

thesis abstract

Plant diversity on high elevation islands – drivers of species richness and endemism

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Abstract. High elevation islands elicit fascination because of their large array of endemic species and strong environmental gradients. First, I define a high elevation island according to geographic and environmental characteristics. Then, within this high elevation island framework, I address local disturbance effects on plant distribution, drivers of diversity and endemism on the island scale, and global patterns of treeline elevation and climate change. Locally, introduced herbivores have strong negative effects on the summit scrub of my model island La Palma (Canary Islands), while roads have unexpected positive effects on endemics. On the island scale, topography and climate drive diversity and endemism. Hotspots of endemism are found in summit regions – a general pattern on high elevation islands. The global pattern of treeline elevation behaves quite differently on islands than on the mainland. A thorough literature review and climate projections suggest that climate change will profoundly affect oceanic island floras.

Keywords. Climate change, disturbance, herbivore, isolation, non-native, road ecology, speciation, topography, treeline

Introduction

Islands contribute disproportionately to global biodiversity by harboring 25% of global species richness but cover only 3% of the land surface area (Kreft et al. 2008). Islands, in general, possess relatively low total species richness but exhibit high degrees of endemism, making them global diversity hotspots (Kier et al. 2009). In particular, this holds true for high elevation islands because these islands are usually larger in area, offer strong environmental continental-scale gradients and display high topographic complexity (Irl 2014). In fact, they can be considered *climatic mini-continents* (Irl et al. 2015) with a high diversity of vegetation zones tracking the changes in climatic conditions and the (often) anisotropic precipitation regime due to stable wind systems such as prevailing trade winds (e.g., Giambelluca et al. 2011, Garzón-Machado et al. 2014). In consequence, high elevation islands are valuable objects for ecological, evolutionary and biogeographic research questions but also important for nature conservation.

High elevation islands are found in every ocean. I consider high elevation islands to possess two main defining features: (i) they can be found from low latitudes to approximately mid latitudes, and (ii) they possess the full range of elevational ecosystems (ranging from the coastal zone to the alpine zone) of their respective geographical position (Irl 2014). Regarding (i), islands at high latitudes with high mountain peaks exist as well, however, the zone of ecological activity (ranging from the coast to the permanent snowline) on high latitude islands is generally quite small. Also, most high latitude islands were more or less completely covered by ice during the last glacial maximum (Egholm et al. 2009), resulting in insufficient time for speciation processes to be relevant in the post-ice age period. Ultimately, this makes high latitude islands less interesting from a diversity- and evolutionary-oriented perspective. With respect to (ii), I consider high elevation islands to offer a wide range of habitats ideally suited to study evolutionary differentiation along environmental gradients. An important ecological feature

of high elevation islands is the presence of a high elevation treeline, which defines the lower limit of the alpine zone (Körner 2012).

Endemic species are an iconic feature of high elevation islands. Endemics on islands are mainly the result of *in situ* speciation (Whittaker et al. 2008) rather than migration and range contraction processes as is the case on continents (Orme et al. 2005). This partly allows inferring evolutionary processes that influence patterns of diversity, especially when focusing on endemics that are only found on a single island within an archipelago (so-called single-island endemics). From a conservation perspective, endemics should be treated with highest priority (Kier et al. 2009), as the extinction of a single-island endemic on its native island will automatically result in a direct loss to global biodiversity.

