

Trait-dependent effects of biotic and abiotic filters on plant regeneration in Southern Ecuador

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Summary

Tropical forests have always fascinated scientists due to their unique biodiversity. However, our understanding of ecological processes shaping the complexity of tropical rainforests is still relatively poor. Plant regeneration is one of the processes that remain understudied in the tropics although this is a key process defining the structure, diversity and assembly of tropical plant communities. In my dissertation, I combine experimental, observational and trait-based approaches to identify processes shaping the assembly of seedling communities and compare associations between environmental conditions and plant traits across plant life stages. By working along a steep environmental gradient in the tropical mountains of Southern Ecuador, I was able to investigate how processes of plant regeneration vary in response to biotic and abiotic factors in tropical montane forests.

My dissertation comprises three complementary chapters, each addressing an individual research question. First, I studied how trait composition in plant communities varies in relation to the broad- and local-scale environmental conditions and across the plant life cycle. I measured key traits reflecting different ecological strategies of plants that correspond to three stages of the plant life cycle (i.e., adult trees, seed rain and recruiting seedlings). I worked on 81 subplots along an elevational gradient covering a large climatic gradient at three different elevations (1000, 2000 and 3000 m a.s.l.). In addition, I measured soil and light conditions at the local spatial scale within each subplot. My findings show that the trait composition of leaves, seeds and seedlings changed similarly across the elevational gradient, but that the different life stages responded differently to the local gradients in soil nutrients and light availability. Consequently, my findings highlight that trait-environment associations in plant communities differ between large and small spatial scales and across plant life stages.

Second, I investigated how seed size affects seedling recruitment in natural forests and in pastures in relation to abiotic and biotic factors. I set up a seed sowing experiment in both habitat types and sowed over 8,000 seeds belonging to seven tree species differing in seed size. I found that large-seeded species had higher proportions of recruitment in the forests compared to small-seeded species. However, small-seeded species tended to recruit better in pastures compared to large-seeded species. I showed that high surface temperature was the main driver of differences in seedling recruitment between habitats, because it limited seedling recruitment of large-seeded species. The results from this experiment show that pasture restoration requires seed addition of large-seeded species and active protection of recruiting seedlings in order to mitigate harmful conditions associated with high temperatures in deforested areas.

Third, I examined the associations between seedling beta-diversity and different abiotic and biotic factors between and within elevations. I applied beta-diversity partitioning to obtain two components of beta-diversity: species turnover and species richness differences. I associated these components of beta-diversity with biotic pressures by herbivores and fungal pathogens and environmental heterogeneity in light and soil conditions. I found that species turnover in seedling communities was positively associated with the dissimilarity in biotic pressures within elevations and with environmental heterogeneity between elevations. Further, I found that species richness differences increased primarily with increasing environmental heterogeneity within elevations. My findings show that the associations between beta-diversity of seedling communities and abiotic and biotic factors are scale-dependent, most likely due to differences in species sorting in response to biotic pressures and species coexistence in response to environmental heterogeneity.

My dissertation reveals that studying processes of community assembly at different plant life stages and spatial scales can yield new insights into patterns and processes of plant regeneration in tropical forests. I investigated how community assembly processes are governed by abiotic

and biotic filtering across and within elevations. I also experimentally explored how the process of seedling recruitment depends on seed size-dependent interactions, and verified how these effects are associated with abiotic and biotic filtering. Identifying such processes is crucial to inform predictive models of environmental change on plant regeneration and successful forest restoration. Further exploration of plant functional traits and their associations with local-scale environmental conditions could effectively support local conservation efforts needed to enhance forest cover in the future and halt the accelerating loss of biodiversity.

1. Introduction

1.1. Plant diversity and ecological processes in the tropics

Tropical forests have always fascinated ecologists, because they harbour an extremely high diversity of plant species. The majority of tree species ever described by botanists belong to tropical forests, whereas thousands of undescribed species are still supposed to be discovered (Cazzolla Gatti et al., 2022). This outstanding species richness in the tropics is reflected also in the prominent diversity of forms and functions hardly comparable to any other ecosystem worldwide (Carson & Schnitzer, 2008). Unsurprisingly, these diversity phenomena were a subject of interest of Darwin, Wallace and Humboldt – the great ecologists of the XIX century, whose ideas have inspired generations of scientists (Diniz-Filho, 2022; Hortal et al., 2023; Violle et al., 2007). Importantly, as tropical plants constitute a vast number of all existing plant species globally, they are entangled in manifold ecological processes, including mutualistic and antagonistic interactions among diverse taxa (Carson & Schnitzer, 2008; Slik et al., 2015; Tietje et al., 2023).

Our understanding of ecological processes in tropical ecosystems has steadily been increasing (Carson & Schnitzer, 2008), nonetheless many processes still remain understudied (Carvalho et al., 2023). One of these key ecological processes that has received little attention so far is plant regeneration (Larson & Funk, 2016; Török et al., 2020). Plant regeneration broadly refers to the steps that a plant undertakes to successfully reproduce (see Box 1 for a Glossary). As such, it involves the sequence from a germinating seed to an established seedling, a surviving sapling and finally, the adult plant (Larson & Funk, 2016). Plant regeneration processes are inherently influenced by the environment in which plants establish and thrive (Díaz & Cabido, 2001; Larson & Funk, 2016). Multiple abiotic and biotic factors may support or limit a plant that seeks to establish in a given community. Abiotic filtering is a process in which abiotic factors (e.g., temperature, precipitation) limit survival and occurrence of an organism, whereas

biotic filtering refers to a process in which other living organisms (e.g. via competition or antagonistic interactions) limit survival and occurrence of an organism (Aicher et al., 2011; Kraft et al., 2015; Larson & Funk, 2016). These processes define the assembly of plant communities (see Box 1) and occur at different temporal and spatial scales (HilleRisLambers et al. 2012; Kraft et al., 2015).

The initial stages of the plant life cycle including plant reproduction and seedling establishment have often been overlooked by previous studies, although these early steps can trigger changes in plant species composition across space and time (Garwood et al., 2023; Moles & Westoby, 2004b; Usinowicz et al., 2017). Thus, extensive studies on plant regeneration are required to understand current diversity patterns and to better predict future changes in ecosystems. In particular, field studies in different tropical ecosystems and regions may be vital for further scientific progress given the significant differences in geographical conditions and evolutionary history across the continents (Dalsgaard et al., 2021; Tietje et al., 2023). For instance, unravelling trait-related aspects of plant regeneration and community assembly might be helpful to better understand plant diversity in a changing world (Báez et al., 2022; Larson & Funk, 2016; Usinowicz et al., 2017).

1.2. Plant functional traits

Functional traits are the morphological, physiological, biochemical and other characteristics of an individual which provide quantitative or qualitative information on its performance and fitness (de Bello et al., 2010; Violle et al., 2007). The concept of functional traits (see Box 1) has become a powerful tool to quantify plants' responses to biotic and abiotic filtering and to precisely measure morphological variation in a community across taxonomic, spatial and temporal scales (De Bello et al., 2010). Plant functional traits can describe trade-offs in ecological strategies and functional linkages in plant communities in relation to abiotic and

biotic filtering (Adler et al., 2014; Lavorel & Garnier, 2002). For instance, seed size is a morphological trait associated with plant regeneration and it can be shaped by both, abiotic and biotic factors (Acosta-Rojas, Barczyk, Espinosa, Tinoco, et al., 2023; Rosbakh et al., 2022). For instance, plants producing small seeds invest in high numbers of seeds and therefore are more likely to disperse their seeds, but usually have a lower recruitment probability than plants producing large seeds (Moles et al., 2004; Moles & Westoby, 2006). Selected functional traits have been measured at several locations globally yielding insightful concepts such as the leaf economics spectrum (Wright et al., 2004). For example, plants tend to invest in either long-lived, “conservative” or nutrient-rich, “acquisitive” leaves corresponding to a resource allocation trade-off. The concept of the leaf economics spectrum was adapted by Díaz et al. (2016) into a global comparative study describing different growth forms and ecological groups of plants. Likewise, such comparisons can be expanded to other traits including roots, seeds and seedlings (Díaz et al., 2016; Umaña et al., 2021; Weemstra et al., 2016).

Disentangling the impact of abiotic and biotic factors on different functional traits has been proposed as a framework to better understand plant diversity and its importance to ecosystems (Lavorel & Garnier, 2002). For instance, it can be remarkably valuable for studying diverse ecosystems, in which the species identification remains challenging. In principle, functional traits should be described at the level of an individual, but in many cases their assessment can be statistically extrapolated to the level of populations, species or communities (Miller et al., 2019; Violle et al., 2007). For example, the measure of functional diversity can describe how different traits are distributed in a given community (de Bello et al., 2013). In turn, functional composition (see Box 1) informs about the presence and dominance of particular plant traits in a community (Díaz & Cabido, 2001). As such, functional trait composition is supposed to reflect the optimal ecological strategy in a community (Báez et al., 2022; Lavorel & Garnier, 2002). For instance, the production of fleshy fruits in certain plant clades reflects an ecological

strategy related to mutualistic interactions with animals (Bolmgren & Eriksson, 2010; Nevo et al., 2019; Onstein et al., 2017). To capture the prevalence of key ecological strategies of plants in a community, relevant traits can be quantified by using community-weighted means (Miller et al., 2019). At the same time, plant functional traits can effectively describe the distribution and prevalence of optimal ecological strategies across environmental gradients or over different time periods (Adler et al., 2014; Lavorel & Garnier, 2002; Moles & Westoby, 2006; Westoby, 1998). It means that a trait-based approach can be used to study the effects of abiotic and biotic filters on the community assembly of plants (Bruehlheide et al., 2018; Kunstler et al., 2016).

1.3. Environmental filtering and biotic interactions

Community assembly of plants (see Box 1) can be strongly mediated by functional traits, but the processes that cause changes in the community can be also directly associated with environmental filtering (Bruehlheide et al., 2018; Kraft et al., 2015). Environmental filtering has been defined as a key process that reduces the probability of survival or occurrence of an organism under certain environmental conditions (Kraft et al., 2015). Because abiotic factors primarily determine how plants can adapt to different environments and whether they are able to thrive in them (Bruehlheide et al., 2018), environmental filtering is supposed to determine species and trait composition across different scales while zooming from a global into a local perspective (Bruehlheide et al., 2018; Díaz et al., 1998; Wilkes et al., 2020). The global assessments of plant functional traits has supported this hypothesis, however, trait-environment associations are by far more complex than they primarily seem (Violle et al., 2007). For instance, variation in leaf traits can be largely explained by climate, as values of given traits can shift across climatic gradients, but it also responds to local abiotic factors (Báez et al., 2022; Bruehlheide et al., 2018; Schmitt et al., 2020; Wright et al., 2004).

Biotic filtering has been considered as a process in which organisms are filtered by both antagonistic and mutualistic biotic interactions (Schemske et al., 2009; Švamberková & Lepš, 2020; Tingstad et al., 2015). In fact, biotic enemies and mutualistic interactions have been considered essential for the high diversity of plants in the tropics (Dalsgaard et al., 2021; Janzen, 1970). For instance, antagonistic interactions, such as herbivory, are known to promote the high diversity of plants across tropical forests by reducing their abundance and therefore enhancing competition between species (Bagchi et al., 2014). In addition, the tight relationship between fleshy-fruited plant species and seed-dispersing frugivores has been a prominent example of mutualism, which universally occurs across all tropical regions (Wang & Smith, 2002). In conclusion, biotic interactions are particularly important at early plant life stages, because their diversity is vital for seed dispersal and regeneration processes (Auffret et al., 2017; Wang & Smith, 2002).

Essentially, the interplay of biotic and abiotic factors is responsible for the composition and the persistence of plant communities (Bagchi et al., 2014), even if these features change over time and differ in space (Báez et al., 2022; Pereira Martins et al., 2020; Werner & Homeier, 2015). There is a lot of evidence that environmental conditions at regional and local scales can filter plant communities with different strength (Buckley & Puy, 2022; Messier et al., 2010) and that different groups of plants respond to them more or less sensitively (Donohue et al., 2010; Muehleisen et al., 2020; Rissanen et al., 2023). Given the variation in such effects on plant communities, it might be important to discern the effects of broad-scale from local-scale processes (Buckley & Puy, 2022; Díaz et al., 1998; Wilkes et al., 2020). For instance, climatic conditions can determine species composition in general, but the topography with its environmental heterogeneity also matters for local plant diversity (Báez et al., 2022; Bruelheide et al., 2018; Buckley & Puy, 2022). Here, the concept of beta-diversity (see Box 1) can be a valuable tool to disentangle scale-dependent mechanisms of community assembly (Arellano,

Tello, et al., 2016). Beta-diversity quantitatively describes how communities differ between each other (Legendre, 2014). Multiple studies have explored plant beta-diversity indices across environmental gradients, because they offer a powerful framework to explain plant-environment associations across different spatial and temporal scales (Legendre & Condit, 2019; Song et al., 2019; Wilkes et al., 2020).

1.4. Plant regeneration

The majority of plants reproduce by yielding seeds, which germinate, establish and grow to finally develop into another fertile individual (Larson & Funk, 2016; Wang & Smith, 2002). In consequence, each individual plant is supposed to resist numerous abiotic and biotic filters before it reaches maturity (Larson & Funk, 2016). In particular, woody plant species face various challenges across their ontogeny, since they are characterised by larger sizes and typically more complex life history if compared to non-woody plants (Dayrell et al., 2018; Westoby, 1998). So far, there have been only a few studies from tropical forests comparing trait-dependent effects of environmental factors on different stages of the plant life cycle (Falster et al., 2018; Larson & Funk, 2016; Visser et al., 2016). One of these studies revealed that key traits, such as seed mass and wood density, result in complex multi-trait interactions within demographic processes inside a tropical lowland forest (Visser et al., 2016). In another study, the functional traits are proposed as a framework to predict how different traits across the life cycle are expected to influence plant growth under differing light conditions (Falster et al., 2018).

Given the long life span of a single tree and that each plant faces different challenges over the ontogeny, plant communities are supposed to respond to environmental filtering and biotic interactions with different intensity depending on their life stage or ecological strategy (Falster et al., 2018; Larson & Funk, 2016; Visser et al., 2016). One study showed that nonwoody plants

at the seedling stage appear to be more affected due to environmental filtering in the understory if compared to seedlings of woody plants in tropical forests (Murphy et al., 2016). Therefore, to better understand community assembly processes it seems important to differentiate what are the effects of abiotic and biotic factors on trait and species composition at different spatial and temporal scales (Aicher et al., 2011; Legendre & Condit, 2019). For instance, seedlings and adult plants respond differently to environmental filtering, because of the differences in size and ecological strategies (Dayrell et al., 2018; Visser et al., 2016). Hence, a seedling stage of a tree might be restricted to only the first year of the plant's life, but passing through multiple abiotic and biotic filters during that time seems inevitable for seedlings in order to establish into a future tree community. The integrative approach embedding different stages of plant regeneration is vital to predict changes in future plant communities (Falster et al., 2018; Westoby et al., 2022).

Field observations and in-situ experiments have been widely used to study plant regeneration in tropical forests (Kraft et al., 2015). The observation-based approach has been often used to model multiple species' responses to environmental filtering and biotic interactions, while field experiments can precisely identify the mechanisms that influence how plant reproduce and communities assemble (Bagchi et al., 2014; Larson & Funk, 2016). Seed sowing experiments are an efficient tool to study ecological response and potential of different species to restore forest ecosystems (Howe et al., 2010; Khurana & Singh, 2001; Turnbull et al., 2000). Studying seedling establishment and the causes of mortality can provide insights into regeneration processes of species which differ in their traits, phylogeny and distribution. Similarly, the experiments that control biotic pressures have contributed to understanding the associations between regenerating plants and their enemies which significantly shape species and trait composition in tropical forests worldwide (Bagchi et al., 2010, 2014; Coley & Kursar, 2014; Williams et al., 2021).

1.5. Tropical mountains

Several montane forests have been considered biodiversity hotspots, but one of the most diverse are the tropical montane forests of the Andes in Ecuador, Peru and Colombia (Myers et al., 2000; Rahbek et al., 2019). The Andes with their complex topography have experienced intense species diversification in the past geological eras and have been called the cradle of biodiversity (Antonelli et al., 2009; Rahbek et al., 2019). The diversity of plants, birds, mammals and numerous other taxa in the tropical Andes and the Amazon is the highest in the world (Antonelli et al., 2018). The flora of Ecuador is estimated to count several thousands of vascular plants, including over 2000 woody plant species (Rahbek et al., 2019). Also, the endemism rates in the Ecuadorian mountains are exceptionally high (Rahbek et al. 2019, Kessler and Kluge, 2008). Nonetheless, this incredible diversity has not been sufficiently explored, and scientists call for an urgent action to protect and study these ecosystems to enhance the understanding of ecological processes shaping this diversity (Beck, 2008; Cueva-Ortiz et al., 2020; Homeier et al., 2013).

Tropical mountains are particularly suitable to study ecological processes because of their elevational gradient. Elevational gradients offer an unique laboratory to study the environmental change and ecological interactions due to their relative climatic stability and geographical proximity (Malhi et al., 2010). Studies across long elevational gradients provide a framework to compare the distribution patterns of biotic interactions, trait composition and plant diversity, and to assess the extent to which they are shaped by environmental conditions (Albrecht et al., 2018; Báez et al., 2022; Feeley et al., 2011; Hulshof et al., 2013; Nowak et al., 2019). There are at least three reasons why tropical mountains are suitable to study ecological processes. First, the climatic and other abiotic conditions typically change between elevations approximating many environmental gradients (Hulshof et al., 2013; Salinas et al., 2011). Second, the closely standing forests are supposed to resemble each other in terms of the species

composition and phylogenetic diversity, because of their joint natural history constrained to similar geographical regions (Malhi et al., 2010; Rahbek et al., 2019; Tietje et al., 2023). Lastly, studying ecological processes across elevations gives the unique insight into scale-dependent processes governing community assembly and the diversity of plants (Browne & Karubian, 2016; Cohen et al., 2016; Kemp et al., 2017; Puglielli & Pärtel, 2023). The large elevational gradients and topographical complexity of tropical mountains have promoted high speciation rates and diversity in these ecosystems (Dalsgaard et al., 2021; Mittelbach et al., 2007; Rahbek et al., 2019). These features have also contributed to their conservation in many countries, where the last remaining forests have persisted along steep mountain ridges (Rahbek et al., 2019).

Tropical forests are facing many challenges worldwide due to human activities (Uriarte & Chazdon, 2016). Despite their huge diversity, tropical montane forests are currently threatened more than ever, with accelerating deforestation rates in many regions (He et al., 2023) and a status that assigns them to the most threatened ecosystems on Earth (He et al., 2023; Rahbek et al., 2019). The conservation and protection of tropical montane forests have been postulated by the scientific community in past decades (He et al., 2023; Myers et al., 2000). That is why the investigation of tropical mountains is crucial to gain insights into plant diversity and related ecological processes. For example, field experiments investigating the restoration potential of native species and their resilience to environmental change have sparked many incentives concerning deforested habitats (Cole et al., 2011; Holl et al., 2000, 2017).

Box 1. Glossary

Beta-diversity – the measure of dissimilarity in species composition between two sampling sites. The idea of beta-diversity as a measurement of ecological dissimilarity was introduced by Whittaker (1972), and later developed into several quantitative metrics, such as Jaccard dissimilarity or species turnover and richness differences (Legendre 2014).

Community assembly – the processes by which the species composition of a community is determined (Mittelbach 2015). There are two key mechanisms underpinning community assembly, namely species sorting, which means that species intensively replace each other in a community, and species coexistence, which refers to the processes that support or limit the number of species in a community (Leibold et al. 2004, Kraft et al. 2015).

Environmental filtering – processes by which environmental conditions select those species that are capable to survive and persist in a given environment (Kraft et al. 2015).

Functional trait – any trait which impacts individual performance and fitness of a plant indirectly via its effects on growth, reproduction and survival (Violle et al. 2007).

Functional trait composition – the functional component of biodiversity, defined as the presence and relative abundance of certain functional traits in a community. Individuals with similar traits tend to share similar responses to the environment (e.g. temperature or nutrients), and have similar effects on ecosystem functioning (e.g. productivity or nutrient cycling, Díaz & Cabido 2005).

Plant regeneration – the process whereby mature individuals of a plant population are replaced by new individuals of the next generation through seed production, seed dispersal, germination, seedling emergence and survival. Each of these steps has the ability to influence plant population and community dynamics (Grubb 1977, Larson & Funk 2016);

2. Dissertation structure and research questions

In my dissertation, I investigated the interactions between plants at different life stages and abiotic and biotic factors at different spatial scales and in different habitats in the tropical mountains of south Ecuador. I explored scale-dependent processes of plant community assembly with the use of different approaches including plant functional traits, a seed sowing experiment and beta-diversity partitioning. I posed three research questions concerning plant-environment interactions to gain insight into plant community assembly inside tropical montane forests. The first question (Q1) aims at answering to what extent environmental conditions shape the trait composition of leaves, seeds and seedlings between and within elevations in tropical montane forests. The second question (Q2) explores the effects of seed size on seedling

recruitment of five native tree species in pastures and forests. Finally, the third question (Q3) describes the scale-dependent effects of biotic pressures and environmental heterogeneity on the beta-diversity of seedling communities in tropical montane forests. To address these questions, I combined a trait-based approach with extensive field observations and a field experiment. I further calculated community-weighted means of traits and applied beta-diversity partitioning. I structured my dissertation into three original research articles, of which one is already published (Barczyk et al. 2023; Appendix A3) and two are under revision (Appendices A1 and A2).

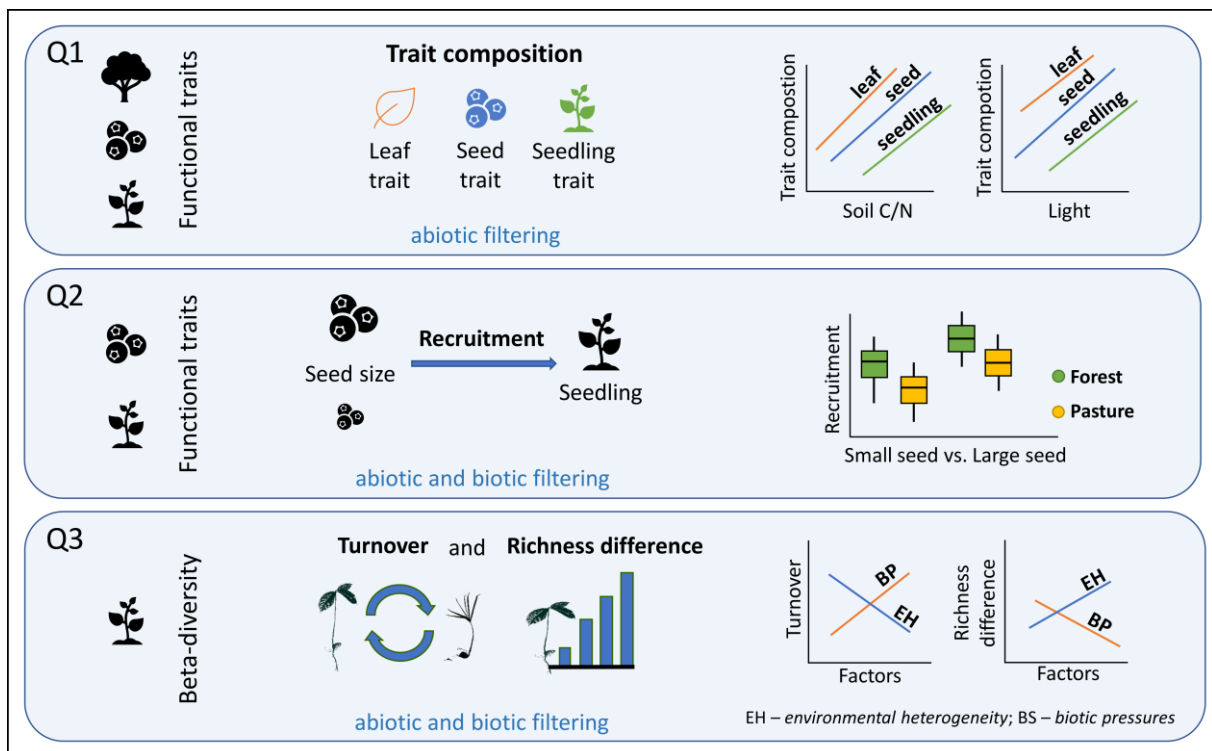


Figure 1. A schematic overview of the dissertation structure. My three research questions aim at studying the associations between plant regeneration and the abiotic and biotic environment in tropical montane forests in Southern Ecuador. Q1: How does trait composition of leaves, seeds and seedlings change across elevations and environmental gradients? Q2: How does seedling recruitment of small- and large-seeded species differ between forests and pastures? Q3: How do biotic and abiotic factors shape beta-diversity of seedling communities? The silhouettes on the left depict the plant life stage(s) studied in the questions (adult trees, seeds and seedlings, respectively). Response variables for each research question are shown in the centre, predictor variables are shown on the right side of each window. To test the importance of abiotic filters on trait composition (Q1) I studied trait-environment associations (coloured lines) across and within elevations in tropical montane forests at 1000, 2000 and 3000 m a.s.l. To verify how seedling recruitment depends on seed size (Q2) I quantified seedling recruitment in a seed sowing experiment in forests and pastures (boxes) using two large-seeded and three small-seeded plant species. To test the associations between beta-diversity components and the environment (Q3), I partitioned beta-diversity of seedling species and measured environmental heterogeneity (blue lines) and biotic pressures (orange lines) within and between elevations in tropical montane forests along the elevational gradient.

2.1. How does trait composition of leaves, seeds and seedlings change across environmental gradients? (Question 1)

I studied how trait composition changes in plant communities at different plant life stages in relation to broad- and local-scale environmental conditions. I measured key traits reflecting different ecological strategies of plants, which correspond to specific stages of the plant life cycle (specific leaf area of adult trees, seed mass in seed rain and initial seedling height of recruiting seedlings). I worked on 81 subplots along an elevational gradient covering large climatic gradients and also measured environmental conditions at all study plots. Subsequently, I associated traits describing ecological strategies of adult trees, seed rain and recruiting seedlings across elevations at the large spatial scale and then soil and light conditions within elevations at the small spatial scale. First, I expected that all selected traits would be similarly filtered across large elevational gradients (Homeier et al., 2021; Rosbakh et al., 2022). Second, I hypothesized that specific leaf area, seed mass and initial seedling height would be positively associated with soil fertility within elevations (Foster et al., 2011; Hodgson et al., 2011; Umaña et al., 2021), while specific leaf area, seed mass and initial seedling height would be differently associated with light availability within elevations (Acosta-Rojas, Barczyk, Espinosa, Tinoco, et al., 2023; Baraloto et al., 2005). In this work I aimed at investigating the mechanisms of environmental filtering at different spatial scales and across the plant life cycle, which are supposed to matter for community assembly processes from a broader perspective of plant regeneration (Auffret et al., 2017; Visser et al., 2016).

2.2. How does seedling recruitment of small- and large-seeded species differ between forests and pastures? (Question 2)

I set up an experiment in the forest and in pastures in which I sowed over 8,000 seeds belonging to seven tree species. I aimed to compare the effect of the seed size on seedling recruitment in two contrasting habitat types and relate them with abiotic and biotic factors. I hypothesised that

seedlings growing from large seeds would recruit in higher numbers because they might be more resistant to environmental filtering (Macera et al., 2017; Moles & Westoby, 2004a). Second, I expected that there will be generally more seedlings recruiting in the forest compared to pastures and that large-seeded species would more successfully recruit in the forest due to harsh abiotic conditions in the pastures (Chacón et al., 2016; Eriksson & Eriksson, 1997). Third, I expected that high temperatures and biotic pressures would reduce recruitment success of both groups of seedlings with more pronounced response in small-seeded species (Bagchi et al., 2014; Engelbrecht et al., 2005). In this question, I focused on trait-dependent patterns in seedling recruitment in forests and pastures. I set up a seed sowing experiment to verify to what extent different habitat types and abiotic and biotic factors may be relevant for the selection of species for active reforestation of pastures in tropical mountains.

2.3. How do biotic and abiotic factors shape beta-diversity of seedling communities? (Question 3)

Third, I explored the associations between beta-diversity of seedlings and different abiotic and biotic factors at two different spatial scales. I studied seedling communities along the elevational gradient in the field and measured environmental conditions and biotic pressures on seedlings at the subplot level. I applied beta-diversity partitioning to obtain species turnover and species richness differences, which I then associated with two variables important for seedling recruitment: biotic pressures and environmental heterogeneity. In this study, I expected that species turnover would be associated with biotic factors within elevations (Bagchi et al., 2014) and with abiotic factors between elevations (Arellano, Tello, et al., 2016; Wallis et al., 2021). I also expected that richness differences would be associated with abiotic factors within elevations (Cornwell & Grubb, 2003; Johnson et al., 2017). By searching scale-dependent relationships of beta-diversity and biotic or abiotic factors I aimed to identify the main processes

of community assembly among seedling communities at the early recruitment phase – one of the rarely investigated stages of the plant life cycle.

3. Study system and study design

I conducted a field experiment and a one-year observation of seedling communities in the area of Podocarpus National Park and San Francisco Reserve in Southern Ecuador (Fig. 2). The Podocarpus National Park spans over 1400 km² and is situated along a large elevational gradient between 900 m a.s.l. and 3500 m a.s.l. The San Francisco Reserve (Reserva Biologica San Francisco) is located at the edge of the Podocarpus National Park at approximately 2000 m a.s.l. next to the main road between Loja and Zamora and above the San Francisco River, embedding also the research facility of Estación Científica San Francisco (ECSF). The whole area belongs to one of the most diverse biodiversity hotspots worldwide (the Tropical Andes hotspot; Myers et al. 2000). It harbours an extraordinary diversity of vascular plant species (>45,000 sp.) of which a high proportion are endemic to the area (>20,000 sp.).

