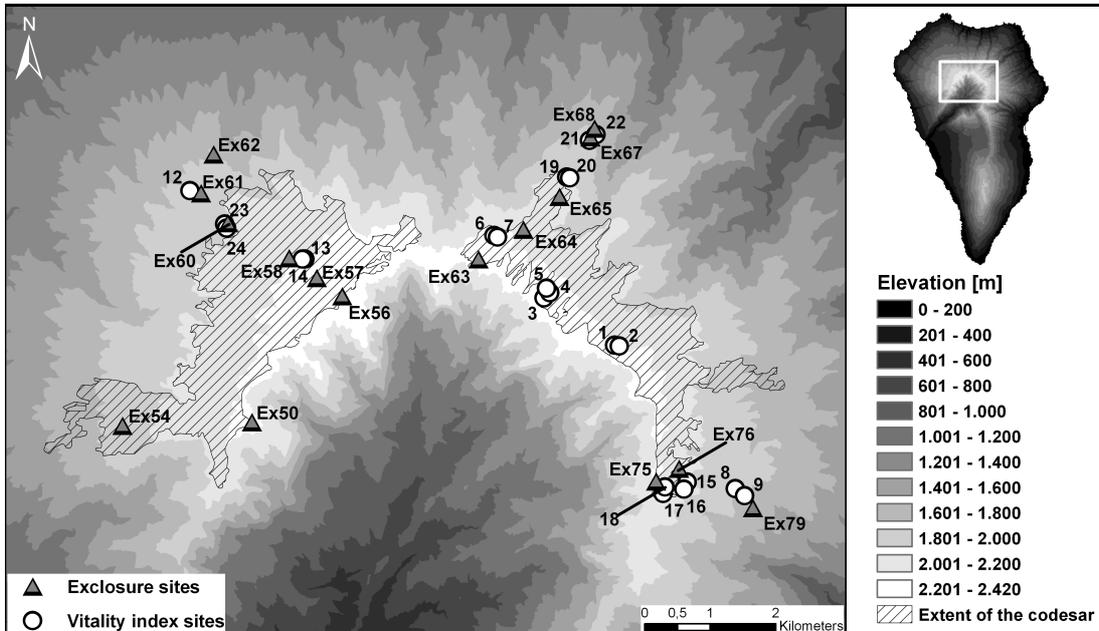

Figure 2. Site location on the Caldera de Taburiente. Circles illustrate the V_i sites, squares the plots for the age/circumference-correlation and triangles the fenced exclosure sites, where growth height was measured. The shaded area depicts the current extent of the codesar (Digital elevation model provided by Dr. Félix Medina of the *Consejería de Medio Ambiente del Cabildo Insular de La Palma*; map created in ArcView 9.3.1).

Study species

The island endemic *Adenocarpus viscosus* ssp. *spartioides* RIVAS-MART. & BELMONTE is a member of the Fabaceaen family (González Henríquez et al., 1986). It produces bright yellow flowers, has small evergreen leaves and a strongly ramified, but rather compact growth form (González Henríquez et al., 1986). The upper surface of its leaves is covered with small spiral hairs, while the bottom side is densely coated with subsessile glands, both morphological traits typical for semi-arid high-elevation vegetation (Lausi & Nimis, 1986). Year rings are produced in its woody branches that reflect a pronounced seasonality in growing conditions.
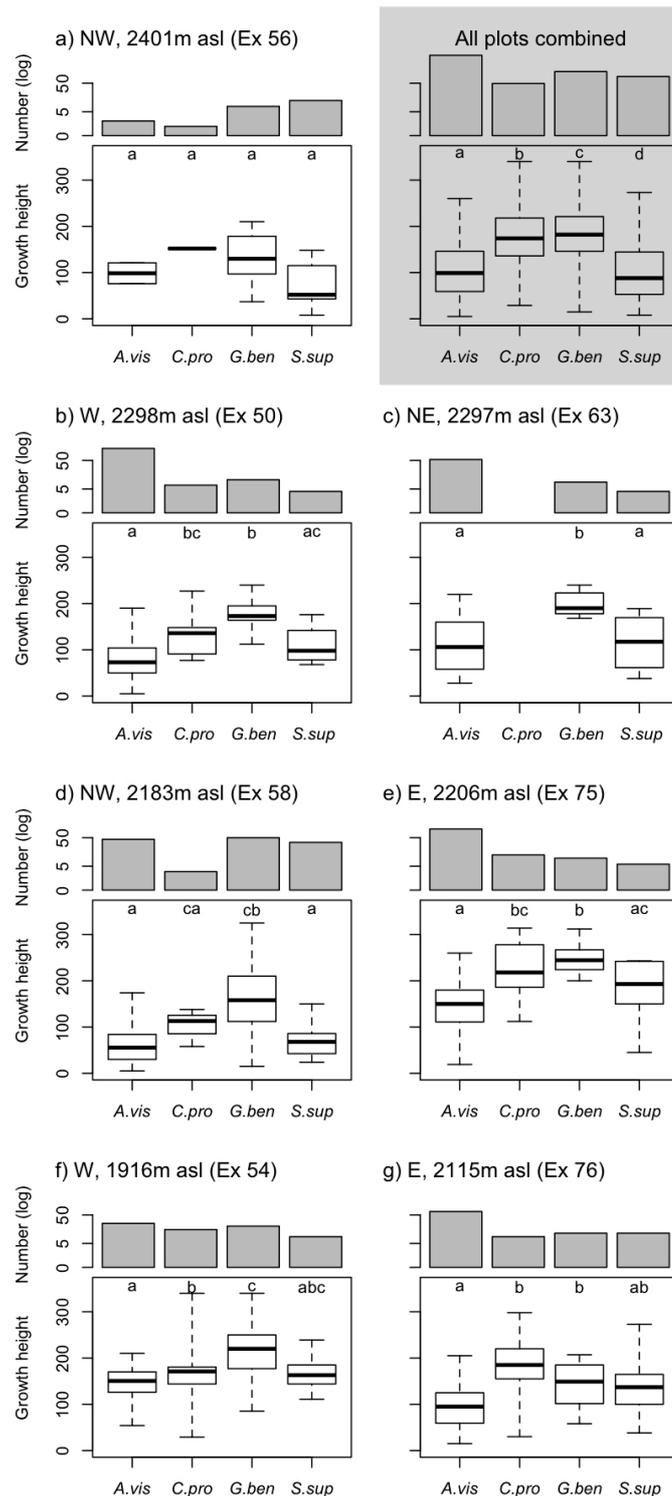
Figure 3. Growth heights of different shrub species according to altitude and island orientation measured in exclosure plots established in 2000 (maximum individual age of 11 years). Boxplots indicate growth height with whiskers extending to the data extremes. The grey barplots depict the number of measured individuals. Lower case letters indicate significant differences (p<0.05). Graphs (a-g) are sorted from top to bottom according to elevation and from left to right according to island orientation. The graph shaded in grey shows the complete dataset. Abbreviations: A.vis = Adenocarpus viscosus spp. spartioides, C.pro = Chamaecytisus proliferus ssp. proliferus, G.ben = Genista benehoavensis, S.sup = Spartocytisus supranubius.

Figure 4. Photo of white-blooming Chamaecytisus proliferus ssp. proliferus reaching from inside an exclosure plot (right-hand side) out into the potential reach of introduced herbivores. Browsing marks are visible on the left-hand side of the fence indicating the maximum height to where herbivores may reach. The picture was taken on the E side of the caldera at around 1800 m a.s.l. (i.e. the transition zone of the Canary Pine forest to the subalpine scrub). (Photo: M.J. Steinbauer, April 2011).
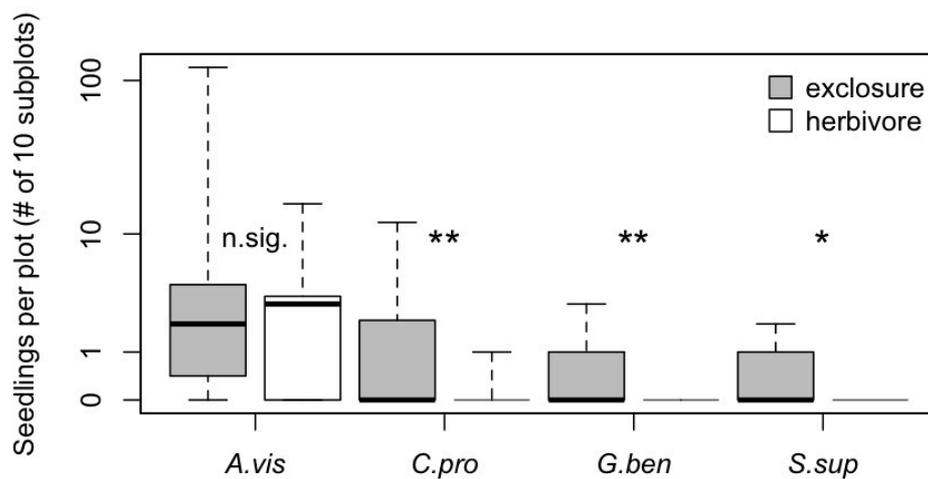

Figure 5. Seedling recruitment of the four target shrub species inside and outside of the exclosures. Seedling recruitment of all species, except for Adenocarpus, decreases significantly from inside to outside of the exclosure displaying the strong negative effect of introduced herbivore presence. Significance is based on mixed effect models of the subplot data. Abbreviations as in figure 3. Whiskers extend to the data extremes.

A. viscosus ssp. *spartioides* is attributed to the Genisto benehoavensis-Adenocarpetum spartioides Sᴀɴᴛᴏꜱ 1983 ɴᴏᴍ. ᴍᴜᴛ. (ᴀʀᴛ. 45) Rɪᴠᴀꜱ-Mᴀʀᴛíɴᴇᴢ ᴇᴛ ᴀʟ. 2001, a subalpine dry open scrub community with ecological similarities to the Spartocytisetum supranubii Oʙᴇʀᴅᴏʀꜰᴇʀ ᴇx Eꜱᴛᴇᴠᴇ 1973 ɴᴏᴍ. ᴍᴜᴛ. (ᴀʀᴛ. 45) Rɪᴠᴀꜱ-Mᴀʀᴛíɴᴇᴢ ᴇᴛ ᴀʟ 2001 of Tenerife both being part of the alliance Spartocytision supranubii (Leuschner, 1996). Fabaceaean species play an important role in all of these communities on comparably young soils in a harsh climate, probably due to their advantageous trait of being able to fix nitrogen.

Today, *A. viscosus* ssp. *spartioides* exhibits virtually mono-dominant stands in the subalpine zone of La Palma. However, a transition zone with the *pinar* exists below the timberline, where our target species contributes substantially to the performance of the vegetation. Its altitudinal amplitude reaches from 1500 to 2400 m a.s.l., although its zone of optimal growth occurs between 1700 and 2000 m a.s.l. (González Henríquez et al., 1986). However, it is not clear, whether the subalpine zone is climatically induced or if it is anthropogenically influenced (see e.g. Leuschner, 1996).

Shrub species diversity of the entire subalpine community has become strongly pauperized through goat and rabbit grazing (Cabrera-Rodriguez, 2008), increased fire frequencies and human disturbances such as collecting branches for firewood and fodder (Palomares Martínez et al., 2004). For this reason, the National Park management of the NP Caldera de Taburiente heads a conservation initiative for endangered native and endemic species. Endangered species include shrubs such as *Bencomia exstipulata*, *Chamaecytisus proliferus* ssp. *proliferus*, *Genista benehoavensis*, *Spartocytisus supranubius* and *Teline stenopetala* ssp. *sericea* (hereafter only genus names will be used; Palomares Martínez et al., 2004). *Genista* is a single island endemic to La Palma, while *Bencomia* and *Spartocytisus* are also found in the subalpine scrub vegetation of Tenerife (Acebes Ginovés et al., 2010). *Adenocarpus* and *Teline* are single island endemic subspecies (Acebes Ginovés et al., 2010). *Chamaecytisus* is found on several other islands of the archipelago. A variety of this species that is endemic only to La Palma is described but not generally accepted (var. *calderae*; Nezadal et al., 1999). Many of these characteristic species have become extremely rare or have nearly been driven to extinction. However, they are still found on inaccessible cliffs and rocky outcrops. In recent years, these historically important species have been sown in their natural habitats in protected exclosures established by the National Park authorities (Palomares Martínez et al., 2004).

Sampling design: factors driving mono-dominance

In this study, seven rectangular 20 x 20 m exclosure plots established by the National Park in 2000 were used to assess the growth potential and competitive success of the present shrub species (*Adenocarpus*, *Bencomia*, *Chamaecytisus*, *Genista, Spartocytisus* and *Teline*) in the absence of herbivores (Fig. 2 and Tab. 1). All vegetation was removed within the exclosures in 2000 and an equal amount of seeds per species (*Genista* and *Spartocytisus*: 3000 seeds/plot; *Teline* and *Chamaecytisus*: 2000 seeds/plot; *Bencomia*: 30000 seeds/plot) was sown (note that seed numbers per species varied strongly due to highly differing germination success between species, as experimentally tested by Palomares

Martínez (1993)). We assumed that seeds of *Adenocarpus* were also present in the seed bank, as this species is omnipresent in the study area. In addition, seeds of the sown shrub species were presumed to be present inside and outside the exclosures in equal quantities because species reach regeneration age after 2 to 5 years (Palomares Martínez, 1993) and natural seed dispersal has therefore been possible for about 6 to 9 years. The plots are fenced and regularly monitored. They differ in altitude and orientation. Only those plots where the access of herbivores was efficiently impeded and no signs (faeces, browsing marks) of their influence were found, were used for biometric measurements. *Bencomia* and *Teline* were excluded from analysis, due to the low number of individuals found in the exclosures. For all other shrub species, growth height of each individual was measured. A control plot of similar size was placed next to the exclosure and growth height of twenty randomly selected individuals of each shrub species was measured here as well.

To study the effect of herbivore presence on regeneration of established plant species, 10 subplots of 1 m² were randomly selected in eleven exclosures and the associated outer plots. Present seedlings (i.e. not yet lignified individuals) of either shrub species were counted. We selected all exclosures that were neither disturbed (e.g. by fire) nor entered by herbivores within the last two years (Fig. 2 and Tab. 1). This resulted in a larger number of suitable sites than those used for the biometric measurements where the criterion was eleven years without disturbance. Note that due to time constraints, some plots included in the biometric measurements were not assessed for the seedling establishment.

Table 1. Overview of the exclosure sites used for growth height and seedling recruitment measurements. For the exact location please compare with map in Fig. 2.

Site	Growth height	Seedling recruitment
Ex50	x	
Ex54	x	
Ex56	x	
Ex57		x
Ex58	x	x
Ex60		x
Ex61		x
Ex62		x
Ex63	x	
Ex64		x
Ex67		x
Ex68		x
Ex75	x	
Ex76	x	x
Ex79		x

Sampling design: life-death pattern of Adenocarpus

In a second step, plotless and transect sampling methods were applied, due to the high density and the partial impassibility of the *codesar*, to assess the pattern of living versus dead organs of *Adenocarpus*. Altitudinal and aspect transects were placed along the caldera flanks. 22 sites (sites 1-9 and 12-24, Fig. 2) were sampled roughly located at three altitudinal levels (transition zone of the *codesar* and the *pinar* between 1800 and 2000 m, mid-*codesar* between 2000 and 2200 m and high-*codesar* above 2200 m) and at three different caldera (macro-) orientations (E, NE, NW; note: the northern flank of the caldera is extremely steep and rocks are too instable for access) with additional plots at the caldera rim. Two sites with different slope (micro-) aspects were selected at each altitudinal level and aspect. 16 randomly selected *Adenocarpus* individuals were sampled for each site. Furthermore, measurements for each site included slope aspect and angle, elevation, maximum growth height per species, circumference of the thickest branch per species and the vitality index V_i. The vitality index V_i describes the estimated percentage of green leaf coverage relative to the number of branches (i.e. V_i: 0 = 0% percentage of green leaf coverage relative to the number of branches, dead; 1 = 1 - 24%; 2 = 25 - 74%; 3 = 75 - 99%; 4 = 100%). For example, a shrub individual with a V_i = 3 had about three-quarters of its branches covered with green leaves.

Besides direct ecological impacts, the performance of the subalpine scrub ecosystem depends also on age structure and population diversity. Therefore, 50 randomly selected branches of *Adenocarpus* individuals were cut to count growth rings. *Adenocarpus* branches generally ramify directly from the point, where the stem protrudes from the soil. A preliminary investigation showed that the thickest branch gives a good estimation of plant age and was therefore used for counting growth rings. In 12 cases of undifferentiated tree rings individuals were excluded from the analysis. A multiple regression with age as dependent variable and circumference and growth height as explanatory variables (including interaction; r^2 of 0.79***, Fig. S1 in supporting information) showed the best age estimate and was therefore preferred to a simple circumference/age correlation (r^2 of 0.57*** Fig. S1 in supporting information). In further analyses the variable "age" is always derived via the interacting relation.

Statistical Analysis

Significant differences in mean growth height between the shrub species within each exclosure were assessed using ANOVA with a post-hoc Tukey test. In addition, all exclosure sites were combined to one analysis using linear mixed models (R-package "nlme" version 3.1-96; Pinheiro et al. 2009) with site as random variable. Again significance was tested using ANOVA with a post-hoc Tukey test. The latter one is implemented in R package "multcomp" (Hothorn et al. 2008). A high number of young and thus small individuals could bias the comparison of mean maximum growth height. Therefore, we additionally restricted our analysis to large individuals (> 2/3 of the growth height of the largest individual of a certain species on a certain site). Finally, linear regression (with r^2 as goodness-of-fit indicator) was applied to quantify the effect of altitude and caldera orientation of the exclosure sites on

growth height. The effect of caldera orientation was tested on the residuals of the linear regression on altitude.

To gain an understanding on the effect of herbivory on seedling establishment, linear mixed models were implemented for each investigated shrub species. We checked whether the number of established seedlings was significantly higher inside or outside of herbivore exclosures. "Site" was selected as random variable to account for possible differences among the plots.

In order to differentiate the joined and independent explanatory power of the essential driving factors, all variables significantly (p>0.001) correlating with V_i (elevation, age, slope aspect and caldera orientation), were compared by a variation partitioning using multiple linear regression models (linear regression and adjusted r^2 as the goodness-of-fit measure) following the guidelines of Legendre (2008).

All analyses and graphics were performed in R (R Development Core Team, 2010). Significance is indicated by * for p<0.05, ** for p<0.01 and *** for p<0.001.

RESULTS

Factors driving mono-dominance

In the absence of herbivory, *Genista* and *Chamaecytisus* are able to grow higher than *Adenocarpus* and *Spartocytisus*. This is true if all individuals (Fig. 3) or if only the large ones (Fig. S2 in supporting information) are compared. However, *Adenocarpus* shows the highest number of individuals in all sampled exclosure sites. No other adult shrub species besides *Adenocarpus* was found outside the fenced sites, where herbivores have unlimited access. If parts of individuals of non-*Adenocarpus* species reached beyond the fence, they were heavily browsed (Fig. 4).

Growth height decreases with elevation at a rate of 8.40 cm/100 m*** (9.4%/100 m; percentage values are calculated in relation to mean growth height) for *Adenocarpus*, 10.6 cm/100 m* (5.9%/100 m) for *Genista* and 17.9 cm/100 m*** (17.5%/100 m) for *Spartocytisus*, while no relation was detected for *Chamaecytisus*.

After correcting for the effect of elevation, a lower growth height of *Adenocarpus* was detected for NW (-52.4 cm***) and W (-22.0 cm) facing sites. *Chamaecytisus* also grows smaller on NW (-94.4 cm*) and W (-52.1 cm*) facing sites, while *Spartocytisus* has a lower growth height on NW sites (-67.8***). No tendency was detected for *Genista,* which seems to be less affected by caldera orientation.

The mean number of seedlings per subplot (1 m^2) without herbivore pressure was 1.30 ±5.91 for *Adenocarpus,* 0.22 ±0.78 for *Chamaecytisus*, 0.05 ±0.21 for *Spartocytisus* and 0.07 ±0.26 for *Genista*. Outside the fences the mean number of seedlings dropped to 0.33 ±1.04 per patch for *Adenocarpus,* while overall only one *Chamaecytisus* seedling and none of the other species was found (Fig. 5). Given the high standard deviation the mixed effect models result in a significant higher seedling number for *Chamaecytisus**, Spartocytisus** and *Genista*** inside the fences, but no significant difference for *Adenocarpus* (p = 0.068).
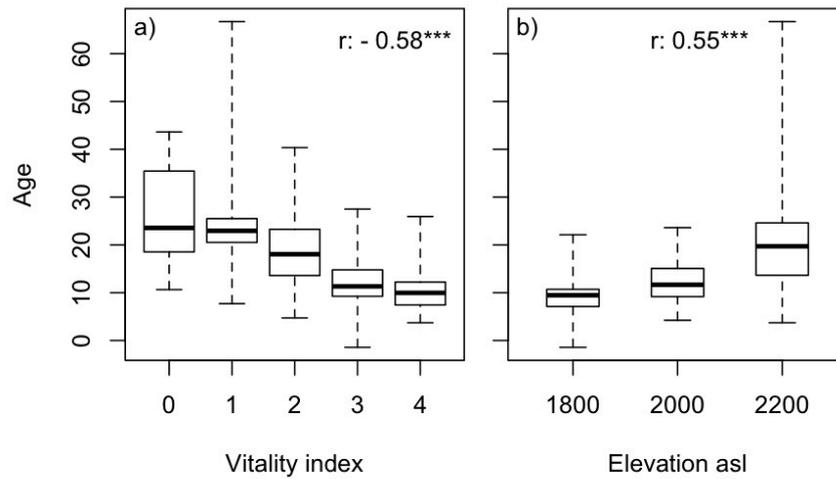
90

Figure 6. Older Adenocarpus individuals are less vital (a), i.e. negatively correlated with age. Mean age of individuals increases with elevation possibly due to higher fire frequency in lower altitudes (b). Correlation is shown as r-values with minus symbols indicating negative correlations.
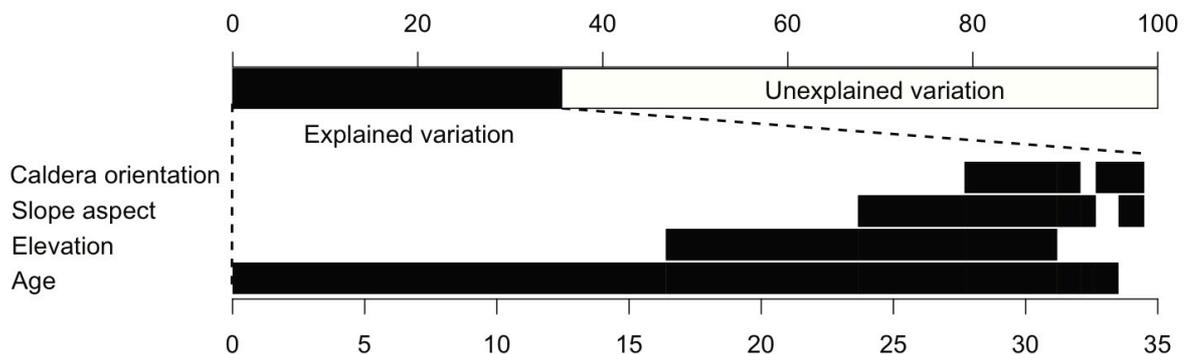

Figure 7. Variance partitioning reveals that vitality of Adenocarpus strongly depends on the age of individuals. A differentiation between this effect and elevation or orientation is hardly possible due to a strong overlap in explained variation. The upper bar illustrates the explained variation (black) in comparison with the unexplained variation (white). Within the explained variation the lower bars show how much the specific variables explain independently (i.e. if there is no horizontal overlap between the variable bars) or jointly (i.e. if a horizontal overlap exists between two or more variable bars). For reasons of simplification and improved comprehensibility only contributions of more than 0.5% are displayed.

Life-death pattern of Adenocarpus

The vitality index V_i exhibits a spatial pattern: vitality is negatively correlated to age (Fig. 6a) and tends to be lower in higher elevations and on the northeastern side of the caldera rim. The age of an individual is the main influence concerning the vitality of *Adenocarpus* explaining 33.5% of variation (in the linear model for variation partitioning). The older plots exhibit lower vitality than the younger plots.

91

Moreover, the variance of the V_i data is higher on the older plots; hence the younger plots are apparently more homogeneous in vitality (see also Fig. S3 in supporting information). Elevation explains 15.2% of the variance of the V_i in the dataset. 10.6% and 6.6% of the variance are explained by slope aspect and caldera orientation, respectively. Variation partitioning reveals that age provided the largest share of explained variation either independently (46%) or jointly with elevation (20%). Only a minor part of the explained variation (4%) is contributed independently from age and elevation (Fig. 7).

Age of *Adenocarpus* individuals is positively related to elevation (Fig. 6b), i.e. higher located sites host populations with a significantly higher mean age than the sites at mid-elevations and in the *pinar*. Sites with a relatively high mean age show a distinct higher variance than young growth sites (Fig. S3 in supporting information).

DISCUSSION

Mono-dominance of Adenocarpus

Adenocarpus is virtually mono-dominant in the subalpine scrub vegetation of La Palma. In the plots next to the exclosures no adult shrub species other than *Adenocarpus* are present, even though seed dispersal from other shrub species such as *Bencomia*, *Chamaecytisus*, *Genista*, *Spartocytisus* and *Teline* from inside the exclosure can be expected due to advanced age, large size and abundant flowers of many target shrubs. However, some adult individuals of the non-*Adenocarpus* shrub species are locally found outside of the exclosures throughout the subalpine scrub independently of the studied exclosures.

Damage and consumption by introduced herbivores, which has been suggested to be one of the four major threats to Canarian endemic plant diversity (Francisco-Ortega et al., 2000), to *Adenocarpus* is by far lower than to any of its other competitor species. This selective grazing, a common phenomenon among herbivores (van Vuren & Coblentz, 1987; Bryant et al., 1991; Rafferty & Lamont, 2007; Traveset et al., 2009; Maher et al., 2010), gives *Adenocarpus* an advantage over other shrub species. Hence, herbivores potentially eliminate non-*Adenocarpus* species from the vegetation cover and restrict them to areas that are outside of their reach, such as rocky outcrops and cliffs (Garzón-Machado et al., 2011). Personal observations in plots, where rabbits managed to enter, support the idea of a selective grazing as only 10% of *Adenocarpus* individuals showed browsing marks, while all other shrubs were heavily damaged (90-100% browsing marks).

Phytochemical analyses have shown that *Adenocarpus* possesses a variety of different alkaloids that could potentially act as defence mechanisms towards mammalian herbivory. Among other alkaloids such as toxic pyrrolizidines (Cheeke, 1988; Greinwald et al., 1992), the main alkaloid, adenocarpine, probably leads to a reduced palatability and digestibility in herbivores. It is a structural derivative of the toxic anabasine found in *Nicotiana glauca* (Schütte et al., 1964) and is particularly enriched in the leaves (Greinwald et al., 1992). The only other species possessing significant amounts of alkaloids (i.e. mainly sparteine) was *Chamaecytisus*, but the amounts showed a pronounced seasonality with high values in

spring and low values in fall (Ventura et al., 2000). High values of sparteine significantly reduced sheep performance and the consumption of *Chamaecytisus* in spring, if herbivores were given the choice (Ventura et al., 2000).

Seedling recruitment in all species is very low. However, *Adenocarpus* is strongly favoured in this respect. It seems to react more or less indifferently to herbivore pressure, even though a tendency towards higher recruitment within the exclosures is discernable. Seedling recruitment of the other species is minimal (*Chamaecytisus*) or non-existent (*Genista*, *Spartocytisus*) outside the plots. In this respect, *Chamaecytisus* might have a slight competitive advantage over *Genista* and *Spartocytisus*, due to the seasonal varying content of alkaloids acting as an herbivore deterrent (Ventura et al., 2000). Due to the large flowering adult individuals found inside the exclosures, seed availability of the three rare shrub species is assumed to be present in their proximity. Herbivores prefer young leaves because of their higher nutrient content and better digestibility (Coley & Barone, 1996), thus exerting an additional pressure on the few seedlings found outside of the exclosures. Estimations by the National Park suggest that as few as one rabbit per hectare is enough to prevent the seedling establishment of the rare shrubs. In general, the presence of introduced herbivores strongly modifies seedling recruitment in the *codesar*, which is in accordance with the results given by Garzón-Machado et al. (2010) for the *pinar* of La Palma and by Kyncl et al. (2006) for the summit scrub of Tenerife. Then again, the overall higher seed rain of *Adenocarpus* compared to the other species might influence seedling recruitment. This potential bias could not be accounted for in the study, particularly when keeping in mind the large seed quantities needed for successful germination (Palomares Martínez, 1993).

Growth performance of shrub species inside the exclosures after 11 years is not distributed uniformly throughout the subalpine vegetation zone. Western caldera orientations seem to have negative effects on shrub growth performance of *Adenocarpus*, *Chamaecytisus* and *Spartocytisus*, possibly due to leeward drought effects on the west-facing sites or to storm impacts coming from the Atlantic Ocean, whereas *Genista* does not seem to display any preferential growth regarding caldera orientation. Similarly, elevation has a negative impact on the growth of *Adenocarpus*, *Genista* and *Spartocytisus*, with a lowest relative decline of growth height per 100 m elevation in *Genista*. Elevation strongly influences environmental conditions on small spatial scales, especially in mountain environments, among others affecting morphological plant features (Körner et al., 1989). Both findings suggest that *Genista* is actually better adapted to the harsh climatic conditions of the subalpine scrub than other naturally occurring shrub species. In fact, it is presumed to have played a more important role in the past, possibly being the dominant shrub species next to *Adenocarpus* (Garzón-Machado et al., 2011).

Growth heights of *Adenocarpus* measured in exclosure plots are significantly lower than those of the other species, especially those of *Chamaecytisus* and *Genista* (Fig. 4), but also those of *Spartocytisus*, when looking a large individuals only (S2 in supporting information). In the densely covered *codesar* the long-term survival of a shrub individual (no matter which species) is only guaranteed by a successful competition for light. The competitive success is thus at least in parts reflected in growth height of the shrub individuals (Aarssen, 1983). This leads to the conclusion that *Adenocarpus* individuals are less

competitive in the absence of herbivores once shrub species have managed to establish. The present mono-dominance is thus proposed to be a direct effect of herbivore pressure.

Age of *Adenocarpus* is positively correlated with elevation. This contradicts the results by González Henríquez et al. (1986), who state that the optimum range of *Adenocarpus* lies between 1500 and 2000 m. Indeed, the oldest individuals and the highest mean age are found in the high-*codesar* (i.e. above 2200 m). This likely reflects the modulating effect of wildfires on the age structure of the *codesar* producing a high abundance of seedlings and saplings and a low abundance of old plants in lower elevations where fire frequencies are highest. However, as previously shown, longevity of shrub species is promoted at high elevations because species tend to grow more slowly causing them to remain in physiologically "younger" state (Diemer, 1998). The data collected in this study can neither conclusively verify nor falsify these hypotheses. Wildfires are a part of the fire-adapted *pinar* ecosystem (Höllermann, 2000; Climent et al., 2004; Del Arco et al., 2010), which often subsequently spread into the subalpine zone. For example, the last big wildfire event in the subalpine scrub occurred in 2005 destroying large parts of the NW low- and mid-*codesar*, but not spreading into the high-*codesar*. Even though regeneration commenced fairly quickly, no other species besides *Adenocarpus* was observed in the 2005 wildfire area in April 2011 (personal observation).

However, it is not only *Adenocarpus* that is potentially able to create a sufficient soil seed bank inbetween fire events. Other shrub species reach reproduction age as quickly as *Adenocarpus* or even quicker as sowing experiments performed by the National Park Caldera de Taburiente show. Here *Teline* reached the earliest reproduction age after 2-3 years, *Adenocarpus, Chamaecytisus* and *Genista* after 3 years, *Spartocytisus* after 4 years and *Bencomia* after 5 years (Palomares Martínez, 1993). Nevertheless, the other shrub species are caught in a detrimental cycle. Regeneration of non-*Adenocarpus* species only occurs very locally, owing to their comparably heavy seeds that cannot be dispersed over long distances (Palomares Martínez, 1993), i.e. the probability of reaching recently burnt areas or other sites potentially adequate for colonization is low.

We suggest that only the combination of both types of disturbance, introduced herbivores and wildfires, supports the development of mono-dominant *Adenocarpus* stands. As shown in the exclosure plots, regeneration after a fire event would favour non-*Adenocarpus* shrub species (Fig. 3), if a sufficient soil seed bank was available or seeds were introduced from neighbouring and unharmed areas. However, the very low abundance of other shrub species strongly reduces propagule availability and the probability of introduction. Moreover, the selective browsing of herbivores gives the few non-*Adenocarpus* seedlings little chance to reach such a height to where browsing damage is non-lethal. Johansson et al. (2010) showed that the dominance between two shrubby *Erica*-species in an Ethiopian subalpine environment shifted by the presence of grazing cattle and cyclic burning. Analogously, the combination of fire and introduced rabbits greatly reduced vegetation cover, plant biomass and species richness in an Australian subalpine ecosystem (Leigh et al., 1987). However, historic land use practices (e.g. goat herding and cyclic burning) probably left its marks on the current species composition of La

Palma's subalpine scrub (see Kyncl et al. (2006) for Tenerife) and the magnitude of this contribution to the legacy of *Adenocarpus* still remains largely unclear.

Life-death pattern in the *codesar*

Age appears to be the main factor influencing the vitality of *Adenocarpus* individuals. This conclusion is supported by the negative correlation between age and the vitality index (V_i). The variance of age in the old growth plots indicates active rejuvenation following a natural pattern (i.e. natural population dynamic). Wiegand et al. (2000) describe a similar behaviour for two shrub species in the South African semi-arid Karoo. Elevation, as a proxy for climatic gradients, serves as the second master variable that explains the behaviour of the vitality index. Together with slope aspect and caldera orientation microclimatic conditions are strongly modified by elevation (Körner et al., 1989).

In contrast to *Adenocarpus*, both *Genista* and *Spartocytisus* alike show seasonal adaptation to harsh winter conditions by reducing the water content in the terminal branches (Á. Palomares Martínez, unpublished). Therefore, *Adenocarpus* is especially sensitive to the strong northern winds that accumulate ice on the branches (personal observation), thus, theoretically disadvantaging it even more compared to other shrub species. Furthermore, this sensitivity may help to explain the observed life-death pattern in the *codesar*. *Chamaecytisus* and *Teline* seem to show no signs of winter adaptation in their terminal branches (Á. Palomares Martínez, unpublished). Consequently, they are very rare (*Chameacytisus*) or not present at all (*Teline*) in the exclosure sites of the high-*codesar*, even though they were equally sown in all plots.

In summary, the effects of introduced herbivores have a fundamental impact on the interspecific competition and distribution of endemic shrub species in the subalpine zone of La Palma, Canary Islands, and lead one species (i.e. *Adenocarpus viscosus* ssp. *spartioides*) to nearly complete mono-dominance. To implement useful conservation strategies for the protection of the endangered endemic shrub species (i.e. *Bencomia exstipulata*, *Chamaecytisus proliferus* ssp. *proliferus*, *Genista benehoavensis*, *Spartocytisus supranubius* and *Teline stenopetala* ssp. *sericea*) further understanding is needed, in particular, regarding the effects of wildfires and winter ice storms. The impact of introduced herbivores on high-elevation ecosystems of oceanic islands has been largely underrepresented in current and past research. With this case study we hope to have contributed to the gaining of insights on the extent of their impact, possibly leading to future conservation initiatives of endangered endemic species of this and comparable systems.

ACKNOWLEDGMENTS

Taburiente (La Palma) for establishing and maintaining the exclosures during the last 11 years and the anonymous reviewers for their valuable comments and suggestions.

REFERENCES

Aarssen, L.W. (1983) Ecological combining ability and competitive combining in plants – toward a general evolutionary theory of coexistence in systems of competition. American Naturalist, 122, 707-731

Acebes Ginovés, J.R., León Arencibia, M.C., Rodríguez Navarro, M.L., del Arco Aguilar, M., García Gallo, A., Pérez de Paz, P.L., Rodríguez Delgado, O., Martín Osorio, V. E. & Wildpret de la Torre, W. (2010) Spermatophyta. In: Lista de especies silvestres de Canarias. Hongos, plantas y animales terrestres. 2009. Arechavaleta, M., Rodríguez, S., Zurita, N. & García, A. (eds.). Gobierno de Canarias, Tenerife, 122-172

Del Arco Aguilar, M.J., González-González, R., Garzón-Marchado, V. & Pizarro-Hernández, B. (2010) Actual and potential natural vegetation on the Canary Islands and its conservation status. Biodiversity and Conservation, 19, 3089–3140.

Bowen, L. & van Vuren, D. (1997) Insular endemic plants lack defenses against herbivores. Conservation Biology, 11, 1249-1254.

Brullo, C., Brullo, S., DeMarco, G., Giusso del Galdo, G. & Guarino, R. (2008) A survey of the orophilous shrubby vegetation of the Teide (Tenerife, Canary Islands). Feddes Repertorium, 119, 63-81.

Bryant, J.P., Provenza, F.D., Pastor, J., Reichardt, P.B., Clausen, T.P. & du Toit, J.T. (1991) Interactions between woody plants and browsing mammals mediated by secondary metabolites. Annual Review of Ecology, Evolution, and Systematics, 22, 431-46.

Cabrera-Rodriguez, F. (2006) Microhabitat selection of the European rabbit on La Palma, Canary Islands, Spain. Acta Theriologica, 51, 435-442.

Cabrera-Rodriguez, F. (2008) Seasonal abundance and management implications for wild rabbits (Oryctolagus cuniculus) on La Palma, Canary Islands, Spain. Wildlife Biology in Practice, 2, 39-47.

Callaway, R.M. & Ridenour, W.M. (2004) Novel weapons: invasive success and the evolution of increased competitive ability. Frontiers in Ecology and the Environment, 2, 436–443.

Campbell, K. & Donlan, C.J. (2005) Feral goat eradications on islands. Conservation Biology, 19, 1362-1374.

Carracedo, H.C., Pérez Torrado, F.J., Ancochea, E., Meco, J., Hernán, F., Cubas, C.R., Casillas, R., Rodriguez, E. & Ahijado, A. (2002) Cenozoic volcanism II: the Canary Islands. The Geology of Spain (ed. by Gibbons, W. and Moreno, T.), pp. 439–472. Geological Society, London.

Caujapé-Castells, J., Tye, A., Crawford, D. J. , Santos-Guerra, A., Sakai, A., Beaver, K., Lobin, W., Florens, F. B. V., Moura, M., Jardim, R., Gómes, I., C. Kueffer. C., (2010) Conservation of oceanic island floras: present and future global challenges. Perspectives in Plant Ecology, Evolution and Systematics, 12, 107-130.

Cheeke, P.R. (1988) Toxicity and metabolism of pyrrolizidine alkaloids. Journal of Animal Science, 66, 2343-2350

Climent, J., Tapias, R., Pardos, J.A. & Gil, L. (2004) Fire adaptations in the Canary Island pine (Pinus canariensis). Plant Ecology, 171, 185-196.

Coblentz, B.E. (1978) The effects of feral goats (Capra hircus) on island ecosystems. Biological Conservation, 13, 279-286.

Coley, P.D. & Barone, J.A. (1996) Herbivory and plant defenses in tropical forests. Annual Review of Ecology and Systematics, 27, 205-335

Courchamp, F., Chapouis, J.L. & Pascual, M. (2003) Mammal invaders on islands: impacts, control and control impact. Biological Reviews, 78, 347-383.

Cushman, J.H., Waller, J.C. & Hoak, D.R. (2010) Shrubs as ecosystem engineers in a coastal dune: influences on plant populations, communities and ecosystems. Journal of Vegetation Science, 21, 821-831.

Darwin, C.R. (1859) On the origin of species by means of natural selection. London, John Murray.

Diemer, M. (1998) Life span and dynamics of leaves of herbaceous perennials in high-elevation environments: 'news from the elephant's leg'. Functional Ecology, 12, 413-425

Fernández-Palacios, J.M. & Whittaker, R.J. (2008) The Canaries: an important biogeographical meeting place. Journal of Biogeography, 35, 379-387.

Francisco-Ortega, J., Santos-Guerra, A., Kim, S.C. & Crawford, D.J. (2000) Plant genetic diversity in the Canary Islands: a conservation perspective. America Journal of Botany, 87, 909-917

Garzón-Machado, V., del Arco-Aguilar, M.J. & Pérez-de-Paz, P.L. (2011) A tool set for description and mapping vegetation on protected natural areas: an example from the Canary Islands. Biodiversity and Conservation, 20, 3605-3625

Garzón-Machado, V., González-Mancebo, J.M., Palomares-Martínez, A., Acevedo-Rodríguez, A., Fernández-Palacios, J.M., Del-Arco-Aguilar, M. & Pérez-de-Paz, P.L. (2010) Strong negative effect of alien herbivores on endemic legumes of the Canary pine forest. Biological Conservation, 143, 2685-2694.

González Henríquez, M.N., Rodrigo Pérez, J.D. & Suárez Rodríguez, C. (1986) Flora y Vegetación del Archipelago Canario, Edirca, Las Palmas de Gran Canaria.

González, M., Mathieu, A., Augusto, L., Gire, C., Bakker, M.R. & Budynek, A. (2010) Gorse seed bank variability in maritime pine stands. Seed Science Research, 20, 31-38.

Greinwald, R., Bachmann, P., Witte, L., Acebes-Ginovés, J.R. & Czygan, F.C. (1992) Taxonomic significance of alkaloids in the Genus Adenocarpus (Fabaceae-Genista). Biochemical Systematics and Ecology, 20, 69-73

Hierro, J.L., Maron, J.L. & Callaway, R.M. (2005) A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. Journal of Ecology, 93, 5–15.

Höllermann, P. (2000) The impact of fire on Canarian ecosystems 1983-1998. Erdkunde, 54, 70-75

Hothorn, T., Bretz, F. & Westfall, P. (2008). Simultaneous inference in general parametric models. Biometrical Journal, 50, 346-363.

Irl, S.D.H. & Beierkuhnlein, C. (2011) Distribution of endemic plant species on an oceanic island – a geospatial analysis of La Palma (Canary Islands). Procedia Environmental Science, 7, 170-175.

Johansson, M., Rooke, T., Fetene, M. & Granström, A. (2010) Browser selectivity alters post-fire competition between Erica arborea and E. trimera in the sub-alpine heathlands of Ethiopia. Plant Ecology, 207, 149-160

Kazakis, G., Ghosn, D., Vogiatzakis, I.N. & Papanastasis, V.P. (2007) Vascular plant diversity and climate change in the alpine zone of the Lefka Ori, Crete. Biodiversity and Conservation, 16, 1603-1615.

Körner, C., Neumayer, M., Palaez Menendez-Reidl, S. & Smeets-Scheel, A. (1989) Functional morphology of mountain plants. Flora, 182, 353-383

Kyncl, T., Suda, J., Wild, J., Wildova, R. & Herben, T. (2006) Population dynamics and clonal growth of Spartocytisus supranubius (Fabaceae), a dominant shrub in the alpine zone of Tenerife, Canary Islands. Plant Ecology, 186, 97-108.

Lausi, D. & Nimis, P.L. (1986) Leaf and canopy adaptations in a high-elevation desert on Tenerife, Canary Islands. Vegetatio, 68, 19-31.

Legendre, P. (2008) Studying beta diversity: ecological variation partitioning by multiple regression and canonical analsysis. Journal of Plant Ecology, 1, 3-8

Leigh, J.H., Wimbush, D.J., Wood, D.H., Holgate, M.D., Slee, A.V., Stanger, M.G. & Forrester, R.I. (1987) Effects of rabbit grazing and fire on a sub-alpine environment .1. Herbaceous and shrubby vegetation. Australian Journal of Botany, 35, 433-464

Leuschner, C. (1996) Timberline and alpine vegetation on the tropical and warmtemperate oceanic islands of the world: Elevation, structure and Floristics. Vegetatio, 123, 193-206.

Lowe, S., Browne, M., Boudjelas, S. & De Poorter, M. (2000) 100 of the world's worst invasive alien species - A selection from the Global Invasive Species Database. Aliens, 12, 1-12

MacArthur, R. & Levins, R. (1967) The limiting similarity, convergence, and divergence of coexisting species. The American Naturalist, 101, 377–385.

Maher, K.A., Hobbs, R.J. & Yates, C.J. (2010) Woody shrubs and herbivory influence tree encroachment in the sandplain heathlands of southwestern Australia. Journal of Applied Ecology, 47, 441-450.

Navarro, J.F., Martín, E. & Rodríguez, A. (1990) Las primeras etapas del programa de excavaciones en las Cuevas de San Juan y su aportación a las dicronías de la prehistoria de Canarias. Investigaciones Arqueológicas en Canarias, 2, 189–201.

Nezadal, W., Lindacher, R. & Welss, W. (1999) Lokalendemiten und Phytodiversität der westkanarischen Inseln La Palma und La Gomera. Feddes Repertorium, 110, 19-30.

Nogales, M., Rodriguez-Luengo, J.L. & Marrero, P. (2006) Ecological effects and distribution of invasive non-native mammals on the Canary Islands. Mammal Review, 36, 49-65.

Mueller-Dombois, D. & Spatz, G. (1975) The influence of feral goats on the lowland vegetation in Hawaii Volcanoes National Park. Phytocoenologica, 3, 1–29.

Palomares Martínez, Á. (1993) El matorral de alta montaña en la isla de La Palma, seguimiento debido al peligro de extinción de la especie Genista benehovensis. In: Ponencias y comunicaciones. Congreso forestal español - Lourizán, 2, 421-425

Palomares Martínez, Á., Méndez Carvajal, C., López Soriano, I. & Delgado Luzardo, A. (2004) Plan de Conservación del Hábitat de las Cumbres del Norte de La Palma. Internal document of the National Park Caldera de Taburiente, El Paso, La Palma.

Parkes. J, (1990) Feral goat control in New Zealand. Biological Conservation, 54, 335-348.

Pinheiro, J., Bates, D., DebRoy, S. & Sarkar D (2009) nlme: Linear and Nonlinear Mixed Effects Models, R package version 3.1-96.

R Development Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project.org/.

Rafferty, C. & Lamont, B.B. (2007) Selective herbivory by mammals on 19 species planted at two densities. Acta Oecologia, 32, 1-13.

Schütte, H.R., Kelling, K.L., Knöfel, D. & Mothes, K. (1964) Zur Biosynthese von Adenocarpin in Adenocarpus viscosus. Phytochemistry, 3, 249-252

Shaben, J. & Myers, J.H. (2010) Relationships between Scotch broom (Cytisus scoparius), soil nutrients, and plant diversity in the Garry oak savannah ecosystem. Plant Ecology, 207, 81-91.

Simberloff, D. (1995) Why do introduced species appear to devastate islands more than mainland areas? Pacific Science, 49, 87-97.

Steinbauer, M. J., Otto, R., Naranjo-Cigala, A., Beierkuhnlein, C. & Fernández-Palacios, J. M. (2011). Increase of island endemism with altitude - speciation processes on oceanic islands. Ecography, 34, 1–10.

Strasberg, D., Rouget, M., Richardson, D.M., Baret, S., Dupont, J. & Cowling, R.M. (2005) An assessment of habitat diversity and transformation on La Réunion Island (Mascarene Islands, Indian Ocean) as a basis for identifying broad-scale conservation priorities. Biodiversity and Conservation, 14, 3015-3032.

Traveset, A., Nogales, M., Alcover, J.A., Delgado, J.D., López-Darias, M., Godoy, D., Igual, J.M. & Bover, P. (2009) A review on the effects of alien rodents in the Balearic (Western Mediterranean Sea) and Canary Islands (Eastern Atlantic Ocean). Biological Invasions, 11, 1653-1670.

Van Vuren, D. & Coblentz, B.E. (1987) Some ecological effects of feral sheep on Santa Cruz Island, California, USA. Biological Conservation, 41, 253-268.

Ventura, M.R., Castanon, J.I.R., Muzquiz, M., Mendez, P. & Flores, M.P. (2000) Influence of alkaloid content on intake of subspecies of Chamaecytisus proliferus. Animal Feed Science and Technology, 85, 279-282

Vitousek, P.M., D'Antonio, C.M., Loope, L.L., Rejmánek, M. & Westbrooks, R. (1997) Introduced species: A significant component of human-caused global change. New Zealand Journal of Ecology, 21, 1-16.

Walker, L.R., Clarkson, B.D., Silvester, W.B. & Clarkson, B.R. (2003) Colonization dynamics and facilitative impacts of a nitrogen-fixing shrub in primary succession. Journal of Vegetation Science, 14, 277-290.

Wiegand, T., Milton, S.J., Esler, K.J. & Midgley, G.F. (2000) Live fast, die young: estimating size-age relations and mortality pattern of shrubs species in the semi-arid Karoo, South Africa. Plant Ecology, 150, 115-131.

SUPPORTING INFORMATION IN ELECTRONIC VERSION OF DISSERTATION

Appendix S1. Relationship of age of Adenocarpus to circumference and growth height.

Appendix S2. Growth heights of large individuals of different shrub species according to elevation and island orientation measured in exclosure plots established in 2000.

Appendix S3. Increase of maximum age of Adenocarpus and heterogeneity in age structure with elevation.

7.4 Manuscript 4

Burned and devoured – Introduced herbivores, fire and the endemic flora of the high elevation ecosystem on La Palma, Canary Islands

Severin D. H. Irl, Manuel J. Steinbauer, Jana Messinger, Gesche Blume-Werry, Ángel Palomares-Martínez, Carl Beierkuhnlein, Anke Jentsch

ABSTRACT

Novel disturbance regimes (e.g., introduced herbivores and fire) are among the major drivers of degradation in island ecosystems. High elevation ecosystems (HEEs) on islands might be especially vulnerable to these disturbances due to high endemism. Here, data from an 11-year exclosure experiment in the HEE of La Palma (Canary Islands) are presented where mammalian herbivores have been introduced. We investigate the combined effect of herbivory and fire on total species richness, seedling richness, and seedling establishment on the whole system and a subset of highly endangered species (target species). Total species richness, seedling species richness, and seedling establishment decreased with herbivory. Five out of eight target species were exclusively found inside the exclosures indicating the negative impact of introduced herbivores on endemic high elevation flora. Target species were generally affected more negatively by introduced herbivores and were subject to significantly higher browsing pressure, probably owing to their lack of defense strategies. A natural wildfire that occurred six years before data sampling substantially increased total species richness and seedling richness in both herbivory exclosure and reference conditions. We conclude that species composition of the HEE has been severely altered by the introduction of non-native herbivores, even though fire seems to have a positive effect on this system.

