

# **Plant functional diversity and seed rain along land-use and elevational gradients in southern Ecuador**

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## **1. Summary**

Seed dispersal is a key ecosystem function for plant regeneration, as it involves the movement of seeds away from the parental plants to particular habitats where they can germinate and transition to seedlings and ultimately adult plants. Seed dispersal is shaped by a diversity of abiotic and biotic factors, particularly by associations between plants and climate and between plants and other species. Due to the ongoing loss of biodiversity and changing global conditions, such interactions are prone to change and pose a severe threat to plant regeneration. One way to address this challenge is to study associations between plant traits and abiotic and biotic factors to understand the potential impacts of global change on plant regeneration. Plant communities have long been analyzed through the lens of vegetative traits, mainly ignoring how other traits interact and respond to the environment. For instance, while associations between vegetative traits (e.g., specific leaf area, leaf nitrogen content) and climate are well studied, there are few case studies of reproductive traits in relation to trait-environment associations in the context of global change.

Thus, the overarching aim of this dissertation is to explore how trait-environment associations, with a special focus on reproductive traits, can improve our understanding of the effect that global change may have on seed dispersal, and ultimately on plant regeneration. To this end, my research focuses on studying associations between plant traits and abiotic and biotic factors along an elevational gradient in both forests and deforested areas of tropical mountains. This dissertation addresses three principal research objectives. First, I investigate the extent to which reproductive (seed and fruit traits) and vegetative traits (leaf traits) are related to abiotic and biotic factors for communities of fleshy-fruited plants in the Ecuadorian Andes. I used multivariate analyses to test associations between four (a)biotic factors and seven reproductive traits and five vegetative traits measured on 18 and 33 fleshy-fruited plant species respectively. My analyses demonstrate that climate and soil conditions are strongly associated with the distribution of both reproductive and vegetative traits in tropical tree communities. The production of “costly” vs. “cheap” seeds, fruits and leaves, i.e., the production of few rewarding fruits and acquisitive leaves versus the production of many less-rewarding fruits and conservative leaves, is primarily limited by temperature, whereas the size of plant organs is more related to variation in precipitation and soil

conditions. My findings suggest that associations between reproductive and vegetative traits and the abiotic environment follow similar principles in tropical tree communities.

Second, I assess how climate and microhabitat conditions affect the prevalence of endozoochorous plant species in the seed rain of tropical montane forests in southern Ecuador. I analyzed seed rain data for an entire year from 162 traps located across an elevational gradient spanning of 2000 m. I documented the microhabitat conditions (leaf area index and soil moisture next to each seed trap) at small spatial scale as well as the climatic conditions (mean annual temperature and rainfall in each plot) at large spatial scale. After a one-year of sampling, I counted 331,838 seeds of 323 species/morphospecies. My analyses demonstrate that the prevalence of endozoochorous plant species in the seed rain increases with temperature across elevations and with leaf area index within elevations. These results show that the prevalence of endozoochory is shaped by the interplay of both abiotic and biotic factors at large and small spatial scales.

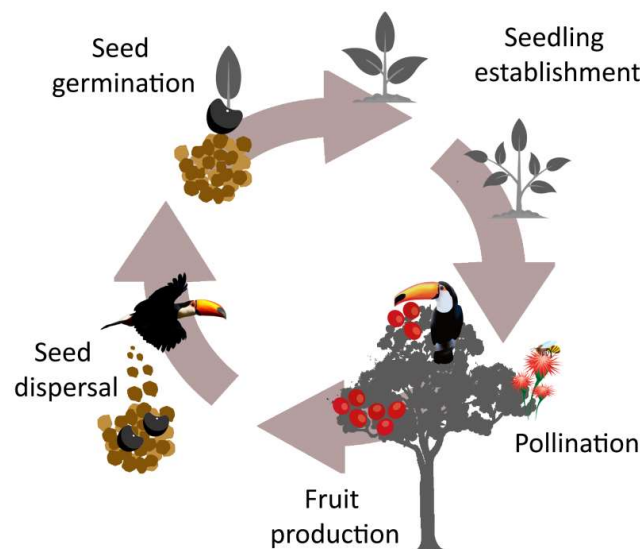
Third, I examine the potential of seed rain to restore deforested tropical areas along an elevational gradient in southern Ecuador. For this chapter, I collected seed rain using 324 seed traps installed in 18 1-ha plots in forests (nine forest plots) and in pastures (nine deforested plots) along an elevational gradient of 2000 m. After a sampling period of three months, I collected a total of 123,039 seeds of 255 species/morphospecies from both forests and pastures along the elevational gradient. I did not find a consistent decrease in the amount and richness of seed rain between forests and pastures, but I detected a systematic change in the type of dispersed seeds, as heavier seeds and a higher proportion of endozoochorous species were found in forests compared to pastures at all elevations. This finding suggests that deforestation acts as a strong filter selecting seed traits that are vital for plant regeneration.

Understanding the role that trait-environment associations play in how plant communities regenerate today could serve as a basis for predicting changes in regeneration processes of plant communities under changing global conditions in the near future. Here, I show how informative the measurement of reproductive traits and trait-environment associations are in facilitating the conservation of forest habitats and the restoration of deforested areas in the context of global change.

## 2. Introduction

### 2.1. Relevance of seed dispersal for plant regeneration

Plant regeneration is a multi-step ecological process essential for the long-term forest stability and resilience (Norden et al., 2009). This complex process involves every transition of the plant life cycle from adult plants to seeds to seedlings to saplings (Figure 1). Some ecosystem functions such as pollination and seed dispersal shape these transitions. Thus, studying transitions between plant stages and ecosystem functions in plant communities is essential to characterize how plant regeneration occurs. Plant regeneration promotes the ongoing persistence of various plant stages in a specific habitat, increasing plants' probabilities of survival in the face of shifting environmental conditions (Nathan & Muller-Landau, 2000; Wang & Smith, 2002). Understanding the mechanisms by which plant regeneration is promoted or disturbed allows us to develop effective strategies to conserve or recover this essential ecological process of ecosystems (Hubbell et al., 1999; Muller-Landau et al., 2002).



**Figure 1:** Plant regeneration cycle for a fleshy-fruited plant species depicting different stages from fruit production to the germination of dispersed seeds. Although this cycle highlights the process of animal-mediated seed dispersal, the same processes also occur in plant species with other seed dispersal modes.

During plant regeneration, seed dispersal is carried out when adult plants produce fruits, and these reproductive structures containing seeds are dispersed away from parental plants (van der Pijl, 1982). As a consequence, the seed rain produced by seed dispersal

creates the first template for shaping the distribution of plant species (Howe & Smallwood, 1982). Seed dispersal is particularly important for plant regeneration because it helps plants to escape from the vicinity of the mother plant to reach suitable microsites (Wenny, 2001) and colonize new habitats (Puerta-Piñero et al., 2013). Seed dispersal provides clear advantages that promote the plant regeneration process due to seed predation and pathogen attack often decrease with increasing distance from the parental plants (Connell, 1970; Janzen, 1970). In addition, seed dispersal contributes to plant distribution at different spatial scales since it also influences the spatial genetic structure in both plant populations and communities (Gelmi-Candusso et al., 2017; Howe & Miriti, 2004).

Seeds may be dispersed over long or short distances depending primarily on fruit and seed traits and specific characteristics of the dispersal vectors (Heleno & Vargas, 2015). In this sense, plants are able to be transported over different distances. Plant species dispersed over long distances are usually dispersed by vertebrate ingestion (endozoochory), by external adhesion to vertebrate fur or feathers (epizoochory), by wind (anemochory) or by oceanic current (hydrochory), while plant species dispersed over short distances lack specialised dispersal structures (Nathan, 2006; Ridley, 1930). Fruits of plant species dispersed by vertebrate ingestion are characterized by edible fleshy pulps and/or appendages with visual or olfactory cues that attract dispersers (Janson, 1983; van der Pijl, 1982). In wind-dispersed species, the fruits or seeds are in the form of dry diaspores with structures such as hairs or wings (Augspurger, 1986). Therefore, both abiotic and biotic factors shape the seed dispersal function and, consequently, shape the regeneration process of plant species. In this sense, the study of plant traits related to the seed dispersal process of specific plant communities is a promising approach to examine how plant regeneration operates in different ecosystems.

## **2.2. Global change impacts on seed dispersal**

Anthropogenic activities are causing significant changes to the Earth (Steffen et al., 2004; Vitousek, 1994), including the raising of atmospheric concentrations of CO<sub>2</sub> and other greenhouse gases and is associated with changes in the climate. Agricultural practices are increasing the amount of nutrients moved around the world and lead to the deposition of high levels of nitrogen in soils and aquatic ecosystems (Dentener et al., 2006; Fowler et al., 2013). Human-mediated movement of species promotes biotic



invasions, which lead to novel species assemblages (Yang & Bao, 2022). Increased urbanization and the expanding agricultural frontier are altering disturbance regimes and changing land use patterns. Humans have also eliminated species from locations that would have otherwise supported them and restricted populations to a portion of their original ranges (Sales et al., 2022). All of these alterations constitute the global changes our planet is currently facing and, as a consequence of changing environmental conditions and species interactions (Turner et al., 2020; Tylianakis et al., 2008; Vitousek, 1994), plant communities are being severely affected (Ellis et al., 2012; Franklin et al., 2016).

Global change drivers, produced by human impacts, reduce overall plant regeneration (Teixido et al., 2022). Animal-mediated seed dispersal is one of the most vulnerable ecological processes in the plant life cycle (Neuschulz et al., 2016). This fragility is attributed to the disruption of animal-plant mutualistic interactions caused by biodiversity loss and shifts in the distribution of functional traits important for trait-matching (Peña et al., 2023). Furthermore, species that are connected through biotic interactions may differ in the way they respond to climatic changes (Fricke et al., 2022), because they react differently to changing environmental conditions as a result of different dispersal strategies or life histories (Chen et al., 2020; Díaz et al., 2016). Therefore, projecting potential impacts of future global change on plant regeneration first requires an improved understanding of how different processes of plant regeneration respond to current abiotic and biotic conditions.

### **2.3. The role of plant traits in seed dispersal**

Plant functional traits are defined as those morpho-physio-phenological characteristics of plants that have an indirect impact on fitness through their effects on growth, reproduction, and survival (de Bello et al., 2010; Díaz et al., 2016; Violle et al., 2007). In turn, plant functional traits (plant traits, hereafter) can mediate the effects of global change on plant regeneration, and on seed dispersal, in particular. For instance, seed size is a central plant trait for seed dispersal and seedling establishment (Fenner and Thompson, 2005; Moles and Westoby 2006; Saatkamp et al., 2019). Large seeds can only be dispersed by large-gaped animals (Bender et al., 2017; Stevenson, 2000), while smaller seeds can be ingested by animal species with a wider variety of gape widths (Muñoz et al., 2017). Therefore, the loss of large-gaped animals has been specifically

associated with the decline of large-seeded plants (Galetti et al., 2013). At the same time, these large-seeded plants are often associated with mycorrhizal fungi (Janos, 1980) and produce large seedlings that tend to be more resistant to herbivory or fungal infections than small seedlings (Moles & Westoby, 2004). Plants with large seeds, therefore, often have superior tolerance to environmental stressors, but their seedlings have greater chances of establishment in shaded environments than in unshaded habitats, such as late-successional plant species (Dalling et al., 1998; Harms & Dalling, 1997; Kitajima, 2002). Consequently, changes in land use that reduce vegetation cover tend to be characterized by a deficient regeneration of large-seeded plants (Saavedra et al., 2015). Thus, global change leads to systematic changes in plant trait distributions.

Plant traits are often correlated with each other and thus shape different dimensions of plants' ecological strategies (Carmona et al., 2021; Díaz et al., 2016; Wright et al., 2004). For instance, two widespread ecological strategies across plant communities are identified within the seed size and seed number trade-off (Harper et al., 1970). Along this trade-off, strongly linked to seed dispersal, plants tend to fall within a *continuum* of two extremes of the spectrum: (Strategy 1) either many small seeds with higher rates of dispersal and colonization, or (Strategy 2) few larger seeds with higher rates of survival during seedling establishment (Moles & Westoby, 2006; Venable, 1992; Westoby et al., 2002). Similarly, general ecological strategies of plants can be found for other plant organs. In particular, leaves balance the cost of their construction against their growth potential along the leaf economics spectrum (Wright et al., 2004). According to this spectrum, plants produce either long-lived leaves with low leaf nitrogen content and low specific leaf area (i.e., 'conservative' leaves) or short-lived leaves with high leaf nitrogen content and high specific leaf area (i.e., 'acquisitive' leaves). Such general principles of plant strategies have been shown to underpin the global variation in plant form and function (Díaz et al., 2016). Despite this general understanding of how specific functional traits are related to particular plant ecological strategies at broad scales, there is still little empirical evidence for the extent to which these associations still persist at the local scale. In addition, it is largely unknown how these functional trait-mediated plant ecological strategies, especially for those involving reproductive traits, are associated with (a)biotic factors that affect plant regeneration by influencing seed dispersal function.

#### **2.4. Fleshy-fruited plant communities**

Approximately 50% of woody plant species worldwide produce fleshy fruits and depend on fruit-eating animals for seed dispersal (Rogers et al., 2021). In the tropical forests, this prevalence increases to 70-90% (Buitrón-Jurado & Ramírez, 2014; Correa et al., 2015; Howe & Smallwood, 1982), and many frugivorous birds and mammals heavily rely on fleshy fruit as part of their diet (Jordano, 2000; Kissling et al., 2009). Fleshy-fruited plant species and fruit-eating animals profit from mutually beneficial interactions (Herrera, 2002). While frugivorous animals receive valuable nutrients and energy from the fruits (Moermond & Denslow, 1985; Quintero et al., 2020), plants are favored by the movement of seeds away from the mother plant (Wang & Smith, 2002) (Figure 1).

The way in which fleshy-fruited plant species respond to environmental conditions affect the regeneration and maintenance of plant communities in tropical forests. For instance, many large trees have large seeds dispersed by animals and are typically late-successional species (Howe & Smallwood, 1982; Paolucci et al., 2019; Tabarelli & Peres, 2002). In tropical forests, the dominant plants are usually fleshy-fruited species (ter Steege et al., 2013). When these dominant species are extirpated tend to have a significant impact on subordinate species, affecting the diversity and structure of the entire plant community (Grime, 1998). In addition, several large fleshy-fruited trees are also hardwood plants (Aldana et al., 2017; Bello et al., 2015), and the decline in the recruitment of such trees may lead to reduced carbon stocks in tropical forests (Bello et al., 2015; Peres et al., 2016). Since fleshy-fruited plant species play such a key role in plant communities, they are an excellent study system, especially in the tropics, to assess the current impacts of abiotic and biotic factors on given plant communities.

#### **2.5. Tropical elevational gradients**

The tropics is the most biodiverse region in the world, and elevational gradients there support a wide variety of fleshy-fruited plants and fruit-eating animals (Jansson & Davies, 2007; Kissling et al., 2009; Tenorio et al., 2023). Tropical forests are responsible for more than one-third of global photosynthesis in terrestrial ecosystems (Melillo et al., 1993) and store approximately 40% of the carbon that resides in vegetation (Lewis et al., 2004). These features make tropical forests the most important

terrestrial carbon sink in the world. Tropical ecosystems are highly threatened by global change and have undergone severe losses in biodiversity (Gardner et al., 2009; Gibson et al., 2011). In this context, elevational gradients are useful research tools because they include a range of different climatic conditions and land-use changes at small spatial scales (Körner, 2000; Sanders & Rahbek, 2012; Tito et al., 2020).

Changes along the abiotic and biotic gradients in tropical mountains may alter plant communities across elevations. For example, temperature (Mokhov & Akperov, 2006) and soil nitrogen content decrease with increasing elevation (Benner & Vitousek, 2010; Soethe et al., 2008; Wilcke et al., 2008; Wolf et al., 2011). This abiotic gradient implies that plant communities located at lower elevations are adapted to warmer conditions and nitrogen-rich soils compared to communities located at higher elevations. As global temperatures rise, montane plant species may respond by tolerating new conditions and persisting, migrating, or going extinct (Jump & Peñuelas, 2005; Walther et al., 2002). In addition to variations in abiotic factors in tropical mountain settings, plant communities are also exposed to variations in biotic conditions along elevations that affect mutualistic interactions with animals. In contrast to high elevations, for instance, low elevations display a greater diversity of interactions and less specialization in plant-frugivore interaction networks (Qutián et al., 2018). Biotic gradients, such as these, across tropical mountains increase the vulnerability of particular plant species, such as fleshy-fruited plant species, which are highly dependent on mutualistic interactions.

The marked abiotic gradients along tropical mountains have been widely used to assess the effect of environmental filtering on plant communities (Homeier et al., 2021; Pierick et al., 2023). The ‘environmental filtering’ hypothesis states that plant species may develop traits with similar values in a given plant community due to selection by abiotic environment (Kraft et al., 2015). For example, the combination of harsher climatic conditions and weaker biotic stressors experienced by plants at higher elevations may lead to a decrease in the variation of interspecific traits in these plant communities (Kergunteuil et al., 2018). Therefore, environmental filtering along elevation gradients in the tropics demonstrates how (a)biotic factors play an important role in determining plant traits in tropical mountains.

### **3. Dissertation structure and research questions**

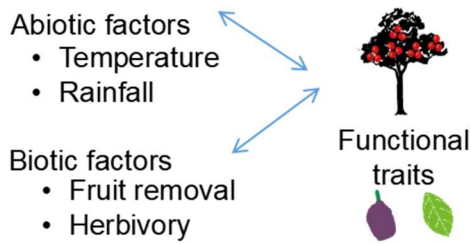
This doctoral thesis investigates how abiotic and biotic factors associated with global changes affect seed dispersal, and ultimately plant regeneration in tropical plant communities. In particular, I am interested to improve the understanding of the current impacts of abiotic and biotic factors on seed dispersal of tropical plant communities. This should provide a basis for predicting changes in plant traits under ongoing global change. In order to accomplish this, I developed three main research questions (Figure 2). The first question (Q1) addresses how plant traits of fleshy-fruited plant species are associated with (a)biotic factors across elevational gradients. The second question (Q2) explores how climate and microhabitat conditions affect endozoochory across elevation gradients. Finally, the third question (Q3) examines how land-use affects seed rain and thus, the potential of seeds to restore deforested areas across elevations.

My dissertation is structured into three research articles, of which one is printed in *Biotropica* (Acosta-Rojas et al., 2023) (appendix A2), one is in revision in *Acta Oecologica* (appendix A1) and the last one is under review to *Applied Vegetation Sciences* (appendix A3).

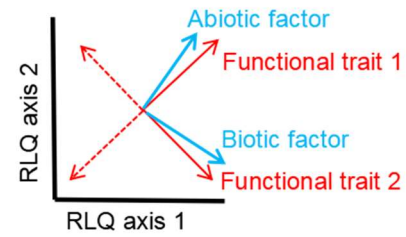
#### **3.1. How are plant functional traits associated with abiotic and biotic factors? (Q1)**

Both abiotic and biotic factors influence how plant traits are distributed in ecological communities (Kraft et al., 2015), yet it is unclear whether different plant traits respond similarly to (a)biotic factors. To assess whether plant traits are related to abiotic and biotic factors in a similar way, I simultaneously studied reproductive and vegetative traits and their associations with (a)biotic factors for tree communities of animal-dispersed plants in the tropical montane forests of southern Ecuador. First, I determined the primary ecological strategies in the community of fleshy-fruited plant species by identifying the main dimensions of variation in seed, fruit and leaf traits. Then, I identified the principal associations between these main dimensions of plant traits and (a)biotic factors. This approach allowed me to describe how two distinct types of plant traits respond to abiotic and biotic factors in the tropical montane forests of southern Ecuador.

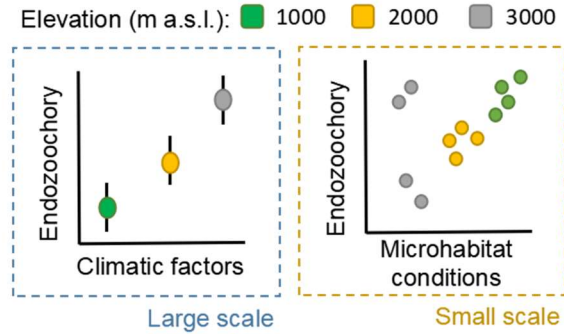
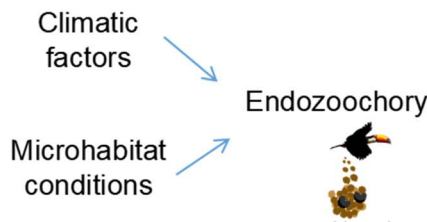
**Q1**



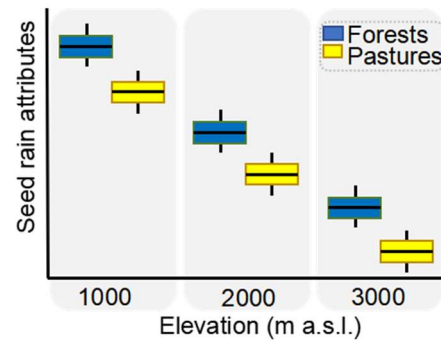
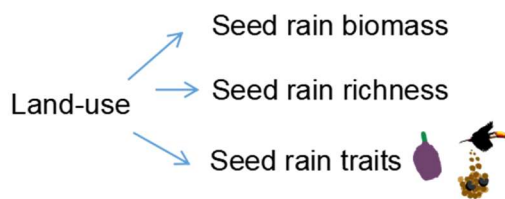
Functional trait spaces:



**Q2**



**Q3**



**Figure 2:** Schematic representation of the structure of my dissertation. I developed three main research questions (Q1, Q2 and Q3) to study how abiotic and biotic factors associated with global change affect seed dispersal in tropical plant communities. Q1: How are plant functional traits associated with abiotic and biotic factors across elevations? Q2: How do climate and microhabitat conditions affect endozoochory across elevations? Q3: How does land-use affect seed rain potential to restore deforested areas across elevations? On the left, I show arrow diagrams with the predictors and response variables for each research question while on the right, I summarize the main predictions for these questions. To address Q1, I measured reproductive (purple fruit icon) and vegetative traits (green leaf icon) and associated these traits (red arrows) with abiotic and biotic factors (blue arrows). To address Q2, I recorded climatic factors and microhabitat conditions at 1000 (yellow circles), 2000 (green circles) and 3000 m a.s.l. (gray circles) and tested how they predicted the prevalence of endozoochory across elevations. To address Q3, I measured three seed rain attributes (seed rain richness, seed rain biomass, and seed traits) in pastures (yellow boxplots) and forests (blue boxplots).

### **3.2. How do climate and microhabitat conditions affect endozoochory? (Q2)**

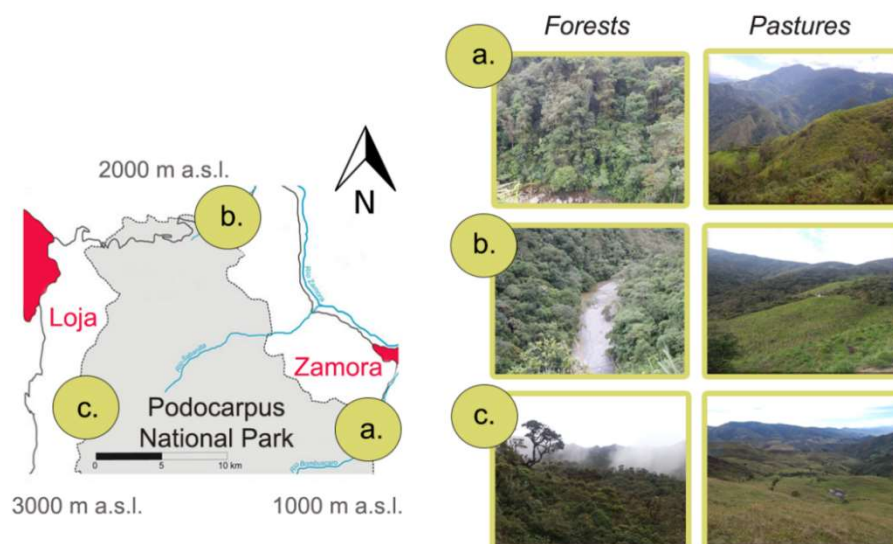
Although endozoochory is the most dominant mode of seed dispersal in tropical forests (Correa et al., 2015), the relationship between endozoochory and local and regional abiotic and biotic factors is still largely unknown. To assess how endozoochory is related to the environment at different scales, I investigated whether the proportion of endozoochorous plant species in the tropical Andes of southern Ecuador was affected by elevation, climate and microhabitat conditions. I hypothesized that: (1) harsher climatic conditions and weaker biotic stressors that usually occur at high elevations should prevent fleshy-fruited species to occur at high elevations (Buitrón-Jurado & Ramírez, 2014), and, in consequence, the proportion of endozoochorous species in the seed rain should decrease with increasing elevation; (2) since productive environments, characterized by the combined effects of high temperature and high rainfall, support the elevated costs of producing fleshy fruits (Bonte et al., 2012; Willson et al., 1989), I expected to find that endozoochory would increase with increasing rainfall and temperature; and finally, (3) that microhabitats favoring late successional plant species would experience higher prevalence of large seeds of fleshy-fruited plant species (de Melo et al., 2006; Tabarelli & Peres, 2002).

### **3.3. How does land-use affect seed rain potential to restore deforested areas across elevations? (Q3)**

Quantification of seed rain is a common method for assessing the natural restoration potential in deforested areas. However, it is unclear which attributes of seed rain these assessments should consider. I compared seed rain between forests and deforested areas along an elevational gradient spanning from 1000 to 3000 m a.s.l. in southern Ecuador. I hypothesized that the disruption of plant-frugivore interactions in deforested areas (Markl et al., 2012; Quitián et al., 2018) would systematically reduce seed rain biomass and richness as well as seed size from forests to pastures across all elevations. In consequence, I also expected to find a decrease in the proportion of endozoochory from forest to pastures with increasing elevation, due to the decline in animal-dispersed species towards higher elevations (Le Bagousse-Pinguet et al., 2017; Šímová et al., 2015; Swenson & Enquist, 2009).

#### 4. Study system and study design

I studied the impacts of (a)biotic factors on plant traits and seed dispersal of plant communities along an elevational gradient in and around Podocarpus National Park and San Francisco Research Station in the tropical Andes of southern Ecuador (Figure 3). This area has a variety of topographic features: elevation ranges from 1000 m a.s.l. at the lowest point of Bombuscaro river valley in the province of Zamora to 3600 m a.s.l. at the Cajanuma ridges in the province of Loja. The study area has a humid tropical climate (Bendix et al., 2008), characterized by a less humid season from December to February and a more humid season from June to August (Beck et al., 2008; Bendix et al., 2006). The mean annual precipitation is generally high, in the range of 2000-4500 mm. Mean annual temperatures along this elevational gradient decrease from about 19.4°C in the lowlands to about 9.4°C in highlands (Bendix et al., 2008).



**Figure 3:** The study area is located in Podocarpus National Park, San Francisco Reserve and the surrounding area, in tropical mountains of southern Ecuador. Specifically, I worked along an elevational gradient from 1000 to 3000 m a.s.l. Letters indicate the location of the three study sites and provide a visual overview of the forests and pastures at the specific elevations: (a.) 1000 m a.s.l., (b) 2000 m a.s.l. and (c) 3000 m a.s.l.

The type of tropical montane forest varies along the elevational gradient. At low elevations (ca. 1000 m a.s.l.) the forest is predominantly evergreen premontane, whereas at mid (ca. 2000 m a.s.l.) and high elevations (ca. 3000 m a.s.l.) the forest



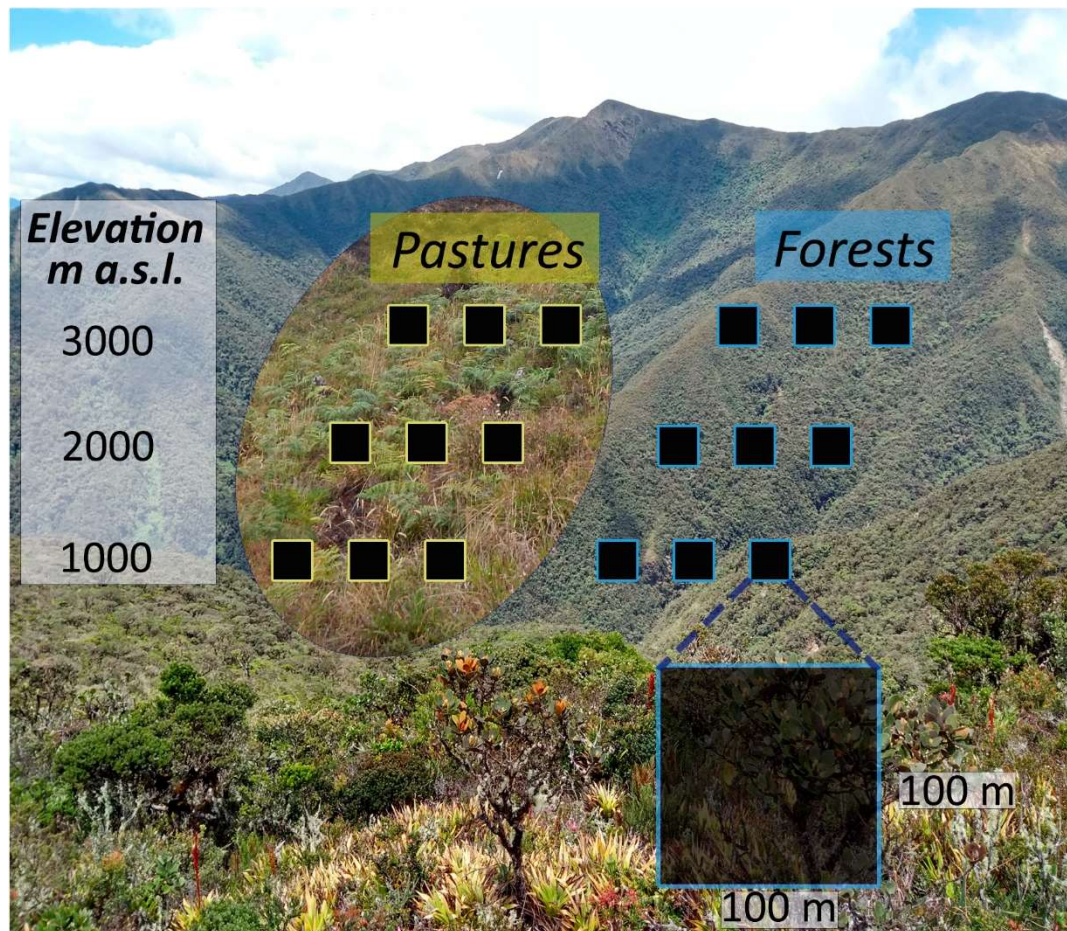
transitions to lower montane forest and upper montane forest, respectively (Homeier et al., 2008). Areas within the Podocarpus National Park and San Francisco Research Station remain mostly unaltered with old-growth forests, while those outside the protected areas have been severely affected by land-use change and are a mixture of secondary and old-growth forest patches, agricultural areas, pastures for livestock grazing, and human settlements.

The extraordinary diversity of climatic and topographic characteristics together with its abundant flora and fauna have led this study area to be recognized as part of the Andean biodiversity hotspot (Beck & Kottke, 2008). In terms of vegetation, Melastomataceae is the most dominant tree family along the elevational gradient (Homeier et al., 2013), and its wide distribution is likely related to its diverse seed dispersal modes (Messeder et al., 2022). However, there is a high turnover of tree species between elevations, and some plant families are more represented in a specific type of montane forest. For example, common tree families in the premontane evergreen forest besides Melastomataceae, are Fabaceae, Moraceae, Myristicaceae, Rubiaceae and Sapotaceae, while in the lower montane forest Euphorbiaceae and Lauraceae are part of the most dominant tree families. In the upper montane forest, Aquifoliaceae, Clusiaceae and Cunoniaceae are tree families highly represented by plant species with a height that rarely exceeds 8–10 m (Homeier et al., 2013).

I collected data at three elevations (1000, 2000 and 3000 m a.s.l.), in two habitat types: (1) forest (for Q1, Q2 and Q3) and (2) pastures used for livestock grazing (for Q3). At each elevation, I worked in three forest plots and three pastures plots of 1-ha plots (i.e. six 1-ha plots per elevation,  $n = 18$  plots along the elevational gradient), established by the DFG research unit RESPECT “Environmental changes in biodiversity hotspot ecosystems of South Ecuador: RESPONSE and feedback EFFECTs (FOR2730)” (more details in Bendix et al., 2021) (Figure 4.).

## **5. Data collection and research methods**

To address the principal research questions of this dissertation, I used three different datasets. I obtained these datasets from fieldwork campaigns conducted in 2018 by other researchers and fieldwork campaigns in 2019 and in 2020 conducted by myself



**Figure 4:** Schematic representation of the plot distribution along the elevational gradient in southern Ecuador. 18 Plots were established in two land-use types: pastures (yellow) and forests (blue). Three plots were established per land-use and elevation. Each plot had an area of 100 m x 100 m (1 ha).

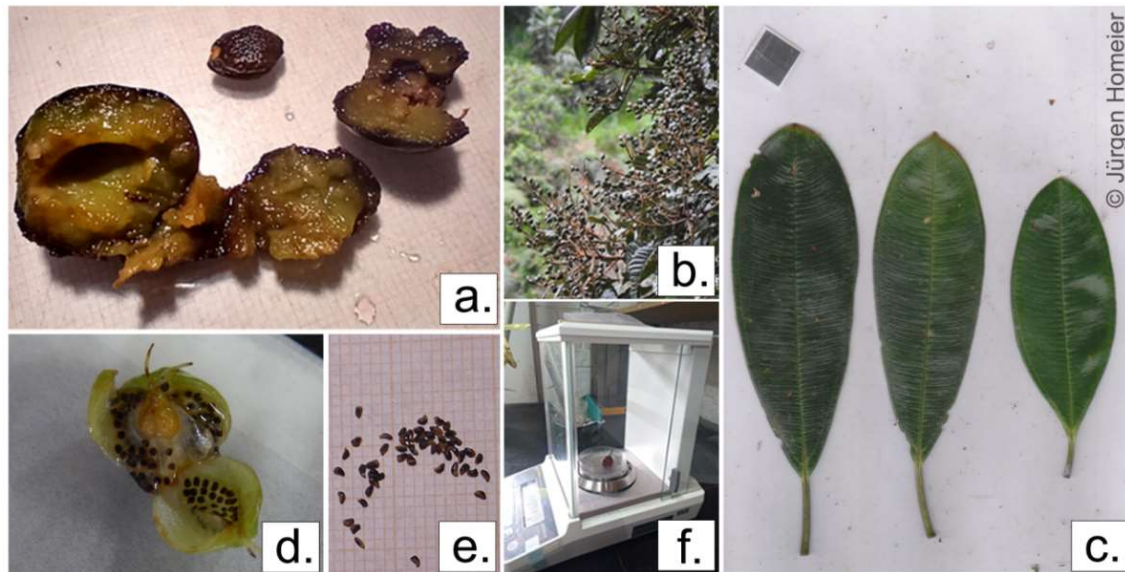
with the support of field assistants. For Q1, the dataset includes plant trait, plant community and plant phylogeny data (Subsections 5.1, 5.2, and 5.3), as well as measurements of abiotic and biotic factors (Subsection 5.5). For Q2, the dataset consists of seed rain records on forests along the elevational gradient over one-year sampling (Subsection 5.4) and measurements of climate and microhabitat conditions (Subsection 5.5). For Q3, the dataset corresponds to seed rain attributes on forests and deforested areas along the elevational gradient over a three-month sampling period (Subsection 5.4).

### 5.1. Trait data of fleshy-fruited plant species

In the field, I collected trait data of seeds and fruits (reproductive traits) as well as compiled leaf trait data (vegetative traits) of fleshy-fruited plant species along the

elevational gradient to test the associations between plant traits and abiotic and biotic factors of fleshy-fruited plant species (Q1). I directly measured and calculated seven reproductive traits from seeds and fruits in the field: (1) seed fresh mass, (2) pulp fresh mass, (3) crop size, (4) pulp C/N ratio, (5) relative yield index, (6) seed C/N ratio and (7) seed number, and compiled five leaf traits from a parallel study in the study area (Homeier et al., 2021): (1) leaf area, (2) specific leaf area, (3) leaf C/N ratio, (4) leaf thickness, and (5) leaf toughness. For reproductive traits, I recorded data by myself on 1-5 individual trees for 18 species, which were the most abundant fleshy-fruit bearing tree species detected in monthly monitoring from May 2019 to March 2020. For the vegetative traits, I compiled data from Homeier et al., (2021) on 8-10 individuals for 33 fleshy-fruited plant species within the study plots between February and March 2019 (Figure 5.).

I selected these seven reproductive traits to capture variability in the rewards offered to animal frugivores (crop size, pulp C/N ratio, relative yield index), in seed and fruit size (seed fresh mass, pulp fresh mass), and in strategies related to seedling establishment (seed C/N ratio, seed number, seed fresh mass) (Fenner & Thompson, 2005; Saatkamp et al., 2019). Crop size was calculated by counting the number of mature fruits on some branches of the tree and multiplying the mean mature fruits per branch by the number of branches with fruits. With the support of field assistants, I harvested at least 10 fruits per tree to record the other six traits. To record seed and pulp fresh mass and count the number of seeds per fruit, I dissected fruits and extracted the seeds. I dried seeds and fleshy pulps at 60 °C for three to four days in Ecuador and export the samples to Germany to determine the carbon (C) and nitrogen (N) concentrations with an elemental analyzer (Vario EL III, Elementar Analysensysteme, Langenselbold, Germany) at the Georg-August-Universität Göttingen. By estimating the C/N ratio for the pulp of fruits and seeds, I was able to summarize the allocation of C and N in fruits and seeds. I also established a relative yield index as the ratio between the fresh mass of the entire fruit and the dry mass of pulp. This measure shows the amount of dry mass that has been gained relative to the total fruit mass (Herrera, 1981). Photos of most plant species' seeds and fruits can be seen in Acosta-Rojas et al., (2021), a field guide on animal-dispersed plants in and around Podocarpus National Park that I have elaborated together with some colleagues during the execution of my dissertation project.



**Figure 5:** Measurement reproductive and vegetative traits of fleshy-fruited plant species in the tropical montane forests of southern Ecuador. (a) Dissection of a ripe fruit of *Guatteria pastazae* with a single seed before measuring seed and pulp fresh mass. (b) Unripe fruits of *Tapirira guianensis subandina* recorded in the fruiting phenology monitoring (c) Scanned leaves of *Miconia calophylla* used to calculate leaf area. (d) Dissection of a ripe fruit of *Sauraria* sp. with multiple tiny seeds before separate seeds from the fresh pulp. (e) Seed number of one fruit of *Miconia cf. jahnii*. (f) Measuring fruit fresh mass of *Matayba inelegans*.

For vegetative traits, I compiled five key leaf traits that capture the variability in leaf size (leaf area), in the cost of leaf production (specific leaf area, leaf C/N ratio) and in plant defense against herbivores (leaf thickness, leaf toughness) (Díaz et al., 2016; Lamarre et al., 2012; Pérez-Harguindeguy et al., 2013; Poorter et al., 2009; Reich et al., 1999; Ruiz-Guerra et al., 2021; Wright et al., 2004). Homeier et al. (2021) collected twenty leaves attached to 2-3 branches from the tree crown under homogeneous exposure to sun radiation. Prior to measurements, each branch was kept entirely in a sealed polyethylene bag with water-soaked tissues. Leaf area (LA, cm<sup>2</sup>) was obtained by scanning 20 undamaged leaves with the software WinFOLIA 2014 (Régent Instruments, Quebec, QC, Canada). After leaves were dried at 60 °C for three to four days in a dryer oven, Homeier et al. (2021) used the ratio of leaf area to leaf dry mass to calculate specific leaf area (SLA, cm<sup>2</sup> g<sup>-1</sup>). Using an elemental analyzer, the C and N content of leaves was measured (Vario EL III Elementar Analysensysteme, Langensfeld, Germany). Leaf thickness (mm) was measured on both sides of the primary leaf vein (Mitutoyo M293- 240-70, Mitutoyo Germany Ltd, Neuss, Germany)

using a digital micrometer. With a digital penetrometer, six punch tests were performed on the leaf surface without the midrib and other major veins to determine the leaf toughness ( $\text{kN m}^{-1}$ ) (fat-ended 2.0 mm diameter steel punch, DS-50 N, Imada Inc., Japan). Homeier et al. (2021) provides more information on the leaf trait techniques and leaf trait data.

## **5.2. Plant community**

In order to explain variations in community composition over abiotic and biotic gradients (Q1), I compiled from another study the presence and abundance of tree species on all nine 1-ha forests plots (Homeier et al., 2021). In the frame of the DFG research unit RESPECT, an inventory of all woody stems with a diameter at breast height (DBH)  $\geq 10$  cm inside each 1-ha plot was carried out. To ensure taxonomic identification in accordance with the herbaria collections of the Universidad Nacional de Loja (UNL) and the University of Göttingen (GOET), all trees were tagged, and herbarium specimens were collected. The number of individual trees per plot served as the measure of each species' abundance.

## **5.3. Plant phylogeny**

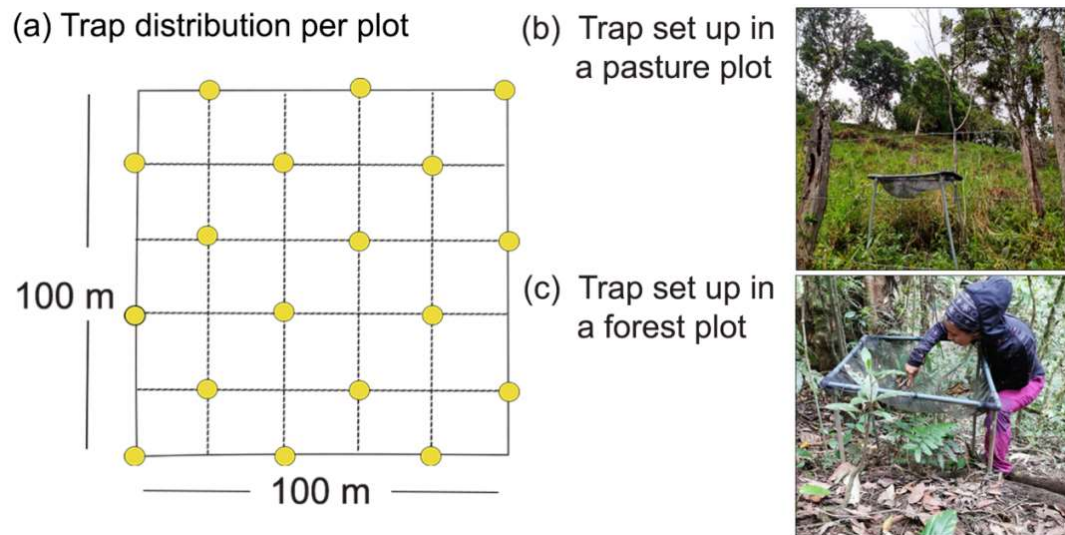
To determine the degree to which a species' phylogenetic history shapes trait-environment relationships (Q1), I built two phylogenetic trees: (1) one for the 18 species of which I measured reproductive traits and another (2) for the 33 species for which I compiled vegetative traits. I used a dated mega-tree implemented in *V.PhyloMaker* (i.e. *GBOTB. extended.tre*). Prior to building the phylogenetic trees, I updated the species nomenclature following the Leipzig Catalogue for Vascular Plants using the R packages *lcvplants* and *LCVP* (Freiberg et al., 2020). I also used the R packages *V.PhyloMaker2* (Jin & Qian, 2022), *ape* (Paradis & Schliep, 2019) and *phytools* (Revell, 2012) for editing the phylogenetic trees. By choosing at random a congeneric species and adding its branch to the phylogenetic tree, the three plant species (*Ocotea* sp., *Saurauia* sp., and *Myrcia* sp.) that could only be recognized to genus level were also included. Therefore, all of the studied species were represented in the phylogenetic trees.

#### **5.4. Seed rain in natural and deforested areas**

In order to explore the effects of climate and microhabitat conditions on endozoochory (Q2) and to examine the potential of seed rain to restore deforested areas (Q3), I collected seed rain in 18 traps per 1-ha plot located along the elevational gradient inside nine forest plots for Q2 and in 18 1-ha plots at forests (9 plots) and deforested areas (9 plots) for Q3. Traps consisted in a PVC frame fitted with 1.5 mm nylon mesh of 0.36 m<sup>2</sup>, suspended 90 cm above the ground by four PVC tubes, that were distanced by approx. 20 m among each other (Figure 6.). In deforested areas, traps were fenced off with wire cable to prevent trampling and damage by cattle. Grasses were cleared below the mesh at each visit. I sampled the content of each trap, with the support of field assistants, every 15 days along an entire year between January 2019 and January 2020 at forests areas (Q2) and between the less rainy season from November 2019 to January 2020 at forest and deforested areas (Q3). I recorded every whole seed, at least 1 mm in length, from woody and herbaceous plants that was captured in each trap. For some species, such as wind-dispersed species, the complete dispersal unit, or diaspore, is made up of the seeds and the surrounding fruit structure. Thus, in this dissertation I refer to all dispersal units as seeds. I counted all seeds and identified them to the lowest possible taxonomic level. To this end, I prepared a reference collection of seeds based on plant material collected from the study area. I also consulted field guides and botanical experts. Taxonomically unidentified seeds were noted as undetermined species/morphospecies. All collected seeds were dried for 3–4 days at 60°C, and weighed using an extremely precise analytical balance (precision 0.0001 g; KERN & SOHN GmbH, Germany).

Based on dried seeds of the seed rain sampling, I measured and calculated two attributes (seed rain biomass and seed rain richness) for Q2 and four attributes (seed rain biomass, seed rain richness, seed mass and seed dispersal mode) for Q3. I calculated seed rain biomass as the sum of the dry mass of the seeds that were gathered for each sample and

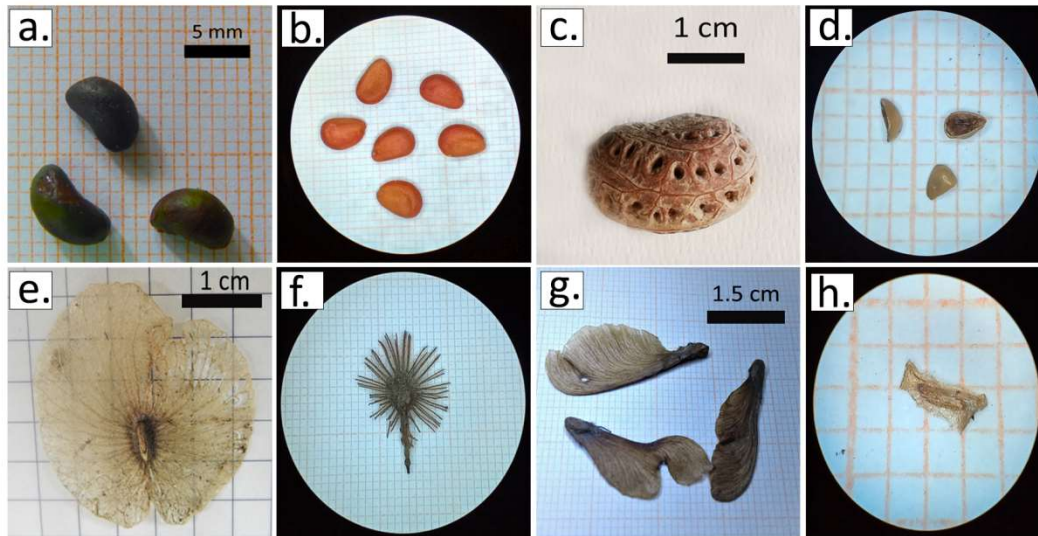




**Figure 6:** Scheme of study design inside 18 1-ha plots installed in forests and pastures along an elevational gradient in southern Ecuador: (a) Distribution of traps inside each plot (the location of each trap is marked with a yellow circle). (b) Seed traps were fenced by wire cable to avoid trap damaging by cattle in the pastures. (c) Seed rain sampling inside forest plots.

seed rain richness as the amount of plant species and morphospecies of seeds collected per trap. In addition, I also calculated a community-wide measure of seed mass, weighing all seeds that were captured in a particular trap on a specific date. To determine the seed dispersal mode of the plant species recorded in the seed rain, I classified each plant species as endozoochorous or non-endozoochorous based on their main seed dispersal mode (Figure 7.). The criteria to assign the seed dispersal modes was based on data on frugivore-plant interactions, sporadic field observations, and seed/fruit morphology (i.e., Bello et al., 2017; Quitián et al., 2019).