I aim at bringing together island ecology with island biogeography and macroecology (Irl 2014) bridging from local scales (e.g., the vegetation of the summit scrub or specific roads) over regional (island scale) to global analyses. Classical island biogeography has typically targeted drivers of diversity and endemism by looking at geographic features of entire islands (e.g., area, elevation, isolation, age, etc.) and comparing these features among islands (e.g., MacArthur and Wilson 1967, Whittaker et al. 2008). Studies on the drivers of diversity and endemism on the within-island scale are underrepresented, although high elevation islands offer unique settings to study continental-scale environmental gradients on the scale of a single island (e.g., Irl et al. 2015, Otto et al. 2016). Both disturbances and environmental features likely determine the patterns of diversity and endemism on the within-island scale, therefore I assess (i) how three globally important disturbances (roads, fire and introduced herbivores) locally affect islands species and (ii) how climate and topography govern species richness and endemism on the island scale. On the global scale, I assess (iii) how climatic features drive island treelines and how climate change might affect oceanic island floras. For details on the methods see Harter et al. (2015), Irl et al. (2012, 2014a,b, 2015, 2016) and Steinbauer et al. (2013).

Study area: La Palma, Canary Islands

La Palma provides an ideal model system to study diversity and endemism on a local and regional scale. The island is an oceanic-volcanic island in a subtropical position with substantial elevation (max. 2426 m a.s.l.). This makes it a typical high elevation island influenced by the trade winds, resulting in a humid windward and a more arid leeward side, as well as an arid summit scrub above the trade wind inversion (Irl and Beierkuhnlein 2011). La Palma harbors its own suite of endemic plant species (Acebes-Ginovés et al. 2010) and a wide range of zonal ecosystems (del Arco-Aguilar et al. 2010). Current checklists indicate that 37 out of the 193 endemic plant species are single-island endemics (Acebes-Ginovés et al. 2010).

Local: Human-associated disturbances on high elevation islands

All high elevation islands worldwide are inhabited by humans and are therefore influenced by direct and indirect human activities. As a consequence, most high elevation islands experience human-associated disturbances (sensu Caujapé-Castells et al. 2010). Especially endemic species, which evolved under the absence of certain disturbances (e.g., mammalian herbivory), might be inadequately adapted to human-associated disturbances, when regarding their evolutionary history (Bowen and Van Vuren 1997). Indeed, the impact of human-associated disturbances such as roads, introduced herbivores and fire on endemic species can be considered as one of the great unknowns in island ecology, making future predictions quite speculative.

A human-associated disturbance that directly affects the environment is roads. However, previous research in road ecology has mainly focused on effects on species richness and the spread of non-native plant species (Trombulak and Frissell 2000). La Palma offers the unique opportunity to study how roads affect endemic species. As roads are often associated with negative impacts on natural vegetation we expected roads to negatively impact endemic richness as well (Irl et al. 2014a). To test this we sampled 48 plot pairs

in roadside and comparable surrounding natural conditions along two mountain roads (one on the humid east and one on the drier western side of the island), both reaching from sea level to the summit of the island. Opposing our expectations, we found endemic richness to be significantly higher in roadside plots than in surrounding vegetation (Irl et al. 2014a). Because of the rugged topography most roads are cut into the side of the mountain producing roadside cliffs. A large subset of endemics on La Palma is probably pre-adapted to rupicolous conditions (Santos-Guerra 1983), and roadside cliffs seem to offer prime virgin cliff habitats highly suitable for cliff dwelling plant species. In addition, cliff habitats (no matter if roadside or natural) can be seen as ‘safe-sites’ protecting endemics from introduced herbivores (Garzón-Machado et al. 2010) and wildfires (Garzón-Machado et al. 2012). However, it is important to stress here that the positive effect of roads on endemics does not outweigh the negative impacts associated with roads (invasive species, pollution, natural habitat destruction, hybridization and homogenization, etc.; Trombulak and Frissell 2000).