INTRODUCTION

Anthropogenic influences have created novel disturbances as well as altered natural disturbance regimes (White and Jentsch, 2001; Hobbs et al., 2006; Catford et al., 2012). Indeed, changes in disturbance regimes are widely recognized as major threats to island biota and ultimately to global biodiversity (Caujapé-Castells et al., 2010). Mammalian herbivores (Courchamp et al., 2003; Campbell and Donlan, 2005), altered fire regimes (Perry et al., 2012; Ramirez et al., 2012), along with land use change, habitat degradation, or climate change (Caujapé-Castells et al., 2010) are of special importance among the threats to native and endemic island biota and insular ecosystems in general. Conservation efforts on islands should have particularly high priority (Kier et al., 2009) because of the outstanding position of islands as hotspots of endemic plant species diversity (Kreft et al., 2008).

A high degree of endemic species (Steinbauer et al., 2012) and their ephemeral evolutionary position (Fernández-Palacios et al., 2014) characterize especially high elevation ecosystems (HEEs) within islands. These ecosystems experience strong environmental (due to increasing climatic harshness with elevation) and geographical isolation (because of increasing distance to comparable ecosystems on other islands or the continent; Steinbauer et al., 2013). As the ocean is an effective filter for terrestrial mammals, most oceanic islands did not possess mammalian herbivores before human colonization. Thus, mammalian herbivory has not influenced the evolution of endemic species on islands (Traveset et al., 2009). As a consequence, endemic plant species have often lost the particular herbivore defense mechanisms and strategies of their continental ancestors due to this lack of selection pressure (Atkinson,

2001). Indeed, evolutionary effects of missing herbivore pressure on plant traits can become apparent even within only decades (Didiano et al. 2014).

Introduced herbivores often profit from the absence of natural enemies, diseases, and pests (Shea and Cheeson, 2002). Thus, introduced mammalian herbivores have not only inflicted damage in the past but continue to inflict great damage on natural island vegetation and endemic plant species (e.g., Campbell and Donlan, 2005; Caujapé-Castells et al., 2010; Irl et al., 2012; Ramirez et al., 2012). Important examples are the feral goat (*Capra hircus*) and the European rabbit (*Oryctolagus cuniculus*), both considered among the world's 100 most invasive species (Lowe et al., 2000).

As an additional driver of change and degradation, human-induced alterations of fire regime (i.e., increased fire frequency or magnitude) can negatively affect island vegetation, even though it may be naturally adapted to occasional wildfires (Arévalo et al., 2001; Perry et al., 2012, Garzón-Machado et al., 2012; Crausbay et al., 2014). Especially combined changes in both disturbances, introduced mammalian herbivores and altered fire regimes, will likely create negative impacts on vegetation dynamics or species richness. Population structure and community composition can be substantially modified via reduced regeneration success after fire events (Johansson et al., 2010; Ramirez et al., 2012).

In contrast to lower elevation ecosystems, HEEs in oceanic islands are still believed to be largely in a natural or at least seminatural state. This is reflected in different forms of nature reserves and protection status. High-elevation nature reserves have been established, for instance, on La Palma and Tenerife (Canary Islands, Spain), Pico (Azores, Portugal), Fogo (Cape Verdes), La Réunion (Mascarene Islands, France), and Hawaii and Maui (Hawaii Islands, United States). The exclusion of intensive land use, settlements and infrastructure and the limited direct human impact in general makes it possible to investigate the dynamics of introduced herbivore pressure and altered fire regimes.

La Palma is a subtropical volcanic-oceanic island with strong environmental gradients (Irl and Beierkuhnlein, 2011). It is inhabited by several globally relevant introduced mammalian herbivores such as the feral goat (*C. hircus*) and the European rabbit (*O. cuniculus*; Garzón-Machado et al., 2010; Irl et al., 2012) but also the recently introduced Barbary sheep (*Ammotragus lervia*) originally from northern Africa. The selective grazing of these herbivores has been shown to cause the virtual mono-dominance of a single shrub species (i.e., the single-island endemic subspecies *Adenocarpus viscosus* subsp. *spartioides*), even though climatically better-adapted shrub species are present in the natural HEE flora (Irl et al., 2012). Fires occur naturally in the subalpine scrub due to the close vicinity to the endemic fire-promoting Canary Pine forest that forms the treeline (Höllermann, 2000; del Arco Aguilar et al., 2010). Both disturbances, fire and herbivory, have been individually studied on the Canary Islands and specifically on La Palma (see Höllermann, 2000, but also Garzón-Machado et al., 2010, or Irl et al., 2012), but an integrative approach to identify the combined effects of both introduced herbivores and altered fire regime with focus on the unique characteristics of HEEs is still missing.

We aimed at exploring the effects of two major disturbances—herbivory and fire—on the high elevation vegetation of La Palma, Canary Islands. Using an 11-year fenced exclosure experiment and

nonfenced counterparts we take the HEEs of La Palma and the transition zone with the Canary Pine forest as a case study. We hypothesize that (1) introduced herbivores negatively affect total species richness, seedling species richness, and seedling establishment; (2) additional fire reduces total species richness, seedling richness, and seedling establishment; and (3) introduced herbivores selectively browse on endemics due to their lack of adaptation to herbivory.

MATERIAL AND METHODS

Study area

The Canary Islands are situated off the northwestern coast of Africa in the Atlantic Ocean. All islands are of volcanic origin (Carracedo et al., 2002). La Palma is located in the NW of the archipelago. At approx. 1.7 Ma it is the second youngest island, spanning an area of 706 km^2 (Carracedo et al., 2002). The HEE of La Palma—also referred to as the subalpine summit scrub (Irl and Beierkuhnlein, 2011; Irl et al., 2012) or summit broom scrub (Garzón-Machado et al., 2011)—is most prominent on the outer flanks of the Caldera de Taburiente complex, ranging from about 2000 to 2400 m a.s.l. It covers an area of 14.3 km^2 (see Fig. 1). The treeline ecotone consists of a transitional zone of the HEE and the Canary Pine forest and ranges between 1800 and 2000 m a.s.l. The inner cliffs of the caldera are too steep for closed vegetation cover. Above the trade-wind induced cloud bank the climatic conditions are characterized by high solar radiation, extensive arid periods of up to 6 months in summer, high diurnal temperature amplitudes, and harsh winter conditions with snow and ice storms at irregular frequencies and magnitude (Garzón-Machado et al., 2013).

No mammalian herbivores exist or have ever existed naturally on the Canary Islands (Traveset et al., 2009). However, aboriginal inhabitants brought the feral goat (*C. hircus*) to the Canary Islands more than 2000 years ago as archaeological studies have shown (Zöller et al., 2003), whereas the Castilian conquerors introduced the European rabbit (*O. cuniculus*) in the 15th and 16th century to the archipelago. Today, rabbits are partially controlled by hunting (Cabrera-Rodriguez, 2006) but are still relatively abundant throughout the whole island. As recently as the 1970s, the Barbary sheep (*Ammotragus lervia*) was deliberately introduced to the Caldera de Taburienta National Park (NP) (Nogales et al., 2006) by the National Institution for Environmental Conservation (ICONA) to stimulate big game hunting as a new economical field.

Forest fires spread upslope from the fire-adapted Canary Pine forest into the HEE at irregular intervals and intensities (del Arco Aguilar et al., 2010), generally affecting the lower HEE regions more than the higher ones. Fire frequency has increased in the last decades (Climent et al., 2004; Palomares Martínez et al., 2004; Garzón-Machado et al., 2012).

The HEE of La Palma is dominated by endemic legume shrub species (Fig. 1; del Arco Aguilar et al., 2010). It has already been shown that, although climatically better adapted legume shrub species such as *Genista benehoavensis*, *Spartocytisus subpranubius*, or *Chamaecytisus proliferus* subsp. *proliferus* are potentially present, the selective grazing of introduced herbivores strongly favors the legume

Adenocarpus viscosus subsp. *spartioides* (Irl et al., 2012). In order to halt extinction dynamics of several very rare and highly endangered endemic plant species the administration of the Caldera de Taburiente NP has established a variety of conservation measures specifically for these endangered endemics, including large-scale fenced exclosures and massive aerial seed dispersal (Palomares Martínez et al., 2004). These endangered endemic species are considered our *target species* (Table 1). All other species are *nontarget species*.
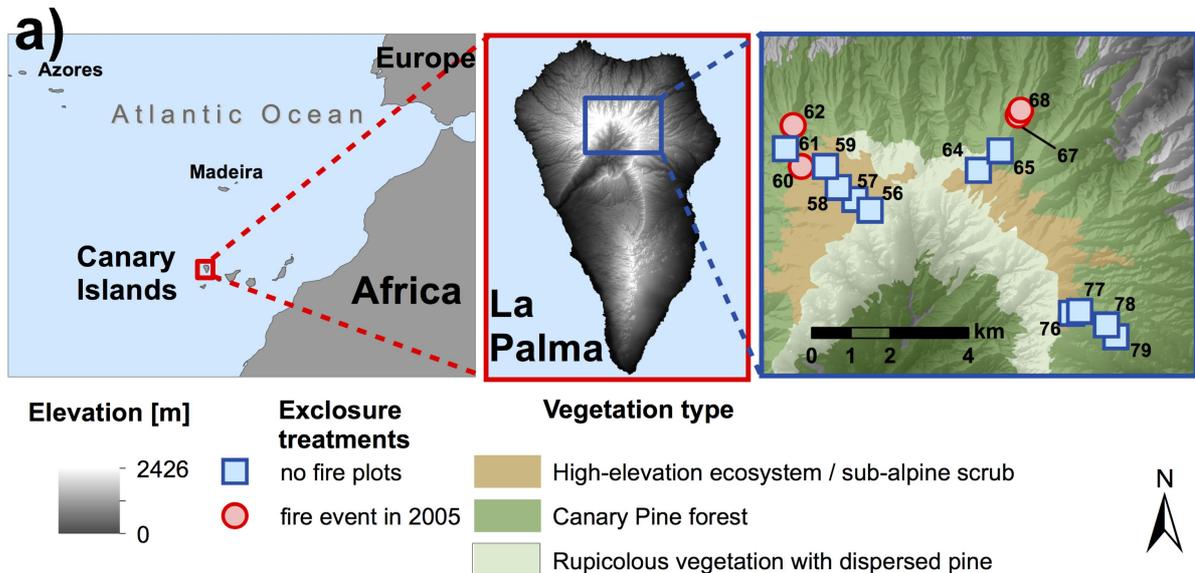

FIGURE 1. (a) Map of the Canary Islands, La Palma, and the study area. (b) A view of the rim of the Caldera de Taburiente from the highest plot (56) at 2400 m a.s.l. The study area is located on the northern part of the island (a, central panel). The symbols depict the sites of exclosures (herbivory exclosure) and their respective herbivory reference pairs: squares = unaffected by 2005 fire and circle = affected by 2005 fire (created with ArcGIS 10, ESRI Inc.). The species inside the exclosure are two of our target species, i.e. *Spartocytisus supranubius* (dark green) and *Genista benehoavensis* (grayish green). Around the telescopes a mono-dominant stand of *Adenocarpus viscosus* subsp. *spartioides* can be seen. Photo by Gesche Blume-Werry.

Sampling design

A paired approach of thirty 20 × 20 m plots (15 pairs) in the presence and absence of introduced herbivores was implemented in this study to assess total species richness, seedling species richness, and establishment success of all vascular plant species of the HEE and transitional zone of La Palma (Fig. 1). The plots are situated outside of the actual Caldera de Taburiente NP but administrated by the park authorities on the outer flanks of the caldera. The first plot of each pair was a fenced exclosure in order to prohibit the access of introduced herbivores (*herbivory exclosure plot*; fence height 1.20 m), The exclosures were established by the Caldera de Taburiente NP in 2000. During the establishment of the herbivory exclosure plots, all aboveground vegetation was removed and eight target species were sown within this area. Target species were sown in equal quantities per plot but differing quantities per species because germination success varied greatly between species (see experimental germination tests done by Palomares Martínez, 1993). See Appendix A1 for the sown seed quantity per species. We assumed that seeds of species, which were not sown, were present in the soil seed bank as these species are more or less widely distributed throughout the study area.

The reference plot of each pair was an unfenced plot permitting full access for introduced herbivores (*herbivory reference plot*). The herbivory reference plot was situated directly next to the herbivory exclosure counterpart and possessed the same size. It was established under comparable site conditions (inclination, soil conditions, fire regime; in the transitional zone, this also included tree cover, etc.), although vegetation was not removed in the herbivory reference plots. Each herbivory reference plot is situated downslope from its herbivory exclosure pair to ensure effective and continuous seed dispersal from within the herbivory exclosure plots. Dispersal ability differs between species, but the Caldera de la Taburiente NP undertook an additional seed rain in 2006 throughout large parts of the study area due to massive aerial seed dispersal of target species. Most target species reach their reproductive age after 2 to 5 years (Palomares Martínez, 1993), indicating that natural seed dispersal from the herbivory exclosure plots to the herbivory reference plots has been possible for a maximum of 6 to 9 yr.

Besides herbivory, a second treatment was present. A wildfire consumed the vegetation of several plot pairs in 2005 (*n* = 4 *herbivory exclosure* plots; *n* = 4 *herbivory reference* plots), thus enabling the assessment of the combined effects of herbivory and fire on total species richness, seedling species richness, and seedling establishment success (Fig. 1). This resulted in a two-factorial sampling design (Table 2).

The plots are distributed throughout the whole HEE reaching from 1800 to 2400 m a.s.l.. They are located at three major aspects (i.e., NW, NE, E) as shown in Figure 1. The distribution of the plots follows the main elevational and aspect gradients and aims at reaching from the transitional zone to the caldera rim. Data sampling took place in April 2011.

Table 1. Total species list including the abbreviations used in the Figures 3 and 4, a classification of their endemism status (SIE = single-island endemic; AE = archipelago endemic; other status = native or non-native), growth form and the species status as target species.

Species	Abbreviation	SIE	AE	Other status	Woody species	Target species
Adenocarpus viscosus subsp. *spartioides*	A.vis	x	x		x	
Asteraceae spec. (2 species)	Ast.	-	-	-		
Bencomia exstipulata	B.exs		x		x	x
Bystropogon origanifolius	B.ori		x		x	
Chamaecytisus proliferus subsp. *proliferus*	C.pro		x		x	x
Cistus symphytifolius	C.sym		x		x	
Descurainia millefolia	D.mil		x		x	
Echium gentianoides	E.gen	x	x		x	x
Echium wildpretii subsp. *trichosiphon*	E.wil	x	x		x	x
Galium spec.	Gal.	-	-	-		
Genista benehoavensis	G.ben	x	x		x	x
Lactuca palmensis	L.pal	x	x			
Lactuca viminea	L.vim			native		
Orchis canariensis	O.can		x			
Pinus canariensis	P.can		x		x	
Pterocephalus porphyranthus	P.por	x	x		x	
Scrophularia glabrata	S.gla		x		x	
Sonchus hierrensis	S.hie		x		x	
Spartocytisus supranubius	S.sup		x		x	x
Teline stenopetala subsp. *sericea*	T.ste	x	x		x	x
Tolpis calderae	T.cal	x	x		x	
Valerianella dentata	V.den			non-native		
Viola palmensis	V.pal	x	x			x

Biotic measurements

Total species richness was recorded within each of the thirty 20 × 20 m plots. All additional biotic measurements took place in 10 × 1 m^2 randomly distributed subplots within each of the thirty 20 × 20 m plots (see Table 2). In each of the ten 1 m^2 subplots seedling identity and abundance of all seedling individuals per species were recorded. Here, we define seedling as a plant individual that has not yet lignified (except for *P. canariensis,* where maximum growth height of 10 cm was chosen as threshold, and the herbaceous *Lactuca palmensis,* which was classified to be juvenile if only juvenile leaves were present). In addition, the absence of flower buds or branch ramifications was mandatory to be considered as seedling. Seedling species richness was calculated by summing up all seedling species. Seedling density (as a measure of seedling establishment success) was calculated by dividing the number of seedlings per species through the total subplot area (i.e., 10 × 1 m^2).

In addition, we measured species-specific browsing intensity of introduced herbivores. Rabbits were able to enter temporarily due to storm-associated fence damage (plot # 56, 59, 77, 78; Fig. 1) in

four herbivory exclosure plots. Temporary rabbit presence did not significantly change total species or seedling richness when compared to the other herbivory exclosure plots (Wilcoxon signed rank test). All plant individuals (i.e., seedlings and adults) were used to identify browsing intensity. Browsing intensity was classified by estimating the percentage of total browsed plant tissue (Table 3).

Statistical analysis

For comparison of total species richness (measured on the 20 × 20 m plot level) and seedling species richness (i.e., integrating all subplots of one plot) between herbivore and no herbivore plots, paired Wilcoxon signed rank tests (R-package *stats*, version 3.1.0) were used. The effect of fire treatments on total species richness and seedling species richness was tested using a mixed-effects model (package *lme4* version 1.1.6; Bates et al., 2014) with herbivory as random effect.

Seedling density was compared between herbivory exclosure and herbivory reference plots for all species separately by using mixed-effects models. Subplots were grouped within pairs by adding a random site factor. The analysis was repeated for all species combined with the factor "species" as an additional random effect.

Model assumptions for mixed-effects models (normality of residuals, homogeneity of variances among treatments) were tested by visual inspection and were not met in all cases. The models were thus repeated with rank transformed data. Results did not differ qualitatively. In the following, results based on the untransformed data are reported.

Browsing intensity between target species and nontarget species was tested using the Mann-Whitney U-test.

Illustrations were created with SigmaPlot 7.0 (Systat Software, 2001) and R version 3.1.0 (R Development Core Team, 2014). The latter was used for all statistical analyses.
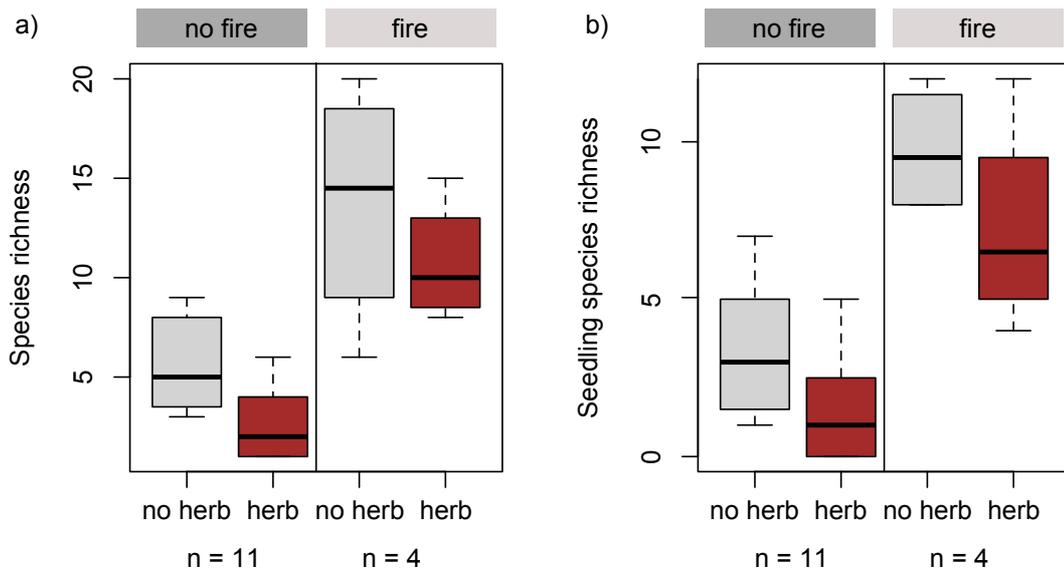
FIGURE 2. (a) Total species richness and (b) seedling species richness varied significantly according to herbivory (herbivory reference = herb; herbivory exclosure = no herb) and fire treatment. Note that the effect of herbivory was tested in a paired t-test (including all plots) and the effect of fire in a mixed-effects model (herbivory as random effect, including all plots).
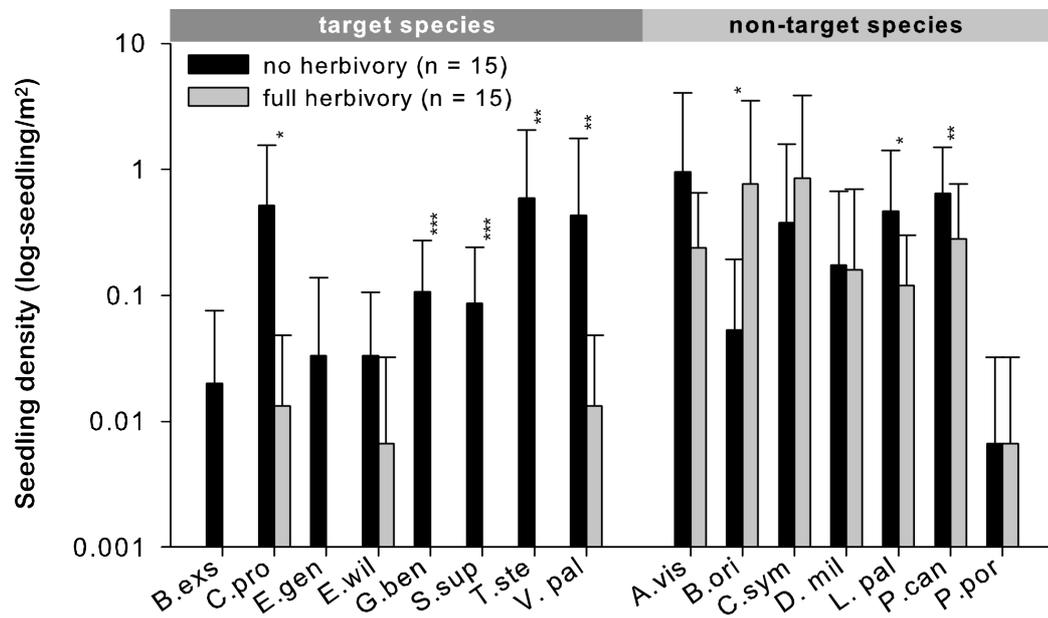

FIGURE 3. Seedling density per target species and nontarget species in the 1 m2 subplots of the herbivory exclosure (black bar; n = 15 plots, 150 subplots) and herbivory reference plots (gray bars; n = 15 plots, 150 subplots). For species abbreviations see Table 2. Significant differences (indicated as asterisks with p-values as $p < 0.05$ = *, $p < 0.01$ = ** and $p < 0.001$ = ***) were assessed using mixed effect models on the subplot data comparing each species individually with a random site factor.

RESULTS

Effects of introduced herbivores on seedling establishment

A total of 24 species was identified in the study sites; 79% (n = 19) of species in the data set were archipelago endemics, 38% La Palma endemics (n = 9; Table 1). The majority of the species were woody perennials (67%).

Total species richness was significantly higher inside the *herbivory exclosure* plots (7.8 ± 5.1; mean ± standard deviation [SD]), when compared to the *herbivory reference* plots (4.9 ± 4.2; paired Wilcoxon signed rank test p < 0.01; Fig. 2, part a). The difference is even more distinct for seedling species richness (paired Wilcoxon signed rank test p = 0.002; Fig. 2, part b; herbivory exclosure*:* 5.1 ± 3.5; herbivory reference: 3.1 ± 3.4).

Plots facing the 2005 fire event were characterized by a significant increase in the total species richness and seedling species richness inside and outside the exclosures (total species richness: 12.3 ± 4.8; seedling species richness: 8.5 ± 2.9) compared to nonfire plots (total species richness: 4.2 ± 2.6; seedling species richness: 2.5 ± 2.1; mixed-effects model p < 0.001 in both cases, Fig. 2). However, the effect of fire is statistically not distinguishable from vegetation type (summit scrub vs. transition zone) or elevation because all burnt areas are situated in or close to the transition zone with the fire-prone pine forest at lower elevations.

In general, the seedling density (as a proxy for seedling establishment) was higher inside the exclosures than outside (p < 0.001; mixed-effects model on subplot level including all species). On average, the herbivory exclosure subplots have a higher seedling density of 0.33 seedlings per m^2 than the herbivory reference subplots. For the majority of target species, this negative effect of herbivory on seedling density was also detectable if analyzed individually (Fig. 3). The same trend is visible for the target species where no significant difference was detectable. However, significance is likely not reached due to very low numbers of individuals. Seedlings of five out of eight target species were exclusively found inside the herbivory exclosure plots (Fig. 3).

Table 2. All possible combinations of the two-factorial design implemented in our sampling design. The number of plots per treatment type is indicated by 'n'.

	Treatment types			
	Herbivory reference	**n**	**Herbivory exclosure**	**n**
No fire	Herbivory reference, no fire	11	Herbivory exclosure, no fire	11
Fire	Herbivory reference, fire	4	Herbivory exclosure, fire	4

Selective browsing on endangered endemic plant species

The target species *T. stenopetala* and *S. supranubius* showed highest browsing damage, followed by *C. proliferus* subsp. *proliferus* and *G. benehoavensis* (Fig. 4). Nontarget species such as *B. origanifolius*

and *L. palmensis* showed a high variability in browsing damage, from no visible browsing marks up to serious damage. Herbivores did not browse *A. viscosus* subsp. *spartioides*. Target species were significantly more heavily browsed than nontarget ones (Mann-Whitney U-test: W = 1067.5, *p* < 0.001).

DISCUSSION

Negative impact of introduced herbivores on seedling richness

Our findings indicate that total species richness, seedling species richness as well as seedling density in insular HEE decreases significantly if introduced herbivores are present (i.e., feral goats, rabbits, or Barbary sheep). Even if plant individuals have reached a certain growth height (i.e., most species of the HEE have a shrubby growth form), rabbit browsing can still cause severe damage, although it remains mostly nonlethal (see Fig. 5). However, under severe drought conditions when other food sources are lacking, the rabbits can turn to browsing the bark of adult shrub individuals (e.g., *G. benehoavensis*, *C. proliferus* subsp. *proliferus*, *B. exstipulata*, *S. supranubius*, *T. stenopetala* subsp. *sericea*) even causing the shrub's death (Palomares Martínez et al., 2011).
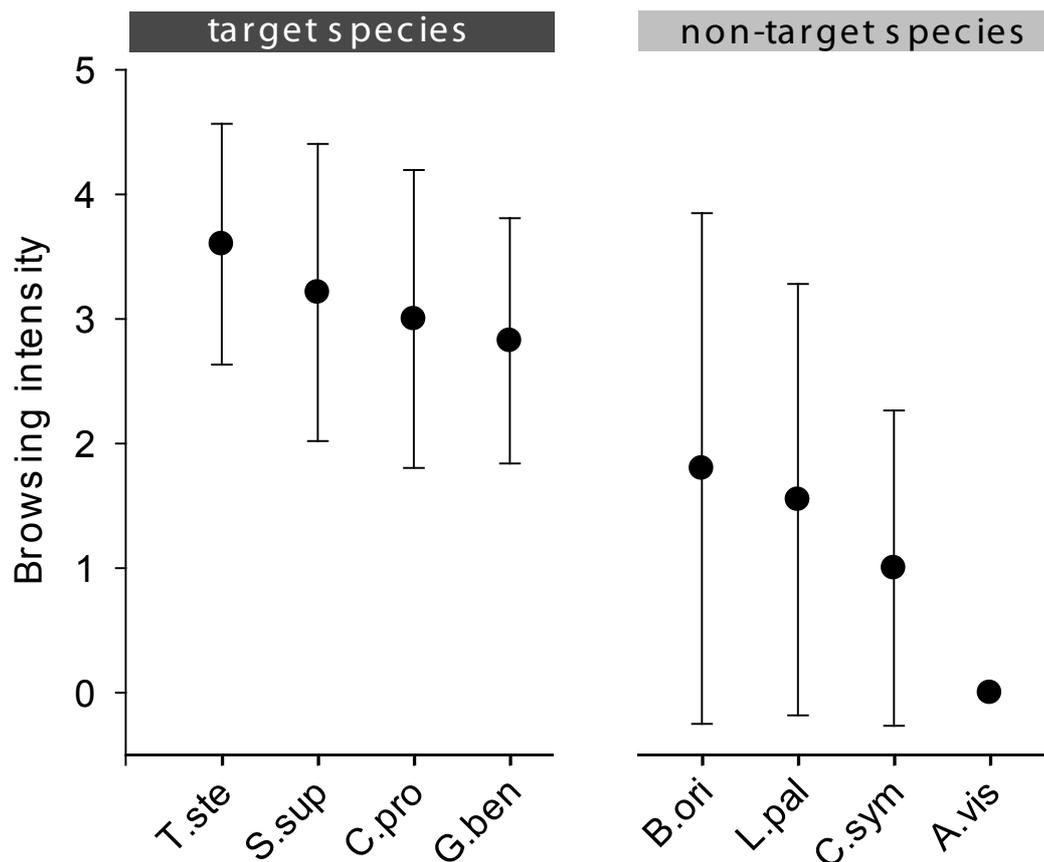

FIGURE 4. Selective grazing indicated by species-specific browsing intensity of introduced herbivores on target and nontarget species present in the herbivory exclosure plot temporarily entered by rabbits. Whiskers indicate the 0.95-confidence interval. Browsing intensity was significantly higher for target species than nontarget species (Mann-Whitney U-test: W = 1067.5, p < 0.001). For browsing classification, see Table 3; for abbreviations, Table 1.

a)

b)

FIGURE 5. Example of selective browsing of introduced herbivores on the single-island endemic *Genista benehoavensis*. The individual at the top is protected from herbivores situated within an exclosure and displaying a vital and healthy growth (growth height about 3.5 m), while the lower individual of the same species has been heavily browsed, reacting with compensational growth (growth height about 0.5 m). Photos by (a) Severin D.H. Irl and (b) Carl Beierkuhnlein.

Both endangered target and the other nontarget species are mainly single-island or—at least—archipelago endemics, in that case mostly restricted exclusively to the two corresponding Canarian HEEs (Acebes Ginovés et al., 2010; del Arco Aguilar et al., 2010). This high degree of endemism is typical for HEEs within an archipelago (Fernández-Palacios et al., 2014). However, some of the nontarget species such as *A. viscosus* subsp. *spartioides* possess a variety of alkaloids possibly functioning as herbivore deterrents (Irl et al., 2012, and references therein), while others are rich in essential oil (e.g. *B. origanifolius* [Economou and Nahrstedt, 1991] and *P. canariensis* [Dob et al., 2005]), or other compounds potentially suitable as herbivore deterrents (e.g., *C. symphytifolius* [Calabuig et al., 1981]). Therefore, these species might have a competitive advantage over the target species. However, recent studies indicate that intraspecific herbivore defense decreases with elevation due to low temperatures and less herbivore pressure (Pellissier et al., 2014).

Similar to the results given by Garzón-Machado et al. (2010) for the Canary Pine forest of La Palma, a large share of target species was exclusively found inside the exclosures in our study area, indicating that introduced herbivores reduce seedling establishment to nearly zero. On the one hand, it cannot be fully excluded that the sampling design (i.e., total vegetation removal and sowing of target species only in the herbivory exclosure plots but not in the herbivory reference twin) might bias our results. On the other hand, aerial seed dispersal by the NP administration (Palomares Martínez et al., 2004) as well as many years of possible seed rain of target species from inside the exclosures to the herbivory reference plots in direct proximity to the exclosures (Palomares Martínez, 1993) should have ensured the possibility of target species to establish also outside of the exclosures. Obviously, this is not the case. In addition, the nonremoval of vegetation in the herbivory reference plots should actually facilitate seedling establishment during the critical period of establishment compared to the herbivory exclosure plots because the removal of the vegetation in the herbivory exclosure plots increases solar radiation and drought stress, and excludes facilitative effects common for high stress HEEs (Anthelme and Dangles, 2012), all affecting seedling establishment and survival negatively.

Extremely few to no seedlings of the target species were found in the *herbivory reference* plots, indicating the poor adaptation of island species to introduced herbivory (Bowen and Van Vuren, 1997). Interestingly, seedlings of some nontarget species (e.g., *B. origanifolius*) are significantly more abundant or do not differ (*A. viscosus* subsp. *sparitoides*, *C. symphytifolius*, *Descurainia millefolia,* and *Pterocephalus porphyranthus*) if introduced herbivores are present, probably profiting from chemical compounds acting as herbivore deterrents, reduced interspecific competition, or increased resource availability outside the exclosures. However, some nontarget species were also negatively affected (*Lactuca palmensis* and *P. canariensis*).

Our data suggest that the environmental niches made available by reducing plant species diversity through introduced herbivores are filled by native and endemic species, and not by non-native plant species commonly associated with disturbed systems at lower elevations (Merlin and Juvik, 1992). Thus, even though this ecosystem is subject to substantial changes in plant species composition and diversity, there is no indication that non-native species abundant in lower elevations of the Canary Islands (Arévalo

et al., 2005) are able to fill the available niches. Exceptions are roadside communities often identified as invasion pathways for non-native plant species (Arévalo et al., 2005; Pauchard et al., 2009) but also for endemics (Irl et al., 2014) into high elevations.

Table 3. Classification of browsing intensity used in Figure 4.

Class	Browsing intensity
0	0% to 5%
1	6% to 25%
2	26% to 50%
3	51% to 75%
4	76% to 95%
5	95% (i.e. lethal damage)

Postfire effects with and without presence of introduced herbivores

Our findings indicate that the legacy of fire has an overall positive effect on total species richness and seedling richness. The negative effects of herbivory seem to be comparable to nonfire conditions. This can result from ameliorated growing conditions owing to the enhanced availability of soil nutrients and the opening of the canopy associated with postfire conditions, the reduced habitat suitability for introduced herbivores, or population decline of herbivores during the fire (Keeley and Fotheringham, 2000). However, the positive effect on total plant species richness and seedling species richness cannot be separated from elevation or vegetation type.

Herbivore impact is still effective as only 37.5% of the target species that occur in no herbivore conditions were actually recorded in the *herbivory reference* plots and then only in very low abundances in postfire conditions. A single shrub species (i.e., *A. viscosus* subsp. *spartioides*) creates almost mono-dominant stands if introduced herbivores are present (Irl et al., 2012). Our data suggest that the effect of introduced herbivores acts on the complete species composition of the entire HEE flora. In addition, fire probably has a positive impact on plant species richness, even though the fire regime is considered an anthropogenically altered disturbance regime mainly due to its elevated reoccurrence frequency (Garzón-Machado et al., 2012).

Implications for conservation and restoration management

Under natural conditions, that is, in the absence of large mammalian herbivores, other species than *A. viscosus* subsp. *spartioides* will probably have played a more important role in the HEE of La Palma, but the reconstruction of prehuman ecosystems remains speculative. Indeed, recent discoveries suggest that a *Juniperus cedrus* woodland might have existed above the Canary Pine forest, which would have encompassed large parts of the current summit scrub (Nogales et al., 2014). Also, even small reductions in species abundance and distributions are likely to have a big impact on the function and structure of species-poor systems such as the HEE of La Palma (sensu the insurance hypothesis; Naeem and Li, 1997).

The definition of a potential natural state of vegetation and ecosystems is difficult if not impossible when environmental conditions and pressures have changed (Chiarucci et al., 2010). Garzón-Machado et al. (2011) assumed that *G. benehoavensis* might be an important species next to *A. viscosus* subsp. *spartioides* in this system, which is confirmed by our data. However, other species such as *C. proliferus* ssp. *proliferus* and *T. stenopetala* subsp. *sericea*, performed well, too. This indicates that these species should also play a vital role in future considerations of conservation and habitat restoration for hypothetical HEEs without introduced herbivores. Also *S. supranubius,* which is very common in the HEE of Tenerife (Kyncl et al., 2006), might be an important species for the highest elevations of La Palma because it seems to be optimally adapted to the harshest HEE conditions (Irl et al., 2012).

Due to their specific growth form and morphology, the La Palma endemics *E. gentianoides* and *E. wildprettii* subsp. *trichosiphon* are not able to dominate the vegetation structure. Yet, their conservation should have top priority because their global distribution is confined to the relatively small area of the HEE of La Palma (Acebes Ginovés et al., 2010; del Arco Aguilar et al., 2010). Interestingly, *A. viscosus* subsp. *spartioides* does not seem to play such a dominant role without introduced herbivores.

All in all, insular HEEs are islands within islands dominated by range-restricted endemics (Fernández-Palacios et al., 2014), and therefore these ecosystems and their species should be considered with high conservation priority. This might become especially relevant because additional pressure is likely exerted on the diversity of island HEEs and their endemic species by anthropogenic climate change, which has the potential to increase the extinction risk of these species (Greenwood and Jump, 2014).

Strong selective browsing influences plant community dynamics

In the HEE of La Palma, introduced herbivores selectively browse on the different species present. Selective browsing is characteristic for many mammalian herbivores (e.g., Rafferty and Lamont, 2007; Traveset et al., 2009; Johansson et al., 2010). In nonadapted systems, it can induce substantial alterations of plant community dynamics and structure in nonadapted ecosystems (Ramirez et al., 2012). In the HEE of La Palma, several plant species, especially the endangered ones, are heavily browsed, while others are less damaged or even remain completely unaffected. Plant species with defense mechanisms possess a

competitive advantage, because unprotected species, even though they are rare, are more likely to be browsed severely than abundant species possessing defense mechanisms (Bryant et al., 1991). In our model system on La Palma this phenomenon can be observed as well. Rare species such as *T. stenopetala* subsp. *sericea*, *S. supranubius*, *C. proliferus* subsp. *proliferus,* or *G. benehoavensis* are preferred by introduced herbivores, while common and widespread species are significantly less damaged. Current rarity, however, reflects the long-lasting legacy of introduced herbivore pressure.

We suppose that the vegetation we see today in the HEE of La Palma strongly deviates from the former "natural" vegetation. As HEEs are very isolated, no introduced or invasive plant species has entered these communities. However, shifting dominance patterns and a local decrease of diversity have likely caused impoverished and almost mono-dominant stands of plants that can cope with current herbivore pressure. Today, many species that can be expected to have been abundant under "natural" conditions (i.e., without mammal herbivory) only occur in refugial locations (e.g., on cliffs or rocky outcrops; nowadays also in large exclosures established for conservation purposes by the Caldera de Taburiente NP) and are highly threatened to become extinct (Palomares Martínez et al., 2004).

Very likely the present ecosystems have been altered by centuries of goat herding and cyclic burning. Such kinds of intense past impacts and land use history can have a long-lasting legacy in local plant species occurrence even after its abolishment (Heubes et al., 2011). In addition, the presence of introduced herbivores has been shown to prevent the recuperation of natural vegetation (Merlin and Juvik, 1992).

CONCLUSION

The results presented from an 11-yr exclosure experiment offer the unique opportunity to identify the long-term impact of introduced mammalian herbivores on an insular HEE in combination with reoccurring fire events. Presumably, the presence of introduced herbivores has substantially altered the species richness and vegetation composition, leading to a strong degradation of this system. This resulted, among others, in a massive coordinated conservation program initiated by the Caldera de Taburiente NP administration to protect the various endangered single-island or archipelago endemics of this system (Palomares Martínez et al., 2004).

Now, the long-term goal should be to preserve the endangered species, create habitats and "safe sites" for these species to expand their current ranges, and, if possible, restore the HEE to a natural state. A necessary step in this direction would be to monitor and strictly control the population of all major herbivores (especially feral goats, rabbits, and Barbary sheep) as well as create awareness among the population about the damages caused by human-induced fires. However, no matter how successful total eradication programs have previously been in enabling the full recovery of natural island vegetation (e.g., Caujapé-Castells et al., 2010, and references therein), it seems unrealistic to achieve this conservation goal on such a large and inhabited island as La Palma that relies heavily on rural and traditional agricultural practices. Nevertheless, total eradication of introduced herbivores from the whole island of

La Palma should be the long-term goal from a conservation perspective to sustainably protect the unique native endemic flora and enable its survival and reestablishment. In the meantime, however, more and larger fenced exclosures might be a promising conservation method to preserve the most endangered species and create patches of restored natural vegetation.

ACKNOWLEDGEMENTS

REFERENCES

Acebes Ginovés, J. R., León Arencibia, M. C., Rodríguez Navarro, M. L., del Arco Aguilar, M., García Gallo, A., Pérez de Paz, P. L., Rodríguez Delgado, O., Martín Osorio, V. E., Wildpret de la Torre, W., 2010: Spermatophyta. In Arechavaleta, M., Rodríguez, S., Zurita, N., and García, A. (eds.), Lista de especies silvestres de Canarias. Hongos, plantas y animales terrestres. La Laguna: Consejería de Politica Territorial y Medio Ambiente del Gobierno de Canarias, 122–172.

Anthelme, F., and Dangles, O., 2012: Plant–plant interactions in tropical alpine environments. Perspectives in Plant Ecology, Evolution and Systematics, 14: 363–372.

Arévalo, J. R., Delgado, J. D., Otto, R., Naranjo, A., Salas, M., and Fernández-Palacios, J. M., 2005: Distribution of alien vs. native plant species in roadside communities along an altitudinal gradient in Tenerife and Gran Canaria (Canary Islands). Perspectives in Plant Ecology, Evolution and Systematics, 7: 185–202.

Arévalo, J. R., Fernández-Palacios, J. M., Jiménez, M. J., and Gil, P., 2001: The effect of fire intensity on the understorey species composition of two Pinus canariensis reforested stands in Tenerife (Canary Islands). Forest Ecology and Management 148: 21–29.

Atkinson, I. A. E., 2001: Introduced mammals and models for restoration. Biological Conservation, 99: 81–96.

Bates, B., Maechler, M., and Bolker, B., 2014: lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-42, http://CRAN.R-project.org/package=lme4.

Bowen, L., and Van Vuren, D., 1997: Insular endemic plants lack defenses against herbivores. Conservation Biology, 11: 1249–1254.

Bryant, J. P., Provenza, F. D., Pastor, J., Reichardt, P. B., Clausen, T. P., and du Toit, J. T., 1991: Interactions between woody plants and browsing mammals mediated by secondary metabolites. Annual Reviews in Ecology and Systematics, 22: 431–446.

Cabrera-Rodriguez, F., 2006: Microhabitat selection of the European rabbit on La Palma, Canary Islands, Spain. Acta Theriologica, 51: 435–442.

Calabuig, M. T., Cortés, M., Francisco, C. G., Hernández, R., and Suárez, E., 1981: Labdane diterpenes from Cistus symphytifolius. Phytochemistry, 20: 2255–2258.

Campbell, K., and Donlan, C. J., 2005: Feral goat eradications on islands. Conservation Biology, 19: 1362–1374.

Carracedo, H. C., Pérez Torrado, F. J., Ancochea, E., Meco, J., Hernán, F., Cubas, C. R., Casillas, R., Rodriguez, E., and Ahijado, A., 2002: Cenozoic volcanism II: the Canary Islands. In Gibbons, W., and Moreno, T. (eds.), The Geology of Spain. London: The Geological Society, 439–472.

Catford, J. A., Daehler, C. C., Murphy, H. T., Sheppard, A. W., Hardesty, B. D., Westcott, D. A., Rejmánek, M., Bellingham, P. J., Pergl, J., Horvitz, C. C., and Hulme, P. E., 2012: The intermediate disturbance hypothesis and plant invasions:

implications for species richness and management. Perspectives in Plant Ecology, Evolution, and Systematics, 14: 231–241.

Caujapé-Castells, J., Tye, A., Crawford, D. J., Santos-Guerra, A., Sakai, A., Beaver, K., Lobin, W., Florens, F. B. V., Moura, M., Jardim, R., Gómes, I., and Kueffer, C., 2010: Conservation of oceanic island floras: present and future global challenges. Perspectives in Plant Ecology, Evolution, and Systematics, 12: 107–130.

Chiarucci, A., Araujo, M. B., Decocq, G., Beierkuhnlein, C., and Fernandez-Palacios, J. M., 2010: The concept of potential natural vegetation: an epitaph? Journal of Vegetation Science, 21: 1172–1178.

Climent, J., Tapias, R., Pardos, J. A., and Gil, L., 2004: Fire adaptations in the Canary Islands pine (Pinus canariensis). Plant Ecology, 171: 185–196.

Courchamp, F., Chapouis, J. L., and Pascual, M., 2003: Mammal invaders on islands: impacts, control and control impact. Biological Reviews, 78: 347–383.

Crausbay, S., Genderjahn, S., Hotchkiss, S., Sachse, D., Kahmen, A., and Arndt, S. K., 2014: Vegetation dynamics at the upper reaches of a tropical montane forest are driven by disturbance over the past 7300 years. Arctic, Antarctic, and Alpine Research, 46: .

Del Arco Aguilar, M. J., González-González, R., Garzón-Marchado, V., and Pizarro-Hernández, B., 2010: Actual and potential natural vegetation on the Canary Islands and its conservation status. Biodiversity and Conservation, 19: 3089–3140.

Didiano, T. J., Turley, N. E., Everwand, G., Schaefer, H., Crawley, M. J., and Johnson, M. T. J., 2014: Experimental test of plant defence evolution in four species using long-term rabbit exclosure. Journal of Ecology, 102: 584–594.

Dob, T., Berramdane, T., Dahmane, T., and Chelghoum, C., 2005: Chemical composition of the needles oil of Pinus canariensis from Algeria. Chemistry of Natural Compounds 41: 165–167.

Economou, D., and Nahrstedt, A., 1991: Chemical, physiological, and toxicological aspects of the essential oil of some species of the genus Bystropogon. Planta Medica, 57: 347–351.

Fernández-Palacios, J. M., Otto, R., Thebaud, C., and Price, J., 2014: Overview of habitat history in subtropical oceanic island summit ecosystems. Arctic, Antarctic and Alpine Research, 46:.

Garzón-Machado, V., del Arco-Aguilar, M. J., and Pérez-de-Paz, P. L., 2011: A tool set for description and mapping vegetation on protected natural areas: an example from the Canary Islands. Biodiversity and Conservation, 20: 3605–3625.

Garzón-Machado, V., del Arco Aguilar, M. J., Valdés González, F., and Pérez-de-Paz, P. L., 2012: Fire as a threatening factor for endemic plants of the Canary Islands. Biodiversity and Conservation, 21: 2621–2632.

Garzón-Machado, V., González-Mancebo, J. M., Palomares-Martínez, A., Acevedo-Rodríguez, A., Fernández-Palacios, J. M., Del-Arco-Aguilar, M., and Pérez-de-Paz, P. L., 2010: Strong negative effect of alien herbivores on endemic legumes of the Canary pine forest. Biological Conservation, 143: 2685–2694.

Garzón-Machado, V., Otto, R., and del Arco Aguilar, M. J., 2013: Bioclimatic and vegetation mapping of a topographically complex oceanic island applying different interpolation techniques. International Journal of Biometeorology (early view). http://dx.doi.org/10.1007/s00484-013-0670-y.

Greenwood, S., and Jump, A. S., 2014: Consequences of treeline shifts for the diversity and function of high altitude ecosystems. Arctic, Antarctic and Alpine Research, 46: .

Heubes, J., Retzer, V., Schmitdlein, S., and Beierkuhnlein, C., 2011: Historical land use explains current distribution of calcareous grassland species. Folia Geobotanica 46: 1–16.

Hobbs, R. J., Arico, S., Aronson, J., Baron, J. S., Bridgewater, P., Cramer, V. A., Epstein, P. R., Ewel, J. J., Klink, C. A., Lugo, A. E., Norton, D., Ojima, D., Richardson, D. M., Sanderson, E. W., Valladares, F., Vilà, M., Zamora, R., and Zobel, M., 2006: Novel ecosystems: theoretical and management aspects of the new ecological world order. Global Ecology and Biogeography, 15: 1–7.

Höllermann, P., 2000: The impact of fire in Canarian ecosystems 1983–1998. Erdkunde, 54: 70–75

Irl, S. D. H., and Beierkuhnlein, C., 2011: Distribution of endemic plant species on an oceanic island—a geospatial analysis of La Palma (Canary Islands). Procedia Environmental Sciences, 7: 170–175.

Irl, S. D. H., Steinbauer, M. J., Babel, W., Beierkuhnlein, C., Blume-Werry, G., Messinger, J., Palomares Martínez, Á., Strohmeier, S., and Jentsch, A., 2012: An 11-yr exclosure experiment in a high-elevation island ecosystem: introduced herbivore impact on shrub species richness, seedling recruitment and population dynamics. Journal of Vegetation Science, 23: 1114–1125.

Irl, S. D. H., Steinbauer, M. J., Epperlein, L., Harter, D. E. V., Jentsch, A., Pätz, S., Wohlfahrt, C., and Beierkuhnlein, C., 2014: The hitchhiker's guide to island endemism—biodiversity and endemic perennial plant species in roadside and surrounding vegetation. Biodiversity and Conservation, 23: 2273–2287, http://dx.doi.org/10.1007/s10531-014-0722-6.

Johansson, M., Rooke, T., Fetene, M., and Granström, A., 2010: Browser selectivity alters post-fire competition between Erica arborea and E. trimera in the sub-alpine heathlands of Ethiopia. Plant Ecology, 207: 149–160.

Keeley, J. E., and Fotheringham, C. J., 2000: Role of fire in regeneration from seed. In Fenner, M., (ed.), Seeds: The Ecology of Regeneration in Plant Communities. 2nd edition. New York: CABI, 311–330.

Kier, G., Kreft, H., Lee, T. M., Jetz, W., Ibisch, P. L., Nowicki, C., Mutke, J., and Barthlott, W., 2009: A global assessment of endemism and species richness across island and mainland regions. Proceedings of the National Academy of Science, 106: 9322–9327.

Kreft, H., Jetz, W., Mutke, J., Kier, G., and Barthlott, W., 2008: Global diversity of island floras from a macroecological perspective. Ecology Letters, 11: 116–127.

Kyncl, T., Suda, J., Wild, J., Wildova, R., and Herben, T., 2006: Population dynamics and clonal growth of Spartocytisus supranubius (Fabaceae), a dominant shrub in the alpine zone of Tenerife, Canary Islands. Plant Ecology, 186: 97–108.

Lowe, S., Browne, M., Boudjelas, S., De Poorter, M., 2000: 100 of the world's worst invasive alien species—a selection from the Global Invasive Species Database. Aliens, 12: 1–12.

Merlin, M. D., and Juvik, J. O., 1992: Relationships among native and alien plants on Pacific islands with and without significant human disturbance and feral ungulates. In Alien Plant Invasions in Native Ecosystems of Hawai'i: Management and Research. Manoa: Cooperative National Park Resources Studies Unit, University of Hawai`i, 597–624.

Naeem, S., and Li, S., 1997: Biodiversity enhances ecosystem reliability. Nature, 390: 507–509.

Nogales, M., Rodriguez-Luengo, J. L., and Marrero, P., 2006: Ecological effects and distribution of invasive non-native mammals on the Canary Islands. Mammal Review, 36: 49–65.

Nogales, M., Rumeu, B., de Nascimento, L., and Fernández-Palacios, J. M., 2014: Newly discovered seed dispersal system of Juniperus cedrus questions the pristine nature of the high elevation scrub of El Teide (Tenerife, Canary Islands). Arctic, Antarctic, and Alpine Research, 46: this special issue.

Palomares Martínez, Á., 1993: El matorral de alta montaña en la isla de La Palma, seguimiento debido al peligro de extinción de la especie Genista benehovensis. Ponencias y comunicaciones. Congreso forestal español. Lourizán 2: 421–425.

