ECOGRAPHY

Research

Onward but not always upward: individualistic elevational shifts of tree species in subtropical montane forests

Kirsten S. W. O'Sullivan, Paloma Ruiz-Benito, Jan-Chang Chen and Alistair S. Jump

K. S. W. O'Sullivan (https://orcid.org/0000-0001-9062-8886) and A. S. Jump, Biological and Environmental Sciences, Faculty of Natural Sciences, Univ. of Stirling, Stirling, UK. – P. Ruiz-Benito, Forest Ecology and Restoration Group, Dept of Life Sciences, Univ. of Alcala, Alcalá de Henares, Spain, and Environmental Remote Sensing Group, Dept of Geology, Geography and Environment, Univ. of Alcala, Alcalá de Henares, Spain. – J.-C. Chen ✉ (zzzjohn@mail.npust.edu.tw), Dept of Forestry, National Pingtung Univ. of Science and Technology, Pingtung, Taiwan.

Ongoing global climate change is driving widespread shifts in species distributions. Trends show frequent upwards shifts of treelines, but information on changes in montane forest below the treeline and in the tropics and subtropics is limited, despite the importance of these areas for biodiversity and ecosystem function. Patterns of species shifts in tropical and subtropical regions are likely to be more complex and individualistic than global averages suggest due to high species diversity and strong influence of competition, alongside direct climatic limitations on distributions. To address the question of how subtropical montane tree species are likely to move as climate changes, we used an extensive national forest inventory to estimate distribution shifts of 75 tree species in Taiwan by comparing the optimum elevation and range edges of adults and juveniles within species. Overall there was a significant difference in optimum elevation of adults and juveniles. Life stage mismatches suggested upward shifts in 35% of species but downward shifts of over half (56%), while 8% appeared stable. Upward elevation shifts were disproportionately common in high elevation species, whilst mid to low elevation species suggested greater variation in shift direction. Whilst previous research on mountain forest range shifts has been dominated by work addressing changes in treeline position, we show that although high elevation species shift up, below the treeline species may shift individualistically, heralding widespread changes in forest communities over coming decades. The wide variation of responses indicated is likely driven by individual species responses to interacting environmental factors such as competition, topography and anthropogenic influences across the broad range of forest types investigated. As global environmental changes continue, more detailed understanding of tree range shifts across a wide spectrum of forests will allow us to prepare for the implications of such changes for biodiversity, ecosystem function and dependent human populations.

Keywords: climate, demography, environmental change, forest inventory, species migrations

Introduction

Ongoing global climate change is contributing towards widespread shifts in species distributions (Parmesan and Yohe 2003, Chen et al. 2011, Pecl et al. 2017, Lenoir et al. 2020), with movements to higher latitudes and elevations expected as species track warming climates (Gosz 1992, Morueta-Holme et al. 2015). Temperatures are predicted to rise to 1.5°C above pre-industrial levels by 2030–2052 (IPCC 2018), with mountain regions expected to experience temperatures up to three times higher than those recorded during the 20th century (Nogués-Bravo et al. 2007). Evidence is accumulating of substantial shifts of montane forest tree distributions in response to climatic pressures (Harsch et al. 2009). The impacts of shifts can vary considerably across species ranges (Wallingford et al. 2020), with upwards shifts of trees threatening many endemic species frequently found at high elevations (Jump et al. 2012). Furthermore, changes in forest distribution and composition can decrease albedo (Pecl et al. 2017) and influence carbon sequestration (Kirby and Potvin 2007). Patchy coverage of assessments of montane forest shifts retards our understanding of the impacts changes are likely to have on biodiversity, ecosystem function and dependent human populations from local to global scales (but see Elsen et al. 2020). Accurate information on species distribution shifts is, therefore, urgently needed for improved bioclimatic modelling and to inform decisions on management, conservation and policy.

While widespread upwards distribution shifts are reported for forest trees, research is largely based on studies of the treeline ecotone of Northern Hemisphere forests (Grabherr et al. 1994, Gehrig-Fasel et al. 2007, Harsch et al. 2009, Dirnböck et al. 2011, Ruiz-Labourdette et al. 2012), with more limited investigation of responses in tropical montane regions (Feeley et al. 2011, 2013, Feeley 2012, Duque et al. 2015, Fadrique et al. 2018, Pouteau et al. 2018). Tropical forests hold the largest species diversity of any terrestrial biome (Potapov et al. 2012), around 70% of the global forest carbon (Pan et al. 2011) and have key roles in stabilising soils (Nilaweera and Nutalaya 1999), maintaining soil fertility (García-Oliva et al. 1994) and regulating global water cycles (Snyder et al. 2004). Consequently, a greater understanding of tree species distributional changes and the implications on tropical ecosystem functioning is needed, due to a general lack of data, with few assessments in Asia, South America and central Africa (Lenoir and Svenning 2015). Generalising patterns of range shifts across regions may be misleading, as environmental conditions vary and there is evidence to suggest climate change affects systems differently (Harsch et al. 2009, Antão et al. 2020, Comte and Lenoir 2020, Lenoir et al. 2020). In the tropics, temperatures do not vary greatly across latitude, but rapidly decline by around 5.2–6.5°C every 1000 m with increasing elevation (Colwell et al. 2008). Therefore, subtle climatic changes could cause rapid shifts in montane community composition (McCarty 2001) and drive the establishment of novel species assemblages (Breshears et al. 2008, Gilman et al. 2010, Alexander et al. 2018). Tropical trees have already been observed living in sub-optimal conditions as they lag behind climate change, and could fall even further behind as climates rapidly alter (Feeley et al. 2011, Fadrique et al. 2018, Esquivel-Muelbert et al. 2019). The high species diversity and complexity of biotic interactions at low latitudes (Schemske et al. 2009) means that multiple factors are likely to interact with temperature, driving strongly individualistic species distribution shifts in tropical forests.

Whilst the general expectation is that species will migrate to higher elevations as the climate warms and bands of suitable environmental conditions shift upwards (Gosz 1992, Feeley 2012, Morueta-Holme et al. 2015), species distributions are limited by multiple interacting factors (Harsch et al. 2009, Ettinger et al. 2011, Wason and Dovciak 2017). Climate change is multifaceted and involves alterations to parameters including temperature mean and range, the amount and duration of rainfall, frequency and duration of fog, location of the cloud base, seasonality and frequency of extreme events (IPCC 2013). Non-climatic factors such as local scale biotic interactions (Lenoir et al. 2009), physiological constraints (Chen et al. 2011), soil nutrient availability (van Breugel et al. 2018), presence and abundance of pests and diseases (Máliš et al. 2016), topography (De Frenne and Verheyen 2016, Lembrechts and Lenoir 2019, Elsen et al. 2020) and anthropogenic land use also influence species distributions (Vilà-Cabrera et al. 2019), and will affect species responses to changing climate. Although upwards species distribution shifts are commonly reported (Harsch et al. 2009, Feeley et al. 2011), studies have also identified downslope movements (Lenoir et al. 2010, Crimmins et al. 2011, Urli et al. 2014) or limited evidence of shifts altogether (Zhu et al. 2012). Large-scale downwards elevational shifts have been noted in some areas, such as in montane vegetation in California (Crimmins et al. 2011). Mountain regions typically have high habitat and environmental heterogeneity (Jobbágy et al. 1996, Morley et al. 2018), so individualistic shifts in montane forest tree species distributions could be particularly likely.

