Long-term monitoring across elevational gradients to assess ecological hypothesis: a description of standardized sampling methods in oceanic islands and first results

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We are launching a long-term study to characterize the biodiversity at different elevations in several Azorean Islands. Our aim is to use the Azores as a model archipelago to answer the fundamental question of what generates and maintains the global spatial heterogeneity of diversity in islands and to be able to understand the dynamics of change across time. An extensive, standardized sampling protocol was applied in most of the remnant forest fragments of five Azorean Islands. Fieldwork followed BRYOLAT methodology for the collection of bryophytes, ferns and other vascular plant species. A modified version of the BALA protocol was used for arthropods. A total of 70 plots (10 m x 10 m) are already established in five islands (Flores, Pico, São Jorge, Terceira and São Miguel), all respecting an elevation step of 200 m, resulting in 24 stations examined in Pico, 12 in Terceira, 10 in Flores, 12 in São Miguel and 12 in São Jorge. The first results regarding the vascular plants inventory include 138 vascular species including taxa from Lycopodiophyta (N=2), Pteridophyta (N=27), Pinophyta (N=2) and Magnoliophyta (N=107). In this contribution we also present the main research question for the next six years within the 2020 Horizon.

Key words: arthropods, bryophytes, elevational gradients, long-term studies, vascular plants

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INTRODUCTION

Islands offer a unique natural laboratory for biogeographical, ecological, evolutionary and conservation research as they represent globally replicated but relatively simplified real world systems (Whittaker & Fernández-Palacios 2007; Kueffer & Fernández-Palacios 2010). Island systems have a leading role in supporting a bulk of theories in the fields of community ecology, biogeography and evolution. Two examples of the extreme importance of islands for biological studies are the formulation of Charles Darwin´s Evolutionary Theory and the classical Equilibrium Model of Island Biogeography (EMIB) (MacArthur & Wilson 1967), intended to explain patterns of species richness on islands based on island area and isolation, but with wider applications in conservation biogeography (Whittaker et al. 2005; Fattorini & Borges 2012).

Oceanic islands have a volcanic origin, emerging from the sea. Volcanos developing at different times contribute to the final shape of the islands, and these may remain quite small and simple (e.g. Corvo Island in Azores) or with rather more complex geomorphology (e.g. Madeira, La Réunion). As archipelagos are made of islands at a different stage of ontogeny Whittaker et al. (2007) proposed "The general dynamic model of oceanic island biogeography" (GDM), which expands the EMIB (MacArthur & Wilson 1967) to incorporate the geological dynamism of oceanic islands and speciation in the explanation of species diversity. Another important feature of islands is their mountainous system, which may be composed of a main large volcano (e.g. Pico in Azores) or a complex of volcanic structures with different levels of topographical complexity. Elevation or maximum altitude of an island is usually used as a surrogate of habitat diversity, and fine scale digital elevation models can be used as metrics of niche diversity (Gray & Cavers 2014). Volcanic islands are thus wonderful systems to study gradients related with altitude.

In the last decades elevational gradients have been increasingly used as model templates for large-scale gradient studies (Rahbek 1995; Körner 2007), since they "present many different environmental and biological shifts and are useful tools for understanding ecosystem dynamics." (Kitching et al. 2011: pp. 238). It is widely recognized that elevational gradients contain many ecotones within a restricted geographical area. Besides the classical biological approaches, studying species turnover and patterns shaping diversity and community structure use elevation gradients (Kitching et al. 2011 and references therein). Climate change is also being investigated using elevation gradients (Merrill et al. 2008; Ashton et al. 2009), either as analogues for latitudinal climate change or assessing the impact on species or communities along these gradients (e.g. Hodkinson 2005 [insects], Odland 2010 [vascular plants]).

There are also limitations associated with studies along elevational gradients. First of all, elevation is not an ecological variable per se, although it may be used as a surrogate of many environmental conditions. It is important to have a detailed description of the sites investigated, since diversity and presence of single taxa often depend on compensating factors such as exposition, distance to major areas of native vegetation, slope degree, etc.

Scale effects should also be considered. As an example, Nogués et al. (2008) report a relationship between scale of extent of the study (the proportion of the complete altitudinal gradient sampled) and the resulting species richness pattern. If the entire gradient was studied, the pattern was hump-shaped, but if the gradient was shortened (smaller extent), the patterns were predominantly monotonic. This strongly advocates for always taking full ecological gradients (best from sea-level to, at least, timberline or mountain tops (Kessler et al. 2011).

Some authors also stated that anthropogenic activities may have caused a global reduction in natural lowland habitats, hindering our ability to detect universal patterns to uncover the mechanisms determining the distribution of biological diversity on Earth (Nogués et al. 2008), which supports the idea that studies should consider the same ecosystems during all the gradient (e.g. native vegetation; streams).

Another criticism associated with the use of altitudinal studies is the entanglement among environmental and biological factors (multicollinearity), leading to possible autocorrelation and variance inflation. Notwithstanding, these relationships give studies based on altitudinal gradients the potential to explore how environmental factors will change across sites and predict how biota will respond (Kitching et al. 2011).

One way to mitigate limitations of elevational studies is to repeat standardized studies in several comparable regions (e.g. islands and archipelagos), at different latitudes (climatic conditions), with different areas, and different distances from the continents (e.g. Odlund 2010). Standardized studies allow for a comparative approach between various ecosystems, providing the means to explore the existence of patterns in the structure of some communities (Magnusson 2009; Culver et al. 2013).

In spite of their obvious interest and importance for the advance of biology, ecology and conservation, there are still few consistent studies about species and communities across elevation gradients in islands. This is the first of a series of papers that aims to document such studies primarily made in permanent native vegetation plots from the Azores archipelago (Portugal), regarding all possible biological groups, starting with phanerogams, cryptogams and invertebrates. Besides conveying the importance of altitudinal studies on volcanic islands, this paper aims to present the Azores as a model archipelago for such efforts and describe the methodologies to study biodiversity at different elevations and scales.

STUDY AREA: THE AZORES ARCHIPELAGO

Location

The Azores archipelago is located in the North Atlantic Ocean (36°55'-39°43' N, 25-310 W), circa 1600 km to the west of Europe (Forjaz 2004). It comprises nine islands and some islets of recent volcanic origin, extending for 600 km and with ages ranging between 0.30 and 8.12 million years old (França et al. 2003). The islands are clustered into three groups: the Western Group (Flores and Corvo), the Central Group (Faial, Pico, São Jorge, Terceira and Graciosa) and the Eastern Group (São Miguel and Santa Maria) (Fig. 1).