Prior to the analyses, for Q2, I used the seed rain biomass to estimate the relative seed rain biomass of endozoochorous species as the seed dry mass of these species divided by the total seed biomass. This term may be also understood as the proportion of endozoochorous species collected per trap along the year. In addition, I used the seed rain richness to estimate the relative seed rain richness of endozoochorous species defined by the number of endozoochorous species sampled in a seed trap over the entire year divided by the total seed richness. Therefore, the relative seed rain richness refers to the proportion of endozoochorous species recorded per trap over the course of a year (logit-transformed before running the analysis with an adjust of 0.025 for the values of



**Figure 7:** Diversity of seeds collected from the seed rain of tropical montane forest between 1000 and 3000 m a.s.l. Endozoochorous species are shown from a-d and non-endozoochorous species from e-h: (a) *Chrysochlamys membranacea* seeds collected at 1000 m a.s.l. (b) *Ternstroemia macrocarpa* seeds embedded in a fine red arile collected at 3000 m a.s.l. (c) *Anomospermum reticulatum* seeds collected at 1000 and 2000 m a.s.l. (d) Melastomataceae seeds collected at 1000 m a.s.l. (e) *Mascagnia* sp. diaspores collected at 1000 m a.s.l. (f) *Heliocarpus americanus* collected at 2000 m a.s.l. (g) Malpighiaceae seeds collected at 2000 m a.s.l. (h) *Clethra revoluta* seeds collected at 2000 and 3000 m a.s.l. The grid on the background of photos without a reference of size is composed of squares of 1 mm<sup>2</sup>.

0 and 1 to avoid undefined values). For Q3, I combined seed rain samples of each trap between November 2019 and January 2020 (a period of three months), since climatic conditions were largely stable throughout this time. Hence, seed rain biomass refers to the total dry mass of seeds gathered per trap throughout all temporal samples (log-transformed). Seed rain richness was defined as the amount of plant species or morphospecies of seeds collected per trap over the three months. Seed mass refers to the average dry mass of seeds collected in each trap over the course of three months (log-transformed). Finally, the proportion of endozoochory was estimated by the number of endozoochorous species and non-endozoochorous in each trap over three-month sampling.



### **5.5. Abiotic and biotic factors at large and small spatial scales**

At the large spatial scale, I compiled key climatic conditions and soil properties in nine 1-ha forest plots from other studies (Bendix et al., 2018a, 2018b; Dobbermann et al., 2018; Velescu et al., 2020a, 2020b, 2020c). Average annual precipitation and temperature were obtained from daily meteorological records between the years 2018 and 2020 from an operational network consisting of automatic climate stations, remote sensing techniques and a regionalization tool developed for the study area (Fries et al., 2009; Rollenbeck & Bendix, 2011). Concentrations of C and N in the soils were obtained by collecting and analyzing mineral soil samples in the A horizon. These concentrations were used to calculate soil C/N ratios in order to approximate the organic matter turnover in the soils and the availability of nutrients to plants. High soil C/N ratios is indicative of low N availability to plants as a result of slower organic matter turnover (Post et al., 1985; Wilcke et al., 2020).

At the small spatial scale, I compiled microhabitat conditions such as canopy structure and soil moisture in a total of 81 subplots inside nine 1-ha forest plots (nine 1 m<sup>2</sup> subplots per 1-ha plot) from a parallel study in the area (Barczyk et al., 2023). For canopy structure, hemispherical photos were taken using a Nikon FC-E8 Fish-Eye Converter (Nikon Corporation, Japan). Barczyk et al., (2023) analyzed hemispherical photos with Gap Light Analyzer version 2.0 (Frazer et al., 1999) to calculate the leaf area index as the amount of one-sided foliage area projected per unit ground surface area (Chen & Black, 1992). High leaf area index values indicate high foliage interception per unit ground surface, resulting in a more complex canopy structure (Chen & Black, 1992). For soil moisture, a tensiometer (SM150 Kit, Delta-T Devices Ltd., UK) was used to record water availability for plants in the soils (Schmugge et al., 1980). Both soil moisture and leaf area index were recorded on the same dates in October 2019.

I compiled avian fruit removal and leaf herbivory at the 1-ha plot scale to quantify two key biotic variables shaping seed, fruit and leaf traits (Galetti et al., 2013; Metcalfe et al., 2014). I used avian fruit removal data from Quitián et al., (2019) and herbivory data sampled on the same plots (Tiede, unpublished data). First, fruit removal was defined as the sum of removed fruits by all frugivorous birds observed on each plot. Only events of fruit and seed removal were considered, i.e., fruit and/or seed dropping events were

excluded (Quitíán et al., 2019). Second, the degree of herbivory was assessed at the community level in the forest plots following Adams et al., (2009). For this purpose, all leaves that reached the traps over 15 days of sampling were collected in the same 162 traps in which seeds were also sampled. Subsequently, leaves were scanned and leaf area loss per leaf and trap were quantified using WinFOLIA 2005 software (Regent Instruments, Inc., Canada). To quantify the total herbivory on each plot, I calculated the proportional leaf area loss for each individual leaf and averaged these values across all leaves in a trap and across all traps located in a forest plot. The mean herbivory rate per plot was given by the mean value over the temporal replicates across the entire year.

## **5.6. Data analyses**

With the purpose of identifying the main ecological plant strategies of the fleshy-fruited species based on the trait data previously collected and compiled (Q1), I conducted two separate principal component analyses (PCA) for (1) reproductive and (2) vegetative traits. To create a straightforward structure where the loading of the traits is maximized along single axes, I used a varimax rotation (Kaiser, 1958). In the PCA with reproductive traits, we included the following seven key traits previously described (see subsection 5.1 of “Data collection and research methods”): crop size, seed fresh mass, pulp fresh mass, seed number, seed C/N ratio, pulp C/N ratio, and the relative yield index. In the PCA with vegetative traits, I used the compiled five leaf traits described also in the subsection 5.1: leaf thickness, leaf toughness, LA, SLA, and leaf C/N ratio. I log-transformed all vegetative traits and some reproductive traits (seed number, seed fresh mass, pulp fresh mass, seed C/N ratio, pulp C/N ratio, and crop mass), before running the analyses in order to approximate a normal distribution of trait data. For both types of traits, I kept only the two first axes of the PCA. I performed PCA and related graphs using the programming language R version 4.0.5 (R Core Team, 2021) with the packages: *psych* (Revelle, 2022) and *ggplot2* (Wickham, 2016).

With the objective to test for a general association between plant traits and abiotic and biotic factors (Q1), I applied individual fourth-corner permutation tests for reproductive and vegetative traits on the sum of the eigenvalues of the first and second axis (Dray et al., 2014). I used the most conservative fourth-corner model six (9999 permutations) to test the null hypothesis that abiotic and biotic factors, species presence, and plant traits are unrelated, according to a random community assembly independent of plant trait

values (Dray et al., 2014). I also applied the same null model to test for axis-specific associations of plant traits and abiotic and biotic factors, based on correlations of the RLQ scores on the first and second axis, respectively (Dray et al., 2014).

So as to test whether the associations between plant traits and abiotic and biotic factors were maintained after controlling for phylogenetic and spatial effects (Q1), I applied an extended version of the RLQ analysis (Pavoine et al., 2011). In addition to the three matrices of the RLQ analysis based on: (1) the mean values of abiotic and biotic factors per plot (i.e., the R matrix), (2) the abundance or presence/absence data of species per plot (i.e., the L matrix) and (3) the plant trait data of species per plot (i.e., the Q matrix) (Dray et al., 2014), this extended RLQ analysis uses two extra matrices based on: (4) the phylogenetic distances between species (i.e., the P matrix) and (5) the spatial configuration of the research plots (i.e., the S matrix) (Pavoine et al., 2011). The analysis includes the covariation by partitioning trait effects into a phylogenetic component due to a phylogenetic clustering of trait values and a trait component that does not depend on the phylogeny. Similarly, the environmental variation is partitioned into a spatial component because of the comparable environmental conditions at neighbouring plots and an environmental component that does not depend on the spatial arrangement of study plots. For the extended RLQ analyses, I applied the same types of fourth-corner permutation tests that I used for the RLQ analyses, but included the phylogenetically and spatially independent components. I performed RLQ-fourth corner analyses using the programming language R version 4.0.5 (R Core Team, 2021) with the packages: *dplyr* (Wickham et al., 2019), *picante* (Kembel et al., 2010), *FD* (Laliberte & Legendre, 2010), *psych* (Revelle, 2022), *ade4* (Dray & Dufour, 2007), and *adiv* (Pavoine, 2020).

To test whether climate and microhabitat conditions affect endozoochory in tropical montane forests (Q2) and whether land-use influences seed rain potential to restore deforested areas (Q3), I used generalized linear mixed-effects models (GLMMs). For Q2, I modelled the effect of elevation on endozoochory with two GLMMs including elevation (1000 m, 2000 m and 3000 m a.s.l.) as a fixed factor and plots as a random factor. Further, I built two full models that included climatic factors (temperature and rainfall) and microhabitat conditions (leaf area index and soil moisture) as predictors and the identity of study plots as a random factor. I used a model with a Gaussian error

distribution when I included the relative biomass of endozoochorous species as a response variable and a model with a Binomial error distribution when the response variable was the relative seed rain richness of endozoochorous species. I generated a set of component models based on the full models, including all potential combinations of predictor variables, and I chose the optimum combination of predictors based on the Akaike's information criterion (Burnham & Anderson, 2004).

For Q3, I first tested the effect of land-use on seed rain biomass (with a Gaussian error distribution) and on seed rain richness (with a Poisson error distribution). Second, I tested the effect of land-use on seed mass (with a Gaussian error distribution) and on the proportion of endozoochours species (with a binomial model). Land-use (forest, pasture) and elevation (1000, 2000, 3000 m a.s.l.) were considered as the fixed factors of the models. For all models, I included the identity of study plots ( $n = 18$ ) as a random factor. I performed GLMMs and related graphs with programming language R version 4.1.2 (R Core Team, 2021), with the use of *car* (Fox & Weisberg, 2019), *glmmTMB* (Magnusson et al., 2020), *r2glmm* (Jaeger, 2017), *MuMIn* (Barton, 2016), *ggplot2* (Wickham, 2016), and *ggpubr* packages (Kassambara, 2018).

## **6. Main results and discussion**

### **6.1. Abiotic factors similarly shape the distribution of fruit, seed and leaf traits in fleshy-fruited tree communities (Q1)**

I assessed plant trait associations and how they relate to both abiotic and biotic factors in fleshy-fruited tree communities in the tropical Andes of southern Ecuador (Acosta-Rojas et al. in revision, appendix A1). First, I identified the main plant ecological strategies in the trade-offs between (i) seed number and seed size as well as in (ii) the production of few costly (N-rich) vs. several cheap (C-rich) fruits. Likewise, leaf trait variation was mainly captured by (i) the leaf economics spectrum between conservative (C-rich) and acquisitive (N-rich) leaves and by (ii) the size spectrum (leaf size). Second, controlling for phylogenetic and spatial covariation, reproductive and vegetative traits were associated with the abiotic and biotic environment. These results show similar trait-environment relationships for both reproductive and vegetative traits, regardless of a species' phylogenetic relatedness. The main ecological strategies related to the

production of fruit and leaves were primarily related to the extent to which environments have a fast (i.e., low soil C/N and a high N availability to plants) or slow turnover of organic matter (i.e., high soil C/N and a low N availability to plants), whereas strategies associated with the size of seeds, fruit, and leaves were mainly associated with rainfall. Therefore, I found similar abiotic constraints for producing different types of seeds, fruit and leaves in the tropical montane forests of southern Ecuador.

I identified the main ecological strategies related to reproductive traits and to seed size and fruit production in particular. Associated with seed size, I distinguished plants producing few large seeds inside large fruits from those producing many small seeds inside small fruits. This trade-off between seed size and number represents two alternative strategies in allocating reproductive resources (Harper et al., 1970). Allocation of biomass to seed and fruit size reflects one of the main constraints in vascular plants around the world (Díaz et al., 2016). Related to fruit production, I was able to differentiate plants producing large crops of C-rich fruits from those producing small crops of protein-rich fruits. This fruit number-reward trade-off, which underpins the cost to produce N-rich fruit, is described in the classic concept of seed dispersal systems proposed by Howe (1993). According to this concept, specialized seed dispersal systems target particular seed dispersers by rewarding fruits (e.g., those with a high lipid or protein content) and modest crop sizes. Contrarily, generalized systems frequently have large crop sizes and sugar-rich fruit that are attractive to a variety of frugivorous animals (Howe, 1993; McKey, 1975). My research shows that the type of resource allocation to fruits is an important trait dimension in the tropical montane forests of southern Ecuador.

Reproductive traits were primarily associated with soil C/N ratio and precipitation. I discovered that plant species with small crops and fruit high in protein (low pulp C/N ratio) were more common in habitats with high N availability (low soil C/N), whereas species with large crops and fruit high in sugar (high pulp C/N ratio) were more common in habitats with low N availability to plants (high soil C/N). According to earlier research (Kaspari et al., 2007), fruit production in tropical forests is influenced by soil nutrients, although other elements such as tree size and competition between nearby trees may also play a role (Minor & Kobe, 2019). Furthermore, I found that size

variation in reproductive traits was related to precipitation. As a result, tree communities in rainy environments were characterized by smaller seeds and fruits. In contrast, less humid environments were characterized by larger diaspores. In line with my findings, seed size is positively correlated with precipitation at larger scales (Moles et al., 2004).

Similar to the main axes for reproductive traits, I identified two different constraints for vegetative traits, which are primarily related to leaf economics and leaf size spectrums. First, I identified that plants produce conservative leaves or produce leaves with an acquisitive use of resources, according to the leaf economics spectrum (Wright et al., 2004). Second, I differentiated small-leaved plants from those with large leaves, reflecting costs and benefits of leaf size for photosynthesis and heat exchange (Givnish, 1987; Kleiman & Aarssen, 2007; Wright et al., 2017). Across all species of fleshy-fruited plants, I found similar restrictions relating to the reproductive and vegetative traits. The cost of generating plant organs is reflected in these trade-offs. For instance, there are restrictions on the size of plant organs as well as the allocation of N and C to seeds, fruit and leaves.

Vegetative traits were mainly related to soil C/N ratio and precipitation, and only marginally related to temperature. I found high soil N availability (i.e., low soil C/N) to be associated with the production of high SLA, N-rich leaves (i.e., low leaf C/N), whereas a low N availability for plants in the soils (i.e., high soil C/N) was associated with the production of leaves with lower N concentration and low SLA values. At both local (Asner et al., 2016; Homeier et al., 2021; Yan et al., 2016) and global scales (Reich & Oleksyn, 2004), soil properties have been recognized as the primary driver of N and phosphorus leaf concentrations. Overall, my results show how important soil C and N concentrations are for determining how these nutrients are allocated to fruit pulp and leaves. Similar patterns of nutrient distribution across fruit and leaves could indicate conservatism in the methods used by plants to distribute nutrients to different types of plant organs (Zhao et al., 2020). Moreover, I found that leaf size is associated with precipitation, and for that reason, large-leaved plants are more abundant in the less rainy environments. Species with large leaves are more frequent in rainy environments with sufficient water supply (Gallagher & Leishman, 2012; Moles et al., 2014; Wright et al., 2017). Interestingly, I found that leaf area was controlled mainly by rainfall variation

even though water is not a limiting factor in the study area. This surprising outcome may be the result of the association between leaf size and another abiotic factors not addressed in my study, such as irradiation (Givnish, 1984; Wright et al., 2017). The positive relationships that I found between fruit and leaf sizes also point to vascular and biomechanical restrictions between plant appendages as a potential explanation for why seed, fruit, and leaf sizes respond to precipitation in a similar manner (Corner, 1949).

## **6.2. An interplay between abiotic and biotic factors at large and small spatial scales shapes the prevalence of endozoochory in tropical mountains (Q2)**

I assessed the prevalence of endozoochory in the seed rain of plant communities along an elevational gradient in the tropical Andes of southern Ecuador. First, I found that the relative seed rain biomass and richness of endozoochorous plant species both decline with increasing elevation. While relative seed rain biomass of endozoochorous species decreases with increasing rainfall, relative seed rain richness of endozoochorous species increases with increasing temperature and higher leaf area index. My findings imply that climatic variables and microhabitat conditions interact to shape the richness of endozoochorous plant species in the seed rain of tropical montane forests.

In the southern Ecuadorian montane forests, the prevalence of endozoochory declined with elevation. In both temperate and tropical montane forests, a reduction in the prevalence of endozoochory along an elevational gradient have previously being reported (Buitrón-Jurado & Ramírez, 2014; Yu et al., 2017). My study reveals two distinct trends in endozoochory in montane forests. First, endozoochorous species' seed rain biomass is similar at 1000 and 2000 m a.s.l., with a subsequent decline toward the upper montane forest at 3000 m a.s.l. This trend may be influenced by fruit production of prolific or large-seeded species, which constitute a significant part of the biomass in seed rain. I suggest that similar values of the relative seed rain biomass of endozoochorous species at low and intermediate elevations may result from the high records of seed rain of large-seeded species at 1000 and 2000 m a.s.l., including the Lauraceae and Menispermaceae spp.

Second, the relative seed richness of endozoochorous species consistently declines with increasing elevation. Systematic change in the species composition of plants at high elevations is likely responsible for the decline in endozoochorous plant species with

elevation. Lower production at the higher elevations (Malhi et al., 2017; Tanner et al., 1998) results in fewer plant taxa that produce fleshy fruits in those upper montane forests. Additionally, abiotic vectors rather than biotic vectors frequently disperse herbaceous plant species, which become more prevalent at high elevations (Arbeláez & Parrado-Rosselli, 2005; Armesto & Rozzi, 1989; Tovar et al., 2020). The decrease in the prevalence of endozoochory along the elevational gradient may also correspond to a decrease in avian frugivores with increasing elevation (Quitíán et al., 2018). For instance, a study in the same montane forests reported a reduced diversity of plant-frugivore interactions at higher elevations, correlating to fewer frugivorous bird species (Quitíán et al., 2018).

In my research, the prevalence of endozoochory in the seed rain was correlated with climatic conditions. The relative seed rain biomass of endozoochorous plant species decreased with increasing rainfall. As a consequence, the positive correlation between endozoochory and rainfall in other Neotropical (Almeida-Neto et al., 2008; Correa et al., 2015) and Paleotropical forests (Zhao et al., 2018) are not supported by my findings. The link between water availability and productivity in our research system may explain these different outcomes. Rainy environments typically have high productivity levels that can support the high cost of producing fleshy fruits (Bonte et al., 2012; Willson et al., 1989). However, excessive rainfall in many tropical mountains is associated with a decline in soil fertility and decreased productivity due to the leaching of soil nutrients (Malhi et al., 2017). At the highest elevation in my study system, decreased productivity might result in a reduction in the production of fleshy fruit. As suggested by Willson et al., (1989), fleshy fruit production in tropical montane forests may be influenced by productivity rather than rainfall.

The relative seed rain richness of endozoochorous plant species increases with increasing temperatures. There is a significant correlation between the proportion of endozoochorous species and mean annual temperature in other montane forests in the northern Andes as well (Buitrón-Jurado & Ramírez, 2014). One explanation of how temperature affects endozoochory could be related to the relationship between productivity and temperature (Pau et al., 2018). On the other hand, low temperatures could harm fleshy fruits (Burke et al., 1976), as they contain a high proportion of water and organic compounds (Coombe, 1976). Moreover, an earlier investigation revealed



that endozoochorous species growing at high elevations may tolerate better warmer temperatures than non-endozoochorous species (Tovar et al., 2020). Therefore, it is likely that a combination of physiological constraints imposed by temperature and related to the production of fleshy fruit determines the prevalence of endozoochorous plant species. Temperature has been shown to positively affect the diversity of frugivorous birds (Santillán et al., 2020), and in another tropical mountain system, indirect associations between plant and bird diversity have been shown to be more significant than direct climatic effects (Vollstädt et al., 2017), suggesting that a greater diversity of endozoochorous plant species can be found in habitats with greater frugivore diversity.

The relative richness of endozoochorous species in the seed rain of tropical montane forests was related to microhabitat conditions in addition to the climatic gradients across the mountain. According to my hypothesis, the prevalence of endozoochory in seed rain richness increases with increasing leaf area index, but it is only weakly related to soil moisture. Several endozoochorous species, the majority of which have relatively large seeds, are likely present in late-successional habitats, which are characterized by increasing canopy complexity (i.e., denser foliage in the canopy) (Unger et al., 2013). The covariation between seed dispersal mode and other plant traits provides more evidence for this explanation. For instance, in Atlantic forests animal-dispersed plants tend to be tall trees with a high wood density (Bello et al., 2015). Since climatic factors operate a large scale while microhabitat conditions act at smaller spatial scales, my research demonstrates how the prevalence of endozoochory in tropical mountains is influenced by an interaction of abiotic and biotic factors operating at different spatial scales.

### **6.3. Importance of measuring different seed rain attributes for informing ecosystem restoration practices (Q3)**

I studied seed rain in old-growth forests and deforested areas along an elevational gradient in tropical mountains located in southern Ecuador. First, I did not find a consistent decline in seed rain biomass and richness between forests and pastures. However, I recovered greater seed mass and a larger proportion of endozoochorous species in forests. My findings show that the community and trait composition of

surrounding old-growth montane forests is considerably different from the template for future plant regeneration provided by seed rain onto pastures.

Contrary to my expectations for the southern Ecuadorian mountains, seed rain biomass and richness were not consistently lower in pasture compared to forests across elevations. In southern Costa Rica, for example, the average number of seeds that fell into forest traps over the course of one year was roughly nine times larger than that for pasture traps (Holl, 1999). The same study also found that forests have more species than pastures do (Holl, 1999). Similarly, mean seed density and species richness of dispersed plant species were higher in the forest than in areas cleared of trees in the tropical Bolivian Andes (Saavedra et al., 2015). The extent to which seeds originate from old-growth montane forests rather than from other sources may be one explanation for the abundance and diversity of seeds in pastures. For instance, the high species turnover between pastures and forests, as well as across elevations, suggests that pastures' seed rain was primarily derived from sources other than old-growth forest vegetation, such as secondary forests, riparian vegetation and hedgerows or remnant trees found within the agricultural land use matrix. My findings suggest that high seed rain richness may not necessarily indicate high natural restoration capability in deforested areas, despite recent research showing that species richness is a good predictor of both resilience (Ratcliffe et al., 2017) and ecological stability (Hautier et al., 2015).

I discovered systematic differences in the predominant seed traits between forests and pastures across elevations, which was in line with my initial expectation. For example, the mean seed mass as well as the percentage of endozoochorous species that arrived on pastures were lower than those recorded in the forests. My findings support previous studies showing that a scarcity of large seeds of late-successional and endozoochorous species may result from seed dispersal into deforested areas under natural regeneration (Saavedra et al., 2015; Tabarelli et al., 2012). In the case of endozoochorous species, seed dispersers visiting the deforested areas studied and feeding on fruit sources located in the agricultural matrix may not be able to eat and disperse the full spectrum of fruit and seed sizes. For example, small-bodied frugivorous birds are limited to swallowing small fruit species, whereas large frugivores can eat small or large fruits (Kitajima, 2002; Wheelwright, 1985). Due to hunting and habitat destruction, especially in tropical

areas, large frugivores constitute a group that is especially vulnerable to local extirpation (Dirzo et al., 2014). Therefore, it is plausible to assume that, as in other tropical areas (Terborgh et al., 2008), the lack of large frugivores arriving in the deforested areas studied here may cause the decline in the dispersal of large-seeded plant species into pastures across these tropical mountains.

## **7. Synthesis and conclusions**

In this dissertation, I explored how trait-environment associations can improve the understanding of the impacts that the abiotic and biotic environment has on plant community responses. This research builds upon empirical measurements of important seed rain-related plant functional traits of entire tree communities, with a particular focus on reproductive traits and fleshy-fruited tree plant species. By integrating multiple types of trait-based analyses for ecological communities, I provide new insights for seed dispersal ecology across tropical mountains. My dissertation has three main findings: (1) I demonstrate that specific plant ecological strategies linked to reproductive and vegetative traits are similarly filtered by abiotic and biotic factors in fleshy-fruited tree communities (Acosta-Rojas et al. in revision, appendix A1), (2) I establish that both climate and microhabitat conditions shape the prevalence of endozoochory in seed rain across elevations in the tropical montane forests (Acosta-Rojas et al. 2023, appendix A2), and (3) I show that measuring plant traits, such as seed mass and seed dispersal mode, in forests and deforested areas along an elevational gradient can be useful for identifying the natural regeneration potential of deforested areas (Acosta-Rojas et al. under review, appendix A3).

Trait-based ecology has long analyzed plant communities through the lens of vegetative traits, mainly ignoring how other traits related to different stages of the plant life cycle interact and respond to the environment (E-Vojtkó et al., 2020; Jiménez-Alfaro et al., 2016). Under this context, my work contributes to a better understanding of an important ecosystem function, seed dispersal, by expanding knowledge of reproductive traits and trait-environment associations across gradients of elevation and land use. In particular, my dissertation constitutes one of the few research studies that (1) investigates trait-environment associations using reproductive traits, (2) integrates reproductive traits with vegetative traits, (3) examines a spectrum of seed and fruit traits,

(4) tests the effect of microhabitat conditions on endozoochory, and (5) demonstrates how land-use can affect reproductive traits. Including reproductive traits to understand the dynamics of plant communities provides additional and essential information about different plant stages and functions (Laughlin, 2014; Rosbakh et al., 2018, 2020). For example, vegetative traits are strongly linked to adult plant growth and survival, while reproductive traits reflect the species' long term persistence of plant species in a given ecosystem (Grubb, 1977).

A trait-based understanding of plant community dynamics constitutes a great source of information for modeling and detecting changes in plant communities undergoing changing environmental conditions. Determining trait-environment associations for fleshy-fruited tree communities across tropical montane forests in this dissertation (Acosta-Rojas et al. in revision, appendix A1) has allowed me to characterize the interactions between endozoochorous plant species and relevant abiotic and biotic factors, as well as to propose potential future scenarios according to the current associations between plant traits and the environment. For example, I detected that the size spectrum of seeds, fruits, and leaves of fleshy-fruited trees is strongly related to rainfall. Thus, high rainfall environments have species producing smaller seeds, fruits and leaves compared to lower rainfall environments where species with larger seeds, fruits and leaves are more dominant. Therefore, projected changes in rainfall patterns under global change may lead to variation in the size of these plant organs. Identifying which plant species have traits that are vulnerable to specific environmental changes can help to optimize and design targeted conservation strategies (da Silva & Tabarelli, 2000).

Detecting trait-environment associations at different scales can help to recognize the importance both large- and small-scale mechanisms driving functional changes in plant communities under global change. For example, I found that both climatic and microhabitat conditions determine the degree of endozoochory in tropical montane forests (Acosta-Rojas et al. 2023, appendix A2). Accordingly, changes in climatic and microhabitat conditions can be expected to lead to changes in the composition of primary dispersal modes of tropical plant communities. Predictive models of tropical forest dynamics under global change should account for such changes in species composition, given the importance of seed dispersal for ecological processes and

ecosystem functions in these forests (Bello et al., 2015; Bendix et al., 2021; Fricke et al., 2022).

Measuring key plant traits across elevations in forests and deforested areas can be useful for identifying the natural regeneration potential of deforested areas and for informing effective restoration practices. I demonstrate that both the plant community and trait composition of the pasture seed rain in tropical mountains are considerably different from the seed rain reaching the nearby old-growth forests (Acosta-Rojas et al. under review, appendix A3). I propose that plant traits such as seed mass and seed dispersal mode can be used as valuable indicators of restoration success. The addition of large-seeded plants in deforested areas could be a useful strategy to promote the establishment of these species (Gallegos et al., 2016), as large-seeded species are more likely than small-seeded species to establish successfully after seed addition (Moles & Westoby, 2002). My research also highlights the need to examine seed traits in ecosystems that have undergone habitat modification in order to direct restoration efforts toward a high level of plant trait diversity. It is possible that the composition of regenerating vegetation will differ substantially from that of the current forest if such active measures are not adopted. Collecting data on seed trait composition is key to developing restoration efforts in deforested areas of tropical mountains.

Trait-environment studies across multiple plant traits are required for detecting the complex impacts of global change on plant regeneration. The unprecedented loss of biodiversity in the tropics demands that ecologists fill the gap between basic ecology on community assembly rules of plant communities and applied science for conservation and restoration purposes (Cabin et al., 2010; Wallington et al., 2005). My dissertation, in particular, picks up on earlier and recent calls that plant trait research should consider multiple traits representing different ecological niches (Craine et al., 2012; Laughlin, 2014; Rosbakh et al., 2022). Therefore, I here provide valuable information from unique and threatened tropical ecosystems that give new insights into the functioning and regeneration potential of tropical mountain forest ecosystems.

## 8. Zusammenfassung

Die Pflanzenverjüngung ist ein mehrstufiger ökologischer Prozess, der für die langfristige Stabilität und Widerstandsfähigkeit von Wäldern unerlässlich ist. Ein wichtiger Aspekt der Pflanzenverjüngung ist die Samenausbreitung, bei der Samen von der Mutterpflanze wegbewegt werden. Die Samenausbreitung spielt eine Schlüsselrolle für die Pflanzenverjüngung, da sie die Bewegung von Samen hin zu bestimmten Lebensräumen ermöglicht, wo sie keimen und sich zu Sämlingen und schließlich zu erwachsenen Pflanzen entwickeln können. Die Ausbreitung von Samen wird durch eine Vielzahl abiotischer und biotischer Faktoren beeinflusst, insbesondere durch die Wechselwirkungen zwischen Pflanzen und Klima sowie zwischen Pflanzen und anderen Tier- und Pflanzenarten. Das Verständnis dieser Wechselwirkungen ermöglicht es, wirksame Strategien zu entwickeln, um zu erhalten oder wiederherzustellen.

Die Erde verändert sich infolge des anthropogenen Handelns erheblich. Aufgrund und der sich verändernden globalen Bedingungen, sind die Wechselwirkungen zwischen Pflanzen und abiotischen und biotischen Faktoren anfällig für Veränderungen, was eine ernsthafte Bedrohung für die Pflanzenregeneration darstellt. Die funktionellen Eigenschaften von Pflanzen sind durch ihre morphologischen, physiologischen und phänologischen Merkmale definiert. Diese Merkmale beeinflussen Wachstum, Fortpflanzung und Überleben von Pflanzen und damit deren Fitness. Um diese potenziellen Auswirkungen des globalen Wandels auf die Pflanzenregeneration zu verstehen, habe ich daher die Zusammenhänge zwischen funktionellen Pflanzenmerkmalen und abiotischen und biotischen Faktoren untersucht.

Die Tropen beherbergen die größte biologische Vielfalt weltweit und sind eines der am stärksten durch den globalen Wandel bedrohten Gebiete der Erde. Sie weisen eine große Vielfalt an Pflanzenarten entlang von Höhengradienten auf, welche durch unterschiedlicher klimatischer Bedingungen und Landnutzungsänderungen auf kleinen räumlichen Skalen gekennzeichnet sind. Die ausgeprägten abiotischen und biotischen Gradienten entlang tropischer Gebirge wurden vielfach genutzt, um die Auswirkungen der Umweltbedingungen auf Pflanzengemeinschaften zu untersuchen. Tropische

Pflanzengemeinschaften wurden lange Zeit vor allem anhand ihrer vegetativen Merkmale analysiert. Die Umweltbeziehungen von Merkmalen, die mit den verschiedenen Phasen des Pflanzenlebenszyklus zusammenhängen, wurden nur selten analysiert. Während beispielsweise die Zusammenhänge zwischen vegetativen Merkmalen (z. B. Blattfläche, Blattstickstoffgehalt) und dem Klima gut untersucht sind, gibt es nur wenige Fallstudien zu reproduktiven Merkmalen, die sich hauptsächlich auf die Samenmasse und deren Beziehung mit der Umwelt konzentrieren.

Das übergeordnete Ziel dieser Dissertation ist es zu untersuchen, wie die Assoziationen zwischen Merkmalen und Umwelt, mit besonderem Schwerpunkt auf reproduktiven Merkmalen, das Verständnis der Auswirkungen des globalen Wandels auf die Samenausbreitung und Pflanzenregeneration verbessern können. Zu diesem Zweck konzentriert sich meine Forschung auf die Untersuchung von Zusammenhängen zwischen funktionellen, reproduktiven Pflanzenmerkmalen und abiotischen und biotischen Faktoren entlang eines tropischen Höhengradienten. Um dies zu erreichen, habe ich in dieser Dissertation drei Forschungsfragen entwickelt. Die erste Frage (Q1) befasst sich mit der Frage, wie Pflanzenmerkmale von endozoochoren Pflanzenarten mit abiotischen und biotischen Faktoren über Höhengradienten hinweg zusammenhängen. Die zweite Frage (Q2) untersucht, wie Klima und Mikrohabitate die Endozoochorie über Höhengradienten hinweg beeinflussen. In der dritten Frage (Q3) wird schließlich untersucht, wie sich die Landnutzung auf den Sameneintrag auswirkt und damit auf das Potenzial der Samen, entwaldete Gebiete in verschiedenen Höhenlagen zu restaurieren.

Ich habe die Datenerhebung selbst durchgeführt und Daten aus anderen Studien zusammengestellt, die in und um den Podocarpus-Nationalpark und die Forschungsstation San Francisco in den tropischen Anden im Süden Ecuadors durchgeführt wurden. Die Gebiete innerhalb des Podocarpus-Nationalparks und der San Francisco-Forschungsstation sind größtenteils naturnah und bestehen aus ungestörtem Bergregenwald, während die Gebiete außerhalb der Schutzgebiete stark von menschlicher Landnutzung betroffen sind und eine Mischung aus gestörten Wäldern, landwirtschaftlichen Flächen, Viehweiden und menschlichen Siedlungen darstellen. Ich sammelte Daten in drei Höhenlagen (1000, 2000 und 3000 m ü. NN) und in zwei Lebensraumtypen: (1) Wald (für Q1, Q2 und Q3) und (2) Weideflächen (für

Q3). In jeder Höhenlage arbeitete ich in drei Waldparzellen und in drei Weideparzellen (jeweils mit einer Größe von 1 ha), die von der DFG-Forschergruppe RESPECT (FOR2730) etabliert wurden.

Zunächst untersuchte ich (Q1), inwieweit reproduktive Merkmale (Samen- und Fruchteigenschaften) und vegetative Merkmale (Blatteigenschaften) mit abiotischen und biotischen Faktoren in Baumgemeinschaften in den ecuadorianischen Anden zusammenhängen. Ich habe die reproduktiven Merkmale selbst gemessen und vegetative Merkmale aus anderen Studien zusammengestellt. Auf den Waldparzellen auf 1000, 2000 und 3000 m ü. NN wurde auch die Häufigkeit dieser Pflanzenarten erfasst. Auf denselben Parzellen sammelte ich Daten zu abiotischen (C/N-Verhältnis des Bodens, mittlere Temperatur und Jahresniederschlag) und biotischen Faktoren (Fruchtfraß durch Vögel und Herbivorie), die für die gemessenen Merkmale potenziell relevant sind. Ich führte multivariate Analysen durch, um die Kovariation zwischen Merkmalen und Umweltbedingungen zu testen, wobei ich die phylogenetische Verwandtschaft der Arten und die räumliche Autokorrelation der Parzellen berücksichtigte. Ich stellte einen trade-off zwischen (i) der Anzahl der Samen und der Samengröße sowie zwischen (ii) der Produktion von wenigen stickstoffreichen und vielen kohlenstoffreichen Früchten fest. Unter Berücksichtigung der phylogenetischen und räumlichen Kovariation wurden die Merkmale von Samen, Früchten und Blättern mit abiotischen und biotischen Faktoren in Verbindung gebracht. Frucht- und Blatteigenschaften, die mit den Produktionskosten zusammenhängen, waren hauptsächlich mit dem C/N-Verhältnis des Bodens korreliert, während Eigenschaften, die mit der Größe von Samen, Früchten und Blättern zusammenhängen, mit der Niederschlagsmenge in Beziehung standen. Interessanterweise deuten meine Ergebnisse darauf hin, dass die Zusammenhänge zwischen reproduktiven und vegetativen Merkmalen und der abiotischen Umwelt in tropischen Baumgemeinschaften ähnlichen grundlegenden Mechanismen folgen.

Zweitens (Q2) untersuchte ich, wie sich die Klima- und Mikrohabitatsbedingungen auf die Häufigkeit endozochorer Pflanzenarten im Sameneintrag tropischer Bergwälder im Süden Ecuadors auswirken. Im Laufe eines Jahres habe ich den Sameneintrag in 162 Samenfallen auf den neun 1 ha großen Waldparzellen auf 1000 m, 2000 m und 3000 m ü. NN erfasst. Die klimatischen Bedingungen (mittlere Jahrestemperatur und



Niederschlag) in jeder Parzelle und die Mikrohabitatsbedingungen (Blattflächenindex und Bodenfeuchtigkeit) in der unmittelbaren Nähe jeder Samenfalle habe ich aus anderen Studien zusammengestellt. Insgesamt erfasste ich 331838 Samen, die zu 323 Morphospezies gehören. Der Anteil der endozoochoren Arten im Samenregen nahm mit der Höhe ab. Die relative Biomasse der endozoochoren Arten nahm mit zunehmender Niederschlagsmenge ab, während der relative Artenreichtum der endozoochoren Arten mit steigender Temperatur und steigendem Blattflächenindex zunahm. Diese Ergebnisse zeigen, dass das Vorkommen endozoochorer Arten in tropischen Wäldern durch das Zusammenspiel abiotischer und biotischer Faktoren auf großen und kleinen räumlichen Skalen bestimmt wird.

Drittens (Q3) untersuchte ich das Potenzial von natürlichem Sameneintrag zur Wiederherstellung entwaldeter tropischer Gebiete entlang eines Höhengradienten im Süden Ecuadors. Für dieses Kapitel erfasste ich drei Monate lang den Sameneintrag mit Hilfe von 324 Samenfallen, die in 18 1-Hektar-Parzellen entlang desselben Höhengradienten von 1000 bis 3000 m ü. NN aufgestellt habe. Die Hälfte der Samenfallen wurde in neun 1-Hektar-Waldparzellen und die andere Hälfte in neun 1-Hektar-Parzellen auf Viehweiden aufgestellt. Ich identifizierte die Samen und erfasste die Biomasse und den Artenreichtum des Sameneintrags in jeder Samenfalle. Außerdem erfasste ich die Eigenschaften der Samen und berechnete für jede Falle den gewichteten Mittelwert der Samenmasse und die Art der Samenausbreitung (Anteil der Endozoochorie). Ich sammelte insgesamt 123039 Samen, die 255 Arten bzw. Morphospezies repräsentieren. Ich konnte keine konsistente Abnahme in der Menge und dem Artenreichtum des Samenregens zwischen Wäldern und Weiden feststellen, jedoch fand ich eine systematische Veränderung in der Zusammensetzung der verbreiteten Samen. Große Samen mit einer hohen Samenmasse und endozoochore Samen waren zahlreich in den Wäldern und nahmen im Vergleich dazu in Weiden in allen Höhenlagen signifikant ab. Meine Ergebnisse deuten darauf hin, dass der Sameneintrag auf den Weiden vor allem aus alternativen Samenquellen und nicht aus den nächstgelegenen Waldhabitaten stammt. Diese Ergebnisse zeigen, dass die Biomasse und der Reichtum des Sameneintrags möglicherweise nicht ausreichen, um das natürliche Regenerationspotenzial entwaldeter Lebensräume zu quantifizieren. Vielmehr sind zusätzliche Informationen über wichtige Samenmerkmale wie die

Samenmasse und die Art der Samenausbreitung wichtig, um die natürliche Regeneration von entwaldeten Gebieten in tropischen Gebirgen zu optimieren.

Meine Dissertation trägt zu einem besseren Verständnis der Samenausbreitung bei, indem sie das Wissen über reproduktive Merkmale und die Beziehungen zwischen diesen Merkmalen und Umweltbedingungen erweitert. Insbesondere stellt meine Dissertation eine der wenigen Forschungsarbeiten dar, die (1) Zusammenhänge zwischen Merkmalen und Umweltbedingungen anhand von reproduktiven Merkmalen untersucht, (2) reproduktive mit vegetativen Merkmalen verknüpft, (3) ein breites Spektrum von Samen- und Fruchteigenschaften untersucht, (4) die Auswirkungen von Mikrohabitatsbedingungen auf die Endozoochorie prüft und (5) zeigt, wie sich menschliche Landnutzung auf die Diversität reproduktiver Merkmale auswirkt. Die Untersuchung von reproduktiven Merkmalen ist für das Verständnis von Pflanzengemeinschaften essentiell und liefert wichtige Informationen über verschiedene Pflanzenstadien und Pflanzenfunktionen hinweg. So sind beispielsweise vegetative Merkmale eng mit dem Wachstum und Überleben adulter Pflanzen verbunden, während reproduktive Merkmale das langfristige Überleben von Pflanzenarten in einem bestimmten Ökosystem abbilden. Meine Ergebnisse erweitern daher das Verständnis, wie sich die Dynamik von Pflanzengemeinschaften im globalen Wandel verändert.

Der beispiellose Verlust an biologischer Vielfalt in den Tropen verlangt von der Ökologie, die Lücke zwischen der Grundlagenforschung und der angewandten Forschung zu schließen. Meine Dissertation zeigt, dass die Erforschung der funktionellen Eigenschaften von Pflanzengemeinschaften unterschiedliche Arten von Merkmalen berücksichtigen sollte, welche verschiedene ökologische Nischen von Pflanzenarten repräsentieren. Daher liefert meine Arbeit wertvolle neue Informationen über die Funktionsweise und das Regenerationspotenzial hoch diverser, tropischer Bergwaldökosysteme. Meine Dissertation zeigt, wie aufschlussreich die Messung von reproduktiven Merkmalen und die Analyse der Beziehung dieser Merkmale mit Umweltbedingungen sein können und wie derartige Analysen zum Erhalt und zur Wiederherstellung entwaldeter Gebiete in den Tropen beitragen können.