Bias in research on forest tree species distribution shifts towards the extremes of species ranges overlooks changes occurring over the whole elevational gradient (Lenoir et al. 2009). Although changes in distribution are typically most obvious at ecotones (Gosz 1992), treeline changes do not necessarily translate to equivalent shifts of all species (Vitasse et al. 2012) or influence dynamics below the treeline. Environmental conditions at ecotones often favour specialists (Fadrique et al. 2018), so distributional changes here are unlikely to be typical of ecosystems as a whole. Species can respond individualistically to climate change (Huntley 1991, Rabasa et al. 2013), with differing capacities to persist or migrate in response to changing environmental conditions (Lenoir and Svenning 2015). Populations of the same species at different locations across the distribution range can also shift

independently (Feeley 2012, Felde et al. 2012), with a meta-analysis of within-species range shifts finding that non-thermal factors considerably influenced patterns, with 42–50% of species showing individualistic shifts despite experiencing similar temperature increases (Gibson-Reinemer and Rahel 2015). Subtle changes within ranges, such as species redistributions or declines, are also likely (Lenoir et al. 2008) and could foreshadow future range shifts (Estrada et al. 2016). The conclusions drawn on forest shifts could, therefore, be substantially different depending on which area or species is assessed (Boisvert-Marsh et al. 2014). For an accurate picture on montane forest tree species distribution shifts, species-specific information is needed (Fadrique et al. 2018), from across the entire elevational gradient.

Given the paucity of information on range shits of tropical montane trees, we sought to determine if evidence exists for species-specific range shifts below the treeline and the extent to which shifts are uniform for the species or individualistic across the elevational gradient. We estimated tree species distribution shifts across an elevation gradient of diverse tropical mountain forests in Taiwan, using a country-wide multi-species forest inventory dataset. We tested the hypothesis that species at high elevations, which are most likely to be temperature limited, will shift upwards, but lower elevation species will display more complex, individualistic patterns due to the greater relative importance of biotic interactions below the treeline. We provide novel insight into distribution shifts of multiple species with elevation and their implications for forest communities in a subtropical montane forest system, contributing key information to better understand forest distribution shifts at a global scale.

Material and methods

Study location

The island of Taiwan straddles the Tropic of Cancer at the margins of the South China Sea. Lowland climates are warm and humid and conditions range through temperate to alpine with increasing elevation in the Central Mountain Range. Elevation is the main driver of temperature differences, whilst monsoons cause substantial variations in rainfall within and between years (Li et al. 2013). Mountains cover 74% of the island (Lu et al. 2001), with over 200 peaks higher than 3000 m a.s.l. (Li et al. 2013). Areas below around 500 m a.s.l. are dominated by urban and agricultural land uses following widespread deforestation, but natural forests are abundant above this elevation, transitioning from broadleaved to mixed and conifer forest with increasing elevation (Li et al. 2013). Landslides occur frequently due to steep topography and unstable geology interacting with earthquakes and typhoons (Lu et al. 2001). High elevation species in Taiwan have been shown to be predominantly shifting upwards (Jump et al. 2012, Greenwood et al. 2014, Morley et al. 2019), but there is a paucity of quantitative information on dynamics in the broader forest below the treeline.

Data

Analyses were undertaken using the 4th Taiwan National Forest Inventory (NFI), a systematic plot-based survey across the forested mountainous areas of Taiwan between the 9 August 2008 and 23 January 2013 (Fig. 1).
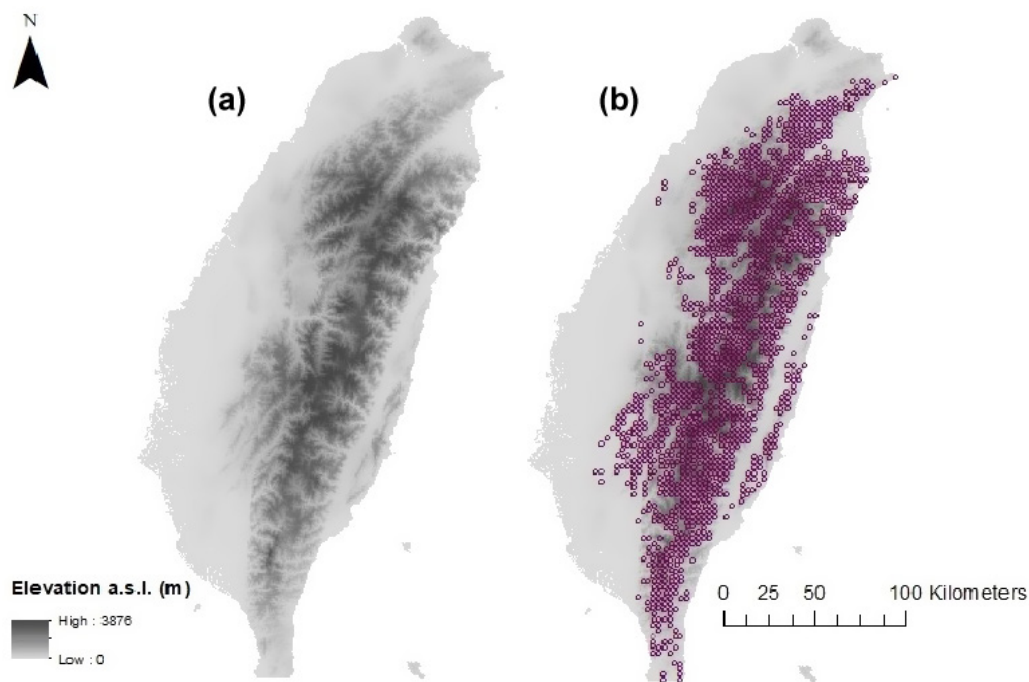

Figure 1. Digital elevation model of Taiwan (a) and the distribution of National Forest Inventory field plots (b).

Plots covered an elevation range from 0 to 3769 m a.s.l. and had a mean spacing of 2871 m between plots (spacing of 3000 m in national forest areas and 1500 m elsewhere). The NFI was spatially extensive, and comprised species information, tree measurements and environmental data over 1564 plots, incorporating 86 306 trees and 516 species. Plots were approximately 0.05 ha (from 0.007 to 0.159 ha), with one plot side of 17.6 m perpendicular to slope and the other side parallel with a variable size to maintain the projected plot area (Supplementary material Appendix 1 Fig. A1). Within each plot, all trees > 5 cm diameter at breast height (dbh) measured at 1.3 m were recorded, with data such as species, dbh and height collected (Supplementary material Appendix 1 Table A1). The elevation of each plot was recorded using a GPS.