Palomares Martínez, Á., Méndez Carvajal, C., López Soriano, I., and Delgado Luzardo, A., 2004: Plan de Conservación del Hábitat de las Cumbres del Norte de La Palma. Internal document of the National Park Caldera de Taburiente, El Paso, La Palma, Canary Islands.

Palomares Martínez, Á., López Graciano, C., Freixes Montes, F., Gómez Gómez, M., Moral del Barrio, M. F., León Pérez, A. M., Lorenzo Pérez, J. H., Balsera Pinar, G., Méndez Carvajal, C., Acevedo Rodríguez, A., Ibáñez de Aldecoa, F. B., Rodríguez Lerin, A., and Fernandez San Martín, J. M., 2011: Memoria anual del Parque Nacional de La Caldera de Taburiente de 2009. Ministerio de Medio Ambiente, y Medio Rural, y Marino, Madrid.

Pauchard, A,. Kueffer, C., Dietz, H. J., Daehler, C., Alexander, J., Edwards, P. J., Arévalo, J., Cavieres, L. A., Guisan, A., Haider, S., Jakobs, G., McDougall, K., Millar, C., Naylor, B., Parks, C., Rew, L., and Seipel, T., 2009: Ain't no mountain high enough: plant invasions reaching new elevations. Frontiers in Ecology and in the Environment, 7: 479–486.

Pellissier, L., Roger, A., Bilat, J., and Rasmann, S., 2014: High elevation Plantago lanceolata plants are less resistant to herbivory than their low elevation conspecifics: is it just temperature? Ecography 37: http://dx.doi.org/10.1111/ecog.00833.

Perry, G. L. W., Wilmshurst, J. M., McGlone, M. S., McWethy, D. B., and Whitlock, C., 2012: Explaining fire-driven landscape transformation during the Initial Burning Period of New Zealand's prehistory. Global Change Biology, 18: 1609–1621.

R Development Core Team, 2014: R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. www.R-project.org.

Rafferty, C., and Lamont, B. B., 2007: Selective herbivory by mammals on 19 species planted at two densities. Acta Oecologia, 32: 1–13.

Ramirez, A. R., Pratt, R. B., Jacobsen, A. L., and Davis, S. D., 2012: Exotic deer diminish post-fire resilience of native shrub communities on Santa Catalina Island, southern California. Plant Ecology, 213: 1037–1047.

Shea, K., and Cheeson, P., 2002: Community ecology theory as a framework for biological invasions. Trends in Ecology & Evolution, 17: 170–176.

Steinbauer, M. J., Irl, S. D. H., and Beierkuhnlein, C., 2013: Elevation-driven ecological isolation promotes diversification on Mediterranean islands. Acta Oecologica, 47: 52–56.

Steinbauer, M. J., Otto, R., Naranjo-Cigala, A., Beierkuhnlein, C., and Fernández-Palacios, J. M., 2012: Increase of island endemism with altitude—speciation processes on oceanic islands. Ecography, 34: 1–10.

Traveset, A., Nogales, M., Alcover, J. A., Delgado, J. D., López-Darias, M., Godoy, D., Igual, J. M., and Bover, P., 2009: A review on the effects of alien rodents in the Balearic (Western Mediterranean Sea) and Canary Islands (Eastern Atlantic Ocean). Biological Invasions, 11: 1653–1670.

White, P. S., and Jentsch, A., 2001: The search for generality in studies of disturbance and ecosystem dynamics. Progress in Botany, 63: 399–449.

Zöller, L., von Suchodoletz, H., and Küster, N., 2003: Geoarchaeological and chronometrical evidence of early human occupation on Lanzarote (Canary Islands). Quaternary Science Reviews, 22: 1299–1307.

Appendix A1. List of sown seed quantity for each of the eight target species.

Species	Sown seed quantity per species
Bencomia exstipulata	30.000
Chamaecytisus proliferus subsp. *proliferus*	2.000
Echium gentianoides	3.000
Echium wildpretii subsp. *trichosiphon*	3.000
Genista benehoavensis	3.000
Spartocytisus supranubius	3.000
Teline stenopetala subsp. sericea	2.000
Viola palmensis	3.000

7.5 Manuscript 5

The Hitchhiker's guide to island endemism - biodiversity and endemic perennial plant species in roadside and surrounding vegetation

Severin D. H. Irl, Manuel J. Steinbauer, Lilith Epperlein, David E. V. Harter, Anke Jentsch, Susanne Pätz, Christian Wohlfahrt, Carl Beierkuhnlein

7.5 Manuscript 5

ABSTRACT

Roadsides are habitats with very specific environmental conditions, often substantially differing from their natural surroundings. However, roads can have a positive effect on local vascular plant species richness. Endemic species on oceanic islands are considered to be less disturbance-adapted than native non-endemics and thus should be negatively affected by roads. Islands provide optimal conditions for testing this, as they possess a large share of clearly defined endemic species. This study focuses on a comparison of endemic plant species in roadside and surrounding communities and the interacting effects of elevation, vegetation type and trade wind-induced precipitation differences. We applied 96 circular plots with 50 m radius along two elevational gradients on the eastern (humid) and western (dry) slope of La Palma, Canary Islands, ranging from 100 m to 2400 m. Interestingly, we found roads to have a significant positive effect on endemic richness and the percentage of endemics as well as the same tendency for plant species richness after correcting for elevation and precipitation. Endemic species turnover was relatively high. The opening of cliffs during construction and, not to be overlooked, the protection from disturbances such as fire and omnipresent introduced herbivores (mainly rabbits or goats) probably leads to a positive effect of roads on endemics. In addition, many endemics might profit from species-specific dispersal capabilities well suited for roadside conditions. However, we do not argue for the use or even construction of roads for nature conservation but suggest protecting existing endemic populations because natural areas have a higher conservation value.

Keywords

Road ecology; disturbance; vascular plant species; endemic richness; elevational gradient; Canary Islands

INTRODUCTION

Roadsides offer a specific composition of plant species and specific moisture, temperature, nutrient and disturbance regimes, which substantially differ from the habitats in the landscapes in their vicinity (Spellerberg 1998; Trombulak & Frissell 2000). In steep mountainous areas, where roads are cut into slopes (Wemple & Jones 2003), this is presumably of particular relevance. Besides having effects on the environmental conditions in their direct surroundings, roads can influence these conditions in natural communities in varying distances from the road verge (Spellerberg 1998). This effect, however, was found to decrease significantly with increasing distance to the road (Watkins et al. 2003).

Oceanic islands of volcanic origin exhibit high rates of endemism due to their geographic isolation and adaptive radiation (Whittaker & Fernández-Palacios 2007). Therefore, compared to their total surface area, islands contribute in a disproportionally substantial manner to global biodiversity (Kreft et al. 2008). This is especially true for oceanic archipelagos such as the Canary Islands (Reyes-Betancort et al. 2008, Steinbauer & Beierkuhnlein 2010). Endemic species are not distributed randomly throughout an island (Steinbauer et al. 2012; 2013a). Often these species are linked to natural vegetation communities

belonging to the zonal vegetation or are confined to habitats that are characteristic for the island topography and microclimate (e.g. volcanic outcrops and cliffs; del Arco-Aguilar et al. 2010). In consequence, one would expect that anthropogenic habitats do not offer adequate conditions for endemic species (Rotholz & Mandelik 2013). However, as roads are correlated with artificial outcrops and low competition pressure, their ruderal habitats may satisfy the needs of endemic species.

It has been widely shown that roads can have a positive effect on plant species richness (e.g. Forman & Alexander 1998). The occurrence of non-native species has been found to be mainly responsible for this (Arévalo et al. 2005) as well as the opening of canopy in forested ecosystems, leading to the establishment of herbaceous species (Watkins et al. 2003). However, to our knowledge a single comparative assessment exists focusing on comparing the percentage of endemic plant species between roadside and surrounding communities (Rotholz & Mandelik 2013). The authors found a significantly lower percentage of endemics in roadside communities than in the adjacent continental Mediterranean shrub land communities owing to high disturbance intensities and frequencies associated with roads. The primary aim of the presented study is to fill this research gap and to assess the effect of roads on endemic species.

The aspect of island habitats (i.e. the location of the habitat in relation to the trade winds) has been shown to influence roadside plant species richness on Tenerife (Arteaga et al. 2009). However, endemic richness is not affected by precipitation differences (Arteaga et al. 2009). Also, there is a tendency towards floristically homogenized roadside communities (i.e. a reduced beta-diversity between communities) (Arévalo et al. 2010). This, however, has mainly to do with non-native and widespread native species in roadside communities along an elevational gradient. So far it has not been tested how endemic species composition responds to roads, especially with regard to the differing environmental conditions between roadside and surrounding communities.

La Palma (Canary Islands) offers steep elevational and environmental gradients spanning from subtropical coastal to treeless summit habitats and from humid evergreen laurel forest and Canary Pine forests to semi-arid succulent scrub (del Arco-Aguilar et al. 2010, Garzón-Machado et al. 2013). In general, the rate of endemic species increases with elevation (Steinbauer et al. 2012, 2013a). Owing to the steep relief, many archipelago as well as single-island endemic species on La Palma are adapted to rupicolous habitats (e.g. species of the genera *Aeonium*, *Aichryson*, *Crambe*, *Micromeria*, *Monanthes*, *Sonchus*, *Teline,* and *Tolpis*; Santos-Guerra 1983). The paved mountain road from near Santa Cruz de La Palma (at sea level on the Eastern side) to the highest point of the island (Roque de los Muchachos; 2426 m a.s.l.) and down again to the coast below Santo Domingo de Garafía on the North-western side offers an excellent opportunity to study roadside habitats and endemic species (Fig. 1 and Fig. 2), by following the main precipitation gradient on the island.

Here, we compare roadside and surrounding communities along two elevational transects on the Western and Eastern side of the island spanning more than 2000 meters in elevation. First, we estimate the effect of roads on plant species richness, endemic richness, percentage of endemics and endemic species composition by comparing roadside communities to their surrounding counterparts. Secondly,

we test the effect of elevation, island side (as a proxy for precipitation differences) and vegetation type (i.e. forest vs. non-forest) on the mentioned indices and how these environmental factors interact with habitat type (i.e. roadside or surrounding community). In general, we expect roads to have a positive effect on plant species richness. However, according to the existing knowledge, roads should negatively impact endemic species richness and the relative contribution of endemics to the communities, respectively.
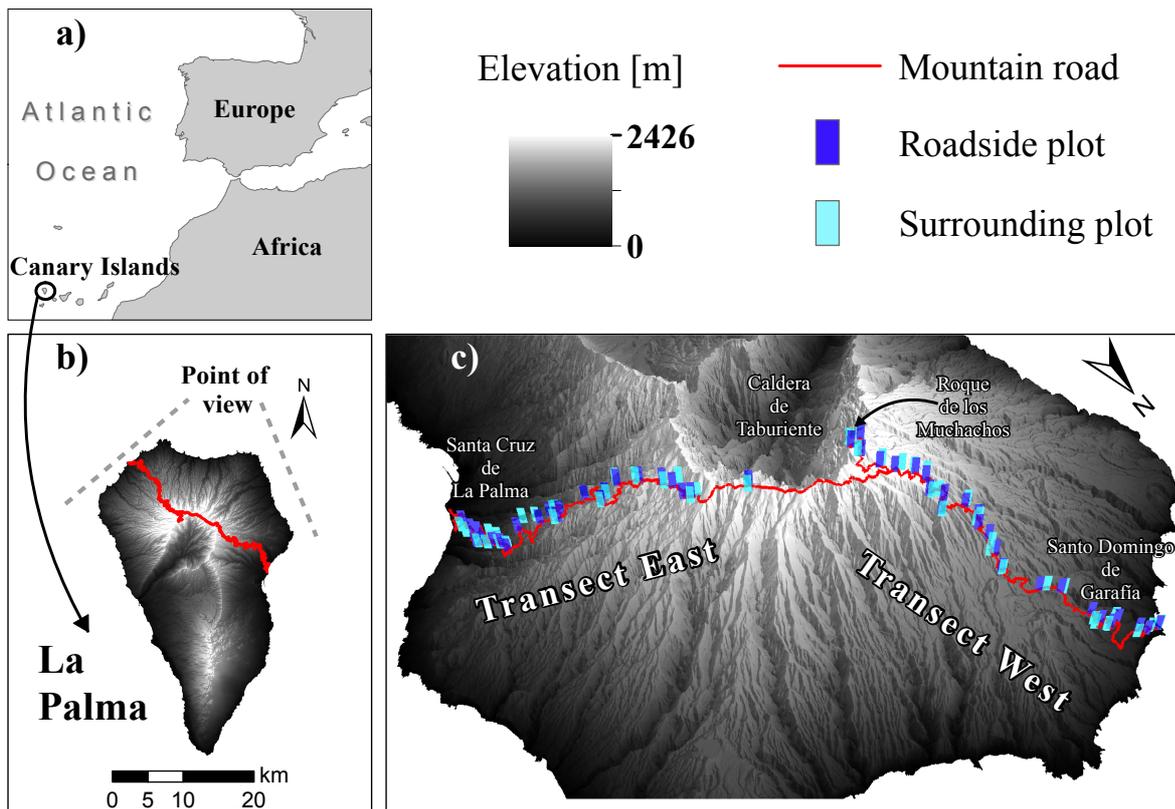

Figure 1. Map of the Canary Islands, La Palma and the study area. Tile a) shows the position of the Canary Islands and La Palma in the Eastern Atlantic Ocean. A digital elevation map of La Palma including the mountain road sampled in this study is displayed in tile b). A 3D view of the Northern part of the island is used to present the roadside and surrounding plots on the eastern and western transect in tile c). Note that the perspective has changed to roughly the Northeast. Vertical exaggeration in 3D view: x2. Figure created in ArcMap 10 and ArcScene 10 (both ESRI Inc., 2010).

MATERIAL AND METHODS

Study Area and Species

La Palma is the northwestern most island of the Canary archipelago, which is located off the Moroccan coast in the Atlantic Ocean (Fig. 1a). The Caldera de Taburiente complex comprising the Northern part of the island is geologically the oldest (i.e. maximum age approx. 1.7 million years), highest and steepest part of the island (Carracedo et al. 2002). Cool oceanic currents produce a relatively

stable and mild climate all year round. Due to its high elevation, the continuous trade winds regularly produce a cloudbank at mid elevations, dividing the island into a humid Eastern and a more arid Western side. Above the cloudbank a thermal inversion exists producing an arid subalpine summit environment subject to strong diurnal temperature amplitudes, high solar radiation and extensive summer drought (Garzón-Machado et al. 2013). The climatic differentiation is directly reflected in a clear vegetation zonation ranging from a semi-arid coastal scrub through thermophilic open woodland in low elevations (del Arco-Aguilar et al. 2010). A humid evergreen laurel forest and a sub-humid *Morella faya*-tree heath forest can be found at mid elevations on the Eastern side, which is exposed to the incoming trade winds (Santos-Guerra, 1983). This is followed by the widely distributed drought-prone and fire adapted endemic Canary Pine forest (*Pinus canariensis*), which is found above the laurel forest on the Eastern and at mid to high elevations on the Western side. A subalpine or summit scrub is found above the treeline (approx. 2000 m a.s.l.; for a detailed map of the distribution of vegetation zones see del Arco et al. 2006). Owing to the steep terrain of La Palma rupicolous communities form different azonal vegetation units at all elevations (del Arco-Aguilar et al. 2010).

According to Acebes Ginovés et al. (2010), La Palma possesses 210 vascular plant species endemic to the Canary Islands. The present study focuses on perennials, as annuals are easily underestimated because (a) they are visible only for short time periods during the year, (b) their appearance depends on specific short-term climatic events leading to high stochasticity and (c) their importance in the flora and overall in the vegetation of the Canary Islands is limited (i.e. most ecosystems are characterized by perennials). About 58% of the native plant species of La Palma and 92% of the endemic plant species of the Canary Islands are perennials (Shmida & Werger 1992). A focus on perennials excludes the potential bias introduced by annuals, as a temporal absence during the sampling period does not necessarily mean that the species is actually absent. Also, perennials integrate over longer time periods better reflecting the actual site conditions.

Sampling design

A two-lane paved road reaching the highest point of the island (Roque de los Muchachos, 2426 m asl) from the East and the Northwest was used for sampling (Fig. 1). The mountain road possessed some variation in road width but was two-lane and therefore consistent throughout the complete study area. The elevational gradient that was sampled in this study spanned from 100 m to 2400 m asl on the Western side and from 100 m to 2200 m asl on the Eastern side of the island. The center of each plot was marked by GPS. Circular plots with a 50 m radius were used at elevational intervals of approximately 100 m. If sampling took place in steep areas (which was mainly the case), plots were limited to about 20 m upslope and downslope from the center point due to the strong increase of available area in steep or even vertical slopes. This sampling approach integrates over all roadside habitats (i.e. road verge, roadside ditch, roadside cliff and other habitats influenced by the road). The center point of the plot was set in the middle of the road (hereafter called *roadside community*) and the presence or absence of all perennial endemic vascular plants was determined. The number of all additional species was counted. Non-native species were not considered. For this study, species were divided into non-endemic and

Canary endemic species (hereafter called *endemics*) following the classification given by Acebes Ginovés et al. (2010).

The same sampling procedure was conducted in sites with a minimum distance of 100 m from the road in the surrounding natural and semi-natural sites (hereafter called *surrounding communities*) at similar elevational levels, aspect and slope. This distance was chosen because the road-effect on the vegetation disappears at distances >50m from the road (Arévalo et al. 2010). The surrounding plots possessed a variety of different habitats, including cliffs and rupicolous habitats as well as other non-cliff habitats, ensuring comparability between roadside and surrounding plots. In order to account for the curvy nature of the mountain road, care was taken that the surrounding communities were not situated in between switchbacks.

Each plot (roadside and surrounding) was classified as forest or non-forest based on a classification map showing the current distribution of vegetation units on La Palma, which was supplied by the island authorities (see Irl & Beierkuhnlein 2011). A 'forest site' was defined as being located in either the Canary Pine forest, the laurel forest or the *Morella faya*-tree heath forest, while all other sites were considered 'non-forest sites'.

Besides recording richness, the percentage of endemic species was calculated (i.e. endemic species richness divided by plant species richness) as this index enables the quantification of endemicity independent of differences in richness (Emerson & Kolm, 2005). Elevation was extracted from a 100 m x 100 m digital elevation model (DEM). Island side was used as a proxy for precipitation, i.e. due to the trade wind influence the Eastern side is generally more humid, the Western drier. Sampling took place in spring 2011 and 2012.

Statistical Analysis

To test the effect of roads on plant species richness, endemic richness and the percentage of endemic species (dependent variables) a conservative statistical approach was chosen. First, the dependent variable was related to other environmental variables (elevation, island side). This model was compared to a model having road as an additional variable. Only if road significantly increased model performance (ANOVA, analysis of variance) was its effect accepted. Thus, a significant effect of road means that it can explain a considerable share of variance after having been corrected for other environmental variables. A similar approach was applied for elevation and island side. Here the effects of the respective other variables were removed before testing significance of the focal variable.

Models were implemented as mixed effect models (package *lme4 version 0.999375-42*, Bates et al. 2011; R Development Core Team 2012) with island side and/or road as a random effect as well as elevation as additional explanatory variable if they were not the variable under focus. Optimal transformation (log, exp, x^2, sqrt, $x + x^2$) of variables was assessed in a pre-analysis with simple linear regression using the transformation, which resulted in the highest R^2 value as basis for the mixed effect models.

The percentage of endemic species was modeled using a binomial family error that accounts for the fact that the reliability of a specific percentage value is influenced by plant species richness and endemic richness (Steinbauer et al. 2012). Models only partly reached final convergence for the percentage values, but results were very similar to generalized linear models with binomial family error but without random effects.

Finally, we analyzed the similarity in endemic species composition between the road and corresponding surrounding plot. Based on presence/absence data, we calculated the Sørensen similarity index for endemic species (see Juransinski et al. 2009 and R package *simba* by Jurasinski & Retzer, 2012). In a second step we tested whether forested plots are less similar in species composition to their related road plot than open non-forested ecosystems.

Figure 2. Typical roadside cliff community of the coastal scrub dominated by endemic plant species. Among others *Aeonium canariense* subsp. *christii* (large light rosettes), of which one individual is flowering in yellow (top left), *Euphorbia canariensis* (cactus-like succulent), *Sonchus hierrensis* (shrubby yellow-flowering Asteraceae; top center) and *Polycarpaea smithii* (dark cliff dweller) are visible. Photo: Manuel J. Steinbauer
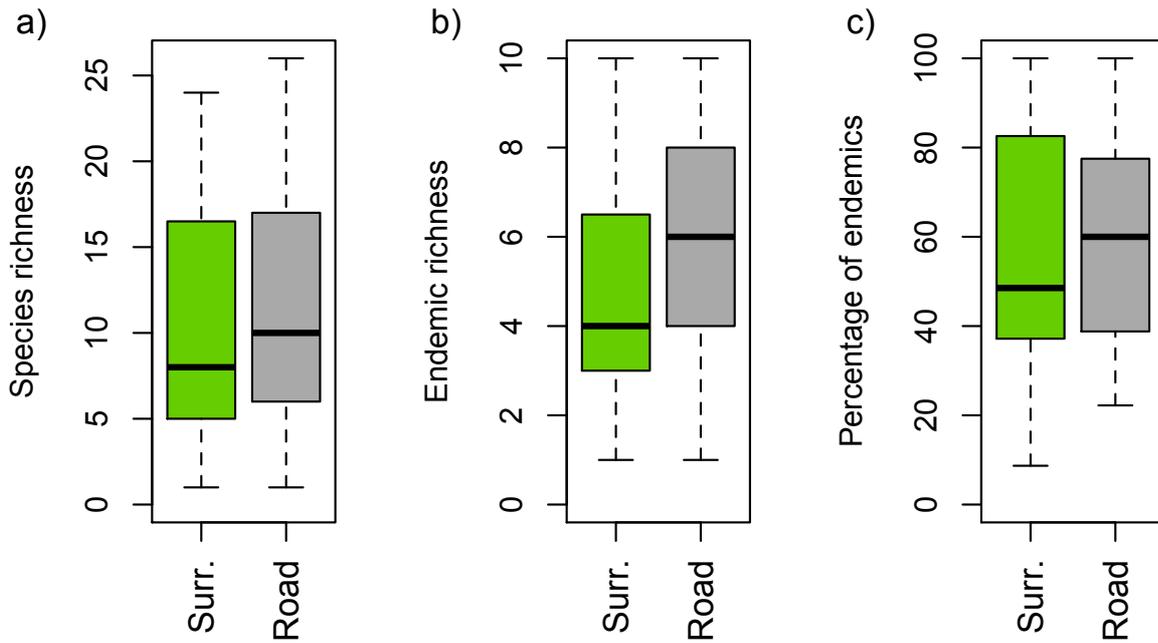
Figure 3. Difference between roadside and surrounding sites for a) species richness, b) endemic richness and c) the percentage of endemic species. The whiskers extend to the data extremes and show non-corrected values along both elevational gradients. Note that the boxplots show an uncorrected comparison between natural and roadside communities. Significant differences were assessed using mixed effect models accounting for the effects of environmental co-variables (see Results section and Tab. 1).

RESULTS

We recorded 57 endemic plant species in 96 plots. 62 plots were located in a forested roadside matrix, 34 in non-forested areas. The 10 most common endemics in all plots were in the following order: *Pinus canariensis* (71 records), *Adenocarpus viscosus* subsp. *spartioides* (47), *Pericallis papyracea* (40) *Sonchus hierrensis* (28), *Chamaecytisus proliferus* subsp. *proliferus* (23), *Kleinia neriifolia* (21), *Descurainia gilva* (16), *Aeonium davidbramwellii* (16), *Sonchus palmensis* (15) and *Rumex lunaria* (15). The complete endemic species list is documented in Tab. S1 (Supplementary Material).

After correcting for elevation and island side, roadside communities had a significantly higher endemic richness ($p < 0.01$; uncorrected mean for roads: 5.9 ± 2.4, uncorrected mean for surrounding communities: 4.5 ± 2.5) and percentage of endemics ($p < 0.05$; uncorrected mean for roads: 60.6 ± 24.6, uncorrected mean for surrounding communities: 57.0 ± 30.0) than surrounding communities. Significance was almost reached for plant species richness ($p = 0.07$) with roadside communities possessing slightly more species (uncorrected mean 11.6 ± 6.7) than surrounding ones (uncorrected mean 10.3 ± 6.8; Fig. 3, Tab. 1).

Endemic richness was negatively related to elevation ($p < 0.05$). Species richness showed a hump shaped pattern ($p < 0.001$) with a maximum at low elevations. Elevation had a positive effect on the

percentage of endemic species (p < 0.001; Fig. 4) because the total species richness declined stronger than the diversity of endemics.

Precipitation-dependent patterns became also apparent (Fig. 4). Significantly higher plant species richness (p < 0.001) and near significant endemic richness (p = 0.09) but lower percentage of endemic species (p < 0.001) were found on the Eastern (humid) compared to the Western (dry) side of the island.

A moderate mean difference in endemic species composition was found between roadside communities and their surrounding counterpart (Sørensen similarity index mean = 0.59 ± 0.19). No significant change in similarity of endemic species composition between roads and corresponding surrounding plots was detected between forest and non-forest ecosystems, and also not with precipitation or with elevation (Fig. 5).
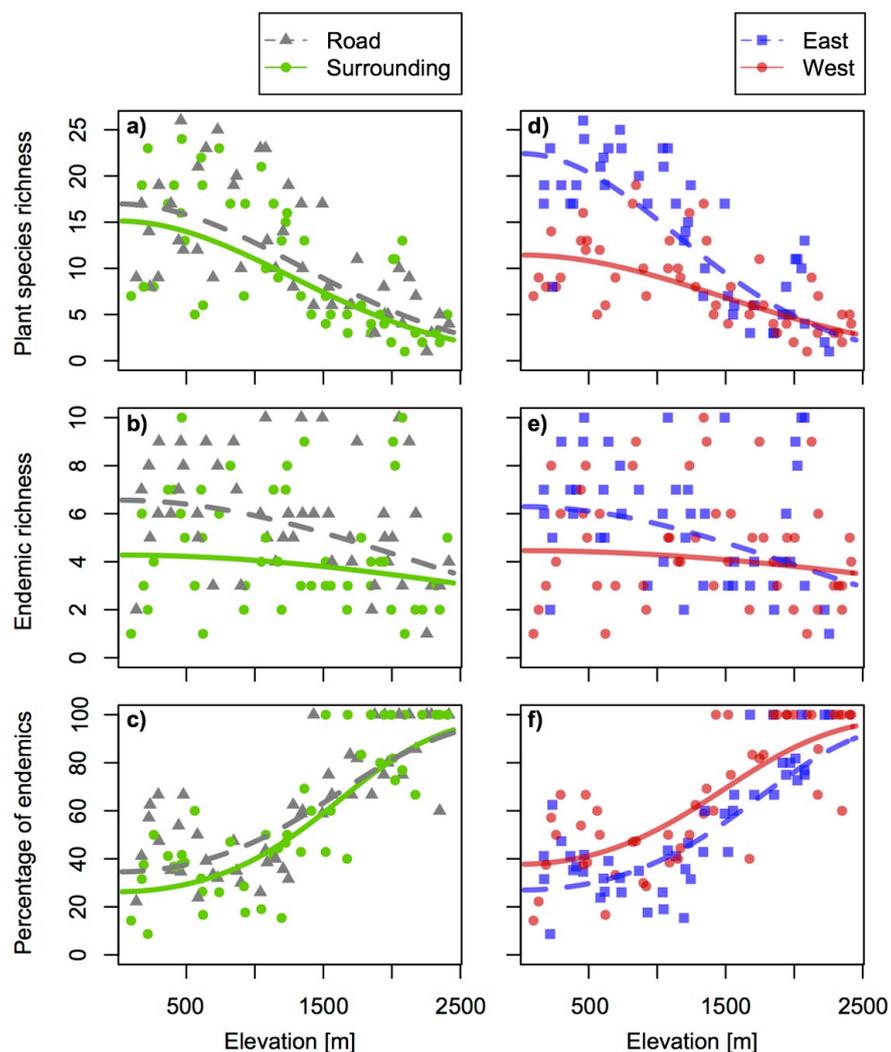
Figure 4. Changes of plant species richness, endemic richness and percentage of endemics with elevation. The coloration in graphs a) – c) indicates the difference between roadside and surrounding sites, in graphs d) – f) the difference between the eastern (humid) and western (dry) transect using the same points. The regression lines are based on simple linear regression. Mixed effect models were used to check the effect including all co-variables in the main analyses.

Figure 5. Similarity in endemic species composition (Sørensen index) between roadside and corresponding surrounding plots does not change between forested (black circles) an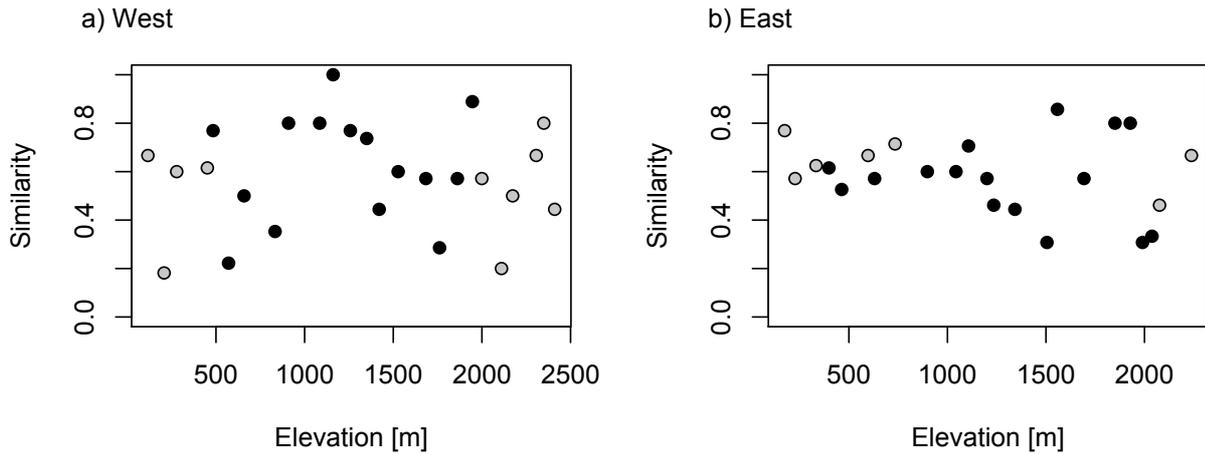d non-forested ecosystems (grey circles) or with elevation on either island side. A value of 0 indicates that the two sites do no share any species, while 1 means that the two sites have the same species composition.

Table 1: Elevation is the best predictor of plant species richness as well as the percentage and number of endemics. Significance of independent variables was assessed by means of mixed effect models. We tested if the focal variable could significantly improve model performance of a null model that already included the other variables (listed under null model). Transformations of the dependent and independent variables were used to achieve best model results. Asterisks indicate significance ($p < 0.05$*; $p < 0.01$**; $p < 0.001$***).

Dependent variable	Independent variable	Null-Modell	
		Fixed effect	Random effect
Log(Endemic richness)	Road **	Elevation^2	Island side
Log(Endemic richness)	Elevation^2*	-	Road + Island side
Log(Endemic richness)	Island side (p = 0 .09)	Elevation^2	Island side
Log(Plant species richness)	Road (p = 0.07)	Elevation + Elevation^2	Island side
Log(Plant species richness)	Elevation + Elevation^2 ***	-	Road + Island side
Log(Plant species richness)	Island side***	Elevation + Elevation^2	Road
Percentage of endemics	Road *	Elevation	Island side
Percentage of endemics	Elevation***	-	Road + Island side
Percentage of endemics	Island side***	Elevation	Road

DISCUSSION

Positive effect of roads on endemic species

Roadside habitats have a positive effect on the occurrence of endemic plant species on La Palma, exhibiting higher endemic richness and percentage of endemics as well as a tendency to higher plant species richness than corresponding surrounding communities. This is surprising as (neo-)endemic species have evolved under the characteristic local conditions of a given island and should be optimally adapted to natural sites. Contrastingly, Rotholz & Mandelik (2013) found a negative effect of roads on the percentage of endemics in a continental Mediterranean shrub land ecosystem, when compared to surrounding communities. The reason for this is probably the high species richness in roadside communities (Forman & Alexander 1998, Rotholz & Mandelik 2013), which has been shown to be mainly associated with non-native species (Arévalo et al. 2005). In consequence, it is not clear if endemic richness differs between surrounding and roadside communities.

In our study we find a surprisingly high number and proportion of endemic plant species along roads. On steep slopes, which are typical for an oceanic island, roads are carved into the mountainside during construction, producing roadside cliffs (Wemple & Jones, 2003). Novel habitats that are created are low in competition and are close to the ecological conditions of young volcanic parent material, which is commonly found on these islands. Such places offer safe sites for germination and establishment of adapted species.

In comparison with other related studies, the high roadside endemic richness and percentage of endemics on La Palma can be also attributed to the fact that we explicitly included outcrops and cliffs that were created by the road construction. Other studies mainly focused on road verges and ditches close to the road (Arévalo et al. 2005, Rotholz & Mandelik 2013). Indeed, Arteaga et al. (2009) found endemic richness to be positively correlated with rock cover and slope steepness, thus supporting the assumption that endemics are mostly confined to relatively undisturbed roadside cliff communities.

Steep slopes, ongoing erosional processes and the resulting abundance of natural cliffs differentiate young volcanic islands from continental systems of comparable climate. In consequence, secondary habitats such as young rocky outcrops along roadsides likely serve as an adequate habitat for endemic plant species on La Palma. Many endemics found in roadside communities are correlated with primary successional stages, are typical cliff dwellers (e.g. *Aeonium davidbramwellii, A. diplocyclum, A. spathulatum, Chamaecytisus proliferus* subsp. *proliferus, Genista benehoavensis, Rumex lunaria, Sonchus hierrensis* or *S. palmensis*) and/or are heliophilous rupicolous legumes (e.g. *Adenocarpus viscosus* subsp. *spartioides, C. proliferus* subsp. *proliferus, G. benehoavensis* or *Teline stenopetala*; Santos-Guerra 1983, del Arco-Aguilar 2010).

Our results suggest roadside cliff communities to be the driver behind the observed patterns. The sampling approach chosen in this study integrates over all habitat types found within each plot and does not strictly focus on roadside cliff communities. However, only few endemic species seem to profit from the accumulated moisture in roadside ditches (e.g. *Pericallis papyracea*) or possess the ability to grow in

ruderal conditions (e.g. *Lotus campylocladus* subsp. *hillebrandii*), emphasizing the importance of roadside cliff communities for endemics.

Despite being part of a man-made infrastructure, these steep roadside cliffs can be considered as 'safe sites' for endemic species because they are virtually free of direct human influence and disturbances after their construction. They protect and potentially favor endemic rupicolous and heliophilous species from the threatening disturbance caused by introduced herbivores (especially rabbits, *Oryctolagus cuniculus*, and goats, *Capra hircus*; Nogales et al. 2006). Endemic species on the Canary Islands have evolved in the absence of large herbivores and are therefore often particularly vulnerable to introduced herbivores (Nogales et al. 2006). It has been shown that herbivores pose an omnipresent threat to natural ecosystems on La Palma (Garzón-Machado et al. 2010) and may even cause shifts in the vegetation structure bringing some single island endemic species to the brink of extinction (Irl et al. 2012).

Roadside cliffs might protect endemics from fire, which is a frequent disturbance in some vegetation zones on the Canary Islands, especially the Canary Pine forest and the summit scrub (del Arco-Aguilar et al. 2010). Roadside cliffs create a direct and indirect protection for endemics from fire owing to the fact that (high) cliffs are often out of the reach of fires and indirect protection because roads are preferentially used by the fire department as firebreaks and as access corridors to wildfires. Indeed, many endemics are not adapted to fire but solely rely on their seed bank for regeneration (Garzón-Machado et al. 2012). Thus, roadside cliffs protecting endemics from fire might be an important issue for conservation as fire frequencies have increased in the last decades, especially due to human-induced actions (Garzón-Machado et al. 2012).

Roads have been shown to function as dispersal corridors for plant species (Forman & Alexander, 1998). Among others, the dispersal ability of a species depends on its diaspore traits (Andersen 1993). Many of the studied endemics of La Palma produce very small seeds (e.g. the genera *Aeonium, Aichryson* and *Monanthes*; Liu 1989) or pappi (e.g. most species of the genera of the Asteraceae family such as *Carlina*, *Pericallis*, *Sonchus* or *Tolpis*; Bramwell & Bramwell 1974) that are readily dispersed by wind. Thus, endemic species possessing such dispersal capabilities likely profit from road-associated dispersal vectors such as vehicle-induced wind drags (e.g. Forman & Alexander, 1998, Zwaenepoel et al. 2006).

Endemic species similarity in roadside vs. surrounding communities

Endemic species similarity between roadside and surrounding communities was consistent along the elevational and precipitation gradient. This indicates that roadside communities offer specific environmental conditions for endemics that surrounding communities do not, and vice versa. Roads have been shown to induce floristic homogenization on the Canary Islands but this was mainly driven by non-native and widely spread natives, and not by endemics (Arévalo et al. 2010). In addition, endemic species turnover between roadside and surrounding communities does not differ between open and forested ecosystems. It also does not change with elevation or island side. This indicates that roads have

a consistent and substantial effect on species composition irrespective of the elevational and precipitation gradient by altering fundamental environmental conditions such as moisture, nutrients and light availability as well as other soil properties (Spellerberg 2002, Trombulak & Frissell 2000). It is likely that endemic pioneer species adapted to the opening of virgin rock surfaces or disturbance tolerant endemics predominate in roadside communities. However, endemics adapted to later successional stages might be increasingly found in the surrounding communities, thus explaining the consistent dissimilarity between roadside and surrounding communities.

Influence of elevation on plant species richness and endemic richness

As expected, plant species richness decreases with elevation as climatic conditions become cooler and area decreases (Körner 2003, Mallen-Cooper & Pickering 2008). Yet, endemic species richness did not show such a pattern as it only declines on the Western dryer transect but not on the Eastern humid transect. In fact, Arévalo et al. (2005) found no significant decline of endemic species richness with elevation in roadside communities on Tenerife, whereas Gran Canaria showed a hump shaped relationship. Other factors than elevation (e.g. fire regime, land use, slope, aspect, changing soil conditions, etc.) might be shaping endemic species distribution (Mallen-Cooper & Pickering 2008). However, they were not explicitly targeted in this study.

Island side and precipitation

Precipitation (i.e. island side in relation to the trade winds) had a positive effect on plant species richness as well as a similar tendency for endemic richness, whereas a negative effect on the percentage of endemics is observed on La Palma. In a local study spanning from the coast to about 650 m Arteaga et al. (2009) found opposing results for total species richness and native species richness in roadside communities on Tenerife. Indeed, if one considers the study by Arévalo et al. (2005) with transects on Tenerife and Gran Canaria to show a precipitation gradient (i.e. the transect on Tenerife is on the Southern dry side, whereas the one on Gran Canaria is located on the Eastern humid side) than comparable results to ours are found (i.e. higher total species richness on Gran Canaria and no significant difference for endemic richness).

In general, humid areas on the Canary Islands are associated with higher plant species richness as well as endemic richness, respectively (von Gaisberg & Stierstorfer 2005, Reyes-Betancort et al. 2008). However, the more pronounced increase of plant species richness than endemic richness in humid areas results in a lower proportion of endemics.

Vegetation-type effect

Vegetation type (i.e. forest or non-forest communities) did not affect plant species richness, endemic richness or percentage of endemics in roadside vs. surrounding communities. This is surprising

as studies by Delgado et al. (2007) and Arévalo et al. (2008) identified edge effects in laurel and pine forest ecosystems on Tenerife, where environmental conditions and species composition changed significantly from inside the forest to the road verge. However, decreasing non-native species richness with increasing distance from the road can be responsible for this. Other studies have shown a negative effect on weedy plants on a photosyntheticaly active radiation gradient ranging from the road verge to the interior of a deciduous Central European forest (Honnay et al. 2002) or strong floristic changes in species composition from road verges to closed forests in managed French oak stands (Avon et al. 2010).

Haider et al. (2010) found a minimum for non-native Mediterranean species on Tenerife at mid-elevations in the cloud layer zone. This indicates that these drought tolerant and light demanding species are negatively affected by the relatively low solar radiation input and probably also by the shading effect of the laurophyllous forest predominant in this elevational zone. However, the relatively large plot area (7800 m^2) used in our study can obscure possible small-scale differences between road verge, roadside ditch, roadside cliff and surrounding communities (which are often heterogeneous in themselves owing to the steep relief).

Implications for management and nature conservation

It is important for road construction to adopt specific criteria to reduce its impact on the surrounding natural and semi-natural ecosystems. Plant species are often adapted to natural surface material (Steinbauer et al. 2013b) or heterogeneity (Leutner et al. 2012). Concrete stabilization of roadside cliffs might be an effective way to impede the spread and further homogenization of endemics, however this should only be used where absolutely necessary and with utmost caution. In cases where roads are widened or additional construction is necessary specific measures should be taken to protect the existing populations of endemic species on roadside cliffs. In general, road construction is often associated with the destruction of natural habitat and increased anthropogenic disturbances, which – among other things – often ameliorate the spread of non-native species (Spellerberg 2002). Therefore, the construction of new roads should be only undertaken where absolutely necessary.

During fieldwork we observed that in large areas of the Canary Pine forest and the summit scrub, roads are regularly used as fire breaks by local firefighters. This is associated with a clearing of understory shrub vegetation that extends roughly 50 m from the road into the surrounding area with obvious effects on the vegetation in relative proximity to the road. Presumably, mainly large shrub individuals or small trees (e.g. *A. viscosus* subsp. *spartioides*, *Cistus symphytifolius*, *Erica arborea*, *Morella faya* and young individuals of *Pinus canariensis*) are extracted, whereas juvenile individuals of these species are not touched. Thus, abundance patterns might change but the patterns of biodiversity and endemicity identified in this study are not influenced by these management actions, also because rupicolous habitats in the roadside but also surrounding plots are not strongly influenced. In addition, it does not seem like time since last road maintenance had a substantially affect on our indices as species richness and the percentage of endemics behave in accordance to other studies with elevation (e.g. Steinbauer et al.

2012, 2013). If time since last road maintenance had an effect this would become apparent in the results, e.g. by observing unexplainable thresholds or breaks in our data.

Roads are continuous structures. Therefore, hybridization and homogenization of endemic species is a major conservation issue on oceanic islands as roads increase the connectivity between previously isolated populations or closely related taxa. Increased connectivity potentially threatens the genetic integrity of many endemics on the Canary Islands (Francisco-Ortega et al. 2000). Already hybridizations have been observed in the genus *Pericallis* on Tenerife, which have been linked to road construction and the resulting increased connectivity (van Hengstum et al. 2012). Roads also have the tendency to homogenize the flora in otherwise heterogeneous communities, reducing the diversity between different habitats and/or ecosystems (Arévalo et al. 2010). Thus, it is necessary for conservation practitioners to create 'safe sites' for endemics, which remain poorly connected to other parts of the island or are altogether inaccessible to humans.

CONCLUSION

We do not suggest seeing roadside habitats as a strategy for conservation practices on La Palma. Obviously, the importance of such habitats for endemic species is context-dependent. Positive effects of roadsides have been shown for endangered taxa (Eversham et al. 1994, Quintana-Ascencio et al. 2007). However, the documented establishment of endemic species populations cannot replace the loss of populations and natural habitats. Top priority in endemic species conservation is the preservation of existing rocky and other natural habitats.

Comparable processes can be expected on other steep young volcanic islands. However, on islands with less dramatic geomorphological features or on the continent, contrasting findings have been reported (Rotholz & Mandelik 2013). If endemic species are not adapted to rupicolous conditions associated with roadsides, negative effects of additional infrastructure on endemic species are likely. Rather the disruptions of natural habitat caused by construction and the fact that roads often function as vectors for the introduction of non-native species could result in the (local) suppression or even loss of biodiversity. Thus, calling the Vogon Constructor Fleet may be a double-edged sword.

REFERENCES

Acebes Ginovés JR, León Arencibia MC, Rodríguez Navarro ML, del Arco Aguilar M, García Gallo A, Pérez de Paz PL, Rodríguez Delgado O, Martín Osorio V E, Wildpret de la Torre W (2010) Spermatophyta. In: Lista de especies silvestres de Canarias. Hongos, plantas y animales terrestres. 2009. Arechavaleta M, Rodríguez S, Zurita N, García A (eds.). Gobierno de Canarias, Tenerife, 122-172.

Andersen MC (1993) Diaspore morphology and seed dispersal in several wind-dispersed Asteraceae. Am J Bot 80:487-492.

del Arco Aguilar MJ, González-González R, Garzón-Marchado V, Pizarro-Hernández B (2010) Actual and potential natural vegetation on the Canary Islands and its conservation status. Biodivers Conserv 19: 3089-3140. doi: 10.1007/s10531-010-9881-2

del Arco Aguilar MJ, Wildpret W, Pérez PL, Rodríguez O, Acebes JR, García A, Martín VE, Reyes JA, Salas M, Díaz MA, Bermejo JA, González R, Cabrera MV, García S (2006) Mapa de Vegetación de Canarias. GRAFCAN, Santa Cruz de Tenerife

Arévalo JR, Delgado J, Fernández-Palacios JM (2008) Changes in plant species composition and litter production in response to roads and trails in the laurel forest of Tenerife (Canary Islands). Plant Biosyst 142: 614-622. doi: 10.1080/11263500802410991

Arévalo JR, Delgado J, Otto R, Naranjo A, Salas M, Fernández-Palacios J (2005). Distribution of alien vs. native plant species in roadside communities along an altitudinal gradient in Tenerife and Gran Canaria (Canary Islands). Perspect Plant Ecol 7: 185 -202. doi: 10.1016/j.ppees.2005.09.003

Arévalo JR, Otto R, Escudero C, Fernández-Lugo S, Arteaga M, Delgado JD, Fernández-Palacios JM (2010) Do anthropogenic corridors homogenize plant communities at a local scale? A case studied in Tenerife (Canary Islands). Plant Ecol 209: 23-35. doi: 10.1007/s11258-009-9716-y

Arteaga MA, Delgado JD, Otto R, Fernández-Palacios JM, Arévalo JR (2009) How do alien plants distribute along roads on oceanic islands? A case study in Tenerife, Canary Islands. Biol Invasions 11: 1071-1086. doi: 10.1007/s10530-008-9329-8

Avon C, Bergès L, Dumas Y, Dupouey JL (2010) Does the effect of forest roads extend a few meters or more into the adjacent forest? A study on understory plant diversity in managed oak stands. Forest Ecol Manag 259: 1546-1555. doi:10.1016/j.foreco.2010.01.031

Bates D, Maechler M, Bolker B (2011) lme4: Linear mixed-effects models using S4 classes: R package version 0.999375-42. http://CRAN.R-project.org/package=lme4

Bramwell D, Bramwell ZI (1974) Wild Flowers of the Canary Islands. Excmo. Cabildo Insular de Tenerife. Stanley Thornes Ltd., London

Carracedo HC, Pérez Torrado FJ, Ancochea E, Meco J, Hernán F, Cubas CR, Casillas R, Rodriguez E, Ahijado A (2002) Cenozoic volcanism II: the Canary Islands. The Geology of Spain (ed. by Gibbons, W. and Moreno, T.), pp. 439–472. Geological Society, London.

Delgado JD, Arroyo NL, Arévalo JR, Fernández-Palacios JM (2007) Edge effects of roads on temperature, light, canopy cover, and canopy height in laurel and pine forests (Tenerife, Canary Islands). Landscape Urban Plan 81: 328-340. doi:10.1016/j.landurbplan.2007.01.005

Emerson BC, Kolm N (2005) Species diversity can drive speciation. Nature 434: 1015–1017.

Eversham BC, Telfer MC (1994) Conservation value of roadside verges for stenotopic heathland Carabidae: corridors or refugia? Biodivers Conserv 3:538–545. doi: 10.1007/BF00115159

Fernández-Palacios JM, de Nicolás JP (1995) Altitudinal pattern of vegetation variation on Tenerife. J Veg Sci 6: 183-190. doi: 10.2307/3236213

Forman RTT, Alexander LE (1998) Roads and their major ecological effects. Annu Rev Ecol Syst 29: 207-231.

Francisco-Ortega J, Santos-Guerra A, Kim SC, Crawford DJ (2000) Plant genetic diversity in the Canary Islands: a conservation perspective. Am J Bot 87: 909-917.

von Gaisberg M, Stierstorfer C (2005) The significance of geological traits for the speciation of endemic angiosperms on El Hierro (Canary Islands). Phytocoenologia 35: 39-52.

Garzón-Machado V, del Arco Aguilar MJ, Valdés González F, Pérez-de-Paz PL (2012) Fire as a threatening factor for endemic plants of the Canary Islands. Biodivers Conserv 21: 2621–2632. doi: 10.1007/s10531-012-0321-3

Garzón-Machado V, González-Mancebo JM, Palomares-Martínez A, Acevedo-Rodríguez A, Fernández-Palacios JM, Del Arco-Aguilar M, Pérez-de-Paz PL (2010) Strong negative effect of alien herbivores on endemic legumes of the Canary pine forest. Biol Conserv 143: 2685-2694. doi:10.1016/j.biocon.2010.07.012

Garzón-Machado V, Otto R, del Arco Aguilar MJ (2013) Bioclimatic and vegetation mapping of a topographically complex oceanic island applying different interpolation techniques. Int J Biometeorol (early view). doi: 10.1007/s00484-013-0670-y

Haider S, Alexander J, Dietz HJ, Trepl L, Edwards PJ, Kueffer C (2010) The role of bioclimatic origin, residence time and habitat context in shaping non-native plant distributions along an altitudinal gradient. Biol Invasions 12: 4003-4018. doi: 0.1007/s10530-010-9815-7

van Hengstum T, Lachmuth S, Oostermeijer JGB, den Nijs HJCM, Meirmans PG, van Tienderen PH (2012) Human-induced hybridization among congeneric endemic plants on Tenerife, Canary Islands. Plant Syst Evol 298:1119–1131. doi 10.1007/s00606-012-0624-6

Honnay O, Verheyen K, Hermy M, (2002) Permeability of ancient forest edges for weedy plant species invasion. Forest Ecol Manag 161: 109–122. doi: 10.1016/S0378-1127(01)00490-X

Irl SDH, Beierkuhnlein C (2011) Distribution of endemic plant species on an oceanic island – a geospatial analysis of La Palma (Canary Islands). Procedia Env Sci 7: 170-175. doi: 10.1016/j.proenv.2011.07.030

Irl SDH, Steinbauer MJ, Babel W, Beierkuhnlein C, Blume-Werry G, Messinger J, Palomares-Martínez Á, Strohmeier S, Jentsch A (2012) An 11-yr exclosure experiment in a high-elevation island ecosystem: introduced herbivore impact on shrub species richness, seedling recruitment and population dynamics. J Veg Sci 23: 1114-1125. doi: 10.1111/j.1654-1103.2012.01425.x

Jurasinski G, Retzer V, Beierkuhnlein C (2009) Inventory, differentiation, and proportional diversity – a consistent terminology for quantifying biodiversity. Oecologia, 159, 15-26. doi:10.1007/s00442-008-1190-z

Jurasinski G, Retzer V (2012) simba: A collection of functions for similarity analysis of vegetation data. R package version 0.3-4. http://CRAN.R-project.org/package=simba

Körner C (2003) Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems (Springer, Berlin).