Elevational gradients in the Andes have become an ideal setting to study ecological processes due to their accessibility, biodiversity and topographic complexity (Báez et al., 2022; Malhi et al., 2010; Wallis et al., 2021). The elevational gradient of Podocarpus National Park spans over 2000 m and has already been studied in research units for decades (Beck, 2008; Bendix et al., 2021). The study area comprises several ecosystems (Beck, 2008). While natural, primary forests and high-elevation paramos are well-protected by the national park and the reserve, the adjacent areas have been deforested and transformed into cattle pastures (Adams et al., 2022; Beck, 2008). These ecosystems differ not only in their general appearance, but also in species composition, associated with a high species turnover across elevations and habitats (Homeier et al., 2010; Wallis et al., 2021).

In my studies, I have worked along an elevational gradient at three elevations (i.e., 1000, 2000 and 3000 m a.s.l.) and in two types of habitats (i.e., forests and pastures; see Figure 2). The study site along the Bombuscaro river (around 1000 m a.s.l.) is covered by evergreen premontane forest. Average temperature is about 20°C and precipitation reaches up to 2500 mm per year. The pasture plots are situated on the steep slopes among forest patches in the northern part of the town of Zamora.

The San Francisco Reserve and the ECSF research station are located at 2000 m a.s.l. (Beck et al., 2020). The reserve spans between the road and the slopes of the main ridge of the Podocarpus NP and is covered by evergreen montane forests. The reserve has been intensively studied in last decades (Bogner et al., 2016; Gradstein et al., 2010). Over 1,200 species of vascular plants have been found in the reserve (Beck, 2008; Homeier et al., 2010). The average temperature reaches about 15.5°C and the precipitation reaches over 2300 mm annually. The steep slopes experience frequent disturbances mainly caused by large-sized landslides (Dislich & Huth, 2012). On the opposite side of the San Francisco valley the mountain slopes have been converted into cattle pastures (Adams et al. 2022; Homeier et al., 2013).

The high-elevation study site, Cajanuma, is placed just below the highest peaks of the Podocarpus NP, at 3000 m a.s.l. This area is covered with evergreen upper montane forest. The temperature in Cajanuma is around 10°C and the precipitation usually exceeds 4000 mm per year. The areas between Loja and the entrance to the national park are settled and the adjacent forests have been converted to pastures.

My study was a part of the research project “RESPECT” funded by the German Research Foundation (DFG). I conducted my field research using the joint plot design established by the RESPECT project along the elevational gradient (Bendix et al., 2021), with nine plots located in forest and nine plots located in pastures (n = 18), each covering 1 ha (Figure 3). The term

“plot” refers to a marked area used by several subprojects in which multiple experiments and observations have been conducted to provide a coherent study framework (Bendix et al., 2021).

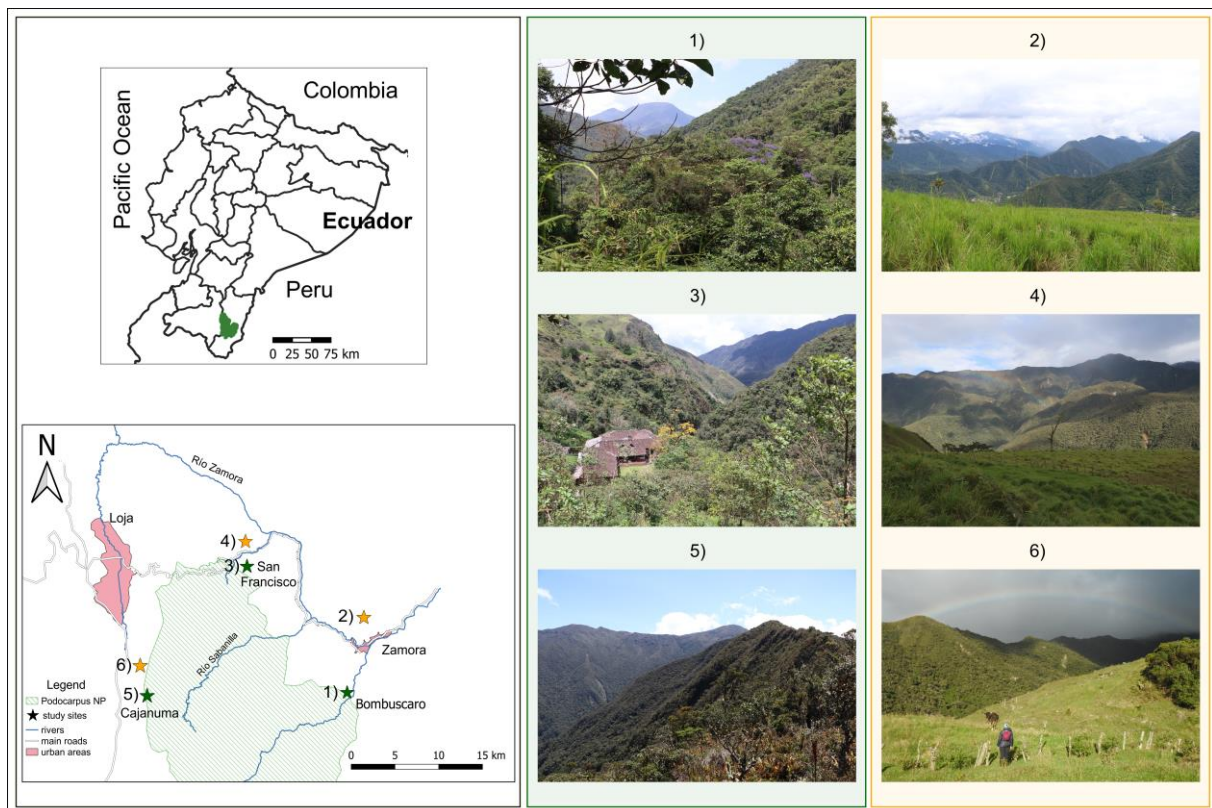


Figure 2. Study system located along the elevational gradient of the tropical Andes in Southern Ecuador. Map of Ecuador (top left) indicates the study area (dark green colour). Map of the study area (bottom left) shows the protected areas of the Podocarpus National Park and San Francisco Reserve (light green colour). The green stars represent study sites in the forest, yellow stars show study sites in the pastures. Photographs show: 1) the premontane rainforest and 2) the pastures close to Zamora both located at around 1000 m a.s.l.; 3) the San Francisco Research Station surrounded by the evergreen montane forests and 4) the pastures close to San Francisco both located at around 2000 m a.s.l.; 5) the upper montane forest and 6) the high-elevation pastures close to Cajanuma located at around 3000 m a.s.l.

4. Data collection and methodology

4.1. Censuses of seedling communities, adult trees and seed rain

I established two types of subplots to study plant regeneration, one experimental and one observational. In 2018, I set up 54 experimental sowing subplots within the 18 plots in the forest and pastures to study seedling recruitment (Fig. 3). In 2019, I established 81 recruitment subplots to study natural forest regeneration along the elevational gradient. During that 1.5-year

period, I was visiting the study subplots to survey seedlings every four months, take measurements and collect data on abiotic and biotic factors. I completed the experiment and the seedling recruitment censuses in July 2020.

All trees inside the forest plots have been surveyed by Jürgen Homeier, who provided information about species occurrence and their abundance. To measure seed rain, our subproject installed regularly distributed seed traps within each of the 18 plots. At the end of 2018, I helped my fellow PhD student Diana Carolina Acosta-Rojas to set up 324 seed traps, which captured seed rain for over a one-year period. Eighteen seed traps, filled with a fine mesh, were placed inside each plot with a minimum distance of 20 m from each other. The seed traps were placed around 80 cm above the ground and covered an area of 0.36 m² (0.6 x 0.6 m). The seed traps in pastures (n = 162) were additionally protected with fences to avoid disturbance by cattle. Seed rain samples were collected from each trap every two weeks in the year 2019. The identification and trait measurements of seeds from seed traps were made by Diana Carolina Acosta-Rojas (Acosta-Rojas, Barczyk, Espinosa, Farwig, et al., 2023; Acosta-Rojas, Barczyk, Espinosa, Tinoco, et al., 2023).

4.2. Seed sowing experiment

I conducted an extensive seed sowing experiment in forests and pastures using seeds of seven different tree species. In November 2018, I established 54 sowing subplots regularly distributed across all study plots, 27 in the forest and 27 in pastures. The sowing subplots in the pastures were protected with fences to avoid cattle tramping. Prior to sowing, I cleared the existing vegetation to prepare the ground for the experiment. Inside each sowing subplot, I set up four 1m² sowing units marked with a red string to easily handle the experiment and spot tiny seedlings. I selected seven tree species growing at different elevations (*Ocotea* sp. and *Saurauia* sp. at 1000 m; *Hieronyma fendleri*, *Clusia ducuoides*, *Cecropia angustifolia* and *Tapirira*

guianensis ssp. *subandina* at 2000 m; *Hedyosmum purpurascens* at 3000 m). Given different times of seed ripening, I sowed each species at a different time of the year (between December 2018 and August 2019). I sowed each species at its elevational origin. Depending on the species' seed size, two large seeds or ten small seeds were sown into the patches of fine mesh, nailed to the ground and protected with a metal tube. Given the large variation in seed availability across the species, I set up between 12 and 20 metal tubes (with two large seeds or ten small seeds inside each tube) per species and sowing subplot.

To measure seedling recruitment, I visited the study subplots every four months after sowing until the end of the experiment in July 2020. At the first visit (four months after sowing), I recorded all recruited seedlings and measured their height. By the subsequent visits I recorded mortality/survival on a binary scale (0 means dead and 1 means alive). At each visit, I tagged every new seedling with a plastic tie with a unique number and measured its height. In addition, I photographed seedlings at each visit to document the occurrence and incidence of herbivores' and fungal pathogens' attacks on the seedlings. I calculated two recruitment variables based on the binary data from seedling censuses: seedling establishment and recruitment success. I distinguished these variables according to their temporal component. Seedling establishment was considered as the proportion of seedlings that established over a one-year-period at each subplot (including those that did not survive until the end of the experiment) in relation to all seeds sown at the subplot. In turn, recruitment success was a measure of relative seedling success one year after sowing, calculated as the proportion of all encountered (i.e., surviving) seedlings after the experimental time in relation to all seeds sown at the subplots.

At the end of the experiment, I measured below- and aboveground biomass of seedlings after the entire experimental period (up to 10-18 months). Precisely, I harvested the seedlings in the field, brought them to the laboratory and separated roots from stems and leaves (belowground and aboveground tissues). I dried the seedlings in the oven for three days at 60 °C and then

weighed them on an analytical balance (KERN & SOHN GmbH, Germany). In consequence, I obtained the below- and aboveground biomass of each seedling encountered at the final visit. In addition, I derived the root-to-shoot ratio by dividing each seedling's belowground biomass by its aboveground biomass.

4.3. Seedling recruitment censuses

In order to measure natural seedling recruitment, I set up 81 natural recruitment subplots regularly distributed within the plots (nine at each plot) in the forest and in the pastures at all three elevations. In May 2019 I cleared the existing vegetation to better spot recruiting seedlings and to exclude herbal plants which often cover the forest floor. I marked each 1m² subplot with a red string to easily find them at later visits. To measure species composition and species traits, I visited the study subplots every four months over a one-year period. At each of the three censuses, I identified all seedlings and measured seedling height. I tagged each recruiting seedling with a plastic tie with a unique ID to easily find it at the subsequent census. I additionally documented all seedlings by taking photographs to ease species identification.

In addition, I established a reference collection of seedlings including alive and dried specimens and seedlings germinating from seeds harvested at the study plots. To do this, I brought several seeds and seedlings to the research station in order to sow/plant them inside the plastic trays (see photo 7 in Fig. 4) and finally to identify the species with the help of local botanists and identification field guides and books. I also took photographs of the reference specimens and compared them with the seedlings I photographed in the field. Selected photographs of collected seedlings have been published in a field guide on fruits and seeds of Podocarpus National Park (Acosta-Rojas et al. 2022).

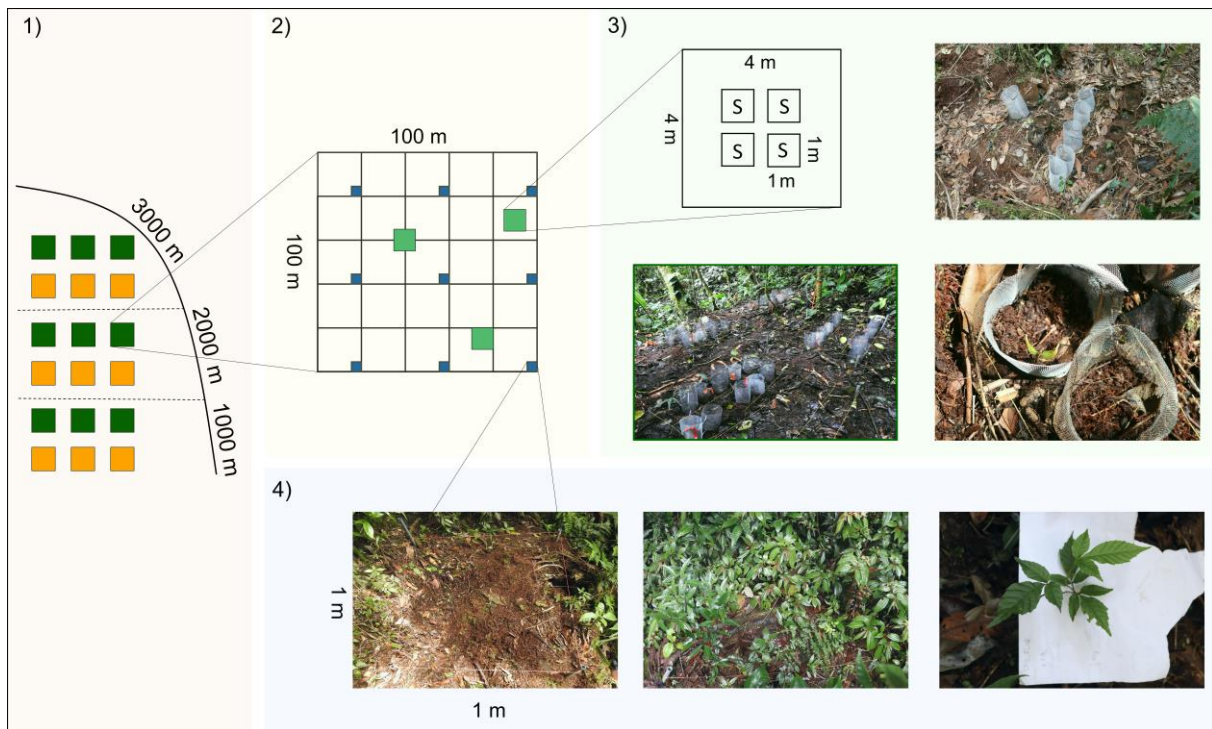


Figure 3. Study design of recruitment experiments and observations. 1) Schematic layout of the study plots in forests and pastures along the elevational gradient. 2) Study plot showing the three experimental sowing subplots (green squares) and nine natural recruitment subplots (blue squares). 3) Study design and photo impressions of the seed sowing experiment: a sowing subplot in the forest, a focus on a sowing unit and metal tubes with recruiting *Tapirira* seedlings. 4) Photo impressions of the natural recruitment observations: after vegetation clearance (left) and one year after clearance (centre), a “reference” photo of a seedling recruiting inside a study subplot (right).

4.4. Plant functional traits

During the recruitment censuses, I measured two functional traits related to seedling growth: initial seedling height and relative growth rate. At each seedling census, I recorded the height of each individual seedling using manual callipers (see photo 6 in Fig. 4). I considered the seedling height as a distance between the stem base and the terminal bud. Because this trait can be highly variable at the individual and species level, I recorded initial seedling height within four months after germination to standardize among species and individuals (Baraloto et al. 2005). Initial seedling height is considered to show the seedling’s capacity to invest into growth after cotyledon development (Baraloto et al., 2005; Westoby et al., 2022). I also calculated the relative growth rate of individual seedlings by taking height measurements of two or three

subsequent censuses. Relative growth rate is a function of seedling growth at given time period (Baraloto et al., 2005), as expressed in the equation: $RGR = \log(\text{seedling height at the census } 2) - \log(\text{seedling height at the census } 1) / \text{number of days}$.

In addition, I compiled plant functional traits of other plant life stages from other sources. In particular, I used seed mass captured in seed rain and specific leaf area of adult trees to answer the trait-related question (Q1). Dry seed mass was measured by Diana Carolina Acosta-Rojas at the level of the individual seeds, all previously collected from seed traps (Acosta-Rojas, Barczyk, Espinosa, Tinoco, et al., 2023) or collected individually from trees (Acosta-Rojas, Barczyk, Espinosa, Farwig, et al., 2023). Specific leaf area is defined as the reverse measure to leaf mass per area (LMA; Wright et al. 2004) calculated as a proportion of leaf area divided by leaf dry mass. Leaf area [cm²] was measured by Jürgen Homeier on five leaves of each individual tree which later were dried in an oven at 60 °C degrees and subsequently weighted on an analytical balance (Homeier et al., 2021).

4.5. Measurements of abiotic and biotic factors

In my study, I measured environmental conditions and biotic pressures to test how abiotic and biotic factors influence the community assembly of seedlings. I recorded canopy openness, soil moisture and photosynthetically active radiation and I assessed pressures of insects and fungal pathogens on seedlings inside all study subplots. Additionally, I recorded soil surface temperature inside the experimental seed sowing subplots.

To quantify canopy openness and canopy closure, I took hemispherical photographs with a Nikon Coolpix 4500 digital camera fitted with a Nikon FC-E8 fish-eye converter. I took photographs at the height of about 70 cm above the ground in the mornings with overcast sky. To process the photographs, I utilised the Gap Light Analyzer ver. 2.0 (1999, Canada/USA).

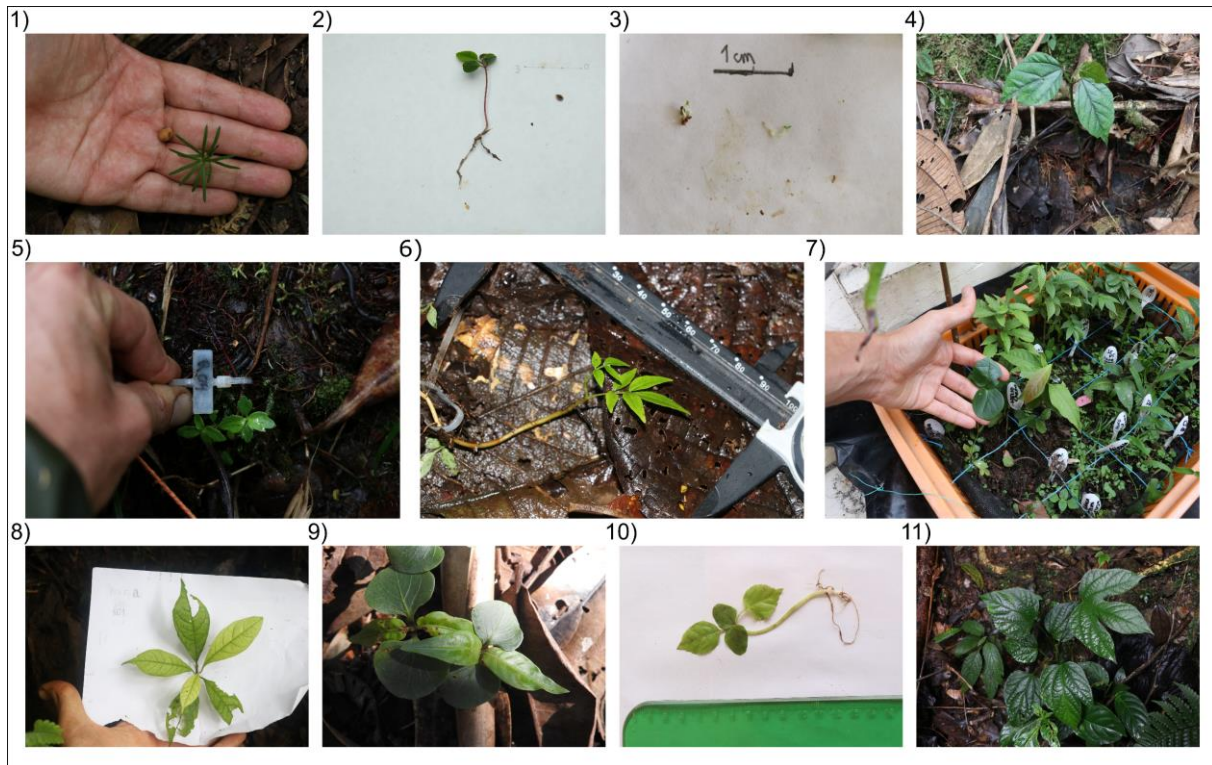


Figure 4. Diversity of seedlings in tropical montane forests in Southern Ecuador. 1) a seed and a seedling of a rare gymnosperm species – *Prumnopitys montana*; 2) a seedling of an abundant species in the plots at 2000 m – *Hieronyma fendleri*; 3) a tiny seedling of a small-seeded pioneer species at 2000 m – *Alzatea verticillata*; 4) a seedling of a rare large-seeded species at 2000 m – *Pourouma montana*; 5) a cable tie used to mark seedlings, here seedlings of *Hedyosmum* sp. at 3000 m; 6) height measurement of a seedling (*Paullinia* sp.) with a manual calliper; 7) seedlings growing in a basket as a "reference collection"; 8) a seedling of *Helicostylis* sp. damaged by herbivores; 9) a seedling of *Psychotria* sp. attacked by fungal pathogens; 10) a four-months-old seedling of *Schefflera* sp. at 2000 m; 11) a one-year-old seedling of *Schefflera* sp. at 2000 m.

I calculated canopy closure as the percentage of canopy covered by vegetation [0-100%] based on the photographs of all study subplots. I also obtained a compatible index of canopy openness by subtracting 100 minus canopy closure. I measured soil moisture with a manual tensiometer (SM150 Kit, Delta-T Devices Ltd., UK). by taking five single measurements inside each subplot during the rainy and less rainy season. Soil moisture was measured as a percentage [0-100%] of water in the soil organic layer (approximately 5 cm deep). I also measured photosynthetically active radiation (PAR) across all study subplots with a LI-1400 Data Logger (LI-COR Biosciences, Nebraska, USA). Finally, to assess the soil surface temperatures in the sowing subplots, I installed 54 iButtons (Maxim/Dallas Semiconductor Corp., Texas, U.S.A)

which measured soil temperature [$^{\circ}$ Celsius] every four hours at a soil depth of about 2 cm. With these records, I calculated two measures related to surface temperature: mean daily mean surface temperature and mean daily maximum surface temperature.

Given that biotic interactions are crucial for plant establishment (Bagchi et al., 2014; Williams et al., 2021), I recorded two biotic variables across my study plots: insect herbivory incidence and fungal pathogen incidence on all established seedlings. To this end, I assessed whether seedlings hold any traces of insect herbivory (incidence of insect herbivory) and traces of fungal pathogens (incidence of fungal pathogens). As insect herbivory I considered any external damage in leaf morphology (e.g. bites or leaf mining), whereas fungal pathogens were identified based on differences of leaf coloration or presence of necrotic spots (Benitez-Malvido & Lemus-Albor, 2005; Muehleisen et al., 2020). Both variables were based on presence/absence data (on a binomial scale) and calculated at the subplot level (separately for the seed sowing experiment and the recruitment census).

Additionally, I used data on abiotic filters from another subproject to answer my first research question, precisely I used the data on soil C/N ratio measured by Velescu et al. (2022). Soil C/N ratio relates to soil fertility because it gives the concentration of soil carbon in relation to the concentration of soil nitrogen. High soil C/N ratios indicate slow turnover of organic matter, resulting in low nitrogen availability to plants (Post et al., 1985; Wilcke et al., 2020).

4.6. Trait-based analyses and beta-diversity partitioning

I integrated trait-based approaches and beta-diversity partitioning at either community or species levels to test for the effects of abiotic and biotic filters on plant regeneration. In my first research question (Q1), I used trait-based analyses to identify patterns in functional trait composition across the environmental gradient. To this end, I calculated community-weighted means (Lavorel & Garnier, 2002) of the key traits measured at the subplot level across all plots.

In consequence, I could compare the mean values of initial seedling height, seed mass and specific leaf area as a function of plant life stage along broad- and local-scale environmental gradients. I scaled all traits separately between and within elevations and tested for an interaction between the life stage and the environmental variables.

In my second research question (Q2), I tested for trait-dependent effects on seedling recruitment of five selected tree species in the forest and in pastures. Precisely, I verified to what extent seedling recruitment is contingent on seed size (large-seeded species with seed mass > 2 g vs. three small-seeded species with seed mass < 2 g; Markl et al. 2012), habitat and different abiotic and biotic variables.

In my third research question (Q3), I applied beta-diversity partitioning according to Legendre (2014). Here, I partitioned the Jaccard dissimilarities between pairs of study subplots located in the forest ($n = 81$ subplots) to calculate the beta-diversity components (i.e., species turnover and richness differences). Simultaneously, I calculated biotic and environmental dissimilarities (i.e. biotic pressures on seedlings and environmental heterogeneity) between the same pairs of forest subplots using Gower's distances. Finally, I averaged the beta-diversity components (i.e., turnover and richness differences) and dissimilarity variables across and within the nine forest plots to test how they relate between each other depending on the spatial scale (i.e., between vs. within elevations).

5. Results and discussion

5.1. Environmental conditions influence trait composition of leaves, seeds and seedlings depending on the spatial scale (Q1)

I aimed to study how the functional trait composition of leaves, seeds and seedling is related to the broad-scale environmental filtering *across* elevations, and to the local-scale environmental

conditions *within* elevations. The community-weighted means of all studied traits decreased with increasing elevation confirming the expected hypothesis. Nevertheless, the community-weighted means of different traits responded differently to the local gradients in soil fertility and light availability. Whereas specific leaf area increased with soil fertility and initial seedling height decreased with light availability, no associations between seed mass and local environmental conditions were detected.

According to our hypothesis, community-weighted means of specific leaf area, seed mass and initial seedling height decreased with increasing elevations. The shift in specific leaf area and seed mass across elevations has previously been detected in tropical and subtropical ecosystems (Duivenvoorden & Cuello A, 2012; Homeier et al., 2021; Hulshof et al., 2013; Rosbakh et al., 2022). Likewise in the mentioned studies, the decrease in community-weighted means of different traits is most likely attributed to the broad-scale environmental filtering related to climatic conditions. I showed that community-weighted means of initial seedling height followed similar patterns, showing that seedlings are generally characterized by small initial seedling height at high elevations. This consistent pattern in trait composition of leaves, seeds and seedlings can be associated with shifts in abiotic and biotic factors along the elevational gradient (Homeier et al., 2021; Peters et al., 2016; Quitián et al., 2018).

My expectation that local effects of soil fertility might be positively associated to all three life stages was only partially consistent with my results. In line with my expectation, specific leaf area was positively associated to soil C/N ratio within elevations. However, I found no effects of soil C/N ratio on seed mass and initial seedling height within elevations. The visible shift in community-weighted mean of specific leaf area with increasing soil C/N ratio reflects a tendency of plants to invest into more acquisitive leaves on fertile soil where there is less limitation in resources (low soil C/N ratio). This significant association has been already reported in studies testing local-scale effects in tropical forests (Hulshof et al., 2013; Schmitt et

al., 2020). In turn, associations between other traits and soil C/N ratio have not been detected in my study. A few studies from lowland tropics reported that soil fertility matters for seed and seedling traits (Foster et al., 2011; Umaña et al., 2021), however it seems that local effects of soil fertility might be secondary in case of seed mass and initial seedling height in tropical montane forests.

Finally, I expected that seedlings under open canopy would be generally more diverse and larger in height due to unlimited access to light. However, initial seedling height decreased with increasing canopy openness within elevations, showing that seedlings with smaller initial seedling height prevail under open canopy. I propose that small-seeded and early-successional species are likely to outnumber large-seeded species with higher seedlings under open canopy. This is in line with other studies which showed that small-seeded pioneer species are more likely to successfully establish in canopy gaps in tropical forests (Baraloto et al., 2005; Dalling et al., 2004; Dalling & Hubbell, 2002). The local effects of canopy openness were not detected for seed mass and specific leaf area, potentially showing that these traits are not sensitive to light availability.

My findings show that trait composition is uniformly filtered across elevations, and that the correlations between different traits and environmental conditions differ depending on the life stage and the environmental factor. This chapter reveals two most important findings. First, I show the consistent shifts in trait composition across elevations of different plant life stages. So far, most studies have identified the effects of environmental conditions on functional traits belonging to one plant life stage, but little is known to what extent traits at different plant life stages are filtered across elevations in tropical montane forests. For instance, Homeier et al. (2021) and Hulshof et al. (2013) revealed that several leaf traits of adult plants differ between elevations, investing more into conservative leaves at highest elevations. A similar outcome was found for several root traits which tend to display distinct strategies along the elevational

gradient (Pierick et al., 2022). My findings show that trait composition of leaves, seeds and seedlings changes gradually with increasing elevations, most likely in relation to intensifying environmental filtering at high elevations.