These remote oceanic islands are part of the Macaronesia biogeographical region, a series of archipelagos (Madeira, Selvagens, Canaries, Azores and Cape Verde) with many shared floristic (Vanderpoorten et al. 2011) and faunistic elements (Fernández-Palacios et al. 2011). The Macaronesian archipelagos have developed many unique species and communities and are integrated in the Mediterranean bioclimatic region, one of the 25 biodiversity hotspots worldwide (Myers et al. 2000).

Climate

The Azorean climate is temperate oceanic and can be characterized by its thermal amenity, with high rates of humidity, regular and abundant rain fall and a strong wind regime (Azevedo et al. 2004). The average annual temperature is about 17.5˚C, being February the coldest month, with medium temperature values ranging between 13-14° C in the coastal areas (Azevedo et al. 2004). On the highest island, Pico, the snow line is usually located at 1200 m during winter. In the archipelago, the solar radiation decreases and precipitation increases from E to W, from 600-800 mm/year in Ponta Delgada (São Miguel Island) to 1400-1600 mm/year in Santa Cruz (Flores Island), with floristic implications among the islands (Azevedo et al. 2004). The orographic mist layer is also a very important variable to consider in ecological studies, since mist provides extra and important additions to the oceanic climate of the islands (Aranda et al. 2014).

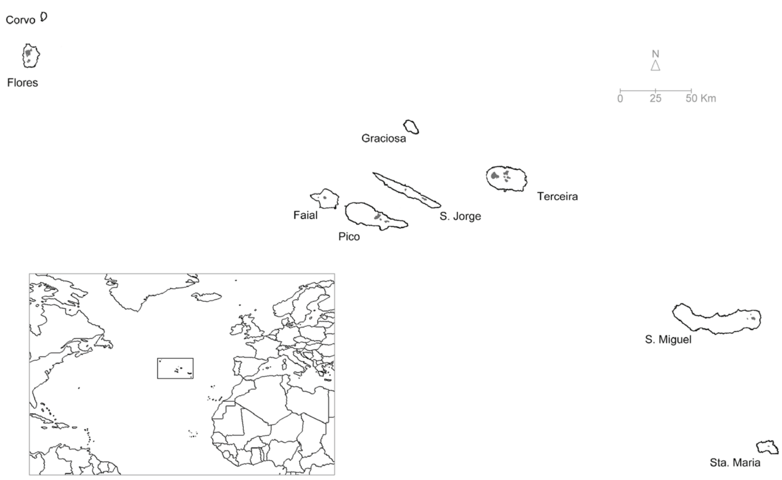

Fig. 1. Location of the Azorean archipelago in the North Atlantic Ocean and Eastern, Central and Western groups of islands (most importat native forest fragments are shaded in grey) (adapted from Gaspar el al. 2008).

Geomorphology and geology

The Azorean islands are volcanic structures that emerged from the ocean due to tectonic movements. Except for Flores and Corvo, all the islands are located on the Azorean microplate, a small, triangular enclave at the junction of the Euro-Asian, African and American plates (França et al. 2003; Forjaz 2004). Although Santa Maria has a maximum geological age of 8.12 My, most areas of Azorean Islands are very young: as much as 65% of the area of Azorean islands have less than 1 My (Triantis et al. 2010b). These areas are mostly the result of highly destructive eruptions of Plinian and Sub-Plinian type (see more examples in Van Riel et al. 2005; Triantis et al. 2010b).

Past and present vegetation

All nine islands of the Azores were once covered with characteristic evergreen forest (Frutuoso 2005a-2005f; Silveira 2013). The native forest, Laurisilva, was the predominant vegetation in the Archipelago before human colonization, in the 15th century (Dias et al. 2007a; Silveira 2013). Since then, the extent of native forests has decreased on every island as a direct consequence of recent human activities (Martins 1993; Triantis et al. 2010a), leading to the loss of endemic species richness and abundance. According to the estimates of Gaspar et al. (2008), less than 5% of the primary natural forests remain in the archipelago; these are dominated by *Juniperus brevifolia* (prevailing from 600 m to 1200 m), *Erica azorica*, *Laurus azorica* and *Ilex perado* subsp. *azorica* (Elias 2007; Elias et al. 2011). The Azorean forests differ from other Macaronesian forests by their paucity of tree species (only one Lauraceae, *Laurus azorica*), trees of small stature and high shrub density (Dias et al. 2007a). Presently, no large areas of natural forest remain below 600 m, where the native vegetation has been replaced mainly by cattle grasslands, exotic forests of *Cryptomeria japonica* and *Eucalyptus* sp. (introduced for timber), and woods of *Pittosporum undulatum* (introduced to provide shelter for orchards but overcoming them, once abandoned) or by crop areas (Haggar et al. 1989; Martins 1993; Silveira 2013). Unsurprisingly, ca. 80% of the vascular plant species reported for the Azores are exotic, some of them invasive (Silva et al. 2010). In fact, the invasion by dangerous plants may be considered one of the most striking features of Azorean islands' ecosystems (Borges et al. 2010a).

Previous elevational studies

Many naturalists referred to the Azores since the XVIII century (Arruda 1998), but only around the middle of the XIX century was the vertical distribution of the vegetation first dealt with by Watson (1843), when describing "An ascent of the peak of Pico". The British scientist states, referring to the mountain: "… which is by much the loftiest of the hills in the Azores, and consequently affords good illustrations of the influence of elevation in modifying their vegetation" (Watson, 1843: 394).

In the XX century, Guppy (1917) and later Tutin (1953) and Dansereau (1970) proposed elevational models of vegetation for the Azores. Guppy (1917) categorized the vegetation in three groups: 1) lower woods, from the coast to around 600 m, with *Morella faya*, *Erica azorica* and *Persea azorica* as the most frequent species, 2) upper woods, divided into two elevation zones (woods proper and scrub), the first between 600 m and 1370 m and the second, from 1370 m to 1670 m, with *Juniperus brevifolia* as the most distinctive species and finally, 3) the *Calluna vulgaris*, *Daboecia azorica* and *Thymus caespititius* zone, from 1670 m to 2300 m. Working mainly with bryophytes, Allorge & Allorge (1946) suggested an altitudinal division of the bryoflora in five stages, from sea level to the summit of Pico Mountain – according to the different species (phanerogams and cryptogams) distribution data. Tutin (1953), after exploring Pico island, elaborated on Guppy's previous classification and defined four vegetation groups for the island, also delimited by elevation: 1) coastal communities, up to 250 m; 2) laurel forest, up to an altitude of 600 m; 3) *Ericetum azoricae* communities, from 600 m or slightly higher up to 1500 m (dominated by *Erica azorica*) and 4) *Callunetum* communities, from 1500 m to the top of the mountain (2351 m). Dansereau (1970) proposed a classification with six groups which slightly overlap across altitudes: 1) the *Myrica faya* zone (0-300 m), 2) the *Laurus azorica* zone

(300-650 m), 3) the *Juniperus brevifolia* zone (450-1100 m), 4) the *Erica azorica* zone (850-1600), 5) the *Calluna vulgaris* zone (1600-2200 m) and 6) the lichen zone (2200-2350 m), a zone virtually lacking vegetation. Other botanists, such as Sjögren (1973), Dias (1996) and Elias (2007) have extensively studied and described the native vegetation of the islands.