The effects of introduced herbivores also clearly left their marks in the summit scrub of La Palma. In the summit scrub a single endemic shrub species (*Adenocarpus viscosus* subsp. *spartioides*) seemingly builds mono-dominant stands, even though other shrubs species are potentially present but extremely rare (Palomares-Martínez et al. 2004). All shrub species of the summit scrub are legumes with a similar spherical growth form. Based on data from 11-year fenced exclosures established by the National Park Caldera de Taburiente, our results show that rare endemic shrub species (i.e., *Genista benehoavensis* and *Chamaecytisus proliferus*) are actually better adapted to the harsh high elevation growth conditions than *A. viscosus* subsp. *spartioides* (Irl et al. 2012). Due to the lack of better-adapted competitors that are suppressed by introduced herbivores (mainly feral goats and rabbits) a suboptimally adapted shrub species (*A. viscosus* subsp. *spartioides*) can create mono-typic stands. Seedling richness strongly decreased under herbivore presence, no matter if

fire was present or not (Fig. 1; Irl et al. 2014b). However, fire generally led to higher seedling richness by providing nutrients and free space, by eradicating competitors for resources and by reducing herbivore pressure in burned areas (Keeley and Fotheringham 2000). Human-associated disturbances seem to effectively control vegetation structure and composition in the summit scrub of La Palma and have substantially altered the system—away from a multi-species system to a single species shrub community.

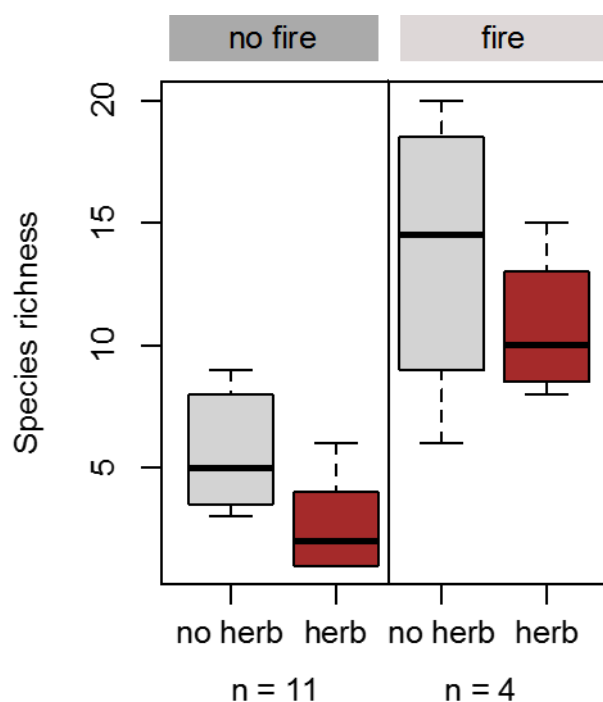


Figure 1. Species richness decreases if non-native herbivores are present, no matter if fire is present or not. However, fire generally leads to an increase in species richness over non-fire conditions, although the negative effect of introduced herbivores is still visible. No herb = herbivore exclosures, herb = herbivores present. Taken from Irl et al. (2014b).

Regional: Patterns of diversity and endemism on a high elevation island

La Palma as an oceanic island permanently isolated from the continent harbors a large array of *in situ* speciated endemics. Thus, it is possible to directly infer the environmental drivers of diversity and indirectly also speciation from patterns found on the landscape scale of a single island, whereas such an inference is much more complicated on the continent where endemism is more often a

result of range contraction and migration processes than *in situ* speciation (Orme et al. 2005). Indeed, La Palma, as a typical trade wind-influenced climatic mini-continent, offers excellent conditions to infer underlying processes from patterns.

A long-standing debate in ecology is how strongly climate and how strongly topography influence diversity but also speciation. Interestingly, we find that climate and topography vary strongly in explaining species richness and endemic richness (both measures of biodiversity; Myers et al. 2000), when compared to endemism (i.e., the percentage of endemics frequently used as a measure of speciation; Emerson and Kolm 2005, Steinbauer et al. 2016). While topography mainly drives endemic richness and climate mainly governs endemism, both climate and topography are of similar importance for species richness (Fig. 2; Irl et al. 2015).