Second, my study has shown that the effects of soil and light conditions on trait composition within elevations differ for leaf, seed and seedling traits. It means that trait composition of leaves, seed and seedlings responds uniformly to large-scale environmental filtering across elevations, and non-uniformly to local-scale environmental filtering within elevations. Most studies so far have compared the filtering mechanisms on different plant functional traits either at broad spatial scales or at the local spatial scale (Baraloto et al., 2005; Dayrell et al., 2018; Visser et al., 2016). However, my findings demonstrate that studying trait-environment associations at different spatial scales can provide new insights into community assembly of plants in tropical mountains. Furthermore, identification of dissimilar associations between traits and local environmental conditions can inform predictive models on the effects of environmental changes on future forest composition.

5.2. Seedling recruitment depends on seed size and habitat type (Q2)

In this research question, I aimed at answering how seedling recruitment depends on seed size in forest and pastures and which environmental factors are most important for early recruitment. First, I found that seedling recruitment of five species was contingent on the interaction between seed size and habitat. Large-seeded species had higher proportions of recruited seedlings compared to small-seeded species in forests. In turn, small-seeded species tended to recruit better in pastures compared to large-seeded species. Moreover, I showed that high surface temperature and, to a lesser extent, high soil moisture had driven these differences between habitats, because high temperatures limited seedling recruitment of large-seeded species and promoted the recruitment of small-seeded species. The results from this experiment showed

that pasture restoration is more likely to succeed if large-seeded plants are sown, and that seedlings of large seeded-species should be actively protected in order to mitigate harmful effects associated with high temperatures in deforested areas.

First, I expected that large-seeded species would recruit better than small-seeded species and that seedlings generally would recruit more successfully in the forest. According to my expectations, I found that the two large-seeded species are more likely to establish than the three small-seeded species. In contrast to my expectation, I found higher recruitment of small-seeded species in pastures compared to the large-seeded species in the forest. Previous studies reported that seedlings growing from large seeds generally tend to establish better than seedlings growing from small seeds (Bruun & Ten Brink, 2008; Macera et al., 2017; Scarpa & Valio, 2008). Other studies reported that seedlings growing in pastures have generally lower recruitment success compared to natural habitats (Howe et al., 2010; Peña-Domene et al., 2017).

Second, I expected that seedling recruitment of all species would be negatively associated with high surface temperatures and biotic factors, and that in particular small-seeded species would be particularly sensitive to high surface temperatures and biotic factors. I did not find support for this hypothesis, because the effects of abiotic and biotic factors on seedling recruitment were dependent on seed size. Large-seeded species were less likely to establish with increasing surface temperatures in contrast to small-seeded species indicating that large-seeded species are more vulnerable to extreme temperatures. Surface temperatures and soil moisture have been identified as the most influential environmental factors for seedlings, showing that abiotic conditions drive differences in seedling recruitment between habitats (Chacón et al., 2016; Peña-Domene et al., 2017). Previous studies have pointed out that abiotic conditions in pastures drive higher mortality of seedlings (Chacón et al., 2016; Eriksson & Eriksson, 1997). In particular, periodic droughts, associated with high surface temperatures and low soil moisture, are supposed to generally hinder seedling recruitment (Engelbrecht et al., 2005; Howe et al.,

2010) and may have masked the positive effects of large seed size that I found in my study. In my experiment, biotic filters have not been found important for seedling recruitment, potentially because they affect seedling recruitment only moderately or with similar intensity regardless of seed size and habitat differences.

My study provides new insights into seedling recruitment in human modified habitats, as interacting effects of habitat and seed size have rarely been reported so far. A better understanding of the trait-dependent mechanisms of plant regeneration in tropical montane forest can be useful for protection and active restoration of these ecosystems. In particular, identification of main abiotic and biotic filters between different habitats and verification of their importance on seedling recruitment can help to further improve reforestation efforts. In conclusion, my results show that seed sowing experiments in tropical mountains can enhance basic knowledge on regeneration strategies of local species with different traits, but also provide ideas for an active reforestation.

5.3. Biotic pressures and environmental heterogeneity shape beta-diversity of seedling communities depending on the spatial scale (Q3)

I investigated the associations between beta-diversity of seedling communities and environmental variables. I found that species turnover and species richness differences depended on different factors at two different spatial scales. First, I found that species turnover was associated with dissimilarity of biotic pressures (herbivores and fungal pathogens) on seedlings within elevations. Second, I detected a similar pattern between species turnover of seedlings and dissimilarity in environmental factors (canopy closure and soil moisture) between elevations. Finally, I showed that species richness differences were positively associated with increasing environmental dissimilarity within elevations.

In line with my first hypothesis, I demonstrated that species turnover within elevations was significantly associated with biotic dissimilarity based on the incidence of insect herbivory and fungal attacks on seedlings. An analogous association has previously been reported from a tropical lowland forest in which seedling communities had been shuffled due to the exclusion of insects and fungal pathogens (Bagchi et al., 2014). Such relationship between biotic pressures on seedlings and changes in species composition have also been reported from other tropical forests and can most likely be linked to the presence of plant enemies, such as small mammals, insect herbivores or fungal pathogens (Bagchi et al., 2010; Janzen, 1970; Spear et al., 2015; Williams et al., 2021). I further expected that species turnover would be positively associated with environmental dissimilarity between elevations, which was confirmed by my findings. Generally, environmental heterogeneity has been considered a good predictor for biodiversity and species composition (Arellano, Fuentes, et al., 2016; Wallis et al., 2021). My findings support the notion that the dissimilarity in environmental conditions may trigger changes in seedling composition at the large spatial scale.

Finally, I expected that richness differences would be positively associated with environmental dissimilarity within elevations, which I could confirm. Previous studies pointed out the potential association that species richness should be related to environmental heterogeneity (Wallis et al., 2021). Environmental factors are known to shape local-scale patterns in species and trait composition and most likely they can also influence how many species can be found in a given space (Johnson et al., 2017; Schmitt et al., 2020). The described associations between the beta-diversity components and abiotic/biotic factors most likely reflect two mechanisms of community assembly – species sorting and species coexistence – in the seedling community. Species sorting in seedlings occurs due to high biotic pressures at the local spatial scale and heterogenous environmental conditions at the large spatial scale (Bagchi et al., 2014; Peguero et al., 2023). In turn, different species of seedlings are supposed to coexist if the local

environmental conditions are more heterogeneous (Johnson et al., 2017). My findings give insights into community assembly processes of a rarely studied plant life stage in a diverse tropical forest. Importantly, the described associations are highly scale-dependent, which potentially reflects the importance of local and regional effects of environmental factors in tropical mountains.

6. Synthesis and conclusions

6.1. Importance of abiotic and biotic filters for trait-mediated plant community assembly

In my dissertation, I could show that plants in tropical mountains non-uniformly respond to environmental filtering and biotic interactions, with a great variability in relation to their life stage, life history and spatial context. My findings support the assumption that trait-mediated processes are likely to play a major role in community assembly in tropical montane forest similarly to what has been described in lowland ecosystems (Bagchi et al., 2014; Peguero et al., 2023). Essentially, abiotic and biotic factors are likely to shape functional trait composition and species composition in seedling communities in tropical montane forests. This is important, because only a minor proportion of studies on plant-environment interactions reckon this particular stage of plant regeneration (Larson & Funk, 2016). In particular, studying seedling communities in tropical mountains could be expanded to reveal the importance of spatio-temporal dynamics in species sorting and species coexistence across the plant life cycle (Garwood et al., 2023; Usinowicz et al., 2012). Future studies should focus on comprehensive field experiments and long-term inventories, because they could further explore the effects of scale-dependency in trait-mediated community assembly in these topographically heterogeneous and diverse ecosystems.

Additionally, in-depth analyses of the species-specific patterns of plant regeneration and the role of abiotic and biotic filtering might be crucial to detect the drivers of community assembly across scales and habitats. Studying trait-environment associations can help to understand how different tree species representing distinct ecological strategies respond to environmental filtering according to their traits (Bruehlheide et al., 2018; Lebrija-Trejos et al., 2010). Principally, my findings show that abiotic and biotic filters are essential for trait composition and species diversity in tropical montane forests. In addition, the complexity of topography and the dissimilar climatic conditions across elevations in tropical mountains can influence the intensity of the processes inside neotropical montane forests (Báez et al., 2022). That is the reason why the assembly processes turn out to be highly dependent on functional traits and spatial scales in the tropical Andes (Arellano, Tello, et al., 2016). Investigating the effects of environmental filtering on particular plant species could be a way to disentangle those trait- and scale-dependencies. The integration of a species' perspective into community ecology may help to shed light on plant community assembly processes, which so far remain poorly explored in tropical mountains (Hallett et al., 2023; Norden et al., 2009).

6.2. Trait-based approach to study plant regeneration and community assembly

In my dissertation, I used a trait-based approach to obtain a more complete picture of community assembly of the early establishment phases of plants in tropical forests. My studies demonstrate that a combination of field observations and field experiments can be particularly useful to explore community assembly of plants at their early life stages. Studying plant regeneration processes can be particularly challenging, because the investigation of the early phases of plant establishment requires time-consuming observations, a lot of expertise in species identification and ideally should be linked to demographic processes of other life stages (Garwood et al., 2023; Larson & Funk, 2016). Future studies should therefore consider inclusion of the early phases of establishment to better explore the mechanisms driving

community assembly of plants in tropical forests. As presented in my research, studying traits across environmental gradients and plant life stages can effectively contribute to exploring patterns of community assembly in tropical forests. Covering different plant life stages might be particularly important, because plant regeneration is supposed to strongly respond to globally changing environmental conditions (Browne et al., 2021; Falster et al., 2018; Sales et al., 2021).

6.3. Understanding and protecting biodiversity today and in the future

The scope of this thesis was restricted to the tropical montane forest in Southern Ecuador. The applied methods, however, can be well expanded to other taxa, regions and countries, at least to those in the neotropics. The findings of my three research questions support this notion, since they present new insights into trait-environment associations within the complex process of plant regeneration in tropical mountains.

First, studying trait-environment associations might be used as a framework in a wider context, for instance in ecological modelling or conservation projects (Hallett et al., 2023; Myers & LaManna, 2016). My research shows that the exploration of seedling recruitment processes across space and time allows to capture the dynamics of plant regeneration. A thorough understanding of plant regeneration processes is particularly important for highly diverse tropical montane forests. It will also help to better predict the consequences of land use and climate changes on natural ecosystems, which is currently not only a common interest of the scientific community, but also of the society as a whole (Bastin et al., 2019; de Bello et al., 2010).

Second, my results showed that trait-based field experiments and observations can help to better predict future scenarios and to promote concrete actions for successful forest restoration. It is particularly important to identify the limiting processes of early plant regeneration to better support seedling establishment by active restoration (Holl et al., 2017; Uriarte & Chazdon,

2016). Growing evidence exists that forest restoration is critical to regrow cleared forests to mitigate climate change effects (Bastin et al., 2019). There is also evidence that secondary forests can resemble the old-growth forests in terms of diversity what gives a reason for hope that many ecological processes that primary forests provide are also maintained by secondary forests (Norden et al., 2009; Rozendaal et al., 2019). The identification of the main environmental filters that plant face during their early establishment phases belongs to one of the main challenges of successful restoration. The results of my field experiment contribute to identifying actionable solutions for successful reforestation in tropical countries. Further exploration of plant functional traits and their associations with local-scale environmental conditions could effectively support local conservation efforts, needed to enhance forest cover in the future and halt the accelerating loss of biodiversity (He et al., 2023; Myers et al., 2000; Rozendaal et al., 2019).

Zusammenfassung

Tropische Regenwälder haben Wissenschaftler aufgrund ihrer einzigartigen Artenvielfalt schon immer fasziniert. Allerdings ist unser Verständnis der oftmals komplexen ökologischen Prozesse in diesen Wäldern, wie zum Beispiel der Verjüngung von Pflanzenpopulationen und Gemeinschaften, immer noch relativ gering. Die Pflanzenverjüngung ist ein der Schlüsselprozess, der die Struktur, Vielfalt und Zusammensetzung von Pflanzengemeinschaften bestimmt. Die Pflanzenverjüngung umfasst die Abfolge von einem keimenden Samen zu einem etablierten Keimling, bis hin zu einer reproduzierenden Pflanze. Die Etablierung und das Überleben von Pflanzen wird hierbei von sogenannten Filtern, also den gegebenen Umweltbedingungen, beeinflusst. Abiotische Filter sind z.B. Temperatur oder Niederschlag, während biotische Filter sich auf die Interaktionen zwischen der Pflanzen mit anderen Organismen bezieht (z.B. Herbivorie, Befall von Pathogenen Pilzen) beziehen. Diese Filter sind entscheidend für die Zusammensetzung von Pflanzengemeinschaften und wirken auf unterschiedlichen räumlichen und zeitlichen Skalen. Bisherige Studien haben die frühen Stadien im Lebenszyklus von Pflanzen, wie die Etablierung von Keimlingen, oft nur wenig untersucht. Dabei sind es insbesondere diese frühen Stadien, die die Zusammensetzung einer Pflanzengemeinschaft über Raum und Zeit hinweg verändern können. Ein umfassendes Verständnis der Pflanzenverjüngung ist daher erforderlich, um die derzeitigen Diversitätsmuster zu verstehen und künftige Veränderungen in Ökosystemen besser vorhersagen zu können.

Merkmalsbasierte Forschung ist besonders nützlich, um die Auswirkungen abiotischer und biotischer Faktoren auf die Pflanzenverjüngung und die Zusammensetzung von Artengemeinschaften zu entflechten. Funktionelle Merkmale sind die Merkmale eines Individuums, die sich auf Wachstum, Fortpflanzung und Überleben auswirken und somit indirekt die Fitness eines Individuums beeinflussen. Zum Beispiel kann die Samengröße einer

Pflanze, deren Verjüngung beeinflussen. Kleinsamige Pflanzen produzieren oft eine große Anzahl von Samen und haben daher eine hohe Chance, dass zumindest einige der Samen für die Verjüngung geeignete Stellen erreichen. Allerdings ist die Etablierungswahrscheinlichkeit kleiner Samen relativ gering. Im Gegensatz dazu produzieren großsamige Pflanzen oftmals weniger Samen, jedoch ist hier die Etablierungswahrscheinlichkeit deutlich höher. Methodisch können Messungen von Merkmalen durch die Messung der funktionalen Vielfalt erweitert werden. Diese beschreibt, wie die Merkmale innerhalb einer Gemeinschaft verteilt sind. So gibt die funktionelle Zusammensetzung einer Pflanzengemeinschaft Aufschluss über das Vorhandensein und die Dominanz bestimmter Pflanzeigenschaften und spiegelt somit die vorherrschenden ökologischen Strategien in einer Pflanzengemeinschaft wider. Abiotische und biotische Faktoren können die funktionelle Zusammensetzung von Pflanzengemeinschaften sowohl auf großräumiger als auch auf lokaler räumlicher Ebene beeinflussen. So können beispielsweise klimatische Bedingungen entlang von Höhengradienten die Artenzusammensetzung bestimmen, während gleichzeitig kleinräumige Prozesse, wie z.B. das Mikroklima, für die lokale Artenzusammensetzung von Bedeutung sind. Das Konzept der Beta-Diversität ist eine wertvolle Methode, um solche skalenabhängigen Prozesse in der Artenzusammensetzung zu entschlüsseln, da es quantitativ beschreibt, wie sich Gemeinschaften untereinander und über Umweltgradienten hinweg unterscheiden.

In meiner Dissertation kombiniere ich experimentelle, beobachtende und merkmalsbasierte Ansätze, um die abiotischen und biotischen Prozesse zu identifizieren, welche die Zusammensetzung von Keimlinggemeinschaften in den tropischen Bergwäldern Süd-Ecuadors bestimmen. Durch meine Arbeit entlang eines Höhengradienten von 1 000 bis 3 000 m über NN konnte ich die Zusammenhänge zwischen Umweltbedingungen und Pflanzenmerkmalen in unterschiedlichen Umwelten und Lebensstadien untersuchen.

Meine Dissertation besteht aus drei Kapiteln, die sich jeweils mit einer Forschungsfrage befassen. In meiner ersten Forschungsfrage (Q1) untersuchte ich, wie sich die Merkmalszusammensetzung in Pflanzengemeinschaften auf großräumiger und lokaler Ebene entlang des Höhengradienten und über verschiedene Lebensstadien der Pflanzen hinweg verändert. Meine zweite Forschungsfrage (Q2) zielte darauf ab, zu untersuchen, wie die Samengröße die Etablierung von Keimlingen in natürlichen Wäldern und auf Weiden beeinflusst und wie diese Unterschiede mit abiotischen und biotischen Faktoren zusammenhängen. In meiner dritten Forschungsfrage (Q3) untersuche ich den Zusammenhang zwischen der Beta-Diversität der Keimlinge und verschiedenen abiotischen und biotischen Faktoren entlang des Höhengradienten. Ich habe umfangreiche Feldbeobachtungen und Experimente im Podocarpus Nationalpark und im San Francisco Reservat in den tropischen Bergwäldern im Süden Ecuadors durchgeführt. Ich habe Daten auf 18 Versuchsflächen in drei Höhenlagen (1000, 2000 und 3000 m ü. NN) und zwei Lebensraumtypen (d. h. geschützte Wälder und aktive Viehweiden) gesammelt. Die Untersuchungsflächen wurden im Rahmen der DFG-Forschergruppe RESPECT (FOR2730) eingerichtet.

Zunächst untersuchte ich (Q1), wie sich die Merkmalszusammensetzung tropischer Pflanzengemeinschaften auf großräumiger und lokaler Ebene und über verschiedene Lebensstadien hinweg verändert. Ich habe dafür Schlüsselmerkmale an drei Lebensstadien gemessen: Blattmerkmale an Bäumen, Samenmerkmale und die Höhe von Keimlingen. Meine Ergebnisse zeigen, dass sich die Merkmalszusammensetzung von Blättern, Samen und Keimlingen über den großräumigen Höhengradienten in ähnlicher Weise veränderte, die verschiedenen Lebensstadien jedoch unterschiedlich auf die lokalen Gradienten in Form von Bodennährstoffen und Lichtverfügbarkeit reagierten. Folglich zeigen meine Ergebnisse, dass die Assoziationen zwischen Pflanzenmerkmalen und der Umwelt von der räumlichen Skala und dem spezifischen Lebensstadium abhängig sind.

Zweitens (Q2) untersuchte ich, wie die Samengröße die Etablierung von Keimlingen in natürlichen Wäldern und auf Weiden in Abhängigkeit von abiotischen und biotischen Faktoren beeinflusst. Ich habe in beiden Lebensraumtypen ein Aussaat-Experiment durchgeführt und über 8.000 Samen von insgesamt sieben Baumarten ausgesät. Ich konnte feststellen, dass sich großsamige Arten in den Wäldern generell besser etablierten als kleinsamige Arten. Kleinsamige Arten etablierten sich hingegen besser auf Weiden als großsamige Arten, da letztere durch die hohen Bodentemperaturen in den Weiden in ihrer Etablierung limitiert waren. Diese Ergebnisse zeigen, dass die Wiederaufforstung von Weideland durch die Zugabe von Saatgut großsamiger Arten aktiv gefördert werden kann.

Drittens (Q3) untersuchte ich die Zusammenhänge zwischen der Beta-Diversität der Keimlinge (Arten-Turnover und Unterschiede im Artenreichtum) und verschiedenen abiotischen und biotischen Faktoren (Licht- und Bodenbedingungen, Inzidenz von Herbivorie und Pilzpathogenen) entlang desselben Höhengradienten. Ich fand heraus, dass der Arten-Turnover in Keimlinggemeinschaften positiv mit dem Auftreten von Herbivoren *innerhalb* der Höhenstufen und mit der Umweltheterogenität *zwischen* den Höhenstufen verbunden war. Außerdem nahmen die Unterschiede im Artenreichtum mit zunehmender Umweltheterogenität *innerhalb* der Höhenlagen zu. Meine Ergebnisse zeigen, dass die Assoziationen zwischen der Beta-Diversität von Keimlinggemeinschaften und den abiotischen und biotischen Faktoren skalenabhängig sind, was sich wahrscheinlich auf unterschiedliche Mechanismen der Koexistenz von Arten auf der großräumigen und lokalen Skala zurückführen lässt.

Meine Dissertation zeigt, dass eine Kombination verschiedener Ansätze, darunter merkmalsbasierte Forschung, Beobachtungen und Aussaatversuche, sowie Beta-Diversitäts-Partitionierung, neue Erkenntnisse über die Prozesse der Pflanzenverjüngung in tropischen Wäldern liefern. Insbesondere zeigen meine Ergebnisse, dass Untersuchungen zur Zusammensetzung von Pflanzengemeinschaften über verschiedene Lebensstadien und

räumliche Maßstäbe hinweg unser Verständnis der räumlich-zeitlichen Dynamik von Pflanzengemeinschaften verbessern. Frühere Studien haben insbesondere die frühen Phasen der Pflanzenregeneration nur wenig erforscht, da die Untersuchung von Keimlingen zeitaufwändige Beobachtungen und spezielle Fachkenntnisse zur Artenbestimmung erfordert. Meine Ergebnisse unterstreichen jedoch, dass künftige Studien besonders die frühen Stadien im Lebenszyklus der Pflanze einbeziehen sollten, um die Mechanismen zur Zusammensetzung von tropischen Pflanzengemeinschaften besser zu erforschen. Die Identifizierung dieser Prozesse ist von entscheidender Bedeutung, um Prognosen der Diversität von Pflanzengemeinschaften unter zukünftigen Landnutzungs- und Klimabedingungen zu erstellen und das Renaturierungspotenzial anthropogen gestörter Wälder abschätzen zu können.

Meine Ergebnisse zeigen weiterhin, dass abiotische und biotische Faktoren für die Merkmalszusammensetzung und die Artenvielfalt in tropischen Bergwäldern von wesentlicher Bedeutung sind. Die Auswirkungen abiotischer und biotischer Faktoren sind jedoch sehr von der räumlichen Skala und dem beobachteten Lebensstadium der Pflanzen abhängig. Zukünftige Untersuchungen zu den Auswirkungen von Umweltfaktoren auf spezifische Pflanzenarten könnten eine Möglichkeit sein, um diese Skalen- und Merkmalsabhängigkeit zu entschlüsseln.

Schließlich zeigen meine Ergebnisse, dass merkmalsbasierte Feldexperimente und Beobachtungen dazu beitragen können, konkrete Maßnahmen für eine erfolgreiche Waldrenaturierung zu untermauern. Es gibt immer mehr Belege dafür, dass die aktive Wiederaufforstung von Wäldern entscheidend für den Renaturierungserfolg gerodeter Wälder ist. Die Ergebnisse meiner Arbeit tragen dazu bei, praktikable Lösungen für eine erfolgreiche Wiederaufforstung in tropischen Ländern zu finden. Zukünftige Forschungen zur Bedeutung funktioneller Pflanzenmerkmale und lokaler Umweltbedingungen für Pflanzenverjüngung könnten Naturschutzbemühungen darin unterstützen Waldflächen zu vergrößern und den Verlust der biologischen Vielfalt aufzuhalten.

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Appendices

Appendix 1: Environmental conditions differently shape leaf, seed and seedling trait composition in tropical montane forest

Appendix 2: Seedling recruitment of large- and small-seeded species in forest and pastures in Southern Ecuador

Appendix 3: Biotic pressures and environmental heterogeneity shape beta-diversity of seedling communities within and between elevations in tropical montane forests

Appendix 4: CV

Appendix 5: Publications and scientific presentations

A1: Environmental conditions differently shape leaf, seed and seedling trait composition in tropical montane forest

Authors: Maciej K. Barczyk, Diana C. Acosta-Rojas, Carlos I. Espinosa, Jürgen Homeier, Boris A. Tinoco, Andre Velescu, Wolfgang Wilcke, Matthias Schleuning and Eike Lena Neuschulz

Title: Environmental conditions differently shape leaf, seed and seedling trait composition in tropical montane forest

Status: submitted

Author contributions:

(1) Concept and design

MB 70%;

ELN, DAR, JH, MS in total 30%

(2) Conducting tests and experiments

MB collected and processed data on seedling recruitment, 100%

MB collected and processed data on canopy properties, 100%

DAR collected and processed data on seeds, 100%

JH surveyed adult trees, identified species, then collected and prepared data on leaf traits, 100%

AV and WW collected and processed data on soil properties 100%

(3) Compilation of data sets and figures

MB, contributed seedling trait and seedling abundance data; 100%;

MB compiled all data for analyses, 100%;

MB prepared all figures and tables, 100%;

JH contributed leaf trait and tree abundance data, 100%;

DAR contributed seed trait and seed abundance data, 100%;

(4) Analysis and interpretation of data

MB calculated community-weighted means, 100%;

MB tested for environmental effects on trait composition across and within elevations, 100%;

MB interpreted the results, 90%

with input from ELN, DAR, JH, MS in total 10%

(5) Drafting of manuscript

MB, 80%;

ELN, JH, MS in total 15%;

AV, BT, CIE, DAR, WW in total 5%

Supplementary material

SI: Methods

Environmental conditions differently shape leaf, seed and seedling trait composition in tropical montane forests

Abstract

The composition of plant functional traits varies in response to environmental conditions due to processes of community assembly and species sorting. However, there is a lack of understanding of how plant trait composition responds to environmental conditions at different spatial scales and across the plant life cycle. We investigated the trait composition of leaves (specific leaf area), seeds (seed mass) and seedlings (initial seedling height) across elevations and within elevations in relation to soil and light conditions in a tropical montane forest in southern Ecuador. We surveyed traits and communities of adult trees, seeds and seedlings on nine plots at three elevations (1000-3000 m a.s.l.) and calculated community-weighted mean trait values to analyse trait variation across and within elevations. In addition, we measured two environmental factors (soil C/N ratio and canopy openness) to quantify local-scale variation in environmental conditions within elevations. We found that community-weighted means of specific leaf area, seed mass and initial seedling height decreased with increasing elevation. Within elevations, mean trait values of trees, seeds and seedlings responded differently to local-scale environmental conditions. Specific leaf area decreased with increasing soil C/N ratio, and initial seedling height decreased with increasing canopy openness. Seed mass was associated neither with soil nor with light conditions. Our findings show that broad-scale and local-scale processes differently shape the composition of leaf, seed and seedling traits in tropical forests, indicating a scale-dependence in trait-environment associations. Furthermore, plant traits corresponding to different life stages were differently related to environmental conditions within elevations. Community assembly processes may therefore lead to differences in species sorting at early and late plant life stages.

Keywords:

Community assembly, community-weighted means, functional traits, plant ecological strategy, Podocarpus National Park

1. Introduction

Investigating variability in plant functional traits contributes to the understanding of demographic processes and the prevalence of ecological strategies in plant communities across environmental gradients (Westoby 1998, Lavorel and Garnier 2002, Moles et al. 2005, Adler et al. 2014, Kraft et al. 2015a). In particular, the composition of plant functional traits in ecological communities can offer insights into processes of community assembly because the functional trait composition varies between and within ecosystems (Díaz and Cabido 2001). Field studies have revealed that environmental filtering along steep environmental gradients leads to shifts in trait values and the dominance of different ecological strategies in distinct locations (Albrecht et al. 2018, Homeier et al. 2021, Pierick et al. 2021, Rosbakh et al. 2022). For instance, climatic or microhabitat differences cause shifts in trait values due to the effects of environmental pressures on plant growth and survival (Lebrija-Trejos et al. 2010, Kraft et al. 2015b, Wiczyński et al. 2019). In addition, plants may switch between different ecological strategies over their ontogeny, because species can maintain high trait plasticity along the plant life cycle in response to changing environmental conditions (Visser et al. 2016, Dayrell et al. 2018) and because species sorting may differently affect plant communities at early and late life stages (Clarke et al. 2001, Foster et al. 2011). Capturing the composition of functional traits that reflect plant growth, reproduction and regeneration can therefore reveal new insights into how plant traits are filtered along environmental gradients (Lebrija-Trejos et al. 2010, Lasky et al. 2014, Larson and Funk 2016).

Leaf traits are powerful predictors of changes in the growth strategies of plants, mainly reflected by the leaf economics spectrum (Wright et al. 2004; Díaz et al. 2016, Maynard et al. 2022). The leaf economics spectrum describes the trade-off between nutrient-rich, ‘acquisitive’ leaves and long-lived, ‘conservative’ leaves. Specific leaf area (leaf area per dry mass; SLA) is a key

functional trait that reflects these trade-offs in investment strategies and variability in resource allocation (Westoby 1998, Diaz et al. 1998, Wright et al. 2004). For instance, species with long-lived, conservative leaves tend to dominate under harsh environmental conditions at high elevations, while species with acquisitive leaves are more abundant in lowland tropical rainforests (Hulshof et al. 2013). In addition, local-scale variation in environmental conditions can trigger shifts in leaf functional traits (Schmitt et al. 2020, Báez et al. 2022).