Without trying to describe general gradients, some scientists have also used altitude as an important variable for their studies. Purvis et al. (1994) studied the lichens distribution of the upper slopes of Pico Island, between 1200 m and 2351 m altitude. Gabriel (2000) studied native forest fragments in Terceira Island, considering both bryophytes and lichens and Elias (2007) analysed the ecology of *Juniperus* forests stands in several islands and at different elevations. More recently, Silva et al. (2005) examined Pico's mountain gradient regarding their vascular flora, and Arosa et al. (2009) investigated the influence of altitude and other variables on spore maturation and release of *Culcita macrocarpa* and *Woodwardia radicans* in the island of São Miguel. For animals, very few elevation studies were made in the Azores. Borges & Brown (1999) used elevation as an indirect indicator of ecological diversity, testing the "altitude range hypothesis" in explaining the richness of arthropod species in three Azorean islands. Besides, Melo (2001), studying grasslands in Terceira Island, evaluated the influence of an elevational gradient in arthropod species diversity. More recently, Ferreira et al. (2013) investigated the reproductive cycle of an endemic land snail in an elevational gradient in Pico Island.

Colonization status of species

According to their colonization status, species may be classified as autochthonous or indigenous (native non-endemic or endemic species) and exotic species. A brief summary of the species registered across Macaronesia to Bryophytes, Vascular plants and Arthropods may be seen in Table 1. One of the most striking result perceived from Table 1 is the unusually high proportion of exotic species present in the Azores (vascular plant species as well as arthropods), highly exceeding the values estimated for other archipelagos, and probably related to the low proportion of native vegetation areas in the archipelago.

Table 1. Diversity of plant taxa and arthropods from Macaronesian archipelagos (percentages estimated considering all the species present at each archipelago) (Frahm et al. 1996; Arechavaleta et al. 2005, 2010; Borges et al. 2008, 2010b, and P.A.V. Borges, unpubl. data) (Nat, native non endemic; End, endemic; Exo, exotic).

			Bryophytes				**Vascular plants**				**Arthropods**			
	Area (km^2)	Max. elev. (m)	All taxa	Nat %	End %	Exo %	All taxa	Nat %	End %	Exo %	All taxa	Nat %	End %	Exo %
Azores	2328	2351	480	97,7	1,5	0,8	1110	12,3	6,6	81,1	2332	46,9	11,5	41,6
Madeira & Selvagens	801	1861	512	97,5	2,1	0,4	1204	51,5	12,8	35,7	3892	58,3	25,2	16,6
Canaries	7493	3718	503	98,0	2,0	0,0	2091	40,7	25,8	33,5	8154	51,8	40,5	7,7
Cape Verde	4033	2829	153	96,1	3,9	0,0	757	30,1	8,7	61,2	1919	69,6	22,7	7,7

The percentage of endemism found in the Azores is quite affected by the high numbers of exotic taxa present on the islands: if only indigenous species (native and endemic) are considered, the endemism rate increases, reaching much higher values for vascular plants (34,8%) as well as for Arthropods (19,7%). Concerning endemism rates of indigenous non-vascular plants, Cape Verde presents the highest (3,9%) and the Azores the lowest (1,5%) values of endemic bryophytes.

MATERIAL AND METHODS

The setting of sampling stations largely followed BRYOLAT methodology (Ah-Peng et al. 2012, 2014). The BRYOLAT project (2007-2010: Altitudinal and latitudinal gradients of bryophyte communities in the Western Indian Ocean) started in the Mascarenes, Madagascar, Comoros and Kenya, and now counts 14 elevational transects around the world, some of them part of the MOVECLIM project (2012-2015: Montane vegetation as listening posts for climate change), which includes the Azorean archipelago.

This methodology was designed for the study of bryophyte diversity and distribution, aiming to obtain a large amount of data, using a stratified sampling strategy along environmental gradients in the tropics and subtropics, aiming to be expedite in the field. It may also be used to characterize the vascular flora, namely ferns, trees, shrubs and grasses, and in other climatic conditions.

This methodological approach involves the delimitation of one transect per island, ideally facing the same orientation where, at 200 m elevation steps, two plots of 10 m x 10 m (P1 and P2), are established at distances varying from 10 to 15 m (Figure 2a and 2b). Different biological taxa require different refinements of the original design.

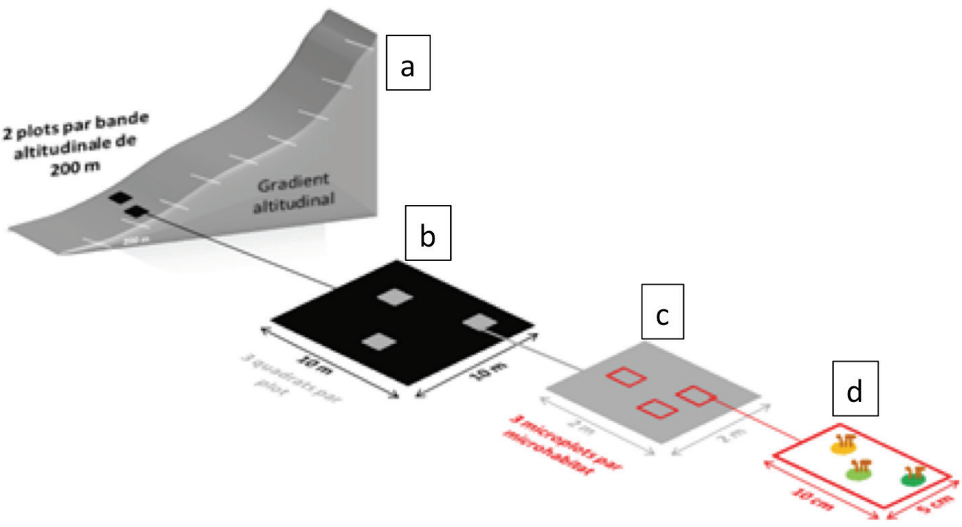

Fig. 2. Representation of the sampling BRYOLAT methodology. (a – transect on the island; at 200 m elevation steps, two plots (black squares, 10 m x 10 m) are placed within 10 to 15 m of each other; b – each plot is divided into 25 quadrats (grey squares, 2 m x 2 m), from which three are sampled; c and d – each quadrat is thoroughly examined for different substrata, and three microplots (red rectangular shapes, 5 cm x 10 cm) are collected on every microhabitat, except on trees, where nine replicates are made.