Tree basal area (m^2) was calculated for each tree and summed to plot level (Kershaw et al. 2017). From the available data, we removed trees with missing elevation, dbh or xy plot coordinates; trees with dbh > 99.99% of values, as these trees had obvious measurement errors, plot x coordinates > 8.8 m and plot y coordinates > 99.99% to remove outliers; plots with basal area < 0.2 m^2 and > 99.99% of basal area, leading to a final number of 84 361 trees and 1548 plots. We checked for plantation forests by identifying plots with > 90% basal area of commonly planted species *Taiwania cryptomerioides*, *Cryptomeria japonica* and *Chamaecyparis formosensis* and checked the coefficient of variation of dbh values. No plots were removed following this process, as only one plot was identified despite trialling less conservative parameter values for basal area (down to > 60%) and dbh coefficient of variation (up to < 0.3), and this plot also showed tree height variation from 5.8 m to 28 m, indicating that it is unlikely to have been planted.

Demographic analysis

To estimate the magnitude and direction of forest tree species distribution shifts at the range optima and range edges we used a demographic approach. A single survey was used to determine the distribution mismatch between adult and juvenile trees as a proxy for change, with juveniles considered to reflect more recent environmental conditions and adults reflecting historic conditions (Lenoir et al. 2009, Rabasa et al. 2013). Two methods of defining adult and juvenile life stages were compared. The first defined juveniles < 1st quartile of dbh values and adults > 1st quartile of dbh values, whilst the second used a species-specific approach, defining juveniles < 0.25 percentile of dbh values for each species and adults > 0.5 percentile. No seedlings were incorporated in the dataset, allowing us to reduce potential influence on the results of ontogenetic niche differentiation (different environmental requirements of different life stages of the same species) and potential time lags between environmental changes and tree responses (Werner 1984, Lenoir et al. 2009, Bertrand et al. 2011, Kroiss et al. 2015, Máliš et al. 2016, Alexander et al. 2018). The distribution of adult and juvenile trees across the landscape for each method was compared, showing similar patterns and therefore indicating that the two methods are unlikely to give substantially different results. However, the second approach was selected as it provides species-specific information and removes trees with intermediate size classes. Distributions were checked again to detect any obvious latitudinal biases in life stages, to determine whether there were any indications of species shifting latitudinally, but no patterns were observed. Data were converted to occurrence records and species selected for analysis if there were at least 30 plots containing the species at the juvenile life stage. The final dataset comprised 62 089 trees, 1526 plots and 84 species.

To explore the shape of species presence along the elevation gradient, we used generalized additive models (GAMs), with most species displaying hump-shaped distributions. These distributions were tested using generalized linear models (GLMs), comparing linear models with quadratic models for each species and life stage. Pseudo R^2 values were calculated as 1 − (residual deviance/null deviance) to determine the predictive power of the models and models were compared using AIC (Akaike information criterion), with lower values suggesting a better fit (with a difference ≥ 2). In accordance with the assumption that species are generally most abundant in the centre of their range (Holt et al. 1997), only data from species which fitted the quadratic model better than the linear model were used for further analysis (75 out of 84 species). Predictions of probability of occurrence were generated for each species, from which, distribution graphs were created and range optima extracted (Supplementary material Appendix 1 Table A2, Fig. A2). The difference in range optima between life stages was calculated for each species and a Wilcoxon signed rank test used to test the general trend of mismatches across all species.

To estimate changes in upper and lower range edges, a data exploration approach was used. We compared elevation at the range edges based on the raw data distributions using the 1st and 9th deciles of the elevation range as they provide a more robust indication of the range edge than extreme values (Lenoir et al. 2009). The difference in range edge positions between life stages was then calculated for each species and Wilcoxon signed rank tests used to test the overall mismatch across all species. All analyses were undertaken in R ver. 3.6.0 (R Core Team).

Results

Differences between life stages at range optima

There was substantial variation in the magnitude and direction of mismatches in range optima between life stages for different species (Fig. 2). Around one third of species (35%) had juvenile optima higher than adults, suggesting upward shifts. However, over half of modelled species (56%) had juvenile range optima at lower elevations than adult optima of the same species, suggesting downward shifts. Shifts in elevational optima between adults and juveniles ranged from
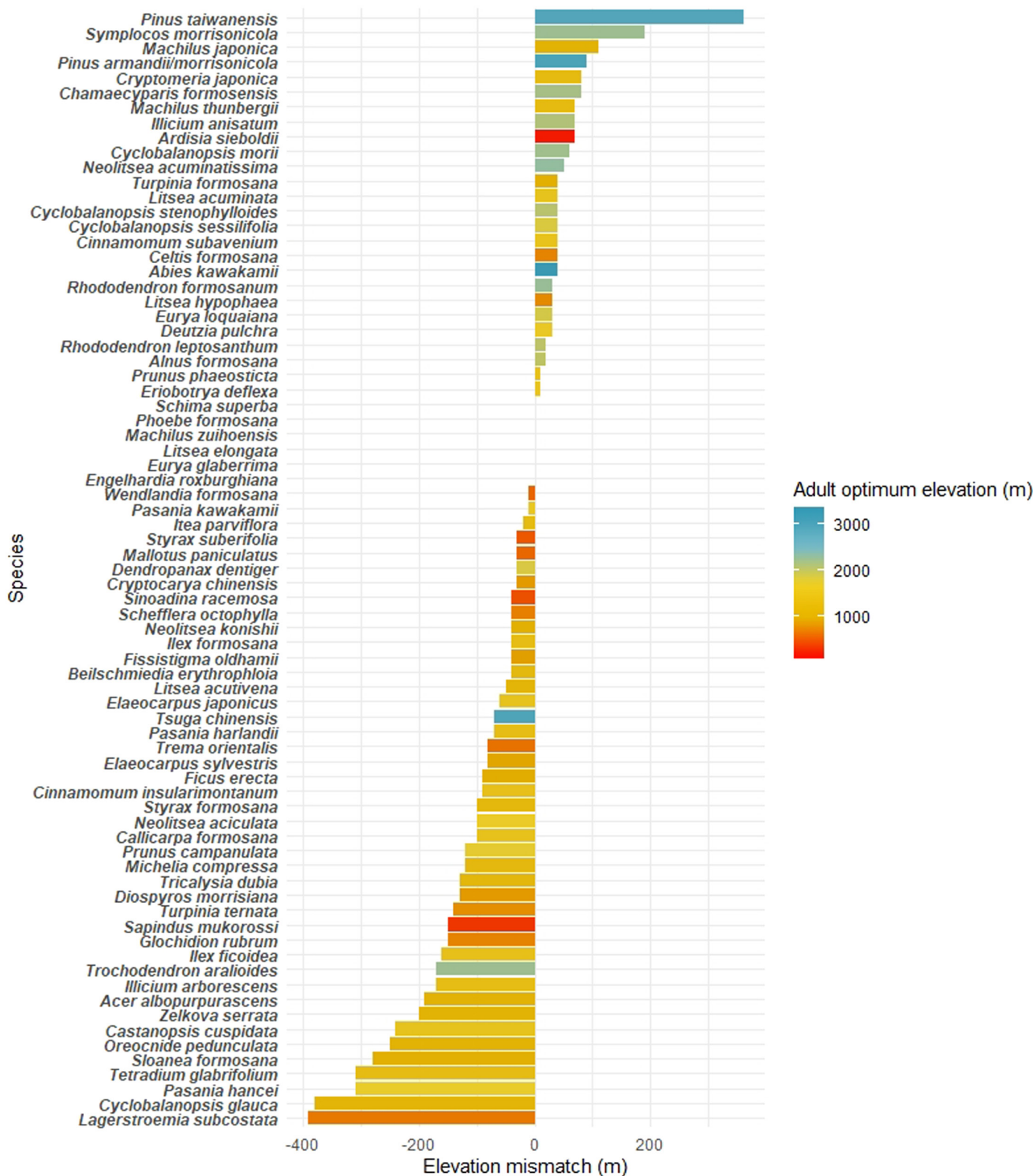
Figure 2. Shifts in optimum elevation (m) between adults and juveniles of 75 subtropical montane tree species calculated as optimum (juvenile) – optimum (adult), using modelled optimum elevations. Negative values indicate juveniles located at lower elevation than their adult counterparts, whilst positive values indicate juveniles located at higher elevations. Juveniles were located at lower elevations than adults for 42 species, higher elevations for 27 species and at the same elevation for 6 species.