Seed traits capture essential trade-offs in plant reproductive strategies of adult plants (Westoby 1998, Moles and Westoby 2006, Bolmgren and Eriksson 2010). Primarily, seed mass influences plant fitness through a trade-off between the costs of seed production and benefits in terms of germination success (Moles and Westoby 2006, Visser et al. 2016, Sales et al. 2021). Consequently, plants may either produce many small seeds or a few large seeds, representing a size-number trade-off in seed production (Moles et al. 2004, Moles and Westoby 2006). As such, differences in seed mass influence seedling survival and growth (Baraloto et al. 2005, Moles and Westoby 2006, Falster et al. 2018), as well as plant fitness and the fate of future plant generations (Terborgh et al. 2008, Canham and Murphy 2016, Kuprewicz and García-Robledo 2019). Several field studies have reported shifts in seed trait composition in plant communities driven by changes in environmental conditions (Moles et al. 2005, Sales et al. 2021). For instance, seed mass has been shown to decrease along elevational gradients with decreasing temperature (Duivenvoorden and Cuello A 2012, Rosbakh et al. 2022). At local spatial scales, canopy properties and soil conditions can trigger variation in seed traits, likely due to changes in allocation strategies in different environments (Acosta-Rojas et al. 2023). Generally, plant species tend to produce larger seeds on fertile soils due to a higher resource allocation into reproduction (Grubb and Coomes 1997, Jager et al. 2015).

Finally, seedling traits have drawn more attention recently, because they are essential for community assembly at early plant life stages (Auffret et al. 2017, Harrison and LaForgia 2019,

Westoby et al. 2022). For instance, the initial seedling height shortly after germination can be a measure of the growth capacity and resistance of young plants (Baraloto et al. 2005). As such, this trait reflects the energy supply provided to a seedling by a seed (Moles et al. 2004, Hu et al. 2017) and, thus, the initial capacity of seedlings to invest into growth (Baraloto et al. 2005, Falster et al. 2018, Umaña et al. 2021a). Initial seedling height can mirror the regeneration strategy of a plant species as seedlings of early- and late-successional species tend to differ in size and growth strategy (Baraloto et al. 2005). Specifically, late-successional species tend to produce larger seeds and seedlings than early-successional species and are more likely to establish in light-limited environments (Dalling and Hubbell 2002, Wright et al. 2003, Visser et al. 2016, Gibert et al. 2016). In contrast, seedlings of small-seeded and early-successional species are more likely to establish in canopy gaps and can surpass large-seeded species in growth rates under open canopy (Dalling and Hubbell 2002, Baraloto et al. 2005). While local variability in soil and light conditions may affect seedling traits (Umaña et al. 2021a, Song et al. 2021), little is known to what extent initial seedling height is associated with broad- and local-scale environmental variation.

Trait-based processes of community assembly can be governed by distinct environmental conditions at different spatial scales (Lasky et al. 2014, Werner and Homeier 2015). Elevational gradients provide powerful means to study this scale-dependency in plant community assembly (Malhi et al. 2010, Albrecht et al. 2018, Rosbakh et al. 2022). Generally, environmental variability across elevations is driven by broad climatic gradients in terms of temperature and precipitation (Hu and Riveros-Iregui 2016, Dantas de Paula et al. 2021, Pierick et al. 2023), whereas soil and light conditions mainly drive local-scale processes within elevations in tropical montane forests (Andersen et al. 2010, Umaña et al. 2021a, Pierick et al. 2021). Studying changes in functional trait composition across and within elevations can contribute to a

mechanistic understanding of plant community assembly at early and late plant life stages in highly diverse tropical ecosystems (Lasky et al. 2014, Homeier et al. 2021, Báez et al. 2022).

Here, we tested how the trait composition of leaves, seeds and seedlings is associated with environmental conditions across and within elevations in tropical montane forests. We calculated community weighted means of key traits assigned to each plant life stage (i.e., specific leaf area, seed mass and initial seedling height) and related them to broad-scale environmental variation across elevations and to variation in local-scale environmental factors (i.e., soil and light conditions) within elevations. First, we expected general shifts in the trait composition across elevations due to harsher climatic conditions at high elevations (Duivenvoorden and Cuello A 2012; Homeier et al. 2021; Umaña et al. 2021a). Second, we expected that trait variation within elevations is associated with local soil and light conditions. In particular, we expected that soil conditions should be associated with mean specific leaf area (Jager et al. 2015, Homeier et al. 2021, Pierick et al. 2021) and seed mass (Grubb and Coomes 1997, Pérez-Ramos et al. 2014, Jager et al. 2015), whereas light conditions should primarily be associated with mean seed mass (Acosta-Rojas et al. 2023) and initial seedling height (Baraloto et al. 2005, Umaña et al. 2021a, Song et al. 2021).

2. Methods

Study design

This study was carried out in the Podocarpus National Park and San Francisco Reserve, located between the Amazon Basin and the main ridge of the Eastern Andes in southern Ecuador. The protected area of the Podocarpus National Park spans over 1400 km² and covers an elevational gradient of more than 2000 meters (ca. 900 m - 3600 m a.s.l.). The area is characterized by mostly intact evergreen montane forests, hosting numerous endemic and undescribed plant

species (Homeier et al. 2008, Kessler & Kluge 2008). The mean annual temperature ranges between 20 °C at 1000 m. a.s.l., 15.5 °C at 2000 m a.s.l. and 10 °C at 3000 m. a.s.l. (Bendix et al. 2008). The mean annual precipitation also varies strongly among elevations: 2432 mm at 1000 m, 2330 mm at 2000 m and 4522 mm at 3000 m (Santillán et al. 2018, Wilcke et al. 2019). Our research was conducted on nine 1-ha plots (three at each elevation; Fig. 1a) in the frame of the DFG Research Unit 2730 (RESPECT) that established these plots along an elevational gradient ranging from 1000 to 3000 m a.s.l. in old-growth forests (Bendix et al. 2021). The lowest study plots were located in evergreen premontane forest along the Bombuscaro River (1000 m a.s.l., 4°6'S, 78°58'W). The plots at mid elevations were placed in lower montane forest in the San Francisco Reserve (2000 m a.s.l., 3°58'S, 79°4'W). The high elevation plots were located in upper evergreen tropical montane forest in Cajanuma (3000 m a.s.l., 4°6'S, 79°10'W). All plots had a minimum pair-wise distance of 100 m (Bendix et al. 2021). While climatic conditions (temperature and precipitation) differ strongly across elevations, local microhabitat conditions (in particular, soil and canopy conditions) also vary strongly among and within plots at the same elevation (Barczyk et al. 2023).

Within each plot, we established several subplots to study the variability in leaf, seed and seedling trait composition. Subplots were differently sized given the different life stages corresponding to each of these traits. To measure leaf traits of adult trees, we divided each 1-ha plot into 25 subplots (tree census; framed with green colour in Fig. 1b), each covering an area of 400 m² (20 x 20 m). In total, this resulted in 225 subplots, where all individual trees were surveyed (75 subplots per elevation). To capture variability in seed trait composition, we established 18 seed traps (0.6 x 0.6 m; seed trap area = 0.36 m²) per plot to capture seed rain, regularly distributed across the plots (seed traps; yellow dots in Fig. 1b). In total, we captured seed rain in 162 seed traps across the elevations (54 traps per elevation). Finally, we set up nine 1-m² subplots (1 x 1 m) within each plot to monitor recruiting seedlings (recruitment census;

blue quadrates in Fig. 1b). In total, we recorded seedling recruitment at 81 subplots (27 subplots per elevation). Hence, we were able to study variability in the respective traits representing different plant life stages with a coherent study design capturing changes in trait composition within and across elevations.

Environmental factors

To quantify environmental conditions within elevations, we measured the soil C/N ratio and canopy openness. We measured these two environmental factors because they are proxies for two crucial resources for plants: nutrients and light (Wright et al. 2003; Umaña et al. 2021b). In 2018, we collected over 400 representative samples from the mineral soil (0-10 cm soil depth) across the nine study plots (Velescu et al., 2022). The soil samples were taken with a soil auger at five locations close to each tree and bulked to a composite sample. They were dried at 40 °C, sieved to <2 mm and an aliquot was milled in a planetary ball mill (PM400, Retsch, Haan, Germany). We determined total carbon (C) and nitrogen (N) concentrations by elemental analyses via thermal combustion at 1020 °C, catalytic reduction and detection by thermal conductivity after chromatographic separation of CO₂ and N₂ (Flash 2000 HT Plus, Thermo Scientific, Bremen, Germany). Because soils were free of carbonates and had a high acidity, all C was assumed to be organic C. Based on C and N concentrations in the soils, mass-related soil C/N ratios were calculated to approximate the organic matter turnover in the soils and the availability of nutrients to plants. High soil C/N ratios indicate slow turnover of organic matter, resulting in low N availability to plants ((Post et al. 1985, Wilcke et al. 2020). Values of soil C/N ratios were averaged for each tree census subplot (n = 225) and mean C/N ratios were assigned to the spatially closest seed trap (n = 162) and recruitment census subplot (n = 81). Thus, soil C/N ratios could be assigned to each individual census (trees, seeds and seedlings) accounting for the different subplots of each life stage.

In October 2019, we visited all study plots to take hemispherical photos and to estimate light conditions. We photographed the canopy 0.7 m above ground at each recruitment census subplot (n = 81). Photos were taken with a Nikon Coolpix 4500 digital camera fitted with a Nikon FC-E8 Fish-Eye Converter Lens (Nikon Corporation, Japan). All photos were taken in the mornings with overcast sky. The hemispherical photos were analysed in Gap Light Analyzer version 2.0 (1999, SFU/IES, Canada/USA). For each photograph representing one subplot, we calculated canopy openness, defined as the percentage of open canopy in relation to full canopy cover (0-100%). Values of canopy openness were matched to the corresponding recruitment census and were then assigned to the spatially closest seed trap and tree census at the subplot level.

Specific leaf area

The tree inventory included all woody stems with a diameter at breast height (DBH) ≥ 10 cm and was conducted on the 25 tree census subplots inside each 1-ha plot (n = 225 subplots in total; Fig. 1). All trees were labelled and herbarium specimens were collected for taxonomic identification. The abundance of each species was defined at the subplot level as the total number of individual stems of a respective species encountered at each subplot. Trait measurements were done on a representative subset of 52 species representing different successional stages and plant families (32 plant families in total). The preselection of species was made by choosing the abundant tree species in the study plots at each elevation which covered different ecological strategies from early-successional pioneers to late-successional tree species and from understory species to tall canopy trees (see also Homeier et al. 2021). The preselected species were representative for the entire community, as they accounted for about 41% of total basal area within the 1-ha plot at 1000 m a.s.l., 50% at 2000 m a.s.l. and 32% at 3000 m a.s.l.; Homeier et al. 2021). All individual trees of the preselected species in the tree

census subplots were marked with a plastic tag. From each individual, we collected 20 leaves attached to two to three branches from the tree crown under a similar exposure to the sun. The entire branches were kept in sealed polyethylene bags with water-soaked tissues prior to measurements. Subsequently, all leaves were dried at 60 °C for 3-4 days to measure leaf dry mass.

To capture variability in the leaf economics spectrum (Wright et al. 2004, Díaz et al. 2016, Maynard et al. 2022), we computed specific leaf area. To this end, we quantified leaf area by scanning 20 undamaged leaves using the software WinFOLIA 2014 (Régent Instruments, Quebec, QC, Canada) and obtained average leaf area of all individual trees [cm²]. Leaf dry mass was obtained with a high precision analytical balance (precision 0.0001 g; KERN & SOHN GmbH, Germany). Specific leaf area [cm² g⁻¹] was then calculated as the proportion between leaf area and leaf dry mass (see Homeier et al. 2021 for further details).

Seed mass

To capture seed rain, we installed a total of 162 seed traps (trap area 0.6m x 0.6m = 0.36 m², 1.5 mm nylon mesh; Fig. 1). The traps were placed about 1 m above the ground and the content was emptied every 15 days in a period between January 2019 and January 2020. The material collected in the traps was separated into fruits and seeds. In most cases, the dispersal units matched seeds in a strict botanical sense, however some diaspores were comprised of seeds and the surrounding fruit structure. Seeds with a length < 1 mm were discarded. We identified the dispersed seeds to the lowest possible taxonomic level using reference plant material from the forest or from herbariums, field guides and the help of botanical experts (Acosta-Rojas et al. 2023). Based on these samples, we obtained the abundance of all (morpho)species at each seed trap pooled over repeated censuses. All seeds were dried at 60 °C for 3-4 days and then weighted

with a high precision analytical balance (precision 0.0001 g; KERN & SOHN GmbH, Germany).

We chose seed mass as a key trait to describe variability in plant reproductive strategy (Moles and Westoby 2006). We measured seed mass [g] of all individual seeds collected from all seed traps. Seed mass was calculated from the dried samples. For tiny seeds, it was calculated as a mean seed mass based on the total weight divided by the number of these seeds in a sample. All further details including the methodology of seed measurements can be found in Acosta-Rojas et al. (2023). In addition, photos of the most abundant species dispersed by animals along the elevational gradient are compiled in Acosta-Rojas et al. (2021).

Initial seedling height

We surveyed seedling recruitment on 81 subplots over a one-year period between May 2019 and July 2020 (Barczyk et al. 2023). Prior to seedling monitoring, we cleared vegetation within the 1-m² subplots to spot recently germinated seedlings. The observations were repeated every four months to capture an entire year of seedling recruitment. We recorded all (morpho) species emerging from seeds (i.e., at least cotyledons had been developed) and classified them into species, genus or family levels. All unidentified individuals were classified as separate morphospecies at each elevation. We obtained the species abundance of surveyed seedlings at each subplot by computing the sum over repeated censuses.

Initial seedling height is a good proxy of a plant's capacity to establish and grow, because it reflects the net energy provision of seeds to seedlings (Moles and Westoby 2004, Baraloto et al. 2005). At each visit, we measured initial seedling height [cm] for each recently established seedling (within the last four months; Baraloto et al. 2005). Precisely, the height of each seedling was measured as a distance between the stem base and the terminal bud using manual

callipers enabling a precision of 1 mm. To validate that initial seedling height is associated with the growth strategy of seedlings, we related initial seedling height with the relative growth rate for a subset of seedlings in the dataset (n = 220 seedling individuals from 83 species). For these seedlings, we calculated the relative growth rate (RGR) as described in Baraloto et al. (2005) with the Equation 1:

$$\text{RGR} = (\ln(\text{height at census time 2}) - \ln(\text{height at the census time 1})) / \text{time interval in days}$$

Initial seedling height was negatively related to RGR within and across species (Linear Mixed Model with a random term of species identity: estimate = -55.08, $p < 0.001$) indicating that seedlings with a small initial height were fast growing, whereas initially large seedlings were slow growing (Fig. S1).

Community-weighted means of traits

In order to obtain community measures of plant trait composition, we calculated the community-weighted mean of each trait (Lavorel and Garnier 2002). First, we log-transformed the trait values of all measured leaves, seeds and seedlings. Based on the log-transformed trait measurements, we calculated mean trait values at the respective subplot (i.e., tree census, seed traps and recruitment census) which allowed us to account for the intraspecific variability in leaf, seed and seedling traits at the subplot level. Further, we extracted the abundance of individuals belonging to the respective species, morphospecies or morphotype observed at the respective subplot corresponding to the studied life stage (i.e., tree census, seed traps and recruitment census). For each subplot and seed trap, we calculated the community-weighted means with Equation 2:

$$\text{CWM} = \sum_{i=1}^n \text{trait}_i \times \text{abundance}_i$$

where $trait_i$ was the mean trait value of a (morpho)species i at each subplot, and $abundance_i$ was the number of individuals (trees, seeds, seedlings) of a (morpho)species i at each subplot.

In order to test for covariation in the composition of different types of traits, we correlated the trait values of leaves, seeds and seedlings at the subplot level ($n = 81$). Community-weighted means of specific leaf area were weakly correlated with seed mass (Pearson's $r = 0.339$, $p < 0.05$) and initial seedling height (Pearson's $r = 0.428$, $p < 0.05$). In contrast, no significant correlation was detected between the community-weighted means of seed mass and initial seedling height (Pearson's $r = 0.106$, $p = 0.061$).

In addition, we tested whether the community weighted-mean of specific leaf area of the focal species at 2000 m a.s.l. ($n = 20$ species) differed from the community-weighted mean of specific leaf area of all individual trees measured at the same study subplots in an enhanced tree census at this elevation ($n = 200$ species). We found no significant difference between the community weighted-mean of the focal species and the entire tree community (paired Wilcoxon signed-rank test: $n = 75$ tree subplots, $W = 1230$, $p = 0.305$), indicating that the tree species included in the analyses were representative for the entire community.

Statistical analyses

We tested the relationship between mean trait values and environmental conditions at two spatial scales (i.e., across and within elevations). At the large spatial scale, we compared community-weighted mean trait values among plots located at different elevations in order to test for changes in trait composition across broad environmental gradients. To control for different scales of trait values in the analysis, we scaled the community-weighted means of each trait to zero mean and unit variance. At the small spatial scale, we analysed patterns within elevations after controlling for the variability in environmental conditions and trait values across elevations. Prior to this analysis, we scaled all environmental variables and community-

weighted mean trait values to zero mean and unit variance within each elevation. That is, we only analysed the variability within elevations in this second analytical step.

We performed Linear Mixed Models (LMMs) to test how community-weighted means of leaf, seed and seedlings varied across and within elevations. The first model tested how the composition of leaf, seed and seedling traits changed across elevations. The second model tested how trait composition was related to environmental variation (i.e., soil C/N ratio and canopy openness) within elevations. To simplify the interpretation of model estimates, we removed the intercepts and main effects of the environmental predictor variables from these models as described in Schielzeth (2010). This model formulation allowed us to test for the trait-specific trends in the variation of leaf, seed and seedling traits across and within elevations. In addition, all models included a random factor of plot identity ($n = 9$ plots) to control for unmeasured variability among plots. All analyses were conducted in R 4.2.3 (R Core Team 2022) and the associated packages “ggplot2” (Wickham 2016), “lme4” (Bates et al. 2015), “lmerTest” (Kuznetsova et al. 2017) and “tidyverse” (Wickham 2011).

As a test of model robustness, we ran a subsampled analysis to control for the uneven number of sample sizes for traits and the respective environmental variables (i.e., soil and light conditions). To this end, we only included those subplots in the analysis for which both trait and environmental data had been measured and did not match environmental variables to the spatially closest subplots or seed traps. These models were based on a restricted sample size and served to test the robustness of the findings of the main analyses including similar number of tree census subplots, seed traps and recruitment census subplots ($n = 81$ subplots).

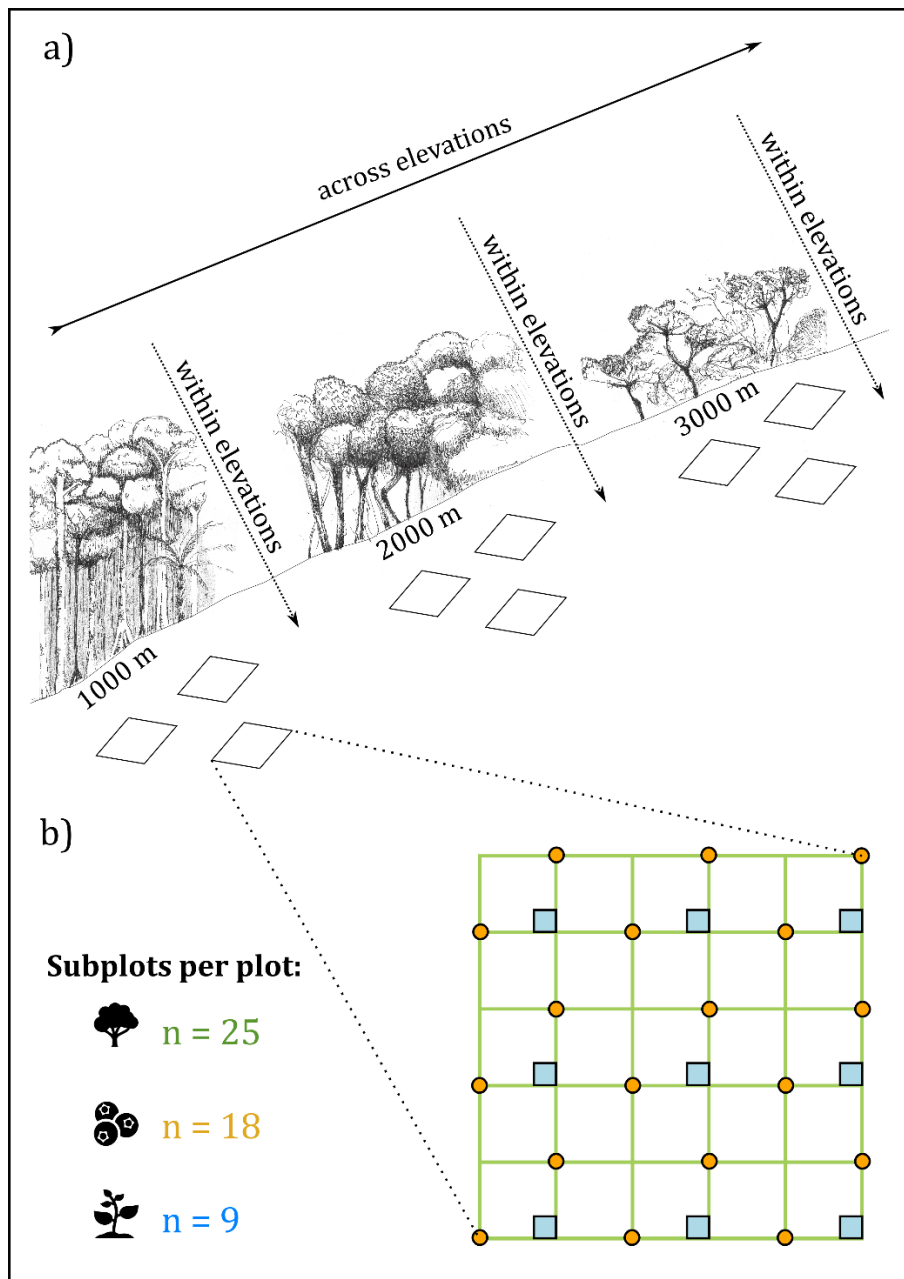


Figure 1. Study design within and across elevations. (a) Nine 1-ha plots were located along the 2000-m elevational gradient at 1000, 2000 and 3000 m a.s.l. (three plots at each elevation). (b) Within each plot, subplots were established to measure trait variation in three distinct life stages: tree census (green frames, 20 x 20 m), seed traps (yellow dots, 0.6 x 0.6 m), and recruitment census (blue quadrates, 1 x 1 m). Analyses within elevations were controlled for variation in trait composition among elevations.

3. Results

We measured specific leaf area on 418 individual trees of 52 plant species (20 species at 1000 m, 20 species at 2000 m and 12 at 3000 m) at 164 subplots (i.e., subplots without the respective

plant species had to be discarded from the analysis). Specific leaf area varied between 26 (*Clusia elliptica* at 3000 m) and 241 cm² g⁻¹ (*Mollia gracilis* at 1000 m).

We captured 2393 individual seeds of 330 morpho(species) [126 species at 1000 m, 121 species at 2000 m and 81 species at 3000 m] in 160 seed traps (i.e., two seed traps did never contain seeds). Seed mass ranged between less than 0.0001 g (e.g., *Meriania sp.* at 3000 m) and more than 2.5 g (e.g., 2.58 g in *Anomospermum reticulatum* at 1000 m). We recorded 548 seedlings of 140 species (82 species at 1000 m, 64 species at 2000 m and 63 species at 3000 m) on 73 subplots (i.e., no seedlings were recorded on eight recruitment subplots). Initial seedling height varied between 0.3 cm (*Miconia sp.* at 1000 m) and 35.4 cm (*Clarisia sp.* at 1000m).

3.1. Changes in trait composition across elevations

Community-weighted means of all plant traits decreased with increasing elevation (Tab. 1). Mean specific leaf area of adult trees decreased from about 116 cm² g⁻¹ at 1000 m to 56 cm² g⁻¹ at 3000 m a.s.l. (Fig. 2a). Mean seed mass decreased from 0.100 g at 1000 m to 0.016 g at 3000 m a.s.l. (Fig. 2b). Mean initial seedling height showed a similar trend and ranged from 5.8 cm at 1000 m to 3.5 cm at 3000 m a.s.l. (Fig. 2c). The decreases in specific leaf area, seed mass and initial seedling height with increasing elevation were highly significant (Tab. 1). The analysis restricted to the subplots directly sampled for both environmental and trait variables showed qualitatively identical patterns (Tab. S1a in Supporting Information).

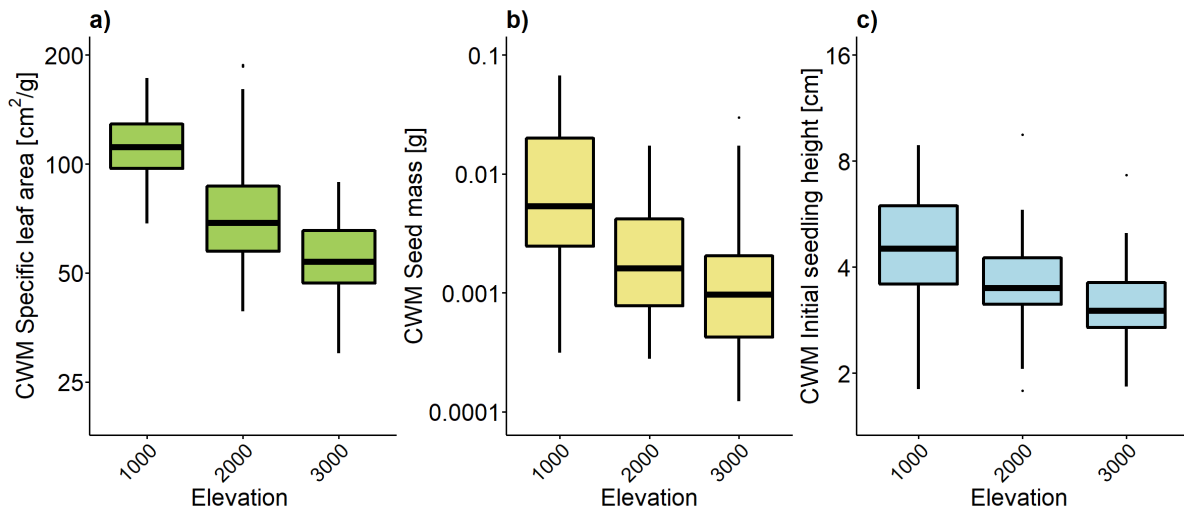


Figure 2. Community-weighted means of leaf, seed and seedling traits across elevations. Shown are: a) specific leaf area of adult trees; b) seed mass captured in seed rain; c) initial seedling height of recruiting seedlings. Community-weighted means are based on trait values and abundances recorded on trees, seeds and seedlings at 164 tree census subplots, 160 seed traps, and 73 recruitment census subplots, respectively. All study subplots were established inside the nine 1-ha plots located across the three elevations [m a.s.l.]. Trait values are presented on a logarithmic y-axis (labels are back-transformed, log₁₀). Summary statistics of the elevational effects on trait composition are shown in Tab. 1. Boxes show 25th and 75th percentiles, with the median indicated, whiskers show data range and dots depict outliers.

Table 1. Linear mixed models testing the effects of elevation on the trait composition of leaves, seeds and seedlings. Estimates indicate the effects of the respective elevational level on leaf, seed and seedling traits relative to the overall mean. Specific leaf area was recorded at 164 tree census subplots, seed mass in 160 seed traps, and initial seedling height at 73 recruitment census subplots, respectively. All study subplots were established inside the 1-ha plots across the three elevations [m a.s.l.]. Plot was included as a random effect (n = 9). Estimates, standard errors, degrees of freedom, t values and probability of tested effects are shown in columns. Traits were log-transformed and community-weighted means were scaled for each trait prior to the analysis so that estimates correspond to standard deviation units for each trait. Significant values (P < 0.05) are marked with bold font.

	Estimate	SE	df	t value	p
1000 m : Specific leaf area (SLA)	0.91	0.16	10.86	5.60	<0.001
1000 m : Seed mass	0.70	0.16	11.19	4.27	0.001
1000 m : Initial seedling height (ISH)	0.52	0.20	27.12	2.56	0.016
2000 m : SLA	-1.07	0.23	10.15	-4.74	<0.001
2000 m : Seed mass	-0.81	0.23	11.10	-3.54	0.005
2000 m : ISH	-0.62	0.28	25.22	-2.18	0.039
3000 m : SLA	-1.83	0.24	12.49	-7.73	<0.001
3000 m : Seed mass	-1.28	0.23	11.19	-5.53	<0.001
3000 m : ISH	-0.81	0.29	27.15	-2.80	0.009

3.2. Changes in trait composition within elevations

Trait composition of leaf, seed and seedling traits responded differently to variation in soil and light conditions within elevations (Tab. 2). Community-weighted means of specific leaf area of adult trees decreased with increasing soil C/N ratio, and were unrelated to canopy openness (Fig. 3a and 3d). Mean seed mass was unrelated to both environmental factors, soil C/N ratio and canopy openness (Fig. 3b and 3e). The community-weighted means of initial seedling height decreased significantly with increasing canopy openness, but were not associated with soil C/N ratio (Fig. 3c and 3f). In the subsampled analysis, community-weighted means of leaf and seedling traits were significantly associated with the same environmental conditions (Tab. 1b in Supporting Information), but the effect of soil C/N ratio on specific leaf area was weaker.

Table 2. Linear mixed models testing the effects of environmental variables on trait composition of leaf, seed and seedling traits within elevations. Estimates indicate differences between leaf, seed and seedling traits to the overall mean and the effects of each environmental predictor variable on the respective trait. Community-weighted means of each trait were computed at subplot level (n = 164, n = 160, n = 73 for leaves, seeds and seedlings, respectively). Plot was included as a random effect (n = 9). Estimates, standard errors, degrees of freedom, t values and probability of tested effects are shown in columns. Both trait and environmental variables were scaled to zero mean and unit variance within each elevation to control for variation across elevations. Significant values ($P < 0.05$) are marked with bold font.