In the Azores, all plots were marked with nylon string and their location signalled with red and white tape, for easier location in the future.

Bryophytes

Three of the 25 quadrats (2 m x 2 m) of each plot (10 m x 10 m) were randomly selected and sampled (Q1, Q2 and Q3). In order to collect the maximum diversity of bryophytes at each quadrat, six types of substrates are examined: rocks (rupicolous), soil (terricolous), humus (humicolous), rotten wood (lignicolous), leaves (epiphyllous) and bark of the most common woody species (corticolous).

Three microplots are collected as replicates from the first five microhabitats, but since each tree is sampled at three heights (TA, from 0 to 50 cm; TB, from 50 to 100 cm; and TC, from 100 to 200 cm) nine corticolous replicates result from bark. Obviously, not all microhabitats are always colonized within the quadrat, and a maximum of 24 microplots (collections of 50 cm2) is possible at each quadrat, resulting in a maximum of 144 samples per elevation. In addition, a number of environmental data were also taken for most bryophyte collections including: substrate samples to calculate pH, slope of the microplot (degree), distance to soil (cm), and three ordinal variables regarding shelter, moisture and light (from 1 [minimum] to 5 [maximum]) according to Gabriel & Bates (2005).

The sample size (microplot) is rather small (5 cm x 10 cm) in order not to over collect, avoiding the destruction of suitable habitats for the colonization of species (ex. fern fronds or tree leaves) and the removal of entire populations of bryophytes. This care will ensure that no harm will be done to bryophyte communities, at all elevations, and particularly at low altitudes where their regeneration is especially slow (e.g., Sjögren 2003).

Vascular plants

The study of vascular plant species largely followed the design presented in the previous section, studying the same plots at the same elevations. Nevertheless, each plot (10 m x 10 m) was divided into four 5 m x 5 m subplots (and not in 2 m x 2 m Quadrats), because that is the minimum area generally considered satisfactory in plant studies. The inventory of vascular plant species was made for each subplot (5 m x 5 m), and the percent cover of each taxa was estimated, using the OTV scale (Ordinal Transform Values) (van der Maarel 1979). Besides, the maximum height of the plants was measured in the centre of each subplot. Whenever woody species were present, the height and dbh (diameter at breast height) of those with more than 5 cm diameter at 130 cm from the soil were measured, following the rules of the International Society of Arboriculture (AFCD 2006). In addition, the height of the 10 tallest trees of each plot was also measured. With few exceptions, all species were identified in the field. Some photographs and notes were made in order to account for the vitality of the species (e.g. presence of flowers).

Arthropods

The first standardized survey in islands targeting most of the arthropod groups was performed in Azores, under the scope of project BALA (Biodiversity of the Arthropods of the Laurisilva of Azores - 2000-2010) (Borges et al. 2005; Ribeiro et al. 2005; Gaspar et al. 2008). In the current study we applied the BALA protocol around the area occupied by the Azorean BRYOLAT plots.

In summary, the following methods were used:

A - Sampling of epigean arthropods - Thirty pitfall traps were used per transect, consisting of plastic cups with 4.2 cm of diameter and 7.8 cm deep. Half of the traps were filled with a non-attractive solution (ethylene glycol, antifreeze solution), and the remaining with a general attractive solution (Turquin), prepared mainly with dark beer and some preservers (chloral hydrate, formalin and acetic acid). The traps were sunken in the soil (with the rim at the surface level) every 5 m, starting with a Turquin trap and alternating with an ethylene trap. All traps were protected from the rain using a plastic plate, at about 5 cm above surface level and fixed to the ground by two pieces of wire. The traps remained in the field for two weeks.

B – Sampling of canopy arthropods - Ten replicate of the three most abundant woody plant species were sampled. In most of the study sites, three species clearly dominated over the remaining plants and the choice was evident; if only one or two plant species dominated in the plots, only these were considered. A branch of each selected plant was chosen at random and beaten with a stick for five times over a beating tray placed beneath. The tray consisted of a cloth- inverted pyramid of 1 m wide and 60 cm deep with a plastic bag at the end.

C – Sampling of flying arthropods - In addition to the BALA protocol, some MOVECLIM plots are being monitored using SLAM traps, aiming to investigate the seasonal and between year variations of the biomass of flying arthropods.

FIRST RESULTS

A total of 70 plots (10 m x 10 m) are already established in five islands (Flores, Pico, São Jorge, Terceira and São Miguel), all respecting an elevation step of 200 m, resulting in 24 stations examined in Pico (data collected in September 2012), 12 in Terceira (also collected in September 2012), 10 in Flores (August 2013), 12 in São Miguel (September 2013) and 12 in São Jorge (August 2014; Table 2-3). Faial is being sampled during 2014/2015. Further contributions will include more information of these plots.

The list of vascular species is shown in Table 3. Taxa are presented following their taxonomic order concerning Division, and alphabetical order on the other categories.

Vascular plants

A total number of 138 vascular plant species was recorded in the 70 plots (280 subplots) across the five studied islands, including taxa from four Divisions, Lycopodiophyta (N=2), Pteridophyta (N=27), Pinophyta (N=2) and Magnoliophyta (N=107). From these, 88 plant species are considered indigenous, 46 exotic, while the origin of four species is doubtful (colonization data according to Silva et al. 2010) (Table 2).

Bryophytes

Bryophytes were collected in all 70 plots (210 quadrats). A maximum of six substrates was sampled per quadrat; phorophytes were represented by 16 woody plants, 12 of which are indigenous (eight endemics) (Table 4).

Table 2. Number of plant species collected in each island for each taxonomic group (exo – exotic origin; ind – indigenous; doub - doubtful origin) (data coming from Borges et al. 2010b; Silva et al. 2010).