## 9. References

- Acosta-Rojas, D.C, Barczyk, M., Espinosa, C., 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*. INABIO. <https://doi.org/10:56787VNKB-t219>
- 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*, 408–417. <https://doi.org/10.1111/btp.13195>
- Adams, J. M., Zhang, Y., Basri, M., & Shukor, N. (2009). Do tropical forest leaves suffer more insect herbivory? A comparison of tropical versus temperate herbivory, estimated from leaf litter. *Ecological Research*, *24*, 1381–1392. <https://doi.org/10.1007/s11284-009-0623-4>
- Aguirre, N. (2007). *Silvicultural contributions to the reforestation with native species in the tropical mountain rainforest region of South Ecuador*. [Doctoral dissertation, Technischen Universität München] <https://mediatum.ub.tum.de/doc/623642/623642.pdf>
- Aldana, A. M., Carlucci, M. B., Fine, P. V. A., & Stevenson, P. (2017). Environmental filtering of eudicot lineages underlies phylogenetic clustering in tropical South American flooded forests. *Oecologia*, *183*, 327–335. <https://doi.org/10.1007/s00442-016-3734-y>
- Almeida-Neto, M., Campassi, F., Galetti, M., Jordano, P., & Oliveira-filho, A. (2008). Vertebrate dispersal syndromes along the Atlantic forest: broad-scale patterns and macroecological correlates. *Global Ecology and Biogeography*, *17*, 503–513. <https://doi.org/10.1111/j.1466-8238.2008.00386.x>
- Arbeláez, M. V., & Parrado-Rosselli, A. (2005). Seed dispersal modes of the sandstone plateau vegetation of the middle Caquetá river region, Colombian Amazonia. *Biotropica*, *37*, 64–72. <https://doi.org/10.1111/j.1744-7429.2005.03077.x>
- Armesto, J. J., & Rozzi, R. (1989). Seed dispersal syndromes in the rain forest of Chiloe: evidence for the importance of biotic dispersal in a temperate rain forest. *Journal of Biogeography*, *16*, 219–226. <https://doi.org/10.2307/2845258>

- Asner, G. P., Knapp, D. E., Anderson, C. B., Martin, R. E., & Vaughn, N. (2016). Large-scale climatic and geophysical controls on the leaf economics spectrum. *Proceedings of the National Academy of Sciences*, *113*, E4043–E4051. <https://doi.org/10.1073/pnas.1604863113>
- Augspurger, C. K. (1986). Morphology and dispersal potential of wind-dispersed diaspores of Neotropical trees. *American Journal of Botany*, *73*, 353–363. <https://doi.org/10.1002/j.1537-2197.1986.tb12048.x>
- Baker, H. G. (1972). Seed weight in relation to environmental conditions in California. *Ecology*, *53*, 997–1010. <https://doi.org/10.2307/1935413>
- Baraloto, C., Forget, P. M., & Goldberg, D. E. (2005). Seed mass, seedling size and neotropical tree seedling establishment. *Journal of Ecology*, *93*, 1156–1166. <https://doi.org/10.1111/j.1365-2745.2005.01041.x>
- 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*, e06538. <https://doi.org/10.1111/ecog.06538>
- Barton, K. (2016). MuMIn: multi-model inference. R package version 1.47.5. R Foundation for Statistical Computing, Vienna, Austria.
- Beck, E., Bendix, J., Breckle, S.-W., Gradstein, S. R., Homeier, J., Kottke, I., Makeschin, F., Mosandl, R., Richter, M., & Werner, F. A. (2008). Potential vegetation and floristic composition of Andean forests in South Ecuador, with a focus on the RBSF. In: Beck, E., Bendix, J., Kottke, I., Makeschin, F., & Mosandl, R. (Eds), *Gradients in a Tropical Mountain Ecosystem of Ecuador* (pp. 87–100). Springer.
- Bello, C., Galetti, M., Montan, D., Pizo, M. A., Mariguela, T. C., Culot, L., Bufalo, F., Labecca, F., Pedrosa, F., Constantini, R., Emer, C., Silva, W. R., da Silva, F. R., Ovaskainen, O., & Jordano, P. (2017). Atlantic frugivory: a plant-frugivore interaction data set for the Atlantic Forest. *Ecology*, *98*, 1729–1729. <https://doi.org/10.1002/ecy.1818>
- Bello, C., Galetti, M., Pizo, M. A., Magnago, L. F. S., Rocha, M. F., Lima, R. A. F., Peres, C. A., Ovaskainen, O., & Jordano, P. (2015). Defaunation affects carbon storage in tropical forests. *Science Advances*, *1*, e1501105. <https://doi.org/10.1126/sciadv.1501105>

- Bender, I. M. A., Kissling, W. D., Böhning-Gaese, K., Hensen, I., Kühn, I., Wiegand, T., Dehling, D. M., & Schleuning, M. (2017). Functionally specialised birds respond flexibly to seasonal changes in fruit availability. *Journal of Animal Ecology*, *86*, 800–811. <https://doi.org/10.1111/1365-2656.12683>
- Bendix, J., Aguire, N., Beck, E., Bräuning, A., Brandl, R., Breuer, L., Böhning-Gaese, K., de Paula, M. D., Hickler, T., Homeier, J., Inclan, D., Leuschner, C., Neuschulz, E. L., Schleuning, M., Suarez, J. P., Trachte, K., Wilcke, W., Windhorst, D., & Farwig, N. (2021). A research framework for projecting ecosystem change in highly diverse tropical mountain ecosystems. *Oecologia*, *195*, 589–600. <https://doi.org/10.1007/s00442-021-04852-8>
- Bendix, J., Dobbermann, M., & Werner, N. (2018a). Climate station data from ECSF Thies station. Available at: [http://www.tropicalmountainforest.org/data\\_pre.do?citid=1788](http://www.tropicalmountainforest.org/data_pre.do?citid=1788) [Accessed 16 May 2023]
- Bendix, J., Dobbermann, M., & Werner, N. (2018b). Climate station data from El Tiro Thies station. Available at: [https://vhrz669.hrz.uni-marburg.de/tmf\\_respect/data\\_pre.do?citid=1714](https://vhrz669.hrz.uni-marburg.de/tmf_respect/data_pre.do?citid=1714) [Accessed 16 May 2023]
- Bendix, J., Rollenbeck, R., & Reudenbach, C. (2006). Diurnal patterns of rainfall in a tropical Andean valley of southern Ecuador as seen by a vertically pointing K-band Doppler radar. *International Journal of Climatology*, *26*, 829–846. <https://doi.org/10.1002/joc.1267>
- Bendix, J., Rollenbeck, R., Richter, M., Fabian, P., & Emck, P. (2008). Climate. In: Beck, E., Bendix, J., Kottke, I., Makeschin, F., & Mosandl, R. (Eds), *Gradients in a Tropical Mountain Ecosystem of Ecuador* (pp. 63–73). Springer.
- Benner, J., Vitousek, P.M., & Ostertag, R. (2010). Nutrient cycling and nutrient limitation in tropical montane cloud forests. In: Bruijnzeel, L.A., Scatena, F.N., & Hamilton, L.S. (Eds), *Tropical Montane Cloud Forests: Science for Conservation and Management* (pp. 90–100). Cambridge University Press.
- Bonte, D., Van Dyck, H., Bullock, J. M., Coulon, A., Delgado, M., Gibbs, M., Lehouck, V., Matthysen, E., Mustin, K., Saastamoinen, M., Schtickzelle, N., Stevens, V. M., Vandewoestijne, S., Baguette, M., Barton, K., Benton, T. G., Chaput-Bardy, A., Clobert, J., Dytham, C., ... Travis, J. M. J. (2012). Costs of dispersal. *Biological Reviews*, *87*, 290–312. <https://doi.org/10.1111/j.1469-185X.2011.00201.x>

- Brown, V. K., & Lawton, J. H. (1991). Herbivory and the evolution of leaf size and shape. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 333, 265–272. <https://doi.org/10.1098/rstb.1991.0076>
- Bruelheide, H., Dengler, J., Purschke, O., Lenoir, J., Jiménez-Alfaro, B., Hennekens, S. M., Botta-Dukát, Z., Chytrý, M., Field, R., Jansen, F., Kattge, J., Pillar, V. D., Schrodte, F., Mahecha, M. D., Peet, R. K., Sandel, B., van Bodegom, P., Altman, J., Alvarez-Dávila, E., ... Jandt, U. (2018). Global trait–environment relationships of plant communities. *Nature, Ecology and Evolution*, 2, 1906–1917. <https://doi.org/10.1038/s41559-018-0699-8>
- Bu, H., Chen, X., Xu, X., Liu, K., Jia, P., & Du, G. (2007). Seed mass and germination in an alpine meadow on the eastern Tsinghai–Tibet plateau. *Plant Ecology*, 191, 127–149. <https://doi.org/10.1007/s11258-006-9221-5>
- Buitrón-Jurado, G., & Ramírez, N. (2014). Dispersal spectra, diaspore size and the importance of endozoochory in the equatorial Andean montane forests. *Flora: Morphology, Distribution, Functional Ecology of Plants*, 209, 299–311. <https://doi.org/10.1016/j.flora.2014.03.009>
- Burke, M. J., Gusta, L. V., Quamme, H. A., Weiser, C. J., & Li, P. H. (1976). Freezing and injury in plants. *Annual Review of Plant Physiology*, 27, 507–528. <https://doi.org/10.1146/annurev.pp.27.060176.002451>
- Burnham, K., & Anderson, D. (2004). *Model Selection and Multimodel*. Springer. <https://doi.org/10.1007/b97636>.
- Cabin, R. J., Clewell, A., Ingram, M., McDonald, T., & Temperton, V. (2010). Bridging restoration science and practice: results and analysis of a survey from the 2009 Society for Ecological Restoration International Meeting. *Restoration Ecology*, 18, 783–788. <https://doi.org/10.1111/j.1526-100X.2010.00743.x>
- Cadotte, M. W., & Tucker, C. M. (2017). Should environmental filtering be abandoned? *Trends in Ecology and Evolution*, 32, 429–437. <https://doi.org/10.1016/j.tree.2017.03.004>
- Camargo, P. H. S. A., Carlo, T. A., Brancalion, P. H. S., & Pizo, M. A. (2021). Frugivore diversity increases evenness in the seed rain on deforested tropical landscapes. *Oikos*, e08028. <https://doi.org/10.1111/oik.08028>
- Carlucci, M. B., Brancalion, P. H. S., Rodrigues, R. R., Loyola, R., & Cianciaruso, M. V. (2020). Functional traits and ecosystem services in ecological restoration. *Restoration Ecology*, 28, 1372–1383. <https://doi.org/10.1111/rec.13279>

- Carmona, C. P., Bueno, C. G., Toussaint, A., Träger, S., Díaz, S., Moora, M., Munson, A. D., Pärtel, M., Zobel, M., & Tamme, R. (2021). Fine-root traits in the global spectrum of plant form and function. *Nature*, *597*, 683–687. <https://doi.org/10.1038/s41586-021-03871-y>
- Chen, J., & Black, T. (1992). Defining leaf area index for non-flat leaves. *Plant, Cell & Environment*, *15*, 421–429. <https://doi.org/10.1111/j.1365-3040.1992.tb00992.x>
- Chen, S., Poschlod, P., Antonelli, A., Liu, U., & Dickie, J. B. (2020). Trade-off between seed dispersal in space and time. *Ecology Letters*, *23*, 1635–1642. <https://doi.org/10.1111/ele.13595>
- Connell, J. (1970). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: Boer, P. J., & Gradwell, G.R. *Dynamics of Numbers in Populations* (pp. 298–312). Center for Agricultural Publishing and Documentation.
- Coombe, B. G. (1976). The development of fleshy fruits. *Annual Review of Plant Physiology*, *27*, 207–228.
- Corner, E. J. H. (1949). The durian theory or the origin of the modern tree. *Annals of Botany*, *13*, 367–414. <https://doi.org/10.1093/oxfordjournals.aob.a083225>
- Correa, D. F., Álvarez, E., & Stevenson, P. (2015). Plant dispersal systems in Neotropical forests: availability of dispersal agents or availability of resources for constructing zoochorous fruits? *Global Ecology and Biogeography*, *24*, 203–214. <https://doi.org/10.1111/geb.12248>
- Craine, J. M., Engelbrecht, B. M. J., Lusk, C. H., McDowell, N. G., & Poorter, H. (2012). Resource limitation, tolerance, and the future of ecological plant classification. *Frontiers in Plant Science*, *3*, 1–10. <https://doi.org/10.3389/fpls.2012.00246>
- Crouzeilles, R., Ferreira, M. S., Chazdon, R. L., Lindenmayer, D. B., Sansevero, J. B. B., Monteiro, L., Iribarrem, A., Latawiec, A. E., & Strassburg, B. B. N. (2017). Ecological restoration success is higher for natural regeneration than for active restoration in tropical forests. *Science Advances*, *3*, e1701345. <https://doi.org/10.1126/sciadv.1701345>
- Cubiña, A., & Aide, T. M. (2001). The effect of distance from forest edge on seed rain and soil seed bank in a tropical pasture. *Biotropica*, *33*, 260–267. <https://doi.org/10.1111/j.1744-7429.2001.tb00177.x>

- Culot, L., Muñoz Lazo, F. J. J., Huynen, M.C., Poncin, P., & Heymann, E. W. (2010). Seasonal variation in seed dispersal by Tamarins alters seed rain in a secondary rain forest. *International Journal of Primatology*, *31*, 553–569. <https://doi.org/10.1007/s10764-010-9413-7>
- da Silva, J. M. C., & Tabarelli, M. (2000). Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. *Nature*, *404*, 72–74. <https://doi.org/10.1038/35003563>
- Dalling, J. W., Hubbell, S. P., & Silvera, K. (1998). Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. *Journal of Ecology*, *86*, 674–689. <https://doi.org/10.1046/j.1365-2745.1998.00298.x>
- Dantas de Paula, M., Forrest, M., Langan, L., Bendix, J., Homeier, J., Velescu, A., Wilcke, W., & Hickler, T. (2021). Nutrient cycling drives plant community trait assembly and ecosystem functioning in a tropical mountain biodiversity hotspot. *New Phytologist*, *232*, 551–566. <https://doi.org/10.1111/nph.17600>
- de Bello, F., Lavorel, S., Díaz, S., Harrington, R., Cornelissen, J. H. C., Bardgett, R. D., Berg, M. P., Cipriotti, P., Feld, C. K., Hering, D., Martins da Silva, P., Potts, S. G., Sandin, L., Sousa, J. P., Storkey, J., Wardle, D. A., & Harrison, P. A. (2010). Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation*, *19*, 2873–2893. <https://doi.org/10.1007/s10531-010-9850-9>
- de Bello, F., Lavorel, S., Lavergne, S., Albert, C. H., Boulangeat, I., Mazel, F., & Thuiller, W. (2013). Hierarchical effects of environmental filters on the functional structure of plant communities: a case study in the French Alps. *Ecography*, *36*, 393–402. <https://doi.org/10.1111/j.1600-0587.2012.07438.x>
- de Melo, F. P. L., Dirzo, R., & Tabarelli, M. (2006). Biased seed rain in forest edges: evidence from the Brazilian Atlantic forest. *Biological Conservation*, *132*, 50–60. <https://doi.org/10.1016/j.biocon.2006.03.015>
- Del Castillo, R. F., & Ríos, M. A. P. (2008). Changes in seed rain during secondary succession in a tropical montane cloud forest region in Oaxaca, Mexico. *Journal of Tropical Ecology*, *24*, 433–444. <https://doi.org/10.1017/S0266467408005142>
- Dentener, F., Drevet, J., Lamarque, J. F., Bey, I., Eickhout, B., Fiore, A. M., Hauglustaine, D., Horowitz, L. W., Krol, M., Kulshrestha, U. C., Lawrence, M., Galy-Lacaux, C., Rast, S., Shindell, D., Stevenson, D., Van Noije, T., Atherton,



- C., Bell, N., Bergman, D., ... Wild, O. (2006). Nitrogen and sulfur deposition on regional and global scales: a multimodel evaluation. *Global Biogeochemical Cycles*, 20, 1–21. <https://doi.org/10.1029/2005GB002672>
- Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A., Dickie, J., Gillison, A. N., Zanne, A. E., ... Gorné, L. D. (2016). The global spectrum of plant form and function. *Nature*, 529, 167–171. <https://doi.org/10.1038/nature16489>
- Dirzo, R., Young, H. S., Galetti, M., Ceballos, G., Isaac, N. J. B., & Collen, B. (2014). Defaunation in the anthropocene. *Science*, 345, 401–406. <https://doi.org/10.1126/science.1251817>
- Dobbermann, M., Bendix, J., & Werner, N. (2018). Climate station data from Bombuscaro Thies station. Available at: [https://vhrz669.hrz.uni-marburg.de/tmf\\_respect/data\\_pre.do?citid=1712](https://vhrz669.hrz.uni-marburg.de/tmf_respect/data_pre.do?citid=1712) [Accessed 16 May 2023]
- Donohue, K., Rubio de Casas, R., Burghardt, L., Kovach, K., & Willis, C. G. (2010). Germination, postgermination adaptation, and species ecological ranges. *Annual Review of Ecology, Evolution, and Systematics*, 41, 293–319. <https://doi.org/10.1146/annurev-ecolsys-102209-144715>
- Dray, S., Choler, P., Dolédec, S., Peres-Neto, P. R., Thuiller, W., Pavoine, S., & Ter Braak, C. J. F. (2014). Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology*, 95, 14–21. <https://doi.org/10.1890/13-0196.1>
- Dray, S., & Dufour, A. B. (2007). The ade4 package: implementing the duality diagram for ecologists. *Journal of Statistical Software*, 22, 1–20. <https://doi.org/10.18637/jss.v022.i04>
- Ellis, E. C., Antill, E. C., & Kreft, H. (2012). All is not loss: plant biodiversity in the anthropocene. *PLOS ONE*, 7, e30535. <https://doi.org/10.1371/journal.pone.0030535>
- Emck, P. A. (2007). *A climatology of South Ecuador with special focus on the major Andean ridge as Atlantic-Pacific climate divide*. [Doctoral dissertation, Technischen Universität München] <https://www.deutsche-digitale-bibliothek.de/item/QEDLQ6N43QUBOOOQ3OVITZ4AZXDSNOH>
- Estrada-Villegas, S., Stevenson, P., López, O., DeWalt, S. J., Comita, L. S., & Dent, D. H. (2023). Animal seed dispersal recovery during passive restoration in a forested

- landscape. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 378. 20210076. <https://doi.org/10.1098/rstb.2021.0076>
- Fenner, M., & Thompson, K. (2005). *The Ecology of Seeds*. Cambridge University Press.
- Fine, P. V. A., Mesones, I., & Coley, P. D. (2004). Herbivores promote habitat specialization by trees in Amazonian forests. *Science*, 305, 663–665. <https://doi.org/10.1126/science.1098982>
- Fowler, D., Coyle, M., Skiba, U., Sutton, M. A., Cape, J. N., Reis, S., Sheppard, L. J., Jenkins, A., Grizzetti, B., Galloway, J. N., Vitousek, P., Leach, A., Bouwman, A. F., Butterbach-Bahl, K., Dentener, F., Stevenson, D., Amann, M., & Voss, M. (2013). The global nitrogen cycle in the twenty-first century. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368, 20130164. <https://doi.org/10.1098/rstb.2013.0164>
- Fox, J., & Weisberg, S. (2019). *An R Companion to Applied Regression*. SAGE.
- Franklin, J., Serra-Diaz, J. M., Syphard, A. D., & Regan, H. M. (2016). Global change and terrestrial plant community dynamics. *Proceedings of the National Academy of Sciences*, 113, 3725–3734. <https://doi.org/10.1073/pnas.1519911113>
- Frazer, G., Canham, C., & Lertzman, K. (1999). Gap Light Analyzer (GLA), Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies.
- Freiberg, M., Winter, M., Gentile, A., Zizka, A., Muellner-Riehl, A. N., Weigelt, A., & Wirth, C. (2020). LCVP, The Leipzig catalogue of vascular plants, a new taxonomic reference list for all known vascular plants. *Scientific Data*, 7, 1–7. <https://doi.org/10.1038/s41597-020-00702-z>
- Fricke, E. C., Ordoñez, A., Rogers, H. S., & Svenning, J. C. (2022). The effects of defaunation on plants' capacity to track climate change. *Science*, 375, 210–214. <https://doi.org/10.1126/science.abk3510>
- Fries, A., Rollenbeck, R., Göttlicher, D., Nauss, T., Homeier, J., Peters, T., & Bendix, J. (2009). Thermal structure of a megadiverse Andean mountain ecosystem in southern Ecuador and its regionalization. *Erdkunde*, 63, 321–335. <https://doi.org/10.3112/erdkunde.2009.04.03>

- Fuentes, M. (1994). Diets of fruit-eating birds: what are the causes of interspecific differences? *Oecologia*, *97*, 134–142. <https://doi.org/10.1007/BF00317917>
- Funk, J. L., & McDaniel, S. (2010). Altering light availability to restore invaded forest: the predictive role of plant traits. *Restoration Ecology*, *18*, 865–872. <https://doi.org/10.1111/j.1526-100X.2008.00515.x>
- Galetti, M., Guevara, R., Côrtes, M. C., Fadini, R., Von Matter, S., Leite, A. B., Labecca, F., Ribeiro, T., Carvalho, C. S., Collevatti, R. G., Pires, M. M., Guimarães, P. R., Brancalion, P. H., Ribeiro, M. C., & Jordano, P. (2013). Functional extinction of birds drives rapid evolutionary changes in seed size. *Science*, *340*, 1086–1090. <https://doi.org/10.1126/science.1233774>
- Gallagher, R. V., & Leishman, M. R. (2012). A global analysis of trait variation and evolution in climbing plants. *Journal of Biogeography*, *39*, 1757–1771. <https://doi.org/10.1111/j.1365-2699.2012.02773.x>
- Gallegos, S. C., Beck, S. G., Hensen, I., Saavedra, F., Lippok, D., & Schleuning, M. (2016). Factors limiting montane forest regeneration in bracken-dominated habitats in the tropics. *Forest Ecology and Management*, *381*, 168–176. <https://doi.org/10.1016/j.foreco.2016.09.014>
- García, D., & Martínez, D. (2012). Species richness matters for the quality of ecosystem services: a test using seed dispersal by frugivorous birds. *Proceedings of the Royal Society B: Biological Sciences*, *279*, 3106–3113. <https://doi.org/10.1098/rspb.2012.0175>
- Gardner, T. A., Barlow, J., Chazdon, R., Ewers, R. M., Harvey, C. A., Peres, C. A., & Sodhi, N. S. (2009). Prospects for tropical forest biodiversity in a human-modified world. *Ecology Letters*, *12*, 561–582. <https://doi.org/10.1111/j.1461-0248.2009.01294.x>
- Gelmi-Candusso, T. A., Heymann, E. W., & Heer, K. (2017). Effects of zoochory on the spatial genetic structure of plant populations. *Molecular Ecology*, *26*, 5896–5910. <https://doi.org/10.1111/mec.14351>
- Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., Peres, C. A., Bradshaw, C. J. A., Laurance, W. F., Lovejoy, T. E., & Sodhi, N. S. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, *478*, 378–381. <https://doi.org/10.1038/nature10425>

- Givnish, T. J. (1984). Leaf and Canopy Adaptations in Tropical Forests. In: Medina, E., H. Mooney, & C. Vázquez-Yanes. (Eds), *Physiological ecology of plants of the wet tropics* (pp. 51–84). Springer. [https://doi.org/10.1007/978-94-009-7299-5\\_6](https://doi.org/10.1007/978-94-009-7299-5_6)
- Givnish, T. J. (1987). Comparative studies of leaf form: assessing the relative roles of selective pressures and phylogenetic constraints. *New Phytologist*, *106*, 131–160. <https://doi.org/10.1111/j.1469-8137.1987.tb04687.x>
- Grime, J. P. (1998). Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, *86*, 902–910. <https://doi.org/10.1046/j.1365-2745.1998.00306.x>
- Grubb, P. J. (1977). The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews*, *52*, 107–145. <https://doi.org/10.1111/j.1469-185X.1977.tb01347.x>
- Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S. J., Loveland, T. R., Kommareddy, A., Egorov, A., Chini, L., Justice, C. O., & Townshend, J. R. G. (2013). High-resolution global maps of 21st-century forest cover change. *Science*, *342*, 850–853. <https://doi.org/10.1126/science.1244693>
- Harms, K. E., & Dalling, J. W. (1997). Damage and herbivory tolerance through resprouting as an advantage of large seed size in tropical trees and lianas. *Journal of Tropical Ecology*, *13*, 617–621. <https://doi.org/10.1017/S0266467400010750>
- Harper, J. L., Lovell, P. H., & Moore, K. G. (1970). The shapes and sizes of seeds. *Annual Review of Ecology and Systematics*, *1*, 327–356. <https://doi.org/10.1146/annurev.es.01.110170.001551>
- Hautier, Y., Tilman, D., Isbell, F., Seabloom, E. W., Borer, E. T., & Reich, P. B. (2015). Anthropogenic environmental changes affect ecosystem stability via biodiversity. *Science*, *348*, 336–340. <https://doi.org/10.1126/science.aaa1788>
- Heleno, R., & Vargas, P. (2015). How do islands become green? *Global Ecology and Biogeography*, *24*, 518–526. <https://doi.org/10.1111/geb.12273>
- Herrera, C. (1981). Are tropical fruits more rewarding to dispersers than temperate ones? *The American Naturalist*, *118*, 896–907. <https://doi.org/10.1086/283882>
- Herrera, C. (2002). Seed dispersal by vertebrates. In: Herrera, C., & Pellmyr, O. (Eds), *Plant–Animal Interactions: an Evolutionary Approach* (pp. 185–208). Wiley-Blackwell.

- Holl, K. D. (1999). Factors limiting tropical rain forest regeneration in abandoned pasture: seed rain, seed germination, microclimate, and soil. *Biotropica*, *31*, 229–242. <https://doi.org/10.1111/j.1744-7429.1999.tb00135.x>
- Holl, K. D. (2012). Restoration of Tropical Forests. In: van Andel, J. & Aronson, J. (Eds), *Restoration Ecology: the New Frontier* (pp. 103–114). Wiley Blackwell.
- Holl, K. D. (2023). *Introducción a la Restauración Ecológica*. CopIt-arXives.
- Holl, K. D., Loik, M. E., Lin, E. H. V., & Samuels, I. A. (2000). Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. *Restoration Ecology*, *8*, 339–349. <https://doi.org/10.1046/j.1526-100x.2000.80049.x>
- Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, *6*, 65–70. <https://doi.org/10.2307/4615733>
- Homeier, J., Leuschner, C., Bräuning, A., Cumbicus, N. L., Hertel, D., Martinson, G. O., Spann, S., & Veldkamp, E. (2013). Effects of Nutrient Addition on the Productivity of Montane Forests and Implications for the Carbon Cycle. In: Bendix, J., E. Beck, A. Bräuning, F. Makeschin, R. Mosandl, S. Scheu, & W. Wilcke. (Eds), *Ecosystem Services, Biodiversity and Environmental Change in a Tropical Mountain Ecosystem of South Ecuador* (pp. 315–329). Springer.
- Homeier, J., Seeler, T., Pierick, K., & Leuschner, C. (2021). Leaf trait variation in species-rich tropical Andean forests. *Scientific Reports*, *11*, 1–12. <https://doi.org/10.1038/s41598-021-89190-8>
- Homeier, J., Werner, F. A., Gradstein, S. R., Breckle, S. W., & Richter, M. (2008). Potential vegetation and floristic composition of Andean forests in South Ecuador, with a focus on the RBSF. In: Beck, E., Bendix, J., Kottke, I., Makeschin, F., & Mosandl, R. (Eds), *Gradients in a Tropical Mountain Ecosystem of Ecuador* (pp. 87–100). Springer.
- Howe, H. F. (1993). Specialized and generalized dispersal systems: where does “the paradigm” stand? *Vegetatio*, *107*, 3–13. <https://doi.org/10.1007/BF00052208>
- Howe, H. F., & Miriti, M. N. (2004). When seed dispersal matters. *BioScience*, *54*, 651–660. [https://doi.org/10.1641/0006-3568\(2004\)054\[0651:WSDM\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2004)054[0651:WSDM]2.0.CO;2)
- Howe, H. F., & Smallwood, J. (1982). Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, *13*, 201–228.
- Hubbell, S. P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press.

- Hubbell, S. P., Foster, R. B., O'Brien, S. T., Harms, K. E., Condit, R., Wechsler, B., Wright, S. J., & de Lao, S. L. (1999). Light-gap disturbances, recruitment limitation, and tree diversity in a Neotropical forest. *Science*, *283*, 554–557. <https://doi.org/10.1126/science.283.5401.554>
- Jaeger, B. (2017). Computes R Squared for Mixed (Multilevel) Models (0.1.2). Available at: <https://github.com/bcjaeger/r2glmm> [Accessed 16 May 2023].
- Janos, D. P. (1980). Mycorrhizae influence tropical succession. *Biotropica*, *12*, 56–64. <https://doi.org/10.2307/2388157>
- Janson, C. H. (1983). Adaptation of fruit morphology to dispersal agents in a neotropical forest. *Science*, *219*, 187–189. <https://doi.org/10.1126/science.219.4581.187>
- Jansson, R., & Davies, T. J. (2007). Global variation in diversification rates of flowering plants: energy vs. climate change. *Ecology Letters*, *11*, 173–183. <https://doi.org/10.1111/j.1461-0248.2007.01138.x>
- Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *The American Naturalist*, *104*, 501–528. <https://doi.org/10.1086/282687>
- Jin, Y., & Qian, H. (2022). V.PhyloMaker2: an updated and enlarged R package that can generate very large phylogenies for vascular plants. *Plant Diversity*, *44*, 335–339. <https://doi.org/10.1016/j.pld.2022.05.005>
- Jordano, P. (2000). Fruits and frugivory. In: Fenner, M. (Ed), *Seeds: the ecology of regeneration in plant communities* (pp. 125–165). CABI Publishing. <https://doi.org/10.1079/9780851994321.0125>
- Jump, A. S., & Peñuelas, J. (2005). Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters*, *8*, 1010–1020. <https://doi.org/10.1111/j.1461-0248.2005.00796.x>
- Kaiser, H. (1958). The varimax criterion for analytic rotation in factor analysis. *Psychometrika*, *23*, 187–200.
- Kaspari, M., García, M. N., Harms, K. E., Santana, M., Wright, S. J., & Yavitt, J. B. (2007). Multiple nutrients limit litterfall and decomposition in a tropical forest. *Ecology Letters*, *11*, 35–43. <https://doi.org/10.1111/j.1461-0248.2007.01124.x>
- Kassambara, A. (2018). ggpubr: “ggplot2” Based Publication Ready Plots. Available at: <https://rpkgs.datanovia.com/ggpubr/> [Accessed 16 May 2023]
- Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., Blomberg, S. P., & Webb, C. O. (2010). Picante: R tools for integrating

- phylogenies and ecology. *Bioinformatics*, *26*, 1463–1464.  
<https://doi.org/10.1093/bioinformatics/btq166>
- Kergunteuil, A., Descombes, P., Glauser, G., Pellissier, L., & Rasmann, S. (2018). Plant physical and chemical defence variation along elevation gradients: a functional trait-based approach. *Oecologia*, *187*, 561–571.  
<https://doi.org/10.1007/s00442-018-4162-y>
- Kissling, D., Böhning-Gaese, K., & Jetz, W. (2009). The global distribution of frugivory in birds. *Global Ecology and Biogeography*, *18*, 150–162.  
<https://doi.org/10.1111/j.1466-8238.2008.00431.x>
- Kitajima, K. (2002). Do shade-tolerant tropical tree seedlings depend longer on seed reserves? Functional growth analysis of three Bignoniaceae species. *Functional Ecology*, *16*, 433–444. <https://doi.org/10.1046/j.1365-2435.2002.00641.x>
- Kleiman, D., & Aarssen, L. W. (2007). The leaf size/number trade-off in trees. *Journal of Ecology*, *95*, 376–382. <https://doi.org/10.1111/j.1365-2745.2006.01205.x>
- Körner, C. (2000). Why are there global gradients in species richness? Mountains might hold the answer. *Trends in Ecology & Evolution*, *15*, 513–514.  
[https://doi.org/10.1016/S0169-5347\(00\)02004-8](https://doi.org/10.1016/S0169-5347(00)02004-8)
- Körner, C. (2003). *Alpine Plant Life*. Springer. <https://doi.org/10.1007/978-3-642-18970-8>
- Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2015). Community assembly, coexistence and the environmental filtering metaphor. *Functional Ecology*, *29*, 592–599. <https://doi.org/10.1111/1365-2435.12345>
- Laliberte, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, *91*, 299–305.  
<https://doi.org/10.1890/08-2244.1>
- Lamarre, G. P. A., Baraloto, C., Fortunel, C., Dávila, N., Mesones, I., Ríos, J. G., Ríos, M., Valderrama, E., Pilco, M. V., & Fine, P. V. A. (2012). Herbivory, growth rates, and habitat specialization in tropical tree lineages: implications for Amazonian beta-diversity. *Ecology*, *93*, S195–S210. <https://doi.org/10.1890/11-0397.1>
- Laughlin, D. C. (2014). The intrinsic dimensionality of plant traits and its relevance to community assembly. *Journal of Ecology*, *102*, 186–193.  
<https://doi.org/10.1111/1365-2745.12187>

- Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Functional Ecology*, *16*, 545–556. <https://doi.org/10.1046/j.1365-2435.2002.00664.x>
- Le Bagousse-Pinguet, Y., Gross, N., Maestre, F. T., Maire, V., Bello, F., Fonseca, C. R., Kattge, J., Valencia, E., Leps, J., & Liancourt, P. (2017). Testing the environmental filtering concept in global drylands. *Journal of Ecology*, *105*, 1058–1069. <https://doi.org/10.1111/1365-2745.12735>
- Lebrija-Trejos, E., Pérez-García, E. A., Meave, J. A., Bongers, F., & Poorter, L. (2010). Functional traits and environmental filtering drive community assembly in a species-rich tropical system. *Ecology*, *91*, 386–398. <https://doi.org/10.1890/08-1449.1>
- Levin, S. A., Muller-Landau, H. C., Nathan, R., & Chave, J. (2003). The ecology and evolution of seed dispersal: a theoretical perspective. *Annual Review of Ecology, Evolution, and Systematics*, *34*, 575–604. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132428>
- Lewis, S. L., Malhi, Y., & Phillips, O. L. (2004). Fingerprinting the impacts of global change on tropical forests. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *359*, 437–462. <https://doi.org/10.1098/rstb.2003.1432>
- Llerena-Zambrano, M., Ordoñez, J. C., Llambí, L. D., van der Sande, M., Pinto, E., Salazar, L., & Cuesta, F. (2021). Minimum temperature drives community leaf trait variation in secondary montane forests along a 3000-m elevation gradient in the tropical Andes. *Plant Ecology and Diversity*, *14*, 47–63. <https://doi.org/10.1080/17550874.2021.1903604>
- Madani, N., Kimball, J. S., Ballantyne, A. P., Affleck, D. L. R., Van Bodegom, P. M., Reich, P. B., Kattge, J., Sala, A., Nazeri, M., Jones, M. O., Zhao, M., & Running, S. W. (2018). Future global productivity will be affected by plant trait response to climate. *Scientific Reports*, *8*, 2870. <https://doi.org/10.1038/s41598-018-21172-9>
- Magnusson, A., Skaug, H. J., Nielsen, A., Berg, C. W., Kristensen, K., Maechler, M., van Benthem, K., Bolker, B., & Brooks, M. E. (2020). Package “glmmTMB”. Generalized Linear Mixed Models using Template Model Builder. Available at: <https://cran.r-project.org/web/packages/glmmTMB/index.html> [Accessed 16 May 2023]



- Malhi, Y., Girardin, C. A. J., Goldsmith, G. R., Doughty, C. E., Salinas, N., Metcalfe, D. B., Huaraca Huasco, W., Silva-Espejo, J. E., del Aguilla-Pasquell, J., Farfán Amézquita, F., Aragão, L. E. O. C., Guerrieri, R., Ishida, F. Y., Bahar, N. H. A., Farfan-Rios, W., Phillips, O. L., Meir, P., & Silman, M. (2017). The variation of productivity and its allocation along a tropical elevation gradient: a whole carbon budget perspective. *New Phytologist*, *214*, 1019–1032. <https://doi.org/10.1111/nph.14189>
- Markl, J. S., Schleuning, M., Forget, P. M., Jordano, P., Lambert, J. E., Traveset, A., Wright, S. J., & Böhning-Gaese, K. (2012). Meta-analysis of the effects of human disturbance on seed dispersal by animals. *Conservation Biology*, *26*, 1072–1081. <https://doi.org/10.1111/j.1523-1739.2012.01927.x>
- Martínez-Garza, C., Flores-Palacios, A., De La Peña-Domene, M., & Howe, H. F. (2009). Seed rain in a tropical agricultural landscape. *Journal of Tropical Ecology*, *25*, 541–550. <https://doi.org/10.1017/S0266467409990113>
- Mazón, M., Aguirre, N., Echeverría, C., & Aronson, J. (2019). Monitoring attributes for ecological restoration in Latin America and the Caribbean region. *Restoration Ecology*, *27*, 992–999. <https://doi.org/10.1111/rec.12986>
- McKey, D. (1975). The ecology of coevolved seed dispersal systems. In: Lawrence E. G. & Raven, P. H. (Eds), *Coevolution of Animals and Plants* (pp. 159–191). University of Texas Press. <https://doi.org/10.7560/710313-009>
- Meli, P., Holl, K. D., Rey Benayas, J. M., Jones, H. P., Jones, P. C., Montoya, D., & Moreno Mateos, D. (2017). A global review of past land use, climate, and active vs. passive restoration effects on forest recovery. *PLOS ONE*, *12*, e0171368. <https://doi.org/10.1371/journal.pone.0171368>
- Melillo, J. M., McGuire, A. D., Kicklighter, D. W., Moore, B., Vorosmarty, C. J., & Schloss, A. L. (1993). Global climate change and terrestrial net primary production. *Nature*, *363*, 234–240. <https://doi.org/10.1038/363234a0>
- Messeder, J. V. S., Guerra, T. J., Pizo, M. A., Blendinger, P. G., & Silveira, F. A. O. (2022). Seed Dispersal Ecology in Neotropical Melastomataceae. In: Goldenberg, R., Michelangeli, F.A., Almeda, F. (Ed), *Systematics, Evolution, and Ecology of Melastomataceae* (pp. 735–759). Springer. [https://doi.org/10.1007/978-3-030-99742-7\\_33](https://doi.org/10.1007/978-3-030-99742-7_33)
- Metcalfe, D. B., Asner, G. P., Martin, R. E., Silva Espejo, J. E., Huasco, W. H., Farfán Amézquita, F. F., Carranza-Jimenez, L., Galiano Cabrera, D. F., Baca, L. D.,

- Sinca, F., Huaraca Quispe, L. P., Taype, I. A., Mora, L. E., Dávila, A. R., Solórzano, M. M., Puma Vilca, B. L., Laupa Román, J. M., Guerra Bustios, P. C., Revilla, N. S., ... Malhi, Y. (2014). Herbivory makes major contributions to ecosystem carbon and nutrient cycling in tropical forests. *Ecology Letters*, *17*, 324–332. <https://doi.org/10.1111/ele.12233>
- Minor, D. M., & Kobe, R. K. (2019). Fruit production is influenced by tree size and size-asymmetric crowding in a wet tropical forest. *Ecology and Evolution*, *9*, 1458–1472. <https://doi.org/10.1002/ece3.4867>
- Moermond, T. C., & Denslow, J. S. (1985). Neotropical avian frugivores: patterns of behavior, morphology, and nutrition, with consequences for fruit selection. *Ornithological Monographs*, *36*, 865–897. <https://doi.org/10.2307/40168322>
- Mokhov, I. I., & Akperov, M. G. (2006). Tropospheric lapse rate and its relation to surface temperature from reanalysis data. *Izvestiya, Atmospheric and Oceanic Physics*, *42*, 430–438. <https://doi.org/10.1134/S0001433806040037>
- Moles, A., Falster, D. S., Leishman, M. R., & Westoby, M. (2004). Small-seeded species produce more seeds per square metre of canopy per year, but not per individual per lifetime. *Journal of Ecology*, *92*, 384–396. <https://doi.org/10.1111/j.0022-0477.2004.00880.x>
- Moles, A., Perkins, S. E., Laffan, S. W., Flores-Moreno, H., Awasthy, M., Tindall, M. L., Sack, L., Pitman, A., Kattge, J., Aarssen, L. W., Anand, M., Bahn, M., Blonder, B., Cavender-Bares, J., Cornelissen, J. H. C., Cornwell, W. K., Díaz, S., Dickie, J. B., Freschet, G. T., ... Bonser, S. P. (2014). Which is a better predictor of plant traits: Temperature or precipitation? *Journal of Vegetation Science*, *25*, 1167–1180. <https://doi.org/10.1111/jvs.12190>
- Moles, A., & Westoby, M. (2000). Do small leaves expand faster than large leaves, and do shorter expansion times reduce herbivore damage? *Oikos*, *90*, 517–524. <https://doi.org/10.1034/j.1600-0706.2000.900310.x>
- Moles, A., & Westoby, M. (2002). Seed addition experiments are more likely to increase recruitment in larger-seeded species. *Oikos*, *99*, 241–248. <https://doi.org/10.1034/j.1600-0706.2002.990204.x>
- Moles, A., & Westoby, M. (2004). Seedling survival and seed size: a synthesis of the literature. *Journal of Ecology*, *92*, 372–383. <https://doi.org/10.1111/j.0022-0477.2004.00884.x>

- Moles, A., & Westoby, M. (2006). Seed size and plant strategy across the whole life cycle. *Oikos*, *113*, 91–105. <https://doi.org/10.1111/j.0030-1299.2006.14194.x>
- Mommer, L., & Weemstra, M. (2012). The role of roots in the resource economics spectrum. *New Phytologist*, *195*, 725–727. <https://doi.org/10.1111/j.1469-8137.2012.04247.x>
- Muller-Landau, H. C., Wright, S. J., Calderón, O., Hubbell, S. P., & Foster, R. B. (2002). Assessing recruitment limitation: concepts, methods and case-studies from a tropical forest. In: Levey, D. J., Silva, W. R., & Galetti, M. (Eds), *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation* (pp. 35–53). CABI Publishing. <https://doi.org/10.1079/9780851995250.0035>
- Muñoz, M. C., Schaefer, H. M., Böhning-Gaese, K., & Schleuning, M. (2017). Importance of animal and plant traits for fruit removal and seedling recruitment in a tropical forest. *Oikos*, *126*, 823–832. <https://doi.org/10.1111/oik.03547>
- Muscarella, R., & Fleming, T. H. (2007). The role of frugivorous bats in tropical forest succession. *Biological Reviews*, *82*, 573–590. <https://doi.org/10.1111/j.1469-185X.2007.00026.x>
- Nathan, R. (2006). Long-distance dispersal of plants. *Science*, *313*, 786–788. <https://doi.org/10.1126/science.1124975>
- Nathan, R., & Muller-Landau, H. (2000). Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution*, *15*, 278–285. <http://www.ncbi.nlm.nih.gov/pubmed/10856948>
- Neuschulz, E. L., Mueller, T., Schleuning, M., & Böhning-Gaese, K. (2016). Pollination and seed dispersal are the most threatened processes of plant regeneration. *Scientific Reports*, *6*, 29839. <https://doi.org/10.1038/srep29839>
- Norden, N., Chazdon, R. L., Chao, A., Jiang, Y.-H., & Vélchez-Alvarado, B. (2009). Resilience of tropical rain forests: tree community reassembly in secondary forests. *Ecology Letters*, *12*, 385–394. <https://doi.org/10.1111/j.1461-0248.2009.01292.x>
- Oliveras, I., Bentley, L., Fyllas, N. M., Gvozdevaite, A., Shenkin, A. F., Peprah, T., Morandi, P., Peixoto, K. S., Boakye, M., Adu-Bredu, S., Schwantes Marimon, B., Marimon Junior, B. H., Salinas, N., Martin, R., Asner, G., Díaz, S., Enquist, B. J., & Malhi, Y. (2020). The influence of taxonomy and environment on leaf trait variation along tropical abiotic gradients. *Frontiers in Forests and Global Change*, *3*, 1–14. <https://doi.org/10.3389/ffgc.2020.00018>

- Palma, A. C., Goosem, M., Fensham, R. J., Goosem, S., Preece, N. D., Stevenson, P., & Laurance, S. G. W. (2021). Dispersal and recruitment limitations in secondary forests. *Journal of Vegetation Science*, *32*, e12975. <https://doi.org/10.1111/jvs.12975>
- Pandit, R., Scholes, R., Montanarella, L., Brainich, A., Barger, N., ten Brink, B., Cantele, M., Erasmus, B., Fisher, J., Gardner, T., Holland, T., Kohler, F., Kotiaho, J., Von Maltitz, G., Nangendo, G., Parrotta, J., Potts, M., Prince, S., Sankaran, M. & Willemsen, L. (2018). Summary for policymakers of the assessment report on land degradation and restoration of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Available at: [https://www.ipbes.net/system/tdf/spm\\_3bi\\_ldr\\_digital.pdf?file=1&type=node&id=28335](https://www.ipbes.net/system/tdf/spm_3bi_ldr_digital.pdf?file=1&type=node&id=28335) [Accessed 16 May 2023]
- Paolucci, L. N., Pereira, R. L., Rattis, L., Silvério, D. V., Marques, N. C. S., Macedo, M. N., & Brando, P. M. (2019). Lowland tapirs facilitate seed dispersal in degraded Amazonian forests. *Biotropica*, *51*, 245–252. <https://doi.org/10.1111/btp.12627>
- Paradis, E., & Schliep, K. (2019). ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, *35*, 526–528. <https://doi.org/10.1093/bioinformatics/bty633>
- Pau, S., Detto, M., Kim, Y., & Still, C. J. (2018). Tropical forest temperature thresholds for gross primary productivity. *Ecosphere*, *9*, e02311. <https://doi.org/10.1002/ecs2.2311>
- Pavoine, S. (2020). adiv: an R package to analyse biodiversity in ecology. *Methods in Ecology and Evolution*, *11*, 1106–1112. <https://doi.org/10.1111/2041-210X.13430>
- Pavoine, S., Vela, E., Gachet, S., de Bélair, G., & Bonsall, M. B. (2011). Linking patterns in phylogeny, traits, abiotic variables and space: a novel approach to linking environmental filtering and plant community assembly. *Journal of Ecology*, *99*, 165–175. <https://doi.org/10.1111/j.1365-2745.2010.01743.x>
- Peña, R., Schleuning, M., Dalerum, F., Donoso, I., Rodríguez-Pérez, J., & García, D. (2023). Abundance and trait-matching both shape interaction frequencies between plants and birds in seed-dispersal networks. *Basic and Applied Ecology*, *66*, 11–21. <https://doi.org/10.1016/j.baae.2022.11.008>

- Peres, C. A., Emilio, T., Schiatti, J., Desmoulière, S. J. M., & Levi, T. (2016). Dispersal limitation induces long-term biomass collapse in overhunted Amazonian forests. *Proceedings of the National Academy of Sciences*, *113*, 892–897. <https://doi.org/10.1073/pnas.1516525113>
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., De Vos, A. C., ... Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, *61*, 167–234. <https://doi.org/10.1071/BT12225>
- Pierick, K., Link, R. M., Leuschner, C., & Homeier, J. (2023). Elevational trends of tree fine root traits in species-rich tropical Andean forests. *Oikos*, *2023*, e08975. <https://doi.org/10.1111/oik.08975>
- Poorter, H., Niinemets, Ü., Poorter, L., Wright, I. J., & Villar, R. (2009). Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist*, *182*, 565–588. <https://doi.org/10.1111/j.1469-8137.2009.02830.x>
- Post, W. M., Pastor, J., Zinke, P. J., & Stangenberger, A. G. (1985). Global patterns of soil nitrogen storage. *Nature*, *317*, 613–616. <https://doi.org/10.1038/317613a0>
- Puerta-Piñero, C., Muller-Landau, H. C., Calderón, O., & Wright, S. J. (2013). Seed arrival in tropical forest tree fall gaps. *Ecology*, *94*, 1552–1562. <https://doi.org/10.1890/12-1012.1>
- Quintero, E., Pizo, M. A., & Jordano, P. (2020). Fruit resource provisioning for avian frugivores: the overlooked side of effectiveness in seed dispersal mutualisms. *Journal of Ecology*, *108*, 1358–1372. <https://doi.org/10.1111/1365-2745.13352>
- Quitíán, M., Santillán, V., Espinosa, C. I., Homeier, J., Böhning-Gaese, K., Schleuning, M., & Neuschulz, E. L. (2018). Elevation-dependent effects of forest fragmentation on plant-bird interaction networks in the tropical Andes. *Ecography*, *41*, 1497–1506. <https://doi.org/10.1111/ecog.03247>
- Quitíán, M., Santillán, V., Espinosa, C. I., Homeier, J., Böhning-Gaese, K., Schleuning, M., & Neuschulz, E. L. (2019). Direct and indirect effects of plant and frugivore diversity on structural and functional components of fruit removal by birds. *Oecologia*, *189*, 435–445. <https://doi.org/10.1007/s00442-018-4324-y>

- R Core Team. (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Ratcliffe, S., Wirth, C., Jucker, T., van der Plas, F., Scherer-Lorenzen, M., Verheyen, K., Allan, E., Benavides, R., Bruelheide, H., Ohse, B., Paquette, A., Ampoorter, E., Bastias, C. C., Bauhus, J., Bonal, D., Bouriaud, O., Bussotti, F., Carnol, M., Castagneyrol, B., ... Baeten, L. (2017). Biodiversity and ecosystem functioning relations in European forests depend on environmental context. *Ecology Letters*, *20*, 1414–1426. <https://doi.org/10.1111/ele.12849>
- Reich, P. B. (2014). The world-wide “fast-slow” plant economics spectrum: A traits manifesto. *Journal of Ecology*, *102*, 275–301. <https://doi.org/10.1111/1365-2745.12211>
- Reich, P. B., Ellsworth, D. S., Walters, M. B., Vose, J. M., Gresham, C., Volin, J. C., & Bowman, W. D. (1999). Generality of leaf trait relationships: a test across six biomes. *Ecology*, *80*, 1955–1969. [https://doi.org/10.1890/0012-9658\(1999\)080\[1955:GOLTRA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[1955:GOLTRA]2.0.CO;2)
- Reich, P. B., & Oleksyn, J. (2004). Global patterns of plant leaf N and P in relation to temperature and latitude. *Proceedings of the National Academy of Sciences*, *101*, 11001–11006. <https://doi.org/10.1073/pnas.0403588101>
- Reich, P. B., Walters, M. B., & Ellsworth, D. S. (1997). From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences*, *94*(25), 13730–13734. <https://doi.org/10.1073/pnas.94.25.13730>
- Reid, J. (2015). Indicators of success should be sensitive to compositional failures: reply to Suganuma and Durigan. *Restoration Ecology*, *23*, 519–520. <https://doi.org/10.1111/rec.12254>
- Reid, J., Wilson, S. J., Bloomfield, G. S., Cattau, M. E., Fagan, M. E., Holl, K. D., & Zahawi, R. A. (2017). How long do restored ecosystems persist? *Annals of the Missouri Botanical Garden*, *102*, 258–265. <https://doi.org/10.3417/2017002>
- Revell, L. J. (2012). phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, *3*, 217–223. <https://doi.org/10.1111/j.2041-210X.2011.00169.x>
- Revelle, W. (2022). psych: procedures for Psychological, Psychometric, and Personality Research. R package version 2.2.5. Available at: <https://cran.r-project.org/package=psych>. [Accessed 16 May 2023]

- Ribeiro, S., Pimenta, H., & Fernandes, G. (1994). Herbivory by chewing and sucking insects on *Tabebuia ochracea*. *Biotropica*, *26*, 302–307.  
<https://doi.org/10.2307/2388851>
- Ricketts, T. (2001). The matrix matters: effective isolation in fragmented landscapes. *The American Naturalist*, *158*, 87–99. <https://doi.org/10.1086/320863>
- Ridley, H. N. (1930). *The Dispersal of Plants Throughout the World*. Reeve & Co. Ltd.
- Rogers, H. S., Donoso, I., Traveset, A., & Fricke, E. C. (2021). Cascading Impacts of Seed Disperser Loss on Plant Communities and Ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, *52*, 641–666.  
<https://doi.org/10.1146/annurev-ecolsys-012221-111742>
- Rollenbeck, R., & Bendix, J. (2011). Rainfall distribution in the Andes of southern Ecuador derived from blending weather radar data and meteorological field observations. *Atmospheric Research*, *99*, 277–289.  
<https://doi.org/10.1016/j.atmosres.2010.10.018>
- Rosbakh, S., Chalmandrier, L., Phartyal, S., & Poschlod, P. (2022). Inferring community assembly processes from functional seed trait variation along elevation gradient. *Journal of Ecology*, *110*, 2374–2387.  
<https://doi.org/10.1111/1365-2745.13955>
- Rosbakh, S., Margreiter, V., & Jelcic, B. (2020). Seedlings of alpine species do not have better frost-tolerance than their lowland counterparts. *Alpine Botany*, *130*, 179–185. <https://doi.org/10.1007/s00035-020-00237-4>
- Rosbakh, S., Pacini, E., Nepi, M., & Poschlod, P. (2018). An unexplored side of regeneration niche: seed quantity and quality are determined by the effect of temperature on pollen performance. *Frontiers in Plant Science*, *9*, 1–16.  
<https://doi.org/10.3389/fpls.2018.01036>
- Ruiz-Guerra, B., García, A., Velázquez-Rosas, N., Angulo, D., & Guevara, R. (2021). Plant-functional traits drive insect herbivory in a tropical rainforest tree community. *Perspectives in Plant Ecology, Evolution and Systematics*, *48*, 125587. <https://doi.org/10.1016/j.ppees.2020.125587>
- Russo, S. E., & Augspurger, C. K. (2004). Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. *Ecology Letters*, *7*, 1058–1067. <https://doi.org/10.1111/j.1461-0248.2004.00668.x>
- Saatkamp, A., Cochrane, A., Commander, L., Guja, L. K., Jiménez-Alfaro, B., Larson, J., Nicotra, A., Poschlod, P., Silveira, F. A. O., Cross, A. T., Dalziell, E. L.,