	Estimate	SE	df	t value	p
Specific leaf area	0.02	0.06	21.87	0.27	0.790
Seed mass	<0.01	0.06	24.73	0.001	0.999
Initial seedling height	-0.08	0.09	79.38	-0.94	0.348
Soil C/N : SLA	-0.47	0.07	127	-7.16	<0.001
Soil C/N : Seed mass	0.06	0.06	175.6	1.08	0.282
Soil C/N : ISH	-0.15	0.09	268.7	-1.72	0.088
Canopy openness : SLA	0.04	0.05	349	0.65	0.517
Canopy openness : Seed mass	-0.02	0.06	347.4	-0.44	0.661
Canopy openness : ISH	-0.27	0.09	349.1	-3.07	0.002

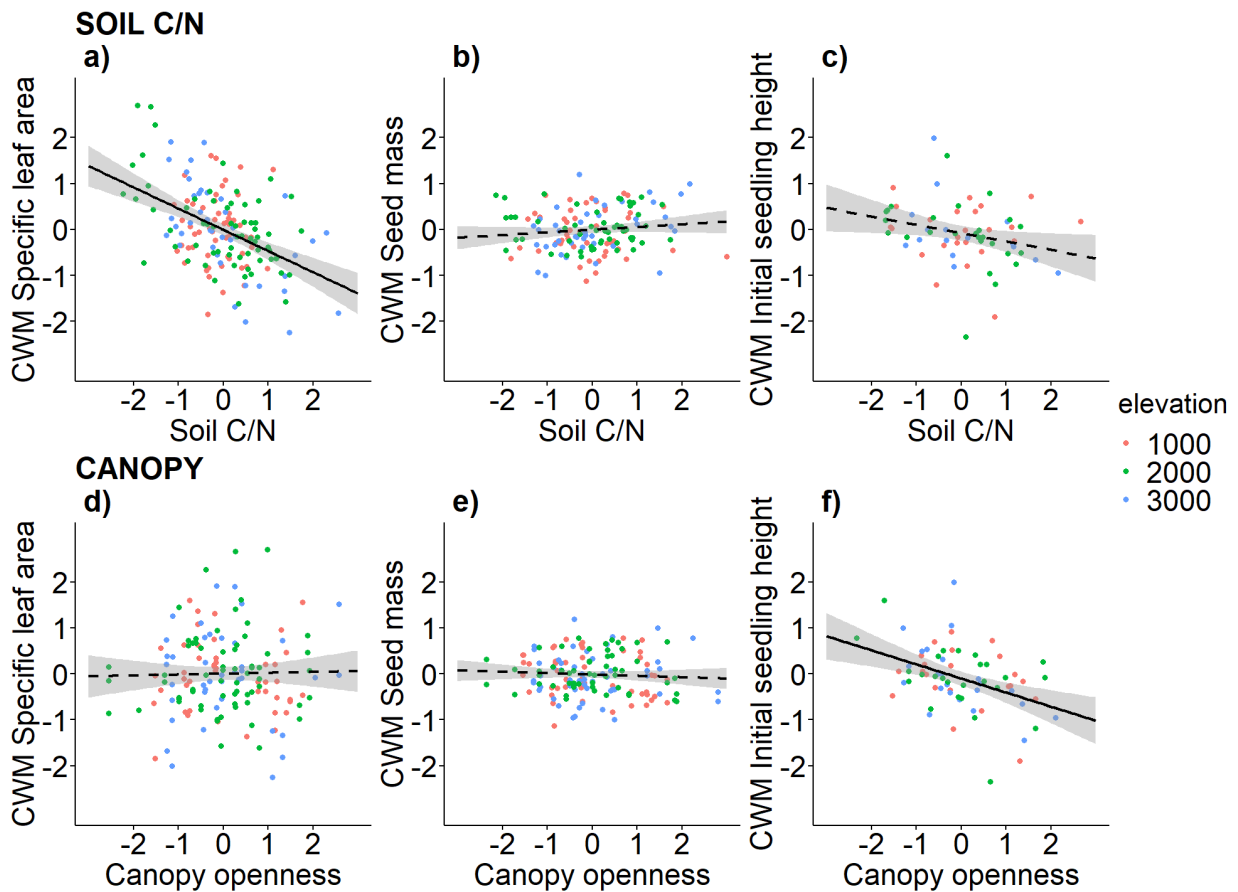


Figure 3. Relationships between community-weighted means of leaf, seed and seedlings traits and soil and light conditions within elevations. Specific leaf area (a, d); seed mass (b, e); and initial seedling height (c, f) in relation to soil C/N ratio (a-c) and canopy openness (d-f). Each point represents the community-weighted mean trait value at one subplot ($n = 164$ tree census subplots, $n = 160$ seed traps, $n = 73$ recruitment census subplots). Both trait and environmental variables were scaled to zero mean and unit variance within each elevation to control for variation across elevations. Summary statistics of the studied trait-environment associations can be found in Tab. 2. Dashed lines show non-significant relationships, while solid lines indicate significant associations.

Discussion

We found a consistent shift in trait values of different plant life stages across elevations, highlighting the important role of environmental filtering at large spatial scales. In contrast, we found that within elevations soil and light conditions were differently associated with traits representing distinct plant life stages. Thus, our investigation revealed that the composition of leaf, seed and seedling traits was related to different environmental factors, and that trait-environment relationships were highly contingent on the plant life stage. Our findings help to understand how environmental conditions shape community assembly of tropical plant communities at small and large spatial scales and across the plant life cycle.

Changes in trait composition across elevations

We found that elevation had consistent effects on the trait composition of different plant life stages, likely because broad-scale environmental filtering of the trait composition of plant communities increased with increasing elevation. Previous studies identified temperature as a major environmental driver causing shifts in species and trait composition across elevational gradients (Nottingham et al. 2018, Homeier et al. 2021b, Acosta-Rojas et al. 2023). Community-weighted means of specific leaf area were gradually decreasing with increasing elevation. This is in line with previous studies on the composition of other leaf traits across elevational gradients in montane forests (Hulshof et al. 2013, Schmitt et al. 2020, Homeier et al. 2021a). Trees growing at high elevations have been shown to invest more into the production of conservative leaves (i.e., leaves with small specific leaf area), which are more resistant and long-lasting to stand harsh climatic conditions (Westoby 1998, Hulshof et al. 2013). Similarly, previous studies have demonstrated that community-weighted mean of seed mass decrease in

tropical mountains along steep environmental gradients because of less favourable climatic conditions at high elevations (Duivenvoorden and Cuello A 2012, Rosbakh et al. 2022). The decline in seed mass with increasing elevation could also be related to the lower diversity of large seed-dispersing animals at high elevations in the study area (Quitán et al. 2018). We further found a significant decrease in community-weighted means of initial seedling height across elevations. This association may be related to the covariation between initial seedling height and seed mass and the general decrease in seed mass with increasing elevation (Moles et al. 2004, Baraloto et al. 2005). Furthermore, this suggests that late successional species producing large seedlings are more prevalent at lower elevations corresponding to the structural changes from taller, more densely covered lower to more open upper montane forests (Homeier et al. 2010, Arellano et al. 2016). Overall, we found that environmental variation at large spatial scales leads to consistent changes in the mean trait values of leaves, seeds and seedlings, suggesting similar shifts in resource allocation patterns across different plant life stages at broad spatial scales (Lasky et al. 2014, Visser et al. 2016, Umaña et al. 2021b). Generally, plants invested into less costly plant organs (e.g., less acquisitive leaves, smaller seeds and seedlings) in the harsher environmental conditions at high elevations.

Changes in trait composition within elevations

We detected pronounced differences in trait-environment associations within elevations. In contrast to our expectation, only specific leaf area, but not seed mass and initial seedling height, was related to variation in soil C/N ratios. Within elevations, specific leaf area was negatively associated with increasing C/N ratio. Previous studies found similar trends and showed that trees growing on more fertile soils (e.g., low C/N ratio) tend to produce acquisitive leaves (i.e., large specific leaf area) (Hodgson et al. 2011, Hulshof et al. 2013, Schmitt et al. 2020, Homeier et al. 2021). This is because plants growing on fertile soils invest more into growth by producing

acquisitive leaves with high photosynthetic capacity to compete for light and accelerate reproduction (Apaza-Quevedo et al. 2015, Falster et al. 2018, Homeier et al. 2021). Both inter- and intra-specific shifts from plants with acquisitive to conservative leaves have been reported along environmental gradients as a consequence of this trade-off (Schmitt et al. 2020). In line with that, recent studies from tropical forests demonstrated that soil fertility is a main driver of plant community assembly, because leaf traits are crucial to mediate species sorting in tropical tree communities (Dantas de Paula et al. 2021, Peguero et al. 2023).

In contrast to our hypothesis, seed size was not significantly associated with soil conditions within elevations. Although previous studies have shown that seed size may decrease in plant communities growing on less fertile soil conditions, such a local effect was not detected in our study (Pérez-Ramos et al. 2014, Jager et al. 2015). One reason for the lack of this relationship could be that seed size is not only driven by abiotic factors, such as soil fertility, but often depends on biotic factors and the diversity of animal seed dispersers (Quitán et al. 2018, Acosta-Rojas et al. 2023). Given that the majority of plants in tropical forests depend on seed dispersal by frugivorous animals, bird and mammal diversity may be closely associated with plant trait composition (Wang and Smith 2002, Vollstädt et al. 2017, Sales et al. 2021).

We found that initial seedling height, but not specific leaf area and seed mass, was related to variation in canopy openness within elevations. Previous studies from other tropical forests have shown that canopy openness fosters seedling growth, as light is a limiting factor for seedling growth in the forest understorey (Baraloto et al. 2005, Umaña et al. 2021a, Song et al. 2021). In our study, we found that seedlings growing under open canopy tended to be smaller than seedlings growing under dense canopy cover. This relationship likely reflects different ecological strategies of plants under different light conditions. Late-successional plant species are usually equipped with large seeds which yield large seedlings (Dalling and Hubbell 2002, Saavedra et al. 2015). Consequently, large-seeded species can better cope with biotic and

abiotic pressures at the seedling stage, and prevail over small-seeded species in the understory (Wright et al. 2003, Baraloto et al. 2005). In fact, shade-tolerant late-successional species are more likely to establish under a dense canopy than early-successional species (Dalling and Hubbell 2002, Falster et al. 2018, Umaña et al. 2021a), but grow more slowly than the small-sized seedlings of early-successional species (Baraloto et al. 2005, see Fig. S1). Overall, our findings imply that community assembly of plants at the initial stage is highly dependent on light conditions at the local scale. It also confirms that initial seedling height is a valuable functional trait that can reflect differences in growth rates and the prevailing successional strategy in different environmental contexts.

In contrast to our hypothesis, seed size was not significantly associated with canopy openness. A study on seed rain from the same area recently demonstrated that canopy openness was negatively related to seed rain richness within elevations (Acosta-Rojas et al. 2023). Hence, local light conditions may influence species richness in seed rain, but were unrelated to mean seed mass at the community level. A very interesting finding of our study is that canopy openness affected the composition of seed and seedling traits differently although the two traits are correlated (Baraloto et al. 2005). This finding depicts differences in filtering mechanisms and species sorting at adult and seedling stage. The upcoming seedling communities appear to be characterised by a different trait composition than the established adult plant communities, indicating high dynamics in the trait composition of tropical plant communities. Disequilibrium dynamics in trait-environment associations may be particularly strong in tropical montane forests that undergo rapid small-scale changes in light conditions, due to frequent natural disturbances (Dislich and Huth 2012).

Conclusions

We found trait-specific variation in the functional composition of plant communities with regard to variation in soil and light conditions within elevations, although large-scale patterns in trait composition of leaves, seeds and seedling were consistent across elevations. These findings suggest that scale-dependent environmental filtering is key to understand community assembly of plants in tropical montane forests. At small spatial scales, leaf trait variation was primarily governed by variation in soil conditions, whereas variation in seedling size depended on changing light conditions. In contrast, the functional composition in terms of seed size seems to be shaped by factors unmeasured in our study or may be in disequilibrium with current abiotic conditions. Our study of plant traits across the plant life cycle shows that plant responses to environmental factors are contingent on their life stage. Community assembly may therefore lead to differences in species sorting at early and late plant life stages so that the diversity of tropical plant communities may emerge through an interplay of assembly processes governing different plant life stages.

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Supporting Information

Tab. S1. Results of sensitivity analysis on a subset of study subplots. Linear mixed models testing the effects of (a) elevation and (b) environmental variables within elevations on trait composition of leaf, seed and seedling traits (n = 81 tree census subplots and seed traps; n = 73 recruitment census subplots). Estimates indicate (a) differences in leaf, seed and seedling traits for each elevation, and (b) effects of each environmental variable on the respective trait values (see Tables 1 and 2 for details). Plots was included as a random effect (n = 9). Estimates, standard errors, degrees of freedom, t values and probability of tested effects are shown in columns. Significant values ($P < 0.05$) are marked with bold font.

	Estimate	SE	df	t value	p
a)					
1000 m : Specific leaf area (SLA)	0.81	0.23	24.02	3.59	0.001
1000 m : Seed mass	0.67	0.21	17.16	3.25	0.005
1000 m : Initial seedling height (ISH)	0.39	0.21	19.00	1.85	0.081
2000 m : SLA	-0.80	0.31	22.01	-2.58	0.017
2000 m : Seed mass	-0.70	0.29	16.77	-2.44	0.026
2000 m : ISH	-0.49	0.29	18.07	-1.66	0.114
3000 m : SLA	-1.88	0.34	29.51	-5.60	<0.001
3000 m : Seed mass	-1.29	0.29	17.16	-4.45	<0.001
3000 m : ISH	-0.68	0.30	19.46	-2.25	0.036
b)					
Specific leaf area (SLA)	0.04	0.10	32.74	0.45	0.653
Seed mass	-0.01	0.09	25.34	-0.10	0.925
Initial seedling height (ISH)	-0.08	0.09	26.93	-0.89	0.383
Soil C/N : SLA	-0.21	0.09	153.37	-2.23	0.027
Soil C/N : Seed mass	0.10	0.09	112.43	1.12	0.266
Soil C/N : ISH	-0.13	0.09	109.60	-1.43	0.155
Canopy openness : SLA	-0.04	0.09	177.16	-0.42	0.679
Canopy openness : Seed mass	-0.09	0.08	177.57	-1.05	0.297
Canopy openness : ISH	-0.26	0.09	176.87	-2.96	0.004

Table S2. Mean daily temperature, daily precipitation and annual precipitation at the plot level. The measurements were obtained from three climate stations (one per elevation) during the study period between June 2019 – June 2020 and then extrapolated to the remaining plots.

Plot name	Elevation (m a.s.l.)	Mean daily temperature [°C]	Mean daily precipitation [mm]	Annual precipitation [mm]
Bombuscaro 1	1000	19.5	6.1	2195.4
Bombuscaro 2	1000	19.4	6.2	2220.7
Bombuscaro 3	1000	19.3	6.2	2239.7
San Francisco 1	2000	15.4	5.3	2036.5
San Francisco 2	2000	15.3	5.5	2121.3
San Francisco 3	2000	15.7	5.8	2229.0
Cajanuma 1	3000	10.3	7.4	2721.7
Cajanuma 2	3000	10.4	7.4	2709.8
Cajanuma 3	3000	10.0	7.8	2797.2

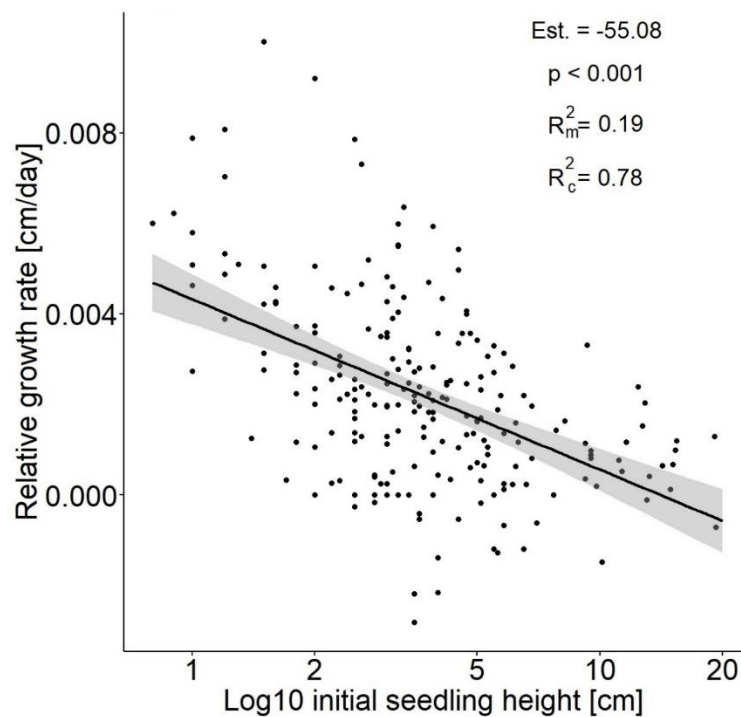


Fig. S1. Relationship between relative growth rate and initial seedling height. Relative growth rate (see Equation 1) was calculated for individual seedlings that were recorded over repeated censuses. Both variables were log-transformed prior to the analysis; the labels on the x-axis were back-transformed (\log_{10}). Given are the model estimate with its associated p-value and the marginal and conditional R^2 values, based on a Linear Mixed Model controlling for random variation among species ($n = 220$ seedlings of 83 species).

A2: Seedling recruitment of large- and small-seeded species in forest and pastures in Southern Ecuador

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Title: Seedling recruitment of large- and small-seeded species in forest and pastures in Southern Ecuador

Status: submitted

Author contributions:

(1) Concept and design

MB, 80%;

ELN, MS in total 20%

(2) Conducting tests and experiments

MB, 75%, and **DAR**, 25%, established the seed sowing experiment

MB 90%, and **DAR** 10%, measured seedlings and assessed seedling recruitment

MB 20% and **DAR** 80%, installed iButtons to measure surface temperature

MB measured abiotic and biotic filters on study plots, 100%

(3) Compilation of data sets and figures

MB processed the seed sowing experiment data, 100%;

MB prepared all data for analyses, 100%;

MB prepared all figures and tables, 100%

(4) Analysis and interpretation of data

MB calculated proportions of seedling establishment and recruitment success, 100%;

MB tested for seed size, habitat and environmental effects on seedling recruitment, 100%;

MB interpreted the results, 85%

with input from **ELN**, **CIE**, **DAR**, **MS** in total 15%

(5) Drafting of manuscript

MB, 85%;

ELN, **CIE**, **DAR**, **MS** in total 15%;

Supplementary material

SI: Methods

Seedling recruitment of small- and large-seeded species in forests and pastures in Southern Ecuador

Abstract

Seedling recruitment is a key process of plant regeneration that often depends on plant functional traits, such as seed size. To optimize forest restoration efforts, we need to better understand how seedling recruitment of different seed sizes varies along environmental gradients with strong variation in abiotic and biotic factors. To understand these interacting effects, we conducted a sowing experiment in forests and pastures in the tropical mountains of southern Ecuador. We quantified seed germination and seedling recruitment in relation to temperature, soil moisture and biotic pressures. We sowed seeds of five tree species of varying seed size at three elevations (1000, 2000 and 3000 m a.s.l.) in primary forest and pastures. We tested (1) how habitat type influences the recruitment of seedlings belonging to three small- and two large-seeded species, and (2) how abiotic and biotic factors limit seedling recruitment of species with different seed sizes. We found that seedlings of the two large-seeded species recruited better than seedlings of the three small-seeded species, but only in the forest habitat. Seedling recruitment of large seeds was primarily limited by high surface temperature, which explains lower recruitment of large seeds in pastures compared to forests. Our study shows that seed size can be a key trait mediating variability in seedling recruitment in tropical ecosystems. We conclude that restoration measures should aim to mitigate extreme temperatures in tropical pastures to aid the natural regeneration of large-seeded tree species.

Introduction

Seedling recruitment is an essential process fostering plant regeneration and forest restoration (Gallegos et al., 2016; Neuschulz et al., 2016). At the seedling stage, environmental filtering by abiotic and biotic stress is a major cause of plant mortality (Alvarez-Clare & Kitajima, 2009; Wright et al., 2005). A key challenge in restoration ecology is therefore to determine the abiotic and biotic factors that limit seedling survival (Palma & Laurance, 2015). However, we still need to understand to what extent environmental filtering limits seedling establishment in forests and human-modified habitats in tropical mountain environments (de la Peña-Domene et al., 2013; García-Hernández et al., 2019).

Environmental gradients in tropical mountains are particularly suited to study shifts in plant communities and demography in relation to changing abiotic conditions (Malhi et al., 2010; Toledo-Aceves et al., 2019). Abiotic factors, such as temperature and precipitation, influence seedling recruitment (Song et al., 2016b) and differ greatly across elevations and habitats (García-Hernández et al., 2019; Holl et al., 2000; Malhi et al., 2010). For instance, constantly high temperatures promote high seedling diversity at lower elevations (Song et al., 2016b), while seedling recruitment locally depends on environmental conditions, such as canopy openness, surface temperature and soil moisture (Comita et al., 2009; Muñoz Mazón et al., 2022; Song et al., 2016a). Moreover, the interplay of different abiotic factors, such as high surface temperature and low soil moisture, may result in periodic droughts, which can be detrimental to seedlings (Martínez-Garza et al., 2013; Slot & Poorter, 2007). In addition, biotic pressures caused by herbivores and fungal pathogens have been shown to be the main driver of high seedling mortality in tropical forests (Bagchi et al., 2014). These antagonistic interactions can significantly limit seedling recruitment, contingent on the ecological context (Bachelot et al., 2016; Galmán et al., 2018; Jeffs et al., 2018; Moreira et al., 2018). For instance, insect herbivory can follow hump-shaped patterns across elevations in tropical mountains (Sam et al.,

2020), and leaf damage of plants is more likely to occur in human-altered habitats than inside natural forests (Morante-Filho et al., 2016).

Plant functional traits mediate environmental effects on plant demography, and hence, plant regeneration (Violle et al., 2007). Moles and Westoby (2004) showed that seed size is one of the most influential traits in plant recruitment. In the tropics, seedlings that emerge from large seeds are more likely to survive than seedlings emerging from small seeds (Macera et al., 2017; Rose & Poorter, 2003). However, this phenomenon may vary depending on the environmental context. For example, seedlings of small-seeded pioneer species grow faster in forest gaps than seedlings of late successional, large-seeded species (Grubb et al., 2013). As interactions between environmental conditions and plant traits can alter the plant regeneration cycle (Larson & Funk, 2016; Norden et al., 2009), we assume that seed size can mediate the effects of abiotic and biotic factors on plant regeneration (Macera et al., 2017; Pereira De Souza & Valio, 2001). Recruitment experiments, involving plant species differing in seed size, are ideally suited to study the interacting effects of environmental conditions and seed size on plant recruitment (Cole et al., 2011; Macera et al., 2017).

Although recent studies have investigated which factors influence seedling recruitment across environmental gradients (Garca-Hernandez et al., 2019; Lin et al., 2017), the effects of abiotic and biotic factors on plant species with different traits have rarely been studied in tropical mountains (Rozendaal et al., 2019; but see Toledo-Aceves et al., 2019). In addition, montane habitats are prone to drastic alterations due to land-use change (Lippok et al., 2013; Sales et al., 2020). Deforestation by humans limits plant recruitment (Gallegos et al., 2016; Granados et al., 2017), yet we lack field experiments that test how seedling recruitment differs among contrasting habitats (Cole et al., 2011; but see de la Pena-Domene et al., 2017; Toledo-Aceves et al., 2019). Ultimately, experiments in forests and human-modified habitats can inform the selection of plant species for forest restoration (Bastin et al., 2019). While previous studies have

recommended using late-successional species and seed nucleation to restore tropical montane forests in Costa Rica (Cole et al., 2011; Palma & Laurance, 2015), there is limited information on seedling recruitment in deforested habitats of other tropical mountains (but see Toledo-Aceves et al. 2021).

We conducted a recruitment experiment with five species of different seed sizes comparing two habitats (i.e., forest and pastures) in the tropical montane forest in the Ecuadorian Andes. First, we tested how the recruitment of seedlings emerging from small and large seeds differs between natural and deforested habitats (i.e., primary forest vs. pastures) at 1000, 2000 and 3000 m a.s.l. We expected higher seedling recruitment of large-seeded plant species than of small-seeded plant species (Macera et al., 2017; Moles & Westoby, 2004) and lower overall recruitment in pastures than in forest due to harsher abiotic conditions in pastures (de la Peña-Domene et al., 2017). We also expected that large-seeded species may recruit better in pastures than small-seeded species, due to their higher robustness against high temperatures and periodic droughts (Martínez-Garza et al., 2013). Second, we analysed the direct effects of abiotic and biotic factors on seedling recruitment of small- and large-seeded species. We expected that harsh abiotic conditions in pastures (high surface temperatures, low soil moisture) would reduce seedling recruitment, due to a high mortality of seedlings emerging from small seeds (Gallegos et al., 2015; Morales et al., 2018). We further hypothesized that biotic pressures, such as insect herbivory, are more likely to reduce the recruitment success of small-seeded species, because leaf damage in seedlings growing from small seeds is more likely to hinder their further development (Green & Juniper, 2004).

Materials and methods

Study area

The field study was conducted in the Podocarpus National Park, San Francisco Reserve and in pastures surrounding these areas in southern Ecuador (see the map in the Appendix A: Fig. A1). This area covers an elevational gradient between 1000 and 3600 m a.s.l., and reaches from premontane forest to upper evergreen tropical montane forest and subpáramo (Homeier et al., 2013; Kessler & Kluge, 2008). The mean annual precipitation ranges from approximately 2000 mm to 4500 mm, and the mean annual temperature ranges from 20°C at 1000 m a.s.l. and 15.5°C at 2000 m a.s.l. to 10°C at 3000 m a.s.l. (Bendix et al., 2008). The surroundings of the National Park have experienced severe deforestation during the last decades. Cleared sites have been overgrown by alien grass species (Homeier et al., 2013) and have been converted into cattle pastures.

Our research was carried out on a total of 18 1-ha plots established in the frame of the DFG research unit RESPECT (Bendix et al., 2021; Fig. 1). At 1000 m a.s.l., three forest plots were located in the lower montane forest of Bombuscaro valley inside the Podocarpus National Park, and three pasture plots were placed outside the National Park close to Zamora. Plots at 2000 m a.s.l. (three forest and three pasture plots) were located on opposite sides of the San Francisco river next to the San Francisco Research Station. The three forest plots at 3000 m a.s.l. were located in the upper montane forest in Cajanuma on the western border of the Podocarpus National Park, while the three pasture plots were located outside the National Park. The distance between plots was at least 100 m.

Seed sowing experiment

On each of the 18 plots, we randomly selected three relatively flat subplots of roughly 15 m² with no trees, resulting in a total of 54 subplots (Fig. 1). The distance between subplots was a minimum of 20 m. Prior to the experiment, we cleared the undergrowth on these subplots of

existing vegetation. All subplots located in the pastures were fenced to avoid trampling by cattle, whereas all forest subplots remained unfenced because of the rarity of large mammals in the forest.

We mainly selected mid- and late-successional fleshy-fruited tree species, because emergence rates of early-successional species producing numerous tiny seeds are very low (Cole et al., 2011). To collect seeds for the experiments, we monitored the fruiting phenology of 30 abundant tree species from September 2018 to August 2019 across the elevational gradient. As the production of fruits in the tropics is characterized by a high asynchrony (Ramirez-Parada et al., 2020), most of the monitored species did not produce sufficient numbers of fruits to be harvested. Because large-seeded species decrease in abundance with increasing elevation (Duivenvoorden & Cuello, 2012), we could not collect large-seeded species at the highest elevation. In 2018 and 2019, we were able to harvest fruits from five common tree species in sufficient quantities. We used species belonging to different families and functional groups to increase the response diversity in the experiment (Palma & Laurance, 2015). The following species were used for the sowing: *Ocotea* sp. (Lauraceae) at 1000 m; *Clusia ducuoides* (Clusiaceae), *Hieronyma fendleri* (Phyllanthaceae) and *Tapirira guianensis* spp. *subandina* (Anacardiaceae) at 2000 m; *Hedyosmum purpurascens* (Chloranthaceae) at 3000 m (see also Appendix A: Table A1 and Acosta Rojas et al., 2021). Species were split into two groups according to their seed size (Markl et al., 2012): three small-seeded species with a mean seed mass smaller than 0.1 g (i.e., *H. fendleri* – 0.0079 g; *C. ducuoides* – 0.0054 g; *H. purpurascens* – 0.0135 g) and two large-seeded species with a mean seed mass larger than 0.1 g (i.e., *Ocotea* sp. – 0.5272 g; *T. guianensis* spp. *subandina* – 0.4063 g).

We sowed seeds of each species in both forest and pasture plots at their elevation of origin. We did not transplant seeds outside of the natural occurrence of the study species, because we aimed to compare differences in seedling recruitment across habitats at the respective home elevation.

None of the species used for the experiment occurred outside the elevation of origin. Sowing times depended on the time of fruiting and therefore occurred between December 2018 and August 2019 reflecting the natural variation among the study species (i.e., *Ocotea sp.* – December 2018; *H. fendleri* and *C. ducuoides* – February 2019; *H. purpurascens* – June 2019; *T. guianensis* ssp. *subandina* – August 2019).