0 m to 390 m, with high variability in upward and downward shifts. Overall, there was a significant difference in the optimum elevation between life stages (V = 679.5, p = 0.002), with the juvenile median 50 m lower than the adult median. There was no difference in range optima between life-stages for 8% of species.

Evidence for upward elevation shifts was disproportionately common in high elevation species (blue to green in Fig. 2). From the 15 species with adult optima > 2000 m a.s.l., upwards shifts were indicated for 12 species, downward shifts for 2 species, whilst 1 remained stable. The species which showed evidence for downward shifts were predominantly from mid to low elevations, with 41 out of 43 species having adult optimum elevations < 2000 m a.s.l. The species which showed no apparent mismatch between life stages were primarily mid-elevation species from the Lauracae, Theaceae and Juglandaceae families, with adult optimum positions ranging from 950 to 2660 m.

Differences between life stages at range edges

Species elevational ranges varied considerably in size (from 363 to 1974 m), with species located at the high and low elevational extremes displaying the smallest ranges (Fig. 3). Most species showed a mismatch between life stages at their lower and upper range edges (1st and 9th decile), with substantial variation between species. Mismatches suggested range expansions in 57% of species and range contractions in 43%. There were 17 species (22.67%) which had mismatches that implied range expansion at both range boundaries, with downward shifts at their lower range boundary and upward shifts at their upper range boundary.

The raw data trends were consistent with the model results. At the lower range edge, around two thirds of species (65.33%) had juvenile lower range edges below adults of the same species, suggesting potential downward shifts. Around a quarter of species (26.67%) had juveniles located higher than adults, suggesting upward shifts at their lower range edge. Mismatches in elevation ranged from 2.4 to 482 m, with considerable variation in the sizes of mismatches in both upward and downward directions. There was no life stage mismatch at the lower range edge for 8% of species. However, overall, there was a significant difference in the lower range edge positions between life stages (V = 1735.5, p = 0.002), with the juvenile median 123.1 m lower than the adult median.

Over half of species (56%) showed mismatches suggesting downward shifts at the upper range edge, with juvenile upper range edges lower than adult upper range edges of the same species. Indications of upward shifts at the upper range edge were evident in 40% of species, with juveniles located higher than adults. Mismatches in elevation ranged from 4.3 to 528.1 m, with considerable variation in the sizes of mismatches in both upward and downward directions. Overall considering all species, whilst the juvenile median was 13 m higher than the adult median, there was no significant difference in the upper range edge positions between life stages (V = 1614, p = 0.0928).

Discussion

By comparing the distribution of adult and juvenile life stages of 75 tree species across an elevation gradient from 0 to 3769 m a.s.l. covering a broad range of forest types, we provide evidence that suggests species distribution shifts along elevational gradients can vary considerably in tropical forests. While it is generally expected that species should shift to higher elevations in response to climate change (Chen et al. 2011), we found highly variable life stage mismatches in range optima and upper and lower range edge positions, with a tendency for juveniles to be located at lower elevations than their adult counterparts. While our evidence suggests high altitude species are largely shifting upwards, mid to low elevation species showed more idiosyncratic patterns. Downward shifts of range optima were more common and were concentrated in mid to low elevation forests where species diversity was higher. Our results suggest that migration could be a common response of montane forest tree species to environmental change, but that species move individualistically and are impacted by factors other than climate warming (Huntley 1991). Range optima and upper and lower range edges of individual species did not shift uniformly in terms of size or direction, and more species underwent range expansions than contractions. Mid-elevation species appeared to be more stable under climate change, with some showing no migrations and no associated population declines, and others displaying range expansions at both edges of their distributions.

The upslope movements at high elevations we observed are likely to have been facilitated by rising temperatures and the potential for trees to expand into non-forest areas, following the expectation that climate change drives species upwards as higher elevations become suitable for tree establishment and growth (Lenoir et al. 2009, Jump et al. 2012, Greenwood et al. 2014, Pouteau et al. 2018). Temperatures in Taiwan's Central Mountain Range have risen to around 1.05°C higher than the 1934–1970 average, with this warming already linked to rapid upwards migrations of high altitude plant species (Jump et al. 2012). Although the overall mismatch at the upper range boundary showed no significant difference across all species, critically, there was substantial difference at an individual species level. Upward shifts were the most common response of high elevation species, which is consistent with high altitude trees generally being more temperature limited than trees from warmer areas (Way and Oren 2010), high elevation montane environments warming at a faster rate than lower elevations (Pepin et al. 2015) and high elevation plant species likely to be competitively excluded under warmer temperatures (Alexander et al. 2015, Morley et al. 2020).