Kreft H, Jetz W, Mutke J, Kier G, Barthlott W (2008) Global diversity of island floras from a macroecological perspective. Ecol Lett 11: 116–127. doi: 10.1111/j.1461-0248.2007.01129.x

Leutner BF, Steinbauer MJ, Müller CM, Früh AJ, Irl S, Jentsch A, Beierkuhnlein C (2012) Mosses like it rough - growth form specific responses of mosses, herbaceous and woody plants to micro-relief heterogeneity. Diversity 4: 59-73. doi:10.3390/d4010059

Liu HY (1989) Systematics of Aeonium (Crassulaceae). Special Publications Number 3, National Museum of Natural Science. Pao-Teh Han Publishing, Taiwan

Mallen-Cooper J, Pickering CM (2008) Linear declines in exotic and native plant species richness along an increasing altitudinal gradient in the Snowy Mountains, Australia. Austral Ecol 33: 684-690. doi:10.1111/j.1442-9993.2008.01835.x

Nogales M, Rodríguez-Luengo JL, Marrero P (2006) Ecological effects and distribution of invasive non-native mammals on the Canary Islands. Mammal Rev 36: 49–65.

Quintana-Ascencio PF, Weekley CW, Menges ES (2007) Comparative demography of a rare species in Florida scrub and road habitats. Biol Conserv 137:263–270. doi:10.1016/j.biocon.2007.02.009

R Development Core Team (2012) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Reyes-Betoncort JA, Santos-Guerra A, Guma IR, Humphries CJ, Carine MA (2008) Diversity, rarity and the evolution and conservation of the Canary Islands endemic flora. Anales del Jardín Botánico de Madrid 65: 25-45.

Rotholz E, Mandelik Y (2013) Roadside habitats: effects on diversity and composition of plant, arthropod, and small mammal communities. Biodivers Conserv 22:1017-1031. doi: 10.1007/s10531-013-0465-9

Santos-Guerra A (1983) Vegetación y flora de La Palma. Editorial Interinsular Canaria, Tenerife.

Shmida A, Werger MJA (1992) Growth form diversity on the Canary Islands. Vegetatio 102: 183-199.

Spellerberg IF (1998) Ecological effects of roads and traffic: A literature review. Global Ecol Biogeogr 7: 317-333.

Spellerberg IF (2002) Ecological effects of roads. Science Publish, Enfield.

Steinbauer MJ, Beierkuhnlein C (2010) Characteristic pattern of species Diversity on the Canary Islands. Erdkunde, 64, 57-71. doi:10.3112/erdkunde.2010.01.05

Steinbauer MJ, Otto R, Naranjo-Cigala A, Beierkuhnlein C, Fernández-Palacios JM (2012). Increase of island endemism with altitude - speciation processes on oceanic islands. Ecography 34: 1–10. doi: 10.1111/j.1600-0587.2011.07064.x

Steinbauer MJ, Irl SDH, Beierkuhnlein C (2013a) Elevation-driven ecological isolation promotes diversification on Mediterranean islands. Acta Oecol 47: 52-56. doi: 0.1016/j.actao.2012.11.004

Steinbauer MJ, Gohlke A, Mahler C, Schmiedinger A, Beierkuhnlein C (2013b) Quantification of wall surface heterogeneity and its influence on species diversity at medieval castles - implications for the environmentally friendly preservation of cultural heritage. J Cult Herit, 14, 219-228. doi:10.1016/j.culher.2012.06.003

Trombulak SC, Frissell CA (2000) Review of ecological effects of roads on terrestrial and aquatic communities. Conserv Biol 14: 18-30. doi: 10.1046/j.1523-1739.2000.99084.x

Watkins RZ, Chen J, Pickens J, Brosofske KB (2003) Effects of Forest Roads on Understory Plants in a Managed Hardwood Landscape. Conserv Biol 17: 411-419. doi: 10.1046/j.1523-1739.2003.01285.x

Wemple BC, Jones JA (2003) Runoff production on forest roads in a steep, mountain catchment. Water Resour Res 39: 1220 .doi:10.1029/2002WR001744

Whittaker RJ, Fernández-Palacios JM (2007) Island Biogeography. Ecology, Evolution, and Conservation. 2nd ed. Oxford University Press, Oxford.

Zwaenepoel A, Roovers P, Hermy M (2006) Motor vehicles as vectors of plant species from road verges in a suburban environment. Basic Appl Ecol 7: 83-93. doi:10.1016/j.baae.2005.04.003

7.6 Manuscript 6

Climate vs. topography – spatial patterns of plant species diversity and endemism on a high-elevation island

Severin D.H. Irl[1,]*, David E.V. Harter[1], Manuel J. Steinbauer[1], David Gallego Puyol[2], José María Fernández-Palacios[3], Anke Jentsch[4], Carl Beierkuhnlein[1]

Submitted to *Journal of Ecology*

[1] *Dept. of Biogeography, BayCEER, University of Bayreuth, 95770 Bayreuth, Germany*

[2] *Dept. Physical, Chemical and Natural Systems, Universidad Pablo de Olavide, 41013 Sevilla, Spain*

[3] *Island Ecology and Biogeography Research Group, Dept. of Ecology, Universidad de La Laguna, La Laguna, 38206, Tenerife, Spain*

[4] *Dept. of Disturbance Ecology, BayCEER, University of Bayreuth, 95770 Bayreuth, Germany*

* Corresponding author: severin.irl@uni-bayreuth.de; Tel.: +49-921-552299; Fax.: +49-921-552315

SUMMARY

1. Climate and topography are among the most fundamental drivers of plant diversity. However, understanding the drivers behind diversity patterns is a complex task as abiotic drivers and human influence might be relevant. Here, we assess the importance of climate and topography in explaining diversity patterns of species richness, endemic richness and endemicity on the landscape scale of an oceanic island, and evaluate the independent contribution of climatic and topographic variables independently to spatial diversity patterns.

2. We constructed a presence/absence matrix of perennial endemic and native vascular plant species (including subspecies) in 890 plots on the environmentally very heterogeneous island of La Palma, Canary Islands. Species richness, endemic richness and endemicity were recorded, interpolated and related to climate (i.e. variables describing temperature, precipitation, variability and climatic rarity) and topography (i.e. topographic complexity, solar radiation, geologic age, slope and aspect). We used multi-model inference, spatial autoregressive models, variance partitioning and linear regression kriging as statistical methods.

3. Species richness is best explained by both climatic and topographic variables. Topographic variables (esp. topographic complexity and solar radiation) explain endemic richness and climatic variables (esp. elevation/temperature and rainfall seasonality) explain endemicity. Spatial patterns of species richness, endemic richness and endemicity were in parts geographically decoupled from each other.

4. *Synthesis*. A combination of eco-evolutionary processes (micro-refugia, *in situ* speciation, preadaptation to rupicolous conditions) and human-induced influence (introduced herbivores, fire) both dependent on topography likely shape the current pattern of endemic richness on La Palma. However, climate mainly drives endemicity, which is connected to speciation. We highlight the importance of incorporating climatic variability into future studies of plant species diversity and endemism. The partially non-overlapping hotspots of species richness, endemic richness and endemicity emphasize the need for conservation management to acknowledge different diversity measures to protect the complete spectrum of spatial diversity. High-elevation islands such as La Palma are highly suitable to study drivers of diversity and endemism, as they offer environmental gradients of continental magnitude on the landscape scale of a single climatic *mini-continent* and a large array of *in situ*-speciated endemics.

Key-words: Canary Islands; climatic rarity; climatic stability; determinants of plant community diversity and structure; island ecology; landscape scale; mini-continent; multi-model inference; spatial ecology

INTRODUCTION

Species and species diversity are not distributed randomly in space (Rosenzweig 1995). Rather they follow distinct spatial patterns (Orme *et al.* 2005; Stohlgren *et al.* 2005) or are distributed along differing environmental gradients (Hortal *et al.* 2013; Slaton 2014). In heterogeneous landscapes, often multiple overlapping and interacting gradients are influential, especially gradients based on topography and climate (Dewar & Richard 2007; Slaton 2014). This complexity results in a key task in ecology, biogeography and evolution: Disentangling the major drivers of species distribution and biodiversity patterns from a diverse array of environmental factors.

In contrast to many other regions, oceanic islands harbour a relatively low species richness but high endemism, i.e. a larger number of endemic species, among which many are single-island endemics (SIEs; Whittaker *et al.* 2008) and high endemicity, i.e. a high proportion of endemics in a given flora or community as an indicator for floristic uniqueness (Gillespie *et al.* 2008). Oceanic islands never had contact to other landmasses (Whittaker & Fernández-Palacios 2007); accordingly, most of their endemic species and especially SIEs are a result of *in situ* speciation (Stuessy *et al.* 2006; Whittaker *et al.* 2008). The spatial distribution of endemism within a given oceanic island can thus give valuable information about origin and drivers of biodiversity patterns on the landscape scale, and have important implications for conservation (Richardson & Whittaker 2010). Several drivers have been proposed to explain small-scale patterns of endemic richness and endemicity over different types of landscapes and scales. We focus on the following three factors: a) precipitation variability (Dewar & Richard 2007), b) climatic rarity (Ohlemüller *et al.* 2008) and c) topographic complexity (Whittaker *et al.* 2008; Kougioumoutzis & Tiniakou 2014).

On the regional scale, islands are characterized by relatively stable oceanic climate conditions (Whittaker & Fernández-Palacios 2007). However, traditionally 'stability' is mainly acknowledged for island temperature regimes, whereas a large spatio-temporal variation in precipitation is a common phenomenon within island archipelagos or even within a single oceanic island (Giambelluca *et al.* 1986, Dewar & Richard 2007). The distribution and amount of precipitation often show large variation on relatively small spatial scales (e.g. Hawaii, Giambelluca *et al.* 1986 or La Palma, Canary Islands, Garzón-Machado et al. 2013). Increasing precipitation variability increases the necessity for species to adapt to these conditions (Dewar & Richard 2007). Isolation is a strong filter for pre-adapted specialists to colonize a new island (Weigelt & Kreft 2013), thus, colonizing species via evolutionary adaptation may use vacant niche space, resulting in the speciation of specialized endemics (Whittaker et al. 2008).

The concept of climatic rarity suggests that in a specific area certain climatic conditions are less common than others (Ohlemüller *et al.* 2008). High climatic rarity is likely connected to spatially restricted selection pressure, which promotes ecological differentiation processes and evolutionary adaptations (Nosil 2012). This might lead to the evolution of local endemics but also to the immigration of already adapted specialist species, while the immigration of non-adapted species is hindered (Nosil

2012). Indeed, Ohlemüller *et al.* (2008) showed that areas containing many small-range species coincided with high climatic rarity and, thus, were environmentally isolated by a surrounding matrix of common climatic conditions. Up to now, climatic rarity is a concept mainly applied on continental scales (Ohlemüller *et al.* 2008). In this study, we transfer, for the first time, this concept to a smaller scale: the landscape scale within a single island.

Topographic complexity positively influences species richness patterns and speciation processes (Whittaker *et al.* 2008; Hortal *et al.* 2009; Trigas *et al.* 2013). Increasing topographic complexity (e.g. variation in slope inclination and aspect) increases habitat diversity, niche space available for niche partitioning and speciation, and thus enables species coexistence (Hortal *et al.* 2009). Therefore, topographic complexity likely results in increased species richness (Hortal *et al.* 2009). In addition, complex topography offers micro-refugia during periods of environmental alterations (e.g. during past climatic fluctuations, or even during rare extreme weather events; Ashcroft *et al.* 2012). This can decrease extinction risk, consequently maintaining species richness and endemic richness over time (Mee & Moore 2014), which is crucial on isolated oceanic islands with low colonization rates. In the case of endemicity, topographic complexity works on large spatio-temporal scales (Whittaker *et al.* 2008), thus a relationship between endemicity and topographic complexity is not expected.

We used the island of La Palma (Canary Islands) as a study system due to its strong elevational and ecological gradients (Garzón-Machado *et al.* 2013) and very complex topography (Carracedo *et al.* 2002, Irl & Beierkuhnlein 2011). In general, we assume that environmental drivers explain the spatial pattern of species richness (i.e. perennial plant species richness), endemic richness and endemicity. Our research aims are to assess, i) which overall contribution climate and topography have in explaining species richness, endemic richness and endemicity of perennial plants on La Palma, ii) how climatic and topographic variables individually contribute to explaining species richness, endemic richness and endemicity, and iii) to determine the resulting high-resolution spatial pattern of species richness, endemic richness and endemicity on the island.

MATERIAL AND METHODS

Study area

La Palma is the north-westernmost island of the Canary Islands, located in the Atlantic Ocean off the coast of north-western Africa (Fig. 1). La Palma covers an area of 706 km^2 and its highest peak is Roque de los Muchachos (2426m; Carracedo *et al.* 2002). La Palma has a subtropical-Mediterranean climate with humid winters and dry summers (Garzón-Machado *et al.* 2013). However, climatic conditions differ considerably within the island. Annual precipitation ranges from about 170 mm to almost 1400 mm (excluding fog drip which can lead to almost threefold amounts of actual precipitation), annual temperature from about 9 °C on the island summit to around 22 °C at the leeward south-western coast (Irl & Beierkuhnlein 2011). The north-eastern trade winds create an elevation-associated climatic divide of the island in a humid windward and a dry leeward side. Above the trade wind-induced cloud

zone exists a thermal inversion layer, generally exhibiting dry conditions with the possibility of snow and ice in winter (Garzón-Machado *et al.* 2013).
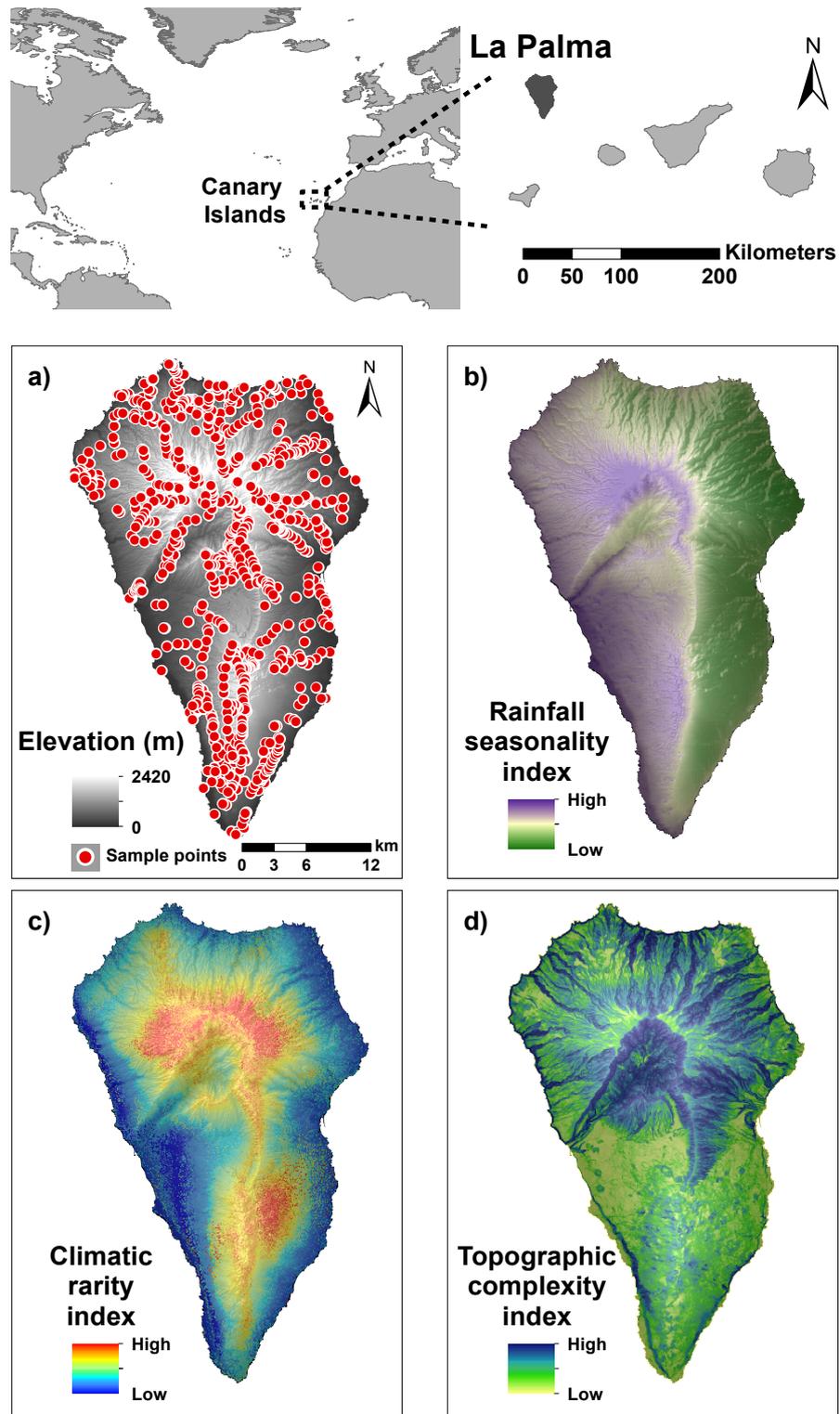

Figure 1. Maps of La Palma within the Canary Islands showing the spatial distribution of a) elevation (including the location of the sampled plots), b) the rainfall seasonality index, c) the climatic rarity index and d) topographic complexity. The large number of sampled plots (n = 890) enabled to cover the whole island and all relevant environmental conditions.

La Palma is geologically divided into two parts. The northern older part is morphologically complex with steep valleys (so-called *barrancos*), coastal cliffs and the massive Caldera de Taburiente complex, which has almost vertical cliffs in its interior reaching 1000 m or more in elevation. The volcanic activity has ceased in the northern part, which is dominated by erosive processes (Carracedo *et al.* 2002). The younger, southern part is still subject to subaerial volcanic ontogeny (the last eruption on the southern tip of the island was documented in 1971) and has gentler slopes with volcanic cones and ash fields (Carracedo *et al.* 2002).

The zonal vegetation directly reflects the climatic conditions of the island (Garzón-Machado *et al.* 2013). These zones range from halophytic communities in arid coastal areas to succulent scrub and thermophilic woodlands in semi-arid lower elevations, through the endemic Canary Pine forest in mid elevations to a high-elevation summit scrub. On the windward side a palaeo-endemic evergreen humid laurel forest and a slightly less humid tree heath *Erica arborea-Morella faya* forest exist at mid elevations in the zone of the trade wind clouds instead of the Canary Pine forest (del Arco Aguilar *et al.* 2010, Garzón-Machado *et al.* 2013). Endemic species are found in all natural vegetation zones (del Arco Aguilar *et al.* 2010). According to Acebes Ginovés *et al.* (2010), La Palma hosts 658 native vascular plant species (including species and subspecies; for simplification reasons hereafter referred to as *species*), of which 193 are archipelago endemics (AEs, i.e. endemic to the Canary Islands). Of the AEs 37 are single-island endemics (SIEs).

Sampling method

The presence and absence of endemic perennial vascular plant species (i.e. all SIEs and AEs) was recorded in 890 plots using a radial sampling approach with a 50 m radius (Fig. 1a; see S1 in Supporting Information for a list of species and S2 for list with plot information). To cover all relevant gradients we accessed sampling sites by all means possible (i.e. roads, tracks, hiking paths, backcountry, non-technical climbing, etc.). In a selected area, a random point was set as centre point of each plot. This centre point was recorded with a GPS device (Garmin Oregon 550). Our sampling approach covers all relevant environmental gradients on La Palma owing to the large number of plots and the good spatial coverage, even though plots were not randomly distributed (Fig. 1a). This sampling approach is very time efficient, allowing for a large sample size, which is essential for differentiated high-resolution spatial analyses in face of a variety of gradients (e.g. elevation, precipitation, geology, seasonality, solar radiation, etc.) and topographic complexity.

We focused on perennial vascular plant species including all woody species but excluding annuals. We excluded annuals for several reasons: (1) Annuals can easily be underestimated as they produce aboveground biomass only for short time periods during the year resulting in wrong absences if aboveground biomass is not present, (2) annuals react very strongly to short-term climatic events, while perennials better integrate over long-term environmental conditions (e.g. climate), (3) their relevance for

the flora, especially the endemic flora, of the Canary Islands is limited, as a study by Shmida & Werger (1992) revealed (i.e. 58% of the native plants of La Palma and 93% of the archipelago endemics are perennials). In addition, this sampling focus strongly increased sampling efficiency, resulting in exceptionally high spatial coverage, which is fundamental for our research objectives.

The numbers of remaining native perennial species (i.e. species that were not SIEs or AEs) were identified in the field and recorded without species' identities as our focus was on endemic diversity (i.e. endemic richness and endemicity). We calculated total perennial species richness per plot (hereafter referred to as *species richness*, abbreviated as SR) by adding the number of recorded endemic perennial species to the remaining native perennial species.

The percentage of single-island endemics (pSIEs) and the percentage of archipelago endemics (pAE) were calculated by dividing the number of single-island endemics (nSIE) and the number of archipelago endemics (nAE) through total species richness, respectively. Percentage indices are independent of richness gradients and are an indicator of taxonomic or, in our case, floristic uniqueness (Gillespie et al. 2008). Nomenclature and endemic status follow Acebes Ginovés *et al.* (2010). Sampling took place in fall 2010 and in spring 2011, 2012 and 2013.

Environmental data

Basic environmental data were derived from raster datasets provided by the Cabildo Insular de La Palma (2 x 2 m digital elevation model and geologic map). The resolution of the digital elevation model was resampled to a raster resolution of 100 x 100 m. All plots were recalculated as centroids of the 100 x 100 m raster. Plots that were located within the same raster cell were homogenized (i.e. species lists were added together). Elevation, slope angle, micro-aspect (northerness and easterness) and macro-aspect (mean aspect per grid cell within a 5 km radius) as well as mean annual solar radiation (using a standard diffuse atmosphere and based on latitude, elevation and slope aspect) were calculated for each plot.

Mean annual precipitation and mean annual temperature were interpolated using data collected from meteorological stations for the Canary Islands (n = 214 for mean annual temperature and n = 288 for mean annual precipitation; see S3a in Supporting Information). Linear regression kriging (R package *gstat*) was applied as interpolation method, with elevation, slope, island, micro- and macro-aspect as co-variables (for details on linear regression kriging see Statistical Analysis section). Three measures of precipitation variability were computed using monthly precipitation data from 47 meteorological stations from the Spanish Federal Meteorology Agency (AEMET) from the Canary Islands (time span: 1969 to 1998; see S3a in Supporting Information) and implementing the same linear regression kriging technique: i) intra-annual variability represented by the 30 year mean of the annual coefficients of variation based on monthly precipitation sums, respectively, ii) inter-annual variability represented by the coefficient of variation for annual precipitation over the 30 year time period, and iii) rainfall seasonality represented by

the rainfall seasonality index by Walsh & Lawler (1981; see the spatial distribution of the rainfall seasonality index for La Palma in Fig. 1a).

Climatic rarity was calculated following the method given by Ohlemüller *et al.* (2008) for two geographic entities: a) based on the climate of the Canary Islands and b) based on the climate of La Palma. For both geographic entities each climatic variable was divided into equal range classes. For mean annual temperature we used a class size of 0.25°C and for mean annual precipitation a class size of 25 mm. According to the temperature and precipitation conditions each 100 x 100 m raster cell was assigned to a respective temperature and precipitation class (e.g. a combination of precipitation ranging from 300 to 325 mm and temperature from 20 to 20.25°C). Then, all cells of each combined temperature and precipitation class on La Palma were summed up, resulting in a spatial index of climatic rarity based on area (in ha). Climatic rarity increases with decreasing index values (Fig. 1b).

Topographic complexity was estimated by calculating the ratio between the 3D and 2D surface area with the following equation (Fig. 1c; Jenness 2004):

$$Topograhic\ complexity\ index\ = \frac{\sum_{100 \times 100\ m}(Area_{2 \times 2\ m}\ /\cos\ (Slope_{2 \times 2\ m}))}{Area_{100 \times 100\ m}}$$

where $Area_{2 \times 2\ m}$ is the area per grid cell from a 2 x 2 m DEM, $Slope_{2 \times 2\ m}$ the slope of each grid cell from the same DEM in degrees, and $Area_{100 \times 100\ m}$ the area per grid cell from a 100 x 100 m DEM containing all 50 x 50 (i.e. 2500) grid cells from the 2 x 2 m DEM. This index increases with increasing topographic complexity (i.e. from 1 = absolutely flat surface to $\propto$).

The linear regression kriging method as well as all other statistical methods were implemented in R Statistics (version 3.0.1; R Core Team 2013). All other GIS features were calculated in ArcMap 10 (ESRI Inc. 2010). A list summarizing all environmental variables used in this study is given in Table 1.

Statistical analysis

First, the linear relationship between response and explanatory variables were assessed by bivariate correlations (Spearman's ρ; see S3b in Supporting Information). To undergo a variable reduction for each response variable (SR, nSIE, nAE, pSIE, pAE), explanatory variables with correlations $-0.1 \leq r \leq 0.1$ were excluded due to weak explanatory power. In a second step collinearity was addressed by testing correlations for each possible pair of explanatory variables. If $|r| > 0.7$, the explanatory variable performing poorer with the response variable was excluded (S3b; see Dormann et al. 2013 for a discussion of collinearity). This resulted in a unique set of climatic and topographic variables for each response variable (see S3c in Supporting Information).

To select the appropriate transformation for each response variable, exploratory linear regression models were applied to each explanatory variable. The following transformations were separately tested to find the best model fit: untransformed, logarithmic, square root, quadratic (x^2) and hump-shaped ($x^2 + x$). Transformation selection was based on AICc values (i.e. second-order Akaike Information Criterion) of the respective regression models (Grueber et al. 2011; see S3d in Supporting Information). The best fitting

transformation of each explanatory variable was implemented in a multiple linear regression (MLR). S3c displays the resulting MLRs for SR, nSIE, nAE, pSIE and pAE. Model fits of each MLR model were visually checked to ensure compliance with model assumptions.

Table 1. List of all environmental variables and their abbreviations used in this study grouped into climate and topography. Units, minimum and maximum value are given for each variable.

Environmental variables

Class	Variable	Abbreviation	Unit	Min. value	Max. value
Climate	Climatic rarity for the Canary Islands	CR_CAN	ha	4	5311
	Climatic rarity for La Palma	CR_LP	ha	2	818
	Elevation	Elev	m a.s.l.	1	2392
	Intra-annual precipitation variability	INTRA_VAR	-	1.18	1.96
	Inter-annual precipitation variability	INTER_VAR	-	0.25	0.48
	Mean annual precipitation	MAP	mm	177	1331
	Mean annual temperature	MAT	°C	8.7	20.0
	Rainfall seasonality index	RSI	-	0.67	0.84
Topography	Annual solar radiation	ASR	Wh/m^2	63650	189110
	Easterness	Easterness	-	0	1
	Geologic age	Age	Ma	0.0005	4
	Macro-aspect	Macro	-	-0.925	0.899
	Northerness	Northerness	-	0	1
	Slope angle	Slope	°	1	55
	Topographic complexity index	TCI	-	1	2.97

The residuals of each MLR were tested for spatial autocorrelation using Moran's I to avoid potential parameter estimate bias and inflation of type I errors (Dormann et al. 2007). No spatial autocorrelation was detected in the residuals of the MLRs for SR (I = -0.001 n.s.) and nSIE (I = -0.002 n.s.), whereas nAE (I = -0.007, $p < 0.001$), pSIE (I = -0.004, $p < 0.001$) and pAE (I = -0.003, $p < 0.05$) resulted in significant spatial autocorrelation. To double-check the effect of spatial autocorrelation simultaneous autoregressive models (SAR) with a spatially dependent error term were implemented based on the same set of explanatory variables as in the MLRs. SARs account for spatial autocorrelation by using a neighbourhood matrix (Dormann et al. 2007). Results were compared with the respective MLR using Nagelkerke's pseudo R^2 as correlation coefficient (Nagelkerke 1991, see S3c). Performance of MLRs and SARs was comparable, even though Nagelkerke's pseudo R^2 was consistently higher. However, this likely resulted from the fact that R^2 and Nagelkerke's pseudo R^2 are not directly comparable and the latter tends to produce higher values. For this reason and because the three significant Moran's I values are very close to zero we conclude that spatial autocorrelation is therefore negligible for the following steps and is sufficiently covered by the explanatory variables in the respective MLRs.

Variance partitioning using MLRs (adjusted R^2 as the goodness-of-fit measure; R package *vegan*) was implemented to assess the overall importance of climate and topography following the guidelines of Legendre (2008). All variables used in this study were pre-classified into being either climatic or topographic drivers (Table 1). The same set of variables as selected for the MLR/SAR approach and their respective best fitting transformations were used for variance partitioning (see S3c). Then, based on this set of variables the independent, overlapping and total contribution of each class (i.e. topography or climate) was calculated based on adjusted R^2 values.

Multi-model inference (MMI) was used to calculate the relative importance of each explanatory variable in relation to each response variable (R package *relaimpo* version 2.2-2). In contrast to traditional null-hypothesis testing, MMI enables inference from more than one model (Johnson & Omland 2004) and has been proposed as a promising method in ecology and biogeography (Millington & Perry 2011). The relative importance and confidence intervals were calculated using bootstrapping (n = 1000) with all possible model combinations. As a result, the explained variation of the MLR for each response variable (indicated as adjusted R^2), and the relative contribution of each explanatory variable (i.e. % contribution to the R^2 of the respective MLR) and its confidence interval are given.

In a last step, the spatial interpolation of the response variables was conducted using linear regression kriging (R package *gstat*). Linear regression kriging uses a statistical approach (MLR) to infer the relationship of explanatory variables to the response variable and then interpolates the residuals into space (Garzón-Machado et al. 2013). All explanatory variables used in the MLRs and their respective transformations according to each response variable (S3c) were used as basis of direct spatial interpolation of species richness, endemic richness and endemicity values.

Statistical significance is indicated in the following as '*' for $p < 0.05$, '**' for $p < 0.01$ and '***' for $p < 0.001$. All correlation coefficients in MLRs, MMI and variance partitioning are given as number of variable-corrected adjusted R^2.

RESULTS

Topography vs. climate

The large number of sampled points ensured a comprehensive and spatially dense coverage of the island, including all relevant environmental gradients (Fig. 1a), and a very high spatial density of plots on this scale (1.26 plots per km^2). 79 AEs were identified (44% of all perennial AEs of La Palma; Acebes Ginovés *et al.* 2010), 31 of which were SIEs (84% of all La Palma SIEs; Acebes Ginovés *et al.* 2010; see species list S1). Species richness ranged from 1 to 57 species per plot, nSIE from 0 to 8 species per plot, nAE from 0 to 24 species per plot, and pSIE as well as pAE from 0 to 100% . The overall explanatory power of the MMIs was good (SR, pSIE and pAE) to moderate (nSIE and nAE), i.e. a moderately large section of unexplained variance remained (Table 2).

Variance partitioning revealed that topography and climate both are more or less equally important for species richness (joint explained variation for climate: $R^2 = 0.41$ and topography: $R^2 = 0.34$,

including a large share of overlapping contribution: R^2 = 0.26; Fig. 2a). However, endemic richness was dominated by the influence of topography for both nSIE (joint explained variation: R^2 = 0.18) and nAE (joint explained variation: R^2 = 0.27), whereas climate had very little influence on endemic richness (joint explained variation: $R^2 \leq 0.06$; Fig. 2b-c). Climate was very important in explaining endemicity for both pSIE (joint explained variation: R^2 = 0.42) and pAE (joint explained variation: R^2 = 0.45; Fig. 2d-e). Moreover, the influence of topography was almost not separable from the explained variation of climate (independent explained variation for pSIE: R^2 = 0.01 and pAE: R^2 = 0.02, overlapping explained variation for pSIE: R^2 = 0.15 and for pAE = R^2 = 0.22). For all values of joint, independent, overlapping and total explained variation of each response variable resulting from variance partitioning see S3e in Supporting Information.

Environmental components of topography and climate

In the MMI species richness was mainly explained by elevation, annual solar radiation, the rainfall seasonality index and the topographic complexity index (Fig. 2f, Table 2a), indicating the joint importance of climate (elevation, rainfall seasonality index) and topography (annual solar radiation, topographic complexity index). However, the relative contribution of each variable was relatively moderate (e.g. elevation as explanatory variable with the highest relative contribution only reaches 27%). Further climatic (climatic rarity, inter-annual precipitation variability, intra-annual precipitation variability) and topographic variables (easterness and slope) only played a subordinate role (Fig. 2f, Table 2a). Overall explained variation was high (R^2 = 0.5; Table 2a); however, half of the variation remained unexplained.

Endemic richness was best explained by different topographic variables, i.e. the topographic complexity index, annual solar radiation and slope for both nSIE and nAE (Fig. 2g-h, Table 2b). The topographic complexity index as largest contributor of relative importance reached 50% and 47% for nSIE and nAE, respectively. Climatic variables only had marginal influence of $\leq 5\%$ (i.e. intra-annual precipitation variability, inter-annual precipitation variability and the rainfall seasonality index), with the slight exception of climatic rarity for La Palma for nAE (12%; Table 2b). Overall explained variation was moderate for both nSIE and nAE and did not surpass R^2 = 0.31 (Table 2b).

Climatic variables had the highest explanatory power for endemicity, whereas topographic variables were of minor importance (Fig 2i-j). For pSIE elevation and the rainfall seasonality index (both climatic variables) as well as annual solar radiation (topographic variable) were the most important variables, ranging from 12% (annual solar radiation) to 50% relative importance (elevation; Table 2c). The climatic variables mean annual temperature (which is strongly linked to elevation; relative importance of 32%) and the rainfall seasonality index (relative importance of 31%) as well as to a certain degree also annual solar radiation (relative importance of 12%) had the highest relative importance for pAE (Table 2c). Other climatic (i.e. intra-annual precipitation variability and inter-annual precipitation variability) and topographic variables (i.e. geologic age and easterness) only had little additional

explanatory power (≤ 6%; Fig. 2i-j, Table 2c). Overall explained variation was high for both pSIE and pAE, almost reaching R^2 values of 0.5 for the latter (Table 2c).
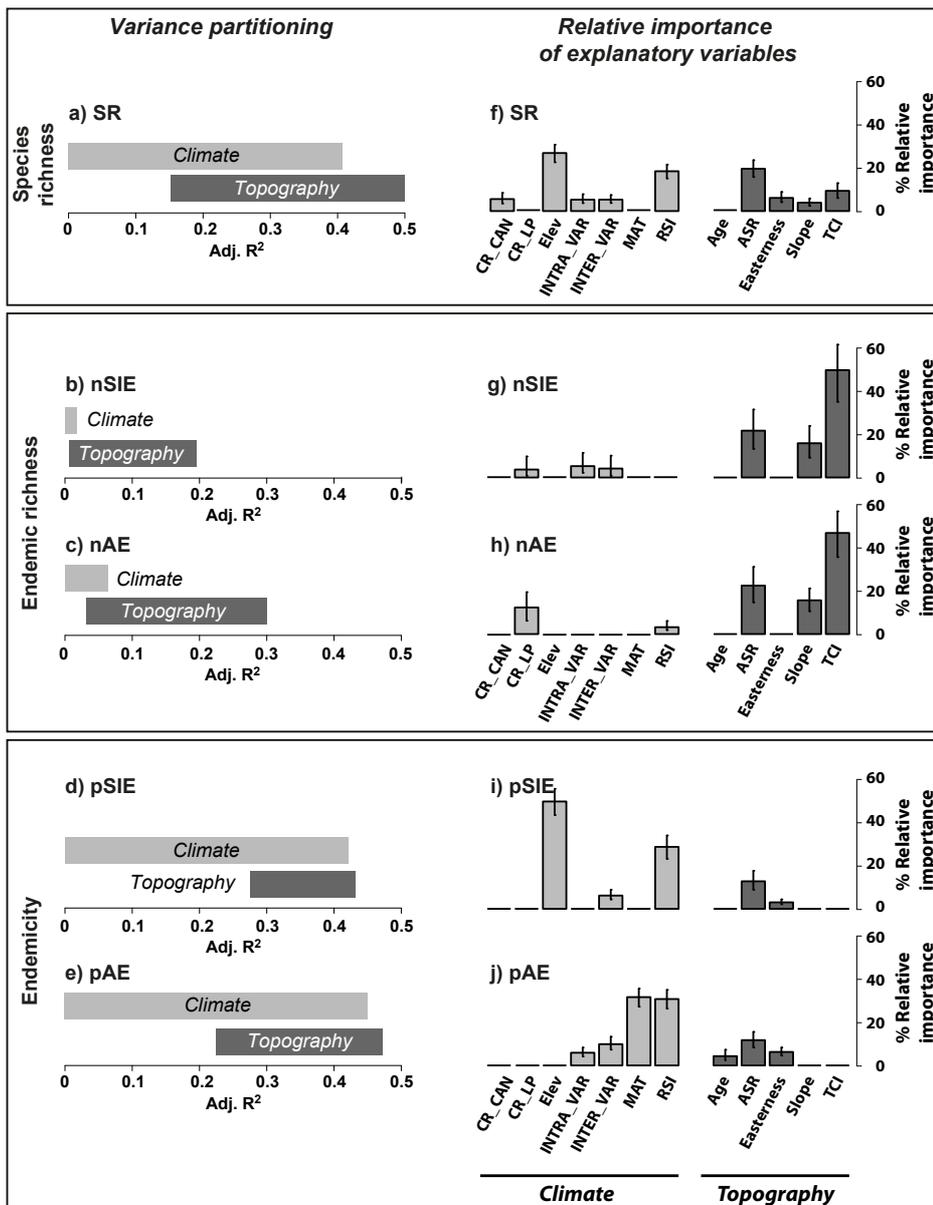

Figure 2. Variance partitioning of the influence of climate and topography (a-d) and relative importance of explanatory variables (f-j) on species richness (SR), endemic richness (nSIE = number of single-island endemics, nAE = number of archipelago endemics) and endemicity (pSIE = percentage of single-island endemics, pAE = percentage of archipelago endemics). Figures a)-d) show the independent and overlapping explained variation of climate and topography as portion of the total adjusted R2 values. For values see S3e in Supporting Information. Figures f)-j) display the relative importance of each explanatory variable calculated by the multimodel inference approach as per cent contribution to the R2 for the respective response variable. Gaps indicate that these variables were removed due to collinearity or during the variable reduction process. Both variance partitioning and relative importance result from multiple linear regressions. For details on both methods please see the Material and Methods section. Abbreviations of explanatory variables: Age: Geologic age; ASR: Annual solar radiation; CR_CAN: Climatic rarity for the Canary Islands; CR_LP: Climatic rarity for La Palma; Elev: Elevation; INTER_VAR: Inter-annual precipitation variability; INTRA_VAR = Intra-annual precipitation variability; MAT = Mean annual temperature; RSI = Rainfall seasonality index; TCI = Topographic complexity index.
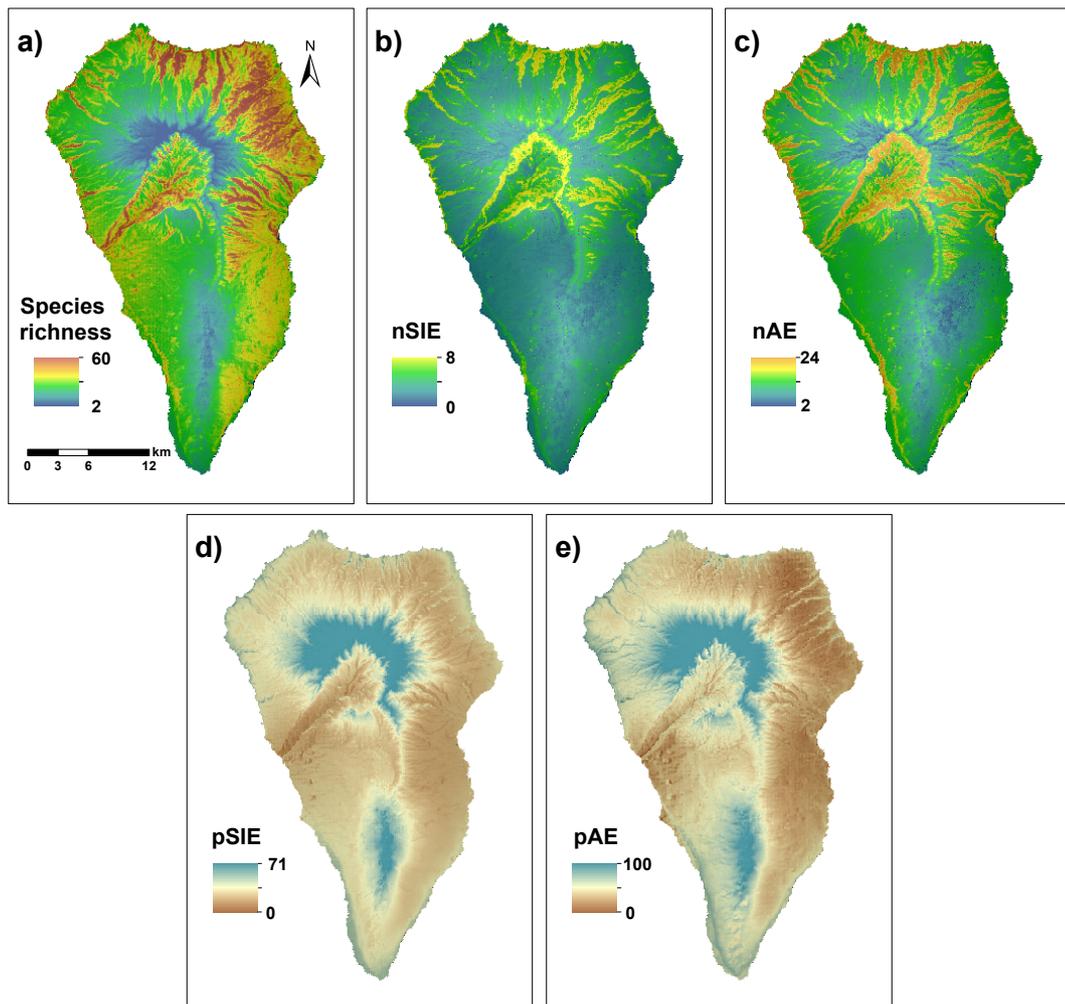
Figure 3. Spatial interpolation maps of a) species richness, b) number of single-island endemics (nSIE), c) number of archipelago endemics (nAE), percentage of single-island endemics (pSIE) and percentage of archipelago endemics (pAE).

Spatial distribution of species richness, endemic richness and endemicity

A complex pattern of species richness, endemic richness and endemicity is visible for La Palma (Fig. 3). Species richness decreased with elevation and from northeast to southwest (Fig. 3a). The highest values of species richness, however, reached values of around 60 species and were located in the steep barrancos and in the coastal cliffs on the northern part of the island, independent of island aspect. Endemic richness for both nSIE and nAE was highest in the steep barrancos of the north but also reached very high values in the inner cliffs of the Caldera de Taburiente complex (around 8 for nSIE and 24 for nAE; Fig. 3b-c). In general, endemic richness decreased with elevation but without the island aspect-driven asymmetry displayed by species richness. Endemicity for both pSIE and pAE strongly increases with elevation reaching values of 71% and around 100% at the highest elevations for pSIE and pAE, respectively (Fig. 3d-e). While strongly decreasing with elevation in eastern aspects, endemicity can

reach quite high values (around 25% for pSIE and 75% for pAE) in barrancos at lower elevations and coastal cliffs of the north, lowland areas of the south and western slopes at mid elevations (esp. for pAE with values between 50 and 70%).

Table 2. Total explained variation and relative importance of each environmental variable in explaining a) species richness, b) endemic richness (nSIE = number of single-island endemics; nAE = number of archipelago endemics) and c) endemicity (pSIE = percentage of single-island endemics; pAE = percentage of archipelago endemics). Total explained variation (given as R2) results from multimodel inference (bootstrap n = 1000). '% of R2' gives the relative contribution of the respective environmental variable to the total explained variation. Explanatory variables are ordered by relative contribution and are grouped as either topographic (italics) or climatic variable (bold). The best fitting transformation is given in 'Transf.'. Tested transformations were: linear, logarithmic, square-root, quadratic and hump-shape (x2 + x). 'Dir.' indicates the direction of correlation (Dir. '+' = positive correlation; '-' = negative correlation; ∩ = hump; ∪ = inverse hump). Abbreviations of variables are given in Table 1. For details see methods section.

a) Species richness

SR Total explained variation: R² = 0.50	% of R²	Dir.	Transf.
Elev	27	∩	hump
ASR	20	∩	hump
RSI	18	∩	hump
TCI	9	+	log
CR_CAN	6	+	log
Easterness	6	∪	hump
INTER_VAR	5	∪	hump
INTRA_VAR	5	∪	hump
Slope	4	+	quad.

b) Endemic richness

nSIE Total explained variation: R² = 0.20	% of R²	Dir.	Transf.
TCI	50	+	sqrt
ASR	22	∩	hump
Slope	16	+	linear
INTRA_VAR	5	∪	hump
CR_LP	4	+	log
INTER_VAR	4	-	linear

nAE Total explained variation: R² = 0.31	% of R²	Dir.	Transf.
TCI	47	+	sqrt
ASR	22	-	sqrt
Slope	16	+	quad.
CR_LP	12	+	log
RSI	3	∩	hump

c) Endemicity

pSIE Total explained variation: R² = 0.44	% of R²	Dir	Transf.
Elev	50	∪	hump
RSI	29	∪	hump
ASR	13	∪	hump
INTER_VA R			
Easterness	6	∩	hump
Easterness	3	-	linear

pAE Total explained variation: R² = 0.48	% of R²	Dir.	Transf.
MAT	32	∪	hump
RSI	31	∪	hump
ASR	12	∪	hump
INTER_VA R			
Easterness	10	∩	hump
Easterness	6	-	linear
INTRA_VA R			
Age	6	∩	hump
Age	4	∪	hump

DISCUSSION

Effects of topography and climate

The presented study shows that topography and climate are important drivers of species richness, endemic richness and endemicity on the landscape scale of the very heterogeneous oceanic island of La Palma. However, we find a shift in the overall importance of either topography or climate in explaining the distribution and spatial patterns of each response variable. The effect of climate and topography on species richness has been widely studied in many different biomes and landscapes, and on varying spatial scales (Field *et al.* 2009) and both climate and topography have been shown to be of great importance (e.g. Hortal *et al.* 2009; Hortal *et al.* 2013; Xu *et al.* 2014).

Several possible explanations, which are not mutually exclusive, exist for the strong positive impact of topography on endemic richness, which in our study is mainly driven by the topographic complexity index. First, a complex topography such as found on La Palma likely renders a high diversity of different habitats and thus a large local niche space (Whittaker *et al.* 2008; Hortal *et al.* 2013; Steinbauer *et al.* 2013a) as well as an increase in area (Leutner *et al.* 2011). Second, the high topographic complexity of La Palma likely offers micro-refugia during periods of climatic fluctuation, thus reducing local extirpation probabilities (Médail & Diadema 2009) and possibly also increasing speciation (Mee & Moore 2014). Third, the low influence of climate on endemic richness on La Palma might indicate that the endemic species set (as a whole) is adapted to the complete range of climatic conditions on the island, as *in-situ* speciation has happened in all climatic conditions on the island (esp. relevant for SIEs; Beard *et al.* 2008). Fourth, many endemic species on La Palma are adapted to rupicolous conditions (del Arco Aguilar *et al.* 2010); conditions that are more likely to be present if topographic complexity is high. Fifth, endemics, which are known to be more palatable to introduced herbivores, lack defence mechanisms (Bowen & Van Vuren 1997), and are therefore preferentially browsed (Irl *et al.* 2012), may be better protected from introduced herbivore impact on steep and morphological complex sites (such as the barrancos and the coastal cliffs). Steep and inaccessible areas might offer 'safe sites' from introduced herbivores to endemics (Irl *et al.* 2014a), which have had detrimental effects on endemic species on La Palma (Garzón-Machado *et al.* 2010, Irl *et al.* 2014b). Sixth, endemics might experience lower fire frequencies (which have generally increased in recent decades; Climent *et al.* 2004) in topographic complex regions probably due to lower vegetation cover and lower productivity. Thus, a combination of eco-evolutionary processes that have triggered adaptations to local environmental conditions and recent human-mediated influence (i.e. introduced herbivores and fire) has likely shaped the current distribution of endemic richness on La Palma.

In contrast to endemic richness, climate has a stronger influence on endemicity than topography on La Palma. Endemicity stands for floristic uniqueness and the relative importance of endemics in a given area (Gillespie *et al.* 2008) but is also interpreted as a measure of speciation (Emerson & Kolm 2005; Steinbauer *et al.* 2013b). Climate and especially climatic changes directly influence speciation, e.g. through specific resource availability in terms of energy or water availability or by establishing specific selection pressures (Hua & Wiens 2013). For example, high elevation ecosystems possess quite

harsh conditions for plant growth, thus selective pressure is very high (Anthelme & Dangles 2012). Idle resources, open niche space and potential isolation effects in high elevation island ecosystems likely stimulate speciation processes (Steinbauer *et al.* 2013b). As a result, endemicity potentially indicates evolutionary *in-situ* specialization to specific environmental conditions (i.e. past adaptive speciation processes); a phenomena, which has been proposed to be relevant for all mountainous islands as well as isolated mainland peaks and mountain systems (Steinbauer *et al.* 2013b).

Precipitation variability and climatic rarity

Precipitation variability, especially the rainfall seasonality index, contributed substantially in explaining species richness and endemicity but not endemic richness on La Palma. As on other scales (Dewar & Richard 2007), areas of La Palma with high precipitation variability host generally fewer species, while stable areas are mainly humid regions supporting relatively high species richness. High species richness likely results from high resource availability and low selective pressure for specialization, suitable for common (mesophytic) species communities (Stohlgren *et al.* 2005; Weigelt *et al.* 2013). However, in drought-prone regions one of the essential resources for plant growth is very limited (i.e. water) and/or connected to a high temporal stochasticity, leading to less favourable growing conditions. This results in an increased importance of specialized endemics and thus a higher floristic uniqueness but lower species richness in high variability conditions (Dewar & Richard 2007). Several studies have shown that centres of endemic richness are connected to long-term climatic stability (Jansson 2003; Platts *et al.* 2012; Weber *et al.* 2014), while endemic richness on La Palma is highest in variable conditions. However, our study used measures of climatic variability on a short-term scale (in the range of several decades), not accounting for stability on geologic timescales. This might indicate that long-term stability and short-term variability are not mutually exclusive, thus timescales have to be considered for climatic stability analyses.