I suggest two main drivers of the pattern of endemic richness on La Palma. On the one hand, species' adaptations to local topography govern this pattern, on the other human-mediated influences might have an influence as well (Irl et al. 2015). On the adaptation side, endemic species are likely pre-adapted to rupicolous conditions

(Santos Guerra 1983) but high topographic complexity (the main predictor) may also enable higher diversity by increasing local niche space (Hortal et al. 2013) and area (Leutner et al. 2011). On the human influence side, La Palma is to some degree degraded by anthropogenic activities. However, anthropogenic activities are not homogeneously distributed throughout an island but, as is the case for La Palma, are aggregated in areas that are easily accessible (i.e. possess a low topographic complexity). Similar to the roadside cliffs (Irl et al. 2014a) but on a larger scale, inaccessible areas might be considered 'safe sites' for endemics, even though these endemics might have a much wider distribution under natural conditions (with subsequent effects on endemic richness).

Endemism, which is linked to speciation, strongly increases with elevation on La Palma. Indeed, an increase in the percentage of endemic species with elevation is a general pattern found on nearly all high elevation islands but also continental mountain systems (Steinbauer et al. 2016). We argue that increasing geographic isolation of species adapted to high elevation systems may limit gene flow and support evolutionary dynamics (*elevation-driven ecological isolation sensu*

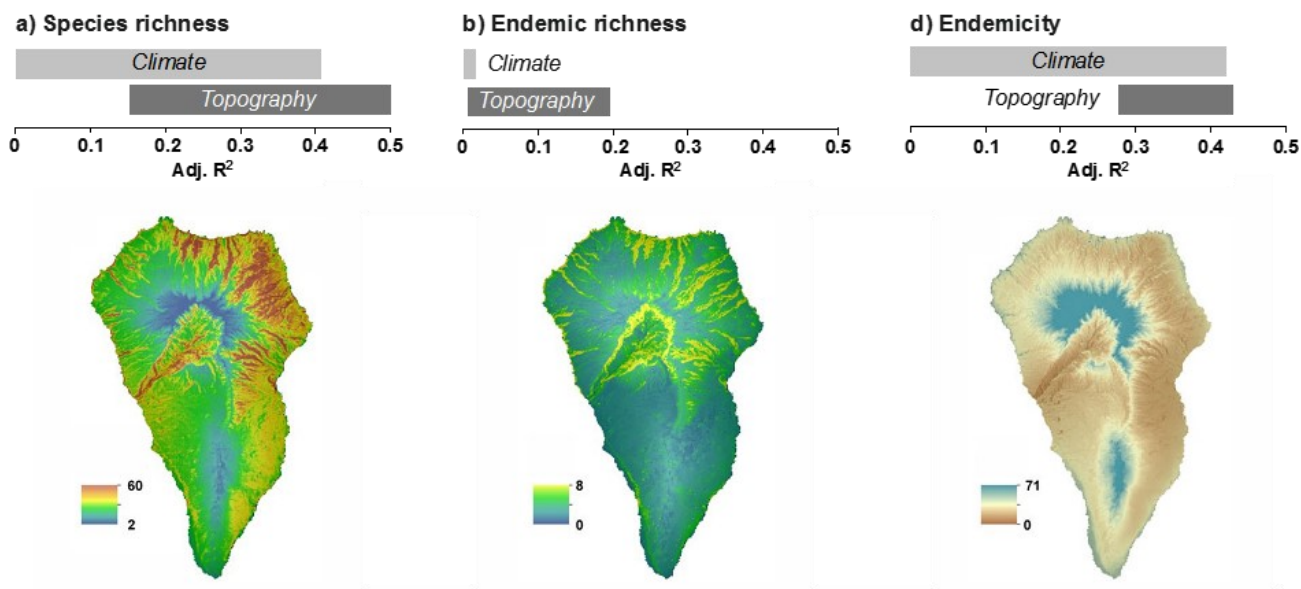


Figure 2. The joint and independent explanatory power of climate and topography (using variance partitioning) on a) species richness, b) endemic richness (number of single-island endemics) and c) endemism (percentage of single-island endemics) on La Palma, Canary Islands. Overlapping bars indicate joint explained variance and single bars independently explained variance. The end of the bar reaching farthest to the right displays total explained variance. The corresponding maps indicate hot- and cold spots of the respective indices within the island (interpolation technique: linear regression kriging). Taken from Irl et al. (2015)

Steinbauer et al. 2013 or Heaney et al. 2005). Recent phylogenetic studies e.g., from tropical Borneo, support this interpretation (Merckx et al. 2015). The authors also show that high elevation endemics are more closely related to taxa in other mountain systems or temperate regions than to taxa from lower elevations even within the same island.