	Lycopodiophyta		**Pteridophyta**		**Pinophyta**		**Magnoliophyta**			**% Exotics**	
	exo	ind	exo	ind	exo	ind	exo	ind	doub	in plots	islands
Flores	0	1	1	16	0	1	8	26	1	16,98	70,45
Pico	0	1	2	17	0	1	19	40	2	26,31	71,31
São Jorge	0	1	3	11	1	1	12	38	2	23,88	70,22
Terceira	0	1	0	10	1	1	6	30	0	14,29	75,23
São Miguel	0	1	5	9	0	1	14	31	0	31,15	77,93

Table 3. List of vascular species registered in the five islands. (Exotic [exo] and doubtful [d] species are signalled after the name of the species; unmarked species assumed to be indigenous; data from Silva et al. 2010).

Division	Class	Order	Family	Species	Colonization	Flores	Pico	São Jorge	Terceira	São Miguel
Lycopodiophyta										
	Lycopodiopsida									
		Lycopodiales								
			Lycopodiaceae	*Huperzia suberecta*			x			
	Selaginellopsida									
		Selaginellales								
			Selaginellaceae	*Selaginella kraussiana*		x	x	x	x	x
Pteridophyta										
	Polypodiopsida									
		Cyatheales								
			Culcitaceae	*Culcita macrocarpa*		x	x	x	x	x
			Cyatheaceae	*Cyathea cooperi*	**exo**					x
		Hymenophyllales								
			Hymenophyllaceae	*Hymenophyllum tunbrigense*		x	x	x	x	x
				Hymenophyllum wilsonii		x			x	
				Trichomanes speciosum			x			
		Osmundales								
			Osmundaceae	*Osmunda regalis*		x	x	x		x
		Polypodiales								
			Aspleniaceae	*Asplenium hemionitis*		x				
				Asplenium marinum		x	x			
				Asplenium obovatum		x	x			
				Asplenium onopteris					x	
			Blechnaceae	*Blechnum spicant*		x	x	x	x	x
				Woodwardia radicans		x		x		x
			Dennstaedtiaceae	*Pteridium aquilinum*		x	x	x	x	x
			Dryopteridaceae	*Cyrtomium falcatum*	**exo**	x	x	x		x
				Dryopteris aemula		x	x	x	x	
				Dryopteris azorica		x	x	x	x	x
				Dryopteris crispifolia			x			
				Elaphoglossum semicylindricum		x	x		x	x
				Polystichum setiferum			x			x

Division	**Class**	**Order**	**Family**	**Species**	**Colonization**	**Flores**	**Pico**	**São Jorge**	**Terceira**	**São Miguel**
			Polypodiaceae	*Polypodium azoricum*		x	x	x	x	
			Pteridaceae	*Adiantum hispidulum*	**exo**					x
				Pteris incompleta		x		x		
			Thelypteridaceae	*Christella dentata*	**exo**		x			x
				Oreopteris limbosperma			x			
				Stegnogramma pozoi			x			
			Woodsiaceae	*Deparia petersenii*	**exo**			x		x
				Diplazium caudatum	**exo**	x	x	x		
Pinophyta										
	Pinopsida									
		Pinales								
			Cupressaceae	*Cryptomeria japonica*	**exo**			x	x	
				Juniperus brevifolia		x	x	x	x	x
Magnoliophyta										
	Magnoliopsida									
		Apiales								
			Apiaceae	*Angelica lignescens*			x			
				Apium graveolens	**exo**	x				
				Chaerophyllum azoricum				x		
				Sanicula azorica			x			
			Araliaceae	*Hedera azorica*		x	x	x	x	x
			Pittosporaceae	*Pittosporum undulatum*	**exo**	x	x	x	x	x
		Aquifoliales								
			Aquifoliaceae	*Ilex perado* subsp. *azorica*		x	x	x	x	x
		Asterales								
			Asteraceae	*Bellis azorica*			x	x		
				Leontodon filii						x
				Leontodon rigens				x		x
				Leontodon saxatilis subsp. *longirostris*	**d**		x			
				Pericallis malvifolia				x		x
				Solidago sempervirens	**d/exo**	x				
				Sonchus oleraceus	**exo**		x			
				Tolpis azorica			x	x		

Division	Class	Order	Family	Species	Colonization	Flores	Pico	São Jorge	Terceira	São Miguel
		Boraginales								
			Boraginaceae	*Myosotis maritima*					x	
		Brassicales								
			Brassicaceae	*Cardamine caldeirarum*				x		
		Caryophyllales								
			Caryophyllaceae	*Cerastium glomeratum*	**exo**		x			
				Sagina maritima					x	
				Silene uniflora subsp. *cratericola*			x			
			Phytolaccaceae	*Phytolacca americana*	**exo**	x	x	x		x
			Polygonaceae	*Polygonum aviculare*	**exo**		x			x
		Dipsacales								
			Adoxaceae	*Viburnum treleasei*		x	x	x	x	x
			Caprifoliaceae	*Leycesteria formosa*	**exo**					x
		Ericales								
			Clethraceae	*Clethra arborea*	**exo**					x
			Ericaceae	*Calluna vulgaris*		x	x	x	x	x
				Daboecia azorica			x	x		
				Erica azorica		x	x	x	x	x
				Vaccinium cylindraceum		x	x	x	x	x
			Myrsinaceae	*Myrsine africana*		x	x	x	x	x
			Primulaceae	*Lysimachia azorica*		x	x	x	x	x
		Fabales								
			Fabaceae	*Acacia melanoxylon*	**exo**					x
				Lotus parviflorus	**exo**					x
				Lotus uliginosus	**exo**			x		
		Fagales								
			Myricaceae	*Morella faya*		x	x	x	x	x
		Gentianales								
			Gentianaceae	*Centaurium scilloides*					x	
			Rubiaceae	*Galium palustre*	**exo**			x		
				Rubia agostinhoi			x	x		x
		Gunnerales								
			Gunneraceae	*Gunnera tinctoria*	**exo**					x