- Dickie, J., Erickson, T. E., Fidelis, A., Fuchs, A., Golos, P. J., Hope, M., Lewandowski, W., Merritt, D. J., ... Walck, J. L. (2019). A research agenda for seed-trait functional ecology. *New Phytologist*, *221*, 1764–1775. <https://doi.org/10.1111/nph.15502>
- Saavedra, F., Hensen, I., & Schleuning, M. (2015). Deforested habitats lack seeds of late-successional and large-seeded plant species in tropical montane forests. *Applied Vegetation Science*, *18*, 603–612. <https://doi.org/10.1111/avsc.12184>
- Sakschewski, B., Von Bloh, W., Boit, A., Poorter, L., Peña-Claros, M., Heinke, J., Joshi, J., & Thonicke, K. (2016). Resilience of Amazon forests emerges from plant trait diversity. *Nature Climate Change*, *6*, 1032–1036. <https://doi.org/10.1038/nclimate3109>
- Sales, L. P., Galetti, M., Carnaval, A., Monsarrat, S., Svenning, J., & Pires, M. M. (2022). The effect of past defaunation on ranges, niches, and future biodiversity forecasts. *Global Change Biology*, *28*, 3683–3693. <https://doi.org/10.1111/gcb.16145>
- San-José, M., Arroyo-Rodríguez, V., Jordano, P., Meave, J. A., & Martínez-Ramos, M. (2019). The scale of landscape effect on seed dispersal depends on both response variables and landscape predictor. *Landscape Ecology*, *34*, 1069–1080. <https://doi.org/10.1007/s10980-019-00821-y>
- San-José, M., Arroyo-Rodríguez, V., & Meave, J. A. (2020). Regional context and dispersal mode drive the impact of landscape structure on seed dispersal. *Ecological Applications*, *30*, e02033. <https://doi.org/10.1002/eap.2033>
- Sanders, N. J., & Rahbek, C. (2012). The patterns and causes of elevational diversity gradients. *Ecography*, *35*, 1–3. <https://doi.org/10.1111/j.1600-0587.2011.07338.x>
- Santillán, V., Quitián, M., Tinoco, B. A., Zárate, E., Schleuning, M., Böhning-Gaese, K., & Neuschulz, E. L. (2020). Direct and indirect effects of elevation, climate and vegetation structure on bird communities on a tropical mountain. *Acta Oecologica*, *102*, 103500. <https://doi.org/10.1016/j.actao.2019.103500>
- Schaefer, H. M., Schmidt, V., & Winkler, H. (2003). Testing the defence trade-off hypothesis: how contents of nutrients and secondary compounds affect fruit removal. *Oikos*, *102*, 318–328. <https://doi.org/10.1034/j.1600-0706.2003.11796.x>



- Schmugge, T. J., Jackson, T. J., & McKim, H. L. (1980). Survey of methods for soil moisture determination. *Water Resources Research*, *16*, 961–979.  
<https://doi.org/10.1029/WR016i006p00961>
- Schupp, E. W., Milleron, T., & Russo, S. E. (2002). Dissemination limitation and the origin and maintenance of species-rich tropical forests. In: Levey, D. J., Silva, W. R., & Galetti, M. (Eds), *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation* (pp. 19–33). CABI Publishing.  
<https://doi.org/10.1079/9780851995250.0019>
- Šimová, I., Violle, C., Kraft, N. J. B., Storch, D., Svenning, J.-C., Boyle, B., Donoghue, J. C., Jørgensen, P., McGill, B. J., Morueta-Holme, N., Piel, W. H., Peet, R. K., Regetz, J., Schildhauer, M., Spencer, N., Thiers, B., Wisser, S., & Enquist, B. J. (2015). Shifts in trait means and variances in North American tree assemblages: species richness patterns are loosely related to the functional space. *Ecography*, *38*, 649–658. <https://doi.org/10.1111/ecog.00867>
- Soethe, N., Lehmann, J., & Engels, C. (2008). Nutrient availability at different altitudes in a tropical montane forest in Ecuador. *Journal of Tropical Ecology*, *24*, 397–406. <https://doi.org/10.1017/S026646740800504X>
- Steffen, W., Sanderson, R., Tyson, P., Jäger, J., Matson, P., Moore III, B., Oldfield, F., Richardson, K., Schellnhuber, H. J., Turner, B., & Wasson, R. (2004). *Global change and the earth system: a planet under pressure*. Springer.
- Stevenson, P. (2000). Seed dispersal by woolly monkeys (*Lagothrix lagothricha*) at Tinigua National Park, Colombia: dispersal distance, germination rates, and dispersal quantity. *American Journal of Primatology*, *50*, 275–289.  
[https://doi.org/10.1002/\(SICI\)1098-2345\(200004\)50:4<275::AID-AJP4>3.0.CO;2-K](https://doi.org/10.1002/(SICI)1098-2345(200004)50:4<275::AID-AJP4>3.0.CO;2-K)
- Stevenson, P. (2001). The relationship between fruit production and primate abundance in Neotropical communities. *Biological Journal of the Linnean Society*, *72*, 161–178. <https://doi.org/10.1006/bijl.2000.0497>
- Swenson, N. G., & Enquist, B. J. (2007). Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. *American Journal of Botany*, *94*, 451–459.  
<https://doi.org/10.3732/ajb.94.3.451>

- Swenson, N. G., & Enquist, B. J. (2009). Opposing assembly mechanisms in a Neotropical dry forest: implications for phylogenetic and functional community ecology. *Ecology*, *90*, 2161–2170. <https://doi.org/10.1890/08-1025.1>
- Tabarelli, M., & Peres, C. (2002). Abiotic and vertebrate seed dispersal in the Brazilian Atlantic forest: implications for forest regeneration. *Biological Conservation*, *106*, 165–176. [https://doi.org/10.1016/S0006-3207\(01\)00243-9](https://doi.org/10.1016/S0006-3207(01)00243-9)
- Tabarelli, M., Peres, C., & Melo, F. (2012). The ‘few winners and many losers’ paradigm revisited: Emerging prospects for tropical forest biodiversity. *Biological Conservation*, *155*, 136–140. <https://doi.org/10.1016/j.biocon.2012.06.020>
- Tanner, E., Vitousek, P., & Cuevas, E. (1998). Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. *Ecology*, *79*, 10–22. [https://doi.org/https://doi.org/10.1890/0012-9658\(1998\)079\[0010:EIONLO\]2.0.CO;2](https://doi.org/https://doi.org/10.1890/0012-9658(1998)079[0010:EIONLO]2.0.CO;2)
- Teixido, A. L., Fuzessy, L. F., Souza, C. S., Gomes, I. N., Kaminski, L. A., Oliveira, P. C., & Maruyama, P. K. (2022). Anthropogenic impacts on plant-animal mutualisms: a global synthesis for pollination and seed dispersal. *Biological Conservation*, *266*, 109461. <https://doi.org/10.1016/j.biocon.2022.109461>
- Tenorio, E. A., Montoya, P., Norden, N., Rodríguez-Buriticá, S., Salgado-Negret, B., & González, M. A. (2023). Mountains exhibit a stronger latitudinal diversity gradient than lowland regions. *Journal of Biogeography*, *23*, 1–11. <https://doi.org/10.1111/jbi.14597>
- ter Braak, C. J. F., Cormont, A., & Dray, S. (2012). Improved testing of species traits–environment relationships in the fourth-corner problem. *Ecology*, *93*, 1525–1526. <https://doi.org/10.1890/12-0126.1>
- ter Steege, H., Pitman, N. C. A., Sabatier, D., Baraloto, C., Salomão, R. P., Guevara, J. E., Phillips, O. L., Castilho, C. V., Magnusson, W. E., Molino, J.-F., Monteagudo, A., Núñez Vargas, P., Montero, J. C., Feldpausch, T. R., Coronado, E. N. H., Killeen, T. J., Mostacedo, B., Vasquez, R., Assis, R. L., ... Silman, M. R. (2013). Hyperdominance in the Amazonian tree flora. *Science*, *342*, 1243092. <https://doi.org/10.1126/science.1243092>
- Terborgh, J., Huanca Nuñez, N., Alvarez Loayza, P., & Cornejo Valverde, F. (2017). Gaps contribute tree diversity to a tropical floodplain forest. *Ecology*, *98*, 2895–2903. <https://doi.org/10.1002/ecy.1991>

- Terborgh, J., Nuñez-Iturri, G., Pitman, N. C. A., Valverde, F. H. C., Alvarez, P., Swamy, V., Pringle, E. G., & Paine, C. E. T. (2008). Tree recruitment in an empty forest. *Ecology*, *89*, 1757–1768. <https://doi.org/10.1890/07-0479.1>
- Tito, R., Vasconcelos, H. L., & Feeley, K. J. (2020). Mountain ecosystems as natural laboratories for climate change experiments. *Frontiers in Forests and Global Change*, *3*, 1–8. <https://doi.org/10.3389/ffgc.2020.00038>
- Tovar, C., Melcher, I., Kusumoto, B., Cuesta, F., Cleef, A., Meneses, R. I., Halloy, S., Llambí, L. D., Beck, S., Muriel, P., Jaramillo, R., Jácome, J., & Carilla, J. (2020). Plant dispersal strategies of high tropical alpine communities across the Andes. *Journal of Ecology*, *108*, 1910–1922. <https://doi.org/10.1111/1365-2745.13416>
- Turner, M. G., Calder, W. J., Cumming, G. S., Hughes, T. P., Jentsch, A., LaDeau, S. L., Lenton, T. M., Shuman, B. N., Turetsky, M. R., Ratajczak, Z., Williams, J. W., Williams, A. P., & Carpenter, S. R. (2020). Climate change, ecosystems and abrupt change: science priorities. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *375*, 20190105. <https://doi.org/10.1098/rstb.2019.0105>
- Tylianakis, J. M., Didham, R. K., Bascompte, J., & Wardle, D. A. (2008). Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, *11*, 1351–1363. <https://doi.org/10.1111/j.1461-0248.2008.01250.x>
- Unger, M., Homeier, J., & Leuschner, C. (2013). Relationships among leaf area index, below-canopy light availability and tree diversity along a transect from tropical lowland to montane forests in NE Ecuador. *Tropical Ecology*, *54*, 33–45.
- United Nations Environment Programme and Food and Agriculture Organization of the United Nations. (2021). *Principles for Ecosystem Restoration to Guide the United Nations Decade 2021–2030*. FAO.
- van der Pijl, L. (1982). *Principles of Dispersal in Higher Plants*. Springer. <https://doi.org/10.1007/978-3-642-87925-8>
- Vancutsem, C., Achard, F., Pekel, J.-F., Vieilledent, G., Carboni, S., Simonetti, D., Gallego, J., Aragão, L. E. O. C., & Nasi, R. (2021). Long-term (1990–2019) monitoring of forest cover changes in the humid tropics. *Science Advances*, *7*, eabe1603. <https://doi.org/10.1126/sciadv.abe1603>
- Velescu, A., Fabian, T., & Wilcke, W. (2020). Chemical properties of forest and pasture soils in Bombuscaro at 1000 m asl. Available at: [http://vhrz669.hrz.uni-marburg.de/tmf\\_respect/data\\_pre.do?citid=1867](http://vhrz669.hrz.uni-marburg.de/tmf_respect/data_pre.do?citid=1867) [Accessed 16 May 2023]

- Velescu, A., Fabian, T., & Wilcke, W. (2020). Chemical properties of forest and pasture soils in San Francisco at 2000 m asl. Available at: [http://vhrz669.hrz.uni-marburg.de/tmf\\_respect/data\\_pre.do?citid=1868](http://vhrz669.hrz.uni-marburg.de/tmf_respect/data_pre.do?citid=1868) [Accessed 16 May 2023]
- Velescu, A., Fabian, T., & Wilcke, W. (2020). Chemical properties of forest and pasture soils in Cajanuma at 3000 m asl. Available at: [http://vhrz669.hrz.uni-marburg.de/tmf\\_respect/data\\_pre.do?citid=1869](http://vhrz669.hrz.uni-marburg.de/tmf_respect/data_pre.do?citid=1869) [Accessed 16 May 2023]
- Venable, D. L. (1992). Size-number trade-offs and the variation of seed size with plant resource status. *The American Naturalist*, *140*, 287–304. <https://doi.org/10.1086/285413>
- Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, *116*, 882–892. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>
- Vitousek, P. M. (1994). Beyond global warming: ecology and global change. *Ecology*, *75*, 1861–1876. <https://doi.org/10.2307/1941591>
- Vollstädt, M. G. R., Ferger, S. W., Hemp, A., Howell, K. M., Töpfer, T., Böhning-Gaese, K., & Schleuning, M. (2017). Direct and indirect effects of climate, human disturbance and plant traits on avian functional diversity. *Global Ecology and Biogeography*, *26*, 963–972. <https://doi.org/10.1111/geb.12606>
- Wallington, T. J., Hobbs, R. J., & Moore, S. A. (2005). Implications of current ecological thinking for biodiversity conservation: a review of the salient issues. *Ecology and Society*, *10*, 1–15. <https://www.jstor.org/stable/26267748>
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, *416*, 389–395. <https://doi.org/10.1038/416389a>
- Wang, B. C., & Smith, T. B. (2002). Closing the seed dispersal loop. *Trends in Ecology & Evolution*, *17*, 379–386. [https://doi.org/10.1016/S0169-5347\(02\)02541-7](https://doi.org/10.1016/S0169-5347(02)02541-7)
- Wenny, D. G. (2001). Advantages of seed dispersal: a re-evaluation of directed dispersal. *Evolutionary Ecology Research*, *3*, 51–74.
- Westoby, M., Falster, D. S., Moles, A., Vesk, P. A., & Wright, I. J. (2002). Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, *33*, 125–159. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150452>

- Wheelwright, N. T. (1985). Fruit-size, gape width, and the diets of fruit-eating birds. *Ecology*, *66*, 808–818. <https://doi.org/10.2307/1940542>
- Wickham, H. (2016). *ggplot2: Elegant Graphics for Data Analysis*. Springer.
- Wickham, H., François, R., Henry, L., & Müller, K. (2019). dplyr: A Grammar of Data Manipulation. Available at: <https://dplyr.tidyverse.org/> [Accessed 16 May 2023]
- Wijdeven, S. M. J., & Kuzee, M. E. (2000). Seed availability as a limiting factor in forest recovery processes in Costa Rica. *Restoration Ecology*, *8*, 414–424. <https://doi.org/10.1046/j.1526-100x.2000.80056.x>
- Wilcke, W., Oelmann, Y., Schmitt, A., Valarezo, C., Zech, W., & Homeier, J. (2008). Soil properties and tree growth along an altitudinal transect in Ecuadorian tropical montane forest. *Journal of Plant Nutrition and Soil Science*, *171*, 220–230. <https://doi.org/10.1002/jpln.200625210>
- Wilcke, W., Velescu, A., Leimer, S., Blotevogel, S., Alvarez, P., & Valarezo, C. (2020). Total organic carbon concentrations in ecosystem solutions of a remote tropical montane forest respond to global environmental change. *Global Change Biology*, *26*, 6989–7005. <https://doi.org/10.1111/gcb.15351>
- Willson, M. F., Irvine, A. K., & Walsh, N. G. (1989). Vertebrate dispersal syndromes in some Australian and New Zealand plant communities, with geographic comparisons. *Biotropica*, *21*, 133–147. <https://doi.org/10.2307/2388704>
- Wolf, K., Veldkamp, E., Homeier, J., & Martinson, G. O. (2011). Nitrogen availability links forest productivity, soil nitrous oxide and nitric oxide fluxes of a tropical montane forest in southern Ecuador. *Global Biogeochemical Cycles*, *25*, 1–12. <https://doi.org/10.1029/2010GB003876>
- Wright, I. J., Ackerly, D. D., Bongers, F., Harms, K. E., Ibarra-Manriquez, G., Martinez-Ramos, M., Mazer, S. J., Muller-Landau, H. C., Paz, H., Pitman, N. C. A., Poorter, L., Silman, M. R., Vriesendorp, C. F., Webb, C. O., Westoby, M., & Wright, S. J. (2007). Relationships among ecologically important dimensions of plant trait variation in seven neotropical forests. *Annals of Botany*, *99*, 1003–1015. <https://doi.org/10.1093/aob/mcl066>
- Wright, I. J., Dong, N., Maire, V., Prentice, I. C., Westoby, M., Díaz, S., Gallagher, R. V., Jacobs, B. F., Kooyman, R., Law, E. A., Leishman, M. R., Niinemets, Ü., Reich, P. B., Sack, L., Villar, R., Wang, H., & Wilf, P. (2017). Global climatic drivers of leaf size. *Science*, *357*, 917–921. <https://doi.org/10.1126/science.aal4760>

- Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., ... Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, *428*, 821–827. <https://doi.org/10.1038/nature02403>
- Wright, J. S. (2002). Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia*, *130*, 1–14. <https://doi.org/10.1007/s004420100809>
- Yan, Z., Li, P., Chen, Y., Han, W., & Fang, J. (2016). Nutrient allocation strategies of woody plants: an approach from the scaling of nitrogen and phosphorus between twig stems and leaves. *Scientific Reports*, *6*, 1–9. <https://doi.org/10.1038/srep20099>
- Yang, Y., & Bao, L. (2022). Scale-dependent changes in species richness caused by invader competition. *Ecological Modelling*, *469*, 109996. <https://doi.org/10.1016/j.ecolmodel.2022.109996>
- Yu, S., Katz, O., Fang, W., Li, D., Sang, W., & Liu, C. (2017). Shift of fleshy fruited species along elevation: temperature, canopy coverage, phylogeny and origin. *Scientific Reports*, *7*, 40417. <https://doi.org/10.1038/srep40417>
- Zhao, N., Yu, G., Wang, Q., Wang, R., Zhang, J., Liu, C., & He, N. (2020). Conservative allocation strategy of multiple nutrients among major plant organs: from species to community. *Journal of Ecology*, *108*, 267–278. <https://doi.org/10.1111/1365-2745.13256>
- Zhao, Y., Cao, H., Xu, W., Chen, G., Lian, J., Du, Y., & Ma, K. (2018). Contributions of precipitation and temperature to the large scale geographic distribution of fleshy-fruited plant species: growth form matters. *Scientific Reports*, *8*, 17017. <https://doi.org/10.1038/s41598-018-35436-x>
- Zimmerman, J. K., Pascarella, J. B., & Aide, T. M. (2000). Barriers to forest regeneration in an abandoned pasture in Puerto Rico. *Restoration Ecology*, *8*, 350–360. <https://doi.org/10.1046/j.1526-100x.2000.80050.x>
- Zvereva, E. L., & Kozlov, M. V. (2014). Effects of herbivory on leaf life span in woody plants: a meta-analysis. *Journal of Ecology*, *102*, 873–881. <https://doi.org/10.1111/1365-2745.12252>

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The field work of my doctoral project in Ecuador, let part of my heart in this beautiful country. I thank all the field and lab assistants for their hard work during the fieldwork of this project there; to Milton David Ortega, Karina González, Víctor Hugo Bustamante, Aini Celena Chamba, Diego Íñiguez, Wilson Ortega, Nohemy Poma, Johana Gusmán, Julia Barczyk, Weronika Gajda-Barczyk, and Wioleta Oleś. I am also grateful to the new friends and kindly people that make me feel at home and enjoy more my time there; to Juljana, Gabo, Samantha, Kenji, Roberth, José, Jorges, Jimmy, family Maldonado Macas, and Felix Matt.

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## 11. Appendices

### **A1: Abiotic factors similarly shape the distribution of fruit, seed and leaf traits in tropical fleshy-fruited tree communities**

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*Status:* in revision

*Author contributions:*

(1) Concept and design

DCAR, 80%;

MS, ELN, in total 20%

(2) Field work/data collection

DCAR collected and measured seed and fruit traits in the field, 90%; MB, 10%.

DCAR prepared all data for analyses, 100%;

DCAR prepared all figures and tables, 100%.

NF, YT contributed herbivory data, 100%;

JH contributed leaf traits data, 100%;

JH recorded the presence and abundance for these species, 100%

AV, WW contributed soil data, 100%;

MS, ELN contributed frugivory data, 100%;

(3) Analysis and interpretation of data

DCAR identified the main ecological plant strategies, 100%;

DCAR tested for associations between main ecological plant strategies and abiotic and biotic factors, 100%;

DCAR tested for phylogenetic and spatial effects, 100%;

DCAR interpreted the results, 90%

with input from MB, CIE, NF, JH, YT, BT, AV, WW, ELN, MS, in total 10%

(4) Drafting of manuscript

DCAR, 80%;

MS, ELN, in total 15%;

MB, CIE, NF, JH, YT, BT, AV, WW, in total 5%

## **Abiotic factors similarly shape the distribution of fruit, seed and leaf traits in tropical fleshy-fruited tree communities**

### **Abstract**

The distribution of plant traits is related to abiotic and biotic factors, but it is unknown whether different types of plant traits respond similarly to these factors. We simultaneously studied seed, fruit and leaf traits and their associations with abiotic and biotic factors for tree communities in the tropical mountains of southern Ecuador. We measured seed, fruit, and leaf traits on 18-33 fleshy-fruited plant species and recorded the abundance for these species on nine 1-ha forest plots located at 1000, 2000, and 3000 m a.s.l. On the same plots, we recorded abiotic (soil C/N ratio, mean temperature, and annual rainfall) and biotic factors (avian fruit removal and herbivory) potentially relevant for the measured traits. We conducted principal component and RLQ analyses to test for trait-environment covariation, controlling for phylogenetic relatedness and spatial autocorrelation. We identified a trade-off between (i) seed number and seed size and between (ii) the production of few costly (nitrogen-rich) vs. many cheap (carbon-rich) fruits. Likewise, leaf trait variation was primarily associated with (i) the leaf economics spectrum and (ii) leaf size. Controlling for phylogenetic and spatial covariation, seed, fruit and leaf traits were associated with abiotic and, to a lesser extent, with biotic factors. Fruit and leaf traits linked to production costs were mainly related to soil C/N ratios, whereas traits associated with the size of seeds, fruits, and leaves were related to rainfall. Our study suggests that associations between seed, fruit and leaf traits and the abiotic environment follow similar principles in tropical tree communities.

### **Key words**

Montane forests; nitrogen allocation; precipitation; soil properties; temperature.

### **Introduction**

Plant traits constitute the main dimensions of variation in plant ecological strategies (Carmona et al. 2021; Díaz et al. 2016; Wright et al. 2004) and are associated with variation in abiotic and biotic factors (Bruehlheide et al. 2018). Understanding these associations is the basis for developing a mechanistic approach to predict changes in plant communities in response to changing environmental conditions (Bendix et al.

2021; Madani et al. 2018). Because plant traits are related to important ecosystem functions, such as carbon stocks of ecosystems (Lavorel and Garnier 2002), such models can be used to project ecosystem change in response to global change (Bendix et al. 2021; Sakschewski et al. 2016).

At global scale, previous studies described large-scale patterns in plant ecological strategies related to plant traits (Wright et al. 2004; Mommer and Weemstra 2012; Reich 2014; Díaz et al. 2016). For instance, a widespread pattern is the trade-off between seed size and seed number (Harper et al. 1970), in which plants produce either many small or few large seeds (Moles and Westoby 2006; Venable 1992; Westoby et al. 2002). Another similarly general pattern across plant communities has been identified through the leaf economics spectrum which describes the variation between ‘conservative’ leaves (i.e., long-lived leaves with low leaf nitrogen content and specific leaf area) and ‘acquisitive’ leaves (i.e., short-lived leaves with high leaf nitrogen content and specific leaf area), balancing leaf construction costs against growth potential (Wright et al. 2004). Such general principles of plant strategies have been shown to underpin the global variation in plant form and function (Díaz et al. 2016).

The effects of abiotic factors, such as climatic conditions and soil properties, have been tested on individual plant traits and on trait combinations related to plant ecological strategies. For instance, mean annual temperature, rather than annual precipitation, was identified to be the main determinant of 21 plant traits across the globe (Moles et al. 2014). Further, large-scale studies have found that large-leaved plant species tend to inhabit sites with higher rainfall and temperature compared to small-leaved species, which inhabit arid conditions and higher elevations (Gallagher and Leishman 2012; Moles et al. 2014; Wright et al. 2017). However, global patterns of covariation between traits and abiotic factors do not always apply to small spatial scales (Oliveras et al. 2020). In fact, plant trait composition at the community level was poorly captured by global climate and soil variables (Bruehlheide et al. 2018). For example, local temperature variation and the type of soil substrate explained the occurrence of conservative and acquisitive leaves in the tree canopy of Andean–Amazon forests (Asner et al. 2016). Plant trait combinations, therefore, might be filtered by a combination of various local abiotic factors (Bruehlheide et al. 2018; Llerena-Zambrano et al. 2021). In addition, plant traits may be related to variation in biotic factors, such as changing compositions of mutualistic and antagonistic animal partners (Galetti et al. 2013; Quitián et al. 2019). This particularly applies to tropical plant communities where

variation in biotic factors has been identified as a key driver of plant diversity (Janzen 1970). In tropical tree communities, up to 90% of tree species produce fleshy fruits and depend on animals for seed dispersal (Howe and Smallwood 1982) and generally face a high intensity of herbivore pressure (Metcalf et al. 2014).

The process of environmental filtering is widely seen as the key mechanism by which abiotic factors structure plant communities (Aldana et al. 2017; Cadotte and Tucker 2017; Lebrija-Trejos et al. 2010), especially under harsh climatic conditions (Swenson and Enquist 2007; de Bello et al. 2013). For instance, Tovar et al. (2020) found that dispersal-related plant traits (i.e., dispersal mode and growth form) were primarily filtered by climatic conditions at high elevations of the tropical Andes. Likewise, in secondary tropical montane forests, community leaf trait variation was primarily constrained by climatic conditions, such as minimum temperature (Llerena-Zambrano et al. 2021). In addition, biotic factors can also filter plant traits through the effects of plant interactions with seed dispersers and herbivores. For example, trait distributions of seed dispersers can lead to changes in seed size distributions of Neotropical and Afrotropical tree communities (Galetti et al. 2013; Vollstädt et al. 2017), whereas herbivores have been shown to promote leaf trait changes in Amazonian forests (Fine et al. 2004).

While fruit, seed and leaf traits may respond to similar abiotic factors, they capture different aspects of plant life. Fruit and seed traits play a key role in plant reproduction and modulate key demographic processes, such as seed dispersal and seedling establishment (Baraloto et al. 2005; Donohue et al. 2010). On another end of the trait spectrum, leaf traits are essential for carbon sequestration and plant growth (Reich et al. 1997; Wright et al. 2004). So far, most studies have investigated either seed or leaf trait associated with environmental factors (e.g., Asner et al. 2016; Tovar et al. 2020; Homeier et al. 2021). Combined studies of seed and leaf trait variation can therefore yield important new insights into how different types of plant traits covary with abiotic and biotic factors (Rosbakh et al. 2022). Because plant traits result from the shared and unshared evolutionary history of species, it is also essential to test to what extent trait-environment associations are imposed by the phylogenetic history of the species (Pavoine et al. 2011).

Here, we investigate associations of seed, fruit and leaf traits with abiotic and biotic factors for a community of fleshy-fruited plants in the Andes of southern Ecuador. Given their dependence on animal seed dispersers, fleshy-fruited tree communities

provide an excellent study system for testing how both abiotic and biotic factors shape different types of plant traits. First, we determined the main plant ecological strategies in the community of fleshy-fruited plant species by identifying the main dimensions of variation in fruit and seed, and leaf traits. Second, we identified the main associations between these trait dimensions and abiotic and biotic factors. Given the phylogenetic non-independence of the studied plant traits, we controlled this analysis for the phylogenetic covariation among species. By using this approach, we are able to show how two distinct types of plant traits respond to abiotic and biotic factors in tropical montane forests of southern Ecuador.

## **Methods**

### **Study system**

Our study was conducted from 2018 to 2020 in a biodiversity hotspot of the Andes in the Podocarpus National Park and San Francisco Reserve, southern Ecuador. We worked along an elevational gradient ranging from 1000 - 3000 m a.s.l. with three main study locations: evergreen premontane forest (ca. 1000 m a.s.l., 4° 6' S, 78° 58' W), lower montane forest (ca. 2000 m a.s.l., 3° 58' S, 79° 4' W) and upper montane forest (ca. 3000 m a.s.l., 4° 6' S, 79° 10' W) (Homeier et al. 2008, Appendix Fig. A.1). At each elevation, we worked on three 1-ha plots, which were located at least 100 m and at maximum 1.5 km apart from each other. All nine plots were located in old-growth forest without visible signs of human disturbance. Plot selection was conducted within the DFG research unit “Environmental changes in biodiversity hotspot ecosystems of South Ecuador: RESponse and feedback effECTs (FOR2730)” (more details in Bendix et al. 2021).

The study area has a tropical humid climate, where the mean annual precipitation increases along the elevational gradient from around 2000 mm/year at the two lowermost sites to up 4500 mm/year in the upper montane forest (Bendix et al. 2008; Emck 2007). During 2019, the year in which we measured plant traits, the highest monthly mean values of rainfall were recorded in January (1589 mm/month at 3000 m a.s.l.), February (875 mm/month at 2000 m a.s.l.) and March (766 mm/month at 1000 m a.s.l.), whereas the lowest monthly mean values were recorded in July (102 mm/month at 1000 m a.s.l.), September (360 mm/month at 3000 m a.s.l.) and November (326 mm/month at 2000 m a.s.l.) (see annual rainfall records in the Appendix, Table B.2).

Along the elevational gradient, mean annual temperature decreases from 20°C at 1000 m a.s.l. to 10°C at 3000 m a.s.l. (Bendix et al. 2008). During the year 2019, the highest values of monthly mean temperature have been recorded in October (16.5° at 2000 m a.s.l.) and November (20.9°C at 1000 m a.s.l. and 11.1°C at 3000 m a.s.l.), while the lowest values have been recorded in July (18.3°C at 1000 m a.s.l.) and August (14.3°C at 2000 m a.s.l. and 9°C at 3000 m a.s.l.) (see annual temperature records in the Appendix, Table B.2). Frost events are very unlikely to occur in the study area below 3400 m a.s.l. (Bendix et al. 2008).

### **Abiotic factors**

For each plot, we recorded key climatic conditions and soil properties. Average annual precipitation and temperature were obtained from daily meteorological records between the years 2018 and 2020 from an operational network consisting of automatic climate stations, remote sensing techniques and a regionalization tool developed for the study area (see more details in Fries et al. 2009; Rollenbeck and Bendix 2011) (see climate data in Appendix, Table C.2).

In 2018, we recorded soil properties (total carbon and nitrogen concentrations) on the same plots where we obtained climatic data. We excavated three soil profiles on each plot and collected samples from the mineral soil (A horizon) to obtain carbon (C) and nitrogen (N) concentrations, resulting in an overall of 27 soil samples from nine 1-ha plots. The samples were dried at 40 °C in a drying oven, the mineral soil was sieved to < 2 mm and an aliquot was milled in a planetary ball mill (Retsch, Haan, Germany). We determined total C and N concentrations by elemental analysis via thermal combustion at 1020 °C, catalytic reduction and detection by thermal conductivity after chromatographic separation of CO<sub>2</sub> and N<sub>2</sub> (Thermo Scientific, Flash 2000 HT Plus Elemental Analyser, 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, 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). Soil data are available from the FOR2730 data warehouse (Velescu et al. 2020a; Velescu et al. 2020b; Velescu et al. 2020c).

### **Biotic factors**

We recorded avian fruit removal and herbivory at the plot scale to quantify two key biotic variables shaping seed, fruit and leaf traits (Galetti et al. 2013; Metcalfe et al. 2014), respectively. To quantify avian fruit removal, plant-bird interactions were observed for 600 h per plot during four time periods between 2014 and 2015 (Quitán et al. 2019). Seven plots were identical to those in which climatic conditions, soil properties and herbivory (see below) were measured. Two plots had been slightly shifted (i.e., plots BO1 at 1000 m a.s.l. and CA3 at 3000 m a.s.l.) after the study of fruit removal but were characterized by a very similar tree species composition and habitat. Fruit removal was defined as the sum of removed fruits by all frugivorous birds observed on each plot, only considering events of fruit and seed removal and excluding events of fruit and/or seed droppings (see more details in Quitán et al. 2019). We are confident that our measure is a good proxy for community-wide fruit removal by birds, because fruit removal and avian frugivore richness per plot were highly correlated ( $n = 9$  plots,  $r = 0.88$ ,  $p = 0.001$ ). As this variable represents a community-wide measure per plot, it is not mandatory that exactly the same plant species were studied in this and the previous study.

To assess the degree of herbivory, we installed 18 litterfall traps (60 cm × 60 cm) on each plot, resulting in 162 traps along the elevational gradient. Litterfall traps were located at 20 m distance from each other. The content of the litterfall traps was collected monthly during the entire year of 2019. All leaves contained in the samples were scanned, and we quantified the leaf area loss per leaf and trap using WinFOLIA 2005 software (Regent Instruments, Inc., Canada), following Adams et al. (2009). To quantify the total herbivory on each plot, we calculated the proportional leaf area loss for each individual leaf and averaged these values across all leaves in a trap and across all traps located in a plot. The mean herbivory rate per plot was given by the mean value over the temporal replicates across the entire year.

### **Tree community**

We recorded the presence and abundance of tree species on all nine 1-ha plots to describe changes in community composition across the abiotic and biotic gradients. To this end, an inventory of all woody stems with a diameter at breast height (DBH)  $\geq 10$  cm was conducted inside each 1-ha plot (Homeier et al. 2021). All trees were marked and herbarium specimens were collected to ensure taxonomic identification in reference



to the herbaria collections of the Universidad Nacional de Loja (UNL) and the University of Göttingen (GOET). The abundance of each species was defined as the number of individual trees per plot (see Appendix, Table C.3 for the relative abundances of each species per plot).

### **Fruit and seed traits**

We monitored the fruiting phenology of the most abundant 36 fleshy-fruited tree species from May 2019 to March 2020 on a monthly basis. We recorded seven fruit and seed traits for all tree species fruiting during that time period (18 fleshy-fruited plant species, each sampled on 1-5 individual trees, Appendix, Fig. D.4). Fruit and seed traits were selected to capture variability in seed and fruit size (seed fresh mass, pulp fresh mass), in the rewards provided to animal frugivores (crop size, pulp C/N ratio, relative yield index) and in strategies of seedling establishment (Seed C/N ratio, seed number) (Fenner and Thompson 2005; Saatkamp et al. 2019).

Crop size was recorded by estimating the number of ripe fruits on each fruiting plant. For other trait measurements, we collected at least 10 fruits per tree. We dissected fruits and extracted seeds to record seed and pulp fresh mass, and to count the number of seeds per fruit (see Online Resource 4, Fig. S4 for a visual explanation). After drying seeds and fleshy pulps at 60 °C for 3-4 days, we analyzed the C and N concentrations, separately for seeds and pulp with an elemental analyzer (Vario EL III, Elementar Analysensysteme, Langensfeld, Germany). We summarized investment of C and N in fruits and seeds by calculating the C/N ratio for the pulp of fruits and seeds. In addition, we calculated a relative yield index as the proportion between the dry mass of pulp and the fresh mass of the whole fruit. This index indicates how much dry material is gained in relation to the whole fruit mass (Herrera 1981). Photos of seeds and fruits of most of the plant species are available in Acosta-Rojas et al. 2021 (see fruit and seed trait values in Appendix, Table E.5).

### **Leaf traits**

We selected 8-10 individuals for 33 out of the 36 target fleshy-fruited plant species within the study plots between February and March 2019. For 15 of these tree species, we were also able to record measurements of seed and fruit traits (see Appendix, Table C.3 for the species list in which we measured seed, fruit and leaf traits). We collected 20 leaves attached to 2-3 branches from the tree crown under a homogeneous exposure

to sun radiation. The whole branches were kept in sealed polyethylene bags with water-soaked tissues prior to measurements. We recorded five key leaf traits related to the leaf economics spectrum and herbivory. Leaf traits were selected to capture the variability in leaf size (leaf area), in the cost of leaf production (specific leaf area, leaf C/N ratio) and in plant defence against herbivores (leaf thickness, leaf toughness) (Díaz et al. 2016; Lamarre et al. 2012; Pérez-Harguindeguy et al. 2013; Poorter et al. 2009; Reich et al. 1999; Ruiz-Guerra et al. 2021; Wright et al., 2004).

We quantified leaf area (LA, cm<sup>2</sup>) by scanning 20 undamaged leaves using the software WinFOLIA 2014 (Régent Instruments, Quebec, QC, Canada) (see Appendix, Fig. D.4 for a visual explanation). Specific leaf area (SLA, cm<sup>2</sup> g<sup>-1</sup>) was calculated as the proportion between leaf area and leaf dry mass. The C and N concentrations of leaves were quantified by using an elemental analyzer (Vario EL III Elementar Analysensysteme, Langenselbold, Germany). Leaf thickness (mm) was measured on both sides of the main leaf vein using a digital micrometer (Mitutoyo M293-240-70, Mitutoyo Germany Ltd, Neuss, Germany). Leaf toughness (kN m<sup>-1</sup>) was based on six punch tests applied to the leaf surface without midrib and other major veins using a digital penetrometer (fat-ended 2.0 mm diameter steel punch, DS-50 N, Imada Inc., Japan). More details of the leaf trait methods and leaf trait data are available in Homeier et al. 2021 (see leaf trait values in Appendix, Table F.6).

## **Phylogeny**

We used a dated mega-tree, implemented in V.PhyloMaker (i.e. GBOTB. extended.tre), to build two phylogenetic trees for the 18 species on which we measured seed and fruit traits and for the 33 species on which we measured leaf traits (see Appendix, Fig. G.7). The phylogenetic trees included all studied species. The three plant species that could only be identified to genus level (*Ocotea* sp., *Saurauia* sp., and *Myrcia* sp.) were included by randomly selecting a congeneric species and adding the branch of this species to the phylogenetic tree. This was justified because the phylogenetic differences among species were largely driven by differences among plant genera, families and orders. Before building the phylogenetic trees, we updated the species nomenclature following the Leipzig Catalogue for Vascular Plants (Freiberg et al. 2020) using the R packages *lcvplants* (Freiberg et al. 2020) and *LCVP* (Freiberg et al. 2020). We also used the R packages *V.PhyloMaker2* (Jin and Qian 2022), *ape* (Paradis et al. 2004) and *phytools* (Revell 2012) for editing the phylogenetic trees.

### **Statistical analysis**

First, we conducted two principal component analyses (PCA) to identify the main ecological plant strategies, given by the main dimensions of trait variation, for (1) fruits/seeds and (2) leaves in the community of fleshy-fruited plant species. We applied a varimax rotation to obtain a simple structure, in which the loading of the traits are maximized on single axes. For both types of traits, we kept only the two first axes. In the PCA, we included the following key traits for seed and fruit: crop size, seed fresh mass, pulp fresh mass, seed number, seed C/N ratio, pulp C/N ratio, and the relative yield index; and leaf traits: leaf thickness, leaf toughness, LA, SLA, and leaf C/N ratio. We log-transformed seed number, seed fresh mass, pulp fresh mass, seed C/N ratio, pulp C/N ratio, and crop mass, as well as all leaf traits, prior to running the analyses to approximate a normal distribution of trait data. All traits were scaled to zero mean and unit variance before running the PCA.

Secondly, we tested whether plant traits and abiotic and biotic factors were systematically associated by combining RLQ analyses with a fourth-corner approach (Dray et al., 2014). The RLQ analysis maximizes the co-variance between traits and environmental data via the use of co-inertia analysis on the three cross-matrixes that include (1) abundance or presence/absence data of the fleshy-fruited plant species per plot (i.e., L matrix), (2) the two main axes of seed and fruit or leaf trait variation (i.e., Q matrix), separately defined for seed and fruit, and leaf traits (see PCA analysis above), and (3) the mean values of abiotic and biotic factors per plot (i.e., R matrix). RLQ analysis calculates the best joint combination of the ordination of plots by their abiotic and biotic factors, the ordination of fleshy-fruited species by their traits, and the simultaneous ordination of species and plots (Dray et al. 2014). Including species abundances in table L yielded qualitatively identical patterns so that we only present results based on presence/absence data which ensures that the patterns were not dominated by the most abundant species. As almost all of the cross-covariance between plant traits and abiotic and biotic factors was explained by the two RLQ axes (>99% of the projected inertia in the cases of both trait types), we restricted the analyses to these two dimensions. To test for a general association between plant traits and abiotic and biotic factors, we applied separate fourth-corner permutation tests for seed and fruit, and leaf traits on the sum of the eigenvalues of the first and second axis (Dray et al. 2014). We selected the most conservative fourth-corner model six (9999 permutations) that tests the null hypothesis that abiotic and biotic factors, species presences, and plant

traits are unrelated, according to a random community assembly independent of plant trait values (Dray et al. 2014). We applied the same null model to test for axis-specific associations of plant traits and abiotic and biotic factors, based on correlations of the RLQ scores on the first and second axis, respectively (Dray et al. 2014).

We tested whether the associations between plant traits and abiotic and biotic factors were maintained after controlling for phylogenetic and spatial effects by applying an extended version of the RLQ analysis (Pavoine et al. 2011). The extended RLQ analysis includes two additional matrices based on the (1) phylogenetic distances among species (i.e., P matrix) and (2) the spatial arrangement of the study plots (i.e., S matrix) (Pavoine et al. 2011). The analysis accounts for covariation by partitioning trait effects into a phylogenetic component due to a phylogenetic clustering of trait values and a trait component that is independent of phylogeny. Accordingly, the environmental variation is partitioned into a spatial component due to similar environmental conditions at neighbouring plots and an environmental component that is independent of the spatial arrangement of study plots. We applied the same types of fourth-corner permutation tests to this extended RLQ analyses, but used the phylogenetically and spatially independent components of the Q and R matrix, respectively.

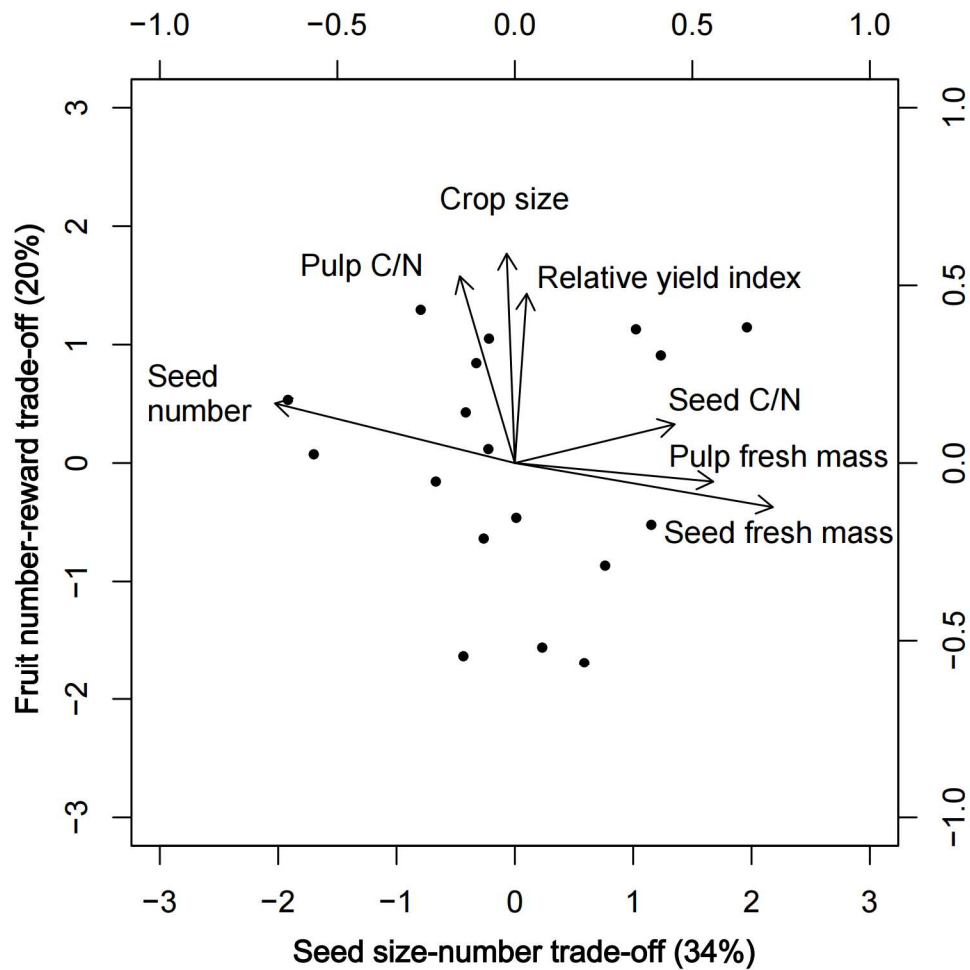
We also tested for correlations between seed and fruit, and leaf traits for the 15 fleshy-fruited plant species for which we had measured both types of traits. Across the 35 pairwise correlations, only leaf area and seed fresh mass ( $r = 0.88$ ,  $p = 0.001$ ), and leaf area and pulp fresh mass ( $r = 0.88$ ,  $p = 0.001$ ) were significantly correlated after correcting for multiple testing using Holm's method (Holm 1979). All statistical analyses were performed using the R version 4.0.5 (R Core Team 2021) with the packages: dplyr (Wickham et al., 2019), picante (Kembel et al. 2010), FD (Laliberte and Legendre 2010), psych (Revelle, 2022), ade4 (Dray and Dufour 2007), and adiv (Pavoine 2020).

## **Results**

### **Fruit and seed traits**

We identified the main dimensions of fruit and seed trait variation in the fleshy-fruited plant community on two main principal components (*eigenvalue axis 1* = 2.53, and *eigenvalue axis 2* = 1.27). The first two axes of the PCA accounted for 54% of the variation in fruit and seed traits. Axis 1 accounted for 34% of the variation and

differentiated between plants with large fruits (seed and pulp fresh mass) with few seeds, and those producing small fruits with several seeds (i.e., reflecting the *seed size-number trade-off*). The second axis explained 20% of the variation and was positively correlated with crop size, pulp C/N ratio and the relative yield index (i.e., representing a *fruit number-reward trade-off*) (Fig. 1).



**Figure 1.** Principal component analysis with varimax rotation of seed/fruit traits of 18 fleshy-fruited plant species (black circles) along an elevational gradient in the tropical mountains of southern Ecuador. The first and second axis together comprise 54% of trait variation. Axes are labelled according to the main ecological strategies or plant traits associated with each axis.

The general associations between fruit and seed traits (represented by the two main trait dimensions) and abiotic and biotic factors were larger than expected under random community assembly although this association was only marginally significant (Table 1). The first ordination axis summarized most of the projected inertia between

fruit and seed traits and abiotic and biotic factors, whereas the second axis comprised only a minor proportion. In separate permutation tests of the ordination axes, associations between plant traits and abiotic and biotic factors were significant for the first axis, but not for the second axis (Table 1). Accounting for phylogenetic and spatial covariation, the projected inertia on each RLQ axis and the associations between RLQ axes, plant traits and abiotic and biotic factors remained qualitatively identical (Table 1). In the RLQ space, the seed size-number trade-off was negatively related to rainfall, reflecting the association of small seeds with high precipitation. Moreover, the fruit number-reward trade-off was positively related to the soil C/N ratios and negatively to fruit removal, suggesting that the production of small crops of N-rich fruits is associated with low soil C/N ratios (high N availability to plants) and high avian fruit removal. Variability in temperature varied largely independently to the variation in the two main seed and fruit trade-offs (Fig. 2).