In each subplot, we set up four quadrates of 1 m² to sow seeds and bordered them with strings. Because large-seeded and small-seeded species differ in germination rates, we sowed a larger number of seeds for small-seeded than for large-seeded species (Paz & Martínez-Ramos, 2003). We sowed ten small or two large seeds into a 10x10 cm patch of mosquito net filled with soil and protected it with a metallic mesh tube that was open at the top to lower seed predation by rodents and birds (Paine & Beck, 2007) and to easily find and handle seedlings at repeated surveys. Insect herbivores were able to access and feed on emerging seedlings. In total, 7214 small and 1248 large seeds were sown (sum = 8462 seeds; see also Appendix A: Table A1 in Supplementary Material). Prior to sowing, all seeds were treated for 1 min in 5% chlorine bleach solution to clean the seeds of any fungal pathogens (Luna et al., 2014).

Every three months, we recorded and marked each emerging seedling with a plastic cable tie. Depending on the study species and the timing of the sowing experiment, the monitoring period lasted between 10 to 18 months: *Ocotea sp.* – 18 months; *H. fendleri* and *C. ducuoides* – 15 months; *H. purpurascens* – 12 months; *T. guianensis* ssp. *subandina* – 10 months. During each visit, we measured seedling height and recorded traces of herbivory and fungal pathogens. We considered any kind of external damage including bites and leaf mining as traces of herbivory (Muehleisen et al., 2020). Likewise, changes in leaf colour and/or necrotic spots on leaves were considered as traces of fungal pathogens (Benítez-Malvido & Lemus-Albor, 2005). At the end of the experiment, we harvested each seedling to measure its dry biomass. After careful cleaning of the seedlings with water, we cut the stems from the roots to separate below- and aboveground

biomass. Roots and stems with leaves were then put into paper bags and dried in the oven at 60°C for 72 h. After drying the samples, we weighed the aboveground- and belowground dry biomass of each seedling with a high precision analytical balance (KERN & SOHN GmbH, Germany). Based on these two measures, we calculated the ratio between below- and aboveground biomass (i.e., root-to-shoot ratio) for each seedling as a relative measure of below-versus aboveground investment.

From the seedling monitoring, we quantified different variables of plant regeneration. To ensure the comparability among study species, establishment and recruitment variables were measured approximately one year after sowing for each study species (10 months in case of *T. guianensis* ssp. *subandina*, 12 months for all other species). “Seedling establishment” was defined as the number of *all* seedlings which germinated and then developed cotyledons or leaves 10 – 12 months after sowing, divided by the total number of seeds sown for each species at each subplot. “Recruitment success” was defined as the number of seedlings with developed leaves encountered 10 – 12 months after sowing, divided by the total number of seeds sown for each species at each subplot. In addition, we analysed differences in below- and aboveground biomass at the end of the experiment and compared the root-to-shoot ratio between habitats and seed sizes. Below- and aboveground biomasses were log-transformed prior to the analysis to approximate normality.

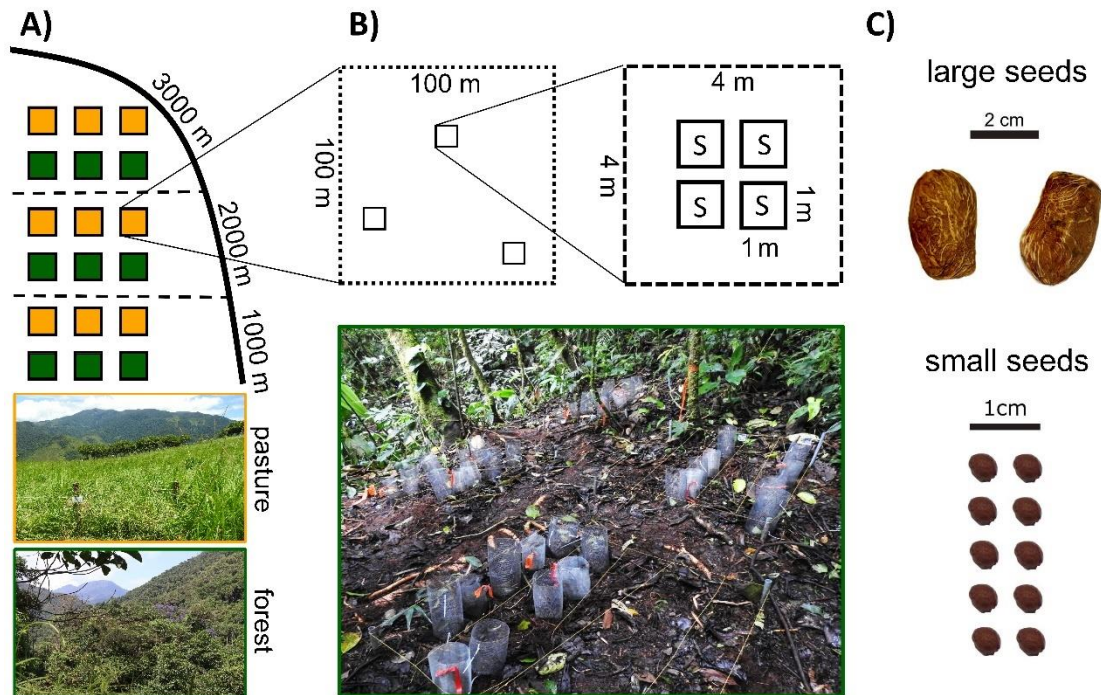


Fig. 1. Design of a sowing experiment with five species in the tropical mountains of South Ecuador. (A) Schematic overview of the location of plots ($n = 18$) at three elevations a.s.l. Green squares correspond to primary forest plots, yellow squares indicate pasture plots. Photographs show habitat differences. (B) Each 1-ha plot contained three subplots ($n = 54$). Within each subplot, four sowing units (S) were established ($n = 216$). Seeds of different species were protected by wire cages that were open at the top (see sowing unit in the forest). (C) Examples of a large-seeded species (*Tapirira guianensis* ssp. *subandina*; 0.406 g) and a small-seeded species (*Hieronyma fendleri*; 0.008 g) used in the experiment. Overall, we were able to sow seeds of one large-seeded species at 1000 m, one large-seeded species and two small-seeded species at 2000 m, and one small-seeded species at 3000 m.

Abiotic factors

We buried several data loggers at the depth of sown seeds (ca. 2 cm deep) to measure surface temperature. Surface temperature was recorded at all 54 subplots using iButton data loggers (Maxim/Dallas Semiconductor Corp., Texas, U.S.A) every 4 h throughout an entire year (June 2019 – June 2020). We calculated two measures related to surface temperature: mean daily mean surface temperature and mean daily maximum surface temperature. We decided to use mean daily maximum surface temperature values for the three driest months (September–November 2019) in the analyses, as extreme temperatures increase seedling mortality by drought stress (Holl, 1999). Average soil moisture was measured at all subplots twice during

two seasons: dry (i.e., less rainy) season (October 2019) and rainy season (May-June 2020) using a tensiometer (SM150 Kit, Delta-T Devices Ltd., UK). We used soil moisture records from the dry season in the analyses, assuming that low soil moisture would increase drought stress in combination with high temperatures. Both abiotic variables were non-correlated at the subplot level (Pearson's $r < 0.15$, $p > 0.05$). Summary statistics (mean and SD) of both abiotic variables are given in the Appendix A: Table A2.

Biotic factors

We quantified the incidence of fungal pathogens and insect herbivory on seedlings. We obtained means of both biotic factors for each census and subplot by dividing the number of seedlings with fungal pathogen and/or herbivory traces by the number of established seedlings, and based on this calculated a mean incidence across the censuses for each subplot. As both biotic variables were measured on individual seedlings, they directly reflect biotic pressures on the recruiting seedlings. Given that the two biotic variables were highly correlated (Pearson's $r = 0.82$, $p < 0.001$) and yielded qualitatively identical results in their effects on seedling recruitment, we selected insect herbivory incidence to be included in the analyses. Both biotic variables were not correlated with abiotic variables at the subplot level (Pearson's $r < 0.15$, $p > 0.05$). Summary statistics (mean and SD) of both biotic variables can be found in the supplementary material (Appendix A: Table A2).

Statistical analysis

All statistical analyses were carried out using R 4.2.1 (R Core Team 2022) and the associated 'dplyr', 'ggplot2', 'lme4', "lmerTest", 'MuMIn' 'plyr' and 'tidyr' packages (cran.r-project.org/web/packages).

We performed analyses of seedling establishment, recruitment success, below- and aboveground biomass and root-to-shoot ratio with (Generalized) Linear Mixed Models. Seedling establishment and recruitment success were analysed with a binomial error distribution, and biomass-related variables with a Gaussian error distribution. All models contained subplots nested in plots and species identities as random effects. Subplot identity controlled for microhabitat effects on recruitment beyond the effects of the respective predictor variables, plot identity controlled for elevational and plot-specific effects on recruitment, and species identity controlled for differences among study species in addition to those of seed size (see Appendix A: Fig. A2 for species-specific differences).

First, we tested the main and interaction effects of habitat and seed size on seedling recruitment and biomass-related variables (Hypothesis 1) according to our experimental design (Fig. 1). The mixed-effect model allowed us to test the interacting effects of habitat and seed size on seedlings, accounting for variation in plot and species identity. Second, we tested the effects of abiotic and biotic factors on seedling recruitment and biomass-related variables of seeds with different sizes (Hypothesis 2). We excluded habitat effects from these models and tested the main and interaction effects of the respective abiotic and biotic factors with seed sizes because abiotic and biotic variables strongly differed between forests and pastures (see the Appendix A: Table A2). In order to simplify these models, we started with a full model including all main and interaction effects and then followed a step-wise procedure to first remove non-significant interaction terms, followed by non-significant main effects. The final models therefore maintained only the significant relationships (i.e., with a p value < 0.05).

Results

Over the entire experimental period, a total of 913 seedlings established out of 8462 sown seeds across habitat types and elevations. Overall, 370 seedlings established out of 1248 large seeds

(29.6%), and 543 seedlings established out of 7214 small seeds (7.5%). After the one-year-period after sowing, seedling establishment and recruitment success differed between species (Appendix A: Fig. A2). The variation in seedling establishment of the three small-seeded species ranged between 0 and 0.40 (shown as a proportion, $n = 32$ subplots at mid and high elevations; see Fig. 1). Recruitment success of the three small-seeded species varied between 0 and 0.30. Similarly, seedling establishment of the two large-seeded species varied between 0.03 and 0.75, and their recruitment success ranged between 0 and 0.50 ($n = 36$ subplots at low and mid elevations). Although seedling establishment and recruitment success of the small-seeded species varied greatly, *Ocotea* sp. and *Tapirira guianensis* ssp. *subandina* (large-seeded species) established and recruited on average better than *Clusia ducuoides*, *Hedyosmum purpurascens* and *Hieronyma fendleri* (small-seeded species, Appendix A: Table A3).

Seedling recruitment of three small- and two large-seeded species in forest and pastures

Seedling establishment and recruitment success were higher for the large-seeded than for the small-seeded species, but differences were contingent on the habitat type (Fig. 2; Table 1). Seedlings growing from large seeds were similarly likely to establish in forest and pastures, whereas establishment of seedlings growing from small seeds was more than twice as high in the pastures than in the forest (Fig. 2A). Recruitment success of seedlings of the two large-seeded species was significantly higher in the forest than in the pastures (Fig. 2B; Table 1), whereas recruitment success of the three small-seeded species was about twice as high in the pastures compared to the forest (Fig. 2B). Fixed effects explained almost 40% of the variation in seedling establishment and more than 30% in recruitment success, whereas the full model including the random terms explained over 85% of the variation in both tested variables (Table 1). Species-level patterns corresponded to these main findings showing that the three small-seeded species established better in the pastures, whereas recruitment success of the two large-seeded species was higher in the forest than in pastures (see Appendix A: Fig. A2). The

interaction between seed size and habitat remained highly significant for recruitment variables while accounting for the entire experimental period (10 – 18 months; see Appendix A: Table A4).

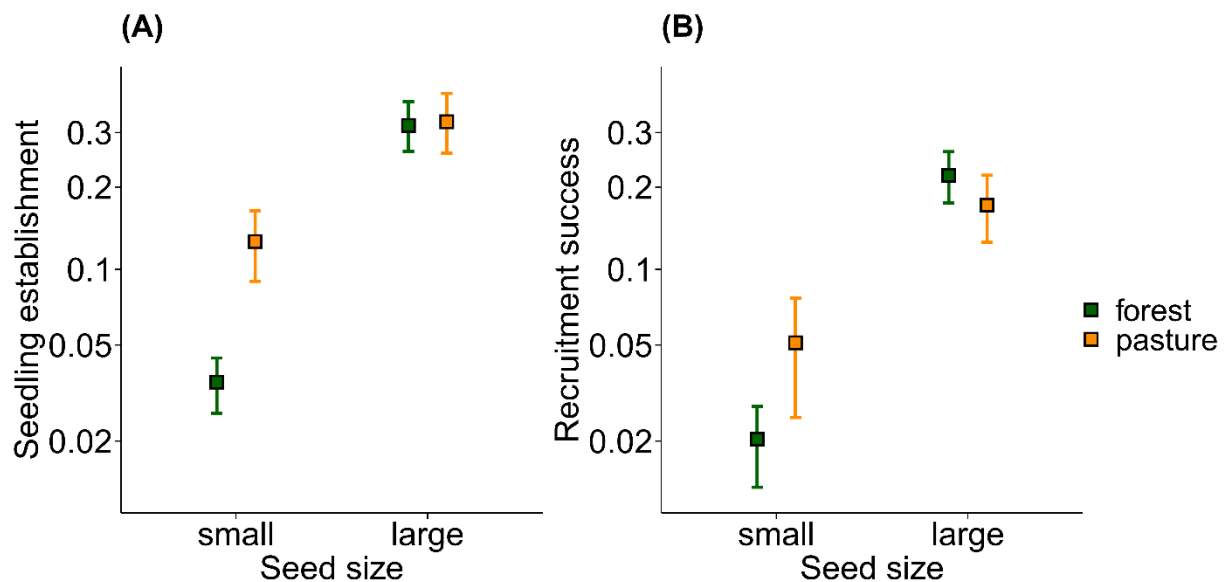


Fig. 2. Seed size-dependent seedling establishment and recruitment success in two habitat types (green: forest, yellow: pasture) in the tropical mountains of South Ecuador. (A) Seedling establishment of three small- and two large-seeded species, shown as the proportion of seedlings established from seeds at the respective sowing units (see Fig. 1B) one year after sowing (10 months in case of *T. guianensis* ssp. *subandina*); (B) recruitment success of three small- and two large-seeded species, shown as the proportion of seedlings recruited one year after sowing (10 months in case of *T. guianensis* ssp. *subandina*). Recruitment variables (A and B) are presented on a logit y-axis (tick labels are back-transformed to the original scale). Summary statistics of the effects of habitat and seed size on seedling establishment and recruitment success, controlling for effects of species identities are shown in Table 1. Squares indicate mean proportions of seedling establishment and recruitment success, respectively, and error bars correspond to 95% confidence intervals around the mean.

Table 1. Generalized linear mixed effect models (GLMMs) testing the interacting effects of habitat and seed size on (A) seedling establishment and (B) recruitment success of five tree species in the tropical mountains of South Ecuador after the one-year-period (10 months in case of *T. guianensis* ssp. *subandina*). Subplot nested in plot and species identity were included as random effects in the models ($n = 54$ subplots; $n = 18$ plots; $n = 5$ species). Estimates, standard errors, z values and p values of tested effects are shown in columns. P values in bold font indicate significant effects. Marginal R^2 (R^2m) and conditional R^2 (R^2c) values of the respective model are shown in the last two columns.

	<i>Estimate</i>	<i>Std. Error</i>	<i>z value</i>	<i>p</i>	R^2m	R^2c
A) Seedling establishment					0.39	0.95

A2: Seedling recruitment of large- and small-seeded species in forest and pastures in Southern Ecuador

(Intercept)	-0.74	0.55	-1.35	0.177		
Seed size (small)	-2.66	0.64	-4.13	<0.001		
Habitat (pasture)	-0.66	0.42	-1.59	0.112		
Seed size (small) x habitat (pasture)	2.08	0.26	8.07	<0.001		
B) Recruitment success					0.33	0.85
(Intercept)	-1.38	0.59	-2.34	0.019		
Seed size (small)	-2.55	0.72	-3.55	<0.001		
Habitat (pasture)	-0.96	0.41	-2.37	0.018		
Seed size (small) x habitat (pasture)	2.02	0.36	5.62	<0.001		

At the end of the experiment, belowground and aboveground biomass differed between seed sizes and habitats (Fig. 3; Table 2). The two large-seeded species had more than ten times larger belowground and aboveground biomass in comparison to the three small-seeded species. Below- and aboveground biomass were slightly, but significantly higher in pastures than in forests for both small-seeded and large-seeded species (Fig. 3; Table 2). The root-to-shoot ratio, a measure of the relative investment into above- vs. belowground biomass, was about two times higher in pastures than in forest for both large- and small-seeded species (Fig. 3C; Table 2). Habitat type and seed size explained about 70% of the variation in the below- and aboveground biomass and about 17% for the root-to-shoot ratio (Table 2).

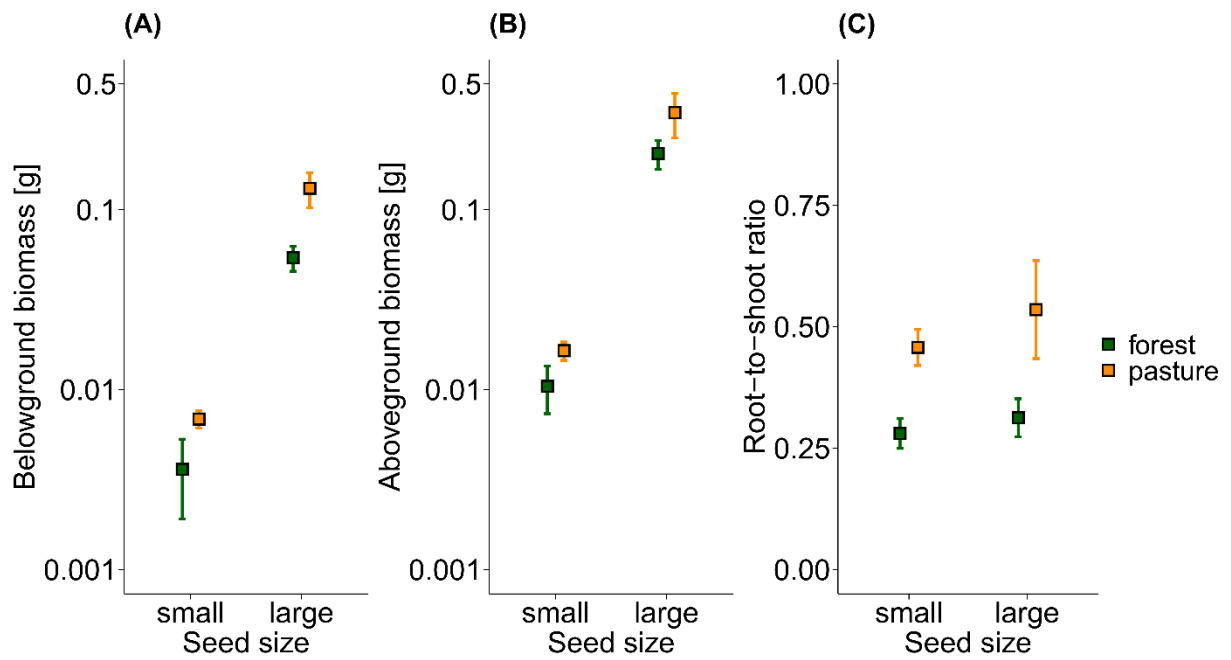


Fig. 3. (A) Belowground biomass, (B) aboveground biomass and (C) root-to-shoot ratio in seedlings of three small- and two large-seeded species in two habitat types (green: forest, yellow: pasture) in the tropical mountains of South Ecuador at the end of the experiment. Biomass variables (A and B) are presented on a logarithmic y-axis (labels are back-transformed, \log_{10}). The output of models testing the effects of habitat and seed size is shown in Table 2. Squares indicate means and error bars correspond to 95% confidence intervals around the mean.

Table 2. Linear mixed effect models (LMMs) testing the effects of seed size and habitat type on the (A) belowground and (B) aboveground biomass and (C) root-to-shoot ratio in seedlings of three small- and two large-seeded species in the tropical mountains of South Ecuador at the end of the experiment. Biomass variables (A and B) were log-transformed prior to the analysis. Subplot nested in plot and species identity were included as random effects in the models (n = 54 subplots; n = 18 plots; n = 5 species). Estimates, standard errors, degrees of freedom, t values and p values of tested effects are shown in columns. P values in bold font indicate significant effects. Marginal R^2 (R^2_m) and conditional R^2 (R^2_c) values of the respective model are shown in the last two columns.

	<i>Estimate</i>	<i>Std. Error</i>	<i>df</i>	<i>t value</i>	<i>p</i>	<i>R²_m</i>	<i>R²_c</i>
A) Log₁₀ belowground biomass						0.71	0.75
(Intercept)	-1.47	0.08	6.57	-18.98	<0.001		
Seed size (small)	-1.34	0.08	3.51	-16.27	<0.001		
Habitat (pasture)	0.47	0.08	13.07	5.70	<0.001		
B) Log₁₀ aboveground biomass						0.72	0.79
(Intercept)	-0.9	0.11	3.3	-7.91	0.003		
Seed size (small)	-1.26	0.14	2.81	-8.98	0.003		
Habitat (pasture)	0.21	0.07	12.05	3.15	0.008		
C) Root-to-shoot ratio						0.17	0.39
(Intercept)	0.32	0.08	3.28	4.11	0.022		
Seed size (small)	-0.08	0.10	2.79	-0.80	0.485		
Habitat (pasture)	0.24	0.04	10.98	5.43	<0.001		

Seedling recruitment of three small- and two large-seeded species in relation to abiotic and biotic factors

Surface temperature was the most important explanatory variable in the models (Table 3) and interacted with seed size in the effects on seedling establishment and recruitment success. Seedling establishment and recruitment success of large-seeded species decreased with increasing temperature, whereas small-seeded species were more likely to establish at high temperatures. According to the model (Table 3), an increase in one standard deviation unit of surface temperature ($\sim 5^\circ\text{C}$) corresponded to a decrease in the odds of establishment and recruitment by about 40%. For small-seeded species, an increase in one standard deviation unit of surface temperature corresponded to an increase of about 60% and 70%, respectively. In addition, the recruitment success of small-seeded species increased with increasing soil

moisture (changes in odds by about 40%, Table 3B). The abiotic variables explained about 30% of the variation in seedling establishment and recruitment success (Table 3). Neither seedling establishment nor recruitment were significantly related to insect herbivory incidence. Below- and aboveground biomass of seedlings were unrelated to abiotic or biotic variables, whereas root-to-shoot ratio was positively associated with surface temperature for both small- and large-seeded species (effect of surface temperature on root-to-shoot ratio: estimate (standard deviation units) = 0.08, t value = 5.23, $p < 0.001$)

Table 3. Generalized linear mixed effect models (GLMMs) testing the interacting effects of abiotic variables and seed size on (A) seedling establishment and (B) recruitment success of three small- and two large-seeded species in the tropical mountains of South Ecuador after the one-year-period (10 months in case of *T. guianensis* ssp. *subandina*). Subplot nested in plot and species identity were included as random effects in the models ($n = 54$ subplots; $n = 18$ plots; $n = 5$ species). Estimates, standard errors, z values and p values of tested effects are shown in columns. P values in bold font indicate significant effects. Marginal R^2 (R^2m) and conditional R^2 (R^2c) values of the respective model are shown in the last two columns. Temperature and soil moisture were scaled to zero mean and unit variance prior to the analyses. Shown are minimum adequate models after removing non-significant main and interaction effects of abiotic and biotic variables. Herbivory incidence was never significant.

	<i>Estimate</i>	<i>Std. Error</i>	<i>z value</i>	<i>p</i>	<i>R²m</i>	<i>R²c</i>
A) Seedling establishment					0.33	0.91
(Intercept)	-0.84	0.69	-1.22	0.221		
Seed size (small)	-1.72	0.88	-1.97	0.049		
Max. temperature	-0.54	0.21	-2.54	0.011		
Seed size (small) x Max. temperature	1.02	0.18	5.64	<0.001		
B) Recruitment success					0.34	0.86
(Intercept)	-1.62	0.68	-2.37	0.018		
Seed size (small)	-1.65	0.87	-1.90	0.058		
Max. temperature	-0.46	0.22	-2.12	0.034		
Soil moisture	-0.05	0.15	-0.32	0.753		
Seed size (small) x Max. temperature	1.01	0.22	4.58	<0.001		
Seed size (small) x Soil moisture	0.38	0.16	2.39	0.017		

Discussion

Overall, we found that patterns of seedling recruitment varied between species with different seed sizes and between forests and pastures. Habitat effects on seedling recruitment were

contingent on seed size. The two large-seeded species (sown at low and mid elevations) established more frequently than the three small-seeded species (sown at mid and high elevations), particularly in forest habitats. Seed-size-specific differences in seedling recruitment were mainly related to the substantially lower recruitment of the two species with large seeds at high surface temperatures in contrast to the three small-seeded species. Our findings emphasize that seed size is a key trait mediating differences in seedling recruitment between forests and pastures and provide important information for restoration efforts of pastures in tropical mountains.

Habitat type and seedling recruitment

We found that seedlings of large-seeded species were more likely to establish than small-seeded species, but only in the forest habitat. Consequently, seed size seems to be a driving factor for differences in the regeneration process between natural and deforested habitats of tropical montane forests. A general advantage of large-seeded species to recruit has been detected in many tropical forests (Dalling & Hubbell, 2002; Muñoz et al., 2017; Paz & Martínez-Ramos, 2003), but the positive relationship between large seed size and seedling survival has not been confirmed as a general rule in ecology (Moles & Westoby, 2004). A previous study on several tree species from tropical mountains by de la Peña-Domene et al. (2018) has shown that seedlings growing in pastures had generally lower establishment than seedlings in forest habitats. We found this pattern only for seedlings of the two large-seeded species from the lower elevations. In contrast, seedling establishment and recruitment success of the three small-seeded species sown at mid and high elevations were more likely in pastures than in forests. Nonetheless, expanding the experiment by adding more species from different elevations would be needed to confirm these interacting effects between habitat type and seed size.

We further found differences in belowground biomass of seedlings growing in different habitats. Belowground biomass was generally higher in pastures than in forests. The root-to-shoot ratio was significantly higher in pastures than in forest for both small-seeded and large-seeded species. This shows that seedlings growing in pastures generally allocate more biomass into roots compared to seedlings growing in forests. We assume that the high investment into root biomass in pastures may be related to frequent droughts in pastures (Markesteyn & Poorter, 2009). Similar trade-offs in biomass allocation strategies have also been reported for several tree seedlings in response to soil nutrients (Umaña et al., 2021). In particular under limited soil P, seedlings have been shown to invest more into roots than into stems to accelerate growth (Umaña et al., 2021). Our study potentially reflected this trade-off in biomass allocation due to differences in resource limitations between forest and pasture habitats. Our findings call for further studies comparing allocation patterns of seedlings across habitat gradients in tropical forests.

Abiotic and biotic factors and seedling recruitment

Surface temperature was the main factor mediating recruitment differences of seedlings belonging to small- and large-seeded species across forest and pasture habitats (Table 3). We found that seedling establishment and recruitment success decreased with surface temperature but only for seedlings of the two large-seeded species sown at the lower elevations. That is, recruitment success of large-seeded species decreased by about 50% with a temperature increase of about 5°C. Surface temperatures were generally higher in pastures than in forests (Appendix A: Table A2), suggesting that this difference was mainly responsible for the lower recruitment of seedlings belonging to the two large-seeded species in pastures. This corresponds with the outcome of a recent study from Northern Peru which showed that maximum temperatures inside montane forests tend to be around 4°C lower compared to outside forests

(Newell 2022). Another study from the slopes of the Peruvian Andes has reported that solar irradiation limited seedling establishment of two *Polylepis* species, possibly due to increased soil temperature during a dry season (Morales et al., 2018). In other studies from tropical mountains, high temperature and seasonal drought in pastures have been identified as a limiting factor for seedling recruitment (de la Peña-Domene et al., 2017; Martínez-Garza et al., 2013). Intriguingly, we found that the three small-seeded species sown at mid and high elevations recruited better than large-seeded species at high surface temperatures and under high soil moisture. Seedlings of small-seeded species were apparently more resistant to extreme temperatures compared to large-seeded species, especially if a high soil moisture was maintained. A reason for this could be related to a lower exposure of these seedlings to high surface temperatures, as small seedlings may be better covered by surrounding vegetation than large ones. In addition, higher allocation into roots may have helped these seedlings to survive drought events in pastures. Previous studies identified species-specific differences in drought resistance across tropical seedlings (Kupers et al., 2019; Slot & Poorter, 2007). Such interspecific differences may be linked to distinct ecological strategies of plant species corresponding to differences in shade tolerance (Kupers et al., 2019).

In our study, seedling establishment and recruitment success were unrelated to herbivory incidence despite an overall high incidence of biotic pressures on seedlings in both forest and pasture habitats. Attacks of insect herbivores and fungal pathogens are especially frequent if large mammals are rare (Williams et al., 2021). Other studies along rainfall gradients showed that seedlings from wet tropical forests experience relatively low damage from insect herbivores (Muehleisen et al., 2020), but are more likely to suffer from fungal diseases (Spear et al., 2015). In the wet tropical mountains of South Ecuador, effects of insect herbivory and fungal pathogens on seedling recruitment seemed to be less important for establishment and recruitment variables than the effects of the pronounced temperature differences between

habitat types. Our findings do not rule out that biotic pressures can limit seedling recruitment in the studied ecosystems, but the variation in recruitment among species and habitat types seems to be primarily driven by abiotic effects. Future experiments with multiple species may help to gain a more complete understanding about the importance of biotic effects on seedling recruitment in tropical montane ecosystems (Pizano et al. 2014).