Division	Class	Order	Family	Species	Colonization	Flores	Pico	São Jorge	Terceira	São Miguel
		Lamiales								
			Lamiaceae	*Mentha aquatica*	**exo**			x		
				Prunella vulgaris	**d**			x		
				Thymus caespititius			x			
			Oleaceae	*Ligustrum henryi*	**exo**			x		
				Picconia azorica		x	x		x	x
			Orobanchaceae	*Parentucellia viscosa*	**exo**			x		
			Plantaginaceae	*Plantago coronopus*				x		x
				Plantago lanceolata	**exo**		x		x	
			Scrophulariaceae	*Sibthorpia europaea*		x	x	x	x	x
		Laurales								
			Lauraceae	*Laurus azorica*		x	x	x	x	x
				Persea indica	**exo**				x	
		Malpighiales								
			Euphorbiaceae	*Euphorbia azorica*			x			
				Euphorbia stygiana			x			
			Hypericaceae	*Hypericum foliosum*		x	x	x	x	x
			Violaceae	*Viola odorata*	**exo**		x			
				Viola palustris subsp. *juresii*		x	x	x		
		Malvales								
			Thymelaeaceae	*Daphne laureola*			x			
		Myrtales								
			Myrtaceae	*Metrosideros excelsa*	**exo**				x	
				Psidium littorale	**exo**	x				
		Ranunculales								
			Papaveraceae	*Fumaria muralis*	**exo**		x			
			Ranunculaceae	*Ranunculus cortusifolius*				x		
				Ranunculus repens	**exo**			x		
		Rosales								
			Moraceae	*Ficus carica*	**exo**	x				
			Rhamnaceae	*Frangula azorica*		x	x	x	x	x
			Rosaceae	*Duchesnea indica*	**exo**		x			
				Fragaria vesca	**d**		x	x		
				Potentilla anglica		x	x	x	x	x

Division	Class	Order	Family	Species	Colonization	Flores	Pico	São Jorge	Terceira	São Miguel
				Prunus azorica						x
				Rubus hochstetterorum		x	x			x
				Rubus ulmifolius	**exo**		x	x		x
		Santalales								
			Santalaceae	*Arceuthobium azoricum*			x			
		Saxifragales								
			Crassulaceae	*Umbilicus horizontalis*			x		x	
				Umbilicus rupestris			x		x	
				Umbilicus sp.					x	
		Solanales								
			Convolvulaceae	*Salpichroa origanifolia*	**exo**		x			
			Solanaceae	*Physalis peruviana*	**exo**		x			
				Solanum mauritianum	**exo**			x		x
				Solanum nigrum	**exo**	x	x			
	Liliopsida									
		Alismatales								
			Araceae	*Zantedeschia aethiopica*	**exo**		x			
				Arum italicum	**exo**		x			
		Asparagales								
			Iridaceae	*Iris foetidissima*	**exo**					x
			Orchidaceae	*Platanthera micrantha*			x	x	x	
		Commelinales								
			Commelinaceae	*Tradescantia fluminensis*	**exo**		x			x
		Liliales								
			Smilacaceae	*Smilax azorica*			x			x
		Poales								
			Cyperaceae	*Carex echinata*				x	x	
				Carex hochstetteriana		x	x	x	x	x
				Carex pendula		x				
				Carex peregrina		x	x			
				Carex pilulifera subsp. azorica					x	
				Carex sp.			x	x		
				Carex viridula subsp. *cedercreutzii*						x
				Carex vulcani			x	x		x

Division	Class	Order	Family	Species	Colonization	Flores	Pico	São Jorge	Terceira	São Miguel
				Eleocharis multicaulis				x	x	
			Juncaceae	*Juncus effusus*		x		x		
				Luzula purpureosplendens		x	x	x	x	x
			Poaceae	*Agrostis* sp.		x	x	x	x	x
				Anthoxanthum odoratum	**exo**		x			
				Arundo donax	**exo**			x		x
				Brachypodium sylvaticum		x		x		x
				Deschampsia foliosa		x	x	x	x	x
				Festuca francoi		x	x	x		x
				Festuca petraea					x	
				Holcus azorica				x		
				Holcus lanatus	**exo**	x	x	x		
				Holcus rigidus		x	x	x	x	x
				Hordeum murinum	**exo**				x	
		Zingiberales								
			Zingiberaceae	*Hedychium gardnerianum*	**exo**	x	x	x	x	x

Table 4 (following page). Total number of bryophyte samples collected in each island, at each elevational station; Tree species (phorophytes) are ordered from the most to the least common. (At each elevation there are a maximum of 18 samples for Rocks, Soil, Humus, Decaying wood and Leaves, but a maximum of 54 samples for tree bark; Phorophytes: ACA - *Acacia melanoxylon*; CAL - *Calluna vulgaris*; CLE - *Clethra arborea*; ERI - *Erica azorica*; EUP – *Euphorbia azorica*; HED - *Hedychium gardnerianum*; ILE - *Ilex perado* subsp. *azorica*; JUN - *Juniperus brevifolia*; LAU - *Laurus azorica*; MYC - *Morella faya*; MYS - *Myrsine africana*; PIC - *Picconia azorica*; PIT - *Pittosporum undulatum*; THY - *Thymus caespititius*; VAC - *Vaccinium cylindraceum;* VIB – *Viburnum treleasei*).

Island / Altitude (m)	Bryophyte substrata						Phorophytes where bryophytes were sampled															
	Rocks	**Soil**	**Humus**	**Decaying wood**	**Leaves**	**Trees**	**ERI**	**JUN**	**VAC**	**ILE**	**PIT**	**LAU**	**MYC**	**CAL**	**MYS**	**PIC**	**EUP**	**VIB**	**CLE**	**HED**	**ACA**	**THY**
TOTAL (5 islands)	361	362	362	478	199	1225	95	75	52	48	45	41	39	24	22	16	6	4	3	3	1	1
Flores	**53**	**53**	**38**	**61**	**29**	**149**	**9**	**18**	**7**	**1**	**9**	**1**	**3**	**0**	**2**	**8**	**0**	**1**	**0**	**0**	**0**	**0**
0	17	18	0	7	0	18	1				3		1			6						
200	18	18	2	16	0	40	6		3		4		2									
400	18	17	0	16	0	38	2				2	1				2		1				
600	0	0	18	16	14	33		8	2	1					2							
800	0	0	18	6	15	20		10	2													
Pico	**155**	**63**	**117**	**141**	**62**	**341**	**42**	**4**	**14**	**23**	**8**	**16**	**14**	**18**	**4**	**3**	**6**	**0**	**0**	**0**	**0**	**1**
0	18	3	0	18	0	27	3	1			1		4									
200	16	5	0	18	0	34					4		9			1						
400	18	11	6	18	0	40	3			1	3	4	1			2						
600	15	0	18	17	17	54	1		1	9		5			1							
800	0	4	18	18	18	54	1		4	3		2			2		6					
1000	3	4	18	18	18	48		3	3	6		5										
1200	6	12	12	13	9	36	9		5	4												
1400	8	12	12	3	0	18	9		1					6	1							1
1600	17	10	12	17	0	21	16							3								
1800	18	2	2	0	0	8								8								
2000	18	0	7	0	0	1								1								
2200	18	0	12	1	0	0																
São Jorge	**69**	**81**	**50**	**84**	**6**	**237**	**4**	**24**	**12**	**14**	**9**	**1**	**19**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**	**0**
0	18	0	2	18	0	43					3		12									
200	15	9	0	12	0	48				7	5		6									
400	17	18	0	18	0	48	4	1	2	7	1	1	1									
600	3	18	15	18	0	54		12	6													
800	2	18	15	18	6	44		11	4													
1000	14	18	18	0	0	0																