### **Leaf traits**

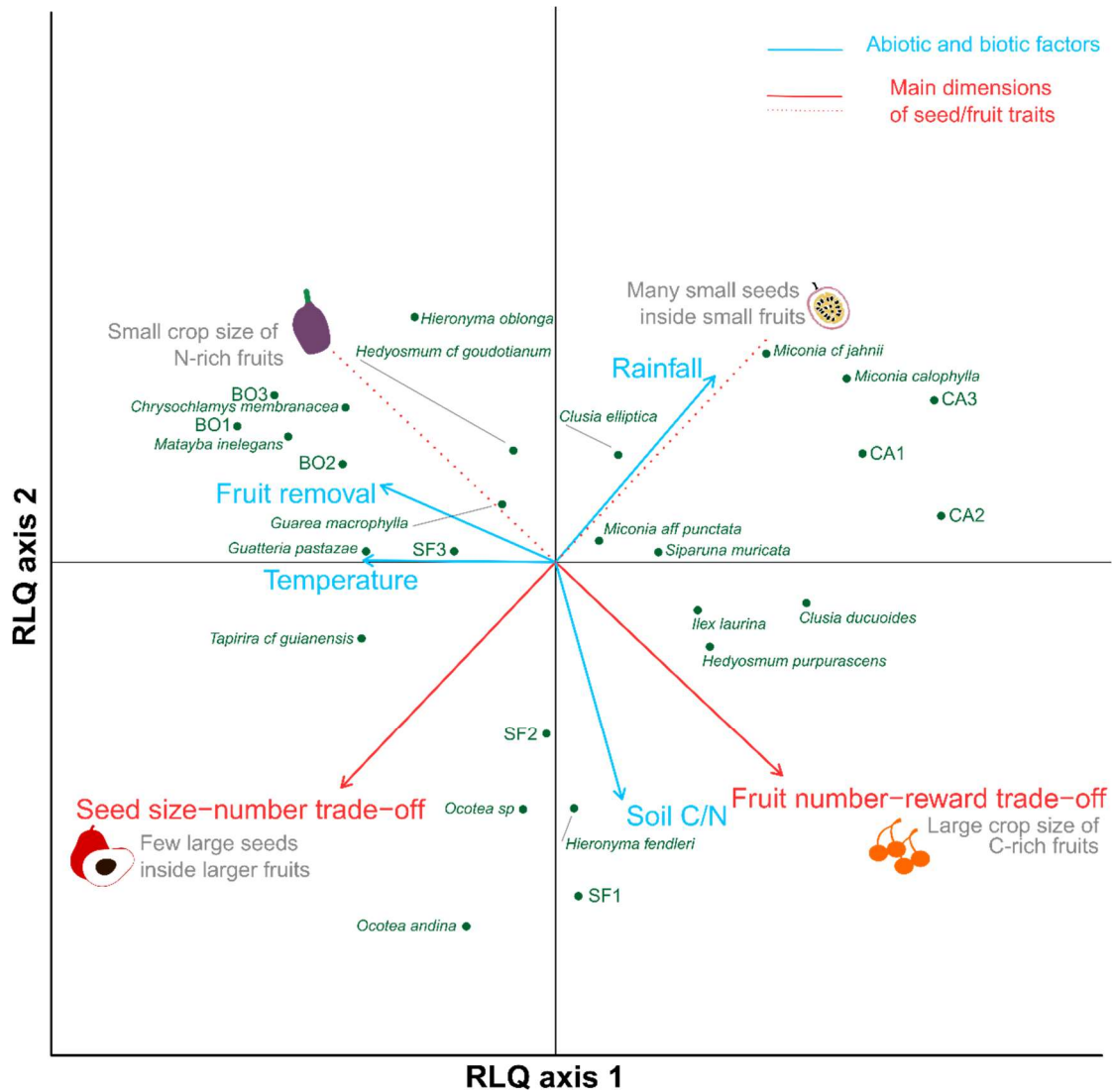
We identified the main dimensions of leaf trait variation in the community of fleshy-fruited plant species on two axes (*eigenvalue axis 1* = 3.28, and *eigenvalue axis 2* = 0.77). The first two axes of the PCA accounted for 81% of the variation in leaf traits. Axis 1 accounted for 57% of the variation and differentiated between leaves with low SLA but high leaf C/N ratio (“conservative” leaves), and those leaves with high SLA and decreasing leaf C/N ratio (“acquisitive” leaves), reflecting variation along the *leaf economics spectrum*. The second axis explained 24% of all variation and was positively correlated with leaf area (Fig. 3).

The general associations between leaf traits and abiotic and biotic factors were larger than expected under random community assembly (Table 2). The first ordination axis described most of the projected inertia between leaf traits and abiotic and biotic factors, whereas the second axis comprised only a very minor proportion. In separate analyses of the two ordination axes, associations between the first axes of leaf traits and abiotic and biotic factors were stronger than expected for the first axes, but not for the second axes (Table 2). In the extended RLQ analysis accounting for phylogenetic and spatial covariation, the projected inertia of the RLQ axes, as well as the associations between RLQ axes, leaf traits, and abiotic and biotic factors were maintained (Table 2).

**Table 1.** Fourth-corner analyses of the associations between seed and fruit traits of 18 fleshy-fruited plant species and abiotic and biotic factors along an elevational gradient in southern Ecuador. Shown are permutation tests for the global association and for specific axes based on a RLQ analysis and an extended RLQ analysis accounting for phylogenetic and spatial covariation among species and plots, respectively. Given are the total inertia (sum of RLQ eigenvalues) and the inertia of each axis, as well as Pearson correlation coefficients between Q and R matrices on the respective axis. P-values are based on 9999 permutations.

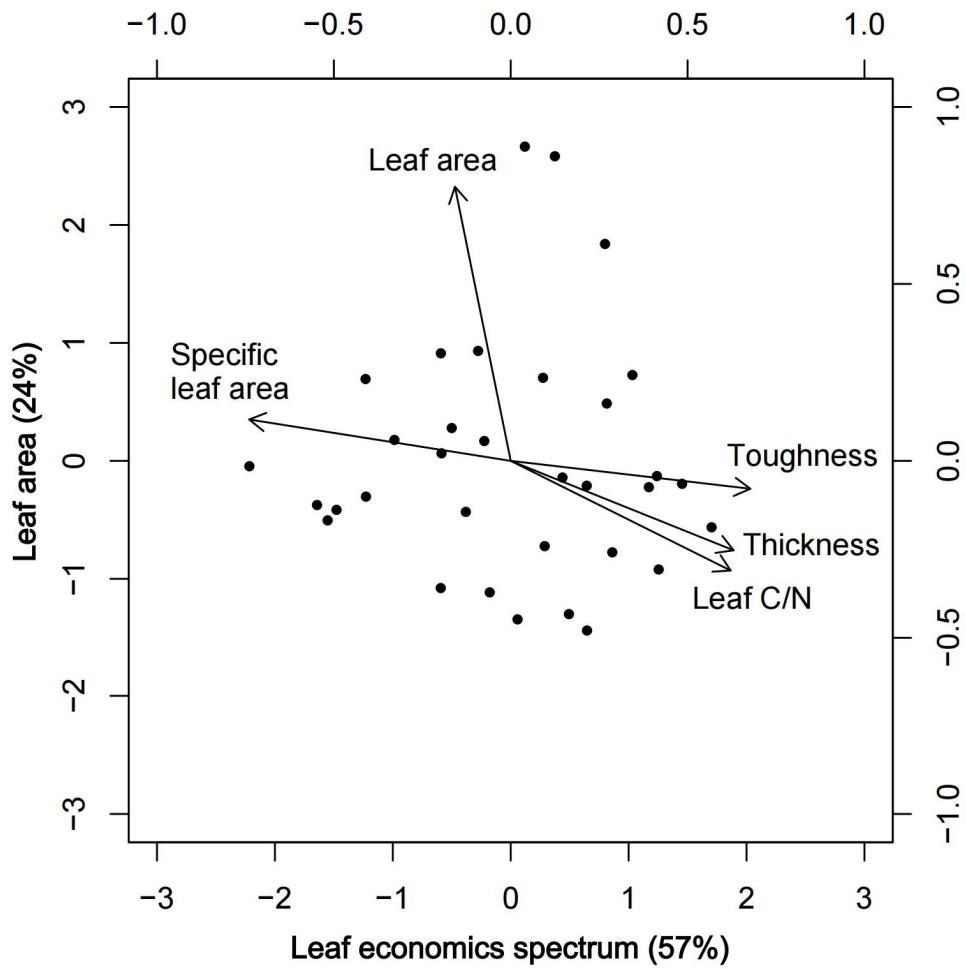
		RLQ analysis	Extended RLQ analysis
General association	<i>Total inertia</i>	0.87	0.68
	<i>p-value</i>	0.09	0.08
Axis 1	<i>Projected inertia</i>	0.82	0.61
	<i>Pearson's r</i>	0.57	0.56
	<i>p-value</i>	0.01	0.02
Axis 2	<i>Projected inertia</i>	0.05	0.07
	<i>Pearson's r</i>	0.19	0.23
	<i>p-value</i>	0.37	0.32

In RLQ space, the leaf economics spectrum ranging from acquisitive to conservative leaves was related to soil C/N ratios. Conservative leaves were associated with environments with high soil C/N ratios (low N availability to plants), while acquisitive leaves were associated with lower soil C/N ratios (high N availability to plants). In addition, leaf area was negatively related to rainfall and, to a lesser extent, positively to herbivory. Temperature was only weakly related to leaf trait variation (Fig. 4).



**Figure 2.** Associations between fruit and seed traits, and abiotic and biotic factors in the fleshy-fruited tree communities of southern Ecuador. Vectors depict the coefficients of the main dimensions of fruit traits (solid red arrows) and abiotic and biotic factors (solid blue arrows) on the first two axes of the RLQ space; dashed arrows extend arrows to the opposite direction for the two main trait dimensions. Species and plots (BO at 1000 m a.s.l., SF at 2000 m a.s.l. and CA at 3000 m a.s.l.) are displayed by green circles and their respective labels. Icons illustrate the extreme trait values for the two main trait trade-offs.

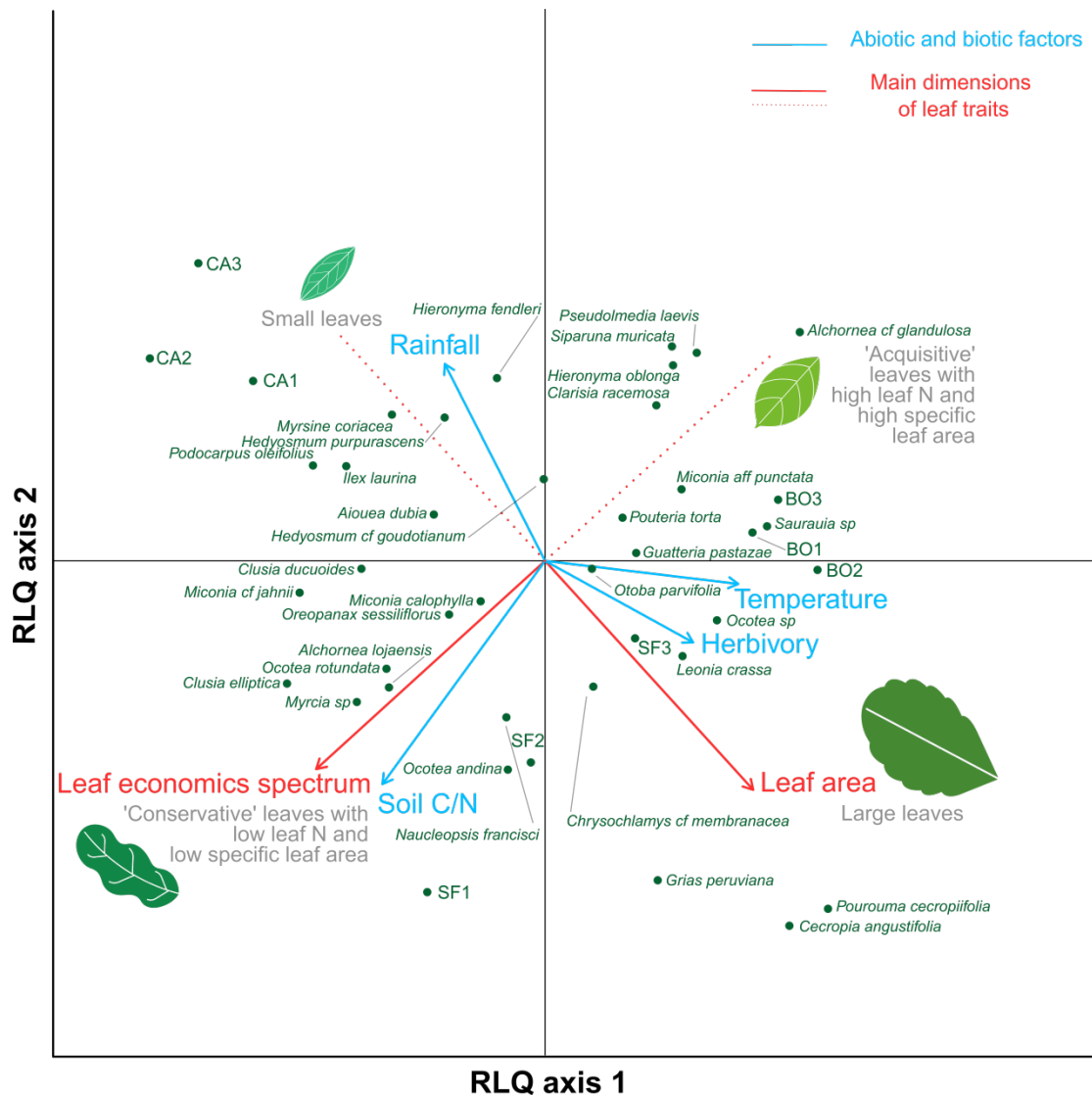




**Figure 3.** Principal component analysis with varimax rotation of leaf traits of 33 fleshy-fruited plant species (black circles) along an elevational gradient in the tropical mountains of southern Ecuador. The first and second axis together comprise 81% of trait variation. Axes are labelled according to the main ecological strategies or plant traits associated with each axis.

**Table 2.** Fourth-corner analyses of the associations between leaf traits of 33 fleshy-fruited plant species and abiotic and biotic factors along an elevational gradient in southern Ecuador. Shown are permutation tests for the global association and for specific axes based on a RLQ analysis and an extended RLQ analysis accounting for phylogenetic and spatial covariation among species and plots, respectively. Given are the total inertia (sum of RLQ eigenvalues) and the inertia of each axis, as well as Pearson correlation coefficients between Q and R matrices on the respective axis. P-values are based on 9999 permutations.

		RLQ analysis	Extended RLQ analysis
General association	sum of RLQ-eigenvalues	1.44	1.35
	<i>p-value</i>	0.01	0.01
Axis 1	Projected inertia	1.42	1.31
	<i>Pearson's r</i>	0.75	0.75
	<i>p-value</i>	0.001	0.0007
Axis 2	Projected inertia	0.02	0.04
	<i>Pearson's r</i>	0.12	0.12
	<i>p-value</i>	0.50	0.51



**Figure 4.** Associations between leaf traits, and abiotic and biotic factors in the fleshy-fruited tree communities of southern Ecuador. Vectors depict the coefficients of the main dimensions of leaf traits (solid red arrows) and abiotic and biotic factors (solid blue arrows) on the first two axes of the RLQ space; dashed arrows extend the arrows to the opposite direction for the main trait dimensions. Species and plots (BO at 1000 m a.s.l., SF at 2000 m a.s.l. and CA at 3000 m a.s.l.) are displayed by green circles and their respective labels. Icons illustrate the extreme trait values for the main trait trade-offs.

### Discussion

Here, we identified plant trait associations and how they relate to abiotic and biotic factors in fleshy-fruited tree communities in the tropical Andes of southern Ecuador. We identified similar trade-offs in trait distributions of seed, fruit and leaf traits related to trait costs and benefits accounting for the phylogenetic and spatial covariation among species and plots, respectively. Variation in seed and fruit traits was associated to

variation in producing many small or few large seeds and to producing many cheap (C-rich) or few rewarding (N-rich) fruits. Similarly, leaf trait variation was mainly captured by the trade-off between conservative (C-rich) and acquisitive (N-rich) leaves. These findings demonstrate similar trait-environment associations for both seed, fruit and leaf traits that were independent of the phylogenetic history of species. The main ecological strategies associated with the production of costly vs. cheap fruits and leaves were primarily related to the extent to which environments have a fast (i.e., low soil C/N and a high N availability to plants) or slow turnover of organic matter (i.e., high soil C/N and a low N availability to plants), whereas strategies associated with the size of seeds, fruits, and leaves were primarily related to rainfall. Hence, our analyses reveal similar abiotic constraints for producing different types of fruits/seeds and leaves in tropical montane forests of southern Ecuador.

### **Plant ecological strategies**

We identified two main ecological strategies related to seed size and fruit production. First, the seed size-number trade-off separated plants producing few large seeds inside large fruits from those with several small seeds inside small fruits. This trade-off represents alternative strategies in allocating reproductive resources (Harper et al. 1970). Investment into diaspore size (i.e. seed and fruit size) reflects one of the main constraints in Neotropical plants (Wright et al. 2007) and vascular plants in general (Díaz et al. 2016). Second, the cost to produce N-rich fruits underpins a fruit number-reward trade-off. Plants either produce large crops of C-rich fruits or small crops of protein-rich fruits. This trade-off is described by the classic concept of seed dispersal systems, proposed by Howe (1993), which differentiates between specialized and generalized systems of fleshy-fruited plant species. Specialized dispersal systems are characterized by rewarding fruits (i.e., containing high lipid or protein content) and small crop sizes, addressing specific types of seed dispersers. In contrast, generalized systems tend to have sugar-rich fruits and large crop sizes, attractive to many different types of frugivorous animals. Our findings suggest that differences in the type of fruit investment are a key trait dimension in the tropical montane forests of southern Ecuador. Similar to the main axes in fruit and seed traits, we identified two distinct constraints related to leaf production and leaf size. First, according to the leaf economics spectrum (Wright et al. 2004), we were able to separate plants producing conservative leaves and plants producing leaves with an acquisitive use of resources. Second, we differentiate

between small and large leaves (i.e. leaf area was associated with the second axis of trait variation), reflecting costs and benefits of leaf size for photosynthesis and heat exchange (Givnish 1987; Kleiman and Aarssen 2007). Overall, we identified similar constraints related to the variation of seed, fruit and leaf traits across fleshy-fruited plant species. These trade-offs reflect the costs to produce plant organs. e.g., in terms of N and C allocation to fruits and leaves, as well as limitations in the size of plant organs.

### **Plant trait associations with abiotic and biotic factors**

In this study, fruit and seed traits were primarily associated with soil C/N ratio and precipitation. We found that plant species with small crops and protein-rich fruits (i.e., low pulp C/N ratio) were more abundant in environments with high N availability (i.e., low soil C/N), whereas species with large crops of sugar-rich fruits (i.e., high pulp C/N ratio) were more abundant in habitats with low N availability to plants (i.e., high soil C/N). Previous studies have shown that fruit production in tropical forests is related to soil nutrients (Kaspari et al. 2007), but can also be related to other factors such as tree size and competition between neighbouring trees (Minor and Kobe 2019). We further found that size variation of fruits and seeds was related to precipitation. As a consequence, tree communities were characterized by smaller seeds and fruits in rainy habitats. In contrast, larger diaspores were produced in less rainy environments. In line with our findings, seed size seems to be positively related to precipitation at broad scales (Moles et al. 2004).

Likewise, leaf traits were primarily related to soil C/N ratio and precipitation, and were only weakly related to temperature. First, the production of N-rich leaves (i.e. low leaf C/N) with high SLA was associated with high N availability (i.e., low soil C/N), while leaves with lower N concentration and decreasing SLA were associated with a with low N availability to plants (i.e., high soil C/N). Soil conditions have been identified as main drivers of N and phosphorus concentrations in leaves at local (Asner et al. 2016; Homeier et al. 2021; Yan et al. 2016) and global scales (Reich and Oleksyn 2004). Overall, our findings highlight the role of the soil C and N concentrations for the allocation of these nutrients to the fleshy-fruited pulps and leaves. These similar patterns of nutrient allocation between fruits and leaves might suggest conservatism in the strategies of how plants allocate nutrients to certain types of plant organs (Zhao et al. 2020). Second, we found that leaf size was associated with precipitation. That is, large-leaved plants were more abundant in the less rainy environments in our study area.

Large-leaved species tend to be more common in rainy environments with sufficient water supply (Gallagher and Leishman 2012; Moles et al. 2014; Wright et al. 2017). Since water is not limiting in our study area (see rainfall records in Table S2), it is somewhat surprising that leaf area was mainly shaped by the variation in precipitation. This rather unexpected result may be due to additional factors associated with leaf size, such as irradiation (Givnish 1984; Wright et al. 2017), that were not covered by our study. Positive correlations between fruit and leaf sizes reported in this study also suggest that vascular and biomechanical constraints between plant appendages (Corner 1949) might explain why seed, fruit and leaf sizes respond similarly to precipitation.

In our system, seed, fruit and leaf traits were also related to fruit removal rates by birds. Protein-rich fruits (i.e., fruits with a low pulp C/N ratio) tended to increase in abundance with increasing avian fruit removal. This suggests that the production of rewarding fruits may be linked to the high availability of animal frugivores (Howe 1993), or that increasing fruit removal by frugivores occurs due to the presence of high-quality fruits (Fuentes 1994; Schaefer et al. 2003). In addition, larger leaves were slightly positively related to increasing herbivory rates. This implies that the production of leaves with a large photosynthetically active surface area may act as a mechanism of resistance for leaves exposed to high levels of herbivory (Zvereva and Kozlov 2014). Alternatively, increasing herbivory rates may be the result of the high availability of leaf biomass in large-leaved plants (Brown and Lawton 1991; Ribeiro et al. 1994; Moles and Westoby 2000).

Despite intensive monitoring of fruiting phenology over 10 months, we were only able to collect leaves (33 species) and fruits and seeds (18 species) from a limited number of representative fleshy-fruited plant species in the study area. The relative small number of sampled species might specifically explain the weaker statistical support for the association between seed, fruit traits and abiotic and biotic factors compared to the analysis of leaf traits (ter Braak et al. 2012). Although the sample size was limited, we are confident that the described patterns are robust given the large trait variation covered by our study species and the fact that the identified trait-environment associations were independent of phylogenetic and spatial sampling effects. Nevertheless, further studies are needed to test these associations in a larger number of plant species, comparing fleshy and non-fleshy fruited plant species in more ecosystem types. Future studies may also try to identify the specific mechanisms underpinning the identified trait-environment relationships.

## **Conclusions**

Our results demonstrate that abiotic and biotic factors are associated with the distribution of seed, fruit and leaf traits in the fleshy-fruited tree communities of tropical montane forests in southern Ecuador. Our findings further suggest similar principles of trait-environment covariation across plant traits in animal-dispersed tree communities that are independent of plant phylogeny. The identification of such associations between plant ecological strategies and environmental conditions can be the basis for predicting changes in plant traits in diverse tropical tree communities under future environmental change (Bendix et al. 2021; Dantas de Paula et al. 2021; Madani et al. 2018).

## **References**

- Acosta-Rojas DC, Barczyk M, Espinosa CI, Gusmán J, Peña J, Neuschulz EL, Schleuning M, Homeier J (Eds) (2021) Guía de campo de plantas dispersadas por animales: frutos y semillas en el parque nacional Podocarpus y sus cercanías/Field guide of animal-dispersed plants: fruits and seeds in and around Podocarpus national park, 1st edn. INABIO, Quito.
- Adams JM, Zhang Y, Basri M, Shukor N (2009) Do tropical forest leaves suffer more insect herbivory? A comparison of tropical versus temperate herbivory, estimated from leaf litter. *Ecol Res* 24:1381–1392. <https://doi.org/10.1007/s11284-009-0623-4>
- Aldana AM, Carlucci MB, Fine PVA, Stevenson PR (2017) Environmental filtering of eudicot lineages underlies phylogenetic clustering in tropical South American flooded forests. *Oecologia* 183:327–335. <https://doi.org/10.1007/s00442-016-3734-y>
- Asner GP, Knapp DE, Anderson CB, Martin RE, Vaughn N (2016) Large-scale climatic and geophysical controls on the leaf economics spectrum. *Proc Natl Acad Sci U S A* 113:E4043–E4051. <https://doi.org/10.1073/pnas.1604863113>
- Baraloto C, Forget PM, Goldberg DE (2005) Seed mass, seedling size and neotropical tree seedling establishment. *J Ecol* 93:1156–1166. <https://doi.org/10.1111/j.1365-2745.2005.01041.x>

- de Bello F, Lavorel S, Lavergne S, Albert CH, Boulangeat I, Mazel F, Thuiller W. (2013) Hierarchical effects of environmental filters on the functional structure of plant communities: A case study in the French Alps. *Ecography* 36:393–402. <https://doi.org/10.1111/j.1600-0587.2012.07438.x>
- Bendix J, Aguire N, Beck E et al (2021) A research framework for projecting ecosystem change in highly diverse tropical mountain ecosystems. *Oecologia* 195:589–600. <https://doi.org/10.1007/s00442-021-04852-8>
- Bendix J, Rollenbeck R, Richter M, Fabian P, Emck P (2008) Climate. In: Beck E, Bendix J, Kottke I, Makeschin F, Mosandl R (eds), *Gradients in a tropical mountain ecosystem of Ecuador*, 1st edn, Springer, Heidelberg, pp 63–73.
- ter Braak C, Cormont A, Dray S (2012) Improved testing of species traits–environment relationships in the fourth-corner problem. *Ecology* 93:1525–1526. <https://doi.org/10.1890/12-0126.1>
- Brown VK, Lawton JH (1991) Herbivory and the evolution of leaf size and shape. *Philos Trans R Soc Lond B Biol Sci* 333:265–272. <https://doi.org/10.1098/rstb.1991.0076>
- Bruelheide H, Dengler J, Purschke O et al (2018) Global trait–environment relationships of plant communities. *Nat Ecol Evol* 2:1906–1917. <https://doi.org/10.1038/s41559-018-0699-8>
- Cadotte MW, Tucker CM (2017) Should environmental filtering be abandoned? *Trends Ecol Evol* 32:429–437. <https://doi.org/10.1016/j.tree.2017.03.004>
- Carmona CP, Bueno CG, Toussaint A et al (2021) Fine-root traits in the global spectrum of plant form and function. *Nature* 597:683–687. <https://doi.org/10.1038/s41586-021-03871-y>
- Corner EJH (1949) The durian theory or the origin of the modern tree. *Ann Bot* 13:367–414. <https://doi.org/10.1093/oxfordjournals.aob.a083225>
- Dantas de Paula M, Forrest M, Langan L et al (2021) Nutrient cycling drives plant community trait assembly and ecosystem functioning in a tropical mountain biodiversity hotspot. *New Phytol* 232:551–566. <https://doi.org/10.1111/nph.17600>
- Díaz S, Kattge J, Cornelissen JHC et al (2016) The global spectrum of plant form and function. *Nature* 529:167–171. <https://doi.org/10.1038/nature16489>



- Donohue K, Rubio De Casas R, Burghardt L, Kovach K, Willis CG (2010) Germination, postgermination adaptation, and species ecological ranges. *Annu Rev Ecol Evol Syst* 41:293–319. <https://doi.org/10.1146/annurev-ecolsys-102209-144715>
- Dray S, Choler P, Dolédec S, Peres-Neto PR, Thuiller W, Pavoine S, Ter Braak CJF (2014) Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology* 95:14–21. <https://doi.org/10.1890/13-0196.1>
- Dray S, Dufour AB (2007) The ade4 package: Implementing the duality diagram for ecologists. *J Stat Softw* 22:1–20. <https://doi.org/10.18637/jss.v022.i04>
- Duarte LDS, Debastiani VJ, Carlucci MB, Diniz-Filho JAF (2018) Analyzing community-weighted trait means across environmental gradients: should phylogeny stay or should it go? *Ecology* 99:385–398. <https://doi.org/10.1002/ecy.2081>
- Emck PA (2007) A climatology of South Ecuador with special focus on the major Andean ridge as Atlantic-Pacific climate divide. PhD dissertation, Faculty of Natural Sciences, Friedrich Alexander University Erlangen-Nuremberg, Erlangen, Bavaria, Germany.
- Fenner M, Thompson K (2005) *The Ecology of Seeds*, 1st edn, Cambridge University Press, Cambridge.
- Fine PVA, Mesones I, Coley PD (2004) Herbivores promote habitat specialization by trees in Amazonian forests. *Science* 305:663–665. <https://doi.org/10.1126/science.1098982>
- Freiberg M, Winter M, Gentile A, Zizka A, Muellner-Riehl A, Weigelt A, Wirth C (2020) LCVP, The Leipzig catalogue of vascular plants, a new taxonomic reference list for all known vascular plants. *Sci Data* 7:416. <https://doi.org/10.1038/s41597-020-00702-z>
- Fries A, Rollenbeck R, Göttlicher D, Nauss T, Homeier J, Peters T, Bendix J (2009) Thermal structure of a megadiverse Andean mountain ecosystem in southern Ecuador and its regionalization. *Erdkunde* 63:321–335. <https://doi.org/10.3112/erdkunde.2009.04.03>
- Fuentes M (1994) Diets of fruit-eating birds: what are the causes of interspecific differences? *Oecologia* 97:134–142. <https://doi.org/10.1007/BF00317917>

- Galetti M, Guevara R, Côrtes MC et al (2013) Functional extinction of birds drives rapid evolutionary changes in seed size. *Science* 340:1086–1090.  
<https://doi.org/10.1126/science.1233774>
- Gallagher RV, Leishman MR (2012) A global analysis of trait variation and evolution in climbing plants. *J Biogeogr* 39:1757–1771. <https://doi.org/j.1365-2699.2012.02773.x>
- Givnish TJ (1987) Comparative studies of leaf form: assessing the relative roles of selective pressures and phylogenetic constraints. *New Phytol* 106:131–160.  
<https://doi.org/10.1111/j.1469-8137.1987.tb04687.x>
- Givnish TJ (1984) Leaf and canopy adaptations in tropical forests. In: Medina E, Mooney H, Vázquez-Yanes C. (eds), *Physiological ecology of plants of the wet tropics*, Springer, Dordrecht, pp 51–84.
- Harper JL, Lovell PH, Moore KG (1970) The shapes and sizes of seeds. *Annu Rev Ecol Syst* 1:327–356. <https://doi.org/10.1146/annurev.es.01.110170.001551>
- Herrera CM (1981) Are tropical fruits more rewarding to dispersers than temperate ones? *Am Nat* 118:896–907. <https://doi.org/10.1086/283882>
- Holm S (1979) A simple sequentially rejective multiple test procedure. *Scand J Stat* 6:65–70. <https://doi.org/10.2307/4615733>
- Homeier J, Seeler T, Pierick K, Leuschner C (2021) Leaf trait variation in species-rich tropical Andean forests. *Sci Rep* 11:1–11. <https://doi.org/10.1038/s41598-021-89190-8>
- Homeier J, Werner FA, Gradstein SR, Breckle SW, Richter M (2008) Potential vegetation and floristic composition of Andean forests in South Ecuador, with a focus on the RBSF. In: Beck E, Bendix J, Kottke I, Makeschin F, Mosandl R. (eds), *Gradients in a Tropical Mountain Ecosystem of Ecuador*, 1st edn, Springer, Heidelberg, pp 87–100.
- Howe HF (1993) Specialized and generalized dispersal systems: where does “the paradigm” stand? *Vegetatio* 107:3–13. <https://doi.org/10.1007/BF00052208>
- Howe HF, Smallwood J (1982) Ecology of seed dispersal. *Annu Rev Ecol Evol Syst* 13:201–228. <https://doi.org/10.1146/annurev.es.13.110182.001221>
- Janzen DH (1970) Herbivores and the number of tree species in tropical forests. *Am Nat* 104:501–528. <https://doi.org/10.1086/282687>

- Jin Y, Qian H (2022) V. PhyloMaker2: An updated and enlarged R package that can generate very large phylogenies for vascular plants. *Plant Divers* 44:335-339. <https://doi.org/10.1016/j.pld.2022.05.005>
- Kaspari M, García MN, Harms KE, Santana M, Wright SJ, Yavitt JB (2007) Multiple nutrients limit litterfall and decomposition in a tropical forest. *Ecol Lett* 11:35–43. <https://doi.org/10.1111/j.1461-0248.2007.01124.x>
- Kembel SW, Cowan PD, Helmus MR et al (2010) Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26:1463–1464. <https://doi.org/10.1093/bioinformatics/btq166>
- Kleiman D, Aarssen LW (2007) The leaf size/number trade-off in trees. *J Ecol* 95:376–382. <https://doi.org/10.1111/j.1365-2745.2006.01205.x>
- Laliberte E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91:299–305. <https://doi.org/10.1890/08-2244.1>
- Lamarre GPA, Baraloto C, Fortunel C et al (2012) Herbivory, growth rates, and habitat specialization in tropical tree lineages: implications for Amazonian beta-diversity. *Ecology* 93:S195–S210. <https://doi.org/10.1890/11-0397.1>
- Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the Holy Grail. *Funct Ecol* 16:545–556. <https://doi.org/10.1046/j.1365-2435.2002.00664.x>
- Lebrija-Trejos E, Pérez-García EA, Meave JA, Bongers F, Poorter L (2010) Functional traits and environmental filtering drive community assembly in a species-rich tropical system. *Ecology* 91:386–398. <https://doi.org/10.1890/08-1449.1>
- Llerena-Zambrano M, Ordoñez JC, Llambí LD, van der Sande M, Pinto E, Salazar L, Cuesta F (2021) Minimum temperature drives community leaf trait variation in secondary montane forests along a 3000-m elevation gradient in the tropical Andes. *Plant Ecol Divers* 14:47–63. <https://doi.org/10.1080/17550874.2021.1903604>
- Madani N, Kimball JS, Ballantyne AP et al (2018) Future global productivity will be affected by plant trait response to climate. *Sci Rep* 8:1–10. <https://doi.org/10.1038/s41598-018-21172-9>
- Metcalf DB, Asner GP, Martin RE et al (2014) Herbivory makes major contributions to ecosystem carbon and nutrient cycling in tropical forests. *Ecol Lett* 17:324–332. <https://doi.org/10.1111/ele.12233>

- Minor DM, Kobe RK (2019) Fruit production is influenced by tree size and size-asymmetric crowding in a wet tropical forest. *Ecol Evol* 9:1458–1472. <https://doi.org/10.1002/ece3.4867>
- Moles AT, Falster DS, Leishman MR, Westoby M (2004) Small-seeded species produce more seeds per square metre of canopy per year, but not per individual per lifetime. *J Ecol* 92:384–396. <https://doi.org/10.1111/j.0022-0477.2004.00880.x>
- Moles AT, Perkins SE, Laffan SW et al (2014) Which is a better predictor of plant traits: temperature or precipitation? *J Veg Sci* 25:1167–1180. <https://doi.org/10.1111/jvs.12190>
- Moles AT, Westoby M (2000) Do small leaves expand faster than large leaves, and do shorter expansion times reduce herbivore damage? *Oikos* 90:517–524. <https://doi.org/10.1034/j.1600-0706.2000.900310.x>
- Moles AT, Westoby M (2006) Seed size and plant strategy across the whole life cycle. *Oikos* 113:91–105. <https://doi.org/10.1111/j.0030-1299.2006.14194.x>
- Mommer L, Weemstra M (2012) The role of roots in the resource economics spectrum. *New Phytol* 195:725–727. <https://doi.org/10.1111/j.1469-8137.2012.04247.x>
- Oliveras I, Bentley L, Fyllas et al (2020) The Influence of taxonomy and environment on leaf trait variation along tropical abiotic gradients. *Front For Glob Change* 3:18. <https://doi.org/10.3389/ffgc.2020.00018>
- Paradis E, Schliep K (2019). *ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R*. *Bioinformatics* 35:526–528. <https://doi.org/10.1093/bioinformatics/bty633>
- Pavoine S, Vela E, Gachet S, De Bélair G, Bonsall MB (2011) Linking patterns in phylogeny, traits, abiotic variables and space: a novel approach to linking environmental filtering and plant community assembly. *J Ecol* 99:165–175. <https://doi.org/10.1111/j.1365-2745.2010.01743.x>
- Pavoine S (2020) *adiv: An R package to analyse biodiversity in ecology*. *Methods Ecol Evol* 11:1106–1112. <https://doi.org/10.1111/2041-210X.13430>
- Pérez-Harguindeguy N, Díaz S, Garnier E et al (2013) New handbook for standardised measurement of plant functional traits worldwide. *Aust J Bot* 61:167–234. <https://doi.org/10.1071/BT12225>

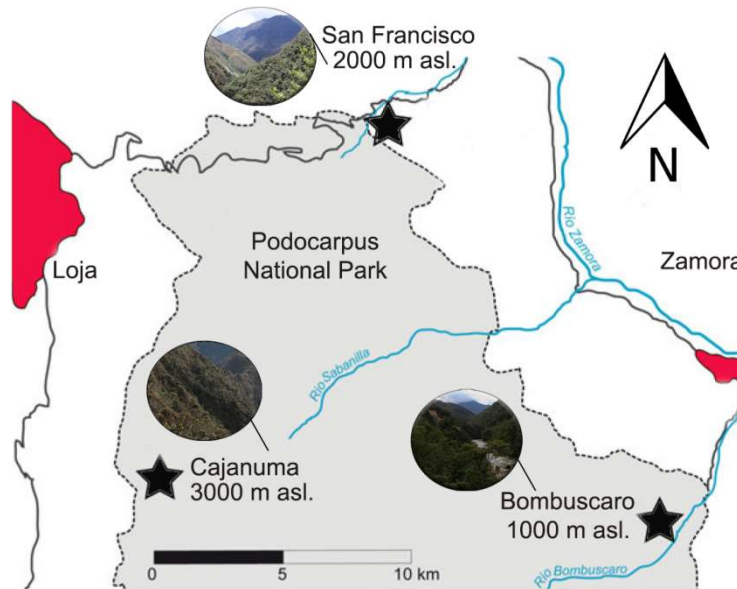
- Poorter H, Niinemets Ü, Poorter L, Wright IJ, Villar R (2009) Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytol* 182:565–588. <https://doi.org/10.1111/j.1469-8137.2009.02830.x>
- Post WM, Pastor J, Zinke PJ, Stangenberger AG (1985) Global patterns of soil nitrogen storage. *Nature* 317:613–616. <https://doi.org/10.1038/317613a0>
- Quitíán M, Santillán V, Espinosa CI, Homeier J, Böhning-Gaese K, Schleuning M, Neuschulz EL (2019) Direct and indirect effects of plant and frugivore diversity on structural and functional components of fruit removal by birds. *Oecologia* 189:435–445. <https://doi.org/10.1007/s00442-018-4324-y>
- R Core Team (2021) R: A language and environment for statistical computing. Available at <http://www.R-project.org>.
- Reich PB (2014) The world-wide “fast-slow” plant economics spectrum: A traits manifesto. *J Ecol* 102:275–301. <https://doi.org/10.1111/1365-2745.12211>
- Reich PB, Ellsworth DS, Walters MB, Vose JM, Gresham C, Volin JC, Bowman WD (1999) Generality of leaf trait relationships: A test across six biomes. *Ecology* 80:1955–1969. [https://doi.org/10.1890/0012-9658\(1999\)080\[1955:GOLTRA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[1955:GOLTRA]2.0.CO;2)
- Reich PB, Oleksyn J (2004) Global patterns of plant leaf N and P in relation to temperature and latitude. *Proc Natl Acad Sci USA* 101:11001–11006. <https://doi.org/10.1073/pnas.0403588101>
- Reich PB, Walters MB, Ellsworth DS (1997) From tropics to tundra: Global convergence in plant functioning. *Proc Natl Acad Sci USA* 94:13730–13734. <https://doi.org/10.1073/pnas.94.25.13730>
- Revell LJ (2012) phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol Evol* 3:217–223. <https://doi.org/10.1111/j.2041-210X.2011.00169.x>
- Revelle W (2022) psych: procedures for psychological, psychometric, and personality research. Available at <https://cran.rstudio.org/web/packages/psych/psych.pdf>
- Ribeiro S, Pimenta H, Fernandes G (1994) Herbivory by chewing and sucking insects on *Tabebuia ochracea*. *Biotropica* 26:302–307. <https://doi.org/10.2307/2388851>
- Rollenbeck R, Bendix J (2011) Rainfall distribution in the Andes of southern Ecuador derived from blending weather radar data and meteorological field observations. *Atmos Res* 99:277–289. <https://doi.org/10.1016/j.atmosres.2010.10.018>

- Rosbakh S, Chalmandrier L, Phartyal S, Poschlod P (2022). Inferring community assembly processes from functional seed trait variation along elevation gradient. *J Ecol* 110:2374–2387. <https://doi.org/10.1111/1365-2745.13955>
- Ruiz-Guerra B, García A, Velázquez-Rosas N, Angulo D, Guevara R (2021) Plant-functional traits drive insect herbivory in a tropical rainforest tree community. *Perspect Plant Ecol Evol Syst* 48:125587. <https://doi.org/10.1016/j.ppees.2020.125587>
- Saatkamp A, Cochrane A, Commander L et al (2019) A research agenda for seed-trait functional ecology. *New Phytol* 221:1764–1775. <https://doi.org/10.1111/nph.15502>
- Sakschewski B, Von Bloh W, Boit A et al (2016) Resilience of Amazon forests emerges from plant trait diversity. *Nat Clim Chang* 6:1032–1036. <https://doi.org/10.1038/nclimate3109>
- Schaefer HM, Schmidt V, Winkler H (2003) Testing the defence trade-off hypothesis: How contents of nutrients and secondary compounds affect fruit removal. *Oikos* 102:318–328. <https://doi.org/10.1034/j.1600-0706.2003.11796.x>
- Swenson NG, Enquist BJ (2007) Ecological and evolutionary determinants of a key plant functional trait: Wood density and its community-wide variation across latitude and elevation. *Am J Bot* 94:451–459. <https://doi.org/10.3732/ajb.94.3.451>
- Tovar C, Melcher I, Kusumoto B et al (2020) Plant dispersal strategies of high tropical alpine communities across the Andes. *J Ecol* 108:1910–1922. <https://doi.org/10.1111/1365-2745.13416>
- Velescu A, Fabian T, Wilcke W (2020a) Chemical properties of forest and pasture soils in Bombuscaro at 1000 m asl. Available at [http://vhrz669.hrz.uni-marburg.de/tmf\\_respect/data\\_pre.do?citid=1867](http://vhrz669.hrz.uni-marburg.de/tmf_respect/data_pre.do?citid=1867)
- Velescu A, Fabian T, Wilcke W (2020b) Chemical properties of forest and pasture soils in Cajanuma at 3000 m asl. Available at [http://vhrz669.hrz.uni-marburg.de/tmf\\_respect/data\\_pre.do?citid=1869](http://vhrz669.hrz.uni-marburg.de/tmf_respect/data_pre.do?citid=1869)
- Velescu A, Fabian T, Wilcke W (2020c) Chemical properties of forest and pasture soils in San Francisco at 2000 m asl. Available at [http://vhrz669.hrz.uni-marburg.de/tmf\\_respect/data\\_pre.do?citid=1868](http://vhrz669.hrz.uni-marburg.de/tmf_respect/data_pre.do?citid=1868)
- Venable DL (1992) Size-number trade-offs and the variation of seed size with plant resource status. *Am Nat* 140:287–304. <https://doi.org/10.1086/285413>

- Vollstädt MGR, Ferger SW, Hemp A, Howell KM, Töpfer T, Böhning-Gaese K, Schleuning M (2017) Direct and indirect effects of climate, human disturbance and plant traits on avian functional diversity. *Glob Ecol Biogeogr* 26:963–972. <https://doi.org/10.1111/geb.12606>
- Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ (2002) Plant ecological strategies: Some leading dimensions of variation between species. *Annu Rev Ecol Sys* 33:125–159. <https://doi.org/10.1146/annurev.ecolsys.33.010802.150452>
- Wickham H, François R, Henry L, Müller K (2019) dplyr: A Grammar of Data Manipulation. R package version. Available at <https://dplyr.tidyverse.org/>
- Wilcke W, Velescu A, Leimer S, Blotevogel S, Alvarez P, Valarezo C (2020) Total organic carbon concentrations in ecosystem solutions of a remote tropical montane forest respond to global environmental change. *Glob Chang Biol* 26:6989–7005. <https://doi.org/10.1111/gcb.15351>
- Wright IJ, Ackerly DD, Bongers F et al (2007) Relationships among ecologically important dimensions of plant trait variation in seven neotropical forests. *Ann Bot* 99:1003–1015. <https://doi.org/10.1093/aob/mcl066>
- Wright IJ, Dong N, Maire V et al (2017) Global climatic drivers of leaf size. *Science* 357:917–921. <https://doi.org/10.1126/science.aal4760>
- Wright IJ, Reich PB, Westoby M et al (2004) The worldwide leaf economics spectrum. *Nature* 428:821–827. <https://doi.org/10.1038/nature02403>
- Yan Z, Li P, Chen Y, Han W, Fang J (2016) Nutrient allocation strategies of woody plants: An approach from the scaling of nitrogen and phosphorus between twig stems and leaves. *Sci Rep* 6:1–9. <https://doi.org/10.1038/srep20099>
- Zhao N, Yu G, Wang Q, Wang R, Zhang J, Liu C, He N (2020) Conservative allocation strategy of multiple nutrients among major plant organs: From species to community. *J Ecol* 108:267–278. <https://doi.org/10.1111/1365-2745.13256>
- Zvereva EL, Kozlov MV (2014) Effects of herbivory on leaf life span in woody plants: A meta-analysis. *J Ecol* 102:873–881. <https://doi.org/10.1111/1365-2745.12252>

## Supporting information

**Appendix Fig. A.1** Map of the study area located in the tropical mountains of southern Ecuador along an elevational gradient from 1000 to 3000 m a.s.l. The three main study locations are marked by black stars. The grey area corresponds to Podocarpus National Park, while red areas are showing the nearest cities.





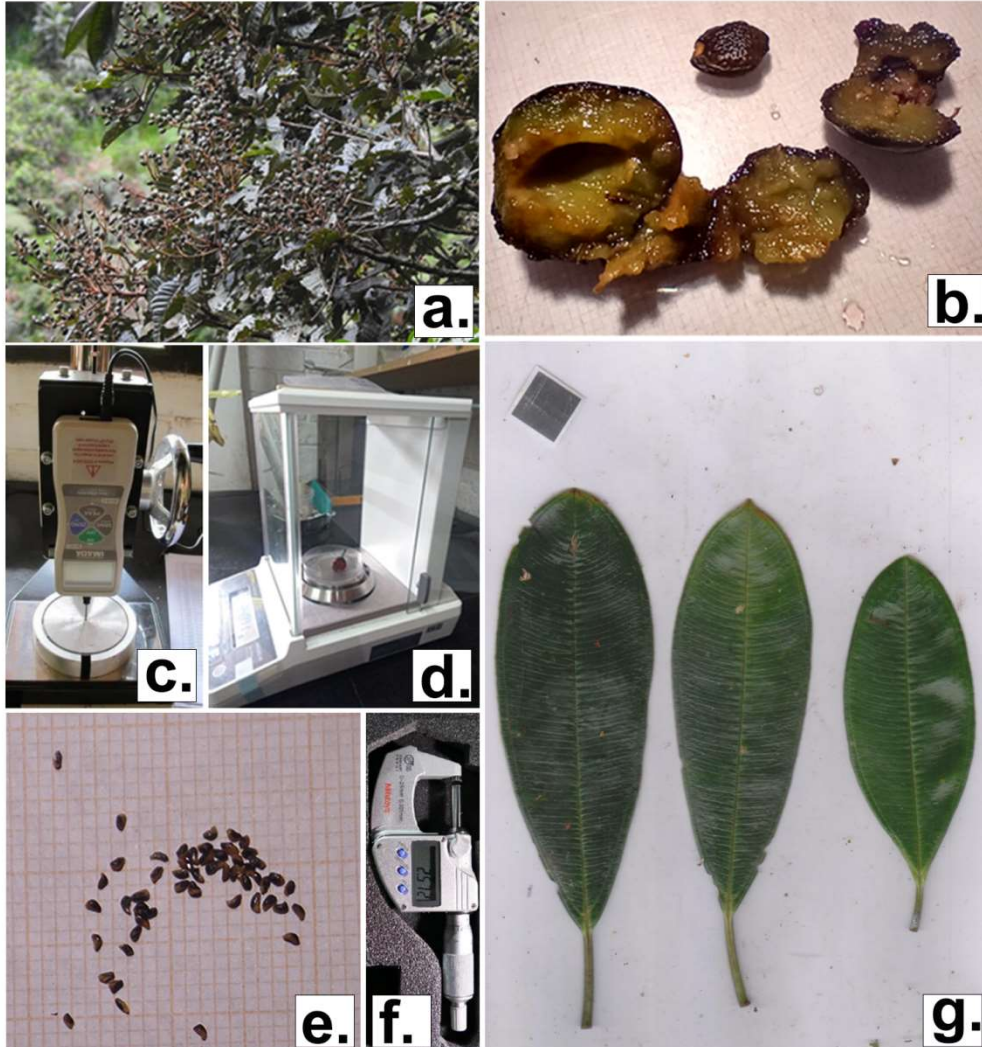
**Appendix Table B.2** Abiotic and biotic factors recorded at plot level in the tropical montane forests of southern Ecuador. Numbers represent mean values of the respective factor; fruit removal corresponds to the total number of removed fruits on a plot. Numbers in brackets indicate the lowest and highest records of the respective abiotic and biotic factor across sampled years (temperature, precipitation), soil samples (soil C/N) and animal-plant interactions (fruit removal and herbivory).