Implications for restoration

Our study highlights the importance of seed size for seedling recruitment in tropical mountains. In particular, we showed that the seed size-dependency of seedling recruitment in forests and pastures is related to different temperature conditions in these habitats. Based on these findings, we suggest two key measures that could contribute to improving forest restoration.

First, we emphasise the advantage of deploying large-seeded species in restoration efforts because of the high recruitment potential of large seeds compared to small seeds. Since our experiment shows that the recruitment of large-seeded species is reduced in pasture habitats, we propose that assisted restoration measures are required to support forest restoration in pastures. Our findings suggest that such measures should specifically aim to reduce high surface temperatures in pasture habitats. For instance, the installation of permeable shading structures could be an option to facilitate seedling survival and to protect the regenerating vegetation from environmental extremes (Bader et al., 2007; Gallegos et al., 2015). Seedling protection against high surface temperature should be implemented early during the establishment phase to facilitate seedling survival.

Second, we show that seed addition to pasture habitats enables recruitment of small-seeded and, to a lesser extent, of large-seeded species. This measure appears to be particularly important, because previous studies have shown that pastures often lack seeds, especially of late-

successional and large-seeded plant species dispersed by animals (de la Peña-Domene et al., 2017; Saavedra et al., 2015). Forest restoration therefore requires active seed addition to facilitate the reforestation of pastures into forest ecosystems (Cole et al., 2010; Holl et al., 2017). Long-term monitoring of seedling establishment and survival followed after seed addition may further help to improve restoration efforts.

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Supplementary material

Table A1. Description of the five species used in the sowing experiment in the tropical mountains of South Ecuador. Extra information and photos can be found in the field guide published by Acosta Rojas et al. (2021).

Species and family	Seed mass [g]	Seeds sown	Starting date and time span	Species characteristics incl. information about seed collection
<i>Ocotea</i> sp. [Lauraceae]	0.5272	528	December 2018 – 18 months	Mid-successional, tall tree, dispersed by birds and the spectacled bear, seeds collected from trees in Bombuscaro (1000m)
<i>Clusia ducuoides</i> [Clusiaceae]	0.0054	2980	March 2019 – 15 months	Late-successional, tall tree, dispersed by birds, seeds collected from trees in San Francisco (2000m)
<i>Hieronyma fendleri</i> [Phyllanthaceae]	0.0079	3600	March 2019 – 15 months	Mid-successional, small tree, dispersed by birds, seeds collected from trees San Francisco (2000m)
<i>Tapirira guianensis</i> <i>subsp. subandina</i> [Anacardiaceae]	0.4063	720	September 2019 – 10 months	Mid-successional, tall tree, dispersed by birds and mammals, seeds collected from trees in San Francisco (2000m)
<i>Hedyosmum purpurascens</i> [Chloranthaceae]	0.0135	634	June 2019 – 12 months	Early-successional, small tree, dispersed by birds, seeds collected from trees in Cajanuma (3000 m)

Table A2. Variation of selected abiotic and biotic factors across habitats and elevations in the tropical mountains of South Ecuador. (A) Mean daily maximum surface temperature of the three driest months; (B) mean daily surface temperature of the three driest months; (C) average soil moisture during the dry (i.e., less rainy) season; (D) mean herbivory incidence on established seedlings; (E) mean fungal pathogen incidence on established seedlings. Mean and standard deviation are shown in columns (n = 9 subplots).

	1000 m Mean ± SD	2000 m Mean ±SD	3000 m Mean ±SD
A) Mean daily max temperature [°C]			
FOREST	21.1 ± 0.7	15 ± 1.1	12 ± 0.6
PASTURE	25.2 ± 2.4	18.8 ± 1.8	25.6 ± 2.7
B) Mean daily mean temperature [°C]			
FOREST	19.3 ± 0.3	12.9 ± 1.1	10.3 ± 0.3
PASTURE	21.1 ± 0.5	14.1 ± 0.5	15.9 ± 0.6
C) Average soil moisture [%]			
FOREST	36 ± 10.2	50.7 ± 5.5	72.7 ± 18.5
PASTURE	59.4 ± 9.7	56.7 ± 12.8	51.2 ± 20.5
D) Mean herbivory incidence [0-1]			
FOREST	0.5 ± 0.3	0.5 ± 0.5	0 ± 0
PASTURE	0.7 ± 0.4	0.4 ± 0.5	0.04 ± 0.06
E) Mean fungal pathogen incidence [0-1]			
FOREST	0.6 ± 0.3	0.5 ± 0.5	0.01 ± 0.02
PASTURE	0.8 ± 0.3	0.4 ± 0.4	0.2 ± 0.2

Table A3. Species-specific variation in seedling establishment and recruitment success in the tropical mountains of South Ecuador. Seedling establishment is defined as the proportion of all established seedlings over the experimental period to the total number of seeds sown at the sowing units [0-1] and recruitment success is defined as a proportion of survived seedlings after the entire experimental period to the total number of seeds sown at the sowing units [0-1].

	Species Mean ± SD	Forest Mean ±SD	Pastures Mean ±SD
<i>Clusia ducuoides</i> (2000 m)			
Seedling establishment	0.09 ± 0.14	0.02 ± 0.03	0.15 ± 0.15
Recruitment success	0.03 ± 0.09	0.004 ± 0.01	0.06 ± 0.11
<i>Hedyosmum purpurascens</i> (3000 m)			
Seedling establishment	0.08 ± 0.08	0.07 ± 0.05	0.07 ± 0.05
Recruitment success	0.08 ± 0.08	0.09 ± 0.14	0.09 ± 0.14
<i>Hieronyma fendleri</i> (2000 m)			
Seedling establishment	0.06 ± 0.07	0.04 ± 0.04	0.03 ± 0.04
Recruitment success	0.02 ± 0.04	0.07 ± 0.09	0.02 ± 0.04
<i>Ocotea</i> sp. (1000 m)			
Seedling establishment	0.50 ± 0.24	0.44 ± 0.25	0.30 ± 0.18
Recruitment success	0.31 ± 0.18	0.56 ± 0.23	0.31 ± 0.19
<i>Tapirira guianensis</i> ssp. <i>subandina</i> (2000 m)			
Seedling establishment	0.14 ± 0.13	0.18 ± 0.14	0.12 ± 0.11
Recruitment success	0.07 ± 0.10	0.09 ± 0.11	0.03 ± 0.07

Table A4. Generalized linear mixed effect models (GLMMs) testing the interacting effects of habitat and seed size on (A) seedling establishment and (B) recruitment success of five tree species in the tropical mountains of South Ecuador after the entire period of the experiment (different monitoring time for each species, see above in the Table A1). Subplot nested in plot and species identity were included as random effects in the models (n = 54 subplots; n = 18 plots; n = 5 species). Estimates, standard errors, z values and p values of tested effects are shown in columns. P values in bold font indicate significant effects. Marginal R² (R²m) and conditional R² (R²c) values of the respective model are shown in the last two columns.

	Estimate	Std. Error	z value	p	R²m	R²c
A) Seedling establishment					0.36	0.89
(Intercept)	-0.85	0.50	-1.71	0.087		
Seed size (small)	-2.50	0.56	-4.45	<0.001		
Habitat (pasture)	-0.75	0.44	-1.73	0.084		
Seed size (small) x habitat (pasture)	2.05	0.26	8.02	<0.001		
B) Recruitment success					0.23	0.82
(Intercept)	-1.00	0.35	-2.86	<0.001		
Seed size (small)	-2.10	0.29	-7.29	<0.001		
Habitat (pasture)	-1.50	0.50	-3.0	0.003		
Seed size (small) x habitat (pasture)	2.18	0.36	6.11	<0.001		

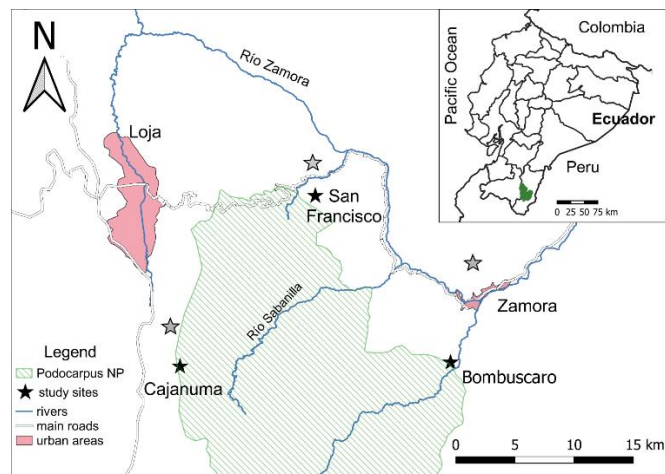


Fig. A1. Map of Podocarpus National Park and surroundings. Map at the top right shows Ecuador with the Podocarpus NP marked with green colour. Black stars symbolize the study sites in forest and grey stars symbolize the study sites in pastures.

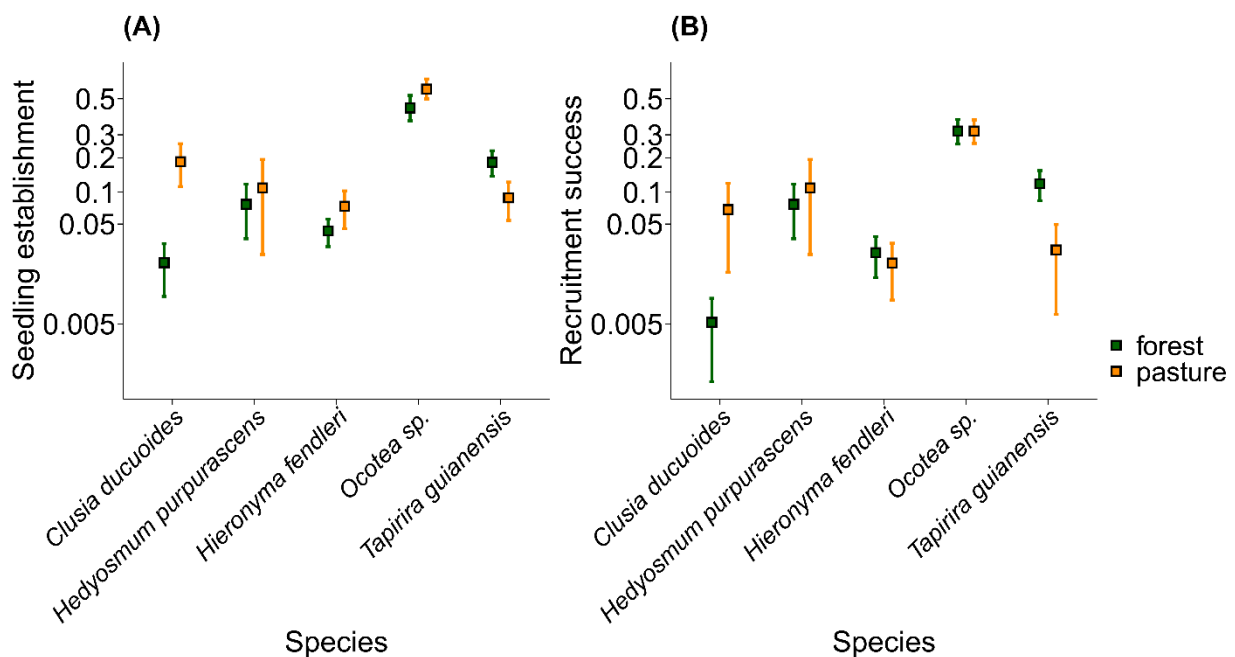


Fig. A2. Species-specific seedling establishment and recruitment success in two habitat types (green: forest, yellow: pasture) in the sowing experiment in the tropical mountains in South Ecuador. (A) Seedling establishment is defined as the proportion of all established seedlings to the total number of seeds sown over the one-year-period (10 months in case of *T. guianensis* ssp. *subandina*); (B) recruitment success is defined as a proportion of seedlings survived after one year (10 months in case of *T. guianensis* ssp. *subandina*) to the total number of seeds sown. Species are ordered according to their seed size; from small (three small-seeded species on the left) to large (two large-seeded species on the right). Each species was sown at the elevation of its origin, i.e. *Ocotea* sp. at 1000 m a.s.l.; *Clusia ducuoides*, *Hieronyma fendleri* and *Tapirira guianensis* ssp. *subandina* at 2000 m a.s.l. and *Hedyosmum purpurascens* at 3000 m a.s.l. Recruitment variables (A and B) are presented on a logit y-axis (tick labels are back-transformed to the original scale). Squares indicate mean proportions of seedling establishment and recruitment success and error bars correspond to 95% confidence intervals around the mean.

Resumen (abstract in spanish)

El reclutamiento de plántulas es un proceso crucial para la regeneración de las plantas y la restauración de los bosques. Sin embargo, se sabe poco sobre cómo los factores abióticos y bióticos limitan el reclutamiento de plántulas de diferentes tamaños a lo largo de gradientes ambientales en las montañas tropicales. Aquí, llevamos a cabo un experimento de siembra con cinco especies de árboles en bosques y pastos a lo largo de un gradiente de elevación en el sur de Ecuador. Para cuantificar el reclutamiento de plántulas en relación con la temperatura, la humedad del suelo y el estrés biótico, sembramos semillas de cinco especies arbóreas de diferente tamaño en tres elevaciones (1000, 2000 y 3000 m s.n.m.) en bosques primarios y pastos. Nosotros probamos (1) cómo el tipo de hábitat influye en el reclutamiento de plántulas de semillas pequeñas y grandes, y (2) cómo los factores abióticos y bióticos limitan el reclutamiento de plántulas de semillas de diferentes tamaños. Nosotros encontramos que las plantas de semillas grandes reclutaron mejor que las de semillas pequeñas, pero sólo en el bosque. El reclutamiento de dos especies con semillas grandes se vio limitado principalmente por la alta temperatura de la superficie, lo que explica el menor reclutamiento de especies con semillas grandes en los pastos en comparación con el bosque. Nuestro estudio muestra que el tamaño de las semillas es un rasgo funcional clave que interviene en la variabilidad del reclutamiento de plántulas en los hábitats de los ecosistemas tropicales. Concluimos que las medidas de restauración deberían tener como objetivo mitigar las temperaturas extremas en los pastos tropicales para ayudar a la regeneración natural de las especies arbóreas con semillas de gran tamaño.

A3: Biotic pressures and environmental heterogeneity shape beta-diversity of seedling communities in tropical montane forests

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Title: Biotic pressures and environmental heterogeneity shape beta-diversity of seedling communities in tropical montane forest

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Author contributions:

(1) Concept and design

MB, 80%;

ELN, CIE, DAR, MS in total 20%

(2) Conducting tests and experiments

MB, established 81 subplots for seedling recruitment census along an elevational gradient, 100 %

MB, collected data on seedling recruitment along an elevational gradient, 100 %

(3) Compilation of data sets and figures

MB identified plant species in the field with the help from botanists, 100%;

MB prepared all data for analyses, 100%;

MB prepared all figures and tables, 100%

(4) Analysis and interpretation of data

MB computed the beta-diversity components, 100%;

MB analysed the associations between beta-diversity components and environmental variables, 100%;

MB interpreted the results, 90%

with input from ELN, MS in total 10%

(5) Drafting of manuscript

MB, 90%;

ELN, CIE, DAR, MS in total 10%

Supplementary material

SI: Methods

ECOGRAPHY

Research article

Biotic pressures and environmental heterogeneity shape beta-diversity of seedling communities in tropical montane forests

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Many theories have been proposed to explain the high diversity of plants in the tropics. However, we lack an understanding of the processes that drive plant diversity and community assembly at different spatial scales. Here, we applied beta-diversity partitioning to test how biotic and abiotic factors are associated with seedling beta-diversity in a tropical montane forest in southern Ecuador. We recorded seedling communities on 81 subplots in nine plots located at three elevations along a 2000 m elevational gradient. We measured biotic pressures (i.e. herbivory and fungal pathogen attacks) and environmental conditions (i.e. soil moisture and canopy closure) in all subplots and related them to species turnover and richness differences in seedling communities within and between elevations. We found that species turnover increased with differences in biotic dissimilarity within elevations, while differences in species richness within elevations increased with increasing environmental dissimilarity. Between elevations, species turnover increased with increasing environmental dissimilarity. Our findings show that species turnover and changes in species richness are related differently to abiotic and biotic factors, and that the importance of these factors for shaping seedling diversity is scale-dependent. Our study contributes to better understand the processes driving seedling beta-diversity and the assembly of plant communities in highly diverse tropical montane forests.

Keywords: community assembly, plant regeneration, Podocarpus National Park, seedling recruitment, species coexistence, species sorting, tropical diversity

Introduction

The diversity of plant species in the tropics is remarkably high (Slik et al. 2015). Many theories have been formulated to explain this phenomenon (Janzen 1970, Giles et al. 2004), principally by seeking to understand the role of environmental filtering (Jones et al. 2008, Stein et al. 2014, Murphy et al. 2016) and spatio-temporal

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patterns of species coexistence (HilleRisLambers et al. 2012, Murphy et al. 2017, Usinowicz et al. 2017). One of the key mechanisms related to environmental filtering is species sorting (Clappe et al. 2018). Plant communities assemble through this mechanism, as species with different functional traits respond differently to changes in local environmental conditions. Eventually, local adaptations in some communities can result in habitat specialization (Leibold et al. 2004, Questad and Foster 2008). Accordingly, environmental heterogeneity can act as a driver of species richness and community composition (Stein et al. 2014). Another important concept of tropical plant diversity is based on the Janzen–Connell hypothesis (Janzen 1970, Connell 1971), which has been extensively tested in many tropical and temperate forests (Bagchi et al. 2010, Comita et al. 2014, Jia et al. 2020). It centres around the interactions between plants and their herbivores and fungal enemies that can moderate plant coexistence and shape diversity patterns in space and time (Bell et al. 2006, Rodríguez-Castañeda et al. 2010, Bachelot et al. 2016, Forrister et al. 2019). Consequently, the variability in biotic pressures plays a major role in shaping tropical plant diversity and the assembly of plant communities (Bagchi et al. 2014, Spear and Broders 2021). Yet, to what extent environmental heterogeneity and biotic interactions drive the diversity and assembly of highly diverse tropical plant communities is not yet resolved (Harms et al. 2000, Arellano et al. 2016a, Johnson et al. 2017).

Beta-diversity concepts facilitate studies of the patterns and drivers of spatial variation in community composition (Whittaker 1972). Beta-diversity, defined as variation in species identities in space, provides effective measures to test the magnitude at which different factors drive dissimilarities in species composition (Anderson et al. 2011). As such, beta-diversity can uncover valuable information on the factors underpinning species turnover and species loss or gain between studied sites (Baselga 2010, Legendre 2014). Effective methods have been established to partition original beta-diversity (i.e. dissimilarity) into two different components, i.e. species turnover (i.e. species replacement) and richness differences (Legendre 2014). While dissimilarity provides quantitative information on how communities resemble each other, species turnover and richness differences provide complementary information on how often species are replaced by each other, and on how locations differ in terms of the number of species. This approach can yield insight into how communities vary across environmental gradients (Baselga 2010, Anderson et al. 2011). The use of beta-diversity partitioning is particularly helpful in revealing factors driving plant diversity. For instance, Pinto-Ledezma et al. (2018) showed that high turnover of plant species occurred mainly in stable climates with higher species richness, while richness differences contributed to beta-diversity of plant communities in less diverse biomes with high environmental variability. So far, most studies investigated the role of environmental filtering to explain regional patterns of beta-diversity (Condit et al. 2002, Swenson et al. 2011, Worthy et al. 2021). However, cross-scale comparisons of beta-diversity are needed to disentangle the effects of

environmental factors and biotic interactions on local and regional diversity in plant communities (Kraft et al. 2011).

Seedling recruitment processes are key for shaping plant community composition (Leck and Outred 2008, Terborgh et al. 2014), because at early life stages plants are particularly exposed to environmental filtering and biotic pressures (Leck and Outred 2008, Browne et al. 2021). Indeed, seedlings of some species are more prone to environmental stress than others. For instance, seedlings with short roots may experience higher mortality under limited water conditions than seedlings developing long roots early on in the establishment phase (Harrison and LaForgia 2019). Likewise, seedlings of species recruiting from large seeds can cope better with pressures by herbivores and pathogens (Moles and Westoby 2004). Because the seedling establishment phase comprises short periods of time relative to plant life span, it is possible to study the processes shaping seedling diversity with observations and experiments over short time periods (Bagchi et al. 2014, Inman-Narahari et al. 2014, Bachelot et al. 2016). Given the critical importance of the seedling life stage, such studies can help to unravel the mechanisms underpinning the assembly of plant communities (Bachelot et al. 2016, Larson and Funk 2016). Studying seedlings in tropical forests is, however, a challenging task, because of the lack of identification tools, high morphological diversity and high seedling mortality (Browne et al. 2021). Given these difficulties, only few studies have sought to disentangle the effects of environmental factors on beta-diversity in tropical seedling communities (Murphy et al. 2016, Worthy et al. 2021).

Tropical mountain ecosystems harbour an extremely high diversity of plant species but, at the same time, they remain relatively little explored (Perrigo et al. 2020). Tropical montane forests offer a unique, natural laboratory to investigate the extraordinary diversity of plants due to high environmental heterogeneity and broad environmental gradients (Malhi et al. 2010, Arellano et al. 2016b). In particular, elevational gradients are very useful to compare processes operating at local and regional scales (Arellano et al. 2016a), as environmental conditions and biotic pressures differ within and between elevations and may contribute to the high diversity of plants in tropical mountains (Arellano et al. 2017, Sam et al. 2020, Wallis et al. 2021). Yet more studies on beta-diversity are required to better understand processes of community assembly in seedling communities (Arellano et al. 2016a, Conradi and Kollmann 2016, Gianuca et al. 2017).

Here, we study the drivers of beta-diversity in seedling communities within and between elevations of tropical montane rainforest in the southern Ecuadorian Andes. Specifically, we attempt to disentangle to what extent species turnover and richness differences are associated with environmental heterogeneity and biotic pressures at two spatial scales (i.e. within and between elevations). We quantified seedling recruitment along a 2000 m elevational gradient over a one-year period and quantified environmental dissimilarity (i.e. soil moisture and canopy closure) and biotic dissimilarity (i.e. herbivory and fungal attacks). We expected

high species turnover in seedling communities within elevations (Swenson et al. 2011) and prominent differences in species richness between elevations (Albrecht et al. 2021). In particular, we expected that differences in species turnover were primarily promoted by 1) environmental dissimilarity between elevations (Johnson et al. 2017) and by 2) biotic dissimilarity within elevations (Bagchi et al. 2014). We further expected 3) an increase in species richness differences associated with environmental dissimilarity, primarily within elevations (Homeier et al. 2010).

Material and methods

Study area

This study was conducted in tropical montane forests in the protected areas of the Podocarpus National Park and adjacent San Francisco Reserve. The Podocarpus National Park spans over 1000 km² in southern Ecuador, bordering on the Amazon Basin at around 1000 m asl and reaching the main ridge of the Andes above 3600 m asl. Main habitats comprise evergreen premontane forest, lower montane forest and upper evergreen tropical montane forest and subpáramo, and are mostly undisturbed due to low human activity (Homeier et al. 2008). The mean annual precipitation ranges between 2000 and 4500 mm with a less rainy season between September and December (i.e. 2432 mm annual precipitation at low elevations, 2079 mm at mid elevations and 4522 mm at high elevations, Santillán et al. 2018). The mean annual temperature ranges between 20°C at 1000 m asl, 15.5°C at 2000 m asl and 10°C at 3000 m asl (Bendix et al. 2008).

Our research was carried out on nine 1 ha plots established in the frame of the DFG Research Unit “RESPECT” along an elevational gradient ranging from 1000 m to 3000 m asl in the primary montane forest (Bendix et al. 2021). Three study plots were located along the Bombuscaro River (1000 m asl, 4°6'S, 78°58'W), three in the San Francisco Valley (2000 m asl, 3°58'S, 79°4'W) and three at Cajanuma (3000 m asl, 4°6'S, 79°10'W) (Homeier et al. 2008). Within each elevation, the three plots represented corresponding forest type (above) and were located at least 100 m apart from each other.

Monitoring of seedling communities

On each of the nine 1 ha plots, we established nine 1 m² subplots with no trees inside, resulting in a total of 81 subplots (Fig. 1). All subplots were situated inside the plots with a distance of 40 m between each other. Prior to the seedling survey starting in May 2019, we manually cleared existing vegetation from the subplots to better spot newly established seedlings and to focus our assessment on the early stages of seedling recruitment. Every four months until July 2020, we recorded all recently recruited seedlings (i.e. at least cotyledons had been developed) and classified them into species and morphotypes. Eventually, we compiled a community matrix, in which columns indicated the presence/absence of

each seedling (morpho)species and rows specified the experimental subplots. In the community matrix, all species identified at the level of genera were treated as distinct (morpho) species for each elevation. The matrix embraced all seedlings encountered at least once over the study period and, thus, comprised seedling species emerging at different times over the study period. Hence, we integrated data over the entire study period and focussed the analyses on our hypotheses concerning spatial patterns in seedling beta-diversity.

Environmental conditions and biotic pressures

Daily measurements of temperature and precipitation were recorded along the entire years 2019 and 2020 at automatic climate stations and were downscaled to the plot scale with the use of remote sensing techniques and a regionalization tool developed for the study area (Fries et al. 2009, Rollenbeck and Bendix 2011). The climatic conditions across the study period were, thus, calculated for each plot separately, but they varied very little within elevations (Supporting information). We therefore calculated the mean annual temperature and precipitation for each elevation and used this value for all plots of an elevation in the analyses. However, the effects of climate on seedling beta-diversity were never significant ($p > 0.1$ in all cases) and we therefore discarded the climatic dissimilarity between elevations from further analyses.

To measure environmental heterogeneity, we recorded soil moisture and canopy closure in all subplots during the less rainy season (October 2019). Average soil moisture was measured using a tensiometer by taking five single measurements inside each subplot. To obtain canopy closure, we took hemispherical photos 0.7 m above ground, with a Nikon Coolpix 4500 digital camera fitted with a Nikon FC-E8 fish-eye converter lens. All photos were taken in the mornings with overcast sky. The hemispherical photos were analysed in Gap Light Analyzer ver. 2.0 (1999, SFU/IES, Canada/USA). We considered soil moisture and canopy closure to be the most relevant proxy for environmental heterogeneity, as they are proxies for two crucial resources exploited by plants: water and light (Leck and Outred 2008).

To assess the degree of biotic pressures, we recorded herbivory traces and fungal pathogens on the seedlings at each of our three visits. As herbivory traces, we considered any kind of external leaf damage including bites, leaf mining and cuts (Muehleisen et al. 2020). As fungal pathogen traces, we considered any kind of leaf damage, including internal changes in leaf colour or external fruiting bodies (Benítez-Malvido and Lemus-Albor 2005).

For each seedling, we recorded the presence or absence of these biotic pressures, corresponding to the presence/absence data on species composition. Based on these data, we calculated the proportion of seedlings with signs of herbivory or fungal pathogens to quantify biotic pressures on seedlings for each subplot and census.

We computed the dissimilarity in environmental conditions and biotic pressures between all pairs of subplots. To this end, we calculated Gower's distances to quantify the

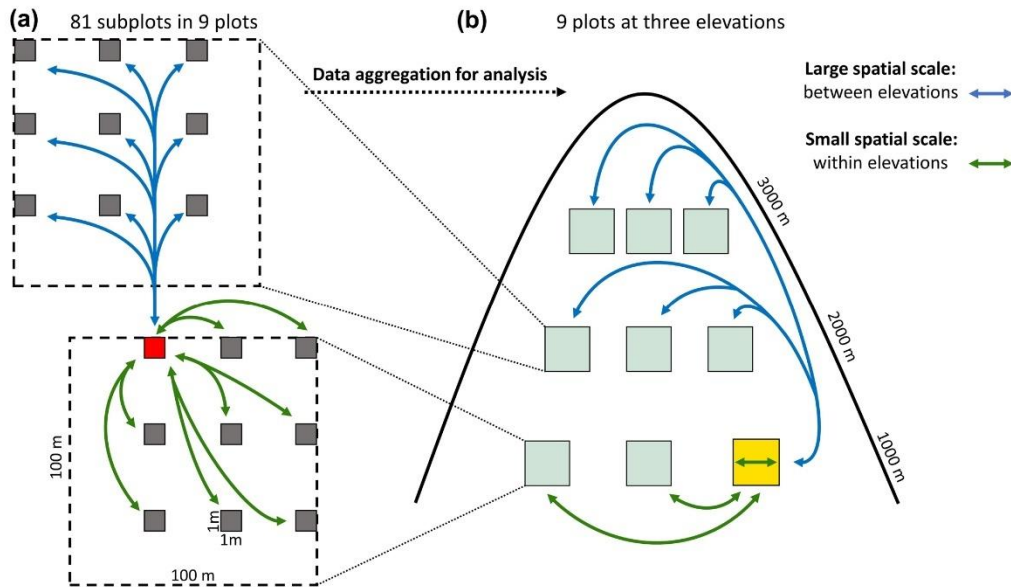


Figure 1. Study design for the analyses of biotic pressures, environmental conditions and seedling communities. We established 81 subplots within nine plots located along an elevational gradient from 1000 to 3000 m asl. (a) Pairwise comparisons of subplots were calculated within each plot, between plots located at the same elevation and between plots located at different elevations. Shown are all pairwise comparisons for an exemplary subplot (red) in relation to subplots within the same plot (green arrows) and to subplots of another plot at another elevation (blue arrows). (b) All subplot comparisons in biotic pressures, environmental conditions and seedling communities were aggregated at plot level for the analysis. The aggregation resulted in a total of 45 plot-based comparisons, both within elevations ($n=18$) and between elevations ($n=27$). Shown are all comparisons for an exemplary plot (yellow) within the same elevation (green arrows) and between elevations (blue arrows).

dissimilarity in environmental conditions (i.e. soil moisture and canopy closure) and biotic pressures (i.e. herbivory attacks and fungal pathogens at each census) between all pairs of subplots. Such data handling allowed matching of the dissimilarity measures and seedling recruitment data, concurrently accounting for temporal variability in biotic pressures typically observed among tropical plant communities (Norden et al. 2007, Pereira Martins et al. 2020). The two dissimilarity matrices were uncorrelated (Mantel tests, $n=9999$, $r=-0.01$, $p=0.529$).