Island / Altitude (m)	Bryophyte substrata						Phorophytes where bryophytes were sampled															
	Rocks	Soil	Humus	Decaying wood	Leaves	Trees	ERI	JUN	VAC	ILE	PIT	LAU	MYC	CAL	MYS	PIC	EUP	VIB	CLE	HED	ACA	THY
Terceira	**54**	**73**	**107**	**97**	**54**	**255**	**25**	**28**	**8**	**5**	**14**	**4**	**2**	**2**	**8**	**3**	**0**	**0**	**0**	**0**	**0**	**0**
0	18	4	18	9	0	21	11															
200	18	1	18	18	0	48	6				9					3						
400	18	18	17	16	0	46	8				5		2		2							
600	0	15	18	18	18	51		1	5	4		4			3							
800	0	18	18	18	18	53		12	2	1					3							
1000	0	17	18	18	18	36		15	1					2								
São Miguel	**12**	**74**	**50**	**87**	**48**	**209**	**15**	**1**	**11**	**5**	**5**	**19**	**1**	**4**	**8**	**2**	**0**	**3**	**3**	**3**	**1**	**0**
0	3	12	0	5	0	24	10						1									
200	9	12	0	15	0	30					5	1				2				3	1	
400	0	11	0	18	12	23	1					7										
600	0	14	18	18	18	54	3	1		3		6			2			3				
800	0	15	14	18	18	52	1		1	2		5			6				3			
1000	0	10	18	13	0	26			10					4								

The most common phorophytes were the endemic species *Erica azorica*, *Juniperus brevifolia*, *Vaccinium cylindraceum* and *Ilex perado* subsp. *ß*, however *Laurus azorica* and the exotic *Pittosporum undulatum* were also among the most collected species. The phorophytes varied across the five islands: for instance, in São Miguel, *Laurus azorica* was the most common species, while in Terceira and São Jorge, it was one of the least represented. The shrub *Calluna vulgaris* was always sampled at high elevations (1000 m or higher).

Considering the number of microplots collected with bryophytes, and comparing those numbers with the maximum possible number of samples for each microhabitat at each elevation step (Figure 3), it is obvious that some microhabitats are much less colonized than others.

In all islands, decaying wood is the habitat with most colonized samples (average of 75,9%), while leaves are the least colonized (average 31,6%); bryophytes colonizing tree barks are also well represented in all islands (average 64,8%).

São Miguel exhibits the lowest percentage of samples collected on rocks. In fact, rocks were hard to find in São Miguel plots, which may be partially explained by the island's high geological age - one of the oldest islands of the Azores, especially the Northeast part, where the samples were made. The youngest island – Pico, presents the highest colonization rate on rocky substrates (comparing to the other islands) and the lowest percentage of soil samples colonized by bryophytes (29%).

The presence of bryophytes growing on leaves is quite low in São Jorge (6,0% of the number of potential samples). This may be due to the

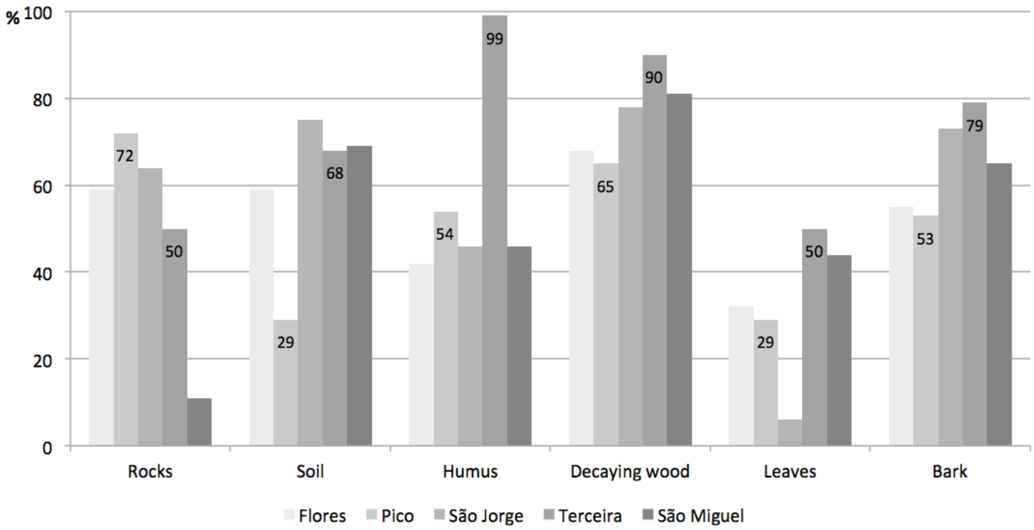

Fig. 3. Percentage of samples collected in each microhabitat in the five islands, considering the maximum of replicates predicted by the model for each elevation station (two plots, six quadrats, three microplots per substrate except for bark [three microplots at three heights]).

dominance of *Juniperus brevifolia* at medium to high altitudes (600 – 800 m), where epiphyllous samples generally are more abundant.

Arthropods

So far, a total of 1087 samples are available for arthropods collected within the 70 MOVECLIM plots. Soil samples of epigean ground–dwelling arthropods are still missing in some altitudinal stations and particularly for Pico Island, canopy samples of arboreal arthropods are missing in most stations. Six phorophytes are well represented with 70 or more samples (Table 5).

A variable number of soil samples (pitfall traps) was placed along the elevation transects on all islands, but the most recurrent technique used to sample arthropods was the sampling of canopies. There are many common vascular plant species between the phorophytes of bryophytes and the species used in the beatings for the collection of arthropods, namely *Juniperus brevifolia, Erica azorica, Laurus azorica, Ilex perado* subsp. *azorica* or *Vaccinium cylindraceum*. The exotic species, Pittosporum undulatum is also part of the sampling in Flores, Terceira and São Miguel Islands. SLAM traps, due to their price, are absent from São Jorge and quite restricted in Flores, Pico and São Miguel islands, where they were placed inside laurel forests.