Our findings support much of the literature indicating widespread upwards shifts at the treeline (Grabherr et al. 1994, Gehrig-Fasel et al. 2007, Harsch et al. 2009, Dirnböck et al. 2011, Ruiz-Labourdette et al. 2012) and high elevation species shifting faster than mid to low elevation species (Lenoir et al. 2008). Furthermore, results based on forest inventory analysis here endorse assessments of treeline
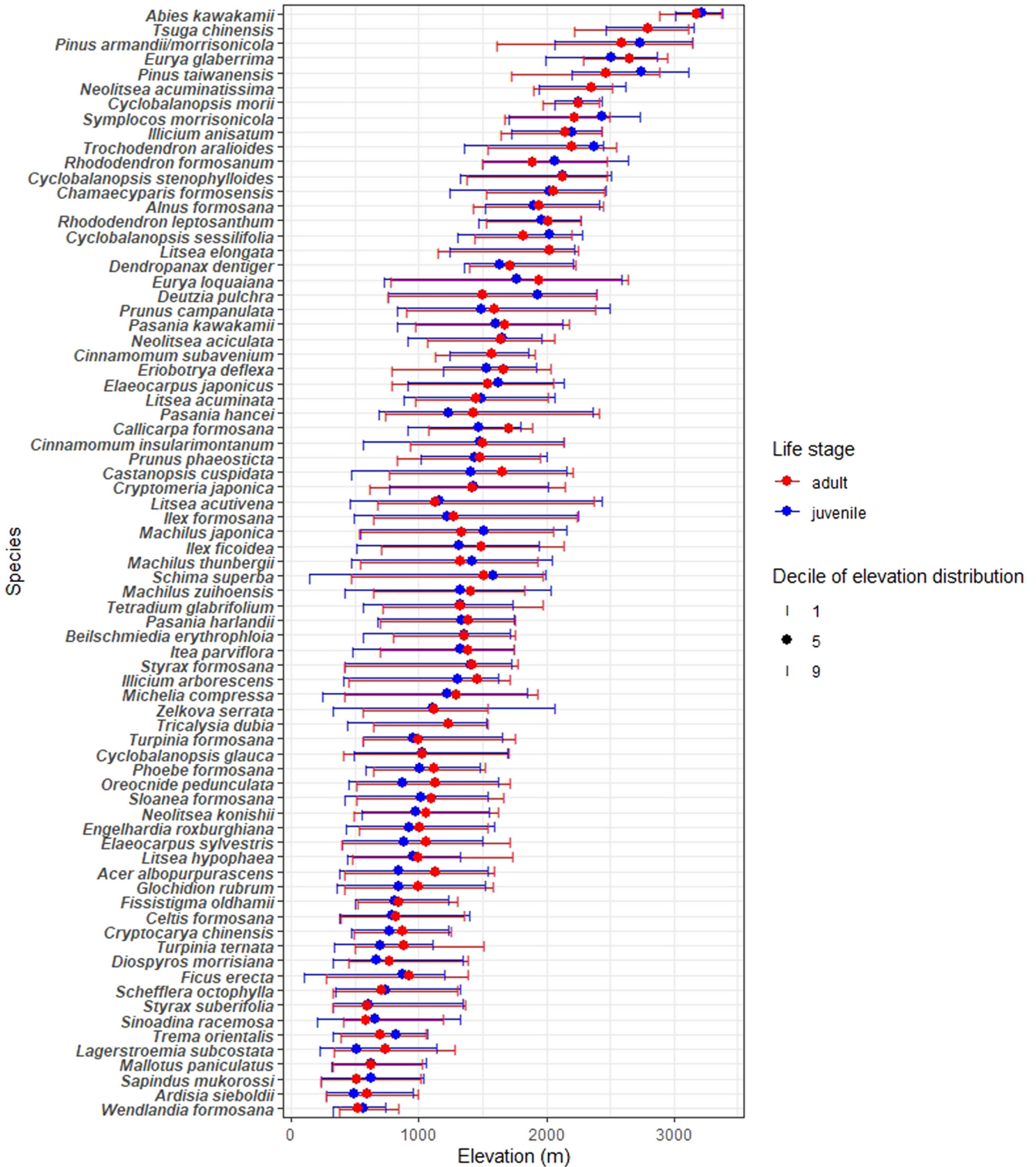
Figure 3. Comparison between juvenile (blue) and adult (red) presence records for 75 subtropical tree species with elevation using the 1st and 9th deciles as the range edges and the 5th decile as the range mid-point.

shifts in the same region based on aerial and satellite imagery (Greenwood et al. 2014). However, while upward shifts are indicated at the highest altitudes, the shifts in range optima that we identify below the treeline are highly individualistic, supporting the expectation that climatic warming can interact with a wide range of non-thermal factors to drive considerable variation in species distributional responses (Lenoir et al. 2010, Crimmins et al. 2011).

Competition for light and nutrients is a major limitation on tree growth and survival (Lewis and Tanner 2000, Coomes and Allen 2007), particularly in diverse tropical forests (Terborgh 2012). Shifts in distributions of some species can reduce the habitat suitability for others (Greenwood et al. 2016), with some species distributions lagging behind climate change whilst others respond more rapidly (Alexander et al. 2018, Lenoir et al. 2020). Ecotones can create barriers for movement, as conditions are typically different than in surrounding forest and can prevent some species colonising (Fadrique et al. 2018), while local variation in edaphic conditions can also restrict the expansion of some species distributions and promote the maintenance of others (Greenwood et al. 2014). Individualistic shifts of species can result in novel community compositions and biotic interactions which can, in turn, cause cascades of species distribution shifts (Huntley 1991, Gilman et al. 2010). Competitive interactions can be further influenced by alterations in plant phenology and physiology in response to climate change (Hughes 2000).

Certain functional traits may facilitate some species survival over others, with traits such as an ability to disperse and colonise new areas early, frequent reproduction and high fecundity likely to aid migrations to new areas (Angert et al. 2011, Alexander et al. 2018) and seed size and number and mode of reproduction likely to influence survival at a new site (Alexander et al. 2018). Effective dispersers may be able to track climate change and out-compete species which are responding more slowly (Urban et al. 2012). Two of the largest shifts in optimum elevation we observed were in *Pinus taiwanensis* and *Lagerstroemia subcostata*, which are common to disturbed areas and habitat margins (Qin et al. 2007, Ruiz-Benito et al. 2015) indicating that they may be well equipped to respond to environmental changes. However, it is important to note that while we focus on distributional differences between life stages, establishment in a new site does not guarantee success as climate continues to change. For example, reductions in *P. taiwanensis* growth have been linked to increasing temperatures, suggesting that performance of established trees may decline under future climate (Ruiz-Benito et al. 2015). Future studies might further explore how altitudinal changes across life stages depend on key functional traits, with dispersal syndrome or ability to track climate change potentially being key plant strategies (Montoya et al. 2008, Ruiz-Benito et al. 2017). For example, species able to migrate rapidly at high elevation have the potential to form outposts in advance of the current treeline where their establishment is facilitated by survival beyond the seedling life stage (Ewald 2012).

Our analyses show wide variation in responses of species across their range, with evidence suggesting the upper edge, optimum and lower edges moving in different directions or at different rates. Differences in shifts across the range of a single species are likely to be due to populations being affected by different processes and drivers of reproduction, dispersal, establishment and growth interacting across a species elevation range. Variation in local adaptation and phenotypic plasticity can cause populations of the same tree species to respond differently to the same environmental challenges (Matías and Jump 2012), with considerable variation in functional traits possible even within single species groups (Hulshof and Swenson 2010). Variations in abiotic environments (Rumpf et al. 2018) and micro-scale climatic conditions also influence where individuals are located (Lembrechts and Lenoir 2019). Mountain environments are highly heterogeneous, with areas of suitable habitat often separated by features such as valleys and outcrops, which restrict migrations (Alexander et al. 2018). Factors such as soil conditions, unstable bedrock, exposed aspects and steep gradients can limit migrations, and have already been linked to individualistic treeline advance in Taiwan (Greenwood et al. 2014, 2015), whilst disturbances such as avalanches and landslides can drive species downwards locally, even within the context of upward shifts facilitated by a warming climate (Cannone et al. 2007, Frei et al. 2010).

Across the region investigated, mid-elevation species appear well equipped to cope with changing climates, with some evidencing persistence and others an ability to migrate. Generalist species with large ranges are considered more likely to succeed under climate change than specialists with narrow ranges (Broennimann et al. 2006, Laurance et al. 2011). The species we observed that did not shift their elevational distributions were all from mid-elevations with large ranges, indicating that they may be able to persist over coming decades and following expectations that generalist species shift less than specialists (Lenoir et al. 2008). While some mid-elevation species look likely to maintain current distributions, others show potential to expand. Of the 17 species with mismatches that suggested range expansions with downwards shifts at their lower range boundary and upwards shifts at their upper range boundary, 11 were characteristic of Pasania–Elaeocarpus montane evergreen broadleaved cloud forest (1200–1600 m a.s.l.) and 10 of Machilus-Castanopsis sub-montane evergreen broadleaved forest (400–1800 m a.s.l.), described by Li et al. (2013). However, such changes will be strongly determined over future decades by shifts in the cloud base, thickness, cover and water content (Ray 2013), which may differ locally due to variation from the East Asian Monsoon and the Massenerhebung effect (Schulz et al. 2017). The pattern of mid-elevation forests faring better than some others under climate change has previously been noted, such as *Pinus jeffreyi* in Nevada rapidly expanding at the mid-elevation point of its range (Gworek et al. 2007). Our results indicate that future forests in Taiwan may show a relative increase in more resilient mid-elevation species.