Beta-diversity components

We applied beta-diversity partitioning based on the presence-absence of seedlings at subplot level. We calculated the pairwise Jaccard dissimilarities between subplots according to the methods of Legendre (2014) (Eq. 1):

$$D_j = (b + c) / (a + b + c) \quad (1)$$

with a referring to the shared number of species between subplot 1 and subplot 2, and b and c defined as the number

of species present only in subplot 1 and subplot 2, respectively. Thus, a gives the minimum number of species in each pairwise comparison; b is the number of species in subplot 1 minus a ; and c is the number of species in subplot 2 minus a .

Furthermore, we computed the species turnover (replacement) and species richness differences as two components of beta-diversity by decomposing the Jaccard dissimilarities with equations (2) and (3):

$$\text{Repl}_j = 2 \times \min(b, c) / (a + b + c) \quad (2)$$

$$\text{RichDiff}_j = |b - c| / (a + b + c) \quad (3)$$

Repl_j describes turnover of species between two different sites, showing the number of species that have been replaced in one community to another. Turnover, known also as replacement, describes the tendency of species to replace each other according to their distinct ecological requirements (Baselga 2010, Swenson et al. 2011).

RichDiff_j defines richness differences between a pair of sites. Richness differences refer to how many species

can coexist together, reflecting differences in the diversity of available niches at different locations (Baselga 2010, Legendre 2014).

Given the fact that species turnover and richness differences derive from beta-diversity partitioning, they complement each other (Legendre 2014) as follows (Eq. 4):

$$D_j = \text{Repl}_j + \text{RichDiff}_j \quad (4)$$

We used the code provided by Legendre (2014) to compute overall beta-diversity (D_j) and to partition beta-diversity into turnover (Repl_j) and richness differences (RichDiff_j). We calculated beta-diversity as well as species turnover and richness differences for all pairwise comparisons of subplots (Fig. 1a).

Statistical analysis

For statistical analyses, we aggregated the pairwise comparisons of subplots at plot level to compare beta-diversity patterns within and between elevations. For within-elevation comparisons, we calculated the mean dissimilarities between subplots of each plot ($n=9$) and for each pair of plots located at the same elevation ($n=9$), totalling 18 plot-based comparisons within elevations (green arrows in Fig. 1b, exemplified for one plot). We further calculated the mean dissimilarities between subplots for each pair of plots between elevations ($n=27$) (blue arrows in Fig. 1b, exemplified for one plot). In total, this resulted in 45 plot-based comparisons for environmental and biotic dissimilarities and the respective components of seedling beta-diversity (Fig. 1b). The aggregation was necessary to account for the non-independence of subplot comparisons within the same plots, and helped to reduce the noise of environmental, biotic and beta-diversity data at the subplot level. The resulting matrices were scaled to zero mean and unit variance to facilitate the further analyses. We used Wilcoxon rank-sum tests to test for differences in environmental and biotic dissimilarities between two spatial scales (within versus between elevations). We also applied Wilcoxon rank-sum tests by comparing the means of the general beta-diversity (D_j) and the two beta-diversity components (Repl_j , RichDiff_j) between the two spatial scales. Additionally, we used a Kruskal–Wallis test to test for differences in the species richness of seedlings among elevations (Supporting information).

We performed linear mixed models (LMMs) to test how beta-diversity components were associated with dissimilarity in environmental conditions and biotic pressures at the two spatial scales. The model included either species turnover or richness differences as response variable tested against the spatial scale (within or between elevations) and the dissimilarities in environmental conditions and biotic pressures, respectively. We included both their respective main effects and their interaction term with spatial scale into the analysis to test for scale-dependent effects of environmental conditions and biotic pressures on seedling beta-diversity. To control for the spatial design of our analysis, we included plot

identities of each plot-based comparison as random effects to the models; the same plot identity was included twice for the nine data points based solely on within-plot comparisons. We focussed the interpretation of these models on the positive associations between beta-diversity components and environmental heterogeneity and biotic pressures, respectively, as we expected positive relationships between species turnover/richness differences and environmental/biotic dissimilarity. This was justified because turnover and richness differences generally related to explanatory variables in opposite directions, given their interdependence (see beta-diversity partitioning in Eq. 4). All analyses were run in R ver. 4.0.2 (www.r-project.org) and the associated packages ‘ggplot2’ (Wickham 2016), ‘lme4’ (Bates et al. 2015), ‘lmerTest’ (Kuznetsova et al. 2017), ‘plyr’ (Wickham 2011), ‘reshape2’ (Wickham 2007), ‘tidyverse’ (Wickham et al. 2019) and ‘vegan’ (Oksanen 2016).

Results

We recorded 156 morphospecies of seedlings belonging to more than 40 families along the 2000 m elevational gradient. Species richness at the subplot level did not differ significantly across elevations (Kruskal–Wallis test, $n=81$, $\text{Chi}^2=5.49$, $p=0.064$; Supporting information) and species composition barely overlapped between different elevations. As expected, beta-diversity (D_j) was significantly higher between elevations than within elevations (Wilcoxon rank-sum test: $n=45$, $W=485$, $p < 0.001$). While species turnover was significantly higher between elevations ($n=45$, $W=357$, $p=0.008$, Fig. 2a), no significant differences between the spatial scales were detected for species richness differences ($n=45$, $W=226$, $p=0.705$, Fig. 2b). Environmental dissimilarity was also significantly higher between elevations than within elevations ($n=45$, $W=385$, $p < 0.001$, Fig. 3a). In turn, biotic dissimilarity was similar at both scales ($n=45$, $W=292$, $p=0.264$, Fig. 3b).

Associations between environmental factors and beta-diversity

Overall, we found a strong indication for scale-dependent effects of environmental and biotic dissimilarity on beta-diversity of seedlings (Table 1). Environmental dissimilarity was positively related to species turnover between elevations (Fig. 4a, Table 1) and to richness differences in seedling communities within elevations (Fig. 4b, Table 1). Biotic dissimilarity was positively related to species turnover within elevations (Fig. 5a). That is, species turnover increased between plots characterized by dissimilar values of biotic pressures. In contrast, biotic dissimilarity was not significantly associated with species turnover between elevations (Table 1). Further, biotic dissimilarity was not significantly related to differences in species richness neither within elevations, nor between elevations (Table 1, Fig. 5b).

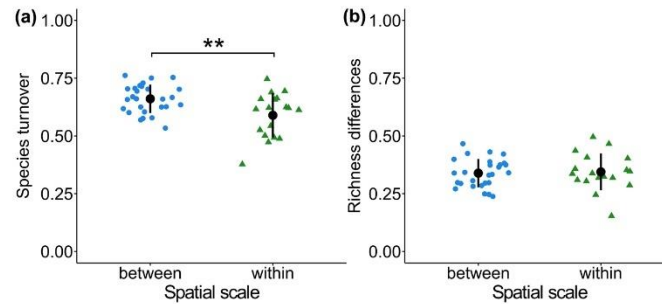


Figure 2. Variation of beta-diversity in seedling communities at two spatial scales in tropical montane forests, showing variability in (a) species turnover and (b) richness differences between seedling communities. Blue dots depict the beta-diversity between elevations, while green triangles correspond to variation within elevations. Values represent 45 plot-based comparisons between elevations ($n=27$) and within elevations ($n=18$) (Fig. 1). Whiskers show 25th and 75th percentiles, with the median indicated with black dots. The asterisks represent statistical significance ($p < 0.01$).

Discussion

We assessed the scale-dependent patterns of species turnover and richness differences in tropical seedling communities and related these to variation in key abiotic and biotic factors. We found that species turnover increased with increasing environmental dissimilarity between elevations and with increasing biotic dissimilarity within elevations. In turn, richness differences in seedling communities increased with environmental dissimilarity within elevations. Our findings show that scale-dependency may be key to understand how different mechanisms shape beta-diversity of seedling communities and, ultimately, the assembly of plant communities in tropical montane forests.

At the large spatial scale, species turnover increased with increasing environmental dissimilarity (Fig. 4a). That is, species turnover between elevations was significantly higher between plots differing in environmental conditions

than between plots with similar environmental conditions. Environmental heterogeneity has been described as a dominant driver of biodiversity for many taxa in the tropical montane forest of Ecuador (Wallis et al. 2021). In line with our findings, beta-diversity patterns in Andean forests are driven by environmental heterogeneity (Arellano et al. 2016b). Essentially, in many tropical forests, high species turnover is associated with changing environmental conditions (Condit et al. 2002, Davidar et al. 2007, Tello et al. 2015). At the same time, a study comparing tree beta-diversity between North and South America found that soil and topography influence species sorting more strongly in temperate forests than in tropical forests, due to the seasonal changes in environmental filtering in temperate ecosystems (Myers et al. 2013). Accordingly, cross-scale dissimilarities in species composition are generally driven by species sorting along steep environmental gradients (Myers et al. 2013, Tello et al. 2015, Zhang et al. 2020). Our findings add to

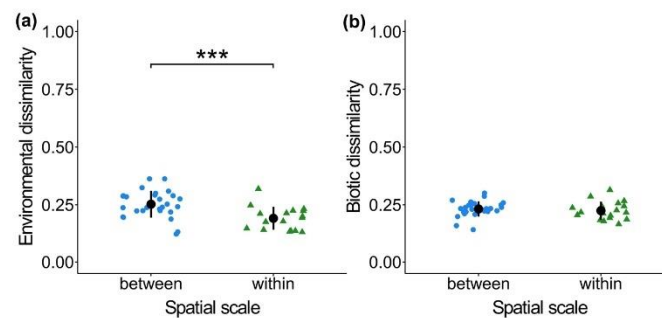


Figure 3. Variation of environmental and biotic dissimilarities at two spatial scales in tropical montane forests, showing (a) environmental dissimilarities based on soil moisture and canopy closure and (b) biotic dissimilarities based on herbivory and fungal pathogens. Blue dots depict the dissimilarities between elevations, while green triangles respond to the dissimilarities within elevations. Values represent 45 plot-based comparisons between elevations ($n=27$) and within elevations ($n=18$) (Fig. 1). Whiskers show 25th and 75th percentiles, with the median indicated with black dots. The asterisks represent statistical significance ($p < 0.001$).

Table 1. Linear mixed models testing the main and interaction effects of biotic and environmental dissimilarities on (a) species turnover and (b) richness differences within and between elevations. Plot identities were included as random factors (n=45 plot-based comparisons). Estimates, standard errors, degrees of freedom, t values and probability of tested effects are shown in columns. Estimates give the differences between the factor variable (within versus between elevations), as well as the linear estimate for the continuous predictor variables (biotic and environmental dissimilarity). The respective interaction terms indicate the effect of biotic and environmental dissimilarity within elevations relative to the effect between elevations (i.e. the differences to the respective main effect of biotic and environmental dissimilarity). Significant values (p < 0.05) are marked with*.

	Estimate	SE	df	t value	p
a) Species turnover					
(Intercept)	0.63	0.02	12.19	25.61	< 0.001***
Within elevations	-0.05	0.02	37.78	-2.32	0.026*
Biotic dissimilarity	0.003	0.01	36.13	0.21	0.834
Environmental dissimilarity	0.047	0.01	36.13	0.21	0.002**
Biotic dissimilarity × within elevations	0.04	0.02	36.78	2.45	0.019*
Environmental dissimilarity × within elevations	-0.08	0.02	33.67	-3.79	< 0.001***
b) Richness differences					
(Intercept)	0.38	0.02	12.79	15.64	< 0.001***
Within elevations	-0.02	0.02	37.70	-0.86	0.396
Biotic dissimilarity	-0.001	0.01	35.23	-0.08	0.935
Environmental dissimilarity	-0.04	0.01	33.95	-3.45	0.002**
Biotic dissimilarity × within elevations	-0.03	0.02	36.68	-1.72	0.094
Environmental dissimilarity × within elevations	0.07	0.02	33.23	4.12	< 0.001***

these studies and show that the environmental heterogeneity between elevations in tropical mountains is a main driver of species turnover in seedling communities.

At the small spatial scale, species turnover increased with increasing biotic dissimilarity (Fig. 5a). In other words, high species turnover within elevations corresponded to increasing differences in biotic pressures on seedlings. Previous field studies revealed the importance of fungal pathogens and insects for community composition of seedlings (Bagchi et al. 2014, Spear and Broders 2021). In line with these findings, the positive association between species turnover and dissimilarity in biotic pressures may be related to differences in the intensity and type of biotic pressures at each plot. This would suggest that herbivores and pathogens drive the detected changes in species composition. However, our findings may also suggest that high species turnover results in changing biotic pressures on seedlings. This interpretation would suggest that different

seedling communities attract different enemies because biotic interactions are often highly specialized, especially in tropical mountains (Rodríguez-Castañeda et al. 2010, Bachelot et al. 2016). While our correlative analyses cannot determine the ultimate mechanism underpinning the reported pattern, both suggested mechanisms are contingent on the host specificity of herbivores and pathogens on specific plant species (Novotny et al. 2006, Bachelot et al. 2016). Independent of the exact mechanism, our findings demonstrate that biotic interactions are more likely to shape species beta-diversity at small than at large spatial scales, consistent with previous concepts (Novotny et al. 2006, Wisz et al. 2013, Cohen et al. 2016). In the future, experimental studies on seedling communities and their enemies could contribute to identify the mechanisms promoting species turnover at small spatial scales.

While the effects of environmental heterogeneity and biotic pressures on plant diversity have been predominantly

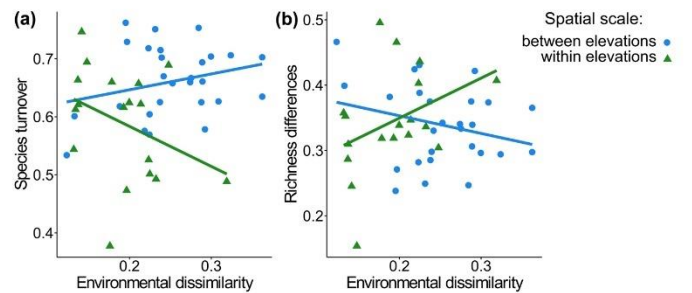


Figure 4. The relationships between environmental dissimilarity (based on soil moisture and canopy closure) and two beta-diversity components: (a) species turnover and (b) species richness differences in seedling communities. Each dot represents the corresponding dissimilarity measure at two different spatial scales (blue – between elevations, green – within elevations), based on 45 plot-based comparisons (Fig. 1). Fitted lines correspond to the univariate association between beta-diversity and the respective predictor variable. Partial effects of environmental dissimilarity on beta-diversity components are given in Table 1.

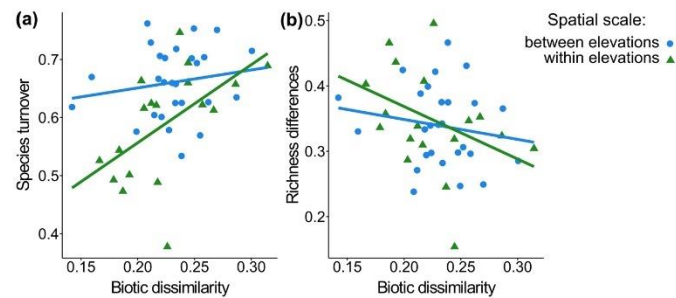


Figure 5. The relationships between biotic dissimilarity (based on herbivory and fungal pathogens) and two beta-diversity components: (a) species turnover and (b) species richness differences in seedling communities. Each dot represents the corresponding dissimilarity measure at two different spatial scales (blue – between elevations, green – within elevations), based on 45 plot-based comparisons (Fig. 1). Fitted lines correspond to the univariate association between beta-diversity and the selected environmental variable. Partial effects of biotic dissimilarity on beta-diversity components are given in Table 1.

reported for tropical lowland forests (Svenning 1999, Bagchi et al. 2014), there is little evidence of how species turnover varies at different spatial scales in tropical montane forests. A previous study from the Bolivian Andes showed that environmental processes contribute to shaping the community composition of trees regardless of the spatial scale (Arellano et al. 2016a). In contrast, a study from a temperate forest showed a strong correlation between environmental filtering and tree species turnover across latitudes (Zhang et al. 2020). Future studies on different growth forms and life stages of plants are required to obtain a more complete picture of species turnover as a result of scale-dependent processes of community assembly (Swenson 2013, Murphy et al. 2016).

We found that species richness differences increased with increasing environmental dissimilarity at the small spatial scale (Fig. 4b). That is, richness differences were particularly high between environmentally heterogeneous localities within elevations. Environmental heterogeneity has been described as very important for species richness across many taxa and at different spatial scales (Stein et al. 2014, Worthy et al. 2021). Additionally, topography has been reported as a prominent driver of the high local diversity of trees in the study area (Homeier et al. 2010). Similarly, coexistence of seedlings was related to niche differences in a tropical montane forest (Inman-Narahari et al. 2014) and to niche partitioning among seedlings in different habitats of tropical lowland forests (Johnson et al. 2017). Thus, certain environmental conditions, e.g. a high light availability under an open canopy, may determine the amount of available niches and therefore promote the coexistence of many species, at least at the early stage of plant regeneration (Giles et al. 2004).

Our study focused on early seedling recruitment, because this initial recruitment phase is especially prone to environmental filtering and biotic pressures (Bagchi et al. 2014, Murphy et al. 2016) and sets a blueprint of community composition for later life stages (Visser et al. 2016, Forrister et al. 2019). Given the high seedling mortality in tropical rainforests, initial seedling recruitment is also considered to be

particularly important for the assembly of tropical plant communities (Maron et al. 2019). In fact, in spite of the relatively short period of our study, we were able to capture a high number of seedling species (Supporting information) and a large variation in beta-diversity (Fig. 2). Despite the asynchrony in seed production in the tropics (Connell and Green 2000), this suggests that our one-year study of seedling communities was able to capture scale-dependent differences in community assembly at this very early stage of plant recruitment. Nevertheless, future long-term studies will be required to test whether patterns in beta-diversity are similar for seedlings and later recruitment stages. In particular, it will be interesting to test whether the importance of abiotic and biotic drivers changes across life stages and subsequent demographic processes (Murphy et al. 2016, Pereira Martins et al. 2020).

We conclude that the processes promoting species turnover and richness differences in seedling communities are scale-dependent and that abiotic and biotic factors shape seedling beta-diversity differently within and between elevations in tropical montane forests. In particular, we reveal that the effects of biotic pressures on seedling communities are particularly pronounced at the local scale within elevations. We conclude that these scale-dependent processes are likely to play a key role in shaping the assembly of seedling and plant communities in tropical montane forests.

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Author contributions

Maciej K. Barczyk: Conceptualization (equal), Data curation (lead), Formal analysis (lead), Investigation (lead), Methodology (equal), Writing – original draft (lead). **Diana C. Acosta-Rojas:** Conceptualization (equal), Investigation-Supporting, Methodology-Supporting, Writing – review and editing-Supporting. **Carlos I. Espinosa:** Funding acquisition-Supporting, Methodology-Supporting, Writing – review and editing-Supporting. **Matthias Schleuning:** Conceptualization (equal), Funding acquisition (equal), Methodology (equal), Supervision (equal), Writing – review and editing (equal). **Eike L. Neuschulz:** Conceptualization (equal), Funding acquisition (equal), Methodology (equal), Supervision (equal), Writing – review and editing (equal).

Transparent peer review

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.3r2280gmh> (Barczyk et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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Supporting information

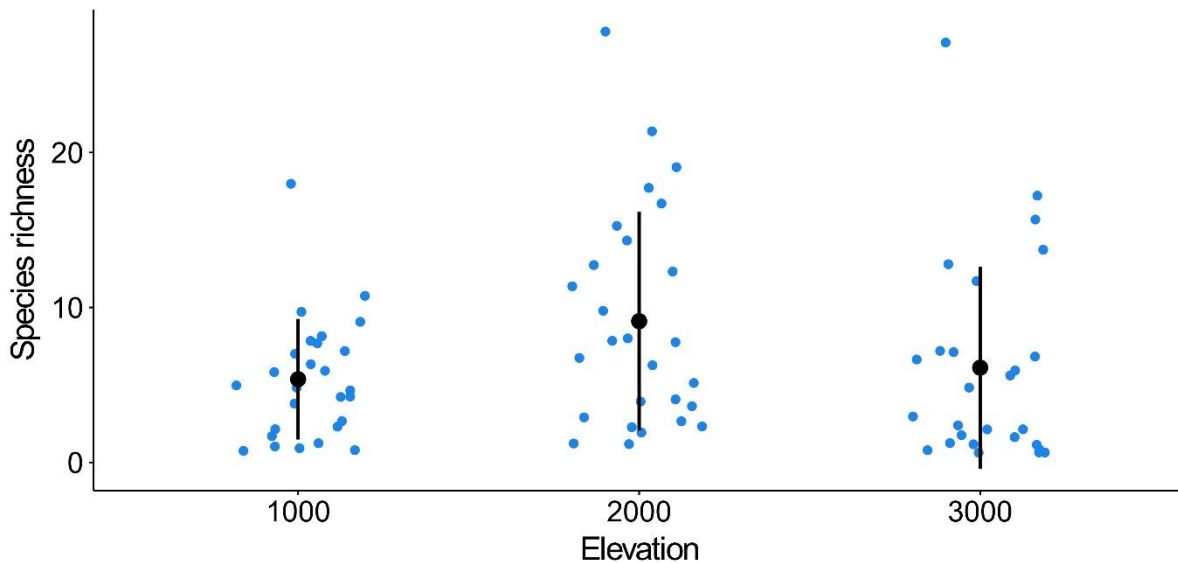


Figure S1. Species richness of seedlings across three elevations (alpha diversity). Blue dots represent the number of species encountered at each studied subplot ($n = 81$ subplots). Whiskers show 25th and 75th percentiles, and the median are indicated with black dots.

Table S1. Mean daily temperature, daily precipitation and annual precipitation, obtained from three climate stations during the time of the experiment (June 2019 – June 2020) and extrapolated for each plot.

Plot name	Elevation (m a.s.l.)	Mean daily temperature [°C]	Mean daily precipitation [mm]	Annual precipitation [mm]
Bombuscaro 1	1000	19.5	6.1	2195.4
Bombuscaro 2	1000	19.4	6.2	2220.7
Bombuscaro 3	1000	19.3	6.2	2239.7
San Francisco 1	2000	15.4	5.3	2036.5
San Francisco 2	2000	15.3	5.5	2121.3
San Francisco 3	2000	15.7	5.8	2229.0
Cajanuma 1	3000	10.3	7.4	2721.7
Cajanuma 2	3000	10.4	7.4	2709.8
Cajanuma 3	3000	10.0	7.8	2797.2

A4: Curriculum Vitae

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EDUCATION

- 09.2018 – present PhD student in Biological Sciences
Senckenberg Biodiversity and Climate Research Centre (SBIK-F)
and **Goethe University Frankfurt**, Frankfurt am Main, Germany
Supervisor: Dr Eike Lena Neuschulz
Dissertation title: “Trait-dependent effects of abiotic and biotic filters on plant regeneration in Southern Ecuador”
- 10.2015 – 10.2017 M.Sc. in Biological Sciences
Jagiellonian University, Kraków, Poland
Supervisor: Dr Marcin Czarnołęski
Master thesis: “Mutualistic relationships between ants and palms in Danum Valley, Borneo”
- 10.2011 – 03.2015 B.S. in Forestry
University of Agriculture, Kraków, Poland
Supervisor: Dr Jan Bodziarczyk
Bachelor thesis: “The structure and dynamics of *Myricaria germanica* L. Desv. bushes on appearing on the gravel bars of the Kamienica Nawojowska river” (in polish)

EMPLOYMENT

- 09.2018 – 10.2022 German Research Foundation (DFG) – PhD in RESPECT project:
Environmental changes in biodiversity hotspot ecosystems of South
Ecuador (FOR2730; www.tropicalmountainforest.org)
- 03.2018 National Science Centre, Poland
Field Project: The impact of interaction between the social information
and the landscape structure on behavior and distribution of birds

COURSES / INTERNSHIPS

- 08.2022 **iDiv Leipzig**, Germany
Summer School in Molecular Evolutionary Ecology
- 05.2019 **Kew Gardens**, UK
Tropical Plant Families Identification Course
- 07.2018 **Tropical Biology Association**, Kenya
Tropical Biology Field Course in Mpala Reserve
- 04 – 06.2017 **Doñana Biological Station (EBD)**, Sevilla, Spain
Field project with the animal-plant interactions group (Erasmus+)
Epigenetic responses to water stress and resistance to extinction in endemic plants
- 03.2017 **Organization for Tropical Studies**, Costa Rica
Field course in “Biology of Neotropical Social Insects”
- 07.2016 **Jagiellonian University**, Kraków, Poland
Tropical ecology – Field Course in Danum Valley Field Centre, Borneo
- 10.2015 – 06.2017 **Jagiellonian University**, Kraków, Poland
Preparatory course for biology teaching at the Pedagogical College
- 11.2011 – 06.2013 **Student Mountain Guides Association (SKPG)**, Kraków, Poland
Practical course for mountain guides in Beskid Mountains (Poland)

A5: Publications and scientific presentations

Publications

Acosta-Rojas, D.C., **Barczyk M. K.**, Espinosa, C.I., Farwig, N., Homeier, J., Tiede, Y., Tinoco, B.A., Velescu, A., Wilcke, W., Neuschulz, E.L. & Schleuning, M. (2023). Abiotic factors similarly shape the distribution of fruit, seed and leaf traits in tropical fleshy-fruited tree communities. *Acta Oecologica*, 121, 103953.

Acosta-Rojas, D. C., **Barczyk, M.**, Espinosa, C. I., Gusmán, J., Peña, J., Neuschulz, E. L., Schleuning, M., & Homeier, J. (2021). Field guide of animal-dispersed plants: fruits and seeds in and around Podocarpus National Park / Guía de campo de plantas dispersadas por animales: frutos y semillas en el Parque Nacional Podocarpus y sus cercanías. 1, 16, INABIO (Quito).

Acosta-Rojas, D. C., **Barczyk M.**, Espinosa, C. I., Tinoco, B. A., Neuschulz, E. L. & Schleuning, M. (2023). Climate and microhabitat shape the prevalence of endozoochory in the seed rain of tropical montane forests. *Biotropica*, 55(2), 408-417.

Barczyk M. K., Acosta-Rojas, D. C., Espinosa, C. I., Schleuning, M. & Neuschulz, E. L. (2023). Biotic pressures and environmental heterogeneity shape beta-diversity of seedling communities in tropical montane forests. *Ecography*, 2023(6), e06538.

Nelson, A.S., Scott, T., **Barczyk, M.**, McGlynn, T. P., Avalos, A., Clifton, E., Das, A., Figueiredo, A., Figueroa, L.L., Janowiecki, M., Pahlke, S., Rana J. D. & O'Donnell, S. (2018). Day/night upper thermal limits differ within *Ectatomma ruidum* ant colonies. *Insectes Sociaux*, 65, 183–189.

Submitted manuscripts

Acosta-Rojas, D. C., **Barczyk M. K.**, Espinosa, C. I., Tinoco, B. A., Neuschulz, E. L. & Schleuning, M. (2023). Systematic reduction in seed rain of large-seeded and endozoochorous species in pastures compared to forests across tropical mountains (submitted)

Barczyk M. K., Acosta-Rojas, D. C., Espinosa, C. I., Schleuning, M. & Neuschulz, E. L. Seedling recruitment of small- and large-seeded species in forests and pastures in Southern Ecuador (submitted)

Barczyk M. K., Acosta-Rojas, D. C., Espinosa, Homeier, J Tinoco, B.A., Velescu, A., Wilcke, Schleuning, M. & Neuschulz, E. L. Environmental conditions differently shape leaf, seed and seedling trait composition in tropical montane forest (submitted)

Presentations at conferences

- 06.2023 Presentation at the European Tropical Ecology Conference in Ceske Budejovice, the Czech Republic (the Merian Award for the 3rd best talk)
“Environmental effects on trait composition in tropical montane forests” – a talk
- 06.2022 Presentation at the European Tropical Ecology Conference in Montpellier, France
“Biotic stress and microhabitat heterogeneity shape beta-diversity of tropical seedling communities in tropical montane forests” – a talk
- 07.2021 Presentation at the Annual Meeting of the Association of Tropical Biology and Conservation, online
“Seed size dependent effects of seedling recruitment in tropical mountain forest” – a lightning talk
- 10.2019 Symposium in Loja, Ecuador
“Trait-dependent effects of abiotic and biotic filters on plant regeneration” – a talk