Table 5. Total number of arthropod samples in each island, and at each elevational station; phorophytes are discriminated from the most to the least common (CAL - *Calluna vulgaris*; ERI - *Erica azorica*; ILE - Ilex perado subsp. azorica; JUN - *Juniperus brevifolia*; LAU - *Laurus azorica*; MYC - *Morella faya*; MYS - *Myrsine africana*; PIT - *Pittosporum undulatum*, VAC - *Vaccinium cylindraceum*).-

Island / alt. (m)	Transects	Soil + Canopy samples	Soil samples	Canopy samples	JUN	ERI	LAU	ILE	VAC	PIT	MYC	MYS	CAL	FRA	SLAM
TOTAL	**27**	**1090**	**420**	**697**	**140**	**110**	**100**	**100**	**90**	**70**	**40**	**20**	**10**	**10**	**12**
Flores	**5**	**180**	**60**	**120**	**20**	**20**	**10**	**10**	**20**	**30**	**10**				**2**
0	1	30		30					10	10	10				
200	1	30		30		10			10	10					
400	1	20		20		10				10					1
600	1	60	30	30	10		10	10							1
800	1	40	30	10	10										
Pico	**4**	**280**	**120**	**160**	**40**	**20**	**20**	**30**	**30**		**10**	**10**			**3**
0	1	60	30	30	10	10					10				
200															
400															
600	1	80	30	50	10	10	10	10	10						1
800	1	70	30	40	10			10	10			10			1
1000	1	70	30	40	10		10	10	10						1
1200 - 2200															
São Jorge	**6**	**180**	**60**	**120**	**20**	**20**	**10**	**30**	**20**		**20**		**10**		**0**
0	1	20		20		10					10				
200	1	20		20				10			10				
400	1	30		30		10	10	10							
600	1	30		30	10				10				10		
800	1	60	30	30	10			10	10						
1000	1	30	30												
Terceira	**6**	**230**	**90**	**140**	**30**	**30**	**20**	**20**	**10**	**20**		**10**			**5**
0	1	10		10		10									1
200	1	20		20		10				10					1
400	1	20		20		10				10					1
600	1	60	30	30	10		10	10							1
800	1	80	30	50	10		10	10	10			10			
1000	1	40	30	10	10										1
São Miguel	**6**	**220**	**90**	**130**	**20**	**20**	**40**	**10**	**10**	**20**				**10**	**2**
0	1	10		10		10									
200	1	20		20			10			10					
400	1	20		20			10			10					
600	1	70	30	40		10	10	10						10	1
800	1	60	30	30	10		10		10						1
1000	1	40	30	10	10										

DISCUSSION

This work aims to investigate differences in the presence and distribution of species in native vegetation, along elevational gradients in the Azores, setting permanent plots to allow future assessments.

In order to have sound and comparable results, the sampling stations were positioned following the full elevation gradient of the islands, with elevation steps of 200 m altitude, and in the best possible areas of native vegetation, roughly within the same geological system. However, the high humanization of the Azorean archipelago, and in particular, the extremely high number of exotic species – accounting for over 80% of all vascular species (Silva et al. 2010), hampers the finding of pristine study areas. It is worth mentioning that species such as *Clethra arborea* and *Gunnera tinctoria* (this one absent from our Plots) are strongly invasive in São Miguel and that Pittosporum undulatum and *Hedychium gardnerianum*, among other invasive species are already present in all Azorean islands and some of our locations. Nonetheless, the selected plots are set in the best fragments that could be found in the Islands, when trying to implement an elevational transect. Besides, the percentage of exotic species inside the plots and on the islands (Table 2) shows that those are relatively natural fragments, since the presence of vascular exotic species is substantially smaller inside the plots. Further analysis, considering the abundance of species inside the plots, and the discrimination per altitude will also be valuable for further description of the plots, and as a baseline of the long term study.

The importance of setting these permanent study sits is crucial at this point in time, since a few habitat restoration projects are going on in areas where some plots were located (ex. Pico da Vara [São Miguel]) (SPEA 2010). A follow up study will ensure an important tool as an independent evaluation (and potential validation) of the consequences of the restoration to the ecosystems, not only to vascular plant species, but also to bryophytes and arthropods, two groups used as monitors to environmental change (Bates 2009; Giordano 2008).

RESEARCH AGENDA FOR THE NEAR FUTURE

We are launching a long-term ecological study (LTER), setting and following permanent plots of Azorean native vegetation over an altitudinal gradient, studying bryophytes, vascular plants and arthropods (and other groups may follow) as a way to gather reliable biodiversity information to address ecological and conservation issues. With this approach we are contributing to answer the fundamental question of what generates and maintains the global spatial heterogeneity of diversity (Brown 2014).

Ecologically it will be possible to pursue the characterization of the island system, collecting long-term ecological data to evaluate species distributions and abundance at multiple spatial and temporal scales and performing studies of the relationship between diversity (taxonomic, functional and phylogenetic) and ecosystem functions, taking advantage of the strong changes of diversity along elevational gradients. Besides, we aim to use species distribution and abundance data in model-based studies of environmental change in different island mountain regions to promote the study of Species-Environment relationships in islands.

Regarding conservation, the priorities would be to predict the likelihood of species extinctions or invasions - identifying pathways impacting on oceanic indigenous assemblages under global change - using the available historical information of species distribution on Azorean islands (see Azorean Biodiversity Portal database; http://www.atlantis.angra.uac.pt/atlantis/; Borges et al. 2010c) and comparing it with data obtained in the standardized survey performed within the project MOVECLIM, and in future surveys. It is also deemed important to evaluate the extent and the mechanisms through which fragmentation of natural habitats affects mountain species communities, including the impact of the non-native habitats in the matrix. In the Azores, it is critical to monitor grazing intensity and invasive species, evaluating how these factors interact with climate change.

In the interface between ecology and conservation, the sustained study of rarity patterns, recording presence and frequency of species along elevational gradients in several islands, should also be explored in detail, since it distinctly contributes to help differentiate taxa that are truly rare, from those that are rare at a given time (e.g. Borges et al. 2008). This has major implications for the definition of the most effective conservation strategies.

Further studies, using different sampling techniques and including different biological groups (especially the less known, such as Fungi, Lichens, Algae and others), should be carried out to improve our knowledge of the system, since each group may respond differently to the same impacts.

Although the islands represent a unique natural laboratory for ecological and evolutionary research, a large proportion of their biota is in danger (Caujapé-Castells et al. 2010; Triantis et al. 2010a), and some taxa have already been extinct (e.g. Cardoso et al. 2010; Rando et al. 2013). Thus, it is necessary to act quickly to safeguard what is possible and avoid permanent losses whose effects, although difficult to predict accurately, are certainly undesirable.

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