Climatic rarity has a positive effect on endemicity and a negative one on species richness. Apart from filtering for pre-adaptation of colonizing species, endemicity in sites with rare climatic conditions is likely to be high, as these areas are generally unsaturated with regards to species richness (Wiens & Graham 2005). Also, they might offer empty ecological niches and are characterized by high selection pressures, due to their inherent climatic peculiarity, differentiating these habitats from the surrounding areas (Ohlemüller *et al.* 2008). Species colonizing isolated oceanic islands are more likely to be adapted to common climatic conditions (Steinbauer *et al.* 2013b, Weigelt & Kreft 2013), leading to a faster saturation of common and mesic-type habitats. In contrast, climatic rarity might generally result in spatially restricted and strong selection pressures (Ohlemüller *et al.* 2008), leading to niche shifts in colonizing organisms, higher speciation rates and higher endemicity (Nosil 2012). Indeed, our results are in accordance with Ohlemüller *et al.* (2008), who stated that, on a continental scale, small-range species are more common in rare climates. On La Palma high endemicity areas are dominated by small-range endemics, which are often specialised to specific and rare climatic conditions. A good example is the summit scrub, which is almost exclusively dominated by perennial woody endemics (Acebes Ginovés *et*

al. 2010; del Arco Aguilar *et al.* 2010), has a small area (~15 km^2) and offers the harshest growing conditions of the whole island (Garzón-Machado *et al.* 2013).

Spatial patterns of species richness, endemic richness and endemicity

The combined negative effect of both the elevation-temperature gradient and annual solar radiation indicate that high species richness is found in steep barrancos and coastal cliffs at low to mid elevations because low temperatures and high solar radiation are stressful for plant growth (Körner 2003). The main drivers of endemic richness on La Palma are topographic complexity, annual solar radiation and slope. Similar to species richness, the highest values of endemic richness are found in the steep barrancos, coastal cliffs and inner cliffs of the Caldera de Taburiente (Fig. 3b-c), although without the trade wind-induced asymmetry shown for species richness. Earlier studies were not able to identify such small-scale differences in endemic richness on the Canary Islands (e.g. Reyes-Betancort *et al.* 2008).

Highest values of endemicity are found at high elevations but also in the barrancos and coastal cliffs at low elevations on the western dry side of the island (Fig. 3d-e). High solar radiation at high elevations might select for adequate adaptation, while impeding the existence of most species that are adapted to conditions of lower radiation (Anthelme & Dangles 2012). This decreases general species richness and facilitates evolutionary adaptation processes, including ecological speciation of specialist endemics via UV-B radiation-induced mutagenesis (Flenley 2011). In addition high UV-B radiation is responsible for the evolution of characteristic life forms in the high elevations ecosystems. On La Palma, this becomes obvious in the presence of giant rosette plants such as several representatives from the genus *Echium*, and morphological adaptations such as pubescence (e.g. *Genista benehoavensis*, *Echium wildpreti* subsp. *trichosiphon*, *Plantago webbii* or *Teline stenopetala* subsp. *sericea*).

Interestingly, hotspots of species richness, endemic richness and endemicity are spatially decoupled on the landscape scale. In consequence, to conserve the whole spectrum of biological variation it is obviously not enough to only focus on species richness as a measure of biodiversity on the continental scale (Orme *et al.* 2005) or the island scale (Di Virgilio *et al.* 2014). Rather it is important to employ conservation strategies for a wide range of different habitats and various definitions of 'hotspot' to adequately cover and preserve the total breadth of species diversity (Stohlgren *et al.* 2005).

CONCLUSION

We suggest that future studies (e.g. using environmental niche modelling) need to acknowledge the effect of spatio-temporal climate variability and climatic rarity but also the equally important effect of topography, especially on the distribution of species richness and endemic richness (Platts *et al.* 2012). On the one hand, the general use of long-term means in modelling of climatic envelops in face of climate change has recently been criticised (Letten et al. 2013). On the other hand, models only based on climate will likely perform poorer than models that also include topographic components, highlighting the importance of using both climate and topography. In addition, we argue that endemics

might be more resilient towards ongoing climate change than previously thought because of their preadaptation to variable precipitation conditions. However, this needs to be investigated in future studies explicitly targeting climate change effects.

In general, high elevation islands such as La Palma offer the opportunity to study continental-scale environmental gradients with high species turnover and clearly defined zonal ecosystems on the landscape scale of a single island. These so-called climatic *mini-continents* host a large array of endemic species, which mainly evolved *in situ* under island conditions (especially SIEs; Whittaker *et al.* 2008). Thus, high elevation islands are optimally suited to provide further insights into the fundamental drivers of diversity and endemism, even possessing the possibility to transfer the gained knowledge to non-island systems.

ACKNOWLEDGEMENTS

REFERENCES

Acebes Ginovés, J.R., León Arencibia, M.C., Rodríguez Navarro, M.L., del Arco Aguilar, M., García Gallo, A., Pérez de Paz, P.L,, Rodríguez Delgado, O., Martín Osorio, V.E. & Wildpret de la Torre, W. (2010) Spermatophyta. In: Lista de especies silvestres de Canarias. Hongos, plantas y animales terrestres. 2009. Arechavaleta M, Rodríguez S, Zurita N, García A (eds.). Gobierno de Canarias, Tenerife, 122-172.

Anthelme, F. & Dangles, O. (2012) Plant–plant interactions in tropical alpine environments. Perspectives in Plant Ecology, Evolution and Systematics, 14, 363-372.

Ashcroft, M.B., Gollan, J.R., Warton, D.I., & Ramp, D. (2012) A novel approach to quantify and locate potential microrefugia using topoclimate, climate stability, and isolation from the matrix. Global Change Biology, 18, 1866–1879.

del Arco Aguilar, M.J., González-González, R., Garzón-Marchado, V. & Pizarro-Hernández, B. (2010) Actual and potential natural vegetation on the Canary Islands and its conservation status. Biodiversity and Conservation, 19, 3089-3140.

Beard, J.S., Chapman, A.R. & Gioia, P. (2008) Species richness and endemism in the Western Australian flora. Journal of Biogeography, 27, 1257-1268.

Bowen, L. & Van Vuren, D. (1997) Insular endemic plants lack defenses against herbivores. Conservation Biology, 11, 1249-1254.

Carracedo, H.C., Pérez Torrado, F.J., Ancochea, E., Meco, J., Hernán, F., Cubas, C.R., Casillas, R., Rodriguez, E. & Ahijado, A. (2002) Cenozoic volcanism II: the Canary Islands. The Geology of Spain (ed. by Gibbons, W. and Moreno, T.), pp. 439–472. Geological Society, London.

Climent, J., Tapias, R., Pardos, J.A. & Gil, L. (2004) Fire adaptations in the Canary Islands pine (Pinus canariensis). Plant Ecology, 171, 185-196.

Dewar, R.E. & Richard, A.F. (2007) Evolution in the hypervariable environment of Madagascar. Proceedings of the National Academy of Sciences, 104, 13723-13727.

Di Virgilio, G., Laffan, S.W., Ebach, M.C. & Chapple, D.G. (2014) Spatial variation in the climatic predictors of species compositional turnover and endemism. Ecology and Evolution, 4, 3264-3278.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., García Marquez J.R., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D. & Lautenbach, S. (2013). Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography, 36, 27-46.

Dormann, C.F, McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F., & Wilson, R. (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. Ecography, 30, 609-628.

Emerson, B.C & Kolm, N. (2005) Species diversity can drive speciation. Nature 434, 1015-1017.

Field, R., Hawkins, B.A., Cornell, H.V., Currie, D.J., Diniz-Filho, J.A.F., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M. & Turner, J.R.G. (2009) Spatial species-richness gradients across scales: a meta-analysis. Journal of Biogeography, 36, 132–147.

Flenley, J.R. (2011) Why is pollen yellow? And why are there so many species in the tropical rain forest? Journal of Biogeography, 38, 809-816.

Garzón-Machado, V., González-Mancebo, J.M., Palomares-Martínez, A., Acevedo-Rodríguez, A., Fernández-Palacios, J.M., Del-Arco-Aguilar, M. & Pérez-de-Paz, P.L. (2010) Strong negative effect of alien herbivores on endemic legumes of the Canary pine forest. Biological Conservation, 143, 2685-2694.

Garzón-Machado, V., Otto, R. & del Arco Aguilar, M.J. (2013) Bioclimatic and vegetation mapping of a topographically complex oceanic island applying different interpolation techniques. International Journal of Biometeorology, Early View, doi: 10.1007/s00484-013-0670-y

Giambelluca, T.W., Nullet, M.A. & Schroeder, T.A. (1986) Rainfall atlas of Hawai'i. Department of Land and Natural Resources, State of Hawai'i

Gillespie, R.G., Claridge, E.M. & Roderick, G.K. (2008) Biodiversity dynamics in isolated island communities: interaction between natural and human-mediated processes. Molecular Ecology, 17, 45-57.

Grueber, C.E. Nakagawa, S., Laws, R.J. & Jamieson, I.G. (2011) Multimodel inference in ecology and evolution: challenges and solutions Journal of Evolutionary Biology, 24, 699-711.

Hortal, J., Triantis, K.A., Meiri, S., Thébault, E. & Sfenthourakis, S. (2009) Island species richness increases with habitat diversity. The American Naturalist, 174, 205-217.

Hortal, J., Carrascal, L.M., Triantis, K.A., Thébault, E., Meiri, S. & Sfenthourakis, S. (2013) Species richness can decrease with altitude but not with habitat diversity. Proceedings of the National Academy of Sciences, 110, E2149–E2150.

Hua, X., & Wiens, J.J. (2013) How does climate influence speciation? The American Naturalist, 182, 1-12.

Irl, S.D.H. & Beierkuhnlein, C. (2011) Distribution of endemic plant species on an oceanic island – a geospatial analysis of La Palma (Canary Islands). Procedia Environmental Sciences, 7, 170-175.

Irl, S.D.H., Steinbauer, M.J., Babel, W., Beierkuhnlein, C., Blume-Werry, G., Messinger, J., Palomares-Martínez, Á., Strohmeier, S. & Jentsch, A. (2012) An 11-yr exclosure experiment in a high-elevation island ecosystem: introduced herbivore impact on shrub species richness, seedling recruitment and population dynamics. Journal of Vegetation Science, 23, 1114-1125.

Irl, S.D.H., Steinbauer, M.J., Epperlein, L., Harter, D.E.V., Jentsch, A., Pätz, S., Wohlfahrt, C. & Beierkuhnlein, C. (2014a) The hitchhiker's guide to island endemism - biodiversity and endemic perennial plant species in roadside and surrounding vegetation. Biodiversity and Conservation, 23, 2273-2287.

Irl, S.D.H., Steinbauer, M.J., Messinger, J., Blume-Werry, G., Palomares-Martínez, Á., Beierkuhnlein, C. & Jentsch, A. (2014b) Burned and devoured—Introduced herbivores, fire, and the endemic flora of the high-elevation ecosystem on La Palma, Canary Islands. Arctic, Antarctic and Alpine Research. Doi: 10.1657/1938-4246-46.4.

Jansson, R. (2003) Global patterns in endemism explained by past climatic change. Proceedings of the Royal Society of London. Series B: Biological Sciences, 270, 583-590.

Jenness, J.S. (2004) Calculating landscape surface area from digital elevation models. Wildlife Society Bulletin, 32, 29–839.

Johnson, J.B., & Omland, K.S. (2004) Model selection in ecology and evolution. Trends in Ecology & Evolution, 19, 101-108.

Kougioumoutzis K. & Tiniakou A. (2014). Ecological factors and plant species diversity in the South Aegean Volcanic Arc and other central Aegean Islands. Plant Ecology & Diversity, DOI: 10.1080/17550874.2013.866989.

Körner, C. (2003) Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems, 2nd edn. Springer, Basel.

Legendre, P. (2008) Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. Journal of Plant Ecology, 1. 3–8.

Letten, A.D., Ashcroft, M.B., Keith, D.A., Gollan, J.R. & Ramp, D. (2013) The importance of temporal climate variability for spatial patterns in plant diversity. Ecography, 36, 1341–1349.

Leutner, B.F., Steinbauer, M.J., Müller, C.M., Früh, A.J., Irl, S.D.H., Jentsch, A. & Beierkuhnlein, C. (2012) Mosses like it rough—Growth form specific responses of mosses, herbaceous and woody plants to micro-relief heterogeneity. Diversity, 4, 59-73.

Médail, F. & Diadema, K. (2009) Glacial refugia influence plant diversity patterns in the Mediterranean Basin. Journal of Biogeography, 36, 1333-1345.

Mee, J.A. & Moore, J.S. (2014) The ecological and evolutionary implications of microrefugia. Journal of Biogeography, 41, 837–841.

Millington, J.D., & Perry, G.L. (2011) Multi-Model Inference in Biogeography. Geography Compass, 5, 448-463.

Nagelkerke, N.J. (1991) A note on a general definition of the coefficient of determination. Biometrika, 78, 691-692.

Nosil, P. (2012) Ecological speciation. Oxford University Press, Oxford.

Ohlemüller, R., Anderson, B.J., Araújo, M.B., Butchart, S.H.M., Kudrna, O., Ridgely, R.S. & Thomas, C.D. (2008) The coincidence of climatic and species rarity: high risk to small-range species from climate change. Biology Letters, 4, 568-572.

Orme, C.D.L., Davies, R.G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V.A., Webster, A.J., Ding, T.S., Rasmussen, P.C., Ridgely, R.S., Sattersfield, A.J., Bennett, P.M., Blackburn, T.M., Gaston, K.J. & Owens, I.P. (2005) Global hotspots of species richness are not congruent with endemism or threat. Nature, 436, 1016-1019.

Platts, P.J., Gereau, R.E., Burgess, N.D., & Marchant, R. (2013) Spatial heterogeneity of climate change in an Afromontane centre of endemism. Ecography, 36, 518-530.

R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Reyes-Betancort, J.A., Santos-Guerra, A., Guma, I.R., Humphries, C.J., Carine, M.A. (2008) Diversity, rarity and the evolution and conservation of the Canary Islands endemic flora. Anales del Jardín Botánico de Madrid, 65, 25-45.

Richardson, D.M., & Whittaker, R.J. (2010) Conservation biogeography – foundations, concepts and challenges. Diversity and Distributions, 16, 313-320.

Rosenzweig, M.L. (1995) Species diversity in space and time. Cambridge University Press, Cambridge.

Shmida, A. & Werger, M. (1992) Growth form diversity on the Canary Islands. Vegetatio, 102, 183-199.

Slaton, M.R. (2014) The roles of disturbance, topography and climate in determining the leading and rear edges of population range limits. Journal of Biogeography, doi: 10.1111/jbi.12406

Steinbauer, M.J., Dolos, K., Field, R., Reineking, B. & Beierkuhnlein, C. (2013a) Re-evaluating the general dynamic theory of oceanic island biogeography. Frontiers in Biogepraphy, 5, 185-194.

Steinbauer, M.J., Irl, S.D.H. & Beierkuhnlein, C. (2013b) Elevation-driven ecological isolation promotes diversification on Mediterranean islands. Acta Oecologica, 47, 52-56.

Stohlgren, T. J., Guenther, D. A., Evangelista, P. H. & Alley, N. (2005) Patterns of plant species richness, rarity, endemism, and uniqueness in an arid landscape. Ecological Applications, 15, 715-725.

Stuessy, T.F., Jakubowsky, G., Salguero Gómez, R., Pfosser, M., Schlüter, P.M., Fer, T., Sun, B.-Y. & Kato, H. (2006) Anagenetic evolution in island plants. Journal of Biogeography, 33, 1259-1265.

Trigas, P., Panitsa, M. & Tsiftsis, S. (2013) Elevational gradient of vascular plant species richness and endemism in Crete – The effect of post-isolation mountain uplift on a continental island system. PLoS ONE, 8, e59425.

Walsh, R.P.D. & Lawler, D.M. (1981) Rainfall seasonality: Description, spatial patterns and change through time. Weather, 36, 201-208.

Weber, L.C., VanDerWal, J., Schmidt, S., McDonald, W.J., & Shoo, L.P. (2014) Patterns of rain forest plant endemism in subtropical Australia relate to stable mesic refugia and species dispersal limitations. Journal of Biogeography, 41, 222-238.

Weigelt, P., Jetz, W., & Kreft, H. (2013) Bioclimatic and physical characterization of the world's islands. Proceedings of the National Academy of Sciences, 110, 15307-15312.

Weigelt, P., & Kreft, H. (2013) Quantifying island isolation–insights from global patterns of insular plant species richness. Ecography, 36, 417-429.

Whittaker, R.J. & Fernández-Palacios, J.M. (2007) Island biogeography – Ecology, evolution, and conservation. 2nd Edition. Oxford University Press, Oxford.

Whittaker, R.J., Triantis, K.A. & Ladle, R.J. (2008) A general dynamic theory of oceanic island biogeography. Journal of Biogeography, 35, 977-994.

Wiens, J.J. & Graham, C.H. (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. Annual Reviews in Ecology, Evolution and Systematics, 36, 519–539.

Xu, C., Huang, Z.Y.X., Chi, T., Chen, B.J.W., Zhang, M. & Liu, M. (2014) Can local landscape attributes explain species richness patterns at macroecological scales? Global Ecology and Biogeography, 23, 436–445.

SUPPORTING INFORMATION IN ELECTRONIC VERSION OF DISSERTATION

Supporting Information. Additional information may be found in the online version of this article.

Appendix S1 List of all species identified in this study.

Appendix S2 List of each sample point, including coordinates, elevation, MAT, MAP, slope aspect, species richness, endemic richness and endemicity per sample point

Appendix S3 Maps of meteorological stations, bivariate correlation matrix of environmental variables, table of best fitting transformations for MLR, table of AICc values of transformations, and table of absolute values of variance partitioning

7.7 Manuscript 7

Impacts of global climate change on the floras of oceanic islands – projections, implications and current knowledge

David E.V. Harter[a,*], Severin D.H. Irl[a,b], Bumsuk Seo[c], Manuel J. Steinbauer[a], Rosemary Gillespie[d], Kostas A. Triantis[e], José-Maria Fernández-Palacios[f], Carl Beierkuhnlein[a]

[a] *Department of Biogeography, BayCEER, University of Bayreuth, 95440 Bayreuth, Germany*

[b] *Disturbance Ecology, BayCEER, University of Bayreuth, 95440 Bayreuth, Germany*

[c] *Biogeographical Modelling, BayCEER, University of Bayreuth, 95440 Bayreuth, Germany; and Ecological Modelling, BayCEER, University of Bayreuth, Dr.-Hans-Frisch-Str. 1-3, 95448 Bayreuth, Germany*

[d] *Department of Environmental Science, Policy and Management, University of California, 130 Mulford Hall, Berkeley, CA 94720, USA*

[e] *Department of Ecology and Taxonomy, Faculty of Biology, National and Kapodistrian University, Athens GR-15784, Greece; and Biodiversity Research Group, Oxford University Centre for the Environment, South Parks Road, Oxford, OX13QY, UK*

[f] *Ecology Department, Biology Faculty, La Laguna University, 38206 La Laguna, Tenerife, Canary Islands, Spain*

* Corresponding author. E-mail: david.harter@uni-bayreuth.de, Tel.: 0049 921 552211

ABSTRACT

Recent climate projections indicate substantial environmental alterations in oceanic island regions during the 21st century, setting up profound threats to insular floras. Inherent characteristics of island species and ecosystems (e.g. small population sizes, low habitat availability, isolated evolution, low functional redundancy) cause a particular vulnerability. Strong local anthropogenic pressures interact with climate change impacts and increase threats. Owing to the high degree of endemism in their floras, a disproportionally high potential for global biodiversity loss originates from climate change impacts on oceanic islands. We reviewed a growing body of research, finding evidence of emerging climate change influences as well as high potentials of future impacts on insular species and ecosystems. Threats from global climate change are not evenly distributed among the world's oceanic islands but rather vary with intrinsic (e.g. island area, structure, age and ecological complexity) and extrinsic factors (regional character, magnitude and rate of climatic alterations, local human influences). The greatest flora vulnerabilities to climate change impacts can be expected on islands of small area, low elevation and homogeneous topography. Islands of low functional redundancies will particularly suffer from high rates of co-modifications and co-extinctions due to climate-change-driven disruptions of ecological interactions. High threat potentials come from synergistic interactions between different factors, especially between climatic changes and local anthropogenic encroachments on native species and ecosystems. In addition, human responses to climate change can cause strong indirect impacts on island floras, making highly populated islands very vulnerable to secondary (derivative) effects. We provide an integrated overview of climate change-driven processes affecting oceanic island plants and depict knowledge gaps and uncertainties. The suitability of oceanic islands and their ecosystems for potential research on the field of climate change ecology is highlighted and implications for adequate research approaches are given.

Keywords: Global warming, island biogeography, island endemics, oceanic buffering, sea-level rise, susceptibility

INTRODUCTION

Oceanic islands have always been stimulating to scientists as natural showcases of ecology, evolution and biogeographical processes (*e.g.* Darwin, 1859; Wallace, 1880; MacArthur and Wilson, 1967; Carlquist, 1974; Whittaker and Fernández-Palacios, 2007). Their origin from oceanic crust and final erosion beneath sea level have been persistent and characteristic traits during all times of earth history, defining special conditions and time scales for evolution and extinction. Isolation from continental landmasses sets up an efficient filter for the immigration of terrestrial organisms to oceanic islands. Successful colonisers are confronted with novel environments and evolutionary opportunities, leading to unique species and species assemblages (MacArthur and Wilson, 1967; Gillespie and Roderick, 2002; Whittaker and Fernández-Palacios, 2007). Thus, oceanic islands generally have lower

overall species numbers per unit area (Whittaker and Fernández-Palacios, 2007) but show higher percentages of endemism than mainland areas (Kier et al., 2009). As a consequence, the extremely limited insular areas host a disproportional high fraction of global biodiversity (Kreft et al., 2008; Kier et al., 2009).

Although most climate change research is focused on continental ecosystems, ocean regions, too, will be affected by global climate change. For many oceanic islands, changing temperatures and precipitation patterns, shifting frequencies and intensities of extreme weather events (*e.g.* droughts, storm surges, hurricanes), have altered patterns of seasonal and mid-term weather systems (El Niño Southern Oscillation, monsoon, etc.) and sea level rise can be expected (IPCC, 2012, 2013b). These changes can pose profound and challenging environmental alterations to terrestrial biota in general (*e.g.* Jump and Peñuelas, 2005; Parmesan, 2006; Cahill et al., 2013), but have specific relevance for island biota (Loope, 1995; Mimura et al., 2007; Caujapé-Castells et al., 2010; Fordham and Brook, 2010; Bramwell, 2011).

This specific relevance is due to several aspects of oceanic islands: First, as a consequence of their isolated evolution, oceanic island species are often insufficiently prepared to changing environments (Cronk, 1997; Gillespie et al., 2008; Fordham and Brook, 2010). For plants on oceanic islands, Carlquist (1974) introduced the "island syndrome", meaningi) a tendency to reduce their dispersability (see also Cody and Overton, 1996; Fresnillo and Ehlers, 2008; Gillespie et al., 2012), ii) a tendency to be poor competitors in the face of introduced species and iii) a lack of defensive mechanisms against (non-native) herbivores (see also Bowen and Vuren, 1997; Vourc'h et al., 2001). Second, the restricted areas of oceanic islands and the surrounding ocean limit the options of island species to migrate and escape potentially deteriorating conditions via range shifts. This requires affected species to either retreat to potential refuge habitats within their island (if available and within reach), adapt rapidly to changing conditions or to become extinct (Gillespie et al., 2008; Levine et al., 2008). Third, due to the restricted size of oceanic islands, the total range of endemics is also comparably small. This is usually connected to a low overall population size, leading to higher vulnerability to stochastic (but also deterministic) threats (Kruckeberg and Rabinowitz, 1985; Gilpin and Soulé, 1986; Frankham, 1998; Gillespie et al., 2008). Especially very narrow endemics, which represent a high percentage of oceanic islands' biodiversity (*e.g.* Sakai et al., 2002), are likely to exhibit low tolerances and a high vulnerability to extrinsic disturbances (Kruckeberg and Rabinowitz, 1985; Lavergne et al., 2004; Hermant et al., 2013). Also, oceanic isolation acts as a very efficient dispersal filter, drastically limiting the potential of species' responses to ecological shifts, such as climate change, by migration to other landmasses.

The imminent sensitivity of many island endemics to rapid environmental changes and extraordinary encroachments is reflected in the disproportionally high numbers of extinctions after human arrival on remote islands (Cronk, 1997; Sadler, 1999; Steadman, 2006; Caujapé-Castells et al., 2010; Fordham and Brook, 2010). Although this pattern is more obvious for animals than for plant species (*e.g.* Sax et al., 2002; Whittaker and Fernández-Palacios, 2007), numerous examples prove novel anthropogenic stressors (introduction of neobiota, selective use or exploitation, land use and habitat destruction) have caused past and current losses of island endemic plant species (*e.g.* Bouchet et al.,

1995; Jaffre et al., 1998; Sadler, 1999; Luz et al., 2003; Fall, 2005; Schäfer, 2005; Prebble and Dowe, 2008; Meyer and Butaud, 2009; Baider et al., 2010; Connor et al., 2012; Restrepo et al., 2012). Besides already irreversible losses, extinction debts and cases of imminent extinctions are also common in oceanic island floras (Sakai et al., 2002; Sax and Gaines, 2008; Kaiser-Bunbury et al., 2010; Heywood, 2011) and other island organisms (Triantis et al., 2010; Halley et al., 2014).

Compared to local human encroachments, global climate change alters environmental conditions beyond the island scale. Despite some climatic buffering effects by the surrounding oceans, climate change thus has the potential to significantly affect island biota. Evidence from Quaternary climatic alterations suggests substantial ecological shifts on oceanic islands, including losses of plant species (*e.g.* Loope and Giambelluca, 1998; Pau et al., 2012; Boer et al., 2013; Nogué et al., 2013). Current observations of vegetation changes due to climate alterations suggest even stronger climate effects on plant life when climatic changes proceed into the future (*e.g.* Roux and McGeoch, 2008; Kapfer et al., 2012; Krushelnycky et al., 2013). Species vulnerability modelling according to 21st century climate change scenarios showed that considerable proportions of island plants are threatened by future conditions, *e.g.* by strong shifts or even complete losses of climatic niches of some species (*e.g.* Fortini et al., 2013 for Hawaiian plants, or Marrero-Gómez et al., 2007; Lloret and González-Mancebo, 2011; Patiño et al., 2013 for the Canary Islands). Taken together, insights from past climatic changes, current trends and projections of future conditions show that oceanic islands and their floras are affected by climatic alterations and that oceanic buffering, although undoubtedly existent, cannot be generally expected to shelter those systems.

Extinctions of oceanic island plants by climate change would contribute disproportionally to global biodiversity decline (Mimura et al., 2007; Fordham and Brook, 2010). This is particularly true considering that about one quarter of all vascular plant species are endemic to islands (sharing only 5 % of the Earth's land area, not considering Greenland), many to oceanic islands (Kreft et al., 2008). However, specific literature on climate change impacts on oceanic island floras is scarce. Apart from case studies of potential local climatic alterations and resulting environmental consequences on selected species (*e.g.* Roux et al., 2005; Marrero-Gómez et al., 2007; Levine et al., 2008; McEachern et al., 2009; Shapcott et al., 2012; Krushelnycky et al., 2013) or on particular ecosystems, single islands or oceanic regions (*e.g.* Sperling et al., 2004; Gillespie et al., 2008; Wetzel et al., 2012; Fortini et al., 2013; Scott and Kirkpatrick, 2013; Bellard et al., 2014), general examinations of impacts and potential influences of global climatic change on island plants are yet missing. Thus, the aims of this study are i) to evaluate current climate change effects on oceanic island floras and discuss possible scenarios of climate-change driven impacts on island plant diversity, ii) to assess how island- and species-specific characteristics may either intensify or attenuate impacts of climate change, and iii) to identify knowledge gaps and research challenges.

CLIMATE CHANGE PATTERNS AMONG ISLAND REGIONS

Global temperature and precipitation change on oceanic islands

Oceanic islands are defined in this study as islands that have never had contact to other landmasses, including islands of volcanic or coralline origin, as well as raised coral or limestone islands and all intermediate forms. We compiled and analysed data on mean annual temperature and mean annual precipitation changes on such islands worldwide, based on median climate simulation outputs by recent CMIP5 model ensembles (Coupled Model Intercomparison Project Phase 5, Taylor et al., 2012) for three future time periods and four greenhouse gas scenarios, respectively.

For this purpose, a dataset of globally distributed islands were obtained from the UNEP-based Island Directory Website (Dahl, 1991; http://islands.unep.ch/isldir.htm), which includes nearly 2000 islands with important island variables, including geological origin. Starting from this dataset we extracted all oceanic islands. Missing geological information on some islands was added if available in the literature and internet sources and all records were checked carefully. Coordinates were corrected (if necessary) and permanent isolation from other landmasses (surrounding sea depth of min. 160 m) was assured by visual assessment of bathymetry in GoogleEarth™ version 7.1.2.2041 (Google Inc. 2013), resulting in a final data set of 787 oceanic islands.

CMIP5-based, multi-model ensemble projections for global mean temperature above surface and precipitation were downloaded from the IPCC AR5 (Intergovernmental Panel on Climate Change fifth assessment report, IPCC, 2013b) publication and data download homepage (http://www.climatechange2013.org/report/full-report/). These data are presented and described in Annex I of the WGI report (IPCC, 2013a) and include twenty-year average changes for the near term (2016–2035), mid-term (2046–2065) and the long term (2081–2100), relative to a reference period of 1986–2005. For each period, data for four Representative Concentration Pathway scenarios (RCP 2.6, RCP 4.5, RCP 6.0 and RCP 8.5; Vuuren et al., 2011) were obtained. From the 42 CMIP5 climate models in total, RCP 2.6 projections are based on an ensemble of 32, RCP 4.5 on the full 42, RCP 6.0 on 25, and RCP 8.5 on 39 model experiments, respectively (IPCC, 2013b). Spatial data was given on a 2.5° grid, consisting of regional median, 25%- and 75%-quantile responses of the respective model ensemble. The conversions of the original netCDF files to raster grids, the extraction of the raster values and their subsequent analyses were carried out with R 2.15.2 (R Core Team, 2012) using the packages 'raster' (Hijmans, 2013) and 'RNetCDF' (Michna, 2012).

To compare climate change projections for oceanic islands with the expected worldwide changes , we additionally analysed projection values from continental grid cells, and, to account for putatively differing coastal climates, from grid cells of coastal areas, including large continental islands. In obtaining continental climate change data, we identified cells that were entirely covering landmasses, i.e. purely inland pixels with no contact to seashores (hereafter termed 'continental'). For 'coastal' climate change expectations, we selected cells that contained shorelines of landmasses bigger than 100000 km^2 (to illustrate, the North Island of New Zealand has an area of 113729 km^2). The latitudinal

range of oceanic islands in our data set ranged from -69° S to 71° N. To assure a reasonable comparison, we restricted the latitudinal range of our coastal and continental grid cell selection to the latitudinal range of -75° S to 75° N, yielding 1331 coastal and 1885 continental pixels in total. Values were extracted from all pixels, respectively, and analysed in the same way as the oceanic island values.

Mean annual temperature is projected to increase appreciably for our set of 787 islands, indicated by consistently positive directions in average change values among greenhouse gas scenarios (Fig. 1A). Model uncertainty for temperature (represented by the vertical extension of boxes in Fig 1A, showing the upper and lower average quartiles) is moderate. According to average median values, RCP 2.6 would likely result in average temperature increases below 1 °C even at the end of the century, whereas this is true in the other scenarios only for the near term future (period 2016 – 2035). For the mid-term (2046 – 2065) future, increases between ~1 °C (RCP 4.5 and RCP 6.0) and 1.5 °C (RCP 8.5) are possible, and for the long-term future (2081 – 2100) temperature increases range from 1.3 °C (RCP 4.5) to 1.6 °C (RCP 6.0) and even 2.8 °C (RCP 8.5).
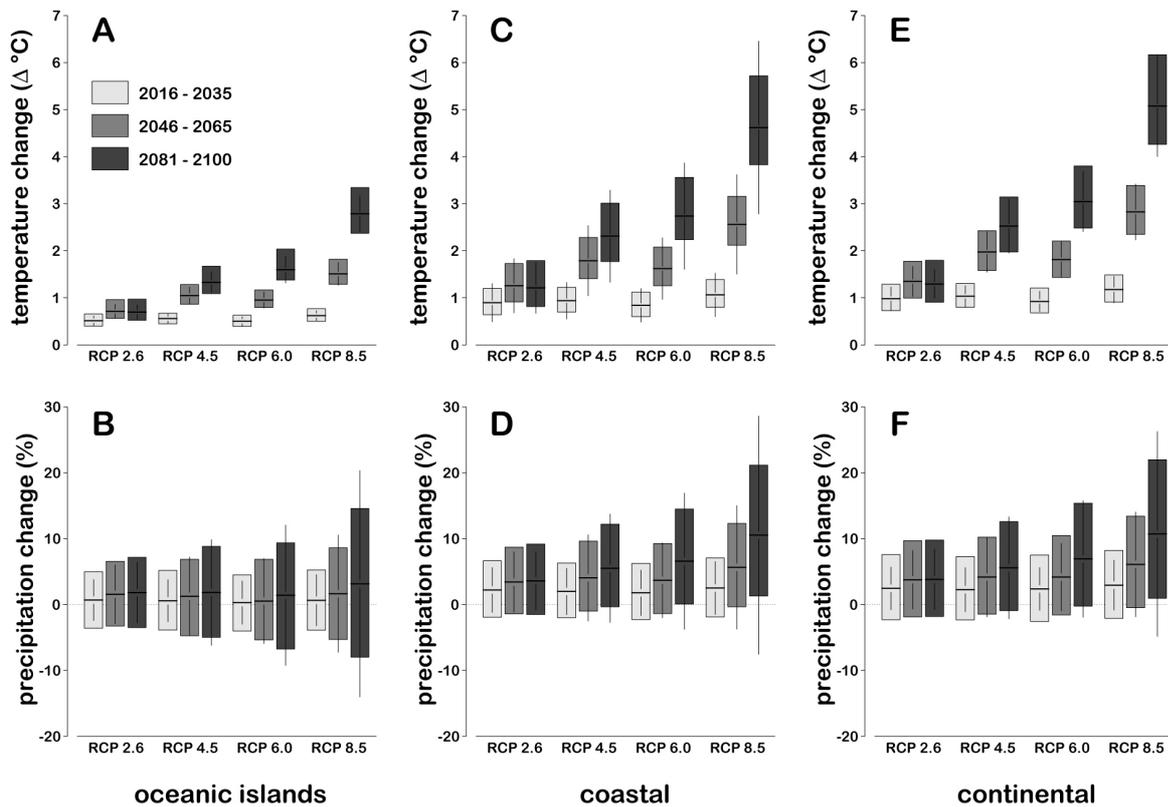

Fig. 1: Average absolute temperature change (A) and percentage precipitation change (B) projections over 787 oceanic islands in the course of the 21st century according to four different greenhouse gas concentration scenarios (RCPs). Single island values were based on regional median model outputs of CMIP5 simulation ensembles (32/42/25/39 out of 42 scenario experiments for RCP 2.6/4.5/6.0/8.5, respectively). Reference period is 1986 – 2005. Boxes show the averaged medians (central horizontal bar) and averaged upper and lower quartiles (upper and lower horizontal bars, respectively) of the climate model ensembles over the whole set of islands to indicate the model variability. The vertical lines depict the standard deviations of averaged medians among islands to show the large differences among islands.

However, there is a large geographic variation (indicated by the error bars in Fig. 1, showing the standard deviation among islands for the given median model response), which increases in long-term projections. Likewise, the overall uncertainty among climate models (the interquartile distance) is higher for the long-term simulation ensembles. For mean annual precipitation, the pattern is less distinctive (Fig. 1B). The average median model response indicates slightly more precipitation for the majority of islands in the future and an increasing trend towards the end of the century (from below 1% in all near-term projections to 1.8 – 3.2% for the period 2081 – 2100, the latter value being the average median for RCP 8.5). Nevertheless, there is a huge variation among islands (standard deviations ranging from 3.4% to 18.1%) and among climate model outputs within simulation ensembles. Both types of variability are indicated to increase from moderate to high greenhouse gas scenario and from near-term to long-term projections. This means strong uncertainties in projecting even the direction of precipitation change for many oceanic islands, considerably depreciating the robustness of assessments of future climatic conditions. Limited predictability of precipitation developments is a known source of uncertainty in climate projections (see below and discussion of precipitation projections and model variance in IPCC, 2013b and Lee and Wang, 2014). Lack of direct observations, methodological uncertainties and high geographical trend variation as well as high variability of major climate drivers like the El Niño-Southern Oscillation (ENSO) and climate oscillations of longer duration (*e.g.* Pacific Decadal Oscillation) may account for this uncertainty (Mote et al., 2011; Keener et al., 2012; IPCC, 2013b).

It should also be noted that large-scale precipitation projections might disregard influences of island topographies on precipitation patterns on smaller scales. High-elevated islands often possess a diversity of mesoclimates due to orographic cloud formation, luv/lee-effects and other topographically determined climatic patterns resulting in heterogeneous precipitation patterns among island regions and/or elevational zones (Whittaker and Fernández-Palacios, 2007). Further on, many oceanic islands have highly structured landscapes of valleys and ridges with broad and steep slopes, which can generate numerous micro-climatic conditions. Both, regional differences within islands and small-scale landscape structures potentially constitute climatic micro-refugia for species during climate change (see *e.g.* Hannah et al., 2014 for general considerations of micro-refugia). Additionally, it is possible that climate change impacts will vary among different areas within islands, *e.g.* increasing humidity in windward slopes but drying conditions in leeward island areas due to disparate changes in cloud formation or cloud layer elevation leading to changing rain shadow effects (Scholl et al., 2007; Chu et al., 2010). While large-scale projections can show regional trends important for general change perspectives, fine resolution island-scale climate models and downscaled climate projections will be necessary to account for geographical variation within high-elevated oceanic islands and to provide better resolved scenarios.

Likewise, large-scale temperature projections in general only refer to air temperatures close to the water surface and thus do not entirely represent the potential changes on small oceanic islands with extents much smaller than the climate model resolution (Mimura et al., 2007; Heywood, 2011; Nurse and McLean, 2014). Air temperature increases above land surfaces on islands might exceed projections

for the surrounding open sea surfaces (Mimura et al., 2007) due to the lower specific thermal capacity of land surface. This could lead to a possible underestimation of temperature changes in current climate models.

The projections for oceanic islands differ from those for coastal and continental regions. Although of appreciable magnitude, temperature increases are projected to be lower on islands (Fig. 1A, C and E). This indicates an oceanic buffering effect that attenuates air temperature increases, probably by the relatively high heat capacity of large water masses surrounding the islands (Kutzbach and Webb III, 1993). While for the near future differences lie within a 1 °C range for all RCP scenarios, mid and long term projections show that average temperature increases in coastal and continental regions may exceed those of oceanic islands by more than 2 °C (RCP 8.5). Interestingly, temperature increase in continental regions is projected to become only very slightly higher than in coastal regions, showing a strong influence of large landmasses to climate conditions even in marginal regions, compared to the peculiar situation of oceanic climates. This difference between oceanic and non-oceanic regions is also true for precipitation change projections (Fig. 1 B, D and F). While no qualitative difference is observable between coastal and continental regions, averaged projections for oceanic islands show lower average increases of precipitation and more drying trends in some climate models. Also, the increase of precipitation during the course of the 21st century seems to be smaller for oceanic islands than for other landmasses. This shows that climate change on oceanic islands may differ in some aspects compared to other terrestrial regions of the world.

Regional variation of change and drivers of variability

Observed and projected changes in climate are known to differ regionally (IPCC, 2013b). For our dataset of 787 islands, projected changes in temperature and precipitation for the period 2081 – 2100 under the medium to high greenhouse gas scenario RCP 6.0 are given in Fig. 2.

Temperature increase is indicated to be highest on arctic and sub-arctic islands (*e.g.* Jan Mayen, Aleutian Islands, Kuril Islands 2.5 – 4.9 °C) and in equatorial regions (*e.g.* Galápagos, Gulf of Guinea islands 2 – 2.5 °C; Fig. 2A). Also, the southernmost Antarctic oceanic islands show high increases (*e.g.* Peter-I-Island 2 – 2.5 °C). However, contrasting to northern-hemispheric regions it is observable that most islands in southern ocean regions seem to expect comparably moderate temperature increases (0.8 – 1.5 °C). According to this, an inversely hump-shaped relationship between the simple latitudinal gradient from the Antarctic oceans to Arctic oceans and projected temperature change explains considerable portions of the spatial variance (R^2 = 0.49; Fig. A.1A, see appendix for a description of regression models).

As already indicated in Fig. 1, coastal and continental regions are projected to receive higher temperature increases in general (Fig. A.1A). However, especially in low (equatorial) latitudes temperature increase projections for islands and coastal regions overlap while continental regions seem to exceed oceanic values more continuously, confirming the oceanic buffering effect. Supporting this, the

increase in temperature on islands is slightly negatively related with distance to the next continent (R^2 = 0.18; Fig. A.1B), which indicates an increasing influence of oceanic buffering and a decreasing influence of continents on climate conditions and climatic changes on islands.

Besides latitude, the position in ocean currents or major climate systems is crucial for the macro- and mesoclimatic conditions of an island or archipelago, which is especially important for precipitation patterns. In our analysis, strong increases of precipitation are indicated in equatorial islands (especially Pacific: southern Line Islands up to 55%, Gilbert Islands up to 50%, Galápagos 30 – 40%; but also Gulf of Guinea islands or Maldives up to 20%) and in polar islands (*e.g.* Jan Mayen, Aleutian Islands, Peter-I.- Island up to 20%; Fig. 2B). Projections vary strongly among regions in mid latitudes. Slight increases (up to 10%) are mainly projected for large parts of the western Pacific and for southern oceanic regions in general. In contrast, projections for central and eastern parts of the Pacific, central parts of the Indian Ocean and most Atlantic Ocean regions, including the Caribbean, indicate decreases in mean annual precipitation. Strongest decreases (-10 to -15.6%) are predicted for southeastern French Polynesia, Pitcairn Islands, Easter Island, Juan Fernández and Desventuradas Islands, some of the Lesser Antilles, Trindade and Martim Vaz, Ascension, Madeira and Aeolian Islands. A moderately distinct overall geographic pattern can thus again be described by an inversely hump-shaped relationship between precipitation change and absolute values of latitude (R^2 = 0.48; Fig. A.1C). This pattern is far more distinct for oceanic islands than for coastal and continental regions due to the exceedingly high precipitation increases in circum-equatorial ocean regions contrasting to declines or constancy in precipitation amounts in subtropical high pressure belt regions (Fig. A.1C), and seems to be a likely future phenomenon (see also Keener et al., 2012; IPCC, 2014; Lee and Wang, 2014; Nurse and McLean, 2014). Additionally, for many regions, trends indicate above average precipitation in regions of originally high precipitation and a further decline in regions of low precipitation (IPCC, 2014), but this pattern is less prominent in the recent CMIP5 results compared to older projections (Lee and Wang, 2014). It has to be noted that increasing precipitation can also have negative effects, especially on originally dry ecosystems (*e.g.* by facilitation of invasive species and outcompeting of dry-adapted endemics), as stated for the Galápagos archipelago by Trueman and d'Ozouville (2010).

However, some differences between outputs of different climate models and their versions account for uncertainties and limited regional predictability, particularly for precipitation. Difficulties in simulating future alterations of precipitation in mid and low latitudes are due to their dependence on rather unpredictable large-scale climate systems. On tropical and subtropical islands, climate changes are often associated with dynamics of El Niño occurrences (*e.g.* Cao et al., 2007. The El Niño-Southern Oscillation (ENSO) interacts with a variety of large-scale atmospheric and oceanic circulation systems and is thus related to inter-annual variability in temperature and precipitation. ENSO variability is naturally very high and its sensitivity to human-induced climate change is still not proven (Collins et al., 2010). However, there is evidence for an increase in ENSO variability during the twentieth-century (Cobb et al., 2013). Higher ENSO activity is associated with larger climate variability and fluctuations of

the Inter-Tropical Convergence Zone (ITCZ) and thus trade wind regimes, which are major determinants of climatic conditions on low and mid latitude islands (Crausbay et al., 2014b).
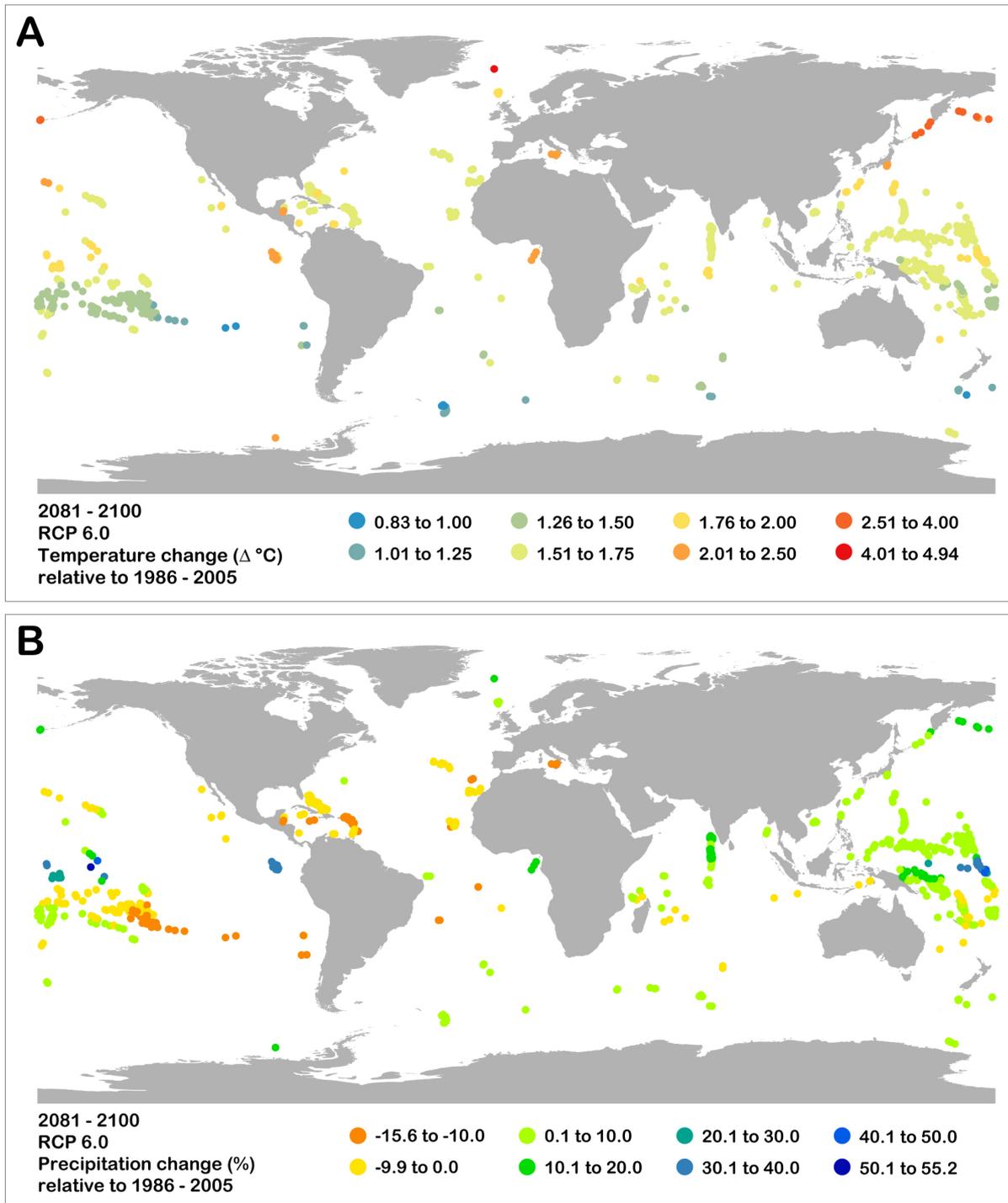
Fig. 2: Maps of (A) projected temperature change and (B) projected precipitation change on 787 oceanic islands for the end of this century (2081 – 2100) under the medium to high greenhouse gas concentration scenario RCP 6.0, based on regional median response projections over 25 climate models. Note that the scale subdivision for temperature change is not linear anymore beyond the 2 °C increase. Data were compiled from the IPCC AR5 publication and data download homepage (http://www.climatechange2013.org/report/full-report/).

Alterations of seasonal patterns may have high impacts on ecosystems, especially when precipitation patterns in the seasonal cycle change (IPCC, 2013b). Global monsoon activity is expected to rise with an increase in global surface temperature. For global oceanic regions this means an 6.3 % spread of the overall monsoon domain, a longer monsoon period duration and increased monsoon rainfall, especially for the northern hemisphere (NH; Lee and Wang, 2014). In large parts of the southern hemispheric (SH) oceanic regions, significant decreases are projected, a pattern due to the higher temperature and thus higher humidity increase in the NH, compared to the SH (Lee and Wang, 2014).

Alterations in temperature seasonality will especially affect islands at higher latitudes, where projected temperature increases are higher and more pronounced for winter periods (IPCC, 2013b). This can extend vegetation periods (Parmesan, 2007) but also may increase the associated potential risks of late frost events (Kreyling, 2010).

Extreme weather events (*e.g.* droughts, heavy precipitation events, heat waves, storms with increased wind speeds, tropical cyclones) can cause very effective pulse disturbances to ecosystems and species, additional to impacts from changes in long-term average conditions (Jentsch and Beierkuhnlein, 2008; IPCC, 2012). This might have particular relevance for oceanic islands due to their small ecosystems and (endemic) species' ranges, allowing for more comprehensive impacts compared to larger continental systems. However, only little information is available on climate and weather extreme shifts in oceanic island regions, which is due to a lack of long-term observational data and high uncertainties in projecting the frequency or strength of such anomalies in oceanic regions (IPCC, 2012).