Elevation	Abiotic and biotic factors	Plots		
		BO1	BO2	BO3
1000 m a.s.l.	Annual precipitation (mm)	2195 (1965 - 2494)	2221 (1992 - 2514)	2240 (2013 - 2530)
	Annual mean temperature (°C)	19.5 (17.1 - 22.2)	19.4 (17 - 22.1)	19.3 (16.9 - 21.9)
	Soil C/N ratio	12 (11.50 - 12.60)	12.10 (12.01 - 12.25)	11.27 (10.30 - 11.86)
	Fruit removal	9210 (20 - 1200)	6400 (10 - 800)	8420 (40 - 1020)
	Mean herbivory rate	0.04 (0.00 - 0.86)	0.04 (0.00 - 0.93)	0.04 (0.00 - 0.94)
2000 m a.s.l.	Annual precipitation (mm)	2037 (1728 - 2175)	2121 (1776 - 2281)	2229 (1904 - 2379)
	Annual temperature (°C)	15.4 (7.8 - 27)	15.3 (7.7 - 26.9)	15.7 (8.1 - 27.3)
	Soil C/N ratio	19.59 (17.36 - 21.45)	17.09 (15.16 - 18.92)	14.45 (12.66 - 15.88)
	Fruit removal	3640 (20 - 600)	4400 (10 - 800)	6880 (10 - 1520)
	Mean herbivory rate	0.04 (0.00 - 0.66)	0.04 (0.00 - 0.58)	0.04 (0.00 - 0.89)
3000 m a.s.l.	Annual precipitation (mm)	2722 (1921 - 3411)	2710 (1913 - 3391)	2797 (2000 - 3557)
	Annual temperature (°C)	10.3 (7 - 12.9)	10.4 (7.1 - 13)	10 (6.7 - 12.5)
	Soil C/N ratio	14.58 (13.86 - 15.20)	15.29 (14.33 - 16.41)	13.57 (12.79 - 14.47)
	Fruit removal	3440 (20 - 1400)	1100 (20 - 300)	1760 (30 - 1000)
	Mean herbivory rate	0.03 (0.00 - 0.68)	0.02 (0.00 - 0.70)	0.03 (0.00 - 0.54)

**Appendix Table C.3** Relative tree abundance of the 36 fleshy-fruited tree species of which we measured seed and fruit traits (SF) and leaf traits (L) traits in the tropical montane forests of southern Ecuador. Values correspond to the proportion of trees per species, expressed as a percentage of the total number of trees recorded per plot.

Family	Species	Traits	Relative tree abundance per plot (%)		
			Plot 1	Plot 2	Plot 3
1000 m a.s.l.					
Euphorbiaceae	<i>Alchornea cf. glandulosa</i>	(L)	8.2	6.2	0.9
Clusiaceae	<i>Chrysochlamys cf. membranacea</i>	(S/F - L)	0.4	0.4	1.5
Moraceae	<i>Clarisia racemosa</i>	(L)	0.9	3.1	3.1
Lecythidaceae	<i>Grias peruviana</i>	(L)	0.2	0.0	2.0
Annonaceae	<i>Guatteria pastazae</i>	(S/F - L)	1.8	0.7	0.0
Phyllanthaceae	<i>Hieronyma oblonga</i>	(S/F - L)	2.0	0.0	0.2
Violaceae	<i>Leonia crassa</i>	(L)	0.4	2.4	4.8
Melastomataceae	<i>Miconia aff. punctata</i>	(S/F - L)	6.2	0.2	0.2
Lauraceae	<i>Ocotea sp.</i>	(S/F - L)	0.2	0.2	4.4
Myristicaceae	<i>Otoba parvifolia</i>	(L)	0.9	2.9	6.3
Urticaceae	<i>Pourouma cecropiifolia</i>	(L)	1.1	0.2	0.0
Sapotaceae	<i>Pouteria torta</i>	(L)	4.4	0.2	0.0
Moraceae	<i>Pseudolmedia laevis</i>	(L)	0.7	1.0	2.6
Actinidiaceae	<i>Saurauia sp.</i>	(L)	0.7	9.6	0.0
Meliaceae	<i>Guarea macrophylla</i>	(S/F)	0.7	0.2	4.4
6 sampled species with seed and fruit traits			11.3	1.7	10.7
14 sampled species with leaf traits			28.0	27.2	25.9
2000 m a.s.l.					
Euphorbiaceae	<i>Alchornea lojaensis</i>	(L)	4.5	3.2	0.0
Urticaceae	<i>Cecropia angustifolia</i>	(L)	0.0	0.7	2.9
Clusiaceae	<i>Clusia ducuoides</i>	(S/F - L)	1.1	4.1	0.0
Chloranthaceae	<i>Hedyosmum cf. goudotianum</i>	(S/F - L)	3.8	4.4	1.1
Phyllanthaceae	<i>Hieronyma fendleri</i>	(S/F - L)	9.7	7.7	0.4
Melastomataceae	<i>Miconia calophylla</i>	(S/F - L)	2.4	1.4	0.0
Myrtaceae	<i>Myrcia sp.</i>	(L)	0.9	1.6	0.0
Primulaceae	<i>Myrsine coriacea</i>	(L)	3.7	1.2	0.0
Moraceae	<i>Naucleopsis francisci</i>	(L)	0.4	3.3	0.0
Lauraceae	<i>Ocotea andina</i>	(S/F - L)	3.1	3.2	0.0
Podocarpaceae	<i>Podocarpus oleifolius</i>	(L)	4.0	2.1	0.1
Sapindaceae	<i>Matayba inelegans</i>	(S/F)	3.8	4.4	0.0
Anacardiaceae	<i>Tapirira guianensis subandina</i>	(S/F)	0.9	1.3	1.5
7 sampled species with seed and fruit traits			24.7	26.6	2.9
11 sampled species with leaf traits			38.1	38.7	5.9
3000 m a.s.l.					
Lauraceae	<i>Aiouea dubia</i>	(L)	1.2	0.1	1.2
Clusiaceae	<i>Clusia elliptica</i>	(S/F - L)	2.5	2.8	1.2
Chloranthaceae	<i>Hedyosmum purpurascens</i>	(S/F - L)	5.5	4.1	3.5
Aquifoliaceae	<i>Ilex laurina</i>	(S/F - L)	4.9	1.0	1.9
Melastomataceae	<i>Miconia cf. jahnii</i>	(S/F - L)	1.3	2.5	0.0
Lauraceae	<i>Ocotea rotundata</i>	(L)	1.7	0.1	0.4
Araliaceae	<i>Oreopanax sessiliflorus</i>	(L)	1.9	0.3	1.9
Siparunaceae	<i>Siparuna muricata</i>	(S/F - L)	1.4	0.0	1.3
5 sampled species with seed and fruit traits			15.7	10.4	7.9
8 sampled species with leaf traits			20.5	10.9	11.4

**Appendix Fig. D.4** Measuring seed, fruit and leaf traits of fleshy-fruited plant species in the tropical montane forests of southern Ecuador. (a) Unripe fruits of *Tapirira guianensis subandina* recorded in the fruiting phenology monitoring. (b) Dissection of a ripe fruit of *Guatteria pastazae* with a unique seed before measuring seed and pulp fresh mass. (c) Digital penetrometer (2.0 mm diameter) used to calculate leaf toughness. (d) Measuring fruit fresh mass of *Matayba inelegans*. (e) Seed number of one fruit of *Miconia cf. jahnii*. (f) Digital micrometer used to measure leaf thickness. (g) Scanned leaves of *Miconia calophylla* used to calculate leaf area.



**Appendix Table E.5** Sample size (n), mean and standard deviation of the seed and fruit traits measured on 18 fleshy-fruited tree species in the tropical montane forests of southern Ecuador. In the sample size column, the first value represents the number of individual trees used to measure crop size, seed fresh mass, pulp fresh mass, seed number and the relative yield index. The second value of the sample size column refers to the number of individual trees used for the chemical analyses to obtain carbon and nitrogen concentrations in the seeds and pulps.

Species	n	Crop size	Seed fresh mass (g)	Pulp fresh mass (g)	Seed number	Seed C/N ratio	Pulp C/N ratio	Relative yield index
1000 m a.s.l.								
<i>Chrysochlamys membranacea</i>	6,3	80.5 ± 22.8	0.065 ± 0.030	0.358 ± 0.626	1.3 ± 0.4	30.7 ± 2.8	38.2 ± 16.1	0.004 ± 0.001
<i>Guarea macrophylla</i>	2,2	312 ± 124.5	0.319 ± 0.036	0.065 ± 0.000	3.6 ± 0.3	20.0 ± 0.2	27.7 ± 7.9	0.004 ± 0.001
<i>Guatteria pastazae</i>	4,3	332 ± 223.5	0.164 ± 0.028	1.433 ± 0.711	1.0 ± 0.0	27.9 ± 1.4	29.4 ± 3.1	0.114 ± 0.009
<i>Hieronyma oblonga</i>	1,1	120	0.008	0.002	1.0	41.7	17.2	0.039
<i>Miconia aff. punctata</i>	5,3	771.2 ± 493.8	0.003 ± 0.001	0.032 ± 0.011	3.2 ± 0.9	56.0 ± 26.1	27.9 ± 1.6	0.201 ± 0.049
<i>Ocotea sp.</i>	1,1	550	0.527	0.405	1.0	39.6	30.4	0.171
2000 m a.s.l.								
<i>Clusia ducuoides</i>	5,3	1462.4 ± 488.7	0.005 ± 0.000	0.007 ± 0.003	3.1 ± 1.9	17.9 ± 2.8	75.8 ± 9.7	0.011 ± 0.002
<i>Hedyosmum cf. goudotianum</i>	5,3	160.6 ± 110.8	0.008 ± 0.001	0.324 ± 0.116	3.0 ± 0.3	28.6 ± 3.5	52.8 ± 5.3	0.074 ± 0.009
<i>Hieronyma fendleri</i>	5,3	13263 ± 12317	0.028 ± 0.004	0.04 ± 0.021	1.0 ± 0.0	161.2 ± 18.1	33.1 ± 6.8	0.051 ± 0.008
<i>Matayba inelegans</i>	2,2	360 ± 339.4	0.426 ± 0.229	0.351 ± 0.07	1.1 ± 0.2	24.5 ± 0.1	15.4 ± 0.9	0.015 ± 0.001
<i>Miconia calophylla</i>	3,3	2536.333 ± 1908	0.00007 ± 0.00001	0.023 ± 0.005	48.4 ± 27.3	22.2 ± 1.2	36.1 ± 4.5	0.098 ± 0.04
<i>Ocotea andina</i>	1,1	886	4.397	4.733	1.0	57.3	45.6	0.135
<i>Tapirira guianensis subandina</i>	5,3	150 ± 131.9	0.266 ± 0.033	0.662 ± 0.179	1.0 ± 0.0	81.9 ± 37.7	33.9 ± 9.3	0.132 ± 0.032
3000 m a.s.l.								
<i>Clusia elliptica</i>	1,1	252	0.019	0.111	11.6	19.5	37.4 ± 0.0	0.015
<i>Hedyosmum purpurascens</i>	5,3	10769.4 ± 21444.5	0.007 ± 0.001	0.378 ± 0.135	4.1 ± 0.4	20.7 ± 0.0	45.2 ± 8.6	0.134 ± 0.031
<i>Ilex laurina</i>	2,2	633 ± 80.6	0.005 ± 0.001	0.02 ± 0.001	3.4 ± 0.3	46.703 ± 27.993	45.118 ± 6.232	0.132 ± 0.002
<i>Miconia cf. jahnii</i>	5,3	442 ± 281.2	0.0002 ± 0.00005	0.016 ± 0.016	39.9 ± 7.0	60.9 ± 62.6	35.4 ± 3.0	0.189 ± 0.062
<i>Siparuna muricata</i>	4,3	265 ± 145.2	0.025 ± 0.000	0.01 ± 0.001	1.7 ± 0.5	19.3 ± 2.1	77.5 ± 50.6	0.005 ± 0.001

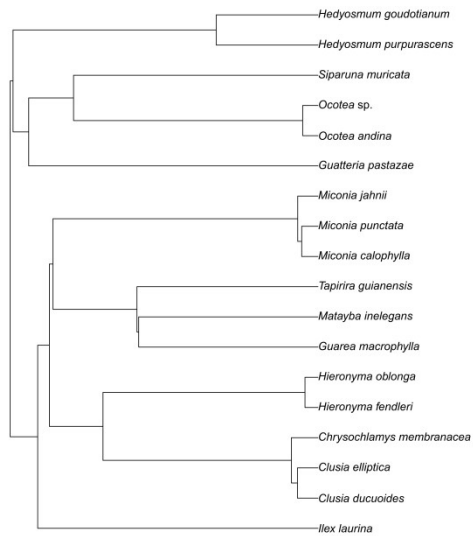
**Appendix Table F.6** Sample size, mean and standard deviation of leaf traits measured on 33 fleshy-fruited tree species in the tropical montane forests of southern Ecuador.

Species	n	Thickness (mm)	Toughness (kN m <sup>-1</sup> )	Leaf area (cm <sup>2</sup> )	Specific leaf area (cm <sup>2</sup> g <sup>-1</sup> )	Leaf C/N ratio
1000 m a.s.l.						
<i>Alchornea cf. glandulosa</i>	9	0.11 ± 0.02	0.66 ± 0.08	72.27 ± 11.57	164.52 ± 21.22	17.53 ± 0.61
<i>Chrysochlamys cf. membranacea</i>	8	0.43 ± 0.03	1.15 ± 0.06	167.80 ± 33.92	100.99 ± 14.08	29.35 ± 2.18
<i>Clarisia racemosa</i>	8	0.17 ± 0.02	1.00 ± 0.05	39.36 ± 11.44	119.29 ± 16.33	20.17 ± 1.53
<i>Grias peruviana</i>	8	0.22 ± 0.02	2.00 ± 0.14	353.23 ± 72.16	72.83 ± 7.99	28.96 ± 2.46
<i>Guatteria pastazae</i>	6	0.22 ± 0.02	0.93 ± 0.18	94.33 ± 21.01	97.98 ± 14.86	27.94 ± 2.80
<i>Hieronyma oblonga</i>	8	0.24 ± 0.03	0.50 ± 0.05	65.77 ± 21.70	133.01 ± 17.87	24.27 ± 1.57
<i>Leonia crassa</i>	8	0.28 ± 0.02	0.98 ± 0.12	183.81 ± 48.78	93.94 ± 9.39	22.08 ± 2.05
<i>Miconia aff. punctata</i>	8	0.28 ± 0.03	0.54 ± 0.04	100.75 ± 21.50	96.10 ± 11.61	20.87 ± 1.12
<i>Ocotea sp.</i>	8	0.30 ± 0.03	0.67 ± 0.05	235.37 ± 19.85	101.09 ± 16.90	21.49 ± 1.97
<i>Otoba parvifolia</i>	8	0.32 ± 0.05	0.87 ± 0.08	97.37 ± 20.18	98.46 ± 12.12	30.76 ± 2.84
<i>Pourouma cecropiifolia</i>	6	0.21 ± 0.01	0.85 ± 0.07	1632.01 ± 713.03	81.49 ± 12.43	25.12 ± 3.08
<i>Pouteria torta</i>	8	0.17 ± 0.03	0.81 ± 0.13	75.43 ± 10.70	86.02 ± 16.68	32.15 ± 3.90
<i>Pseudolmedia laevis</i>	8	0.16 ± 0.03	0.59 ± 0.10	54.15 ± 12.79	127.28 ± 32.38	22.41 ± 1.55
<i>Saurauia sp.</i>	8	0.21 ± 0.05	0.53 ± 0.10	239.50 ± 81.42	129.13 ± 27.65	23.68 ± 2.01
2000 m a.s.l.						
<i>Alchornea lojaensis</i>	*9	0.48 ± 0.06	1.60 ± 0.21	34.78 ± 22.82	47.62 ± 12.57	35.95 ± 5.87
<i>Cecropia angustifolia</i>	10	0.28 ± 0.02	0.71 ± 0.06	1354.33 ± 541.20	60.14 ± 6.24	22.91 ± 2.91
<i>Clusia ducoides</i>	*8	0.53 ± 0.06	1.29 ± 0.12	22.25 ± 5.75	60.39 ± 4.20	39.96 ± 2.16
<i>Hedyosmum cf. goudotianum</i>	*8	0.38 ± 0.04	0.82 ± 0.08	41.01 ± 8.52	88.52 ± 12.23	25.26 ± 2.26
<i>Hieronyma fendleri</i>	9	0.32 ± 0.02	0.75 ± 0.06	22.8 ± 4.84	95.79 ± 35.89	32.17 ± 1.88
<i>Miconia calophylla</i>	8	0.34 ± 0.03	0.97 ± 0.09	52.68 ± 11.19	61.56 ± 5.28	37.60 ± 3.25
<i>Myrcia sp.</i>	8	0.48 ± 0.06	1.47 ± 0.12	37.80 ± 38.93	44.53 ± 3.94	46.66 ± 2.92
<i>Myrsine coriacea</i>	8	0.32 ± 0.06	0.85 ± 0.11	15.40 ± 2.40	69.46 ± 12.73	46.39 ± 11.34
<i>Naucleopsis francisci</i>	9	0.35 ± 0.04	1.65 ± 0.30	57.54 ± 15.51	50.28 ± 6.40	24.68 ± 1.16
<i>Ocotea andina</i>	9	0.36 ± 0.04	1.47 ± 0.12	101.69 ± 23.02	52.28 ± 5.59	32.62 ± 3.06
<i>Podocarpus oleifolius</i>	9	0.32 ± 0.03	2.25 ± 0.36	6.72 ± 2.82	66.32 ± 13.96	39.97 ± 4.97
3000 m a.s.l.						
<i>Aiouea dubia</i>	8	0.34 ± 0.04	1.32 ± 0.20	17.22 ± 8.70	58.23 ± 6.16	28.16 ± 3.33
<i>Clusia elliptica</i>	8	0.60 ± 0.05	1.64 ± 0.27	22.93 ± 8.05	41.46 ± 7.68	49.37 ± 5.78
<i>Hedyosmum purpurascens</i>	8	0.44 ± 0.04	0.99 ± 0.06	13.82 ± 3.41	72.50 ± 8.91	24.21 ± 1.98
<i>Illex laurina</i>	8	0.35 ± 0.05	1.06 ± 0.12	11.89 ± 2.91	53.07 ± 6.65	44.28 ± 4.82
<i>Miconia cf. jahnii</i>	*8	0.50 ± 0.08	1.41 ± 0.38	13.62 ± 3.90	39.72 ± 11.72	41.23 ± 6.09
<i>Ocotea rotundata</i>	8	0.43 ± 0.05	1.74 ± 0.27	29.66 ± 6.00	49.43 ± 7.57	36.33 ± 14.56
<i>Oreopanax sessiliflorus</i>	8	0.39 ± 0.04	1.27 ± 0.11	34.97 ± 12.87	54.77 ± 8.13	31.32 ± 3.07
<i>Siparuna muricata</i>	8	0.29 ± 0.02	0.39 ± 0.04	41.98 ± 27.49	86.99 ± 13.57	15.68 ± 2.00

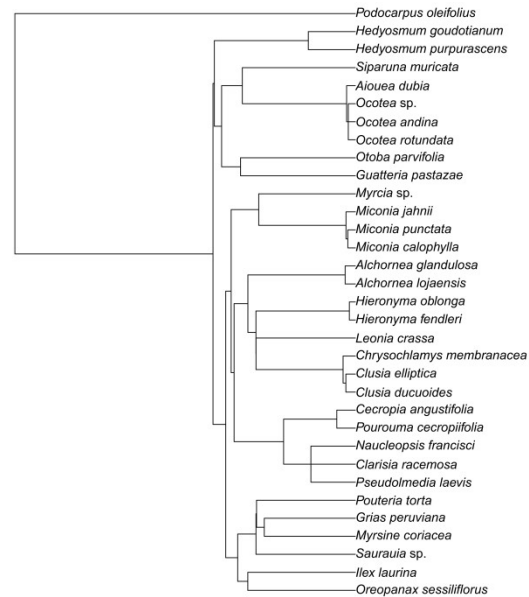
\* SLA was measured on 7 individuals of *Clusia ducoides*, Leaf C/N ratio was measured on 8 individuals of *Alchornea lojaensis*, and 7 individuals of *Miconia cf. jahnii*

**Appendix Fig. G.7** Phylogenetic trees for (a) 18 and (b) 33 fleshy-fruited plant species studied in southern Ecuador. Phylogenetic trees were built based on the dated mega-tree implemented in V.PhyloMaker (i.e. GBOTB. extended.tre). Plant species nomenclature was updated following the Leipzig Catalogue for Vascular Plants (Freiberg et al. 2020) using the R packages lcplants (Freiberg et al. 2020) and LCVP (Freiberg et al. 2020). For editing the phylogenetic trees, we additionally used the R packages ape (Paradis et al. 2004), phytools (Revell, 2012), and V.PhyloMaker2 (Jin & Qian 2022).

(a) Fleshy-fruited plant species with seed/fruit traits



(b) Fleshy-fruited plant species with leaf traits



## **Appendix 8. Abstract in Spanish**

### **Los factores abióticos determinan de forma similar la distribución de los rasgos de los frutos, las semillas y las hojas en las comunidades tropicales con frutos dispersados por animales**

**Preguntas:** La variabilidad en la distribución de los rasgos funcionales de las plantas está asociada tanto al entorno abiótico como al biótico. La identificación de los principios generales de cómo los rasgos de las plantas y los factores ambientales covarían es clave para desarrollar una comprensión mecanicista de la estructura de la comunidad, especialmente en los ecosistemas tropicales ricos en especies. Nosotros estudiamos simultáneamente los rasgos de los frutos, las semillas y las hojas de las comunidades arbóreas en un punto caliente de biodiversidad tropical. Nuestro objetivo era identificar las principales estrategias ecológicas en la comunidad de especies arbóreas de frutos dispersados por animales y preguntar cómo estas estrategias relacionadas con los rasgos se asociaban con la variación de los factores abióticos y bióticos.

**Ubicación:** Bosques montanos maduros a lo largo de un gradiente de elevación que va desde 1000 hasta 3000 m.s.n.m., Parque Nacional Podocarpus y Reserva San Francisco, al sur de la cordillera de Los Andes en Ecuador.

**Métodos:** Se midieron siete rasgos funcionales de semilla/fruto y cinco rasgos de hoja para 18 y 33 especies de árboles de fruto carnoso, respectivamente. Para cada una de estas especies de plantas, registramos su presencia y abundancia en nueve parcelas de bosque de 1 ha situadas a 1.000, 2.000 y 3.000 m de altitud. En las mismas parcelas, se midieron factores abióticos, como las propiedades del suelo (relación C/N del suelo) y las condiciones climáticas (temperatura, precipitaciones), y se registraron factores bióticos relevantes, como la frecuencia en la remoción de frutos por parte de las aves y la herbivoría. Se realizaron análisis de componentes principales y RLQ para identificar los principales ejes de variación de los rasgos funcionales y la covariación entre los rasgos funcionales de las plantas y los factores abióticos y bióticos, controlando por la covariación filogenética y espacial entre especies y parcelas, respectivamente.

**Resultados:** Identificamos dos estrategias ecológicas principales basadas en los rasgos de las semillas y los frutos: (i) un compromiso entre el número y el tamaño de las semillas, y (ii) un compromiso entre la producción de frutos “costosos” (ricos en nitrógeno) frente a la producción de “frutos baratos” (ricos en carbono). Asimismo, identificamos dos estrategias principales basadas en los rasgos de las hojas: (i) una estrategia que diferencia entre hojas de corta vida (“adquisitivas”, ricas en nitrógeno) frente a hojas de larga vida (“conservadoras”, ricas en carbono), y (ii) otra estrategia en la que las plantas tienen hojas de tamaño pequeño o grande. Las distribuciones de los rasgos de las semillas, los frutos y las hojas se asociaron significativamente con el entorno abiótico y biótico, especialmente a lo largo de los primeros ejes RLQ. Las asociaciones entre estos rasgos de las plantas y el ambiente se confirmaron con un análisis RLQ ampliado que tuvo en cuenta la covariación filogenética entre especies vegetales y la autocorrelación espacial de las parcelas. Las estrategias ecológicas asociadas a la producción de frutos y hojas se relacionaron principalmente con la relación C/N del suelo, mientras que las estrategias asociadas al tamaño de las semillas, frutos y hojas se relacionaron con las precipitaciones.

**Conclusiones:** Nuestros resultados demuestran que las relaciones de los rasgos funcionales de las semillas, frutos y hojas con el ambiente abiótico siguen principios similares en las comunidades arbóreas tropicales. La identificación de estos principios generales en la forma en que los rasgos de las plantas covarían con los factores abióticos y bióticos puede aportar al desarrollo de modelos mecanicistas que permitan entender el cambio de la biodiversidad en ecosistemas tropicales muy diversos.



## **A2: Climate and microhabitat shape the prevalence of endozoochory in the seed rain of tropical montane forests**

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*Author contributions:*

(1) Concept and design

DCAR, 80%;

MS, ELN, in total 20%

(2) Field work/data collection:

DCAR set-up of seed traps along the elevational gradient, 50%; MB, 50%;

DCAR collected, categorized (taxonomically and in terms of seed dispersal mode) and measured of seeds, 100%;

DCAR prepared all data for analyses, 100%;

DCAR prepared all figures and tables, 100%.

MB measured microhabitat conditions, 100%.

MS, ELN contributed climatic data, 100%;

(3) Analysis and interpretation of data

DCAR tested hypotheses with generalized linear mixed effects models (GLMMs), 100%;

DCAR interpreted the results, 90%

with input from MB, CIE, BT, ELN, MS, in total 10%

(4) Drafting of manuscript

DCAR, 90%;

MS, ELN, in total 5%;

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## Climate and microhabitat shape the prevalence of endozoochory in the seed rain of tropical montane forests

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### Abstract

Endozoochory, the dispersal of seeds by animal ingestion, is the most dominant mode of seed dispersal in tropical forests and is a key process shaping current and future forest dynamics. However, it remains largely unknown how endozoochory is associated with environmental conditions at regional and local scales. Here, we investigated the effects of elevation, climate, and microhabitat conditions on the proportion of endozoochorous plant species in the seed rain of the tropical Andes of southern Ecuador. Over 1 year, we measured seed rain in 162 seed traps on nine 1-ha forest plots located at 1000, 2000, and 3000 m a.s.l. We recorded climatic conditions (mean annual temperature and rainfall) in each plot and microhabitat conditions (leaf area index and soil moisture) adjacent to each seed trap. In total, we recorded 331,838 seeds belonging to 323 morphospecies. Overall, the proportion of endozoochorous species in the seed rain decreased with elevation. The relative biomass of endozoochorous species decreased with increasing rainfall, whereas the relative seed richness of endozoochorous species increased with increasing temperature and leaf area index. These findings suggest an interplay between climate factors and microhabitat conditions in shaping the importance of endozoochorous plant species in the seed rain of tropical montane forests. We conclude that changing climatic and microhabitat conditions are likely to cause changes in the dominant dispersal modes of plant communities which may trigger changes in the current and future dynamics of tropical forests.

Abstract in Spanish is available with online material.

### KEYWORDS

animal seed dispersal, canopy structure, dispersal syndromes, leaf area index, rainfall, soil moisture, southern Ecuador, temperature

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## 1 | INTRODUCTION

Endozoochory is, by far, the most important dispersal mode worldwide with about 50% of woody plant species depending on fruit-eating animals for seed dispersal (Rogers et al., 2021). In tropical mountains, where biodiversity hotspots (Myers et al., 2000) and high vulnerability to environmental changes converge (Elsen & Tingley, 2015), the prevalence of endozoochory as a dispersal mode for woody plants can reach up to 70% (Buitrón-Jurado & Ramírez, 2014; Correa et al., 2015). Understanding how abiotic and biotic factors shape the prevalence of endozoochory in tropical montane forests is important for projecting the consequences of changing environmental conditions on ecological communities and ecosystem functioning in these vulnerable ecosystems (Bendix et al., 2021; Madani et al., 2018).

Seed dispersal by endozoochory plays an important role in several ecosystem processes. For instance, it influences the dynamics of plant populations such as avoiding negative density dependence (Howe & Smallwood, 1982; Janzen, 1970), reaching suitable microsites (Wenny, 2001), colonizing new habitats (Puerta-Piñero et al., 2013), and increasing the capacity of plants to track climate change (Fricke et al., 2022). Hence, seed dispersal by endozoochory is a key ecosystem service shaping the distribution of plant species, especially in tropical ecosystems (Aslan et al., 2019; Bello et al., 2015).

Endozoochory can be predicted from the morphological traits of seeds and fruits (Pérez-Harguindeguy et al., 2013; Rojas et al., 2022; van der Pijl, 1982). Endozoochorous plant species are characterized by thick-coated seeds inside edible fleshy fruits which are attractive to mutualistic animal partners (Snow, 1981; Stevenson et al., 2002). In contrast, in nonendozoochorous plant species, seed dispersal often depends on the attachment of seeds to animals' fur or on seed dispersal by abiotic factors such as wind, water, or gravity (Howe & Smallwood, 1982; van der Pijl, 1982). These plant species usually have dry diaspores and specific structures, such as hooked spines, arists, stiff hairs, or wings (Janson, 1983; Jara-Guerrero et al., 2011; Tovar et al., 2020; van der Pijl, 1982). Therefore, by studying the composition of seed and fruit morphological traits, it is possible to identify the main modes of seed dispersal in plant communities.

Plant species are more likely to bear fleshy fruits toward the tropics (Chen et al., 2017; vander Wall & Beck, 2012). In addition, the dominance of different seed dispersal modes can vary along elevational gradients in tropical ecosystems (Buitrón-Jurado & Ramírez, 2014). In the northern Andes, for example, the dominance of anemochorous (i.e., wind-dispersed) species increases with increasing elevation (Frantzen & Bouman, 1989; Melcher et al., 2000). Since elevational gradients reflect gradients in climatic conditions, the dominance of certain seed dispersal modes along elevations may be driven by abiotic factors. Indeed, different abiotic factors are associated with the proportion of plant species dispersed by animals. For instance, species with fleshy fruits and large seeds

are more common in wet forests than in dry forests (Almeida-Neto et al., 2008; Gentry, 1983; Tabarelli et al., 2003), corresponding to a general increase in endozoochory with increasing rainfall in the Neotropics (Correa et al., 2015). Despite this, the proportion of endozoochorous species was related to temperature rather than to rainfall in 64 Andean montane forests (Buitrón-Jurado & Ramírez, 2014). Generally, productive forest ecosystems with high rainfall and temperature appear to support more endozoochorous plant species given the high costs involved in the production of fleshy fruits (Bonte et al., 2012; Willson et al., 1989).

In addition to climatic factors, microhabitat conditions influence the distribution of plant species (Chanthorn et al., 2016; Stark et al., 2015) and also the seed deposition patterns of animal seed dispersers (García-Cervigón et al., 2018; Morán-López et al., 2020; Schupp et al., 2010). Within tropical forests, early and late successional plant species are favored by distinct microhabitat conditions related to canopy complexity and, to a lesser extent, to soil properties (Cheng et al., 2022). Wind-dispersed and light-demanding plant species are generally more abundant in early successional habitats (Tabarelli & Peres, 2002), characterized by an open canopy structure. These habitats can either be characterized by high soil moisture due to low rainfall interception and plant transpiration (Muscolo et al., 2014) or by low soil moisture due to high solar radiation and increased evaporation (Camargo & Kapos, 1995). On the contrary, endozoochory and seed size tend to increase in importance in late successional habitats (Bello et al., 2015). In these habitats, the canopy structure is more complex (Unger et al., 2013) and there may be high or low water retention in the soils (Camargo & Kapos, 1995; Muscolo et al., 2014). Variation between early and late successional habitats in fruit biomass and canopy complexity is also associated with habitat use and seed deposition patterns of frugivorous species, all of which affect the proportion of seeds dispersed to different habitats (Ferber et al., 2014; Holl, 1998; Hollander & Vander Wall, 2004; Loayza & Rios, 2014). So far, there are no studies testing how climate conditions at the large scale and microhabitat conditions at the small scale are related to the distribution of seed dispersal modes in the seed rain of tropical plant communities.

In this study, we investigated the importance of endozoochory in plant communities located along an elevational gradient in the tropical Andes in southern Ecuador. Based on seed rain data from 162 traps and across an entire year, we hypothesized that (a) the proportion of endozoochorous species in the seed rain of tropical montane forests decreases with increasing elevation because of the combined effects of high temperature and rainfall at low elevations that tend to favor fleshy-fruited species (Buitrón-Jurado & Ramírez, 2014); (b) endozoochory increases with increasing rainfall and temperature because productive environments support the high costs of producing fleshy fruits (Bonte et al., 2012; Willson et al., 1989); and finally, (c) a higher prevalence of endozoochory in microhabitats that favor late successional plant species with large seeds and endozoochorous seed dispersal (de Melo et al., 2006; Tabarelli & Peres, 2002).

2 | METHODS

2.1 | Study system

The study area was located in the Andes of southern Ecuador. This area is covered by mature forest along an elevational gradient ranging from 1000 to 3000 m a.s.l. Specifically, we established three study sites in Podocarpus National Park and San Francisco Reserve: (1) "Bombuscaro" around 1000 m a.s.l., located in the evergreen premontane forest (4°6' S, 78°58' W); (2) "San Francisco" around 2000 m a.s.l., located in the lower montane forest (3°58' S, 79°4' W); and (3) "Cajanuma" around 3000 m a.s.l., located in the upper montane forest (4°6' S, 79°10' W) (Homeier et al., 2008) (Figure 1a). The mean annual temperature decreases from 20 to 10°C with increasing elevation (Bendix et al., 2008), but temperature conditions are relatively stable throughout the year within each of the three study sites (see the monthly variation in temperature in Figure S1). Mean annual rainfall increases to up to 4500 mm/year at the upper montane forest, whereas rainfall is similarly high at mid (i.e., 2128.9 mm/year at 2000 m a.s.l.) and low elevations (i.e., 2218.6 mm/year at 1000 m a.s.l.) (Bendix et al., 2008; Emck, 2007). The entire study area is subject to constant rainfall throughout the entire year (see the monthly variation in rainfall in Figure S1). Given these patterns, temperature decreases with increasing rainfall along the elevational gradient ( $r = -.82, p < .0001$ ). At each elevation, we worked on three 1-ha plots (i.e., nine plots in total) established by the DFG research unit "Environmental changes in biodiversity hotspot ecosystems of South Ecuador: RESPONSE and feedback EFFECTs (FOR2730)" (more details in Bendix et al., 2021).

2.2 | Seed rain and seed dispersal modes

At each 1-ha plot, we installed 18 regularly spaced seed traps (trap area = 0.36 m<sup>2</sup>, 1.5 mm nylon mesh, Figure 1b,c). The traps were hanging at approximately 90 cm above the ground and the content of each trap was recovered every 15 days for a period of 1 year (January 2019–January 2020). The material collected in the traps was dried, and all intact dispersal units  $\geq 1$  mm in length were counted and identified to the lowest possible taxonomic level using reference plant material from the forest, field guides, and the help of botanical experts. We classified seeds as endozoochorous or nonendozoochorous species based on the evidence from scientific literature, the consultancy with experts, and seed morphology (e.g., seeds of fleshy fruits or arillated seeds vs. ornamented seeds with wings, hair, or hooks). The seeds that could not be classified into endozoochorous or nonendozoochorous species were excluded from the analyses. In most cases, the dispersal units corresponded to seeds in a strict botanical sense. However, for some nonendozoochorous species, the dispersal units (diaspores) were made up of seeds and the surrounding fruit structure. All diaspores are referred to as seeds in the following. After drying seeds at 60°C for 3–4 days, we weighted them with a high precision analytical balance (precision 0.0001 g; KERN & SOHN GmbH). From the dried samples, we calculated seed rain biomass as the total dry mass of seeds collected for each sample. We also calculated seed rain richness as the number of plant species and morphospecies of seeds collected per trap. Photos of the most abundant endozoochorous species found along the elevational gradient are compiled in Acosta-Rojas et al. (2021).

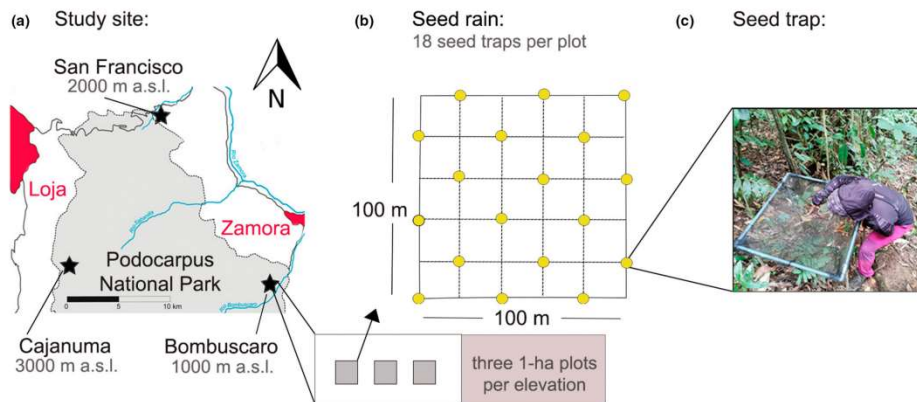


FIGURE 1 Scheme of study design along the elevational gradient in southern Ecuador: (a) the locations of the three study sites are marked with black stars (redrawn based on Homeier et al., 2012). We established three 1-ha plots at each elevation. (b) Seed trap distribution inside each plot; the position of each of the 18 seed traps is marked with a yellow circle. (c) Seed trap design.



### 2.3 | Climatic conditions

For each plot, we recorded two climatic factors: mean annual rainfall (mm) and mean annual temperature (°C). Both variables were obtained by calculating the annual means of the total amount of rainfall and temperature recorded over a period of 3 years (2018–2020). Climatic data were derived from an operational network consisting of automatic climate stations, remote sensing techniques, and a regionalization tool developed for the study area (see more details in Fries et al., 2009; Rollenbeck & Bendix, 2011).

### 2.4 | Microhabitat conditions

To characterize microhabitat conditions, we recorded canopy structure and soil conditions in nine 1 m<sup>2</sup> subplots per plot (i.e., each subplot was located adjacent to two seed traps characterized by similar canopy structures). For canopy structure, we measured the leaf area index which indicates how much of one-sided foliage area is projected per unit ground surface area (Chen & Black, 1992). To calculate the leaf area index, one hemispherical photo was taken per subplot with a Nikon FC-E8 Fish-Eye Converter (Nikon Corporation). The camera was placed 0.7 m above ground and oriented toward the sky. All photos were taken in the mornings with an overcast sky. Leaf area index values were estimated from hemispherical photos with Gap Light Analyser version 2.0 (Frazer et al., 1999). High leaf area index values indicate high foliage interception per unit of ground surface resulting in a more complex canopy structure (Chen & Black, 1992). For soil conditions, we recorded soil moisture which refers to water available for plants in the soils (Schmugge et al., 1980). We used a tensiometer (SM150 Kit, Delta-T Devices Ltd.) to measure soil moisture at five different points on the surface layer of soil in each subplot. Both soil moisture and leaf area index were recorded on the same dates (in October 2019). Since we were not able to measure the leaf area index close to two seed traps at 1000 m a.s.l., we extrapolated these two values from the closest traps. Soil moisture and leaf area index values were log-transformed prior to the analyses and were uncorrelated ( $n = 162$  traps,  $r = .12$ ,  $p = .12$ ). Microhabitat and climatic conditions were only weakly related ( $n = 9$  plots, rainfall vs. leaf area index,  $r = -.33$ , adjusted  $p = 1$  (Holm's method), rainfall vs. soil moisture,  $r = .20$ , adjusted  $p = 1$  (Holm's method); temperature vs. leaf area index,  $r = .76$ , adjusted  $p = .09$  (Holm's method), temperature vs. soil moisture,  $r = -.12$ , adjusted  $p = 1$  (Holm's method)) (see climate and microhabitat conditions recorded per elevation in Table S2).

### 2.5 | Statistical analysis

We tested our three hypotheses (a–c) with data on both seed rain biomass and seed richness by pooling seed rain samples across the entire study year, given the relatively constant environmental conditions throughout the year. First, for each seed trap, the relative seed rain biomass was calculated as the seed dry mass of endozoochorous

species divided by the total seed biomass. This term, also understood as the proportion of endozoochorous species collected per trap along the year, was logit-transformed prior to the analyses (adjusting values of 0 and 1 by 0.025). Second, the relative seed rain richness was defined by the number of endozoochorous species sampled in a seed trap over the entire year divided by the total seed richness. Therefore, the relative seed rain richness refers to the proportion of endozoochorous species recorded per trap throughout the year. We tested relative seed rain richness with a binomial model including the classification of the two species groups as response variables ("yes" = endozoochorous species, "no" = nonendozoochorous species).

We tested the hypotheses (a–c) with generalized linear mixed-effects models (GLMMs) including the identity of study plots ( $n = 9$ ) as a random factor. Hypothesis (a) was tested by including elevation (1000, 2000, and 3000 m a.s.l.) as a fixed factor. Hypotheses (b and c) were tested in a joint model including climatic and microhabitat variables as continuous predictors. We defined a full model that included climatic factors (temperature and rainfall) and microhabitat conditions (leaf area index and soil moisture). All predictors were standardized to zero mean and unit variance to control for different units of measurement among predictors. Based on the full model, we generated a set of component models with all possible combinations of predictor variables and identified the best combination of predictors according to Akaike's information criterion (Burnham & Anderson, 2002). The model with the lowest AICc value was selected as the most parsimonious model, but all models with a delta AICc value < 4 relative to the best model are shown (see Table S4 and S5). For all final models, we measured the proportion of variance explained by fixed factors ( $R^2$  marginal) and random and fixed factors ( $R^2$  conditional). All statistical analyses and graphs were performed with R statistical software version 4.1.2 (R Core Team, 2021), with the use of car (Fox & Weisberg, 2019), glmmTMB (Brooks et al., 2017), MuMIn (Barton, 2019), ggplot2 (Wickham, 2016), and ggpubr packages (Kassambara, 2018).

## 3 | RESULTS

Overall, we recorded a total of 331,838 seeds over the 1-year sampling period along the elevational gradient. Seeds were collected in 160 seed traps because two traps never contained seeds (one at 1000 m a.s.l., one at 3000 m a.s.l.). About 76.4% of the seeds (61.3% of the morphospecies) could taxonomically be identified, others remained classified as undetermined morphospecies. Overall, the seed rain consisted of 323 species/morphospecies distributed over 51 plant families (see the complete list of species/morphospecies in Table S3). Melastomataceae and Lauraceae were the most widespread families of the endozoochorous species, while Asteraceae and Melastomataceae were the most dominant families of the non-endozoochorous plant species. The mean seed dry mass per species (mean seed mass = 0.06 g, SD = 0.22,  $n = 300$ ) ranged from tiny seeds with 0.005 µg (Family Ericaceae) to heavy seeds such as those

TABLE 1 Generalized linear mixed effect models (GLMMs) of the effect of elevation on (a) relative seed rain biomass and (b) relative seed richness of endozoochorous species

Model	Elevation	Estimate	SE	z	p value	R <sup>2</sup> <sub>m</sub>	R <sup>2</sup> <sub>c</sub>
(a)							
Seed rain biomass	Intercept	2.55	0.23	11.12	<.001	0.10	0.10
	2000 m.a.s.l.	0.12	0.32	0.37	.714		
	3000 m.a.s.l.	-1.11	0.32	-3.42	<.001		
(b)							
Seed rain richness	Intercept	1.45	0.12	12.07	<.001	0.22	0.22
	2000 m.a.s.l.	-0.54	0.15	-3.67	.001		
	3000 m.a.s.l.	-0.76	0.16	-4.65	<.001		

Note: Given are estimates, standard errors (SE), z values, and p values. Marginal R<sup>2</sup> (R<sup>2</sup><sub>m</sub>) and conditional R<sup>2</sup> (R<sup>2</sup><sub>c</sub>) are shown in the final columns. The sample size corresponds to 160 traps. Identities of plots (n = 9) were included as random effects in both models.

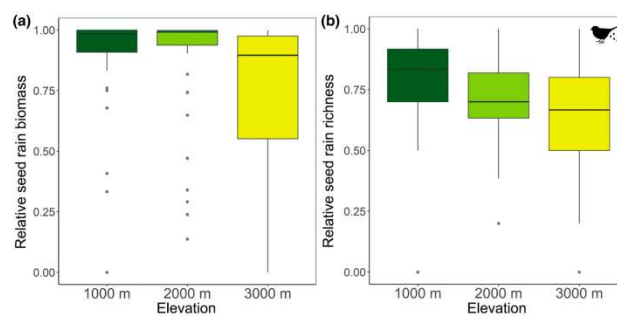


FIGURE 2 Relative seed rain biomass and richness across the elevational gradient in southern Ecuador. (a) Relative seed rain biomass is defined as the proportion of dry biomass of endozoochorous species relative to the total dry biomass of species per trap over the entire year; (b) relative seed rain richness is defined as the proportion of endozoochorous species relative to the total number of species per trap over the entire year. Boxes show 25th and 75th percentiles, with the median indicated, whiskers show data range and gray points are outliers.

of *Anomosperrum reticulatum* (Family: Menispermaceae) with 2.6 g. Overall, endozoochorous species represented 83% of the total seed rain richness.

The relative seed rain biomass and richness of endozoochorous species were both associated with elevation. At low and mid elevations, the relative seed rain biomass of endozoochorous species was similar, but it declined in the upper montane forest (Table 1, Figure 2a). In contrast, the relative seed rain richness of endozoochorous species decreased continuously along the elevational gradient (Table 1, Figure 2b).

Climate and microhabitat conditions explained a significant part of the variation in the prevalence of endozoochory across and within elevations. The most parsimonious model of the proportion of seed rain biomass of endozoochorous species retained rainfall as predictor variables (Table 2). The second-best model included rainfall and soil moisture as predictors (delta AICc relative to the best model = 1.14, all model combinations with delta AICc < 4 are shown in Table S4). Relative seed rain biomass of endozoochorous plant species was negatively associated with rainfall (Table 2, Figure 3a). According to

the most parsimonious model, relative seed rain richness was related to temperature and leaf area index (Table 2). The second-best model included temperature, leaf area index, and soil moisture (delta AICc relative to the best model = 1.93, all model combinations with delta AICc < 4 are shown in Table S5). In the two most parsimonious models, temperature and leaf area index were positively related to the relative seed rain richness of endozoochorous plant species (Table 2, Figures 3b and 4).