Whilst ecological and environmental factors influence species distributions, anthropogenic land-use changes also shape how species are located across the landscape and may have an important role in driving the complex species distribution shifts we observed. Around 60% of mountainous regions across the globe are exposed to intensive anthropogenic land use pressures (Elsen et al. 2020). Agricultural activities are creeping upwards in Taiwan as the human population grows (Chou and Tang 2016), with orchards, tea, vegetables and betel nut now planted locally at mid to high elevations (Lu et al. 2001). Tourism and recreation have also increased in recent decades in forested mountain regions, with associated development expanding, particularly along roads (Lu et al. 2001). Although large scale land-use change in the lowlands would most likely drive forests upwards (Guo et al. 2018), small disturbances may allow certain species to colonise areas previously unavailable to them and temporarily increase species richness (Connell 1978, Molino and Sabatier 2001, Lembrechts et al. 2017).

Both historic forest cover and recent interventions can influence the rate of climate-driven shifts (Guo et al. 2018), particularly at lower edges of species distributions (Vilà-Cabrera et al. 2019). Forests in Taiwan are mostly protected for water resources, slope stability and biodiversity, and there is a strong public appreciation for the value of forests (Lu et al. 2001). However, timber harvesting has occurred, and was particularly intense in some parts of the island during the 1940s (Lu et al. 2001). Localised forest thinning is undertaken for conservation purposes in some areas (Weng et al. 2007, Zhuang et al. 2014, Lin et al. 2015), providing potential for infilling from higher elevations. The legacy of past land use should not be overlooked in driving current forest composition and performance (Perring et al. 2016, 2018, Alfaro-Sánchez et al. 2019).

As the climate continues to change, information on the mechanisms, drivers and implications of forest redistributions are urgently needed. Here, we have addressed an important knowledge gap, demonstrating that tree distribution shifts in tropical montane forests are complex and are likely driven by more than direct effects of climate alone. We followed a similar, but adjusted, demographic approach used in previous studies (Lenoir et al. 2009, Vitasse et al. 2012, Rabasa et al. 2013), which can be applied to forest regions across the world to rapidly assess changes using a single survey in the absence of suitable historic records. Therefore, we suggest this approach will be particularly valuable in data poor regions, such as understudied tropical forests where one large-scale survey could indicate the magnitude and direction of potential tree species changes.

One argument against our interpretation of species distribution shifts could be that differences in the abundance and local distribution of adults and juveniles of a species can be linked to ontogenetic niche differentiation (Werner 1984, Bertrand et al. 2011). However, we argue that findings presented here can indicate anticipated changes through time because: 1) the observed directional patterns can be explained by climate change drivers, but they are not consistent with ontogenetic shifts (i.e. higher tolerance of juveniles than adults at high elevations (Lenoir et al. 2009); and 2) we excluded seedlings that are expected to show the greatest ontogenetic niche differences not linked to temporal changes (Máliš et al. 2016). Further integrated analysis of climate, at both a micro and macro scale (Lembrechts and Lenoir 2019), landscape, land use history and species traits is valuable to provide greater detail. With predictions of future movements essential for effective conservation and resource management, further research into approaches such as trait based range shift predictions are needed (Pöyry et al. 2009, Angert et al. 2011, Estrada et al. 2016). Assessments combining multiple parts of species ranges are scarce (Lenoir and Svenning 2015), yet are much needed and important for gaining a thorough understanding of distribution shift dynamics.

Conclusions

Whilst previous predictions suggest widespread upwards shifts of tree species as the climate warms, trends of montane forest change in the tropics and subtropics are likely to be more complex than global averages suggest. Here, we estimated distribution shifts of 75 tree species in Taiwan to assess the extent to which species respond individualistically to current environmental changes. While frequent upward shifts were indicated for high elevation species, in contrast to expectations, we found evidence suggesting downward shifts to be widespread at mid to low elevations in subtropical montane forest. There was great variability in responses between species and across different parts of the ranges of single species. The wide variation of responses we identified is most likely driven by biotic interactions in high diversity forest and individual species and population responses to interacting environmental factors such as topography and anthropogenic influences. These factors are common to many other tropical and subtropical forests, suggesting such individualistic responses should be frequent and indicating a high likelihood of widespread forest community change over coming decades. With global environmental changes ongoing, accounting for complexity in shifts in montane forest species distributions is needed to provide insight on the implications for ecosystems and the people who depend on them.

Data availability statement

We do not have permission to publicly share these data.

References

Alexander, J. M. et al. 2015. Novel competitors shape species' responses to climate change. – Nature 525: 515–518.

Alexander, J. M. et al. 2018. Lags in the response of mountain plant communities to climate change. – Global Change Biol. 24: 563–579.

Alfaro-Sánchez, R. et al. 2019. Land use legacies drive higher growth, lower wood density and enhanced climatic sensitivity in recently established forests. – Agric. For. Meteorol. 276–277: 107630.

Angert, A. L. et al. 2011. Do species' traits predict recent shifts at expanding range edges? – Ecol. Lett. 14: 677–689.

Antão, L. H. et al. 2020. Temperature-related biodiversity change across temperate marine and terrestrial systems. – Nat. Ecol. Evol. 4: 927–933.

Bertrand, R. et al. 2011. Niches of temperate tree species converge towards nutrient-richer conditions over ontogeny. – Oikos 120: 1479–1488.

Boisvert-Marsh, L. et al. 2014. Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes. – Ecosphere 5: 1–33.

Breshears, D. D. et al. 2008. Vegetation synchronously leans upslope as climate warms. – Proc. Natl Acad. Sci. USA 105: 11591–11592.

Broennimann, O. et al. 2006. Do geographic distribution, niche property and life form explain plants' vulnerability to global change? – Global Change Biol. 12: 1079–1093.

Cannone, N. et al. 2007. Unexpected impacts of climate change on alpine vegetation. – Front. Ecol. Environ. 5: 360–364.

Chen, I. et al. 2011. Rapid range shifts of species associated with high levels of climate warming. – Science 333: 1024–1026.

Chou, C.-H. and Tang, H.-Y. 2016. Conservation of biodiversity in Taiwan. – Bot. Orient. J. Plant Sci. 10: 1–5.

Colwell, R. K. et al. 2008. Global warming, elevational range shifts and lowland biotic attrition in the wet tropics. – Science 322: 258–261.

Comte, L. and Lenoir, J. 2020. Decoupled land–sea biodiversity trends. – Nat. Ecol. Evol. 4: 901–902.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. – Science 199: 1302–1310.

Coomes, D. A. and Allen, R. B. 2007. Effects of size, competition and altitude on tree growth. – J. Ecol. 95: 1084–1097.