Heavy precipitation events have showed a decrease in frequency since the 1950s in many Pacific regions, *e.g.* Hawaii (Chu et al., 2010; Elison-Timm et al., 2011), Guam (Lander and Guard, 2003) or Pohnpei Island, Micronesia (Lander and Khosrowpanah, 2004). Nevertheless, large scale projections for the 21st century indicate regionally highly variable trends for frequencies and intensities of heavy rain days as well as for drought events for large parts of the south-western Pacific (Australian Bureau of Meteorology and CSIRO, 2014). While there is high confidence for increasing frequencies of daily temperature extremes in almost any analysed region, considerable uncertainties remain in projections of precipitation extremes. Depending on the region and model, decreasing, stable and increasing extreme event frequencies and intensities have been projected, with very variable confidence statements (Australian Bureau of Meteorology and CSIRO, 2014). For the Indian Ocean, Cai *et al.* (2014) found that anomalously dry condition events due to decadal occurrences of wind and oceanic current reversals (positive Indian Ocean Dipole events) will appear nearly three times more often in the 21st compared to the 20th century. This will probably result in higher frequencies of extremely high precipitation events in north-western parts of the Indian Ocean but negative rainfall anomalies especially in equatorial western and in tropical and sub-tropical regions of the southern hemispheric Indian Ocean.

Tropical cyclone activity and intensity especially in the Pacific is influenced by the ENSO (Chand et al., 2013). Generally, surface temperatures and the resulting availability of more energy directly affect

tropical cyclones. There is remaining uncertainty about the future frequency but large consensus that these storm systems (also known as hurricanes or typhoons) will increase in intensity (2–11 % by 2100; Knutson et al., 2010) and shift polewards (Graff and LaCasce, 2012; see also Arozena Concepción et al., 2008 for effects of a storm surge on laurel forests on Tenerife and Whinam et al., 2014 for damage on the Macquarie Island endemic *Azorella macquariensis* by changing wind conditions). Besides tsunamis (which occur much less often), tropical cyclones are associated with the most extreme temporal sea level rises (Walsh et al., 2012) and can strongly affect species composition and ecosystem dynamics on oceanic islands (Terry and Chui, 2012; Webb et al., 2014).

Most of the overall biodiversity of oceanic islands is located on high elevation islands in the tropics and subtropics. On many of those islands, trade wind-induced orographic uplift of humid air masses and orographic cloud formation provide considerable direct or indirect (fog drip) precipitation (Scholl et al., 2007) and thus account for (elevational) zonation of ecosystems, each with own species assemblages. However, cloud layer elevations and orographic cloud formation (and thus rainfall, solar radiation, temperature and humidity patterns on islands) depend on the trade wind inversion layer, which shows increasing variability in its occurrence and elevation (e.g. Cao et al., 2007; Lauer et al., 2013). Concomitant changes of precipitation distributions on these islands pose the most significant uncertainty for ecosystems and could be main drivers of biodiversity change on high oceanic islands (Loope and Giambelluca, 1998; Diaz et al., 2011). Especially windward cloud forests with their high endemism do strongly depend on constant humid or wet conditions (Crausbay and Hotchkiss, 2010). Locally there are contrasting projections about whether the thermal inversion layer and the associated cloud formation is shifting upward (Still et al., 1999) or downward (Sperling et al., 2004; Lauer et al., 2013), both of which would endanger highly adapted ecosystems. Again, the ENSO and fluctuations of the ITCZ have a large influence on the occurrence and height of trade wind inversions and have been shown to strongly affect regional climate variation and local plant life (Trueman and d'Ozouville, 2010; Crausbay et al., 2014b).

Sea level rise

Rising sea levels due to thermal extension of oceanic water volumes and melting glaciers and polar ice caps probably pose the most apparent threats for flat islands like atolls but also for coastal plains of higher elevated islands. IPCC projections range from 0.26 m to 0.82 m with regional differences until the end of this century compared to the 1980 – 1999 period (IPCC, 2013b). Other estimates indicate sea level rises between 0.7 – 1.2 m (Horton et al., 2014) or 0.75 – 1.9 m (Vermeer and Rahmstorf, 2009; Jevrejeva et al., 2014) in high warming scenarios. Assuming a rapid melt of global ice-sheets, which is also reported for past global warming periods in the Pleistocene, even up to more than six meters to the end of the century can be possible (Overpeck et al., 2006). Also, recent satellite-based actual ice loss detections (McMillan et al., 2014),updates of glacier retreat and ice drainage velocity in Antarctica (Rignot et al., 2014) as well as new data on glacial valley depth and subaqueous glacier

melting in Greenland (Morlighem et al., 2014) suggest that sea level rise projections might have to be corrected upwards.

Landward shifts of shorelines and concomitant loss of habitat area would have consequences for coastal island ecosystems (Menon et al., 2010; Wetzel et al., 2012; Bellard et al., 2014). Sea level rises will most likely lead to the total and permanent inundation of low elevation islands and island states (such as Kiribati, Maldives, Marshall Islands, Tuvalu; Wong et al., 2005). Wetzel *et al.* (2013) calculated for islands the Southeast Asian Pacific region that a sea level rise of 1 m leads to complete inundation losses of 14.7 % (61.7 % with 6 m sea level rise) of the considered islands, and that 18.9 % (20.5 %) of all islands would lose 50 – 99 % of their terrestrial area. For Oceania (with major Pacific island regions, including Hawaii) this would mean a 3.9 % (14.5 %) loss of island area in total (Wetzel et al., 2013). It has to be noted though that the most affected low islands and atolls host comparably low numbers of endemics, which might limit direct effects of sea level rise to global biodiversity changes. However, affected islanders might have to translocate their settlements and land-use to higher regions (Wetzel et al., 2012) or congregate on other (higher elevated) islands, potentially causing secondary effects to primarily unaffected regions.

FACTORS CONTRIBUTING TO OCEANIC ISLAND PLANT VULNERABILITIES TO GLOBAL CLIMATE CHANGE

Oceanic islands vary in geographical, ecological and anthropogenic settings, which determine the specific risks and vulnerabilities towards different climate change impacts. In the following subchapters we discuss the most important factors and their interactions with climate change impacts regarding oceanic island floras. Tab. 1 gives a summary of the introduced concepts.

Vulnerability is defined here as the degree to which climatic changes are capable to result in significant (mostly negative) responses and modifications of a system, applying for individuals, populations, species, ecosystems or entire islands and regions, and being determined by the system's exposure to climate change impacts, its sensitivity to these impacts, and its capacity to respond (*e.g.* tolerate, adapt, migrate).

Island area

The role of area and habitat space for intra-island range shifts

Species' distributions and abundances depend on climatic factors, forcing species to track their climatic demands by range shifts during periods of climate changes (Parmesan, 2006; Thomas, 2010). The most fundamental prerequisite for successful dispersal is the availability of suitable habitats including adequate substrate or biotic interactions (*e.g.* pollinators), and without anthropogenic restrictions (*e.g.* fragmentation, settlements, land use). Referring to the large-scale climatic changes and the comparably small spatial extent of islands, the opportunities for island species to shift their ranges in climate-relevant

latitudinal (or longitudinal) extents and to maintain population size and genetic variability are very restricted. Nevertheless, the existence of old (pre-Pleistocenic) relict species (*e.g. Laurus novocanariensis* and *Woodwardia radicans* on the Macaronesian Islands) and neo-endemic lineages document the long-term persistence of island populations (see also Fernández-Palacios et al., 2011). Larger islands often contain more habitat space and diversity, likely providing more spatial and ecological opportunities for species to escape unfavourable conditions than small islands (see Triantis et al., 2003 and Kisel et al., 2011 for general consideration of area and habitat diversity).

Large islands also tend to have higher elevations than small islands (Weigelt et al., 2013). Referring to rising temperatures, upward shift on mountainous elevations can provide compensation of lost habitats. However, area declines with elevation, wind speed may increase, and precipitation patterns may differ from original habitats, which makes the finding of suitable conditions in high elevations uncertain for species from lower zones. It has been shown that water stress is an important determinant of high elevation species distributions on oceanic islands (*e.g.* Brito et al., 2014; Crausbay et al., 2014b). Considering strong temperature increases in high elevations (Giambelluca et al., 2008; Keener et al., 2012), stable or decreasing moisture conditions in the future thus can powerfully restrict upslope migration, generating great vulnerabilities of high elevation island species to climate change (Crausbay et al., 2014b). Also, on many islands in the tropics and subtropics, trade wind inversion layers create a strong elevational zonation in precipitation, including a sharp transition on the windward sectors from very humid conditions in cloud contact elevations to dry conditions above those cloudbanks. These ecotones potentially act as barriers for plant species' upward shifts.

Island area shaping population sizes

An island's carrying capacity for a particular species (*i.e.* its maximum population size) is determined, among other factors, by habitat availability, which in turn is a function of the area of the island. Therefore, island area controls overall population sizes and, thus, response or adaptation capacity of populations (Hanski, 2010). Small populations are more exposed to risks of decline or extinction than larger populations, mainly due to demographic and environmental stochasticity (Gilpin and Soulé, 1986; Marrero-Gómez et al., 2007; Caujapé-Castells et al., 2010). Also, low genetic variability and an associated limitation of adaptational potential (Willi et al., 2006), higher inbreeding rates (homozygosity, genetic erosion) and higher impacts of genetic drift may cause instability in small populations (Ellstrand and Elam, 1993; Frankham, 1997; Schaal and Leverich, 2005). In consequence, rare or spatially very restricted species are expected to be more vulnerable to climate change impacts (Ditto and Frey, 2007; Williams et al., 2008; Thomas et al., 2011; Fortini et al., 2013). This suggests that the area of an island correlates negatively with vulnerabilities of inhabiting plant species to climate change, especially for single island endemics. However, small islands host few endemic plants (often none at all, but see Junak and Philbrick, 1999; Florens and Baider, 2006), limiting their general contribution to potential global biodiversity loss. It should also be mentioned that rarity (*i.e.* small population sizes) does not necessarily imply proneness to extinction (Gaston, 1994; Mace and Kershaw, 1997). Some naturally rare species

have evolved resistance to inbreeding and mutational load and show traits that can be seen as adaptations to conditions and processes associated with their rarity, *e.g.* increased self-compatibility or asexuality, reduced dispersal or specialised floral traits (Karron, 1997; Orians, 1997).

Island origin and topography

Geological, topographic and edaphic structuring

Although originally based on volcanism, oceanic islands embrace diverse island types with different geological origination. Generally, the following formation histories are shared: i) volcanic birth and submarine formation of a seamount, ii) further growth by lava eruption above the sea level, iii) reaching of maximum elevational extent dependent on duration and intensity of volcanic activity and expiration of the (main) volcano, iv) subsequent erosion and radial drainage channels, v) ongoing flattening and reduction to a low-altitude plain and vi) terminal decline and subsidence beneath sea level to shape a guyot (Menard, 1986; Nunn, 1994; Fernández-Palacios et al., 2011). In tropical regions, coral accretion is likely to occur in the island periphery during the last stages and even after submergence, and atolls or reef islands will originate as secondary islands (Menard, 1986; Nunn, 1994; Forbes et al., 2013). With the exception of tectonically raised atolls (*e.g.* Makatea, Tuamotus; Aldabra, Seychelles or Henderson Island, Pitcairn Islands) and emergent limestone islands (*e.g.* Bahamas), atolls and most reef islands exhibit little topographical structures and are less heterogeneous in terms of habitat types. However, structural heterogeneity, depending on the geological composition, elevation, topography, soil characteristics and zonation along different geographic and ecological gradients of an island increases the diversity of micro- and mesoclimatic opportunities, habitats and ecosystems (Fernández-Palacios and Andersson, 2000; Whittaker and Fernández-Palacios, 2007). In turn, structural heterogeneity on elevated islands will likely decrease the vulnerability to climate change impacts by providing micro-refugia for endangered plant populations (Fig. 3). For example, mesic plants may evade increases of temperature and/or decreasing moisture conditions by finding sheltering habitats in gorges or at cloud-affected locations in higher elevations as indicated for droughts during the Quaternary on Santa Cruz, Galápagos (Collins et al., 2013). Additionally, specific geomorphological and micro-climatic conditions have generated different ecological and evolutionary histories among islands types (Stuessy et al., 2006; Stuessy, 2007; Whittaker et al., 2008), implying very different species adaptations and variable (but unknown) ecological tolerances and response capacities towards climatic shifts.

The role of elevation

Sea level rise during the 21st century results in increased coastal erosion and temporal or permanent inundations of flat coastal zones or even entire islands and facilitates salt water intrusion into island groundwater (Wong et al., 2005; Woodroffe, 2008; IPCC, 2012; Terry and Chui, 2012; Nurse and McLean, 2014). Degradation and subsidence of whole islands and substantial habitat loss in low-

elevated areas can be expected, potentially resulting in extinctions of endemics if upward shifts of species are not possible (Heywood, 2011; IPCC, 2012; Bellard et al., 2014).

Steep coastlines built of firm rock are less affected by rising sea levels or substantial wave erosion (Forbes et al., 2013). However, higher elevated oceanic islands can also suffer from sea level rise if coastal plains or terraces lie within the elevational range of rise. Accordingly, it has been shown for O'ahu and Maui (Hawaii) that considerable areas in coastal plains are under risk from direct (marine) flooding, and even more from groundwater inundation, *i.e.* localised flooding due to sea level-driven uplift of groundwater tables (Rotzoll and Fletcher, 2012; Cooper et al., 2013). Although indicated for urban regions, the risk is also apparent for natural areas, including critical habitats and protection areas (Kane et al., in review). However, if affected urban areas cannot be adaptively protected from inundation, secondary effects on hinterland ecosystems are possible due to potential habitat destruction by settlement relocations (*e.g.* Wetzel et al., 2012).
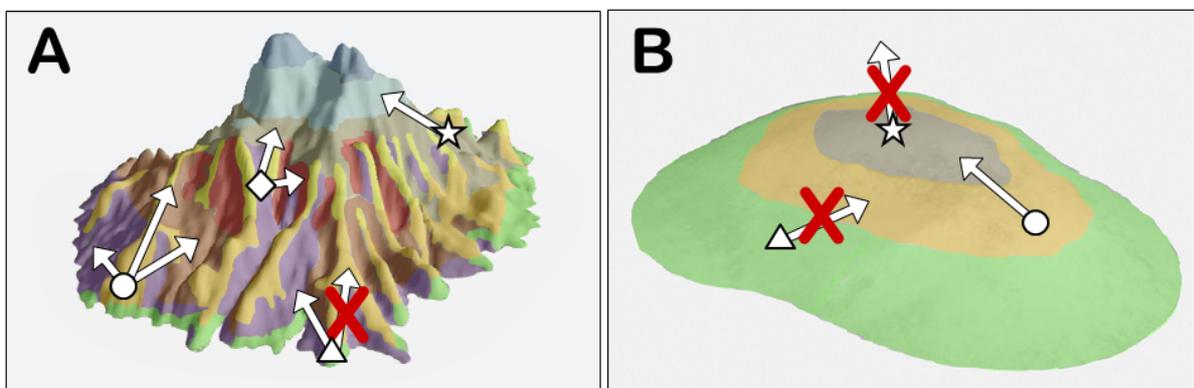

Fig. 3: Effects of island elevation, topography and habitat diversity on range shift potentials of plant species. Habitat types are symbolised by different colours; arrows indicate migration into new habitats in response to climatic alterations. Red crosses symbolise impossibility of an indicated migration into a certain target habitat due to ecological or spatial constraints (e.g. predominant competitor species, lacking interaction partners, absence of specific soil properties, etc.). On highly elevated and topographically structured islands with greater habitat diversity (A), plant species have different options to find adequate micro-refugia (note movements into different types of habitat). On flat and less structured islands (B) many species will face limited possibilities to find adequate and accessible micro-refugia. Insuperable dispersal or establishment filters in a certain direction, or lacking higher elevations might cause problems to species if they fail to adapt to the novel climatic conditions in their original habitats.

Increases in sea levels, solely and in combination with storm surges, are projected to affect freshwater lenses on islands (Kundzewicz and Döll, 2009; Terry and Chui, 2012). This will have serious effects on flat atolls and reef islands or on coastal plain ecosystems where saltwater intrusion can affect upper soil water quality for root water uptake (*e.g.* Spennemann, 2006; Ross et al., 2009; Greaver and Sternberg, 2010). Consequently, ecosystem degradation and plant population declines due to climate change-driven changes of water supply and quality are less likely on elevated volcanic oceanic islands where freshwater aquifers are more salt water-independent and a larger and more resistant groundwater

body is present (Menard, 1986; Kundzewicz and Döll, 2009). However, high elevation islands may also be threatened by saltwater intrusions if precipitation patterns change and groundwater recharge decreases. This can result in upward shifts of the fresh groundwater-saline water boundaries as indicated for Rishiri Island, Japan as a consequence of changing snow fall amounts and altered temporal snowmelt patterns (Mandal and Zhang, 2012).

High elevation islands (like most Hawaiian islands, the Marquesas, some Macaronesian Islands, Society Islands, Samoa, Fiji, Granitic Seychelles, etc.) can induce barrier effects on rain clouds and orographic cloud formation and hence often generate higher precipitation and more freshwater for their ecosystems than low islands (Basist et al., 1994; Scholl et al., 2007). In the course of climate change, potential shifts of cloud layer altitudes might result in modified elevational zonation of vegetation types and species assemblages, *e.g.* of cloud forests, including species losses (Loope and Giambelluca, 1998; Still et al., 1999; Sperling et al., 2004; Scholl et al., 2007; James, 2008; Lloret and González-Mancebo, 2011). It is yet unclear if and how cloud layer altitudes will respond to climate change and how this could differ regionally. Cao *et al.* (2007) found only weak and inconsistent (slightly increasing to slightly decreasing) trends of altitudinal change of the trade wind inversion in Hawaiian Islands in observational data for the period 1979 – 2003. Nevertheless, recent downscaling of 10 CMIP5 models for the two warming scenarios RCP4.5 and RCP8.5 done by Lauer *et al.* (2013) indicates a significant and robust downward shift of the trade wind inversion in the Hawaiian region until the end of the century (2090 – 99 compared to 1990 – 99). In RCP4.5 experiments, elevational changes of the trade wind inversion ranged between 12 and -167 m (multimodel mean -52 m), while in RCP8.5 experiments a decrease between -46 and -355 m (multimodel mean -157 m) was projected (Lauer et al., 2013). Increased occurrence of low-level clouds in the past and future downward trends of cloud layer altitudes are also indicated for the Canary Islands with modelled cloud base level shifts of 15 to -58 m (Sperling et al., 2004). Crausbay *et al.* (2014a) suggested a subsidence of the trade wind inversion during periods of increased ENSO frequencies in the past three millennia for Maui, Hawaii. Decreases in cloud base altitudes may suggest that humid-adapted ecosystems can extend their range downslope where more area is available, resulting in a beneficial situation. However, on islands with elevations above the cloud layer, observations of drying conditions across the trade wind inversion (Sperling et al., 2004) and projected trade wind inversion subsidence (Lauer et al., 2013) imply a future loss of suitable habitat in the upper ranges of cloud contact-dependent species and ecosystems and may reduce the possibility of elevational movements to keep within thermal limits of species ranges. Also, potential soil characteristics constraints or competing human land use might hinder downslope migration, meaning that lower cloud layers do not necessarily mean a benefit for species of humid-adapted ecosystems (Sperling et al., 2004)). However, for dry-adapted high elevation endemics living beyond the trade wind inversion, subsidence of cloud layers might increase potential habitat ranges.

In contrast to downward shift projections, indications for cloud layer upward shifts under warming conditions and associated drastic changes in precipitation are reported for past glacial cycles (Suchodoletz et al., 2010). Higher cloud layers (upward shifts of up to over 200 m) were also projected

for some tropical montane cloud forest sites on continents under increased CO_2 concentrations and climate change conditions (Still et al., 1999). In such scenarios, humid-adapted species might profit from the provision of valuable habitat and temperature conditions for upward shifts in a warming climate. Concomitantly, this would cause risks for dry-adapted high elevation ecosystems above the primary cloud contact elevation (*e.g.* above trade wind inversion layers) due to increasing humidity and invasion of upward-shifting humid-adapted species and ecosystems, as indicated in climate change scenarios for Madeira (Cruz et al., 2010). It is also imaginable that some islands could completely lose humid elevational zones that depend on cloud contact if cloud layer shifts above the island's maximum elevation occurred (potentially applying for some mid-elevation islands, *e.g.* Pohnpei, Kosrae Rapa Iti, Lord Howe and others).

Ecological complexity

Lacking functional redundancy

Generally, biotic interactions, niche overlap, resource competition and facilitation effects between sympatric species, which are more probable to occur with high species numbers, are factors that can facilitate ecosystem resilience to perturbations and increasing environmental variability (Chapin, III et al., 1997; Yachi and Loreau, 1999; Beierkuhnlein and Jentsch, 2005; Hooper et al., 2005).

Compared to continental ecosystems, oceanic islands have relatively low species numbers, simple biotic community structures and can be characterised as 'closed communities' with limited biotic exchange (Whittaker and Fernández-Palacios, 2007; Gilman et al., 2010). Thus, changes in the abundance of single members of functional groups (*e.g.* pollinators, diaspore dispersers, herbivore control) can affect the structure and functional integrity of an island's ecosystem more strongly than is the case in more species-rich continental systems. According to this lack of functional redundancy, the ecological integrity of island ecosystems is relatively fragile. Concomitant to that, a higher proportion of species acts as 'keystone' or 'umbrella' species. Alterations on these species' abundances or functional performance will have dramatic effects for island species (Cushman, 1995; Aslan et al., 2013; Boyer and Jetz, 2014).

Several examples are documented where extinctions of single bird species induced co-extinctions of a number of endemic plant taxa on oceanic islands due to lost mutualism (*e.g.* Cox and Elmqvist, 2001; Fall, 2005; Kingston and Waldren, 2005). Regarding the great role of birds on oceanic islands as pollinators and dispersers, ekercio lu *et al.* (2004) projected that by 2100, 28 – 56 % of all native bird species on oceanic islands worldwide might be functionally extinct (*i.e.* without appreciable contribution to ecosystem processes, see also Boyer and Jetz, 2014). One specific risk from climate change comes from the facilitation of spread and transmission of introduced avian malaria for which endemic birds of oceanic islands often lack adaptation (Garamszegi, 2011). With rising temperatures, spread of the avian malaria mosquito vector to the high elevation thermal refugia of affected birds, as indicated for Kaua'i, Hawaiian Islands (Atkinson et al., 2014), can further diminish their remaining diversity and ecological

functions (pollination, diaspore dispersal, herbivore predation, etc.). At least in such high elevation refuge regions, which often also harbour endangered plant endemics, the loss of ecological services from birds might cause indirect climate change impacts for depending plant species.

It is likely that abundances, spatial distributions, behaviour and competitive capacities of species that interact with plants will be altered by climate change impacts, including potential extirpations (Aslan et al., 2013). Trophic and competitive balances or demographic proportions in mutualistic interactions might be changed, thus affecting community structures, ecosystem functioning and therefore, single plant species (Jump and Peñuelas, 2005; Roux et al., 2005; Gilman et al., 2010; Cahill et al., 2013). Various ecological interactions have been shown to be vulnerable to climatic changes, which likely can be transferred to oceanic island ecosystems: Dependence on single pollinator species and phenology shifts (Memmott et al., 2007) or species declines (for mutualism disruptions on oceanic islands see Caujapé-Castells et al. 2010, Kaiser-Bunbury et al. 2010 and Aslan et al. 2013), expiration of control of herbivore or parasite populations by particular predators (Wilmers et al., 2006; Spiller and Schoener, 2007; Thomson et al., 2010), alteration of plant community structures essential for microclimate (Roux et al., 2005; Royer et al., 2011), lack of maintenance of substrate characteristic by soil organisms, bioturbation or nutrient decomposers (Smith and Steenkamp, 1990; Blankinship et al., 2011) and pest and disease facilitation induced by climatic alterations (Pautasso et al., 2010; Putten et al., 2010).

Depending on the differences in species richness, ecological complexity and functional redundancy of plant interaction partners, impacts of climatic alterations on native floras will differ among oceanic islands. Islands of higher numbers of ecologically closely related species will undergo less climate change-induced extinction cascades than species-poor islands of low functional redundancy. Trøjelsgaard et al. (2013a) showed that plant specialisation on particular pollinator species increases with island age, potentially indicating a higher vulnerability to co-modification. However, rescue from lacking functional redundancy can come from alien species. Neobiota may integrate themselves into local ecosystems and build up novel interactions. This may lead to dependable performances of mutualistic interaction services or even prevent species from co-extinctions (Kaiser-Bunbury et al., 2010; Traveset et al., 2013).

Species richness and migration within islands

Species have to bear up against challenges of new habitats during migratory shifts. Often this means lacking ecological interaction partners that did not follow, for example, adequate tree hosts for epiphytes (Hsu et al., 2012). Another challenge is an altered competitive setting for the shifting species as well as for the species in the receiving community (Caplat et al., 2008; Lavergne et al., 2010). This can be a deleterious or at least strongly filtering factor (Norberg et al., 2012; Urban et al., 2012; Corlett and Westcott, 2013). Species under climatic range shift pressure and potentially resulting new ecological interactions along migration routes, including competition and exclusion, can be assumed to increase with species number on an island. This means that islands rich in species may hold more biotic filters for

potential climate change-induced migrations into new habitats than species-poor islands. However, filtering functions of biodiversity in target areas of shifting species are widely unclear (see Corlett and Westcott, 2013 and references therein). Further on, invasibility of ecosystems by migrating plant species could change due to changing disturbance regimes like wildfire frequency (Wong et al., 2005; James, 2008, see also Angelo and Daehler, 2013) or new forest gap dynamics due to more frequent and/or severe tropical storms (*e.g.* Arozena Concepción et al., 2008; Graff and LaCasce, 2012). In rare cases, asynchronous range shifts also might offer chances for newly co-occurring species to benefit from each other by being driven into new ecological interactions and micro-evolutionary trajectories (Corlett and Westcott, 2013). For example, novel pollinator interactions (see *e.g.* Hembry et al., 2013) or new mycorrhiza alliances could evolve. In the long run, trait adaptations to the new environmental conditions might occur (Lavergne et al., 2010; Hoffmann and Sgrò, 2011; Franks and Hoffmann, 2012).

So far, empirical evidence for novel species interactions induced by climate change-driven range shifts, including establishment rates, the development of novel ecosystems or novel evolutionary pathways of affected species, has not been provided for oceanic islands. Nevertheless, novel community compositions according to species-specific variation in temperature rise-mediated upward range shifts are evidenced by le Roux and McGeoch (2008) on Marion Island.

Interactions between ecosystems

Ecosystems interact with each other especially via matter and energy flows and organismic exchanges (Gauthier et al., 2011 and references therein). On some oceanic islands, the integrity of high elevation forests is an important factor for the hydrologic budget and discharge to lower elevational zones (Izquierdo et al., 2011; Pryet et al., 2012). These ecosystems are especially vulnerable to climate change (*e.g.* by shifting precipitation regimes, see above; Loope and Giambelluca, 1998; Foster, 2001; Sperling et al., 2004). Erosion control by vegetation cover in mountainous zones is also an essential ecotone-crossing service for lowland ecosystems. On some islands mangrove belts protect shorelines and coastal plains from coastal erosion and interact with coral reefs and other marine ecosystems, which in turn deliver their own suite of services to an island`s ecological (and human socio-economic) processes (Field, 1995; Barbier et al., 2011).

Interactions between ecosystems are of relevance for the persistence of their species. However, resource flows and trophic connections across ecotones are themselves vulnerable to climatic alterations. For example, nutrient allocation by piscivorous sea birds affects coastal plant communities (Polis and Hurd, 1996; Anderson and Polis, 1999). Such communities are dependent on the abundance of bird prey, which can be affected by climatic alterations (*e.g.* Roessig et al., 2004; Harley et al., 2006). Decomposition of hurricane-deposited seaweed also increases nutrient availability for coastal plants (Spiller et al., 2010), indicating a potential effect of increasing hurricane frequency spreading across ecosystems. Therefore, ecosystem interdependencies must be included when considering possible climate change impacts (*e.g.* Gauthier et al., 2011). Especially floras of islands rich in ecological

gradients and ecotones, such as high elevation volcanic islands, might receive ecosystem co-modifications. Species living in primarily unimpaired ecosystems thus can be at risk from climate change impacts on interacting ecosystems.

Species characteristics

The risk to sustain negative impacts or to become extinct from climate change is not equally distributed among species (Díaz and Cabido, 1997; Buckley and Kingsolver, 2012; Fortini et al., 2013). It rather varies with specific external (*e.g.* affiliation to specific island types, regional type and strength of climatic alterations, ecosystem and biotic interaction dynamics) and inherent factors (*e.g.* species traits, eco-physiological tolerance, plasticity, dispersal capability). Island endemics are especially affected due to their limited opportunities to escape unfavourable conditions.

Spatial distribution and environmental niche

Endemic plant species are not only geographically isolated but are often also strongly bound to certain environmental conditions (Kruckeberg and Rabinowitz, 1985; Hermant et al., 2013). At the global scale, high levels of endemism are associated to stable climatic conditions since the last glacial maximum (Jansson, 2003). Many island endemics have a small distribution and are confined to specific climatic and edaphic conditions and realise narrow ecological niches (Bramwell, 2011), which generally increases their risk of extinction under changing climatic conditions. For example, *Cheirolophus junonianus*, a single island endemic of La Palma (Canary Islands), is restricted to a particular rocky outcrop and counts only about a hundred individuals (Garnatje et al., 1998). Its area of distribution was minimised to its present extent by recent volcanic activity changing the surrounding soil conditions and geologic properties and thus prohibiting a recuperation of its range to its previous extent (Garnatje et al., 1998). However this also prohibits suchlike species from migrating to track changing climates within their islands, making them highly dependent on more or less consistent habitat conditions, high eco-physiological tolerances, or on rapid evolutionary adaptation. Also, cloud forest species on island mountaintops probably are threatened by their ecological restrictions to very specific, stable and spatially restricted climatic conditions. Even if some adaptive potential is existent, changes in precipitation (or cloud contact) and temperature could alter growing conditions beyond the tolerances of these species (see *e.g.* Shapcott et al., 2012 for the palm species *Lepidorrhachis mooreana* endemic to one single mountain top on Lord Howe Island).

Endemic species are not necessarily specialists on their respective islands. Rather, they can represent 'keystone' species in their inhabited insular environments and ecosystems, often dominating vegetation composition and structure. On all Hawaiian islands, the endemic *Metrosideros polymorpha* is the predominant tree species, being distributed from sea level to the tree line at around 2500 m asl., and along a mean annual precipitation gradient ranging from less than 400 to more than 6000 mm (Cordell et al., 1998). *M. polymorpha* is capable of morphologically and physiologically adapting to a large variety

177

of environments (Cordell et al., 1998). Similarly, the endemic Canary Pine (*Pinus canariensis*) is in large parts of the Canary Islands virtually the only occurring tree species. Potentially it occupies about 15 % of the total archipelagic area (del Arco Aguilar et al., 2010). The species can tolerate fire and in addition, its long needles can comb out water from passing clouds, improving the water supply for the ecosystem (del Arco Aguilar et al., 2010). Generalist species are less likely to be threatened by climatic alterations, as indicated in several studies of continental plant species (*e.g.* Thuiller et al., 2005; Broennimann et al., 2006), but also in comparative modelling of Hawaiian species' niche projections (Fortini et al., 2013). Supporting this, le Roux and McGeoch (2008) have found higher rates of upward shift in generalists related to rising temperatures since 1966 on Marion Island, contrasting to specialist species with lower opportunities of finding appropriate habitats. However, it is not clear yet, if generalist species might even be facilitated by climatic alterations on oceanic islands (*e.g.* range extractions or increases in abundance)

The relative contribution of endemic species increases with elevation (Steinbauer et al., 2012), owing to geographical and environmental isolation to areas with comparable conditions (Steinbauer et al., 2013). High elevation ecosystems on oceanic islands are small, rare and isolated, yet they significantly contribute to the endemic species richness of a given island and are often still undisturbed. However, these ecosystems are also particularly threatened by climate change. An example from Maui on the Hawaiian archipelago shows that the abundance decline of the iconic silversword *Argyroxyphium sandwicense* ssp. *macrocephalum*, which is restricted to the highest parts of the Haleakala crater, is associated with decreasing precipitation (Krushelnycky et al., 2013). Consequently, the future outlook for this species is bleak as drought conditions in the associated alpine ecosystem are projected to increase. Similarly, the high-elevation single island endemic *Helianthemum juliae* found on Tenerife, Canary Islands is highly at risk of extinction if precipitation decreases as predicted (Marrero-Gómez et al., 2007). Marrero-Gómez *et al.* (2007) even suggest translocating this species to more humid areas of the island to ensure its survival.

Indeed, alpine insular ecosystems and their specialised species are especially endangered by climate change due to changes in precipitation patterns (Sperling et al., 2004; Cao et al., 2007; Diaz et al., 2011), disproportional high temperature increase (Giambelluca et al., 2008; Diaz et al., 2011) and the fact that further upward shift is not possible for species already at the highest elevations. Furthermore, a study from Taiwan (Jump et al., 2012) suggests that potential climate change-related upward shifts of plant species from lower elevational zones into summit ecosystems might threaten high elevation endemics on islands. However, for oceanic islands, indications for substantial changes in elevational zonation of ecosystems in summit areas are still lacking.

Table 1: Concepts of climate change vulnerability of island floras and species. Main factors, their potential influence on or interaction with climate change impacts, as well as the underlying mechanisms are depicted, respectively. In the second column the potential effects of the respective factor are shown, either lowering climate change impacts on ecosystems and species (+) or increasing vulnerability and risks (-). Additionally, important references and research potential on the different issues are given. SDMs: species distribution models; VAs: viability analyses (populations and/or species).

Factor	Potential influence or interaction	Effect on climate change impacts on plants	Framework references / Consultable research	Research potential for species vulnerability estimation
Island area	habitat area and diversity +	potential refuge habitats and habitat space for range shifts	Foufopoulos et al., 2011: lizards on Greek islands; Biber, 2002: extinction and threatening patterns of bird species	palaeoecological and palynological comparisons of past climatic change effects among islands of different sizes, phylogeographic analyses, SDMs
	carrying capacity +	large populations less vulnerable to stochastic events and inbreeding; more resilient/adaptive to environmental changes	Frankham, 1998; Ditto and Frey, 2007; Gillespie et al., 2008	VAs of oceanic islands endemic species and populations (including genetic characterisation, *e.g.* bottleneck detections) comparative for different island types
Island age and geology	elevation +	less inundation and coastal erosion, less impacts from saltwater intrusion into groundwater	Woodroffe, 2008; Ross et al., 2009; Mandal and Zhang, 2012; Rotzoll and Fletcher, 2012; Forbes et al., 2013	combination of comparative geomorphological and geohydrological analyses with species distributions
	elevation +	potential upward range shift target areas	Biber, 2002: extinction and threatening patterns of bird species	SDMs
	geological heterogeneity, topographical structuring +	amount of potential micro-refugia	Ashcroft et al., 2009: general micro-refugia identification; Fortini et al., 2013 for Hawaii	comparative fine scale SDMs, micro-refugia identification, palaeoecological and palynological comparisons of past climatic change effects
Ecological complexity	species richness, functional redundancy and ecosystem resilience +	stable ecosystem processes, less extinctions	Cushman, 1995; Putten et al., 2010; no research on climate change vulnerability of island ecosystems according to ecosystem complexity yet (but see Smith and Steenkamp, 1990)	species removal/addition experiments, use of "natural experiments" (*e.g.* extreme events), understanding of ecosystem processes and potential resilience
	ecosystem interactions -	negative influences from proximate ecosystems, potential co-degradations	Polis and Hurd, 1996; Anderson and Polis, 1999; Gauthier et al., 2011 for continental islands	understanding of oceanic island ecological systems and potential effects of ecotones-crossing climate change impacts
	species richness - / +	-: community interaction challenges for shifting species, dispersal/establishment filters +: functional redundancy for species interactions	Caplat et al., 2008; Roux and McGeoch, 2008; Hsu et al., 2012; Norberg et al., 2012 and Urban et al., 2012 for general models of competition effects between resident and range shifting species; Gilman et al., 2010; Aslan et al., 2013	comparative SDMs of interaction partner species, experimental approaches on potential new species combinations, understand effects of recent species range shifts
Species characteristics	niche size / habitat specialist -	low tolerance against environmental change, low range shift capability, high risk of extinction	Frankham, 1997; Jansson, 2003; Roux and McGeoch, 2008; Fortini et al., 2013; Krushelnycky et al., 2013	climate experiments, field studies on range shifts, comparative SDMs
	dispersal capability +	high dispersal capacity enables species to rapidly track climatic alterations to new habitats	Fordham and Brook, 2010; Fortini et al., 2013	data on dispersal capabilities are needed (fruit set analyses, gene flow analyses); include dispersal capability estimates into SDMs or use different dispersal capability scenarios
	short life cycles, genetic variation	high dispersal rates, adaptational potential, lower	Díaz and Cabido, 1997; Jump and Peñuelas, 2005;	population genetic studies, evolutionary studies (*e.g.*

Human influences	prior and parallel human impairments on ecosystems and species -	higher prior vulnerability towards climatic changes; interactions between climate change impacts and additional stressors	Brook et al., 2008; Caujapé-Castells et al., 2010; Fordham and Brook, 2010; Fortini et al., 2013; Vorsino et al., 2014	VAs; understanding of interactions of human disturbance and climate change impacts; assessments of future human land use; link of SDMs for invasive neobiota and endemic species SDMs
	human climate refugees and climate-induced land use or subsistence changes -	further habitat destruction, fragmentation, degradation	Fordham and Brook, 2010; Wetzel et al., 2012	combinations of SDMs, inclusion of human population and land use forecasts and scenarios in risk studies
	conservation measures +	decreased extinction risk	Küffer et al., 2007; Caujapé-Castells et al., 2010; Fordham and Brook, 2010	understanding of conservation potential and possibilities in the face of global climate change on small islands

Life history effects on migration and adaptation abilities to climatic changes

Several species-specific life history traits are likely to influence a given species predisposition to cope with climatic changes. One of the striking trends in island endemics is the tendency towards decreased dispersal capabilities (*e.g.* Carlquist, 1974; Whittaker and Fernández-Palacios, 2007; Bellemain and Ricklefs, 2008, but see also Vaza ová and Münzbergová, 2014). However, the capability to quickly reach adequate new growing sites when the original habitat conditions change to unsuitability is of fundamental importance for climate change-induced range shift of endemics (Fordham and Brook, 2010). Species with poor dispersal capability will have trouble tracking rapidly increasing temperatures or changes in precipitation patterns (Roux and McGeoch, 2008; Bramwell, 2011). Consequently, endemics will have to migrate upward within an island following the temperature isocline at an adequate speed, diminish to refugia (*e.g.* sheltering gorges), or, if possible, move to small-scale micro-refugia "around the bend" (*sensu* Scherrer and Körner, 2009; see also Fig. 3). Indeed, le Roux and McGeoch Roux and McGeoch, 2008 demonstrated species-specific responses in the flora of a sub-Antarctic island to increased temperatures during the last 50 years. They found novel communities with non-analogue species assembly at mid and high elevations due to different range expansion rates among species. Species abundance increases and compositional changes over the last 80 years have also been demonstrated by Kapfer *et al.* Kapfer et al., 2012 on the sub-Arctic island of Jan Mayen.

Furthermore, it is plausible that species' life cycles influence their ability to cope with climatic changes, regarding both range shifts and local persistence. Generation times vary considerably in island floras. Many island floras are characterised by the longevity of endemic woody species belonging to genera or families that are dominated by herbaceous species (Carlquist, 1974), which often correlates with prolonged individual generation times (Bramwell, 2011). Carlquist Carlquist, 1974 argues that the increased longevity resulting in island woodiness is driven by the adaptation to comparably stable past island climates and low seasonal fluctuations. Increasing extreme events and climatic variation on islands (Mimura et al., 2007; IPCC, 2012; Nurse and McLean, 2014) thus may select negatively for island endemics adapted to stable environments (Bramwell, 2011). In contrast, short life cycles, mediated by higher reproductive rates, are advantageous according to dispersal capacities and for evolutionary adaptations to altering environmental conditions (Jump and Peñuelas, 2005; Donnelly et al., 2012). However, the proportion of annual species in island floras is relatively small, *e.g.* only roughly 7% of the endemics of the Canary Islands are annuals (Shmida and Werger, 1992).

Adaptation to changing climatic conditions is more difficult to assess than range shifts, although not less important (Jump and Peñuelas, 2005). Climatic alterations have repeatedly taken place on most oceanic islands and the majority of existing species have endured these environmental changes. According to the special nature of isolated oceanic islands this evidently shows that adaptational processes must have occurred. However, in comparison to Tertiary and Quaternary climatic shifts and oscillations, which have resulted from geological and geophysical processes, the recent anthropogenic changes are proceeding much more rapidly (Diffenbaugh and Field, 2013), making species' adaptations in necessary rates difficult if not impossible (Huntley, 1991; Jump and Peñuelas, 2005). This is especially

true for oceanic island plants due to two main reasons. First, numerous co-occurring (anthropogenic) stressors and impairments are causing additional pressure. Second, island species tend to have low genetic variability (Frankham, 1997; Johnson et al., 2000; Crawford et al., 2001; Stuessy, 2007; Stuessy et al., 2013), potentially contributing to low adaptive capacities by lacking 'option values' *sensu* Jump *et al.* Jump et al., 2009. In combination with reduced dispersal capability, those two aspects are likely to disproportionally increase threats and extinction risk of many endemics facing global climate change. However, some endemics on very isolated and highly dynamic islands show surprisingly large intraspecific ecological variation and/or phenotypic plasticity as a consequence of niche breadth and frequent disturbances (*e.g. Metrosideros polymorpha* in Hawaii; Cordell et al., 1998). Such species can be expected to cope with climatic changes (Jump and Peñuelas, 2005).

Mutualistic species interactions

Many island endemics, too, have developed mutualistic species interactions and dependencies and will only be able to perform range shifts or adapt to a changing environment if their mutualistic partners are able to do the same (Memmott et al., 2007; Tylianakis et al., 2008; Aslan et al., 2013, but see also Hembry et al., 2013). Due to the relatively low species richness of islands the probability is low that if one mutualistic partner is lost, another species will be able to take over its function, possibly resulting in indirect impacts on island plant communities. However, some island endemics have been described as 'super generalists' (Olesen et al., 2002; Traveset et al., 2013; Trøjelsgaard et al., 2013b), meaning species that have very high linkage levels (Olesen et al., 2002). At least for some island plants, certain ecological interactions with other species thus are not as important as in more obligate species interdependencies.

Local human influences

Since human arrival (especially since colonisation by Europeans), many oceanic island species and ecosystems have suffered from anthropogenic influence, drastically changing environmental settings and ecological integrities (*e.g.* Whittaker and Fernández-Palacios, 2007; Caujapé-Castells et al., 2010; Triantis et al., 2010; Heywood, 2011; Walker and Bellingham, 2011). Besides high direct and primary impact on island systems and island species extinctions, it is likely that past and present human impacts can amplify vulnerabilities towards additional disturbances, and that human activity can synergistically intensify impacts of climate change on species and ecosystems (*e.g.* Brook et al., 2008; Caujapé-Castells et al., 2010). Among the most affecting human activities on oceanic islands are non-sustainable land use, overexploitation, pollution and introduction of invasive neobiota (Millenium Ecosystem Assessment, 2005; Wong et al., 2005; Caujapé-Castells et al., 2010).

Land-use, overexploitation and habitat degradation

Land-use (settlements, infrastructure, agriculture, etc.) often leads to habitat destruction or alteration, fragmentation, and pollution by eutrophication, pesticides or waste. These factors can lower natural species' population sizes, affect their ecological integrity and modify their vulnerability to additional stressors (Gilpin and Soulé, 1986; Gillespie et al., 2008; Caujapé-Castells et al., 2010). Human-induced increases of fire frequency or intensity lead to non-natural disturbance regimes and can cause ecosystem impoverishments and the decline and weakening of native species and populations on oceanic islands (Walker and Bellingham, 2011; Connor et al., 2012; Garzón-Machado et al., 2012). Over-exploitation of freshwater resources for agriculture, settlements and tourism demands can lower groundwater tables, deteriorate groundwater quality, and facilitate saltwater intrusion (Gössling, 2001; Praveena and Aris, 2009; Abdullah et al., 2010), leading to habitat degradation and decreased stress tolerance and resilience of species and ecosystems. The same is true for the effects of non-sustainable exploitation of economically valuable taxa. In species with limited population sizes and restricted habitats (like many island species), reduction of population sizes can diminish genetic variation and adaptive potential (Crawford et al., 2001; Willi et al., 2006; James, 2008; Jump et al., 2009; Stuessy et al., 2013). Fragmentation often leads to subsequent Allee effects and higher inbreeding (see Frankham, 1998; Gigord et al., 1999; Ricci, 2006; Caujapé-Castells et al., 2008; James, 2008; Finger et al., 2012; Morrison et al., 2012 for island plants). As a consequence, the vulnerability to genetic erosion, but also to stochastic extinction events is raised (Gilpin and Soulé, 1986; Kingston and Waldren, 2005; Gillespie et al., 2008). Furthermore, potential range shift pathways or target areas for species are often obstructed by human presence or activity, lowering their prospects to escape deteriorating conditions (*e.g.* James, 2008). Disproportionally high proportions of island endemic plants show outcrossing reproduction behaviour and limited dispersal capabilities, which intensifies the impacts of fragmentation (Carlquist, 1974; Francisco-Ortega et al., 2000; Bramwell, 2011).

Reductions of island species populations thus decreases their viability, adaptability and resistance potential against additional threats such as climatic alterations (Frankham, 1997; Caujapé-Castells et al., 2010; Heywood, 2011). Supporting this, Sedlacek *et al.* (2012) experimentally showed that shifting precipitation regimes (drought stress) interact with inbreeding due to small population sizes towards higher extinction risks in the case of a rare and threatened endemic species on Tenerife, Canary Islands. Fortini *et al.* (2013) projected that rare and threatened plant species in the Hawaiian archipelago show the highest vulnerability to climate change threats. However, common species (especially obligate outcrossers) might suffer even more from potential population size reductions, habitat fragmentation and resultant genetic erosion (Honnay and Jacquemyn, 2007; Aguilar et al., 2008). Mating systems and life histories of such species often are not adapted to small population sizes, decreased connectivity and/or low individual density, which can cause extreme endangerment when their numbers are suddenly reduced (Aguilar et al., 2008). Contrastingly, naturally rare species might be adapted to genetic disadvantages of small population sizes (Karron, 1997; Orians, 1997; see above). Therefore, population histories have to be considered when assessing ecological or conservational consequences of rarity in species or populations (naturally small or fragmented populations *vs.* originally common but recently declined or fragmented species/populations; Huenneke, 1991; Aguilar et al., 2008).

Only little is known about relationships between population sizes and extinction risks for oceanic island species, mostly due to lacking knowledge on breeding systems and the histories of species and populations, making direct inferences difficult (Caujapé-Castells et al., 2010). Nevertheless, declines of common species (by local human action, but prospectively also by climate change impacts) should be taken more into consideration for conservation plans as those species can be inherently prone to genetic erosion (Aguilar et al., 2008). Consequential reductions of their biological fitness, resistance capability, viability and thereby population sizes might result in losses of their ecological functions and cause structural risks for ecosystems (Chapin, III et al., 1997; Hooper et al., 2005). It is thus crucial for considerations of climate change impacts on islands to include preceding human detrimental impacts and the degree of human presence and/or influence. Regarding prior degradation of species and ecosystems and the potential of amplifications of climate change threats by local human perturbation (Brook et al., 2008; Fordham and Brook, 2010), densely populated islands with high human impacts on ecosystems are presumably more prone to plant species loss due to climate change influences than more pristine islands.

Invasive neobiota

Invasive neobiota (plants, animals, fungi and microbes) constitute one of the greatest threats to island floras and ecosystems (*e.g.* Cushman, 1995; Millenium Ecosystem Assessment, 2005; Gillespie et al., 2008; Sax and Gaines, 2008; Caujapé-Castells et al., 2010; Küffer et al., 2010; Irl et al., 2014). Many invasive neobiota can directly or indirectly affect island taxa (*e.g.* as competitors, herbivores, predators, parasites, hybridizing congeners, diseases or disease vectors). Climate change impacts are expected to interact with species invasions (Walther et al., 2009; Mainka and Howard, 2010) which will likely intensify impacts on island ecosystems and the challenges of management and control of invasives (Hellmann et al., 2008; Vorsino et al., 2014). In a simple example, moderate changes in temperature or precipitation may only lead to mild modifications of a particular ecosystem and may lie within the capabilities of response of its species (*e.g.* tolerance, plasticity, slight range shifts of populations or even adaptation). However, additional stressors, such as a newly facilitated alien species (*e.g.* a plant competitor) that is now able to establish in the already affected ecosystem can set up profound synergistic effects on climatically weakened native plant species. Such effects are likely to be greater than simple additive effects of single stressors (Brook et al., 2008) and can cause important ecological consequences of climatic changes to oceanic islands.

In contrast to many island endemics, invasive species often show higher rates of dispersal and reproduction, or possess high phenotypic plasticity and climatic tolerance, resulting in comparably high adaptive potentials and relative performance advantages over specialised endemics, especially when confronted with environmental alteration like climatic disturbances and change (Hellmann et al., 2008; Mainka and Howard, 2010; Willis et al., 2010; Chuine et al., 2012). Specialisation in oceanic island endemics and their reduced competitiveness against alien species due to their evolution in isolation

raises a particularly high threat potential from interactions and synergies between climate change and species invasion to oceanic islands.

Climatic changes in habitats or higher intensity and/or frequency of extreme events can facilitate the introduction and colonisation of alien species by increased transport of propagules, opening of new areas and increased growth or survival of colonising neobiota (Loope and Giambelluca, 1998; Walther et al., 2009; Huang et al., 2011; Chuine et al., 2012). Further on, reproduction, competitiveness relative to natives, and thus establishment rates of alien species after colonisation in ecosystems might be enhanced (Chown et al., 2008; Sax and Gaines, 2008; Walther et al., 2009), and finally, climate change impacts might extend suitable areas for alien colonisers, enabling spread and invasion into larger areas of an island (Loope and Giambelluca, 1998; Walther et al., 2009; Vorsino et al., 2014). However, some invasive species on oceanic islands might also experience range contractions due to climatic alterations (Taylor and Kumar, 2014; Vorsino et al., 2014). Nevertheless, the presence of invasive neobiota or neobiota that have potential to become invasive is one of the most important co-factors for the climate change vulnerability of an island flora (e.g. Sax and Gaines, 2008; Bramwell, 2011; Vorsino et al., 2014). Regarding this particular relevance for oceanic islands, it is thus surprising that only few studies exist on neobiota-climate change interactions in such systems.

Human-mediated secondary effects of climate change

Feedbacks can also come from interacting stressors related to the presence and climate change-response of human populations. Climatic alterations and sea level rise may force human islanders to relocate low-lying coastal dwellings, agriculture or infrastructure upwards into the hinterland or to other, *e.g.* larger, higher-elevated or less degraded,islands (Nunn, 2013). Islands have high portions of their human populations living in coastal areas, bearing large potential for climate change migration (McGranahan et al., 2007; Nunn, 2013).