#### 4 | DISCUSSION

We studied the importance of endozoochory in the seed rain of plant communities located along an elevational gradient in the tropical Andes of southern Ecuador. Increasing elevation led to a decrease in the relative seed rain biomass and richness of endozoochorous plant species. Relative seed rain biomass of endozoochorous species decreased with increasing rainfall, whereas relative seed rain richness of endozoochorous species increased with increasing temperature

TABLE 2 Generalized linear mixed effect models (GLMMs) of the effects of climatic and microhabitat conditions on (a) relative seed rain biomass and (b) seed rain richness of endozoochorous species

Model	Fixed terms	Estimate	SE	z	p value	R <sup>2</sup> <sub>m</sub>	R <sup>2</sup> <sub>c</sub>	
(a)	Relative seed rain biomass	(Intercept)	2.22	0.13	16.92	<.001	0.11	0.11
		Rainfall	-0.58	0.13	-4.41	<.001		
(b)	Relative seed rain richness	(Intercept)	1.01	0.06	17.00	<.001	0.25	0.25
		Temperature	0.20	0.08	2.39	<.001		
		Leaf area index	0.18	0.08	2.66	.017		

Note: Given are estimates, standard errors (SE), z values, and p values for each best model. Estimates are directly comparable because all predictors were scaled to zero mean and unit variance prior to the analysis. Marginal R<sup>2</sup> (R<sup>2</sup><sub>m</sub>) and conditional R<sup>2</sup> (R<sup>2</sup><sub>c</sub>) are shown in the two last columns. Identities of plots (n = 9) were included as random effects. The sample size was 160 traps.

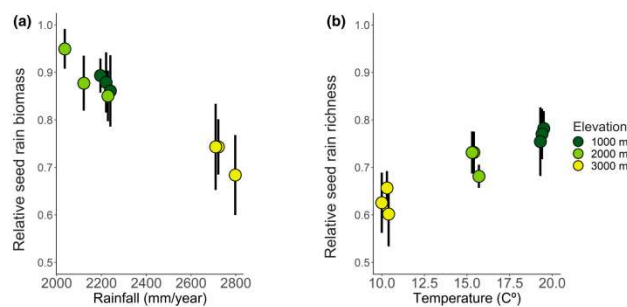


FIGURE 3 Effects of climatic factors on the seed rain of endozoochorous species across the elevational gradient in southern Ecuador. (a) Relative seed rain biomass of endozoochorous species in relation to mean annual rainfall, and (b) relative seed rain richness of endozoochorous species in relation to mean annual temperature. Every point represents mean values of seed rain at the respective nine 1-ha plot levels, and the vertical lines are the corresponding standard deviations in seed rain biomass and richness across the 18 seed traps in each plot.

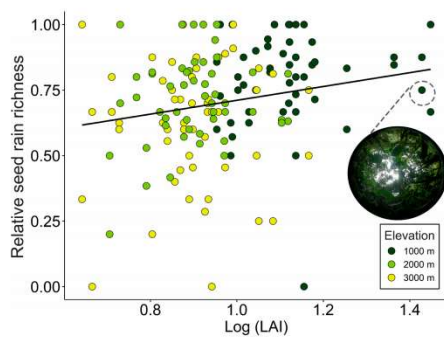


FIGURE 4 The relationship between relative seed rain richness and leaf area index (LAI). Points represent values for each seed trap (n = 160), and the line shows the linear trend in the relationships (see Table 2 for the results from generalized linear mixed effect models). LAI is log-transformed. The hemispherical photo on the low right side illustrates an LAI of 4.15 at 1000 m a.s.l.

and higher leaf area index. Our analyses suggest an interplay between climate factors and microhabitat conditions shaping the variability of endozoochorous plant species in the seed rain of tropical montane forests.

According to our expectations, the prevalence of endozoochory decreased with increasing elevation in the montane forests of southern Ecuador. This decline in the importance of endozoochory has been previously reported in other montane forests along an elevational gradient in the tropical Andes (Buitrón-Jurado & Ramírez, 2014) as well as in temperate forests (Yu et al., 2017). Here, we identified two specific trends of endozoochory in montane forests. First, we detected similar proportions of seed rain biomass of endozoochorous species at 1000 and 2000 m a.s.l. with a subsequent decay toward the upper montane forest at 3000 m a.s.l. This trend might be driven by the fruit production of abundant and large-seeded plant species contributing a large fraction to seed rain biomass. We suspect that similar values of the relative seed rain biomass of endozoochorous species at low and intermediate elevations may derive from the high records of seed rain of abundant small-seeded species (e.g., Moraceae, Melastomataceae spp.) as well as of



several large-seeded species (e.g., Lauraceae, Menispermaceae spp.) at 1000 and 2000 m.a.s.l.

Second, relative seed rain richness of endozoochorous species systematically decreased with increasing elevation. The decrease of endozoochorous plant species with increasing elevations might be due to a systematic shift in plant species composition at the high elevation. Decreased productivity at high elevations (Malhi et al., 2017; Tanner et al., 1998) leads to a reduction of plant taxa producing fleshy fruits at the highest elevation. In addition, herbaceous plant species, which increase in dominance at high elevations, are often dispersed by abiotic agents rather than by biotic vectors (Arbeláez & Parrado-Rosselli, 2005; Armesto & Rozzi, 1989; Tovar et al., 2020). The continuous decline in the importance of endozoochory is also consistent with a decline of avian frugivores along the elevational gradient (Quitán et al., 2018). This study in the same montane forests found lower diversity of plant–frugivore interactions at high elevations, corresponding to a decreased number of frugivorous bird species in the upper montane forest.

In our study, climatic conditions were associated with the prevalence of endozoochory in seed rain. Relative seed rain biomass of endozoochorous plant species decreased with increasing rainfall. This finding is not consistent with the positive association between rainfall and the abundance of endozoochorous plants that have been found in other Neotropical (Almeida-Neto et al., 2008; Correa et al., 2015) and Paleotropical forests (Zhao et al., 2018). These contrasting results might be associated with the relationship between water availability and productivity in our study system. Generally, rainy environments have high productivity that supports the high costs involved in the production of fleshy fruits (Bonte et al., 2012; Willson et al., 1989). In many tropical mountains, however, extremely high rainfall is associated with a decrease in soil fertility and lowered productivity because of the leaching of soil nutrients (Malhi et al., 2017). Lowered productivity may result in reduced production of fleshy fruits at the highest elevation in our study system. As proposed by Willson et al. (1989), fleshy fruit production may be driven by productivity rather than by rainfall in tropical montane forests.

The relative seed rain richness of endozoochorous plant species increased with increasing temperatures. The proportion of endozoochorous species was also positively correlated with the mean annual temperature for other montane forests in the northern Andes (Buitrón-Jurado & Ramírez, 2014). One potential explanation for the temperature effect on endozoochory could be related to the continuous decrease in productivity with decreasing temperature (Pau et al., 2018). In addition, low temperatures may damage fleshy fruits (Burke et al., 1976) which are characterized by high levels of organic compounds and water (Coombe, 1976). A previous study has shown that endozoochorous species growing at high elevations tolerate higher temperatures than nonendozoochorous species (Tovar et al., 2020). Therefore, it is likely that the prevalence of endozoochorous plant species is determined by a combination of physiological constraints imposed by temperature and involved in the production of fleshy fruits.

An additional explanation for the increase of endozoochorous species towards warmer environments is that temperature modulates the diversity of animal seed dispersers (Peters et al., 2016) and thereby indirectly affects the relative richness of endozoochorous plant species. In line with that, positive effects of temperature have been reported on the diversity of frugivorous birds (Santillán et al., 2020) and indirect associations between plant and bird diversity have been shown to be more important than direct climatic effects in another tropical mountain system (Vollstädt et al., 2017). This suggests that a higher number of endozoochorous plant species can be found in environments with a more diverse community of animal frugivores.

In addition to the climatic gradients across the mountain, microhabitat conditions were also related to the relative richness of endozoochorous species in the seed rain of tropical montane forests. In line with our hypothesis, the prevalence of endozoochory in seed rain richness increased with increasing leaf area index, while endozoochory was only weakly related to soil moisture. It is likely that late successional habitats, characterized by increased canopy complexity (i.e., with denser foliage in the canopy, Unger et al., 2013), harbor numerous endozoochorous species, most of which produce rather large seeds. We find further support for this explanation in the covariation between seed dispersal mode and other plant traits. For instance, it has been shown that animal-dispersed plants in Atlantic forests tended to be tall trees with a high wood density (Bello et al., 2015).

Future studies are required for a mechanistic understanding of how microhabitat conditions shape the importance of endozoochory in the seed rain of tropical forests. Such studies should also test to what extent the diversity of plant–frugivore interactions increases in late successional habitats (Morante-Filho et al., 2018). Higher interaction diversity between plants and animals may further contribute to the increase in endozoochorous seeds in late successional microhabitats. Another interesting aspect for future work could be the study of establishment success of endozoochorous and nonendozoochorous species. Large-seeded species dispersed by animals are likely to have a higher recruitment capacity in shaded conditions of late successional forest habitats (Baraloto et al., 2005; Bolmgren & Eriksson, 2005).

## 5 | CONCLUSIONS

We show that the importance of endozoochory in the seed rain of tropical montane forests is shaped by an interplay of climatic and microhabitat conditions at large and small spatial scales. Changing climatic and microhabitat conditions are therefore likely to jointly lead to compositional changes in the dominant dispersal modes of tropical plant communities. Given the importance of seed dispersal for ecological processes and ecosystem functions (Bello et al., 2015; Fricke et al., 2022), such changes in species composition will need to be considered in predictive models of the dynamics of tropical forest ecosystems under global change (Bendix et al., 2021).



**AUTHOR CONTRIBUTIONS**

D.C.A.R., M.B., E.L.N., and M.S. conceived the research idea; C.I.E., B.T., E.L.N., and M.S. conceived the general project ideas and experimental design; D.C.A.R. and M.B. collected data; D.C.A.R. analyzed the data and wrote the first manuscript draft; all authors discussed the results and commented on the manuscript.

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**CONFLICT OF INTEREST**

The authors declare no potential conflict of interest.

**DATA AVAILABILITY STATEMENT**

All data used in this manuscript have been uploaded to the Dryad Repository and are accessible using the following DOI: <https://doi.org/10.5061/dryad.6hd7sr4v>.

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**REFERENCES**

Acosta-Rojas, D., Barczyk, M., Espinosa, C., Gusmán, J., Peña, J., Neuschulz, E., Schleuning, M., & Homeier, J. (2021). *Field guide of animal-dispersed plants: Fruits and seeds in and around Podocarpus National Park*. INABIO. <https://doi.org/10.5678/vnkb-t219>

Almeida-Neto, M., Campassi, F., Galetti, M., Jordano, P., & Oliveira-Filho, A. (2008). Vertebrate dispersal syndromes along the Atlantic forest: Broad-scale patterns and macroecological correlates. *Global Ecology and Biogeography*, 17(4), 503–513. <https://doi.org/10.1111/j.1466-8238.2008.00386.x>

Arbeláez, M. V., & Parrado-Rosselli, A. (2005). Seed dispersal modes of the sandstone plateau vegetation of the middle Caquetá river region, Colombian Amazonia. *Biotropica*, 37(1), 64–72. <https://doi.org/10.1111/j.1744-7429.2005.03077.x>

Armesto, J. J., & Rozzi, R. (1989). Seed dispersal syndromes in the rain forest of Chiloe: Evidence for the importance of biotic dispersal in a temperate rain forest. *Journal of Biogeography*, 16(3), 219–226. <https://doi.org/10.2307/2845258>

Aslan, C., Beckman, N. G., Rogers, H. S., Bronstein, J., Zurell, D., Hartig, F., Shea, K., Pejchar, L., Neubert, M., Poulsen, J., HilleRisLambers, J., Miriti, M., Loiselle, B., Effiom, E., Zambrano, J., Schupp, G., Pufal, G., Johnson, J., Bullock, J. M., ... Zhou, Y. (2019). Employing plant functional groups to advance seed dispersal ecology and conservation. *AoB PLANTS*, 11(2), plz006. <https://doi.org/10.1093/aobpl/afz006>

Baraloto, C., Forget, P.-M., & Goldberg, D. E. (2005). Seed mass, seedling size and neotropical tree seedling establishment. *Journal of Ecology*, 93(6), 1156–1166. <https://doi.org/10.1111/j.1365-2745.2005.01041.x>

Barton, K. (2019). *MuMIn: Multi-model inference*. R Foundation for Statistical Computing. <https://cran.r-project.org/package=MuMIn>

Bello, C., Galetti, M., Pizo, M. A., Magnago, L. F. S., Rocha, M. F., Lima, R. A. F., Peres, C. A., Ovaskainen, O., & Jordano, P. (2015). Defaunation affects carbon storage in tropical forests. *Science Advances*, 1(11), e15011105. <https://doi.org/10.1126/sciadv.1501105>

Bendix, J., Rollenbeck, R., Richter, M., Fabian, P., & Emck, P. (2008). Climate. In E. Beck, J. Bendix, I. Kottke, F. Makeschin, & R. Mosandl (Eds.), *Gradients in a tropical mountain ecosystem of Ecuador* (pp. 63–73). Springer.

Bendix, J., Aguire, N., Beck, E., Bräuning, A., Brandl, R., Breuer, L., Böhning-Gaese, K., de Paula, M. D., Hickler, T., Homeier, J., Inclan, D., Leuschner, C., Neuschulz, E. L., Schleuning, M., Suarez, J. P., Trachte, K., Wilcke, W., Windhorst, D., & Farwig, N. (2021). A research framework for projecting ecosystem change in highly diverse tropical mountain ecosystems. *Oecologia*, 195(3), 589–600. <https://doi.org/10.1007/s00442-021-04852-8>

Bolmgren, K., & Eriksson, O. (2005). Fleshy fruits – origins, niche shifts, and diversification. *Oikos*, 109(2), 255–272. <https://doi.org/10.1111/j.0030-1299.2005.12663.x>

Bonte, D., Van Dyck, H., Bullock, J. M., Coulon, A., Delgado, M., Gibbs, M., Lehoucq, V., Matthysen, E., Mustin, K., Saastamoinen, M., Schtickzelle, N., Stevens, V. M., Vandewoestijne, S., Baguette, M., Barton, K., Benton, T. G., Chaput-Bardy, A., Clobert, J., Dytham, C., ... Travis, J. M. J. (2012). Costs of dispersal. *Biological Reviews*, 87(2), 290–312. <https://doi.org/10.1111/j.1469-185X.2011.00201.x>

Brooks, M. E., Kristensen, K., van Benthem, K., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Machler, M., & Bolker, B. (2017). "glmmTMB" Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *The R Journal*, 9(2), 378–400. <https://journal.r-project.org/archive/2017/RJ-2017-066/index.html>

Buitrón-Jurado, G., & Ramírez, N. (2014). Dispersal spectra, diaspore size and the importance of endozoochory in the equatorial Andean montane forests. *Flora - Morphology, Distribution, Functional Ecology of Plants*, 209(7), 299–311. <https://doi.org/10.1016/j.flora.2014.03.009>

Burke, M. J., Gusta, L. V., Quamme, H. A., Weiser, C. J., & Li, P. H. (1976). Freezing and injury in plants. *Annual Review of Plant Physiology*, 27(1), 507–528. <https://doi.org/10.1146/annurev.pp.27.060176.002451>

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. Springer.

Camargo, J. L., & Kapos, V. (1995). Complex edge effects on soil moisture and microclimate in central Amazonian forest. *Journal of Tropical Ecology*, 11(2), 205–221. <https://doi.org/10.1017/S026646740000866X>

Chanthorn, W., Ratanapongsai, Y., Brockelman, W. Y., Allen, M. A., Favier, C., & Dubois, M. A. (2016). Viewing tropical forest succession as a three-dimensional dynamical system. *Theoretical Ecology*, 9(2), 163–172. <https://doi.org/10.1007/s12080-015-0278-4>

- Chen, J. M., & Black, T. A. (1992). Defining leaf area index for non-flat leaves. *Plant, Cell and Environment*, 15(4), 421–429. <https://doi.org/10.1111/j.1365-3040.1992.tb00992.x>
- Chen, S.-C., Cornwell, W. K., Zhang, H.-X., & Moles, A. T. (2017). Plants show more flesh in the tropics: Variation in fruit type along latitudinal and climatic gradients. *Ecography*, 40(4), 531–538. <https://doi.org/10.1111/ecog.02010>
- Cheng, Y., Leung, L. R., Huang, M., Koven, C., Detto, M., Knox, R., Bisht, G., Brefeld, M., & Fisher, R. A. (2022). Modeling the joint effects of vegetation characteristics and soil properties on ecosystem dynamics in a Panama tropical forest. *Journal of Advances in Modeling Earth Systems*, 14(1), e2021MS002603. <https://doi.org/10.1029/2021M5002603>
- Coombe, B. G. (1976). The development of fleshy fruits. *Annual Review of Plant Physiology*, 27(1), 207–228. <https://doi.org/10.1146/annurev.pl.27.060176.001231>
- Correa, D. F., Álvarez, E., & Stevenson, P. R. (2015). Plant dispersal systems in Neotropical forests: Availability of dispersal agents or availability of resources for constructing zoochorous fruits? *Global Ecology and Biogeography*, 24(2), 203–214. <https://doi.org/10.1111/geb.12248>
- Elsen, P. R., & Tingley, M. W. (2015). Global mountain topography and the fate of montane species under climate change. *Nature Climate Change*, 5(8), 772–776. <https://doi.org/10.1038/nclimate2656>
- Emck, P. A. (2007). *A climatology of South Ecuador with special focus on the major Andean Ridge as Atlantic-Pacific climate divide*. University Erlangen-Nürnberg.
- Ferger, S. W., Schleuning, M., Hemp, A., Howell, K. M., & Böhning-Gaese, K. (2014). Food resources and vegetation structure mediate climatic effects on species richness of birds. *Global Ecology and Biogeography*, 23(5), 541–549. <https://doi.org/10.1111/geb.12151>
- Fox, J., & Weisberg, S. (2019). *An R companion to applied regression* (3rd ed.). Sage. <https://socialsciences.mcmaster.ca/jfox/Books/Companion/>
- Frantzen, N. M. L. H. F., & Bouman, F. (1989). Dispersal and growth form patterns of some zonal páramo vegetation types. *Acta Botanica Neerlandica*, 38(4), 449–465. <https://doi.org/10.1111/j.1438-8677.1989.tb01376.x>
- Frazier, G. W., Canham, C. D., & Lertzman, K. P. (1999). *Gap Light Analyzer (GLA). Version 2.0: Imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation*. Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies.
- Fricke, E. C., Ordoñez, A., Rogers, H. S., & Svenning, J.-C. (2022). The effects of defaunation on plants' capacity to track climate change. *Science*, 375(6577), 210–214. <https://doi.org/10.1126/science.abk3510>
- Fries, A., Rollenbeck, R., Göttlicher, D., Nauß, T., Homeier, J., Peters, T., & Bendix, J. (2009). Thermal structure of a megadiverse Andean mountain ecosystem in southern Ecuador and its regionalization. *Erdkunde*, 63(4), 321–335. <https://doi.org/10.3112/erdkunde.2009.04.03>
- García-Cervigón, A. I., Zywiec, M., Delibes, M., Suárez-Esteban, A., Perea, R., & Fedriani, J. M. (2018). Microsites of seed arrival: Spatio-temporal variations in complex seed-disperser networks. *Oikos*, 127(7), 1001–1013. <https://doi.org/10.1111/oik.04881>
- Gentry, A. (1983). Dispersal ecology and diversity in neotropical forest communities. In K. Kubitzki (Ed.), *Dispersal and distribution* (pp. 303–314). Velag Paul Parey.
- Holl, K. D. (1998). Do bird perching structures elevate seed rain and seedling establishment in abandoned tropical pasture? *Restoration Ecology*, 6(3), 253–261. <https://doi.org/10.1046/j.1526-100X.1998.00638.x>
- Hollander, J. L., & Vander Wall, S. B. (2004). Effectiveness of six species of rodents as dispersers of singleleaf piñon pine (*Pinus monophylla*). *Oecologia*, 138(1), 57–65. <https://doi.org/10.1007/s00442-003-1393-2>
- Homeier, J., Hertel, D., Camenzind, T., Cumbicus, N. L., Maraun, M., Martinsin, G. O., Poma, L. N., Rillig, M. C., Sandmann, D., Scheu, S., Veldkamp, E., Wilcke, W., Wullaert, H., & Leuschner, C. (2012). Tropical Andean forests are highly susceptible to nutrient inputs - rapid effects of experimental N and P addition to an Ecuadorian montane forest. *PLoS One*, 7, e47128. <https://doi.org/10.1371/journal.pone.0047128>
- Homeier, J., Werner, F. A., Gradstein, S. R., Breckle, S. W., & Richter, M. (2008). Potential vegetation and floristic composition of Andean forests in South Ecuador, with a focus on the RBSF. In E. Beck, J. Bendix, Ingrid Kottke, Franz Makeschin, Reinhard Mosandl (Eds.), *Gradients in a tropical mountain ecosystem of Ecuador*. (pp. 87–100). Springer.
- Howe, H. F., & Smallwood, J. (1982). Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, 13(1), 201–228. <https://doi.org/10.1146/annurev.es.13.110182.001221>
- Janson, C. H. (1983). Adaptation of fruit morphology to dispersal agents in a neotropical forest. *Science*, 219(4581), 187–189. <https://doi.org/10.1126/science.219.4581.187>
- Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *The American Naturalist*, 104(940), 501–528. <https://doi.org/10.1086/282687>
- Jara-Guerrero, A., De la Cruz, M., & Méndez, M. (2011). Seed dispersal spectrum of woody species in south Ecuadorian dry forests: Environmental correlates and the effect of considering species abundance. *Biotropica*, 43(6), 722–730. <https://doi.org/10.1111/j.1744-7429.2011.00754.x>
- Kassambara, A. (2018). *ggpubr: "ggplot2" based publication ready plots*. R Foundation for Statistical Computing. <https://cran.r-project.org/package=ggpubr>
- Loayza, A. P., & Rios, R. S. (2014). Seed-swallowing toucans are less effective dispersers of *Guettarda viburnoides* (Rubiaceae) than pulp-feeding jays. *Biotropica*, 46(1), 69–77. <https://doi.org/10.1111/btp.12070>
- Madani, N., Kimball, J. S., Ballantyne, A. P., Affleck, D. L. R., van Bodegom, P. M., Reich, P. B., Kattge, J., Sala, A., Nazeri, M., Jones, M. O., Zhao, M., & Running, S. W. (2018). Future global productivity will be affected by plant trait response to climate. *Scientific Reports*, 8(1), 2870. <https://doi.org/10.1038/s41598-018-21172-9>
- Malhi, Y., Girardin, C. A. J., Goldsmith, G. R., Doughty, C. E., Salinas, N., Metcalfe, D. B., Huaraca Huasco, W., Silva-Espejo, J. E., del Aguilla-Pasquell, J., Farfán Amézquita, F., Aragão, L. E., Guerrieri, R., Ishida, F. Y., Bahar, N. H. A., Farfan-Rios, W., Phillips, O. L., Meir, P., & Silman, M. (2017). The variation of productivity and its allocation along a tropical elevation gradient: A whole carbon budget perspective. *New Phytologist*, 214(3), 1019–1032. <https://doi.org/10.1111/nph.14189>
- Melcher, I. M., Bouman, F., & Cleef, A. M. (2000). Seed dispersal in páramo plants: Epizoochorous and hydrochorous taxa. *Plant Biology*, 2(1), 40–52. <https://doi.org/10.1055/s-2000-9146>
- Melo, F. P. L., Dirzo, R., & Tabarelli, M. (2006). Biased seed rain in forest edges: Evidence from the Brazilian Atlantic forest. *Biological Conservation*, 132(1), 50–60. <https://doi.org/10.1016/j.biocon.2006.03.015>
- Morán-López, T., González-Castro, A., Morales, J. M., & Nogales, M. (2020). Behavioural complementarity among frugivorous birds and lizards can promote plant diversity in island ecosystems. *Functional Ecology*, 34(1), 182–193. <https://doi.org/10.1111/1365-2435.13476>
- Morante-Filho, J. C., Arroyo-Rodríguez, V., Pessoa, M. D. S., Cazetta, E., & Faria, D. (2018). Direct and cascading effects of landscape structure on tropical forest and non-forest frugivorous birds. *Ecological Applications*, 28(8), 2024–2032. <https://doi.org/10.1002/eap.1791>
- Muscolo, A., Bagnato, S., Sidari, M., & Mercurio, R. (2014). A review of the roles of forest canopy gaps. *Journal of Forestry Research*, 25(4), 725–736. <https://doi.org/10.1007/s11676-014-0521-7>
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403(6772), 853–858. <https://doi.org/10.1038/35002501>



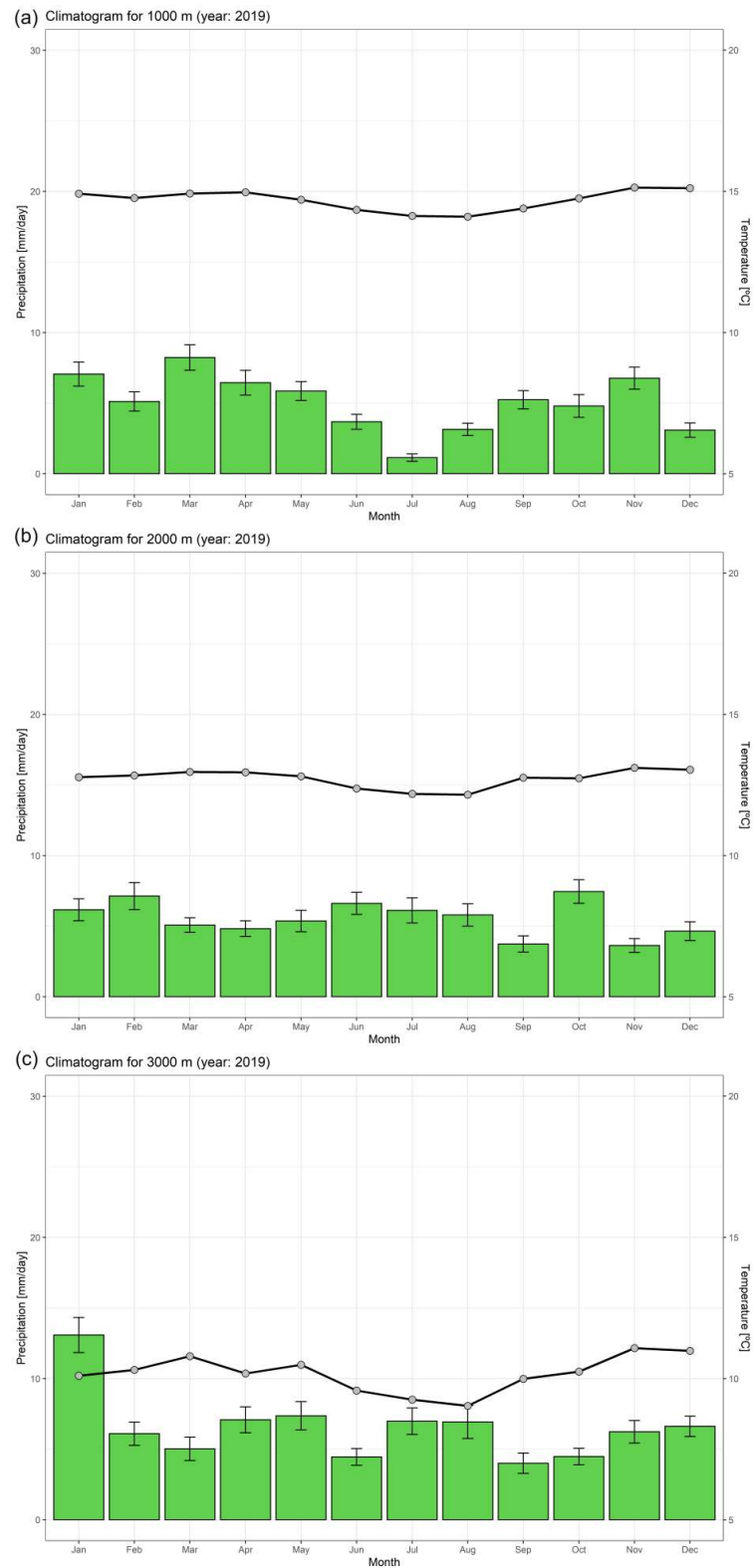
- Pau, S., Detto, M., Kim, Y., & Still, C. J. (2018). Tropical forest temperature thresholds for gross primary productivity. *Ecosphere*, 9(7), e02311. <https://doi.org/10.1002/ecs2.2311>
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P. B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., ... Cornelissen, J. H. C. (2013). New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, 61(3), 167–234. <https://doi.org/10.1071/BT12225>
- Peters, M. K., Hemp, A., Appelhans, T., Behler, C., Classen, A., Detsch, F., Ensslin, A., Ferger, S. W., Frederiksen, S. B., Gebert, F., Haas, M., Helbig-Bonitz, M., Hemp, C., Kindeketa, W. J., Mwangomo, E., Ngeresa, C., Otte, I., Röder, J., Rutten, G., ... Steffan-Dewenter, I. (2016). Predictors of elevational biodiversity gradients change from single taxa to the multi-taxa community level. *Nature Communications*, 7(1), 13736. <https://doi.org/10.1038/ncomms13736>
- Puerta-Piñero, C., Muller-Landau, H. C., Calderón, O., & Wright, S. J. (2013). Seed arrival in tropical forest tree fall gaps. *Ecology*, 94(7), 1552–1562. <https://doi.org/10.1890/12-1012.1>
- Quitán, M., Santillán, V., Espinosa, C. I., Homeier, J., Böhning-Gaese, K., Schleuning, M., & Neuschulz, E. L. (2018). Elevation-dependent effects of forest fragmentation on plant-bird interaction networks in the tropical Andes. *Ecography*, 41(9), 1497–1506. <https://doi.org/10.1111/ecog.03247>
- R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <http://www.R-Project.org>
- Rogers, H. S., Donoso, I., Traveset, A., & Fricke, E. C. (2021). Cascading impacts of seed disperser loss on plant communities and ecosystems. *Annual Review of Ecology, Evolution, and Systematics*, 52(1), 641–666. <https://doi.org/10.1146/annurev-ecolsys-012221-111742>
- Rojas, T. N., Zampini, I. C., Isla, M. I., & Blendinger, P. G. (2022). Fleshy fruit traits and seed dispersers: Which traits define syndromes? *Annals of Botany*, 129(7), 831–838. <https://doi.org/10.1093/aob/mcab150>
- Rollenbeck, R., & Bendix, J. (2011). Rainfall distribution in the Andes of southern Ecuador derived from blending weather radar data and meteorological field observations. *Atmospheric Research*, 99(2), 277–289. <https://doi.org/10.1016/j.atmosres.2010.10.018>
- Santillán, V., Quitán, M., Tinoco, B. A., Zárate, E., Schleuning, M., Böhning-Gaese, K., & Neuschulz, E. L. (2020). Direct and indirect effects of elevation, climate and vegetation structure on bird communities on a tropical mountain. *Acta Oecologica*, 102, 103500. <https://doi.org/10.1016/j.actao.2019.103500>
- Schmugge, T. J., Jackson, T. J., & McKim, H. L. (1980). Survey of methods for soil moisture determination. *Water Resources Research*, 16(6), 961–979. <https://doi.org/10.1029/WR016i06p0961>
- Schupp, E. W., Jordano, P., & Gómez, J. M. (2010). Seed dispersal effectiveness revisited: A conceptual review. *The New Phytologist*, 188(2), 333–353. <https://doi.org/10.1111/j.1469-8137.2010.03402.x>
- Snow, D. W. (1981). Tropical frugivorous birds and their food plants: A world survey. *Biotropica*, 13(1), 1–14. <https://doi.org/10.2307/2387865>
- Stark, S. C., Enquist, B. J., Saleska, S. R., Leitold, V., Schiatti, J., Longo, M., Alves, L. F., Camargo, P. B., & Oliveira, R. C. (2015). Linking canopy leaf area and light environments with tree size distributions to explain Amazon forest demography. *Ecology Letters*, 18(7), 636–645. <https://doi.org/10.1111/ele.12440>
- Stevenson, P. R., Castellanos, M. C., Pizarro, J. C., & Garavito, M. (2002). Effects of seed dispersal by three ateline monkey species on seed germination at Tinigua National Park, Colombia. *International Journal of Primatology*, 23, 1187–1204. <https://doi.org/10.1023/A:1021118618936>
- Tabarelli, M., & Peres, C. A. (2002). Abiotic and vertebrate seed dispersal in the Brazilian Atlantic forest: Implications for forest regeneration. *Biological Conservation*, 106(2), 165–176. [https://doi.org/10.1016/S0006-3207\(01\)00243-9](https://doi.org/10.1016/S0006-3207(01)00243-9)
- Tabarelli, M., Vicente, A., & Barbosa, D. C. A. (2003). Variation of seed dispersal spectrum of woody plants across a rainfall gradient in north-eastern Brazil. *Journal of Arid Environments*, 53(2), 197–210. <https://doi.org/10.1006/jare.2002.1038>
- Tanner, E. V. J., Vitousek, P. M., & Cuevas, E. (1998). Experimental investigation of nutrient limitation of forest growth on wet tropical mountains. *Ecology*, 79(1), 10–22. [https://doi.org/10.1890/0012-9658\(1998\)079\[0010:EIONLO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[0010:EIONLO]2.0.CO;2)
- Tovar, C., Melcher, I., Kusumoto, B., Cuesta, F., Cleef, A., Meneses, R. I., Halloy, S., Llambí, L. D., Beck, S., Muriel, P., Jaramillo, R., Jácome, J., & Carilla, J. (2020). Plant dispersal strategies of high tropical alpine communities across the Andes. *Journal of Ecology*, 108(5), 1910–1922. <https://doi.org/10.1111/1365-2745.13416>
- Unger, M., Homeier, J., & Leuschner, C. (2013). Relationships among leaf area index, below-canopy light availability and tree diversity along a transect from tropical lowland to montane forests in NE Ecuador. *Tropical Ecology*, 54(1), 33–45. <http://www.sciopus.com/inward/record.url?eid=2-s2.0-84866093113&partnErID=MN8TOARS>
- van der Pijl, L. (1982). *Principles of dispersal in higher plants*. Springer. <https://doi.org/10.1007/978-3-642-87925-8>
- Vander Wall, S. B., & Beck, M. J. (2012). A comparison of frugivory and scatter-hoarding seed-dispersal syndromes. *The Botanical Review*, 78(1), 10–31. <https://doi.org/10.1007/s12229-011-9093-9>
- Vollstädt, M. G. R., Ferger, S. W., Hemp, A., Howell, K. M., Töpfer, T., Böhning-Gaese, K., & Schleuning, M. (2017). Direct and indirect effects of climate, human disturbance and plant traits on avian functional diversity. *Global Ecology and Biogeography*, 26(8), 963–972. <https://doi.org/10.1111/geb.12606>
- Wenny, D. G. (2001). Advantages of seed dispersal: A re-evaluation of directed dispersal. *Evolutionary Ecology Research*, 3, 51–74.
- Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer. <https://ggplot2.tidyverse.org>
- Willson, M. F., Irvine, A. K., & Walsh, N. G. (1989). Vertebrate dispersal syndromes in some Australian and New Zealand plant communities, with geographic comparisons. *Biotropica*, 21(2), 133–147. <https://doi.org/10.2307/2388704>
- Yu, S., Katz, O., Fang, W., Li, D., Sang, W., & Liu, C. (2017). Shift of fleshy fruited species along elevation: Temperature, canopy coverage, phylogeny and origin. *Scientific Reports*, 7(1), 40417. <https://doi.org/10.1038/srep40417>
- Zhao, Y., Cao, H., Xu, W., Chen, G., Lian, J., Du, Y., & Ma, K. (2018). Contributions of precipitation and temperature to the large scale geographic distribution of fleshy-fruited plant species: Growth form matters. *Scientific Reports*, 8(1), 17017. <https://doi.org/10.1038/s41598-018-35436-x>

#### SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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## Supplementary material



**Figure S1.** Mean daily temperature and precipitation along the elevational gradient in southern Ecuador for the year 2019. All the study plots are located at (a) 1000, (b) 2000 and (c) 3000 m a.s.l.

**Table S2.** Climate and microhabitat conditions registered at plot level in the tropical montane forests of southern Ecuador. For climate conditions (temperature and rainfall), numbers represent mean values per plot over a period of three years (2018-2020). Since microhabitat conditions were measured at subplot level (soil moisture and leaf area index close to every 162 traps), the first number corresponds to the mean value and the second value to the standard deviation per elevation.

<b>Elevation</b>	<b>Plot</b>	<b>Temperature (C°)</b>	<b>Rainfall (mm/year)</b>	<b>Soil moisture (%)</b>	<b>Leaf area index</b>
1000 m a.s.l.	BO1	19.50	2195.40	34.44 ± 17.64	2.83 ± 0.17
	BO2	19.40	2220.70	27.55 ± 6.36	3.14 ± 0.42
	BO3	19.30	2239.70	45.03 ± 9.29	3.36 ± 0.42
2000 m a.s.l.	SF1	15.40	2036.50	30.24 ± 3.28	2.43 ± 0.27
	SF2	15.30	2121.30	38.62 ± 11.07	2.50 ± 0.29
	SF3	15.70	2229.00	30.09 ± 9.45	2.47 ± 0.12
3000 m a.s.l.	CA1	10.30	2721.66	50.40 ± 12.10	2.53 ± 0.26
	CA2	10.40	2709.85	27.29 ± 7.31	2.38 ± 0.30
	CA3	10.00	2797.24	35.36 ± 14.30	2.47 ± 0.30

**Table S3.** Seed dispersal mode and number of seeds collected per species/morphospecies in the tropical montane forests of southern Ecuador. Seeds were collected along an elevational gradient between 1000 and 3000 m a.s.l. The amount of seeds correspond to the sum of number of seeds collected in the 162 traps along the entire year. Taxonomic identity is indicated by family and species/morphospecies. Seed dispersal modes correspond to either endozoochorous (E) or non-endozoochorous (NE) species.

Family	Species/morphospecies	Elevation (m a.s.l.)	Seed dispersal mode	Amount of seeds
Acanthaceae	<i>Mendoncia aff gracilis</i>	1000, 2000	E	11
	<i>Saurauia sp1</i>	1000	E	6
Actinidaceae	<i>Saurauia sp2</i>	1000	E	1837
	<i>Saurauia sp3</i>	2000	E	1324
Alzateaceae	<i>Alzatea verticillata</i>	2000	NE	18216
Amaranthaceae	<i>Amaranthaceae sp1</i>	2000	E	1
Anacardiaceae	<i>Tapirira guianensis subandina</i>	2000	E	372
Annonaceae	<i>Guatteria pastazae</i>	1000	E	40
	<i>Annonaceae sp1</i>	2000	E	1
Aquifoliaceae	<i>Ilex sp</i>	2000	E	13
	<i>Ilex laurina</i>	3000	E	7
	<i>Schefflera aff morototoni</i>	1000	E	18
Araliaceae	<i>Araliaceae sp1</i>	1000	E	276
	<i>Araliaceae sp2</i>	3000	E	1072
	<i>Geonoma aff undata</i>	3000	E	5
	<i>Wettinia aequatorialis</i>	2000	E	2
Arecaceae	<i>Ceroxylon sp</i>	3000	E	15
	<i>Arecaceae sp1</i>	1000	E	1
	<i>Arecaceae sp2</i>	2000	E	1
	<i>Bidens sp</i>	1000	NE	1840
	<i>Critoniopsis sp</i>	1000	NE	97
	<i>Sonchus sp</i>	2000	NE	1
Asteraceae	<i>Asteraceae sp1</i>	1000	NE	161
	<i>Asteraceae sp2</i>	1000	NE	32
	<i>Asteraceae sp3</i>	2000	NE	376
	<i>Asteraceae sp4</i>	2000	NE	300
	<i>Asteraceae sp5</i>	2000	NE	154
	<i>Asteraceae sp6</i>	2000	NE	35
	<i>Asteraceae sp7</i>	3000	NE	72
Asteraceae	<i>Asteraceae sp8</i>	3000	NE	218
	<i>Asteraceae sp9</i>	3000	NE	7
	<i>Asteraceae sp10</i>	3000	NE	38
Bignoniaceae	<i>Handroanthus chrysanthus</i>	2000	NE	57
	<i>Bignoniaceae sp1</i>	2000	NE	2
	<i>Bignoniaceae sp2</i>	2000	NE	1
Burseraceae	<i>Dacryodes sp</i>	1000	E	104
	<i>Protium sp</i>	1000	E	15
Cannabaceae	<i>Celtis iguanaea</i>	1000	E	98

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	<i>Hedyosmum sp1</i>	1000	E	24
	<i>Hedyosmum sp2</i>	2000	E	8
Chloranthaceae	<i>Hedyosmum sp3</i>	3000	E	46
	<i>Hedyosmum sp4</i>	3000	E	9
	<i>Hedyosmum sp5</i>	3000	E	6
Clethraceae	<i>Clethra revoluta</i>	2000, 3000	NE	476
	<i>Clusia ducuoides</i>	2000	E	127
	<i>Clusia sp1</i>	1000	E	67
Clusiaceae	<i>Clusia sp2</i>	3000	E	61
	<i>Clusia sp3</i>	3000	E	3
	<i>Clusiaceae sp1</i>	2000	E	11
	<i>Clusiaceae sp2</i>	3000	E	55
Cunnoniaceae	<i>Weinmania pubescens</i>	3000	NE	235
	<i>Ericaceae sp1</i>	1000	E	50
	<i>Ericaceae sp2</i>	1000	E	1371
Ericaceae	<i>Ericaceae sp3</i>	2000	E	1560
	<i>Ericaceae sp4</i>	2000	E	7
	<i>Ericaceae sp5</i>	2000	E	1729
	<i>Alchornea lojaensis</i>	2000	E	53
	<i>Alchornea sp1</i>	1000	E	61
	<i>Alchornea sp2</i>	1000	E	66
Euphorbiaceae	<i>Alchornea sp3</i>	2000	E	6
	<i>Sapium sp1</i>	1000	E	160
	<i>Sapium sp2</i>	2000	E	128
	<i>Euphorbiaceae sp</i>	1000	E	4
	<i>Centrolobium sp</i>	2000	NE	13
	<i>Inga sp1</i>	1000	E	13
Fabaceae	<i>Inga sp2</i>	2000	E	2
	<i>Fabaceae sp</i>	1000	E	6
Hypericaceae	<i>Vismia vanillesiana</i>	2000	E	500
	<i>Aniba muca</i>	2000	E	5
	<i>Ocotea calophylla</i>	3000	E	3
	<i>Persea ferruginea</i>	3000	E	3
	<i>Persea weberbaueri</i>	2000	E	4
	<i>Ocotea sp</i>	1000	E	30
	<i>Persea sp1</i>	2000	E	99
	<i>Persea sp2</i>	2000	E	5
	<i>Persea sp3</i>	2000	E	5
Lauraceae	<i>Lauraceae sp1</i>	1000	E	4
	<i>Lauraceae sp2</i>	1000	E	18
	<i>Lauraceae sp3</i>	1000	E	11
	<i>Lauraceae sp4</i>	1000	E	1
	<i>Lauraceae sp5</i>	1000	E	7
	<i>Lauraceae sp6</i>	2000	E	1
	<i>Lauraceae sp7</i>	2000	E	29
	<i>Lauraceae sp8</i>	2000	E	3
	<i>Lauraceae sp9</i>	2000	E	79

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Lauraceae	<i>Lauraceae sp10</i>	2000	E	14
	<i>Mascagnia sp</i>	1000	NE	9
Malpighiaceae	<i>Banisteriopsis sp</i>	2000	NE	26
	<i>Malpighiaceae sp2</i>	3000	NE	2
Malvaceae	<i>Heliocarpus americanus</i>	2000	NE	4
	<i>Mollia gracilis</i>	1000	NE	2091
	<i>Malvaceae sp</i>	1000	NE	1556
Marcgraviaceae	<i>Marcgraviaceae sp</i>	2000	E	21
	<i>Meriania tomentosa</i>	3000	NE	3584
	<i>Miconia punctata</i>	2000	E	882
	<i>Miconia aff punctata</i>	1000	E	514
	<i>Meriania sp1</i>	2000	NE	77985
	<i>Meriania sp2</i>	2000	NE	272
	<i>Meriania sp3</i>	2000	NE	11809
	<i>Meriania sp4</i>	2000	NE	84
	<i>Meriania sp5</i>	3000	NE	365
	<i>Meriania sp6</i>	3000	NE	17096
	<i>Meriania sp7</i>	3000	NE	1647
	<i>Meriania sp8</i>	3000	NE	3241
	<i>Meriania sp9</i>	3000	NE	113
	<i>Meriania sp10</i>	3000	NE	200
	<i>Miconia sp</i>	3000	E	4057
Melastomataceae	<i>Melastomataceae sp1</i>	1000	E	139
	<i>Melastomataceae sp2</i>	1000	E	78
	<i>Melastomataceae sp3</i>	1000	E	383
	<i>Melastomataceae sp4</i>	2000	E	8208
	<i>Melastomataceae sp5</i>	2000	E	1287
	<i>Melastomataceae sp6</i>	2000	E	10
	<i>Melastomataceae sp7</i>	2000	E	2653
	<i>Melastomataceae sp8</i>	2000	E	17
	<i>Melastomataceae sp9</i>	3000	E	581
	<i>Melastomataceae sp10</i>	3000	E	871
	<i>Melastomataceae sp11</i>	3000	E	51
	<i>Melastomataceae sp12</i>	3000	E	4470
	<i>Melastomataceae sp13</i>	3000	E	108
	<i>Melastomataceae sp14</i>	3000	E	56
	<i>Melastomataceae sp15</i>	3000	E	54
Meliaceae	<i>Cedrela odorata</i>	2000	NE	44
	<i>Guarea macrophylla</i>	1000	E	13
	<i>Ruagea aff glabra</i>	2000	E	3
	<i>Anomospermum reticulatum</i>	1000	E	14
	<i>Abuta sp</i>	2000	E	8
Menispermaceae	<i>Cissampelos sp</i>	1000	E	92
	<i>Odontocarya sp</i>	1000	E	12
	<i>Menispermaceae sp1</i>	1000	E	2
	<i>Menispermaceae sp2</i>	1000	E	2
Moraceae	<i>Naucleopsis francisci</i>	2000	E	1



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	<i>Ficus sp1</i>	1000	E	15127
	<i>Ficus sp2</i>	1000	E	14168
Moraceae	<i>Ficus sp3</i>	1000	E	238
	<i>Ficus sp4</i>	2000	E	1803
	<i>Ficus sp5</i>	2000	E	99
	<i>Ficus sp6</i>	2000	E	261
Myricaceae	<i>Morella pubescens</i>	2000, 3000	E	86
Myristicaceae	<i>Otoba parvifolia</i>	1000	E	1
Pentaphragaceae	<i>Ternstroemia macrocarpa</i>	3000	E	64
	<i>Hieronyma fendleri</i>	2000	E	1439
Phyllanthaceae	<i>Hieronyma sp1</i>	1000	E	1
	<i>Hieronyma sp2</i>	1000	E	1
	<i>Hieronyma sp3</i>	2000	E	14
Piperaceae	<i>Piperaceae sp1</i>	2000	E	35253
	<i>Piperaceae sp2</i>	2000	E	1582
	<i>Chusquea falcata</i>	2000	E	883
Poaceae	<i>Panicum sp</i>	2000	NE	143
	<i>Valeriana sp</i>	2000	NE	2
	<i>Poaceae sp1</i>	1000	NE	66
	<i>Poaceae sp2</i>	2000	NE	745
Podocarpaceae	<i>Podocarpus oleifolius</i>	2000	E	4
	<i>Muehlenbeckia tamnifolia</i>	3000	E	9
Polygonaceae	<i>Triplaris sp</i>	1000	E	1
	<i>Polygonaceae sp</i>	1000	E	1
	<i>Myrsine coriacea</i>	2000	E	93
Primulaceae	<i>Myrsine sp</i>	1000	E	5
	<i>Primulaceae sp1</i>	3000	E	2
	<i>Primulaceae sp2</i>	3000	E	97
	<i>Rubus sp</i>	1000	E	3
Rosaceae	<i>Prunus sp1</i>	3000	E	2
	<i>Prunus sp2</i>	3000	E	2
	<i>Ladenbergia oblongifolia</i>	1000	NE	1716
	<i>Guettarda aff hirsuta</i>	3000	E	2
	<i>Faramea sp1</i>	1000	E	1
	<i>Faramea sp2</i>	2000	E	40
	<i>Faramea sp3</i>	3000	E	1
	<i>Guettarda sp1</i>	1000	E	1
	<i>Guettarda sp2</i>	2000	E	2
Rubiaceae	<i>Rubiaceae sp1</i>	1000	E	2
	<i>Rubiaceae sp2</i>	1000	NE	2
	<i>Rubiaceae sp3</i>	1000	E	1
	<i>Rubiaceae sp4</i>	2000	E	48
	<i>Rubiaceae sp5</i>	2000	E	5
	<i>Rubiaceae sp6</i>	2000	E	8
	<i>Rubiaceae sp7</i>	3000	E	31
	<i>Rubiaceae sp8</i>	3000	E	9
Sabiaceae	<i>Meliosma meridensis</i>	3000	E	2