Crimmins, S. M. et al. 2011. Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. – Science 331: 324–327.

De Frenne, P. and Verheyen, K. 2016. Weather stations lack forest data. – Science 351: 234.

Dirnböck, T. et al. 2011. Disproportional risk for habitat loss of high-altitude endemic species under climate change. – Global Change Biol. 17: 990–996.

Duque, A. et al. 2015. Thermophilization of adult and juvenile tree communities in the northern tropical Andes. – Proc. Natl Acad. Sci. USA 112: 10744–10749.

Elsen, P. R. et al. 2020. Topography and human pressure in mountain ranges alter expected species responses to climate change. – Nat. Commun. 11: 1–10.

Esquivel-Muelbert, A. et al. 2019. Compositional response of Amazon forests to climate change. – Global Change Biol. 25: 39–56.

Estrada, A. et al. 2016. Usefulness of species traits in predicting range shifts. – Trends Ecol. Evol. 31: 190–203.

Ettinger, A. K. et al. 2011. Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers. – Ecology 92: 1323–1331.

Ewald, J. 2012. Vegetation databases provide a close-up on altitudinal tree species distribution in the Bavarian Alps. – Biodivers. Ecol. 4: 41–48.

Fadrique, B. et al. 2018. Widespread but heterogeneous responses of Andean forests to climate change. – Nature 564: 207–212.

Feeley, K. J. 2012. Distributional migrations, expansions and contractions of tropical plant species as revealed in dated herbarium records. – Global Change Biol. 18: 1335–1341.

Feeley, K. J. et al. 2011. Upslope migration of Andean trees. – J. Biogeogr. 38: 783–791.

Feeley, K. J. et al. 2013. Compositional shifts in Costa Rican forests due to climate-driven species migrations. – Global Change Biol. 19: 3472–3480.

Felde, V. A. et al. 2012. Upward shift in elevational plant species ranges in Sikkilsdalen, central Norway. – Ecography 35: 922–932.

Frei, E. et al. 2010. Plant species' range shifts in mountainous areas-all uphill from here? – Bot. Helv. 120: 117–128.

García-Oliva, F. et al. 1994. Forest-to-pasture conversion influences on soil organic carbon dynamics in a tropical deciduous forest. – Oecologia 99: 392–396.

Gehrig-Fasel, J. et al. 2007. Tree line shifts in the Swiss Alps: climate change or land abandonment? – J. Veg. Sci. 18: 571–582.

Gibson-Reinemer, D. K. and Rahel, F. J. 2015. Inconsistent range shifts within species highlight idiosyncratic responses to climate warming. – PLoS One 10: e0132103.

Gilman, S. E. et al. 2010. A framework for community interactions under climate change. – Trends Ecol. Evol. 25: 325–331.

Gosz, J. R. 1992. Gradient analysis of ecological change in time and space: implications for forest management. – Ecol. Appl. 2: 248–261.

Grabherr, G. et al. 1994. Climate effects on mountain plants. – Nature 369: 448.

Greenwood, S. et al. 2014. Strong topographic sheltering effects lead to spatially complex treeline advance and increased forest density in a subtropical mountain region. – Global Change Biol. 20: 3756–3766.

Greenwood, S. et al. 2015. Temperature and sheltering determine patterns of seedling establishment in an advancing subtropical treeline. – J. Veg. Sci. 26: 711–721.

Greenwood, S. et al. 2016. Community change and species richness reductions in rapidly advancing tree lines. – J. Biogeogr. 43: 2274–2284.

Guo, F. et al. 2018. Land-use change interacts with climate to determine elevational species redistribution. – Nat. Commun. 9: 1–7.

Gworek, J. R. et al. 2007. Changes in biotic interactions and climate determine recruitment of Jeffrey pine along an elevation gradient. – For. Ecol. Manage. 239: 57–68.

Harsch, M. A. et al. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. – Ecol. Lett. 12: 1040–1049.

Holt, R. D. et al. 1997. On the relationship between range size and local abundance: back to basics. – Oikos 78: 183–190.

Hughes, L. 2000. Biological consequences of global warming: is the signal already. – Trends Ecol. Evol. 15: 56–61.

Hulshof, C. M. and Swenson, N. G. 2010. Variation in leaf functional trait values within and across individuals and species: an example from a Costa Rican dry forest. – Funct. Ecol. 24: 217–223.

Huntley, B. 1991. How plants respond to climate change: migration rates, individualism and the consequences for plant communities. – Ann. Bot. 67: 15–22.

IPCC 2013. Climate change 2013: the physical science basis. – In: Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change. Cambridge Univ. Press.

IPCC 2018. Summary for policymakers. – In: Masson-Delmotte, V. et al. (eds), Global warming of 1.5°C. An IPCC special report on the impacts of global warming of 1.5°C above pre-industrial levels and related global greenhouse gas emission pathways, in the context of strengthening the global response to the threat of climate change. World Meteorological Organization, Geneva, Switzerland, pp. 1–32.

Jobbágy, E. G. et al. 1996. Vegetation heterogeneity and diversity in flat and mountain landscapes of Patagonia (Argentina). – J. Veg. Sci. 7: 599–608.

Jump, A. S. et al. 2012. Rapid altitudinal migration of mountain plants in Taiwan and its implications for high altitude biodiversity. – Ecography 35: 204–210.

Kershaw, J. A. J. et al. 2017. Forest mensuration, 5th ed. – Wiley–Blackwell.

Kirby, K. R. and Potvin, C. 2007. Variation in carbon storage among tree species: implications for the management of a small-scale carbon sink project. – For. Ecol. Manage. 246: 208–221.

Kroiss, S. J. et al. 2015. Recruitment limitation of long-lived conifers: implications for climate change responses. – Ecology 96: 1286–1297.

Laurance, W. F. et al. 2011. Global warming, elevational ranges and the vulnerability of tropical biota. – Biol. Conserv. 144: 548–557.

Lembrechts, J. J. and Lenoir, J. 2019. Microclimatic conditions anywhere at any time! – Global Change Biol. 26: 337–339.

Lembrechts, J. J. et al. 2017. Mountain roads shift native and non-native plant species' ranges. – Ecography 40: 353–364.

Lenoir, J. and Svenning, J. C. 2015. Climate-related range shifts – a global multidimensional synthesis and new research directions. – Ecography 38: 15–28.

Lenoir, J. et al. 2008. A significant upward shift in plant species optimum elevation during the 20th century. – Science 320: 1768–1771.

Lenoir, J. et al. 2009. Differences between tree species seedling and adult altitudinal distribution in mountain forests during the recent warm period (1986–2006). – Ecography 32: 765–777.

Lenoir, J. et al. 2010. Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. – Ecography 33: 295–303.

Lenoir, J. et al. 2020. Species better track climate warming in the oceans than on land. – Nat. Ecol. Evol. 4: 1–16.

Lewis, S. L. and Tanner, E. V. J. 2000. Effects of above- and below-ground competition on growth and survival of rain forest tree seedlings. – Ecology 81: 2525–2538.

Li, C. F. et al. 2013. Classification of Taiwan forest vegetation. – Appl. Veg. Sci. 16: 698–719.