Global: Oceanic islands floras in a changing world

As demonstrated by the dependency of endemics to climatic conditions in the previous section, climate change has the potential to drastically affect oceanic islands floras. Climate change might profoundly impact endemics in multiple, interacting ways. Oceanic islands might be particularly vulnerable because of their high degree of isolation, small area, low species richness, high degree of endemism and low functional redundancy (Fordham and Brook 2010). To assess the risk of island floras and their endemic species generated by climate change, we conducted an exhaustive literature survey and assessed how different climate change scenarios might affect oceanic islands ($n = 787$), among them many high elevation islands (Harter et al. 2015).

Although the surrounding ocean might buffer extreme climatic changes, mean annual temperature as well as mean annual precipitation are predicted to change substantially for oceanic islands ranging from the tropics to high latitudes (Harter et al. 2015). Using CMPI5 model ensemble data (Coupled Model Inter-comparison Project Phase 5; Taylor et al. 2012) temperature increases of 1.3 to 2.8°C are predicted for the time period 2081-2100 depending on the scenario and geographic location of the island. Precipitation changes are more complex and changes within the range between -12% to +20% are likely.

Climate change will likely alter environmental conditions as well as threaten endemic species on high elevation islands. Climatic changes in combination with human land use changes might have a substantial impact on high elevation islands (e.g., changes in altitude, intensity and frequency of trade wind cloud formation or extreme drought

and heavy rain events; Harter et al. 2015). Although upward shifts are possible for species on high elevation islands, high elevation endemics will likely not be able to track these changes because they already occupy the highest areas, leading to a high extinction risk (Poteau and Birnbaum 2016).

Global: Treelines on islands

The high elevation treeline, another feature of islands driven by climate, is a defining element of high elevation islands (Irl 2014) and one of the most important life form boundaries (Körner 2012). A classic topic in biogeography, treeline science, however, has predominantly focused on mainland mountain systems (reviewed in Körner 2012), strongly neglecting islands (but see Leuschner 1996). However, islands have the potential to deliver valuable insights into the processes governing treeline formation because confounding effects of continentality are not relevant here. Using a novel sampling method in treeline science (i.e. Google Earth) we compiled the largest dataset on island treelines up to date ($n = 87$; $n = 58$ for continental islands and $n = 29$ for oceanic islands; Irl et al. 2016).

I used this dataset, which differentiates between oceanic islands (permanently isolated) and continental islands (often complex geologic history of contact and isolation with the mainland), to quantify for the first time that treeline elevation decreased significantly from mainland mountain systems through continental islands to oceanic islands (Fig. 3a), if the effect of latitude was accounted for. I attribute this to the oceanic climate found on islands (high cloudiness and low solar radiation reduce microclimatic amelioration), low mass elevation effect compared to large mainland mountain systems (Leuschner 1996) and drought-induced treelines on trade wind islands (Crausbay et al. 2014).