Wetzel *et al.* (2012; 2013) stated for islands of Southeast Asia and the Pacific region that under different sea-level rise scenarios (1 m, 3 m, or 6 m) considerable portions of the coastal zones and their ecosystems could be lost (inundation and erosion). This would cause 8 – 52 million people to become climate change migrants and force them to reclaim formerly unaffected area in the interior of their island, impairing local ecosystems and species' actual or potential habitat (secondary effects; Wetzel et al., 2012). These investigations are based solely on land loss and human land occupancy. Potential side-effects that might affect adjacent areas, such as increased exploitation of resources, pollution, eutrophication and spread of neobiota are likely to encroach plant species and biodiversity as well (Gillespie et al., 2008; Fordham and Brook, 2010; Heywood, 2011).

Climatic alterations may force (or enable) island societies to drastically rearrange their economies. Besides tourism and fishery, agriculture is the main economic sector. Water availability, soil fertility, salinisation, temperature, length of growing season, extreme events, increase of CO_2-concentration, weeds, pest and disease risks are factors potentially affected by, or co-occurring with, climate change.

Performances of crop species and livestock can change (Fuhrer, 2003; Chartzoulakis and Psarras, 2005). Adaptations in agricultural systems are then required, concerning the selection of crop species and cultivars, demands and distributions of farmland, use of fertilisers and pesticides or freshwater withdrawal (Wong et al., 2005; Mimura et al., 2007; Nurse and McLean, 2014). Additionally, on formerly unsuitable islands or in previously unfavourable elevational zones, climatic changes can improve the conditions for farming or livestock breeding (Mimura et al., 2007). This would especially affect high-latitude islands with warming climates or originally dry islands that receive more precipitation in the course of climate change. However, it is also imaginable that climate change impacts force islanders to abandon agricultural sites or even settlements, potentially resulting in local recoveries of natural processes and conditions.

Another effect of climate change impacts on island societies might be a reduction of conservation efforts due to changing socio-economic priorities. Currently, a lot of threatened species on oceanic island persist only in refugial habitats under continued conservation efforts, *i.e.* 'conservation-reliant species' (*e.g.* Whittaker and Fernández-Palacios, 2007). If island societies find themselves faced with climate change impacts, the viability of these long-term conservation efforts is doubtful (Heywood, 2011). Resource allocations to afford climate change mitigation measures may lead in turn to severe reductions or even complete cessation of conservation expenditures and therefore could indirectly result in species extinctions.

Conservation and adaptation measures to climate change impacts

On islands with greater possibilities and political will to continuously allocate socio-economic resources to protection and management efforts, some climate change impacts on species and ecosystems may be mitigated or even forestalled. Well-designed (in the best case pre-emptive) conservation measures could lessen the vulnerability of species to climate change.

Strategies might include recovery from preceding anthropogenic encroachments in order to increase resistance potentials of threatened species or ecosystems against disturbances, for example by habitat rehabilitation and establishment of protected areas (Whittaker and Fernández-Palacios, 2007; Caujapé-Castells et al., 2010). Regional modelling (downscaled climate projections and ecological niche modelling) as well as identification of emerging threats must be included in planning and area prioritisation for such reserve-based measures to adapt conservation strategies to the challenges and dynamic nature of climate change impacts (Hannah et al., 2002; Küffer et al., 2007; Heywood, 2011). For oceanic islands, it might be particularly reasonable to establish protected areas and managed dispersal corridors along relevant environmental gradients to enable species range shifts (*e.g.* elevational or rainfall gradients). In contrast to large continental systems, gradients on oceanic islands are often very steep, potentially lowering efforts in establishment and management, and less likely to exceed natural dispersal capabilities of species trying to track their climatic habitats. However, it might be needed to control potential negative effects of such corridors, like facilitation of invasive species spread (see *e.g.*

Haddad et al., 2014). Alagador *et al.* (2014) also suggested dynamically shifting conservation areas, including sequential scheduling of conservation area designation, followed by the release of areas that stopped contributing to long-term conservation goals. Such approaches would account for the expectable dynamics in niche shifts during climatic changes and might be especially adequate for oceanic islands, where budgets and available area for conservation are often very limited.

On a larger scale, management of the matrix (areas outside and between protected areas) and improved regional coordination are important to improve range shift potentials and species persistence during climatic changes (Hannah et al., 2002). On oceanic islands, this particularly includes the control of invasive species (*e.g.* competitive alien plants or herbivores; Luz et al., 2003; Kingston and Waldren, 2005; Whittaker and Fernández-Palacios, 2007; Cole and Litton, 2014). Also, augmenting population connectivity and gene flow (*e.g.* by decreasing habitat fragmentation), active genetic management ('genetic rescue'), and population reinforcements by (re-)introductions of plant individuals into natural habitats from *ex situ* breeding programmes ('demographic rescue') would benefit from regional coordination and may help to increase adaptive potential and resistance against disturbances in natural populations (*e.g.* Küffer et al., 2007; Caujapé-Castells et al., 2008).

However, for species of particularly narrow ecological niches, climate change impacts might exceed physiological tolerances or include overwhelming pulse disturbances (*e.g.* fire frequency), precluding sustainable *in situ* conservation (Cahill et al., 2013; Fortini et al., 2013; Krushelnycky et al., 2013). If affected species cannot escape by natural migration to refugia, human-mediated relocations could save them from being decoupled from their climatic niche (see Vitt et al., 2010 for a general consideration). Also, permanent habitat loss (*e.g.* by sea level rise) might call for relocation strategies, including translocations to other islands (for general considerations and case studies from the Florida Keys see Maschinski et al., 2011). Generally, establishments of seed banks and other *ex situ* collections in time would avert total loss of species (Caujapé-Castells et al., 2010). Some efforts in the past were successful in preventing island species from extinction (*e.g.* summarised in Whittaker and Fernández-Palacios, 2007). From a global perspective, however, it is likely that in the face of climatic deteriorations and limited resources for human subsistence on oceanic islands, sustainability and conservation will be sacrificed in many places (see above; Bramwell, 2011; Heywood, 2011).

It is imaginable, however, that some native species could profit from human adaptation measures. Agricultural land, settlements or infrastructure can be abandoned or transformed to restore or conserve ecosystems and their services. These could include coastal preservation (*e.g.* through restoration of mangrove belts), slope reinforcement against landslide and soil erosion (reforestation of hill slope forests), preservation of water accumulation, retention and filtering in watershed areas (groundwater recharge effects; *e.g.* by forest restoration, *e.g.* Perkins et al., 2014), and general services like the supply of wood, food or medicine, *e.g.* by agroforestry (Hills et al., 2013). Conservation of biodiversity also contributes to maintain or restore the natural attractiveness of an island for lucrative tourism. Here, particular species or ecosystems are likely to be favoured due to their rarity, popularity or iconic and charismatic value (Duarte et al., 2008; Hambler and Canney, 2013; Krushelnycky et al., 2013).
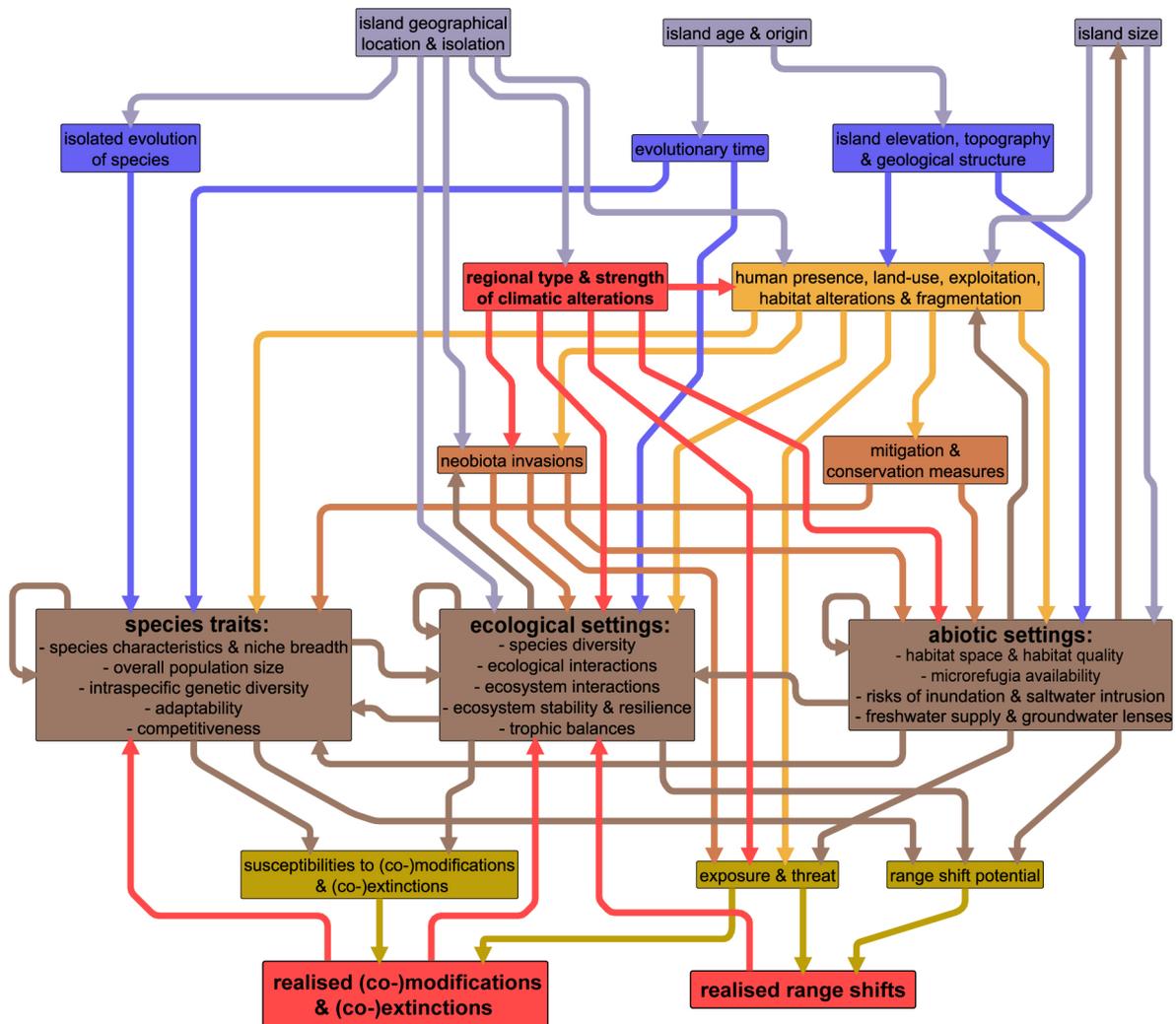
Fig. 4: Flowchart depicting the influences of the most important factors and interaction pathways on species susceptibilities to climatic changes on oceanic islands. Arrows symbolise the direction of influence. Roughly, higher order factors (independent parameters) are positioned at the top, whereas factors of lower order (dependent on others) are positioned towards the bottom. Modifications and co-modifications mean all potential changes in population sizes, structures and viabilities of species and ecosystems, including extinctions and co-extinctions. See digital manuscript for a color-coded version of the figure.

OUTLOOK

General patterns

Global climate change will most likely have direct and dramatic consequences for oceanic island plants and ecosystems. In many cases climate change will also affect island biota indirectly or interact with other drivers, leading to habitat degradation, population decrease and extinction of endemic species. However, oceanic islands are not homogenous in terms of climatic changes and vulnerability. They differ in abiotic, biotic and anthropogenic aspects. Oceanic island plants also differ in their vulnerability and threats due to specific ecological interactions, traits, population viability and response

capability. Some patterns can thus be assumed to have general relevance for impacts of global climate change on island floras, although large uncertainties and knowledge gaps are present that preclude more distinct statements about their vulnerabilities. In the following paragraphs, the most important considerations are given, and a conceptual summary of processes related to island characteristics is provided in Tab. 1, including research challenges.

1. The estimated change in climate is not evenly distributed but depends on geographic location and the associated atmospheric circulation patterns of an island. While temperature is generally increasing (although with variable magnitude), strong differences are assumed for trends in precipitation. There is also a tendency towards intensifying and more frequent extreme events for some island regions.

2. We expect the greatest flora vulnerabilities on oceanic islands of small area, low elevation and simple topographic structuring (with flat atolls and reef islands being threatened most, due to high inundation risks and saltwater intrusions). Nevertheless, these island types possess relatively low numbers of native plant species and only few endemics (Kreft et al., 2008), limiting their role for potential terrestrial plant biodiversity loss in the face of global climate change. In addition, low functional redundancy and strong interactions between ecosystems are likely to increase risks of co-modifications on different organisational levels.

3. In contrast, we presume islands of high topographic and ecological heterogeneity to provide potential refugial habitats. Also, species-rich island communities are probably more resistant or resilient to climatic disturbances and the loss of single species functions.

4. Probably the greatest challenges for island species from climatic alterations are to be expected from interactions and synergies with local anthropogenic pressures. Previous ecosystem alterations, as well as current human impacts parallel to or, as a consequence of, climatic alterations can be fatal for an island's flora and its endemics. Alien species invasions and their detrimental effects are likely to intensify with climate change. Human encroachments in general can be assumed to play major roles in threatening oceanic island floras and may even supersede effects of climatic alterations in some ecosystems or entire islands (*e.g.* Caujapé-Castells et al., 2010).

5. Beside local anthropogenic impacts and synergistic factor-interactions, we suggest that secondary (indirect) effects (*e.g.* trophic cascades, co-extinctions, problems arising from climate-induced human migration) are major threats to oceanic island floras facing climatic alterations.

6. On the species level, low dispersal capacity and high ecological specialisation (narrow ecological niches, including strict dependencies on single interacting species) amplify the risks of decline and extinction. The potentials of rapid evolutionary adaptation to novel climates are not clear, but likely to be negligible.

Main drivers and their interactions are summarised in a flowchart (Fig. 4), providing an overview on the inter-relatedness of factors and mechanisms. Self-amplifying mutual inter-relationships between different factors will probably have more impact than additive singular effects. Moderate primary effects of a single threat factor can turn into harsh encroachments if further interacting stressors come into play.

Suitability and potential of oceanic islands for climate change research

Albeit following logical considerations and being supported by island case studies as well as research on continental systems, various assumptions on climate change vulnerability of island floras are hypothetical and need validation. On oceanic islands, research on ecological consequences of climate change is lagging far behind continental systems, making empirical inference on patterns and processes difficult. However, the disproportionate importance of oceanic islands for global phytodiversity in combination with their special sensitivity calls for comprehensive risk assessments. These are urgently needed for adequate decision-making on counteraction and conservation programmes.

Oceanic islands stimulated the development of fundamental and seminal theories in the fields of ecology, evolution and biogeography that have significantly improved our understanding of natural systems (Whittaker and Fernández-Palacios, 2007). It is therefore surprising that the opportunities of studying oceanic islands to gain general insights and understanding of climate change outcomes on natural systems have been largely unexploited so far. Many aspects of oceanic islands make them best suited model systems for constitutive research on climate change ecology with potential relevance and applicability for the understanding and conservation of non-island systems as well (see *e.g.* Küffer et al., 2014):

i) The clear spatial and ecological delimitation combined with the large number and variability of oceanic islands provides possibilities for replications and comparisons in multi-island data sets. Setting up sound hypotheses and controlling for island idiosyncrasies would make it possible to generate knowledge on basic processes and mechanisms of climate change impacts on plant communities and ecosystems.

ii) Oceanic islands host relatively species-poor and simple ecosystems compared to most continental regions (Whittaker and Fernández-Palacios, 2007; Kreft et al., 2008). As it is difficult to disentangle influencing factors and interactions in more complex systems, this brings great advantages. Straightforward interpretation of ecological processes in field study data as well as target-oriented experimental designs and modelling approaches can be implemented.

iii) Volcanic islands often exhibit high elevations with steep and fissured slopes. This causes outstanding ecological heterogeneity and sequences of different ecosystems within small spatial scales (elevational zonation, island side differences, topographical structure, etc.). Steep ecological gradients and small-scale heterogeneity provide excellent natural experiments to researchers, for example by translating these gradients into potential climatic alteration series (Crausbay and Hotchkiss, 2010).

iv) Considerable portions of plants on oceanic islands are endemic, meaning that the area of their island represents their entire global distribution. This might benefit analyses and inferences on potential evolutionary and biogeographic responses during past climatic changes. Species distribution (or ecological niche) modelling, species and population viability analyses, population

genetic and phylogeographic studies, as well as combinations of these, can yield more meaningful results compared to continental species of wider distribution.

v) In contrast to most continental systems, oceanic islands are ecologically sharply delimited without significant natural biotic exchange to other regions, simplifying hypotheses and their testing in many possible scientific approaches.

vi) A wide array of open questions exists concerning mechanisms, processes and consequences of the upcoming climatic alterations (Tab. 1), calling for extensive use of oceanic islands and their research opportunities by global change ecologists.

Knowledge gaps and suggestions for research approaches

Besides differences in ecological settings, types and magnitudes of climatic impacts and socio-economic structures, the availability of scientific knowledge and necessary data, as well as of resources for potential research is very heterogeneously distributed among islands and island regions. Based on these differences and capabilities, varying research efforts are necessary to set the scientific base for robust assessments of ecological climate change impacts and to enable knowledge-based prioritisation of conservation and mitigation measures. The interdisciplinary work of field biologists, climatologists, social scientists and human geographers, ecological experimenters and modellers, palaeontologists and island biogeographers is needed. Here, we provide a brief summary of research options and data required to advance the understanding of ecological outcomes of climate change on islands (see also Tab. 1 for conceptual summarisation):

i) <u>Botanical surveys and species threats:</u> The floras of many oceanic islands are still largely unexplored and need fundamental botanical surveys (species distributions, individual abundances, population structures, etc.). For those islands with explored floras, long-term monitoring studies may identify changes in species assemblages and abundances. Species and populations at risk need to be identified and prioritisation regarding needs of research and conservation measures must be done. For selected taxa, demographic and population genetic analyses or viability assessments should be carried out.

ii) <u>More detailed climatic data:</u> Baseline data on current and future climatic conditions are certainly needed for almost any study on potential climate change impacts. The amount and spatial distribution of weather stations is not satisfactory on many islands, making consistent and spatially well-arranged long-term data hardly available. Additionally, most oceanic islands are rather small and existing spatial climate data and projections offer insufficient resolutions (grid side lengths of one to several hundreds of kilometres; *e.g.* WorldClim: Hijmans et al., 2005) with some islands even completely slipping through the grid of climate models and being 'unseen' by them (Heywood, 2011). Considering spatial climate patterns and related ecological processes within topographically structured islands (*e.g.* by elevational differences, luv/lee-effects, seasonality differences) is often not yet possible. Thus, there is a need for more and better climate data and models on the island scale.

iii) <u>Anthropogenic factors:</u> Future scenarios for human demographics, land use and socio-economic changes and settings on islands are needed. These will allow for ecological assessments and modelling approaches on interacting effects between climatic alterations and local anthropogenic disturbances on species and ecosystems (Brook et al., 2008; Heywood, 2011). Combinations of species distribution models with scenarios of human population, socio-economic structure, tourism, and potential adaptation strategies to climate change will yield more realistic vulnerability assessments of oceanic island floras. For example, Wetzel *et al.* (2012) assessed land loss and forced human migration on islands due to sea-level rise. Beck (2013) modelled ecological suitability for agriculture under future climate conditions, which could be adapted to island scales. Such approaches can identify potential conflicts between human responses to climate change and range developments of island plant species.

iv) <u>Experiments and field studies:</u> Response capacities towards disturbances from climatic alterations is widely lacking for oceanic island species and their ecological interactions, impeding the mechanistic understanding of climate change outcomes on island ecosystems (Fordham and Brook, 2010; Heywood, 2011). Different experimental approaches are conceivable to gain knowledge about the susceptibility of species and ecosystems to climate change impacts and their potential responses. *In situ* experiments might profit from different island settings, simple ecosystems and steep ecological gradients ('natural experiments') (*e.g.* Roux et al., 2005; Ross et al., 2008; Levine et al., 2010; Anderson et al., 2011 for consultable research on continental islands). Experimental manipulations of climatic parameters and/or adding or removal of potentially important species and invasibility experiments would provide important insights into biodiversity effects under climate change and general response potentials. Field studies and molecular data can bring knowledge on basic ecological demands, demographical dynamics, dispersal capacities, gene flow patterns and adaptability of insular plant species and populations (see *e.g.* Levine et al., 2008; Roux and McGeoch, 2008; Sedlacek et al., 2012; Shapcott et al., 2012; Krushelnycky et al., 2013). Specific studies are most important for rare and presumably threatened species or ecosystems (*e.g.* high elevation ecosystems, ecosystems under inundation risk, rare specialist species) but the climate change response of 'keystone' species might also be of great interest. Potential impacts of climate change on species interactions and ecosystem processes could be analysed by benefitting from the ecological outcomes of 'natural experiments'. Extreme weather events such as abnormal heat waves, droughts, heavy rainfalls, hurricanes, storm surges, inundations and saltwater intrusions might be seen as frequent or even constant future conditions for particular islands or archipelagos. Moreover, adaptabilities of neobiota and their potential to affect island endemic plants can be investigated in experimental settings, enabling adequate decision making for conservation approaches.

v) <u>Modelling approaches:</u> One of the most powerful tools for analysing susceptibilities and range shift prospects of species and ecosystems towards environmental changes is niche distribution and viability modelling (for island studies see *e.g.* 2005; Attorre et al., 2007; 2010; Fortini et al., 2013).

However, biotic, landscape and anthropogenic factors have to be included in such models to cover the whole complexity of potential ecological and distributional changes of species and ecosystems in the future (see Fortini et al., 2013 for a straightforward and comprehensive approach to quantify Hawaiian plant species climate change vulnerability). Among the often neglected (mainly due to lack of data) but very important factors are dispersal capacities (*e.g.* Corlett and Westcott, 2013; Fortini et al., 2013), ecological interactions (dependencies on particular ecosystem processes and structures, availability or co-migration potentials of interacting partner species, competition; *e.g.* Wisz et al., 2013), migration path suitability (*e.g.* Fortini et al., 2013), and availability of micro-refugia (*e.g.* Ashcroft et al., 2009; Fortini et al., 2013). Furthermore, island populations, economies and land use can be expected to change during global change. Thus we have to include current patterns and future scenarios of human impacts (*e.g.* habitat degradation and fragmentation, resource exploitation, effects of invasive species, pollution) into species models to get the best possible projections of species' susceptibility and range shift potentials (e.g. Fordham and Brook, 2010; Vorsino et al., 2014).

vi) Island biogeographic analyses: Comparative studies between islands (*e.g.* within archipelagos) on past ecological responses to climatic changes can reveal potential influences of island biogeographical parameters (area, topography, elevational range, species richness, etc.). Linking vegetation histories to past climatic changes could help to assess future impacts of climate alterations on species and ecosystems. Pollen records can be used to document past extinctions and rates of species turnover (*e.g.* Nascimento et al., 2008; Connor et al., 2012; Boer et al., 2013; Collins et al., 2013; Nogué et al., 2013). Additionally, phylogeographic analyses can detect species histories and responses to past climatic shifts (Davison and Chiba, 2008; Rodríguez-Robles et al., 2010; Bisconti et al., 2013 for studies on island animals). Palynological and phylogeographic results can then be related to the characteristics of specific islands. However, time scales and island histories must be considered to adequately take the dynamics of island areas, topographies and geographical settings (isolation, fusions and fissions etc., see Rijsdijk et al., 2014) into account in order to relate species dynamics to past climatic alterations.

Between-island comparisons of (modelled) intra-island species range shift potentials may reveal benefitting or impeding island features for species responses to climatic changes. Islands that are geographically close to each other and share similar macro-climatic conditions, but differ in an island feature of hypothesised relevance (*e.g.* topographical structure), would provide suitable study systems. This would be possible with species that realistically occur on the islands under comparison. However, meaningful insights into the role of island features would also be possible with species that occur only on one island but whose climatic niche is also existent on another, *i.e.* with comparing "half-hypothetical" species distribution models.

In conclusion, oceanic islands and their unique and diverse flora are at particular risk from global climate change, which poses a high potential for global biodiversity loss. Thus, climate change impacts on islands deserve more scientific interest, not least because of the special suitability of oceanic islands

for diverse climate change-related scientific approaches, and their potential to extend their established function as 'test tubes' in ecology and evolution to model systems for basic and applied climate change research.

Climate change impacts on oceanic island ecology have not been comprehensively examined before. This review offers an initial conceptual framework by i) providing considerations to generalise the findings of case studies and single aspects of island ecology for the climate change vulnerability of oceanic island floras, ii) categorising relevant known and presumable factors and interactions, and iii) depicting uncertainties and research potentials. The paper may thus help to identify specific research needs for different islands, which is important considering the complex and variable risks from climatic alterations, the lack of necessary data for adequate conservation planning and prioritisation, as well as the limited resources for research and conservation in most islands. We hope to stimulate an integrative and multi-disciplinary scientific discussion aiming to better understand and protect the unique biodiversity on oceanic islands with respect to climate change.

ACKNOWLEDGEMENTS

REFERENCES

Abdullah, M.H., Praveena, S.M., Aris, A.Z., 2010. A numerical modelling of seawater intrusion into an oceanic island aquifer, Sipadan Island, Malaysia. Sains Malays. 39, 525–532.

Aguilar, R., Quesada, M., Ashworth, L., Herrerias-Diego, Y., Lobo, J., 2008. Genetic consequences of habitat fragmentation in plant populations: susceptible signals in plant traits and methodological approaches. Mol. Ecol. 17, 5177–5188.

Alagador, D., Cerdeira, J.O., Araújo, M.B., Saura, S., 2014. Shifting protected areas: scheduling spatial priorities under climate change. J Appl Ecol 51, 703–713.

Anderson, S.H., Kelly, D., Ladley, J.J., Molloy, S., Terry, J., 2011. Cascading effects of bird functional extinction reduce pollination and plant density. Science 331, 1068–1071.

Anderson, W.B., Polis, G.A., 1999. Nutrient fluxes from water to land: seabirds affect plant nutrient status on Gulf of California islands. Oecologia 118, 324–332.

Angelo, C.L., Daehler, C.C., 2013. Upward expansion of fire-adapted grasses along a warming tropical elevation gradient. Ecography 36, 551–559.

Arozena Concepción, E.M., Dorta Antequera, P., Panareda Clopés, J.M., Beltrán Yanes, E., 2008. The wind storm effect in the Anaga´s laurel forest (Tenerife. Canary Islands). The Delta storm on November 2005. Scripta Nova 12.

Ashcroft, M.B., Chisholm, L.A., French, K.O., 2009. Climate change at the landscape scale: predicting fine-grained spatial heterogeneity in warming and potential refugia for vegetation. Glob. Change Biol. 15, 656–667.

Aslan, C.E., Zavaleta, E.S., Tershy, B., Croll, D., Nogues-Bravo, D., 2013. Mutualism disruption threatens global plant biodiversity: A systematic review. PLoS One 8, e66993.

Atkinson, C.T., Utzurrum, R.B., Lapointe, D.A., Camp, R.J., Crampton, L.H., Foster, J.T., Giambelluca, T.W., 2014. Changing climate and the altitudinal range of avian malaria in the Hawaiian Islands - an ongoing conservation crisis on the island of Kaua'i. Glob. Change Biol. 20, 2426–2436.

Attorre, F., Francesconi, F., Taleb, N., Scholte, P., Saed, A., Alfo, M., Bruno, F., 2007. Will dragonblood survive the next period of climate change? Current and future potential distribution of Dracaena cinnabari (Socotra, Yemen). Biol. Conserv. 138, 430–439.

Australian Bureau of Meteorology, CSIRO, 2014. Climate variability, extremes and change in the western tropical Pacific: New science and updated country reports: Pacific-Australia Climate Change Science and Adaptation Planning Program technical report, Melbourne, Australia, pp. 358. http://www.pacificclimatechangescience.org/.

Baider, C., Florens, F.B.V., Baret, S., Beaver, K., Matatiken, D., Strasberg, D., Küffer, C., 2010. Status of plant conservation in oceanic islands of the Western Indian Ocean, in: Proceedings of the Fourth Global Botanic Gardens Congress. Fourth Global Botanic Gardens Congress, Dublin.

Barbier, E.B., Hacker, S.D., Kennedy, C., Koch, E.W., Stier, A.C., Silliman, B.R., 2011. The value of estuarine and coastal ecosystem services. Ecol. Monogr. 81, 169–193.

Basist, A., Bell, G.D., Meentemeyer, V., 1994. Statistical relationships between topography and precipitation patterns. J. Climate 7, 1305–1315.

Beck, J., 2013. Predicting climate change effects on agriculture from ecological niche modeling: who profits, who loses? Climatic Change 116, 177–189.

Beierkuhnlein, C., Jentsch, A., 2005. Ecological importance of species diversity, In: Henry, R.J. (Ed.) Plant diversity and evolution. Genotypic and phenotypic variation in higher plants. CABI Pub., Wallingford, pp. 249–285.

Bellard, C., Leclerc, C., Courchamp, F., 2014. Impact of sea level rise on the 10 insular biodiversity hotspots. Global Ecol. Biogeogr. 23, 203–212.

Bellemain, E., Ricklefs, R.E., 2008. Are islands the end of the colonization road? Trends Ecol. Evol. 23, 461–468.

Biber, E., 2002. Patterns of endemic extinctions among island bird species. Ecography 25, 661–676.

Bisconti, R., Canestrelli, D., Nascetti, G., Lalueza-Fox, C., 2013. Has living on islands been so simple? Insights from the insular endemic frog Discoglossus montalentii. PLoS One 8, e55735.

Blankinship, J.C., Niklaus, P.A., Hungate, B.A., 2011. A meta-analysis of responses of soil biota to global change. Oecologia 165, 553–565.

Boer, E.J. de, Hooghiemstra, H., Florens, F.B.V., Baider, C., Engels, S., Dakos, V., Blaauw, M., Bennett, K., 2013. Rapid succession of plant associations on the small ocean island of Mauritius at the onset of the Holocene. Quaternary Sci. Rev. 68, 114–125.

Bouchet, P., Jaffre, T., Veillon, J.-M., 1995. Plant extinction in New Caledonia: protection of sclerophyll forests urgently needed. Biodivers. Conserv. 4, 415–428.

Bowen, L., Vuren, D. van, 1997. Insular endemic plants lack defenses against herbivores. Conserv. Biol. 11, 1249–1254.

Boyer, A.G., Jetz, W., 2014. Extinctions and the loss of ecological function in island bird communities. Global Ecol. Biogeogr. 23, 679–688.

Bramwell, D., 2011. Climate change and island floras, In: Bramwell, D., Caujapé-Castells, J. (Eds.) The biology of island floras. Cambridge University Press, Cambridge, New York, pp. 443–451.

Brito, P., Lorenzo, J.R., González-Rodríguez, Á.M., Morales, D., Wieser, G., Jimenez, M.S., 2014. Canopy transpiration of a Pinus canariensis forest at the tree line: implications for its distribution under predicted climate warming. Eur J Forest Res 133, 491–500.

Broennimann, O., Thuiller, W., Hughes, G.O., Midgley, G.F., Alkemade, J.M.R., Guisan, A., 2006. Do geographic distribution, niche property and life form explain plants' vulnerability to global change? Glob. Change Biol. 12, 1079–1093.

Brook, B.W., Sodhi, N.S., Bradshaw, C.J., 2008. Synergies among extinction drivers under global change. Trends Ecol. Evol. 23, 453–460.

Buckley, L.B., Kingsolver, J.G., 2012. Functional and phylogenetic approaches to forecasting species' responses to climate change. Annu. Rev. Ecol. Evol. S. 43, 205–226.

Cahill, A.E., Aiello-Lammens, M.E., Fisher-Reid, M.C., Hua, X., Karanewsky, C.J., Yeong Ryu, H., Sbeglia, G.C., Spagnolo, F., Waldron, J.B., Warsi, O., Wiens, J.J., 2013. How does climate change cause extinction? P. R. Soc. B. 280, 1–10.

Cai, W., Santoso, A., Wang, G., Weller, E., Wu, L., Ashok, K., Masumoto, Y., Yamagata, T., 2014. Increased frequency of extreme Indian Ocean Dipole events due to greenhouse warming. Nature 510, 254–258.

Cao, G., Giambelluca, T.W., Stevens, D.E., Schroeder, T.A., 2007. Inversion variability in the Hawaiian trade wind regime. J. Climate 20, 1145–1160.

Caplat, P., Anand, M., Bauch, C., 2008. Interactions between climate change, competition, dispersal, and disturbances in a tree migration model. Theor. Ecol. 1, 209–220.

Carlquist, S.J., 1974. Island biology. Columbia University Press, New York, ix, 660.

Caujapé-Castells, J., Marrero-Rodríguez, Á., Baccarani-Rosas, M., Cabrera-García, N., Vilches-Navarrete, B., 2008. Population genetics of the endangered Canarian endemic Atractylis arbuscula (Asteraceae): implications for taxonomy and conservation. Plant Syst. Evol. 274, 99–109.

Caujapé-Castells, J., Tye, A., Crawford, D.J., Santos-Guerra, A., Sakai, A.K., Beaver, K., Lobin, W., Florens, F.B.V., Moura, M., Jardim, R., Gómes, I., Küffer, C., 2010. Conservation of oceanic island floras: Present and future global challenges. Perspect. Plant. Ecol. 12, 107–129.

Chand, S.S., L. McBride, J., Tory, K.J., Wheeler, M.C., Walsh, K.J.E., 2013. Impact of different ENSO regimes on southwest pacific tropical cyclones. J. Climate 26, 600–608.

Chapin, F.S., III, Walker, B.H., Hobbs, R.J., Hooper, D.U., Lawton, J.H., Sala, O.E., Tilman, D., 1997. Biotic control over the functioning of ecosystems. Science 277, 500–504.

Chartzoulakis, K., Psarras, G., 2005. Global change effects on crop photosynthesis and production in Mediterranean: the case of Crete, Greece. Agr. Ecosyst. Environ. 106, 147–157.

Chown, S.L., Lee, J.E., Shaw, J.D., 2008. Conservation of Southern Ocean Islands: invertebrates as exemplars. J. Insect Conserv. 12, 277–291.

Chu, P.-S., Chen, Y.R., Schroeder, T.A., 2010. Changes in precipitation extremes in the Hawaiian Islands in a warming climate. J. Climate 23, 4881–4900.

Chuine, I., Morin, X., Sonié, L., Collin, C., Fabreguettes, J., Degueldre, D., Salager, J.-L., Roy, J., 2012. Climate change might increase the invasion potential of the alien C4 grass Setaria parviflora (Poaceae) in the Mediterranean Basin. Divers. Distrib. 18, 661–672.

Cobb, K.M., Westphal, N., Sayani, H.R., Watson, J.T., Di Lorenzo, E., Cheng, H., Edwards, R.L., Charles, C.D., 2013. Highly variable El Nino-Southern Oscillation throughout the Holocene. Science 339, 67–70.

Cody, M.L., Overton, J.M., 1996. Short-term evolution of reduced dispersal in island plant populations. J. Ecol. 84, 53–61.

Cole, R.J., Litton, C.M., 2014. Vegetation response to removal of non-native feral pigs from Hawaiian tropical montane wet forest. Biol. Invasions 16, 125–140.

Collins, A.F., Bush, M.B., Sachs, J.P., 2013. Microrefugia and species persistence in the Galápagos highlands: a 26,000-year paleoecological perspective. Front. Genet. 4.

Collins, M., An, S.-I., Cai, W., Ganachaud, A., Guilyardi, E., Jin, F.-F., Jochum, M., Lengaigne, M., Power, S., Timmermann, A., Vecchi, G., Wittenberg, A., 2010. The impact of global warming on the tropical Pacific Ocean and El Niño. Nature Geosci. 3, 391–397.

Connor, S.E., Leeuwen, J.F.N. van, Rittenour, T.M., Knaap, W.O. van der, Ammann, B., Björck, S., 2012. The ecological impact of oceanic island colonization - a palaeoecological perspective from the Azores. J. Biogeogr. 39, 1007–1023.

Cooper, H.M., Chen, Q., Fletcher, C.H., Barbee, M.M., 2013. Assessing vulnerability due to sea-level rise in Maui, Hawai'i using LiDAR remote sensing and GIS. Climatic Change 116, 547–563.

Cordell, C., Goldstein, G., Mueller-Dombois, D., Webb, D., Vitousek, P.M., 1998. Physiological and morphological variation in Metrosideros polymorpha, a dominant Hawaiian tree species, along an altitudinal gradient: the role of phenotypic plasticity. Oecologia 113, 188–196.

Corlett, R.T., Westcott, D.A., 2013. Will plant movements keep up with climate change? Trends Ecol. Evol. 28, 482–488.

Cox, P.A., Elmqvist, T., 2001. Pollinator extinction in the Pacific islands. Conserv. Biol. 14, 1237–1239.

Crausbay, S., Genderjahn, S., Hotchkiss, S., Sachse, D., Kahmen, A., Arndt, S.K., 2014a. Vegetation dynamics at the upper reaches of a tropical montane forest are driven by disturbance over the past 7300 years. Arct. Antarct. Alp. Res. 46, 787–799.

Crausbay, S.D., Frazier, A.G., Giambelluca, T.W., Longman, R.J., Hotchkiss, S.C., 2014b. Moisture status during a strong El Niño explains a tropical montane cloud forest's upper limit. Oecologia 175, 273–284.

Crausbay, S.D., Hotchkiss, S.C., 2010. Strong relationships between vegetation and two perpendicular climate gradients high on a tropical mountain in Hawai'i. J. Biogeogr. 37, 1160–1174.

Crawford, D.J., Ruiz, E., Stuessy, T.F., Tepe, E., Aqeveque, P., Gonzalez, F., Jensen, R.J., Anderson, G.J., Bernardello, G., Baeza, C.M., Swenson, U., Silva O., M., 2001. Allozyme diversity in endemic flowering plant species of the Juan Fernandez Archipelago, Chile: Ecological and historical factors with implications for conservation. Am. J. Bot. 88, 2195–2203.

Cronk, Q.C.B., 1997. Islands: Stability, diversity, conservation. Biodivers. Conserv. 6, 477–493.

Cruz, M.J., Aguiar, R., Correia, A., Tavares, T., Pereira, J.S., Santos, F.D., 2010. Impacts of climate change on the terrestrial ecosystems of Madeira. International Journal of Design and Nature and Ecodynamics 4, 413–422.

Cushman, J.H., 1995. Ecosystem-level consequences of species additions and deletions on islands, In: Vitousek, P.M., Loope, L.L., Adsersen, H. (Eds.) Islands. Biological diversity and ecosytem function. Springer, Berlin, pp. 135–147.

Dahl, A.L., 1991. Island directory. UNEP Regional Seas Directories and Bibliographies 35, Nairobi, pp. 573.

Darwin, C.R., 1859. On the origin of species by means of natural selection: or the preservation of favoured races in the struggle for life. John Murray, London.

Davison, A., Chiba, S., 2008. Contrasting response to Pleistocene climate change by ground-living and arboreal Mandarina snails from the oceanic Hahajima archipelago. Philos. T. R. Soc. B. 363, 3391–3400.

del Arco Aguilar, M.-J., González-González, R., Garzón-Machado, V., Pizarro-Hernández, B., 2010. Actual and potential natural vegetation on the Canary Islands and its conservation status. Biodivers. Conserv. 19, 3089–3140.

Diaz, H.F., Giambelluca, T.W., Eischeid, J.K., 2011. Changes in the vertical profiles of mean temperature and humidity in the Hawaiian Islands. Global Planet. Change 77, 21–25.

Díaz, S., Cabido, M., 1997. Plant functional types and ecosystem function in relation to global change. J. Veg. Sci. 8, 463–474.

Diffenbaugh, N.S., Field, C.B., 2013. Changes in ecologically critical terrestrial climate conditions. Science 341, 486–492.

Ditto, A.M., Frey, J.K., 2007. Effects of ecogeographic variables on genetic variation in montane mammals: implications for conservation in a global warming scenario. J. Biogeogr. 34, 1136–1149.

Donnelly, A., Caffarra, A., Kelleher, C.T., O'Neill, B.F., Diskin, E., Pletsers, A., Proctor, H., Stirnemann, R., O'Halloran, J., Peñuelas, J., Hodkinson, T.R., Sparks, T.H., 2012. Surviving in a warmer world: environmental and genetic responses. Clim. Res. 53, 245–262.

Duarte, C.M., Dennison, W.C., Orth, R.J.W., Carruthers, T.J.B., 2008. The charisma of coastal ecosystems: Addressing the imbalance. Estuar. Coast. 31, 233–238.

Elison-Timm, O., Diaz, H.F., Giambelluca, T.W., Takahashi, M., 2011. Projection of changes in the frequency of heavy rain events over Hawaii based on leading Pacific climate modes. J. Geophys. Res. 116, D04109.

Ellstrand, N.C., Elam, D.R., 1993. Population genetic consequences of small population size: Implications for plant conservation. Annu. Rev. Ecol. Syst. 24, 217–242.

Fall, P.L., 2005. Vegetation change in the coastal-lowland rainforest at Avai'o'vuna Swamp, Vava'u, Kingdom of Tonga. Quaternary Res. 64, 451–459.

Fernández-Palacios, J.M., Andersson, C., 2000. Geographical determinants of the biological richness in the Macaronesian region. Acta Phytogeographica Suecica 85, 41–50.

Fernández-Palacios, J.M., Nascimento, L. de, Otto, R., Delgado, J.D., García-del-Rey, E., Arévalo, J.R., Whittaker, R.J., 2011. A reconstruction of Palaeo-Macaronesia, with particular reference to the long-term biogeography of the Atlantic island laurel forests. J. Biogeogr. 38, 226–246.

Field, C.D., 1995. Impact of expected climate change on mangrove. Hydrobiologia 295, 75–81.

Finger, A., Kettle, C.J., Kaiser-Bunbury, C.N., Valentin, T., Mougal, J., Ghazoul, J., 2012. Forest fragmentation genetics in a formerly widespread island endemic tree: Vateriopsis seychellarum (Dipterocarpaceae). Mol. Ecol. 21, 2369–2382.

Florens, F.B.V., Baider, C., 2006. On the discovery of a new endemic Cynanchum (Apocynaceae) on Gunner's Quoin, Mauritius. Phelsuma 14, 7–12.

Forbes, D.L., James, T.S., Sutherland, M., Nichols, S.E., 2013. Physical basis of coastal adaptation on tropical small islands. Sustain. Sci. 8, 327–344.

Fordham, D.A., Brook, B.W., 2010. Why tropical island endemics are acutely susceptible to global change. Biodivers. Conserv. 19, 329–342.

Fortini, L.B., Price, J., Jacobi, J., Vorsino, A., Burgett, J., Brinck, K., Amidon, F., Miller, S., 'Ohukani'ohi'a III, S., Koob, G., Paxton, E., 2013. A landscape-based assessment of climate change vulnerability for all native Hawaiian plants. Technical Report 044. Hawai i Cooperative Studies Unit, University of Hawai'i, Hilo, HI, pp. 45.

Foster, P.N., 2001. The potential negative impacts of global climate change on tropical montane cloud forests. Earth. Sci. Rev. 55, 73–106.

Foufopoulos, J., Kilpatrick, A.M., Ives, A.R., 2011. Climate change and elevated extinction rates of reptiles from Mediterranean islands. Am. Nat. 177, 119–129.

Francisco-Ortega, J., Santos-Guerra, A., Kim, S.-C., Crawford, D.J., 2000. Plant genetic diversity in the Canary Islands: A conservation perspective. Am. J. Bot. 87, 909–919.

Frankham, R., 1997. Do island populations have less genetic variation than mainland populations? Heredity 78, 311–327.

Frankham, R., 1998. Inbreeding and extinction: Island populations. Conserv. Biol. 12, 665–675.

Franks, S.J., Hoffmann, A.A., 2012. Genetics of climate change adaptation. Annu. Rev. Genet. 46, 185–208.

Fresnillo, B., Ehlers, B.K., 2008. Variation in dispersability among mainland and island populations of three wind dispersed plant species. Plant Syst. Evol. 270, 243–255.

Fuhrer, J., 2003. Agroecosystem responses to combinations of elevated CO2, ozone, and global climate change. Agr. Ecosyst. Environ. 97, 1–20.

Garamszegi, L.Z., 2011. Climate change increases the risk of malaria in birds. Glob. Change Biol. 17, 1751–1759.

Garnatje, T., Susanna, A., Messeguer, R., 1998. Isozyme studies in the genus Cheirolophus (Asteraceae: Cardueae-Centaureinae) in the Iberian Peninsula, North Africa and the Canary Islands. Plant Syst. Evol. 213, 57–70.

Garzón-Machado, V., Arco Aguilar, M.J. del, González, F.V., Pérez-de-Paz, P.L., 2012. Fire as a threatening factor for endemic plants of the Canary Islands. Biodivers. Conserv. 21, 2621–2632.

Gaston, K.J., 1994. Rarity. Chapman & Hall, London, pp. 205.

Gauthier, G., Berteaux, D., Bêty, J., Tarroux, A., Therrien, J.-F., McKinnon, L., Legagneux, P., Cadieux, M.-C., 2011. The tundra food web of Bylot Island in a changing climate and the role of exchanges between ecosystems. Ecoscience 18, 223–235.

Giambelluca, T.W., Diaz, H.F., Luke, M.S.A., 2008. Secular temperature changes in Hawai'i. Geophys. Res. Lett. 35.

Gigord, L., Picot, F., Shykoff, J.A., 1999. Effects of habitat fragmentation on Dombeya acutangula (Sterculiaceae), a native tree on La Réunion (Indian Ocean). Biol. Conserv. 88, 43–51.

Gillespie, R.G., Baldwin, B.G., Waters, J.M., Fraser, C.I., Nikula, R., Roderick, G.K., 2012. Long-distance dispersal: a framework for hypothesis testing. Trends Ecol. Evol. 27, 52–61.

Gillespie, R.G., Claridge, E.M., Roderick, G.K., 2008. Biodiversity dynamics in isolated island communities: interaction between natural and human-mediated processes. Mol. Ecol. 17, 45–57.

Gillespie, R.G., Roderick, G.K., 2002. Arthropods on islands: Colonization, speciation, and conservation. Annu. Rev. Entomol. 47, 595–632.

Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W., Holt, R.D., 2010. A framework for community interactions under climate change. Trends Ecol. Evol. 25, 325–331.

Gilpin, M.E., Soulé, M.S., 1986. Minimum viable populations: Process of species extinction, In: Soulé, M.S. (Ed.) Conservation biology. The science of scarcity and diversity. Sinauer Associates, Inc., Sunderland, Massachusetts, pp. 19–34.

Gössling, S., 2001. The consequences of tourism for sustainable water use on a tropical island: Zanzibar, Tanzania. J. Environ. Manage. 61, 179–191.

Graff, L.S., LaCasce, J.H., 2012. Changes in the extratropical storm tracks in response to changes in SST in an AGCM. J. Climate 25, 1854–1870.

Greaver, T.L., Sternberg, L.S.L., 2010. Decreased precipitation exacerbates the effects of sea level on coastal dune ecosystems in open ocean islands. Glob. Change Biol. 16, 1860–1869.

Haddad, N.M., Brudvig, L.A., Damschen, E.I., Evans, D.M., Johnson, B.L., Levey, D.J., Orrock, J.L., Resasco, J., Sullivan, L.L., Tewksbury, J.J., Wagner, S.A., Weldon, A.J., 2014. Potential negative ecological effects of corridors. Conserv. Biol. 28, 1178–1187.

Halley, J.M., Sgardeli, V., Triantis, K.A., 2014. Extinction debt and the species-area relationship: a neutral perspective. Global Ecol. Biogeogr. 23, 113–123.

Hambler, C., Canney, S.M., 2013. Conservation. Cambridge University Press, Cambridge, 1 online resource (424.

Hannah, L., Flint, L., Syphard, A.D., Moritz, M.A., Buckley, L.B., McCullough, I.M., 2014. Fine-grain modeling of species' response to climate change: holdouts, stepping-stones, and microrefugia. Trends Ecol. Evol. 29, 390–397.

Hannah, L., Midgley, G.F., Millar, D., 2002. Climate change-integrated conservation strategies. Global Ecol. Biogeogr. 11, 485–495.

Hanski, I., 2010. The theories of island biogeography and metapopulation dynamics, In: Losos, J.B., Ricklefs, R.E. (Eds.) The theory of island biogeography revisited. Princeton University Press, Princeton, pp. 187–213.

Harley, C.D.G., Randall Hughes, A., Hultgren, K.M., Miner, B.G., Sorte, C.J.B., Thornber, C.S., Rodriguez, L.F., Tomanek, L., Williams, S.L., 2006. The impacts of climate change in coastal marine systems. Ecol. Lett. 9, 228–241.

Hellmann, J.J., Byers, J.E., Bierwagen, B.G., Dukes, J.S., 2008. Five potential consequences of climate change for invasive species. Conserv. Biol. 22, 534–543.

Hembry, D.H., Kawakita, A., Gurr, N.E., Schmaedick, M.A., Baldwin, B.G., Gillespie, R.G., 2013. Non-congruent colonizations and diversification in a coevolving pollination mutualism on oceanic islands. P. R. Soc. B. 280, 20130361.

Hermant, M., Prinzing, A., Vernon, P., Convey, P., Hennion, F., 2013. Endemic species have highly integrated phenotypes, environmental distributions and phenotype-environment relationships. J. Biogeogr. 40, 1583–1594.

Heywood, V.H., 2011. The hazardous future of island floras, In: Bramwell, D., Caujapé-Castells, J. (Eds.) The biology of island floras. Cambridge University Press, Cambridge, New York, pp. 488–510.

Hijmans, R.J., 2013. raster: Geographic data analysis and modeling. R package version 2.1-66.

Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25, 1965–1978.

Hills, T., Carruthers, T.J.B., Chape, S., Donohoe, P., 2013. A social and ecological imperative for ecosystem-based adaptation to climate change in the Pacific Islands. Sustain. Sci. 8, 455–467.

Hoffmann, A.A., Sgrò, C.M., 2011. Climate change and evolutionary adaptation. Nature 470, 479–485.

Honnay, O., Jacquemyn, H., 2007. Susceptibility of common and rare plant species to the genetic consequences of habitat fragmentation. Conserv. Biol. 21, 823–831.

Hooper, D., Chapin, F.S., III, Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J., Wardle, D.A., 2005. Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. Ecol. Monogr. 75, 3–35.

Horton, B.P., Rahmstorf, S., Engelhart, S.E., Kemp, A.C., 2014. Expert assessment of sea-level rise by AD 2100 and AD 2300. Quaternary Sci. Rev. 84, 1–6.

Hsu, R.C.-C., Tamis, W.L.M., Raes, N., Snoo, G.R. de, Wolf, J.H.D., Oostermeijer, G., Lin, S.-H., 2012. Simulating climate change impacts on forests and associated vascular epiphytes in a subtropical island of East Asia. Divers. Distrib. 18, 334–347.