Lin, W. R. et al. 2015. The impacts of thinning on the fruiting of saprophytic fungi in *Cryptomeria japonica* plantations in central Taiwan. – For. Ecol. Manage. 336: 183–193.

Lu, S.-Y. et al. 2001. Managing forests for watershed protection in Taiwan. – For. Ecol. Manage. 143: 77–85.

Máliš, F. et al. 2016. Life stage, not climate change, explains observed tree range shifts. – Global Change Biol. 22: 1904–1914.

Matías, L. and Jump, A. S. 2012. Interactions between growth, demography and biotic interactions in determining species range limits in a warming world: the case of *Pinus sylvestris*. – For. Ecol. Manage. 282: 10–22.

McCarty, J. P. 2001. Ecological consequences of recent climate change. – Conserv. Biol. 15: 320–331.

Molino, J. and Sabatier, D. 2001. Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. – Science 294: 1702–1704.

Montoya, D. et al. 2008. Animal versus wind dispersal and the robustness of tree species to deforestation. – Science 320: 1502–1504.

Morley, P. J. et al. 2018. Integrating remote sensing and demography for more efficient and effective assessment of changing mountain forest distribution. – Ecol. Inform. 43: 106–115.

Morley, P. J. et al. 2019. Quantifying structural diversity measures to better estimate change at mountain forest margins. – Remote Sens. Environ. 223: 291–306.

Morley, P. J. et al. 2020. Montane forest expansion at high elevations drives rapid reduction in non-forest area despite no change in mean forest elevation. – J. Biogeogr. doi: 10.1111/jbi.13951

Morueta-Holme, N. et al. 2015. Strong upslope shifts in Chimborazo's vegetation over two centuries since Humboldt. – Proc. Natl Acad. Sci. USA 112: 12741–12745.

Nilaweera, N. S. and Nutalaya, P. 1999. Role of tree roots in slope stabilisation. – Bull. Eng. Geol. Environ. 57: 337–342.

Nogués-Bravo, D. et al. 2007. Exposure of global mountain systems to climate warming during the 21st century. – Global Environ. Change 17: 420–428.

Pan, Y. et al. 2011. A large and persistent carbon sink in the world's forests. – Science 333: 988–993.

Parmesan, C. and Yohe, G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. – Nature 421: 37–42.

Pecl, G. T. et al. 2017. Biodiversity redistribution under climate change: impacts on ecosystems and human well-being. – Science 355: 1389.

Pepin, N. et al. 2015. Elevation-dependent warming in mountain regions of the world. – Nat. Clim. Change 5: 424–430.

Perring, M. P. et al. 2016. Global environmental change effects on ecosystems: the importance of land-use legacies. – Global Change Biol. 22: 1361–1371.

Perring, M. P. et al. 2018. Global environmental change effects on plant community composition trajectories depend upon management legacies. – Global Change Biol. 24: 1722–1740.

Potapov, P. V. et al. 2012. Quantifying forest cover loss in Democratic Republic of the Congo, 2000–2010, with Landsat ETM+ data. – Remote Sens. Environ. 122: 106–116.

Pouteau, R. et al. 2018. Will climate change shift the lower ecotone of tropical montane cloud forests upwards on islands? – J. Biogeogr. 45: 1326–1333.

Pöyry, J. et al. 2009. Species traits explain recent range shifts of Finnish butterflies. – Global Change Biol. 15: 732–743.

Qin, H. et al. 2007. Lythraceae. – In: Wu, Z. Y. et al. (eds), Flora of China. Vol. 13 (Clusiaceae through Araliaceae). Science Press, Beijing and Missouri Botanical Garden Press, St Louis, pp. 274–289.

Rabasa, S. G. et al. 2013. Disparity in elevational shifts of European trees in response to recent climate warming. – Global Change Biol. 19: 2490–2499.

Ray, D. K. 2013. Tropical montane cloud forests. – In: Climate vulnerability: understanding and addressing threats to essential resources. Elsevier, pp. 79–85.

Ruiz-Benito, P. et al. 2015. Climatic stress during stand development alters the sign and magnitude of age-related growth responses in a subtropical mountain pine. – PLoS One 10: e0126581.

Ruiz-Benito, P. et al. 2017. Climate- and successional-related changes in functional composition of European forests are strongly driven by tree mortality. – Global Change Biol. 23: 4162–4176.

Ruiz-Labourdette, D. et al. 2012. Forest composition in Mediterranean mountains is projected to shift along the entire elevational gradient under climate change. – J. Biogeogr. 39: 162–176.

Rumpf, S. B. et al. 2018. Range dynamics of mountain plants decrease with elevation. – Proc. Natl Acad. Sci. USA 115: 1848–1853.

Schemske, D. W. et al. 2009. Is there a latitudinal gradient in the importance of biotic interactions? – Annu. Rev. Ecol. Evol. Syst. 40: 245–269.

Schulz, H. M. et al. 2017. Mapping the montane cloud forest of Taiwan using 12 year MODIS-derived ground fog frequency data. – PLoS One 12: e0172663.

Snyder, P. K. et al. 2004. Evaluating the influence of different vegetation biomes on the global climate. – Clim. Dyn. 23: 279–302.

Terborgh, J. 2012. Enemies maintain hyperdiverse tropical forests. – Am. Nat. 179: 303–314.

Urban, M. C. et al. 2012. On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change. – Proc. R. Soc. B 279: 2072–2080.

Urli, M. et al. 2014. Inferring shifts in tree species distribution using asymmetric distribution curves: a case study in the Iberian mountains. – J. Veg. Sci. 25: 147–159.

van Breugel, M. et al. 2018. Soil nutrients and dispersal limitation shape compositional variation in secondary tropical forests across multiple scales. – J. Ecol. 107: 566–581.

Vilà-Cabrera, A. et al. 2019. Refining predictions of population decline at species' rear edges. – Global Change Biol. 25: 1–12.

Vitasse, Y. et al. 2012. Tree recruitment of European tree species at their current upper elevational limits in the Swiss Alps. – J. Biogeogr. 39: 1439–1449.

Wallingford, P. D. et al. 2020. Adjusting the lens of invasion biology to focus on the impacts of climate-driven range shifts. – Nat. Clim. Change 10: 398–405.

Wason, J. W. and Dovciak, M. 2017. Tree demography suggests multiple directions and drivers for species range shifts in mountains of northeastern United States. – Global Change Biol. 23: 3335–3347.

Way, D. A. and Oren, R. 2010. Differential responses to changes in growth temperature between trees from different functional groups and biomes: a review and synthesis of data. – Tree Physiol. 30: 669–688.

Weng, S. H. et al. 2007. Microclimatic responses to different thinning intensities in a Japanese cedar plantation of northern Taiwan. – For. Ecol. Manage. 241: 91–100.

Werner, E. E. 1984. The ontogenetic niche and species interactions in size-structured populations. – Annu. Rev. Ecol. Syst. 15: 393–425.

Zhu, K. et al. 2012. Failure to migrate: lack of tree range expansion in response to climate change. – Global Change Biol. 18: 1042–1052.

Zhuang, S. et al. 2014. Effect of forest thinning on soil net nitrogen mineralization and nitrification in a *Cryptomeria japonica* plantation in Taiwan. – J. For. Res. 25: 571–578.