I show that both oceanic and continental islands displayed a single tropical peak in the treeline elevation-latitude relationship compared to the mainland subtropical double-hump (Fig. 3b). Surprisingly, the clearly dominating island feature determining treeline elevation was maxi-

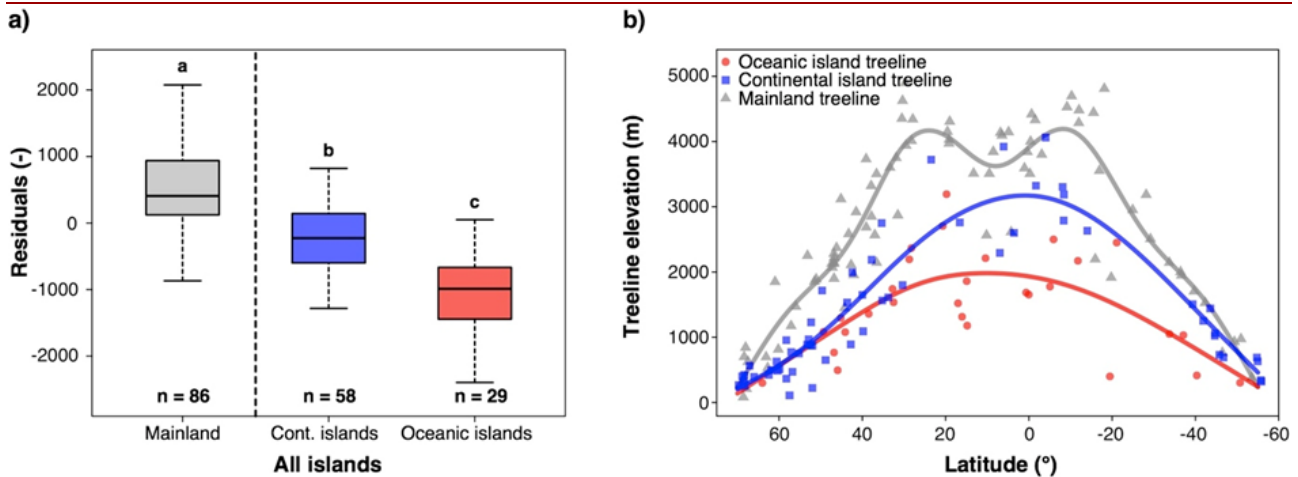


Figure 3. a) Decreasing treeline elevation from mainland mountains through continental islands to oceanic islands, if the effect of latitude is accounted for in a linear model (hence, the residuals). Lowercase letters indicate significant groups from a Tukey HSD post-hoc test after performing an ANOVA. b) Treeline elevation-latitude relationship for oceanic islands, continental islands and the mainland. I used general additive models as smoothing fit. Taken from Irl et al. (2016).

mum island elevation – an easy-to-measure surrogate for mass elevation effect on islands – rather than the island’s latitudinal position, which would be assumed based on previous knowledge (Jobbágy and Jackson 2000, Körner and Paulsen 2004). Although mass elevation in absolute terms is small on islands compared to the mainland, it nevertheless has a substantial effect among islands, independently explaining between about 40 and 50% of the variance (Irl et al. 2016).

Conclusion

High elevation islands, such as La Palma, are highly useful model systems and are important for conserving global biodiversity owing to their (often threatened) endemic species. Disturbances strongly influence the distributional patterns of diversity and endemism on local scales. I suggest a two-fold approach to contain the severe effects of introduced herbivores. For short-term protection fenced enclosures have proven to be effective, however for long-term preservation only strict population control and ultimately total eradication is mandatory, if politically feasible. On a regional scale, topography and climate shape diversity and endemism. However, hotspots of endemic richness and endemism, two important measures of diversity, do not generally overlap, with implications for nature conservation. If the

aim is to protect all facets of diversity, it is important to simultaneously use different measures of diversity – a ‘diversity of diversity measures’ so to say. This might be a predicament of nature conservation agencies in deciding where to allocate their (often) limited resources (Stohlgren et al. 2005). Endemism, as an important aspect of diversity, has a spatial pattern within an island, particularly by increasing with elevation. This increase with elevation is a general phenomenon highlighting the importance of high elevation insular systems for conservation. Future changes, especially interactive effects of climate change and land use change, constitute a considerable threat to island systems and endemic species – a topic which will need intensive future research and a solid scientific base to accurately assess extinction risks and ecosystem threats.

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