Huang, D., Haack, R.A., Zhang, R., 2011. Does global warming increase establishment rates of invasive alien species? A centurial time series analysis. PLoS One 6, e24733.

Huenneke, L.F., 1991. Ecological implications of genetic variation in plant populations, In: Falk, D.A., Holsinger, K.E. (Eds.) Genetics and conservation od rare plants. Oxford University Press, New York, pp. 31–44.

Huntley, B., 1991. How plants respond to climate change: Migration rates, individualism and the consequences for plant communities. Ann. Bot.-London 67, 15–22.

IPCC (Ed.), 2012. Managing the risks of extreme events and disasters to advance climate change adaptation: A special report of working groups I and II of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

IPCC, 2013a. Annex I: Atlas of global and regional climate projections, In: IPCC (Ed.) Climate change 2013: The physical science basis. Working group I contribution to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

IPCC (Ed.), 2013b. Climate change 2013: The physical science basis: Working group I contribution to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK, pp. 1535.

IPCC (Ed.), 2014. Climate change 2014: Impacts, adaptation, and vulnerability: Working group II contribution to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Irl, S.D.H., Steinbauer, M.J., Messinger, J., Blume-Werry, G., Palomares-Martinez, Á., Beierkuhnlein, C., Jentsch, A., 2014. Burned and devoured - Introduced herbivores, fire, and the endemic flora of the high-elevation ecosystem on La Palma, Canary Islands. Arct. Antarct. Alp. Res. 46, 859–869.

Izquierdo, T., Heras, P. de las, Márquez, A., 2011. Vegetation indices changes in the cloud forest of La Gomera Island (Canary Islands) and their hydrological implications. Hydrol. Process. 25, 1531–1541.

Jaffre, T., Bouchet, P., Veillon, J.-M., 1998. Threatened plants of New Caledonia: Is the system of protected areas adequate? Biodivers. Conserv. 7, 109–135.

James, S.A., 2008. Climate change impacts on native plant communities in Melanesia, In: Leisz, S.J., Burnett, J.B. (Eds.) Climate change and biodiversity in Melanesia.

Jansson, R., 2003. Global patterns in endemism explained by past climatic change. P. R. Soc. B. 270, 583–590.

Jentsch, A., Beierkuhnlein, C., 2008. Research frontiers in climate change: Effects of extreme meteorological events on ecosystems. C. R. Geosci. 340, 621–628.

Jevrejeva, S., Grinsted, A., Moore, J.C., 2014. Upper limit for sea level projections by 2100. Environ. Res. Lett. 9, 104008.

Johnson, K.P., Adler, F.R., Cherry, J.L., 2000. Genetic and phylogenetic consequences of island biogeography. Evolution 54, 387–396.

Jump, A.S., Huang, T.-J., Chou, C.-H., 2012. Rapid altitudinal migration of mountain plants in Taiwan and its implications for high altitude biodiversity. Ecography 35, 204–210.

Jump, A.S., Marchant, R., Peñuelas, J., 2009. Environmental change and the option value of genetic diversity. Trends Plant Sci. 14, 51–58.

Jump, A.S., Peñuelas, J., 2005. Running to stand still: adaptation and the response of plants to rapid climate change. Ecol. Lett. 8, 1010–1020.

Junak, S.A., Philbrick, R., 1999. Flowering plants of the San Benito Islands, Baja California, Mexico, in: Proceedings of the Fifth California Islands Symposium, Camarillo, California, p. 235–235.

Kaiser-Bunbury, C.N., Traveset, A., Hansen, D.M., 2010. Conservation and restoration of plant–animal mutualisms on oceanic islands. Perspect. Plant. Ecol. 12, 131–143.

Kane, H.H., Fletcher, C.H., Frazer, L.N., Anderson, T., Barbee, M.M., in review. Modeling sea-level rise vulnerability of coastal wetlands using ranked management concerns. Climatic Change.

Kapfer, J., Virtanen, R., Grytnes, J.-A., Cousins, S., 2012. Changes in arctic vegetation on Jan Mayen Island over 19 and 80 years. J. Veg. Sci. 23, 771–781.

Karron, J.D., 1997. Genetic consequences of different patterns of distribution and abundance, In: Kunin, W.E., Gaston, K.J. (Eds.) The biology of rarity. Causes and consequences of rare-common differences. Chapman & Hall, London, pp. 174–189.

Keener, V.W., Marra, J.J., Finucane, M.L., Spooner, D., Smith, M., 2012. Climate change and Pacific islands: Indicators and impacts: Report for the 2012 Pacific Islands Regional Climate Assessment (PIRCA). Island Press, Washington, DC.

Kier, G., Kreft, H., Lee, T.M., Jetz, W., Ibisch, P.L., Nowicki, C., Mutke, J., Barthlott, W., 2009. A global assessment of endemism and species richness across island and mainland regions. P. Natl. Acad. Sci. USA 106, 9322–9327.

Kingston, N., Waldren, S., 2005. A conservation appraisal of the rare and endemic vascular plants of Pitcairn Island. Biodivers. Conserv. 14, 781–800.

Kisel, Y., McInnes, L., Toomey, N.H., Orme, C.D.L., 2011. How diversification rates and diversity limits combine to create large-scale species-area relationships. Philos. T. R. Soc. B. 366, 2514–2525.

Knutson, T.R., McBride, J.L., Chan, J., Emanuel, K., Holland, G., Landsea, C., Held, I., Kossin, J.P., Srivastava, A.K., Sugi, M., 2010. Tropical cyclones and climate change. Nature Geosci. 3, 157–163.

Kreft, H., Jetz, W., Mutke, J., Kier, G., Barthlott, W., 2008. Global diversity of island floras from a macroecological perspective. Ecol. Lett. 11, 116–127.

Kreyling, J., 2010. Winter climate change: a critical factor for temperate vegetation performance. Ecology 97, 1939–1948.

Kruckeberg, A.R., Rabinowitz, D., 1985. Biological aspects of endemism in higher plants. Annu. Rev. Ecol. Syst. 16, 447–479.

Krushelnycky, P.D., Loope, L.L., Giambelluca, T.W., Starr, F., Starr, K., Drake, D.R., Taylor, A.D., Robichaux, R.H., 2013. Climate-associated population declines reverse recovery and threaten future of an iconic high-elevation plant. Glob. Change Biol. 19, 911–922.

Küffer, C., Beaver, K., Kaiser, C., 2007. Seychelles plant conservation research agenda 2008 - 2015. Ministry of Environment, Natural Resources and Transport (MENRT) and Plant Conservation Action Group (PCA), Victoria, Seychelles.

Küffer, C., Daehler, C.C., Torres-Santana, C.W., Lavergne, C., Meyer, J.-Y., Otto, R., Silva, L., 2010. A global comparison of plant invasions on oceanic islands. Perspect. Plant. Ecol. 12, 145–161.

Küffer, C., Drake, D.R., Fernández-Palacios, J.M., 2014. Island biology: looking towards the future. Biol. Letters 10, 20140719.

Kundzewicz, Z.W., Döll, P., 2009. Will groundwater ease freshwater stress under climate change? Hydrolog. Sci. J. 54, 665–675.

Kutzbach, J.E., Webb III, T., 1993. Conceptual basis for understanding Late-Quaternary climates, In: Wright, H.E., Jr., Kutzbach, J.E., Webb III, T., Ruddiman, W.F., Street-Perrott, F.A., Bartlein, P.J. (Eds.) Global climates since the last glacial maximum. University of Minnesota Press, Minneapolis, pp. 5–11.

Lander, M.A., Guard, C.P., 2003. Creation of a 50-year rainfall database, annual rainfall climatology, and annual rainfall distribution map for Guam. Technical Report 102. University of Guam.

Lander, M.A., Khosrowpanah, S., 2004. A rainfall climatology for Pohnpei Island, Federated States of Micronesia. Technical Report 103. University of Guam.

Lauer, A., Zhang, C., Elison-Timm, O., Wang, Y., Hamilton, K., 2013. Downscaling of climate change in the Hawaii region using CMIP5 results: On the choice of the forcing fields. J. Climate 26, 10006–10030.

Lavergne, S., Mouquet, N., Thuiller, W., Ronce, O., 2010. Biodiversity and climate change: Integrating evolutionary and ecological responses of species and communities. Annu. Rev. Ecol. Evol. S. 41, 321–350.

Lavergne, S., Thompson, J.D., Garnier, E., Debussche, M., 2004. The biology and ecology of narrow endemic and widespread plants: a comparative study of trait variation in 20 congeneric pairs. Oikos 107, 505–518.

Lee, J.-Y., Wang, B., 2014. Future change of global monsoon in the CMIP5. Clim. Dyn. 42, 101–119.

Levine, J.M., McEachern, A.K., Cowan, C., 2008. Rainfall effects on rare annual plants. J. Ecol. 96, 795–806.

Levine, J.M., McEachern, A.K., Cowan, C., 2010. Do competitors modulate rare plant response to precipitation change? Ecology 91, 130–140.

Lloret, F., González-Mancebo, J.M., 2011. Altitudinal distribution patterns of bryophytes in the Canary Islands and vulnerability to climate change. Flora 206, 769–781.

Loope, L.L., 1995. Climate change and island biological diversity, In: Vitousek, P.M., Loope, L.L., Adsersen, H. (Eds.) Islands. Biological diversity and ecosytem function. Springer, Berlin, pp. 123–132.

Loope, L.L., Giambelluca, T.W., 1998. Vulnerability of island tropical montane cloud forests to climate change, with special reference to East Maui, Hawaii. Climatic Change 39, 503–517.

Luz, J.L.L. de la, Rebman, J.P., Oberbauer, T., 2003. On the urgency of conservation on Guadalupe Island, Mexico: is it a lost paradise? Biodivers. Conserv. 12, 1073–1082.

MacArthur, R.H., Wilson, E.O., 1967. The theory of island biogeography. Princeton University Press, Princeton and Oxford.

Mace, G.M., Kershaw, M., 1997. Extinction risk and rarity on an ecological timescale, In: Kunin, W.E., Gaston, K.J. (Eds.) The biology of rarity. Causes and consequences of rare-common differences. Chapman & Hall, London, pp. 130–149.

Mainka, S.A., Howard, G.W., 2010. Climate change and invasive species: double jeopardy. Integr Zool 5, 102–111.

Mandal, A.K., Zhang, J., 2012. Climate change and the future of freshwater resources of the island: a case study on the Rishiri Island, Japan. Environ. Earth Sci. 66, 1309–1319.

Marrero-Gómez, M.V., Oostermeijer, J.G.B., Carqué-Álamo, E., Bañares-Baudet, Á., 2007. Population viability of the narrow endemic Helianthemum juliae (Cistaceae) in relation to climate variability. Biol. Conserv. 136, 552–562.

Maschinski, J., Ross, M.S., Liu, H., O'Brien, J., Wettberg, E.J. von, Haskins, K.E., 2011. Sinking ships: conservation options for endemic taxa threatened by sea level rise. Climatic Change 107, 147–167.

McEachern, A.K., Thomson, D.M., Chess, K.A., 2009. Climate alters response of an endemic island plant to removal of invasive herbivores. Ecol. Appl. 19, 1574–1584.

McGranahan, G., Balk, D., Anderson, B., 2007. The rising tide: assessing the risks of climate change and human settlements in low elevation coastal zones. Environ. Urban. 19, 17–37.

McMillan, M., Shepherd, A., Sundal, A., Briggs, K., Muir, A., Ridout, A., Hogg, A., Wingham, D., 2014. Increased ice losses from Antarctica detected by CryoSat-2. Geophys. Res. Lett. 41, 3899–3905.

Memmott, J., Craze, P.G., Waser, N.M., Price, M.V., 2007. Global warming and the disruption of plant-pollinator interactions. Ecol. Lett. 10, 710–717.

Menard, H.W., 1986. Islands. Scientific American Library, New York, pp. 230.

Menon, S., Soberón, J., Li, X., Peterson, A.T., 2010. Preliminary global assessment of terrestrial biodiversity consequences of sea-level rise mediated by climate change. Biodivers. Conserv. 19, 1599–1609.

Meyer, J.-Y., Butaud, J.-F., 2009. The impacts of rats on the endangered native flora of French Polynesia (Pacific Islands): drivers of plant extinction or coup de grâce species? Biol. Invasions 11, 1569–1585.

Michna, P., 2012. RNetCDF: R Interface to NetCDF Datasets. R package version 1.6.1-2.

Millenium Ecosystem Assessment, 2005. Ecosystems and human well-being: Biodiversity synthesis. World Resources Institute, Washington, DC.

Mimura, N., Nurse, L., McLean, R., Agard, J., Briguglio, L., Lefale, P., Payet, R., Sem, G., 2007. Small islands, In: IPCC (Ed.) Climate change 2007: Impacts, adaptation and vulnerability. Contribution of working group II to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK, pp. 687–716.

Morlighem, M., Rignot, E., Mouginot, J., Seroussi, H., Larour, E., 2014. Deeply incised submarine glacial valleys beneath the Greenland ice sheet. Nature Geosci. 7, 418–422.

Morrison, C., Rounds, I., Watling, D., 2012. Conservation and management of the endangered Fiji Sago palm, Metroxylon vitiense, in Fiji. Environ. Manage. 49, 929–941.

Mote, P.W., Brekke, L., Duffy, P.B., Maurer, E., 2011. Guidelines for constructing climate scenarios. Eos 92, 257–264.

Nascimento, L. de, Willis, K.J., Fernández-Palacios, J.M., Criado, C., Whittaker, R.J., 2008. The long-term ecology of the lost forests of La Laguna, Tenerife (Canary Islands). J. Biogeogr. 36, 499–514.

Nogué, S., Nascimento, L. de, Fernández-Palacios, J.M., Whittaker, R.J., Willis, K.J., 2013. The ancient forests of La Gomera, Canary Islands, and their sensitivity to environmental change. J. Ecol. 101, 368–377.

Norberg, J., Urban, M.C., Vellend, M., Klausmeier, C.A., Loeuille, N., 2012. Eco-evolutionary responses of biodiversity to climate change. Nat. Clim. Change 2, 747–751.

Nunn, P.D., 1994. Oceanic islands. Blackwell, Oxford, pp. 413.

Nunn, P.D., 2013. The end of the Pacific? Effects of sea level rise on Pacific Island livelihoods. Singap. J. Trop. Geogr. 34, 143–171.

Nurse, L., McLean, R., 2014. Chapter 29. Small Islands, In: IPCC (Ed.) Climate change 2014: Impacts, adaptation, and vulnerability. Working group II contribution to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

Olesen, J.M., Eskildsen, L.I., Venkatasamy, S., 2002. Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists. Divers. Distrib. 8, 181–192.

Orians, G.H., 1997. Evolved consequences of rarity, In: Kunin, W.E., Gaston, K.J. (Eds.) The biology of rarity. Causes and consequences of rare-common differences. Chapman & Hall, London, pp. 190–208.

Overpeck, J.T., Otto-Bliesner, B.L., Miller, G.H., Muhs, D.R., Alley, R.B., Kiehl, J.T., 2006. Paleoclimatic evidence for future ice-sheet instability and rapid sea-level rise. Science 311, 1747–1750.

Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. Annu. Rev. Ecol. Evol. S. 37, 637–669.

Parmesan, C., 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Glob. Change Biol. 13, 1860–1872.

Patiño, J., Medina, R., Vanderpoorten, A., González-Mancebo, J.M., Werner, O., Devos, N., Mateo, R.G., Lara, F., Ros, R.M., Linder, P., 2013. Origin and fate of the single-island endemic moss Orthotrichum handiense. J. Biogeogr. 40, 857–868.

Pau, S., MacDonald, G.M., Gillespie, T.W., 2012. A dynamic history of climate change and human impact on the environment from Kealia Pond, Maui, Hawaiian Islands. Ann. Assoc. Am. Geogr. 102, 748–762.

Pautasso, M., Dehnen-Schmutz, K., Holdenrieder, O., Pietravalle, S., Salama, N., Jeger, M.J., Lange, E., Hehl-Lange, S., 2010. Plant health and global change - some implications for landscape management. Biol. Rev. 85, 729–755.

Perkins, K.S., Nimmo, J.R., Medeiros, A.C., Szutu, D.J., Allmen, E. von, 2014. Assessing effects of native forest restoration on soil moisture dynamics and potential aquifer recharge, Auwahi, Maui. Ecohydrology, n/a.

Polis, G.A., Hurd, S.D., 1996. Linking marine and terrestrial food webs: Allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. Am. Nat. 147, 396–423.

Praveena, S.M., Aris, A.Z., 2009. A review of groundwater in islands using SWOT analysis. World Rev. Sci. Tech. Sust. Dev. 6, 186–203.

Prebble, M., Dowe, J.L., 2008. The late Quaternary decline and extinction of palms on oceanic Pacific islands. Quaternary Sci. Rev. 27, 2546–2567.

Pryet, A., Domínguez, C., Tomai, P.F., Chaumont, C., d'Ozouville, N., Villacís, M., Violette, S., 2012. Quantification of cloud water interception along the windward slope of Santa Cruz Island, Galapagos (Ecuador). Agr. Forest Meteorol. 161, 94–106.

Putten, W.H. van der, Macel, M., Visser, M.E., 2010. Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. Philos. T. R. Soc. B. 365, 2025–2034.

R Core Team, 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Restrepo, A., Colinvaux, P., Bush, M., Correa-Metrio, A., Conroy, J., Gardener, M.R., Jaramillo, P., Steinitz-Kannan, M., Overpeck, J.T., 2012. Impacts of climate variability and human colonization on the vegetation of the Galápagos Islands. Ecology 93, 1853–1866.

Ricci, M., 2006. Conservation status and ex situ cultivation efforts of endemic flora of the Juan Fernández Archipelago. Biodivers. Conserv. 15, 3111–3130.

Rignot, E., Mouginot, J., Morlighem, M., Seroussi, H., Scheuchl, B., 2014. Widespread, rapid grounding line retreat of Pine Island, Thwaites, Smith, and Kohler glaciers, West Antarctica, from 1992 to 2011. Geophys. Res. Lett. 41, 3502–3509.

Rijsdijk, K.F., Hengl, T., Norder, S.J., Otto, R., Emerson, B.C., Ávila, S.P., López, H., van Loon, E. Emiel, Tjørve, E., Fernández-Palacios, J.M., Heaney, L., 2014. Quantifying surface-area changes of volcanic islands driven by Pleistocene sea-level cycles: biogeographical implications for the Macaronesian archipelagos. J. Biogeogr. 41, 1242–1254.

Rodríguez-Robles, J.A., Jezkova, T., Leal, M., 2010. Climatic stability and genetic divergence in the tropical insular lizard Anolis krugi, the Puerto Rican 'Lagartijo Jardinero de la Montaña'. Mol. Ecol. 19, 1860–1876.

Roessig, J.M., Woodley, C.M., Cech, J.J., Jr., Hansen, L.J., 2004. Effects of global climate change on marine and estuarine fishes and fisheries. Rev. Fish Fisher. 14, 251–275.

Ross, L.C., Lambdon, P.W., Hulme, P.E., 2008. Disentangling the roles of climate, propagule pressure and land use on the current and potential elevational distribution of the invasive weed Oxalis pes-caprae L. on Crete. Perspect. Plant. Ecol. 10, 251–258.

Ross, M.S., O'Brien, J.J., Ford, R.G., Zhang, K., Morkill, A., 2009. Disturbance and the rising tide: the challenge of biodiversity management on low-island ecosystems. Front. Ecol. Environ. 7, 471–478.

Rotzoll, K., Fletcher, C.H., 2012. Assessment of groundwater inundation as a consequence of sea-level rise. Nat. Clim. Change 3, 477–481.

Roux, P.C. le, McGeoch, M.A., 2008. Rapid range expansion and community reorganization in response to warming. Glob. Change Biol. 14, 2950–2962.

Roux, P.C. le, McGeoch, M.A., Nyakatya, M.J., Chown, S.L., 2005. Effects of a short-term climate change experiment on a sub-Antarctic keystone plant species. Glob. Change Biol. 11, 1628–1639.

Royer, P.D., Cobb, N.S., Clifford, M.J., Huang, C.-Y., Breshears, D.D., Adams, H.D., Villegas, J.C., 2011. Extreme climatic event-triggered overstorey vegetation loss increases understorey solar input regionally: primary and secondary ecological implications. J. Ecol. 99, 714–723.

Sadler, J.P., 1999. Biodiversity on oceanic islands: a palaeoecological assessment. J. Biogeogr. 26, 75–87.

Sakai, A.K., Wagner, W.L., Mehrhoff, L.A., 2002. Patterns of endangerment in the Hawaiian flora. Syst. Biol. 51, 276–302.

Sax, D.F., Gaines, S.D., 2008. Species invasions and extinction: The future of native biodiversity on islands. P. Natl. Acad. Sci. USA 105, 11490–11497.

Sax, D.F., Gaines, S.D., Brown, J.H., 2002. Species invasions exceed extinctions on islands worldwide: A comparative study of plants and birds. Am. Nat. 160, 766–783.

Schaal, B.A., Leverich, W.J., 2005. Conservation genetics: Theory and practice. Ann. Mo. Bot. Gard. 92, 1–11.

Schäfer, H., 2005. Endemic vascular plants of the Azores: an updated list. Hoppea 66, 275–283.

Scherrer, D., Körner, C., 2009. Infra-red thermometry of alpine landscapes challenges climatic warming projections. Glob. Change Biol. 16, 2602–2613.

Scholl, M.A., Giambelluca, T.W., Gingerich, S.B., Nullet, M.A., Loope, L.L., 2007. Cloud water in windward and leeward mountain forests: The stable isotope signature of orographic cloud water. Water Resour. Res. 43, 1–13.

Scott, J.J., Kirkpatrick, J.B., 2013. Changes in the cover of plant species associated with climate change and grazing pressure on the Macquarie Island coastal slopes, 1980–2009. Polar Biol. 36, 127–136.

Sedlacek, J., Schmid, B., Matthies, D., Albrecht, M., Ollerton, J., 2012. Inbreeding depression under drought stress in the rare endemic Echium wildpretii (Boraginaceae) on Tenerife, Canary Islands. PLoS One 7, e47415.

ekercio lu, Ç.H., Daily, G.C., Ehrlich, P.R., 2004. Ecosystem consequences of bird declines. P. Natl. Acad. Sci. USA 101, 18042–18047.

Shapcott, A., Hutton, I., Baker, W.J., Auld, T.D., 2012. Conservation genetics and ecology of an endemic montane palm on Lord Howe Island and its potential for resilience. Conserv. Genet. 13, 257–270.

Shmida, A., Werger, M.J.A., 1992. Growth form diversity on the Canary Islands. Vegetatio 102, 183–199.

Smith, V.R., Steenkamp, M., 1990. Climatic change and its ecological implications at a subantarctic island. Oecologia 85, 14–24.

Spennemann, D.H., 2006. Freshwater lens, settlement patterns, resource use and connectivity in the Marshall Islands. Transforming Cultures eJournal 1, 44–63.

Sperling, F.N., Washington, R., Whittaker, R.J., 2004. Future climate change of the subtropical North Atlantic: Implications for the cloud forests of Tenerife. Climatic Change 65, 103–123.

Spiller, D.A., Piovia-Scott, J., Wright, A.N., Yang, L.H., Takimoto, G., Schoener, T.W., Iwata, T., 2010. Marine subsidies have multiple effects on coastal food webs. Ecology 91, 1424–1434.

Spiller, D.A., Schoener, T.W., 2007. Alteration of island food-web dynamics following major disturbance by hurricanes. Ecology 88, 37–41.

Steadman, D.W., 2006. Extinction & biogeography of tropical Pacific birds. University of Chicago Press, Chicago, pp. 594.

Steinbauer, M.J., Irl, S.D.H., Beierkuhnlein, C., 2013. Elevation-driven ecological isolation promotes diversification on Mediterranean islands. Acta Oecol. 47, 52–56.

Steinbauer, M.J., Otto, R., Naranjo-Cigala, A., Beierkuhnlein, C., Fernández-Palacios, J.M., 2012. Increase of island endemism with altitude - speciation processes on oceanic islands. Ecography 35, 23–32.

Still, C.J., Foster, P.N., Schneider, S.H., 1999. Simulating the effects of climate change on tropical montane cloud forests. Nature 398, 608–610.

Stuessy, T.F., 2007. Evolution of specific and genetic diversity during ontogeny of island floras: The importance of understanding process for interpreting island biogeographic patterns, In: Ebach, M.C., Tangney, R.S. (Eds.) Biogeography in a changing world. CRC Press, Boca Raton, FL.

Stuessy, T.F., Jakubowsky, G., Gomez, R.S., Pfosser, M., Schluter, P.M., Fer, T., Sun, B.-Y., Kato, H., 2006. Anagenetic evolution in island plants. J. Biogeogr. 33, 1259–1265.

Stuessy, T.F., Takayama, K., López-Sepúlveda, P., Crawford, D.J., 2013. Interpretation of patterns of genetic variation in endemic plant species of oceanic islands. Bot. J. Linn. Soc., n/a.

Suchodoletz, H. von, Oberhänsli, H., Hambach, U., Zöller, L., Fuchs, M., Faust, D., 2010. Soil moisture fluctuations recorded in Saharan dust deposits on Lanzarote (Canary Islands) over the last 180 ka. Quaternary Sci. Rev. 29, 2173–2184.

Taylor, K.E., Stouffer, R.J., Meehl, G.A., 2012. An overview of CMIP5 and the experiment design. B. Am. Meteorol. Soc. 93, 485–498.

Taylor, S., Kumar, L., 2014. Climate Change and Weed Impacts on Small Island Ecosystems: Lantana camara L. (Magnoliopsida: Verbenaceae) Distribution in Fiji 1. Pac. Sci. 68, 117–133.

Terry, J.P., Chui, T.F.M., 2012. Evaluating the fate of freshwater lenses on atoll islands after eustatic sea-level rise and cyclone-driven inundation: A modelling approach. Global Planet. Change 88-89, 76–84.

Thomas, C.D., 2010. Climate, climate change and range boundaries. Divers. Distrib. 16, 488–495.

Thomas, C.D., Hill, J.K., Anderson, B.J., Bailey, S., Beale, C.M., Bradbury, R.B., Bulman, C.R., Crick, H.Q.P., Eigenbrod, F., Griffiths, H.M., Kunin, W.E., Oliver, T.H., Walmsley, C.A., Watts, K., Worsfold, N.T., Yardley, T., 2011. A framework for assessing threats and benefits to species responding to climate change. Method. Ecol. Evol. 2, 125–142.

Thomson, L.J., Macfadyen, S., Hoffmann, A.A., 2010. Predicting the effects of climate change on natural enemies of agricultural pests. Biol. Control 52, 296–306.

Thuiller, W., Lavorel, S., Araujo, M.B., 2005. Niche properties and geographical extent as predictors of species sensitivity to climate change. Global Ecol. Biogeogr. 14, 347–357.

Traveset, A., Heleno, R., Chamorro, S., Vargas, P., McMullen, C.K., Castro-Urgal, R., Nogales, M., Herrera, H.W., Olesen, J.M., 2013. Invaders of pollination networks in the Galapagos Islands: emergence of novel communities. P. R. Soc. B. 280, 20123040.

Triantis, K.A., Borges, Paulo A. V., Ladle, R.J., Hortal, J., Cardoso, P., Gaspar, C., Dinis, F., Mendonça, E., Silveira, Lúcia M. A., Gabriel, R., Melo, C., Santos, Ana M. C., Amorim, I.R., Ribeiro, S.P., Serrano, Artur R. M., Quartau, J.A., Whittaker, R.J., 2010. Extinction debt on oceanic islands. Ecography, no.

Triantis, K.A., Mylonas, M., Lika, K., Vardinoyannis, K., 2003. A model for the species–area–habitat relationship. J. Biogeogr. 30, 19–27.

Trøjelsgaard, K., Báez, M., Espadaler, X., Nogales, M., Oromí, P., La Roche, F., Olesen, J.M., Triantis, K.A., 2013a. Island biogeography of mutualistic interaction networks. J. Biogeogr. 40, 2020–2031.

Trøjelsgaard, K., Olesen, J.M., Shipley, B., 2013b. Macroecology of pollination networks. Global Ecol. Biogeogr. 22, 149–162.

Trueman, M., d'Ozouville, N., 2010. Characterizing the Galapagos terrestrial climate in the face of global climate change. Galapagos Research 67, 26–37.

Tylianakis, J.M., Didham, R.K., Bascompte, J., Wardle, D.A., 2008. Global change and species interactions in terrestrial ecosystems. Ecol. Lett. 11, 1351–1363.

Urban, M.C., Tewksbury, J.J., Sheldon, K.S., 2012. On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. P. R. Soc. B. 279, 2072–2080.

Vaza ová, K., Münzbergová, Z., 2014. Dispersal ability of island endemic plants: What can we learn using multiple dispersal traits? Flora 209, 530–539.

Vermeer, M., Rahmstorf, S., 2009. Global sea level linked to global temperature. P. Natl. Acad. Sci. USA 106, 21527–21532.

Vitt, P., Havens, K., Kramer, A.T., Sollenberger, D., Yates, E., 2010. Assisted migration of plants: Changes in latitudes, changes in attitudes. Biol. Conserv. 143, 18–27.

Vorsino, A.E., Fortini, L.B., Amidon, F.A., Miller, S.E., Jacobi, J.D., Price, J.P., Gon, S.'., Koob, G.A., 2014. Modeling Hawaiian ecosystem degradation due to invasive plants under current and future climates. PLoS One 9, e95427.

Vourc'h, G., Martin, J.-L., Duncan, P., Escarré, J., Clausen, T.P., 2001. Defensive adaptations of Thuja plicata to ungulate browsing: a comparative study between mainland and island populations. Oecologia 126, 84–93.

Vuuren, D.P. van, Edmonds, J., Kainuma, M., Riahi, K., Thomson, A., Hibbard, K., Hurtt, G.C., Kram, T., Krey, V., Lamarque, J.-F., Masui, T., Meinshausen, M., Nakicenovic, N., Smith, S.J., Rose, S.K., 2011. The representative concentration pathways: an overview. Climatic Change 109, 5–31.

Walker, L.R., Bellingham, P., 2011. Island environments in a changing world. Cambridge University Press, Cambridge, New York, xiv, 324.

Wallace, A.R., 1880. Island life: Or, the phenomena and causes of insular faunas and floras, including a revision and attempted solution of the problem of geological climates. Macmillan & Co., London.

Walsh, K.J., McInnes, K.L., McBride, J.L., 2012. Climate change impacts on tropical cyclones and extreme sea levels in the South Pacific — A regional assessment. Global Planet. Change 80-81, 149–164.

Walther, G.-R., Roques, A., Hulme, P.E., Sykes, M.T., Pysek, P., Kühn, I., Zobel, M., Bacher, S., Botta-Dukát, Z., Bugmann, H., Czúcz, B., Dauber, J., Hickler, T., Jarosík, V., Kenis, M., Klotz, S., Minchin, D., Moora, M., Nentwig, W., Ott, J., Panov, V.E., Reineking, B., Robinet, C., Semenchenko, V., Solarz, W., Thuiller, W., Vilà, M., Vohland, K., Settele, J., 2009. Alien species in a warmer world: risks and opportunities. Trends Ecol. Evol. 24, 686–693.

Webb, E.L., van de Bult, Martin, Fa'aumu, S., Webb, R.C., Tualaulelei, A., Carrasco, L.R., 2014. Factors affecting tropical tree damage and survival after catastrophic wind disturbance. Biotropica 46, 32–41.

Weigelt, P., Jetz, W., Kreft, H., 2013. Bioclimatic and physical characterization of the world's islands. P. Natl. Acad. Sci. USA 110, 15307–15312.

Wetzel, F.T., Beissmann, H., Penn, D.J., Jetz, W., 2013. Vulnerability of terrestrial island vertebrates to projected sea-level rise. Glob. Change Biol. 19, 2058–2070.

Wetzel, F.T., Kissling, W.D., Beissmann, H., Penn, D.J., 2012. Future climate change driven sea-level rise: secondary consequences from human displacement for island biodiversity. Glob. Change Biol. 18, 2707–2719.

Whinam, J., Abdul-Rahman, J.A., Visoiu, M., di Folco, M.-B. F., Kirkpatrick, J.B., 2014. Spatial and temporal variation in damage and dieback in a threatened subantarctic cushion species. Aust. J. Bot. 62, 10.

Whittaker, R.J., Fernández-Palacios, J.M., 2007. Island biogeography: Ecology, evolution and conservation, 2nd ed. Oxford University Press, New York, xii, 401 s.

Whittaker, R.J., Triantis, K.A., Ladle, R.J., 2008. A general dynamic theory of oceanic island biogeography. J. Biogeogr. 35, 977–994.

Willi, Y., Buskirk, J. van, Hoffmann, A.A., 2006. Limits to the adaptive potential of small populations. Annu. Rev. Ecol. Evol. S. 37, 433–458.

Williams, S.E., Shoo, L.P., Isaac, J.L., Hoffmann, A.A., Langham, G., 2008. Towards an integrated framework for assessing the vulnerability of species to climate change. PLoS Biol. 6, 2621–2626.

Willis, C.G., Ruhfel, B.R., Primack, R.B., Miller-Rushing, A.J., Losos, J.B., Davis, C.C., 2010. Favorable climate change response explains non-native species' success in Thoreau's woods. PLoS One 5, e8878.

Wilmers, C.C., Post, E., Peterson, R.O., Vucetich, J.A., 2006. Predator disease out-break modulates top-down, bottom-up and climatic effects on herbivore population dynamics. Ecol. Lett. 9, 383–389.

Wisz, M.S., Pottier, J., Kissling, W.D., Pellissier, L., Lenoir, J., Damgaard, C.F., Dormann, C.F., Forchhammer, M.C., Grytnes, J.-A., Guisan, A., Heikkinen, R.K., Høye, T.T., Kühn, I., Luoto, M., Maiorano, L., Nilsson, M.-C., Normand, S., Öckinger, E., Schmidt, N.M., Termansen, M., Timmermann, A., Wardle, D.A., Aastrup, P., Svenning, J.-C., 2013. The role of biotic interactions in shaping distributions and realised assemblages of species: implications for species distribution modelling. Biol. Rev. 88, 15–30.

Wong, P.P., Marone, E., Lana, P., Fortes, M., 2005. Chapter 23: Island systems Millenium Ecosystem Assessment. Current state and trends. Island Press, Washington DC, Covelo, London, pp. 663–680.

Woodroffe, C.D., 2008. Reef-island topography and the vulnerability of atolls to sea-level rise. Global Planet. Change 62, 77–96.

Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. P. Natl. Acad. Sci. USA 96, 1463–1468.

SUPPORTING INFORMATION IN ELECTRONIC VERSION OF DISSERTATION

Appendix A1 Relationship of latitude (A) and distance to the next continent (B) to the projected change of temperature and of absolute values of latitude to changes of precipitation (C).

Appendix A2 Description of spatial pattern analysis.

8. Summary

In the seven manuscripts presented in this dissertation I contribute to our understanding of the drivers of plant diversity, endemism and speciation by using empirical, experimental and theoretical approaches. I introduce and define the concept of high elevation islands (HEI), which – in my opinion – are ideal research objects to address ecological and biogeographic questions. I intend to bridge the gap between island biogeography (i.e. by focusing on the global scale) and island ecology (i.e. by addressing the within-island scale). As a model HEI the mountainous island of La Palma (Canary Islands) is used and all field-related research was conducted there.

HEIs are found in all major oceans from mid to low latitudes. Characteristic features are elevational range reaching more than 1000m a.s.l. and possessing ecosystems ranging from coastal to alpine systems. The alpine treeline, as the borderline between forest and treeless alpine systems, is therefore fundamental in describing HEIs. Interestingly, I demonstrate that globally treeline elevation on HEIs, which is generally lower on HEIs than on the mainland, is mainly driven by island elevation, and not, as expected, by latitude. Another characteristic feature of HEIs is the phenomenon described by the *elevation-driven ecological isolation* hypothesis, which suggests increasing speciation rates with elevation due to geographical and environmental isolation. Although island climates are generally considered to be buffered by the surrounding ocean, the reviewed literature indicates that global climate change poses a considerable threat to HEIs, especially to systems adapted to climatic stability (e.g. cloud or laurel forests) and alpine ecosystems.

La Palma is a typical trade wind-dominated subtropical HEI hosting a variety of different environmental gradients, subsequent vegetation zones and a rich endemic flora. Topography and climate (including different measures of precipitation variability) express varying importance in explaining the distribution of species richness, endemic richness and endemicity (i.e. floristic uniqueness) on La Palma. Besides environmental gradients, I show that island ecological processes and patterns on La Palma are in a large measure shaped by human-mediated disturbances. Harsh environmental conditions, a high degree of endemism and the presence of several introduced herbivores, especially the European rabbit *Oryctolagus cuniculus* and the feral goat *Capra hircus*, characterize the high elevation ecosystem of La Palma. In a 11-yr exclosure experiment I am able to show that introduced herbivores have likely led to a vegetation shift in the high elevation ecosystem, which changed from a diverse shrub community to the mono-dominance of a single shrub species (*Adenocarpus viscosus* subsp. *spartioides*). In addition, introduced herbivores selectively browse rare endemics (some even on the brink of extinction) and reduce endemic seedling establishment to nearly zero, making a recuperation of the natural system impossible without substantial herbivore control measures and conservation efforts. Although fire frequencies have increased due to human interference, fire seems to have a positive effect on species richness and seedling establishment in the high elevation ecosystem. Contrary to our expectations, roads have a positive effect on endemic species on La Palma. Many rupicolous endemics profit from roadside cliffs because these cliffs function as 'safe sites' and protect them from introduced herbivores and fire.

As a result of this dissertation several intriguing research questions have arisen in HEI science. These questions focus on within-island patterns of plant species diversity and especially endemism, the novel field of disturbance-driven island ecology, and global and macroecological patterns. HEI science is a promising research field with the potential to substantially advance our knowledge of ecology and biogeography in the future.

9. Zusammenfassung

Diese Dissertation, die aus sieben Manuskripten besteht, trägt zum Verständnis über die Treiber von Pflanzendiversität, Endemismus und Artbildung bei, indem empirische, experimentelle und theoretische Ansätze gewählt werden. Das Konzept der Gebirgsinseln (HEI), die meiner Meinung nach ideale Untersuchungsobjekte sind um ökologische und biogeographische Fragestellungen zu bearbeiten, wird des Weiteren vorgestellt und definiert. Es ist mir ein Anliegen in dieser Dissertation inselbiogeographische (d.h. mit einem Fokus auf die globale Skala) und inselökologische Aspekte (d.h. mit einem Fokus auf die Subinselskala) zu verknüpfen. Als Model-HEI wurde die gebirgige Kanareninsel La Palma ausgewählt und alle Geländestudien dieser Arbeit wurden vor Ort durchgeführt.

Man findet HEIs von den mittleren bis zu den niederen Breiten in allen großen Ozeanen. Die wichtigsten Charakteristika sind eine Mindesthöhe von mehr als 1000 m ü.N.N. und das Vorhandensein der gesamten Bandbreite von Ökosystemen, von der Küstenzone bis zu alpinen Systemen. Daher ist die alpine Baumgrenze, also die Grenze zwischen Wald und baumlosen alpinen Ökosystemen, von zentraler Bedeutung um HEIs zu beschreiben. Interessanterweise konnte ich zeigen, dass die Baumgrenzenhöhe auf HEIs, die durchschnittlich niedriger ist als auf dem Kontinent, vor allem durch die Inselhöhe bestimmt wird und nicht, wie angenommen, durch den Breitengrad. Ein weiteres Charakteristikum von HEIs wird von der Hypothese zur höhenbeeinflussten ökologischen Isolation beschrieben, welche postuliert, dass die Artbildungsrate bedingt durch zunehmende geographisch und ökologische Isolation mit der Höhe zunimmt. Obwohl üblicherweise angenommen wird, dass Inselklimate durch den umgebenden Ozean gepuffert werden, zeigt eine umfassende Literaturstudie, das der globale Klimawandel eine substantielle Bedrohung für die Floren und Ökosysteme von HEIs darstellen könnte. Insbesondere könnten Systeme, die an anhaltende klimatische Stabilität angepasst sind, wie z.B. Nebel- oder Lorbeerwald, aber auch alpine Ökosysteme und deren Arten gefährdet sein.

La Palma ist eine typische, vom Passatwind beeinflusste HEI in den Subtropen, die eine Vielzahl an Umweltgradienten, davon abhängige Vegetationszonen und eine reiche endemische Flora besitzt. Topographie und Klima, welches auch verschiedene Maße von Niederschlagsvariabilität beinhaltet, haben einen unterschiedlichen Einfluss auf Artreichtum, Endemitenreichtum und Endemizität (d.h. die floristische Einzigartigkeit) von La Palma. Neben den Umweltgradienten zeige ich, dass inselökologische Prozesse und Muster auf La Palma zu großen Teilen durch menschengemachte Störungen gesteuert werden. Ungünstige Umweltbedingungen, ein hoher Endemismusanteil und die Präsenz einiger eingeschleppter Herbivoren, v.a. des Wildkaninchens *Oryctolagus cuniculus* und der Wildziege *Capra hircus*, charakterisieren das Hochlagenökosystem von La Palma. In einem 11-jährigen Auszäunungsexperiment konnte ich zeigen, dass wahrscheinlich eine Vegetationsverschiebung im Hochlagenökosystem durch eingeschleppte Herbivoren verursacht wurde, welche zu einer Veränderung des Systems von einer diversen Strauchgesellschaft zur Monodominanz einer einzigen Strauchart (*Adenocarpus viscosus* subsp. *spartioides*) geführt hat. Zusätzlich dazu fressen eingeschleppte Herbivoren bevorzugt seltene Endemiten (von denen sich einige sogar am Rande der Extinktion befinden)

und reduzieren die Etablierung von endemischen Keimlingen fast komplett, was eine Erholung des natürlichen Systems ohne substantielle Herbivorenkontroll- und Naturschutzmaßnahmen unmöglich macht. Obgleich Feuerfrequenzen durch menschliches Zutun zugenommen haben, deutet vieles darauf hin, dass Feuer einen positiven Effekt auf Artreichtum und die Etablierung von Keimlingen im Hochlagensystem hat. Im Gegensatz zu unseren Erwartungen haben Straßen einen positiven Einfluss auf Endemiten auf La Palma. Viele felsenbewohnende Endemiten profitieren von den straßennahen Felswänden, weil diese Felswände als Refugium agieren und die Endemiten vor nicht-heimischen Herbivoren und Feuer schützen können.

Aus dieser Dissertation ergeben sich eine Reihe spannender Forschungsfragen in den HEI-Wissenschaften. Der Fokus dieser Fragen liegt v.a. auf Pflanzendiversität und Endemismus auf der Subinselskala, das neuartige Forschungsfeld der störungsabhängigen Inselökologie und globale sowie makroökologische Muster gerichtet. Die Wissenschaft der HEI ist ein vielversprechendes Forschungsfeld mit dem Potenzial unser Wissen in der Ökologie und Biogeographie in der Zukunft substantiell zu erweitern.

10. Acknowledgements

La Palma really is the *isla bonita*, a wonderful island with dramatic landscapes, a rich and unique endemic flora, great food, beautiful black sand beaches and friendly locals! Every time when I was preparing a field trip to La Palma, my non-scientist friends would make jokes about how I was always going on holidays financed by their tax money. And what can I say? They were right, at least to some degree. No matter what you do on La Palma, research, work, travel or whatever it might be, it always feels a little like going on vacation…

Many people have aided me in the completion of this dissertation. First of all I would like to thank Anke for being so supportive of my work, for giving me the freedom that I needed to develop my own research interests and ideas, for motivating me and making things seem possible to achieve, for the valuable advice and help that you gave me, for the good relationship that we have developed over the years and the great times together on La Palma! I am also very appreciative of learning almost everything I know about writing papers, publishing in scientific journals and communicating science from you.

Carl, you also deserve a big thank-you because you sparked my interest in science in the first place, always supported me (even as a student), introduced me to islands, island ecology and island biogeography, and gave me the opportunity to do ecological research.

Of course, I have to mention the highly influential and renowned Island Boy Group, consisting of Manuel, David and Andi (who doesn't actually work on islands but belongs to the Island Boy Group anyway): Rock on!

Dominik and Reinhold are THE GIS gurus! Nough said.

I really had a great time working with the Disturbance Ecology and Biogeography workgroup. Thank you very much for being so supportive and helpful whenever needed and for the great and positive atmosphere you helped to create!

Ángel Palomares Martínez, the director of the National Park Caldera de Taburiente, was always so kind, helpful and supportive of all our crazy ideas and took the time to deal with our inquiries whenever we needed him. I would also like to mention Ángel Rebolé for taking me into the cliffs of the caldera, helping me identify many species and even showing me a Guanche burial site. My gratitude goes to the many employees of the Caldera de Taburiente NP for establishing and maintaining the exclosure plots for all these years. A special thank you goes to Dr. Félix "Feluco" Medina from the Cabildo Insular de La Palma for the numerous export permissions and the many laughs we had together!

I will always have special memories of the *Grupo Alpino* with Wolfgang and Stefan because that was my first real contact with island ecology and La Palma, and because we worked in snow, rain and storms while others were chilling at the beach!

Lots of people deserve to be mentioned here because they made this dissertation possible after all. Many thanks go to:

- The Elite Netzwerk Bayern and Global Change Ecology for financing my research,
- Philipp and Vanessa for their enduring help in the field and for supplying me with great pictures of La Palma,
- Numerous students of the La Palma Summer School (esp. Susi, Jana, Gesche, Wolle and Lilith) for the great work they did and for realizing your research projects,
- Lisa for her great work on island treelines,
- José Mari for being the nicest person ever,
- David Gallego Puyol, whom I have never met, but who was so friendly to supply me with high quality meteorological data from the Canary Islands,
- James Juvik and Jon Price for the financial support allowing me to come to the specialists' conference in Hawaii,
- Fabien Anthelme for the great time we had on Hawaii and the knowledgeable comments on treelines,
- The many anonymous reviewers who improved my manuscripts with constructive comments and suggestions,
- Olivia for the cover design,
- Karina for the great accommodation and Holiday Cars for being so relaxed about our inappropriate off-road driving,
- The people of La Palma, who spared my life, even though their reckless driving did not make this an easy task,
- My friends Marcus, Sarah, Tobi and Stephan for their disrespect towards ecology and science in general (who alternatively called me "der Bleamesammler" or "der Urlauber" or "Wanderstudent"). You're great anyway!
- My parents aka the surprisingly professional parental proofreading team for fostering my interest in natural sciences, being supportive of whatever I do, and, of course, for all the proofreading,
- And my brothers, Sam and Max, for making multilingual rap songs about my research and being my best buddies.

Above all, I would like to thank my wife Andrea for being such a wonderful person, whom I can rely on, who always supports me and is always there for me, and with whom I have had the best time ever.

Photography

Page vi: Panorama of the Caldera de Taburiente at sunset. Picture taken from the Cumbre Vieja facing north. Picture taken by Severin D.H. Irl.

Page 20: Afternoon light in the Barranco de las Angustias, the largest and steepest valley of the La Palma and the only outflow of the Caldera de Taburiente complex. Picture taken by Philipp Gnoyke.

Page 28: View of the snowcapped Pico de Teide on the neighboring island of Tenerife. The picture was taken above the trade wind inversion layer on the eastern slopes of the Caldera de Taburiente of La Palma. Picture taken by Philipp Gnoyke.

Page 32: Trade wind cloud flowing over the Cumbre Nueva and evaporating on its way down. The picture was taken on the southern slope of the Bejenado looking into the El Paso valley on the west side of the island. A nice stand of the archipelago endemic *Pinus canariensis* can be seen in the foreground. Picture taken by Severin D.H. Irl.

Page 36: Measurements on the rare single-island endemic *Genista benehoavensis* just below the Roque de los Muchachos (2426 m), the highest point of the island, on a winter's day. The shrub is covered with a considerable layer of ice because the night before northern winds had brought humid but freezing conditions to the summit area. Picture taken by Manuel J. Steinbauer.

Page 40: Sunset at the southern tip of the island near the most recently erupted volcano (Teneguía) showing typical low elevation scrub. Picture taken by Philipp Gnoyke.

Page 48: A nice individual of the single island endemic and iconic *Aeonium nobile*. The rosette has a diameter of about 40 cm. Picture taken by Philipp Gnoyke.

Page 188: View of the north coast of La Palma. The many steep barrancos substantially contribute to the high topographic complexity of this region and many endemics are found in these barrancos. On the lower right hand side a well-preserved grove of the famous Canary dragon tree (*Dracaena draco* subsp. *draco*) can be seen. Picture taken by Philipp Gnoyke.

Page 192: One of the three remaining sites of the single-island endemic *Lotus pyranthus* with its flame-resembling flower. The site has been fenced to protect the species from introduced herbivores. Picture taken by Anke Jentsch.

Page 196: View from the rim of the caldera into the Caldera de Taburiente NP. In the background the geologically younger and topographically softer Cumbre Vieja is visible. Picture taken by Severin D.H. Irl.

Page 200: Windswept and dry coast in the northwest of La Palma. An impressive individual of the cactus-like archipelago endemic *Euphorbia canariensis* can be seen on the right hand side. Picture taken by Philipp Gnoyke.

Page 202: View of the interior of the Caldera de Taburiente as seen from the northern cliff of the Bejenado. Picutre taken by Philipp Gnoyke.

11. Declarations

(Eidesstattliche) Versicherungen und Erklärungen

(§ 5 Nr. 4 PromO)

Hiermit erkläre ich, dass keine Tatsachen vorliegen, die mich nach den gesetzlichen Bestimmungen über die Führung akademischer Grade zur Führung eines Doktorgrades unwürdig erscheinen lassen.

(§ 8 S. 2 Nr. 5 PromO)

Hiermit erkläre ich mich damit einverstanden, dass die elektronische Fassung meiner Dissertation unter Wahrung meiner Urheberrechte und des Datenschutzes einer gesonderten Überprüfung hinsichtlich der eigenständigen Anfertigung der Dissertation unterzogen werden kann.

(§ 8 S. 2 Nr. 7 PromO)

Hiermit erkläre ich eidesstattlich, dass ich die Dissertation selbständig verfasst und keine anderen als die von mir angegebenen Quellen und Hilfsmittel benutzt habe.
Ich habe die Dissertation nicht bereits zur Erlangung eines akademischen Grades anderweitig eingereicht und habe auch nicht bereits diese oder eine gleichartige Doktorprüfung endgültig nicht bestanden.

(§ 8 S. 2 Nr. 9 PromO)

Hiermit erkläre ich, dass ich keine Hilfe von gewerblichen Promotionsberatern bzw. –vermittlern in Anspruch genommen habe und auch künftig nicht nehmen werde.

Bayreuth, October 27th, 2014

....
(gez. Severin Irl)