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Sapindaceae	<i>Matayba inelegans</i>	2000	E	16
Sapotaceae	<i>Sapotaceae sp</i>	2000	E	4
Siparunaceae	<i>Siparuna muricata</i>	3000	E	12
	<i>Siparuna sp</i>	2000	E	1
Solanaceae	<i>Solanaceae sp1</i>	1000	E	226
	<i>Solanaceae sp2</i>	2000	E	209
	<i>Solanaceae sp3</i>	2000	E	61
Staphyleaceae	<i>Turpinia occidentalis</i>	1000, 2000	E	28
Symplocaceae	<i>Symplocaceae sp1</i>	3000	E	3
	<i>Symplocaceae sp2</i>	3000	E	1
	<i>Symplocaceae sp3</i>	3000	E	1
	<i>Symplocaceae sp4</i>	3000	E	2
	<i>Symplocaceae sp5</i>	3000	E	1
	<i>Symplocaceae sp6</i>	3000	E	1
Theaceae	<i>Gordonia aff fruticosa</i>	3000	NE	28
Urticaceae	<i>Cecropia angustifolia</i>	2000	E	463
Violaceae	<i>Leonia crassa</i>	1000	E	4
Vitaceae	<i>Vitaceae sp1</i>	2000	E	8
	<i>Vitaceae sp2</i>	2000	E	3
Undetermined	<i>MB007</i>	1000	E	12
	<i>MB008</i>	1000	E	6
	<i>MB010</i>	1000	E	1
	<i>MB012</i>	1000	E	2
	<i>MB028</i>	1000	E	207
	<i>MB034</i>	1000	E	2
	<i>MB037</i>	1000	E	4
	<i>MB039</i>	1000	E	2
	<i>MB042</i>	1000	E	37
	<i>MB044</i>	1000	E	1
	<i>MB045</i>	1000	E	86
	<i>MB052</i>	1000	E	2
	<i>MB057</i>	1000	E	1
	<i>MB059</i>	1000	E	3
	<i>MB062</i>	1000	E	2
	<i>MB063</i>	1000	E	60
	<i>MB064</i>	1000	E	2619
	<i>MB070</i>	1000	E	1
	<i>MB071</i>	1000	E	1
	<i>MB072</i>	1000	E	2
<i>MB074</i>	1000	E	16	
<i>MB077</i>	1000	E	1	
<i>MB079</i>	1000	E	2	
<i>MB084</i>	1000	E	1	
<i>MB085</i>	1000	E	1	
<i>MB087</i>	1000	E	2	
<i>MB088</i>	1000	E	3	
<i>MB089</i>	1000	E	5	
<i>MB092</i>	1000	E	3	

*A2: Climate and microhabitat shape the prevalence of endozoochory in the seed rain of tropical montane forests*

	<i>MB095</i>	1000	E	5
	<i>MB101</i>	1000	E	7
	<i>MB113</i>	1000	E	11
	<i>MB128</i>	1000	E	6
	<i>MB129</i>	1000	E	24
Undetermined	<i>MB130</i>	1000	E	1
	<i>MB140</i>	1000	E	1
	<i>MB142</i>	1000	E	3
	<i>MB148</i>	1000	E	1
	<i>MB149</i>	1000	E	2
	<i>MB150</i>	1000	E	1
	<i>MB151</i>	1000	E	3
	<i>MB154</i>	1000	E	2
	<i>MB155</i>	1000	E	24
	<i>MB157</i>	1000	E	4
	<i>MB170</i>	1000	E	4
	<i>MB177</i>	1000	E	2
	<i>MB187</i>	1000	E	6
	<i>MB197</i>	1000	E	1
	<i>MB206</i>	1000	E	2
	<i>MB208</i>	1000	E	2
	<i>MB218</i>	1000	E	2
	<i>MB228</i>	1000	E	1
	<i>MB231</i>	1000	E	1
	<i>MB240</i>	1000	E	2
	<i>MB241</i>	1000	E	1
	<i>MB245</i>	1000	E	1
	<i>MB246</i>	1000	E	1
	<i>MB026</i>	1000	NE	5
	<i>MB031</i>	1000	NE	3
	<i>MB035</i>	1000	NE	4
	<i>MB065</i>	1000	NE	3104
	<i>MB112</i>	1000	NE	2
	<i>MSF011</i>	2000	E	7
	<i>MSF013</i>	2000	E	1
	<i>MSF020</i>	2000	E	1
	<i>MSF029</i>	2000	E	28
	<i>MSF034</i>	2000	E	437
	<i>MSF040</i>	2000	E	1
	<i>MSF042</i>	2000	E	44
	<i>MSF043</i>	2000	E	1
	<i>MSF046</i>	2000	E	87
	<i>MSF048</i>	2000	E	771
	<i>MSF055</i>	2000	E	2
	<i>MSF056</i>	2000	E	153
	<i>MSF059</i>	2000	E	1
	<i>MSF063</i>	2000	E	1
	<i>MSF070</i>	2000	E	2

*A2: Climate and microhabitat shape the prevalence of endozoochory in the seed rain of tropical montane forests*

	<i>MSF082</i>	2000	E	6
	<i>MSF088</i>	2000	E	1
	<i>MSF095</i>	2000	E	22
	<i>MSF098</i>	2000	E	2
	<i>MSF109</i>	2000	E	3
Undetermined	<i>MSF112</i>	2000	E	6
	<i>MSF124</i>	2000	E	1
	<i>MSF127</i>	2000	E	4
	<i>MSF128</i>	2000	E	13
	<i>MSF129</i>	2000	E	2
	<i>MSF130</i>	2000	E	1
	<i>MSF140</i>	2000	E	92
	<i>MSF147</i>	2000	E	2
	<i>MSF150</i>	2000	E	787
	<i>MSF155</i>	2000	E	4
	<i>MSF157</i>	2000	E	1
	<i>MSF159</i>	2000	E	1
	<i>MSF171</i>	2000	E	55
	<i>MSF173</i>	2000	E	1
	<i>MSF175</i>	2000	E	4
	<i>MSF069</i>	2000	NE	139
	<i>MSF126</i>	2000	NE	68062
	<i>MC002</i>	3000	E	28
	<i>MC015</i>	3000	E	2
	<i>MC031</i>	3000	E	5
	<i>MC038</i>	3000	E	8
	<i>MC041</i>	3000	E	3
	<i>MC042</i>	3000	E	3
	<i>MC045</i>	3000	E	13
	<i>MC059</i>	3000	E	1
	<i>MC060</i>	3000	E	2
	<i>MC063</i>	3000	E	2
	<i>MC065</i>	3000	E	1
	<i>MC079</i>	3000	E	2
	<i>MC085</i>	3000	E	22
	<i>MC087</i>	3000	NE	1
	<i>MC089</i>	3000	E	4
	<i>MC106</i>	3000	E	1
	<i>MC108</i>	3000	E	20
	<i>MC119</i>	3000	E	107
	<i>MC120</i>	3000	E	1
	<i>MC121</i>	3000	E	3
	<i>MC127</i>	3000	E	1
	<i>MC149</i>	3000	E	1
	<i>MC154</i>	3000	E	1
	<i>MC012</i>	3000	NE	669
	<i>MC037</i>	3000	NE	6
	<i>MC061</i>	3000	NE	4

**Table S4.** Generalized linear mixed models (GLMMs) used to test the effect of climate and microhabitat conditions on the relative seed rain biomass of endozoochorous species. Eight of sixteen component models run to select the most fitted model are show in this table with  $\Delta AICc < 4$ . Given are degrees of freedrom (df), logLik, AICc, delta AICc, and AICc weight of the models. In all models, sample size corresponds to 160 plots and the identities of plots (plots = 9) were included as random effects.

No. model	Predictors	df	logLik	AICc	delta AICc	Weight AIC
1	Rainfall	4	-322.05	652.35	0.00	0.28
2	Rainfall, ln(soil moisture)	5	-321.55	653.49	1.14	0.17
3	Rainfall, ln(leaf area index)	5	-321.81	654.01	1.66	0.13
4	Rainfall, temperature	5	-322	654.39	2.05	0.11
5	Rainfall, ln(soil moisture), ln(leaf area index)	6	-321.2	654.94	2.6	0.08
6	Rainfall, ln(leaf area index), temperature	6	-321.33	655.2	2.86	0.07
7	Rainfall, ln(soil moisture), temperature	6	-321.52	655.58	3.23	0.06
8	Rainfall, ln(soil moisture), temperature, ln(leaf area index)	7	-320.59	655.92	3.57	0.05

**Table S5.** Generalized linear mixed models (GLMMs) used to test the effect of climate and microhabitat conditions on the relative seed rain richness of endozoochorous species. Eight of sixteen component models run to select the most fitted model are show in this table with delta AICc<4. Given are degrees of freedrom (df), logLik, AICc, delta AIC and weight AIC of the models. In all models, sample size corresponds to 160 plots and the identities of plots (plots = 9) were included as random effects.

No. model	Predictors	df	logLik	AICc	delta AICc	Weight AIC
1	Temperature, ln(leaf area index)	4	-275.79	559.84	0	0.35
2	Temperature, ln(leaf area index), ln(soil moisture)	5	-275.69	561.76	1.93	0.13
3	Temperature, ln(leaf area index), rainfall	5	-275.79	561.96	2.13	0.12
4	ln(leaf area index), rainfall	4	-276.9	562.05	2.21	0.12
5	Temperature	3	-278.69	563.54	3.7	0.06
6	ln(leaf area index), ln(soil moisture), rainfall	5	-276.7	563.78	3.94	0.05

**A3: Systematic reduction in seed rain of large-seeded and endozoochorous species in pastures compared to forests of tropical mountains**

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*Title:* Systematic reduction in seed rain of large-seeded and endozoochorous species in pastures compared to forests of tropical mountains

*Status:* under review

*Author contributions:*

(1) Concept and design

DCAR, 80%;

MS, ELN, in total 20%

(2) Field work/data collection

DCAR set-up of seed traps along the elevational gradient, 50%; MB, 50%;

DCAR collected, categorized (taxonomically and in terms of seed dispersal mode) and measured of seeds, 100%;

DCAR prepared all data for analyses, 100%;

DCAR prepared all figures and tables, 100%.

(3) Analysis and interpretation of data

DCAR tested hypotheses with generalized linear mixed effects models (GLMMs), 100%;

DCAR interpreted the results, 90%

with input from MB, CIE, BT, ELN, MS, in total 10%

(4) Drafting of manuscript

DCAR, 85%;

MS, ELN, in total 10%;

MB, CIE, BT in total 5%

## **Systematic reduction in seed rain of large-seeded and endozoochorous species in pastures compared to forests of tropical mountains**

### **Abstract**

**Questions:** (a) How do seed rain biomass and richness change from old-growth tropical forests to pastures at different elevations? (b) Do seed mass and seed dispersal mode change from forests to pastures across these elevations? (c) What implications do these changes have for the recovery of deforested areas in tropical mountains?

**Location:** Old-growth montane forests and livestock pastures along an elevational gradient (1000 to 3000 m a.s.l.), located at Podocarpus National Park, San Francisco Reserve and surrounding agricultural lands, Andes of southern Ecuador.

**Methods:** We collected seed rain for a three-month period using 324 traps installed at 18 1-ha plots across elevations. Half of the traps were installed in nine 1-ha forests plots, and the other half in nine 1-ha pasture plots. For each trap, we identified the seeds and measured seed rain biomass and richness, and we also recorded seed traits and calculated community-weighted mean of seed mass and seed dispersal mode (proportion of endozoochory).

**Results:** Forests received a higher seed rain biomass than pastures, but only at the lowest elevation. Seed rain richness did not differ between habitat types. Community-weighted mean of seed mass and the proportion of endozoochorous species declined from forest to pastures and tended to decrease with increasing elevation.

**Conclusions:** Although seed rain biomass and richness were overall similar between forest and pastures, large seeds and endozoochorous species were poorly represented in the seed rain of pastures compared to that of forests. Our findings suggest that seed rain in pastures came from alternative seed sources rather than from the nearest old-growth forests. We show that biomass and richness of seed rain may be insufficient to quantify the restoration potential of deforested areas. Additional information on key seed traits, such as seed mass and seed dispersal mode, is important to optimize restoration efforts in tropical mountains.

**Keywords:** deforestation, Ecuador, elevational gradient, endozoochory, functional traits, restoration, seed dispersal limitation, seed dispersal mode, seeds, tropical montane forests.



## **Introduction**

Tropical mountains are being cleared at an alarming rate, due to human land use for agriculture and livestock grazing (Hansen et al., 2013; United Nations Environment Programme and Food and Agriculture Organization of the United Nations, 2021; Vancutsem et al., 2021). Restoration strategies are therefore urgently needed to halt and reverse the loss of biodiversity and ecosystem functioning in tropical mountains (Pandit et al., 2018). Deforested areas can, sometimes, recover swiftly and natural restoration can take place when human land use has ceased (Crouzeilles et al., 2017; Meli et al., 2017). However, in other deforested areas, the abandonment of human use only results in slow recovery dynamics without active restoration (Holl, 2012). Given the complexity of restoration dynamics in deforested areas, and the limited resources to actively restore forests, it is crucial to understand the ecological forces driving the recovery of tropical forests (Holl, 2023).

Seed dispersal is a key process in plant regeneration because it determines the ability of plants to colonize new areas (Howe & Smallwood, 1982; Levin et al., 2003; Muscarella & Fleming, 2007). Seed dispersal provides the initial spatial template for tree recruitment (Schupp et al., 2002; Russo & Augspurger, 2004), and thereby predetermines the recovery of plant diversity (Hubbell, 2001; Wright, 2002; Terborgh et al., 2017). Given that human land use such as agriculture severely reduces the availability of seeds and seedlings in the soils of deforested areas (Wijdeven & Kuzee, 2000; Palma et al., 2021), quantifying seed rain is important for evaluating the potential of plant regeneration (Cubiña & Aide, 2001; Ricketts, 2001; Del Castillo & Ríos, 2008; Culot et al., 2010; San-José et al., 2019; San-José et al., 2020).

The restoration potential provided by seed rain is greatly determined by the quantity and diversity of arriving seeds (Cubiña & Aide, 2001; García & Martínez, 2012). Seed-rain indicators based on seed numbers and taxonomic diversity are widely used in restoration studies (Reid, 2015; Mazón et al., 2019; Reid et al., 2017) and usually require moderate technical expertise to be measured (Estrada-Villegas et al., 2023). Previous studies have shown that seed rain richness and density declined with distance from the forest edge in abandoned livestock pastures (Zimmerman et al., 2000; Saavedra et al., 2015). In such deforested areas, it is also known that seed rain richness increases as time passes after degradation (Del Castillo & Ríos, 2008), in particular if there is a high activity of seed dispersing animals (Camargo et al., 2021). However, the extent to which seed number and species richness of arriving seeds vary between old-

growth forests and active livestock pastures has been less studied (but see Cubiña and Aide, 2001; Martínez-Garza et al., 2009). Given the abundance of active livestock pastures in tropical mountains, they are particularly suitable for studying the restoration potential of seed rain to recover deforested areas and to design recovery strategies even before the abandonment of livestock grazing.

Successful regeneration of deforested areas, however, also crucially depends on the type of seeds that arrive and eventually germinate and recruit. Measuring traits of seeds arriving to deforested areas is less widely done in restoration studies in the tropics (Mazón et al., 2019), because it takes more effort and requires additional expertise (Estrada-Villegas et al., 2023). Previous studies have shown that large seeds, in particular, promote recruitment in shaded conditions, while the small seeds of pioneer species are more frequently dispersed to open, sparsely vegetated areas (Harms & Dalling, 1997; Dalling et al., 1998; Kitajima, 2002). Therefore, seed limitation in deforested areas is particularly strong for large-seeded species (Saavedra et al., 2015), and for late-successional woody plants dependent on animals for seed dispersal (Martínez-Garza et al., 2009). Hence, the seed rain in deforested areas can be dominated by wind-dispersed species (Holl et al., 2000; Martínez-Garza et al., 2009), despite the general dominance of fleshy-fruited tree species dispersed by animals in tropical forests (Howe & Smallwood, 1982; Jordano, 2000). In this sense, the study of plant traits such as seed mass and the prevalence of the most dominant seed dispersal mode in the seed rain of deforested tropical areas could provide valuable information on the composition of key traits of future plant communities.

Here, we compare the seed rain between old-growth montane forests and deforested areas (i.e., active livestock pastures, hereafter: pastures) at three elevations in southern Ecuador to investigate how differences in seed rain between natural and human-modified habitats vary along the elevational gradient. Specifically, we asked: (a) How do seed rain biomass and richness change from forests to pastures at the three elevations? (b) Do seed traits, such as seed mass and seed dispersal mode (proportion of endozoochory), change from forests to pastures across these elevations? and (c) What implications do these changes have for the recovery of deforested areas in tropical mountains? We predict that seed rain biomass and richness as well as seed mass and the proportion of endozoochory will decline towards pastures across all elevations, due to the detrimental effects of deforestation on plant-frugivore interactions and seed

dispersal by animals (Stevenson, 2001; Markl et al., 2012; Quitián et al., 2018). Furthermore, we expect that differences in seed mass and the proportion of endozoochory between forest and pastures decrease with increasing elevation, due to the decrease in animal-dispersed species towards higher elevations (Swenson & Enquist, 2009; Šímová et al., 2015; Le Bagousse-Pinguet et al., 2017; Acosta-Rojas et al., 2023).

## Methods

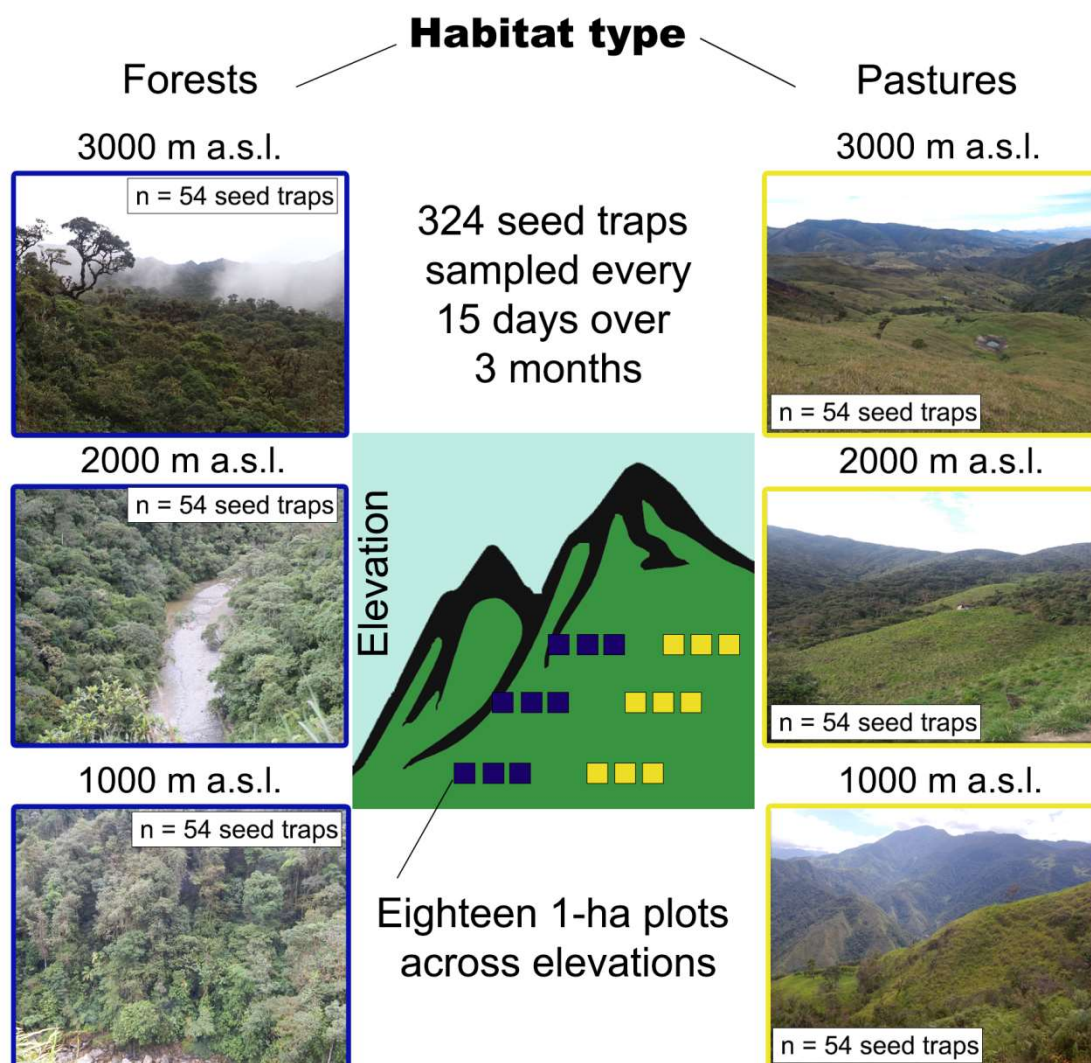
### Study site

This study was conducted in and around the Podocarpus National Park and the San Francisco Reserve along an elevational gradient of 2000 m. Specifically, we worked at three elevations: 1000 m a.s.l. (i.e., low elevation), 2000 m a.s.l. (i.e., mid elevation) and 3000 m a.s.l. (i.e., high elevation) in the Andes of southern Ecuador. The study area is covered by protected old-growth montane forests surrounded by urban areas and land used for agriculture (Figure 1). Low and mid elevations receive a similar amount of annual rainfall (2219 and 2129 mm, respectively), whereas at high elevation rainfall increases to up to 4500 mm per year (Bendix et al., 2008). Temperature decreases from 20°C to 10°C with increasing elevation, but it is relatively constant throughout the year along the elevational gradient (Bendix et al., 2008).

We selected study sites located along the three elevations and corresponding to two habitat types per elevation: (1) *forest* and (2) *pastures* (Figure 1). At each elevation, we worked in six 1-ha plots (i.e. three in the forest and three in the pastures,  $n = 18$ ). The plots were established by the DFG research unit “Environmental changes in biodiversity hotspot ecosystems of South Ecuador: RESPonse and feedback effECTs (FOR2730)” (more details in Bendix et al., 2021). Forest plots at 1000 m a.s.l. were located in Podocarpus National Park and corresponded to an evergreen premontane forest (4°6' S, 78°58' W). Forest plots at 2000 m a.s.l. were located inside the San Francisco Reserve, at a lower montane forest (3°58' S, 79°4' W). Finally, forest plots around 3000 m a.s.l. were located in the Podocarpus National Park, at an upper montane forest (4°6' S, 79°10' W) (Homeier et al., 2008) (Figure 1).

In proximity to each forest location, we selected pastures of active livestock grazing, located within a matrix of forest patches, agricultural areas, and human settlements. The distances from pastures to the nearest old-growth montane forest ranged from 325 to 846 m (Appendix S1). In the pastures, exotic grasses (*Setaria sphacelata* and *Melinis minutiflora*) dominate the area. Due to regular burning, bracken

fern (*Pteridium arachnoideum*) is also widespread in these deforested areas (Aguirre, 2007). Pastures are not completely cleared of woody vegetation, and isolated shade trees such as *Erythrina* sp. at low elevations, and *Heliocarpus americanus* at mid elevations are present. Furthermore, hedgerows comprising woody plant species such as *Tibouchina* sp. often mark the boundaries between pastures (see vegetation structure inside and around pastures in Figure 1 and Appendix S2).



**Figure 1.** Scheme of the study design along an elevational gradient in the tropical montane forests of southern Ecuador. Seed rain was sampled at 1000, 2000 and 3000 m a.s.l in two habitat types: forests (photos shown with blue frames) and pastures (photos shown with yellow frames). Seeds were collected every fifteen days over a period of three months from 324 traps. 18 traps were installed in each of the eighteen 1-ha plots (three per elevation and habitat type).

### **Seed rain measurements**

At each 1-ha plot, we collected seed rain in 18 traps (trap area = 0.6 m × 0.6 m) that were distanced by approx. 20 m among each other (see plot distribution in Appendix S2). Traps were constructed of PVC frames, fitted with 1.5 mm nylon mesh and suspended 90 cm above the ground. In the pastures, traps were fenced by wire cable to avoid trampling and damage by cattle (Appendix S2). Due to the high growth rate of the grasses in the pastures, we cleared the grasses below the mesh at each visit and repaired traps and meshes if necessary. We sampled the content of each trap every 15 days during three months between November 2019 and January 2020. We chose this time period with comparatively little rain and wind because seed traps were prone to damage in the open pastures. Moreover, we found similarly high seed rain throughout the year in another study restricted to the forest plots (Acosta-Rojas et al., 2023). We are therefore confident that we chose a representative sampling period for both habitat types.

We recorded all intact seeds collected in each seed trap  $\geq 1$  mm in length, including both herbaceous and woody plants. For some species, seeds and the surrounding fruit structure constituted the entire dispersal unit (i.e., diaspore). In the following, all dispersal units are referred to as seeds. We counted all seeds and identified them to the lowest possible taxonomic level. To this end, we prepared a reference collection of seeds based on plant material collected from the study area. We also consulted field guides and botanical experts. Taxonomically unidentified seeds were maintained as undetermined species/morphospecies (99 morphospecies in total). Photos of the most abundant endozoochorous species found along the elevational gradient are compiled in Acosta-Rojas et al., (2021).

Upon collection, all seeds were dried at 60 °C for 3-4 days and weighted with a high precision analytical balance (precision 0.0001 g; KERN & SOHN GmbH, Germany). We further recorded two functional traits of seeds: (1) seed mass and (2) seed dispersal mode. To obtain a community-wide measure of seed mass, we weighed all seeds that were collected in a given trap on a specific date. To determine the seed dispersal mode, we classified each plant species considering its primary seed dispersal modes as either endozoochorous or non-endozoochorous species (Appendix S3). These dispersal modes were assigned based on seed/fruit morphology, occasional field observations and data on frugivore-plant interactions (Bello et al., 2017; Quitián et al.,

2019). Ten species that could not be classified into endozoochorous or non-endozoochorous species were excluded from this analysis.

We pooled seed rain samples of each trap across the three months, given the relatively constant environmental conditions throughout this period. We then calculated four measures of seed rain at trap level ( $n = 324$ ): (1) seed rain biomass, (2) seed rain richness, (3) community-weighted mean of seed mass and (4) the proportion of endozoochory. Seed rain biomass was defined as the sum of total dry mass of seeds collected per trap over all temporal samples (log-transformed prior to the analysis). Seed rain richness was the number of plant species or morphospecies of seeds collected per trap over the three months. Community-weighted mean of seed mass (hereafter referred to as seed mass) was defined as the mean dry mass of seeds collected per trap over the three months, calculated as the ratio between the total seed rain biomass and the number of collected seeds per trap (log-transformed, prior to the analysis). Finally, the proportion of endozoochory was estimated by the number of endozoochorous species and non-endozoochorous in each trap over the course of three months.

### **Statistical analysis**

We used mixed-effects models to test for main and interaction effects of elevation (1000, 2000 and 3000 m a.s.l.) and habitat type (forest and pastures) on seed rain biomass and richness (question, a). We tested seed rain biomass with a Gaussian error distribution and seed rain richness with a Poisson error distribution. The identity of study plots ( $n = 18$ ) was included as a random factor to account for the variation within the plots in both models.

In addition, we used mixed-effects models to test for main and interaction effects of elevation and habitat type on seed mass and seed dispersal mode (question, b). We tested seed mass with a Gaussian error distribution and the proportion of endozoochours species with a binomial model including the number of species in the respective group as response variable number of endozoochorous species vs. number of non-endozoochorous species). Both models included the identity of study plots ( $n = 18$ ) as a random factor.

For each model, we quantified the proportion of variance explained by fixed factors ( $R^2$  marginal) and random and fixed factors ( $R^2$  conditional) (Jaeger, 2017). All statistical analyses and graphs were performed with R environment version 4.1.2 (R Core Team, 2021), glmmTMB (Magnusson et al., 2020), MuMIn (Barton, 2016),

r2glmm (Jaeger, 2017), ggplot2 (Wickham, 2016), and ggpubr packages (Kassambara, 2018).

## Results

We collected a total of 123,039 seeds in forests and pastures along the elevational gradient over the 3-month sampling period. The majority of seeds (101,061 seeds, 82%) was collected in the forests, whereas 28% (21,978) of seeds was recorded in the pastures. Overall, we recorded 255 species/morphospecies, of which 74 were identified to family, 49 to genera, and 33 to species level. Seed rain consisted of 149 species/morphospecies in the forests, and 110 species/morphospecies in the pastures. Four species (*Hedyosmum purpurascens*, *Morella pubescens*, *Bidens* sp. and *Melinis* sp.) were recorded in both habitat types. The exotic grass *Setaria sphacelata* was the unique species recorded in pastures at all three elevations. Overall, only six species were shared between at least two elevations (Appendix S3) indicating a very high turn-over of species between habitats and elevations.

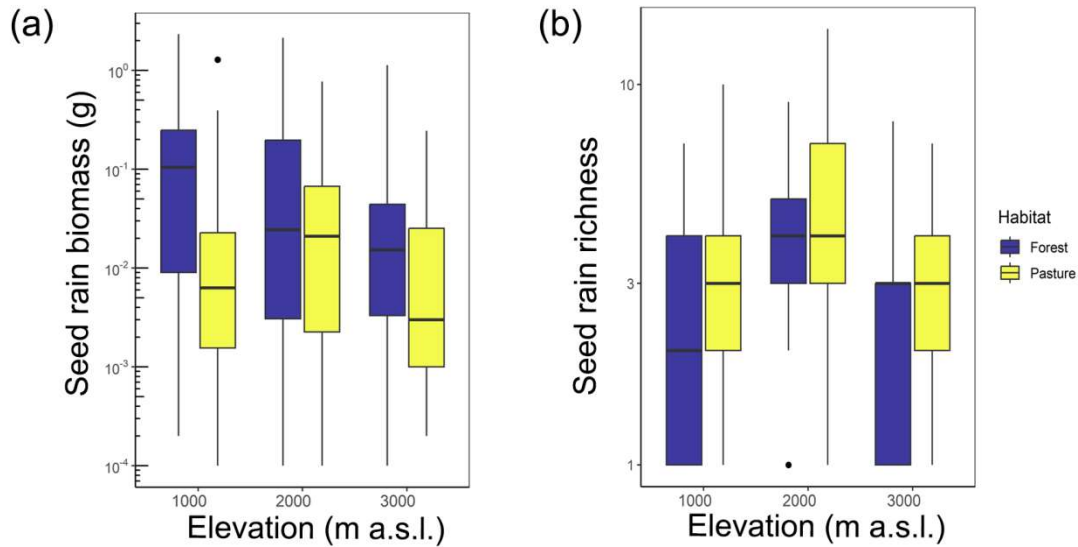
Seed rain biomass was highly variable across seed traps (ranging from 0.0001 g to 2.32 g of seeds per seed trap). Seed rain biomass decreased from forests to pastures, but this was only significant at the lowest elevation (see significant habitat type x elevation interaction terms in Table 1, Figure 2a). In addition, seed rain biomass consistently declined towards high elevations in forests, while it remained constant in pastures across elevations.

Seed rain richness varied among traps ranging from traps with seeds from a single plant species to traps with seeds belonging to up to fourteen species. Seed rain richness was highest at 2000 m, but was not affected by habitat type or by the interaction between elevation and habitat type (Table 1, Figure 2b).

Seed mass ranged from 0.000018 g to 0.72 g per trap. It declined from forest to pastures, in particular at the two lower elevations (see significant habitat type x elevation interaction term in Table 2, Figure 3a). In addition, seed mass consistently declined with increasing elevation in forests. A similar trend was observed in pastures although the decline in seed mass was less pronounced at the highest elevation (see significant habitat type x elevation interaction term in Table 2, Figure 3a).

Endozoochorous species represented 52.8% of the total plant species recorded in the seed rain across all elevations and habitat types. 76% of species were dispersed by endozoochory in the forest, and 58% in the pastures (Table S1). The proportion of

endozoochory generally decreased from forests to pastures (Table 2, Figure 3b) and consistently decreased with increasing elevation in forests and pastures. Across the four models, habitat type and elevation explained most variation in models of seed mass and proportion of endozoochory compared to models of seed rain biomass and richness (see  $R^2$  values given in Tables 1 and 2).



**Figure 2.** Seed rain biomass and richness in forest and pastures across elevations in southern Ecuador. (a) Seed rain biomass is shown log<sub>10</sub>-transformed and is defined as the total dry biomass of seeds collected per trap over three months; (b) Seed rain richness is defined as the total number of species per trap over three months. Boxes show 25th and 75th percentiles, with the median indicated, whiskers show data range and black points are outliers.

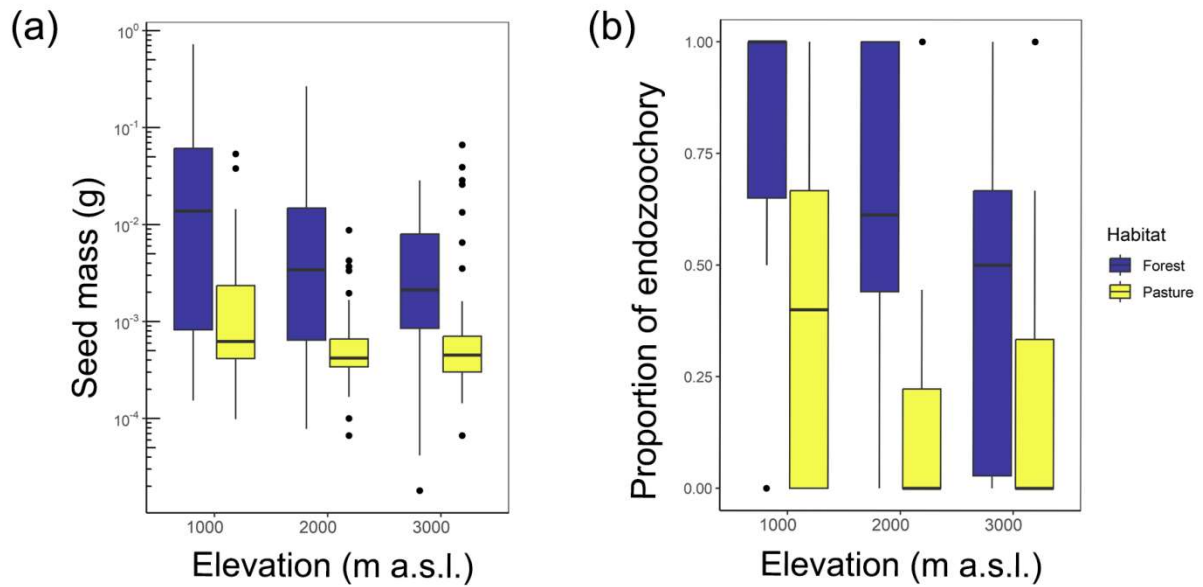


**Table 1.** Generalized linear mixed effect models (GLMMs) of the main and interaction effects of habitat and elevation on seed rain biomass and richness. The model of seed rain biomass was fitted with a Gaussian error distribution, and the model of seed rain richness with a Poisson error distribution. Given are estimates, standard errors (SE),  $z$  values and  $p$ -values. The proportion of variance explained by fixed factors ( $R^2_m$ ) and random and fixed factors ( $R^2_c$ ) are shown in the final columns. Sample size corresponds to 324 traps. Identities of plots ( $n = 18$ ) were included as a random effect. Bold letters indicate that the difference is statistically significant.

Model	Elevation	Estimate	SE	$z$	$p$ -value	$R^2_m$	$R^2_c$
Seed rain biomass	Intercept	-1.31	0.13	-9.97	< <b>0.001</b>		
	Habitat pasture	-0.88	0.17	-5.14	< <b>0.001</b>		
	2000 m	-0.37	0.17	-2.21	<b>0.03</b>	0.09	0.09
	3000 m	-0.64	0.17	-3.72	< <b>0.001</b>		
	Habitat pasture x 2000 m	0.72	0.23	3.12	<b>0.002</b>		
	Habitat pasture x 3000 m	0.51	0.24	2.13	<b>0.03</b>		
Seed rain richness	Intercept	0.99	0.13	7.49	< <b>0.001</b>	0.13	0.21
	Habitat pasture	0.17	0.18	0.96	0.34		
	2000 m	0.34	0.18	1.92	0.05		
	3000 m	0.06	0.18	0.33	0.74		
	Habitat pasture x 2000 m	0.11	0.24	0.49	0.63		
	Habitat pasture x 3000 m	-0.16	0.26	-0.61	0.54		

**Table 2.** Generalized linear mixed effect models (GLMMs) of the main and interaction effects of habitat type and elevation on seed mass and the proportion of endozoochorous species. The model of seed mass was fitted with a Gaussian error distribution, and the model of the proportion of endozoochorous species with a binomial error distribution. Given are estimates, standard errors (SE),  $z$  values and  $p$ -values. The proportion of variance explained by fixed factors ( $R^2_m$ ) and random and fixed factors ( $R^2_c$ ) are shown in the final columns. Sample size corresponds to 324 traps. Identities of plots ( $n = 18$ ) were included as a random effect. Bold letters indicate that the difference is statistically significant.

Model	Elevation	Estimate	SE	$z$	$p$ -value	$R^2_m$	$R^2_c$
Seed mass	Intercept	-2.08	0.12	-18.01	< <b>0.001</b>	0.22	0.23
	Habitat pasture	-0.92	0.16	-5.73	< <b>0.001</b>		
	2000 m a.s.l.	-0.44	0.16	-2.80	< <b>0.01</b>		
	3000 m a.s.l.	-0.65	0.16	-4.13	< <b>0.001</b>		
	Habitat pasture x 2000 m a.s.l.	0.13	0.22	0.60	0.55		
	Habitat pasture x 3000 m a.s.l.	0.50	0.22	2.22	<b>0.03</b>		
Proportion of endozoochory	Intercept	1.44	0.28	5.07	< <b>0.001</b>	0.46	0.50
	Habitat pasture	-1.66	0.37	-4.52	< <b>0.001</b>		
	2000 m a.s.l.	-1.00	0.36	-2.79	< <b>0.001</b>		
	3000 m a.s.l.	-1.13	0.37	-3.06	< <b>0.001</b>		
	Habitat pasture x 2000 m a.s.l.	-0.42	0.49	-0.87	0.39		
	Habitat pasture x 3000 m a.s.l.	0.06	0.51	-0.13	0.90		



**Figure 3.** Seed mass and the proportion of endozoochory in forest and pastures across elevations in southern Ecuador. (a) Seed mass per trap is shown log<sub>10</sub>-transformed and is defined as the mean dry mass of all seeds collected per trap over three months (Community-weighted mean of seed mass); (b) The proportion of endozoochorous species in the seed rain of each trap over three months. Boxes show 25th and 75th percentiles, with the median indicated, whiskers show data range and black points are outliers.

## Discussion

We studied seed rain in forest and deforested areas along an elevational gradient in tropical mountains located in southern Ecuador. In contrast to our expectation, we did not find a consistent decline in the amount and diversity of seed rain between forest and pastures. However, we found a systematic shift in the type of dispersed seeds because the seed mass and the proportion of endozoochorous species were higher in the forest than in pastures across elevations.

Our findings contrast with previous studies that have reported a decline in seed rain richness as well as in the number of seeds arriving at deforested areas in montane ecosystems (Holl, 1999; Saavedra et al., 2015). For instance, throughout the course of an entire year, the average quantity of seeds that fell into forest traps in southern Costa Rica was nearly nine times higher than the average number of seeds that did so in pasture traps (Holl, 1999). The same study recorded a higher number of species in forests than in pastures (Holl, 1999). Likewise, in the tropical mountains of the Bolivian

Andes, mean seed density and species richness of dispersed plant species were higher in the forest than in deforested areas (Saavedra et al., 2015). One potential explanation for the high amount and diversity of seeds in pastures may be related to the extent to which seeds originate from old-growth montane forests rather than from alternative seed sources. For example, the high turnover of species between forests and pastures and across elevations indicates that seed rain in pastures was mainly coming from other seed sources, such as riparian vegetation, small patches of secondary forest, hedgerows or remnant trees within the agricultural land use matrix. Despite previous evidence that species richness is a good predictor of resilience (Ratcliffe et al., 2017) and stability of ecosystems (Hautier et al., 2015), our results suggest that high seed rain richness does not necessarily indicate high natural restoration potential in deforested areas.

In line with our prediction, we found systematic changes in the dominant seed traits between forests and pastures across elevations. We recorded a decline in mean seed mass and in the proportion of endozoochorous species arriving in pastures. Our results are consistent with the findings of previous studies showing that the seed dispersal into deforested areas may cause a lack of large seeds of late-successional and endozoochorous species in regenerating areas (Tabarelli et al., 2012; Saavedra et al., 2015).

Interestingly, the difference in seed mass between forest and pastures was less pronounced at high elevations. This may be driven by a general decrease in mean seed size in the forest at the highest elevation because low temperatures may limit the amount of available resources and energy for investment into seed development (Baker, 1972; Körner, 2003; Bu et al., 2007). In addition, seed size is subject to allometric constraints and can be limited by the overall size of plants. A general decrease in plant size in forests at high elevations may therefore also contribute to this effect (Tovar et al., 2020).

### **Implications for restoration**

Analyzing different measures of seed rain increases understanding of how seed rain processes can shape the regeneration of deforested areas without assisted restoration (Carlucci et al., 2020). Our results demonstrate that seed rain into pastures provides a template for future plant regeneration that is very different to the community and trait composition of nearby old-growth montane forests. The reforestation potential of these areas by natural seed dispersal therefore seems to be limited. However, our results also

suggest that small-seeded plants and those that do not rely on dispersal by animals are more likely to reach deforested habitats. Consequently, we recommend prioritizing large-seeded plant species and those dispersed by endozoochory in the restoration efforts of tropical mountains. Importantly, large-seeded species are more likely to experience successful seedling establishment than small-seeded species in response to seed addition (Moles & Westoby, 2002). Therefore, the addition of large-seeded plants in deforested areas could be a key strategy to promote the establishment of these species (Gallegos et al., 2016). Our study demonstrates the need to investigate seed traits in human-modified habitats to target restoration measures towards a high plant trait diversity. If such active measures are not taken, it is likely that the composition of the regenerating vegetation will be very dissimilar to that of current forests. Restoration efforts should be based on collecting data on seed trait composition (Funk & McDaniel, 2010), as well as quantifying the limited number of seeds and species in deforested areas of tropical mountains.

## References

- Acosta-Rojas, D., Barczyk, M., Espinosa, C., Gusmán, J., Peña, J., Neuschulz, E., Schleuning, M., & Homeier, J. (2021) Field guide of animal-dispersed plants: fruits and seeds in and around Podocarpus National Park. Quito: INABIO.
- 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, 408–417. <https://doi.org/10.1111/btp.13195>
- Aguirre, N. (Ed) (2007) Silvicultural contributions to the reforestation with native species in the tropical mountain rainforest region of South Ecuador. München: Technischen Universität München eingereicht.
- Baker, H. G. (1972) Seed weight in relation to environmental conditions in California. *Ecology*, 53, 997–1010. <https://doi.org/10.2307/1935413>
- Barton, K. (2016) MuMIn: multi-model inference. Available at: <https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf> [Accessed 16 May 2023]
- Bello, C., Galetti, M., Montan, D., Pizo, M. A., Mariguela, T. C., Culot, L., et al. (2017) Atlantic frugivory: a plant-frugivore interaction data set for the Atlantic Forest. *Ecology*, 98, 1729–1729. <https://doi.org/10.1002/ecy.1818>

- Bendix, J., Aguire, N., Beck, E., Bräuning, A., Brandl, R., Breuer, L., et al. (2021) A research framework for projecting ecosystem change in highly diverse tropical mountain ecosystems. *Oecologia*, *195*, 589–600. <https://doi.org/10.1007/s00442-021-04852-8>
- Bendix, J., Rollenbeck, R., Richter, M., Fabian, P., & Emck, P. (2008) Climate. In: Beck, E., Bendix, J., Kottke, I., Makeschin, F., & Mosandl, R. (Eds), *Gradients in a Tropical Mountain Ecosystem of Ecuador*. Heidelberg: Springer Berlin, pp. 63–73.
- Bu, H., Chen, X., Xu, X., Liu, K., Jia, P., & Du, G. (2007) Seed mass and germination in an alpine meadow on the eastern Tsinghai–Tibet plateau. *Plant Ecology*, *191*, 127–149. <https://doi.org/10.1007/s11258-006-9221-5>
- Camargo, P. H. S. A., Carlo, T. A., Brancalion, P. H. S., & Pizo, M. A. (2021) Frugivore diversity increases evenness in the seed rain on deforested tropical landscapes. *Oikos*, *00*, 1–13. <https://doi.org/10.1111/oik.08028>
- Carlucci, M. B., Brancalion, P. H. S., Rodrigues, R. R., Loyola, R., & Cianciaruso, M. V. (2020) Functional traits and ecosystem services in ecological restoration. *Restoration Ecology*, *28*, 1372–1383. <https://doi.org/10.1111/rec.13279>
- Crouzeilles, R., Ferreira, M. S., Chazdon, R. L., Lindenmayer, D. B., Sansevero, J. B. B., Monteiro, L., et al. (2017) Ecological restoration success is higher for natural regeneration than for active restoration in tropical forests. *Science Advances*, *3*, e1701345. <https://doi.org/10.1126/sciadv.1701345>
- Cubiña, A., & Aide, T. M. (2001) The effect of distance from forest edge on seed rain and soil seed bank in a tropical pasture. *Biotropica*, *33*, 260–267. <https://doi.org/10.1111/j.1744-7429.2001.tb00177.x>
- Culot, L., Muñoz, F. J. J., Huynen, M.C., Poncin, P., & Heymann, E. W. (2010) Seasonal variation in seed dispersal by Tamarins alters seed rain in a secondary rain forest. *International Journal of Primatology*, *31*, 553–569. <https://doi.org/10.1007/s10764-010-9413-7>
- Dalling, J. W., Hubbell, S. P., & Silvera, K. (1998) Seed dispersal, seedling establishment and gap partitioning among tropical pioneer trees. *Journal of Ecology*, *86*, 674–689. <https://doi.org/10.1046/j.1365-2745.1998.00298.x>
- Del Castillo, R. F., & Ríos, M. A. P. (2008) Changes in seed rain during secondary succession in a tropical montane cloud forest region in Oaxaca, Mexico. *Journal of Tropical Ecology*, *24*, 433–444. <https://doi.org/10.1017/S0266467408005142>

- Estrada-Villegas, S., Stevenson, P., López, O., DeWalt, S. J., Comita, L. S., & Dent, D. H. (2023) Animal seed dispersal recovery during passive restoration in a forested landscape. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 378, 20210076. <https://doi.org/10.1098/rstb.2021.0076>
- Funk, J. L., & McDaniel, S. (2010) Altering light availability to restore invaded forest: the predictive role of plant traits. *Restoration Ecology*, 18, 865–872. <https://doi.org/10.1111/j.1526-100X.2008.00515.x>
- Gallegos, S. C., Beck, S. G., Hensen, I., Saavedra, F., Lippok, D., & Schleuning, M. (2016) Factors limiting montane forest regeneration in bracken-dominated habitats in the tropics. *Forest Ecology and Management*, 381, 168–176. <https://doi.org/10.1016/j.foreco.2016.09.014>
- García, D., & Martínez, D. (2012) Species richness matters for the quality of ecosystem services: a test using seed dispersal by frugivorous birds. *Proceedings of the Royal Society B: Biological Sciences*, 279, 3106–3113. <https://doi.org/10.1098/rspb.2012.0175>
- Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., et al. (2013) High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science*, 342, 850–853. <https://doi.org/10.1126/science.1244693>
- Harms, K. E., & Dalling, J. W. (1997) Damage and herbivory tolerance through resprouting as an advantage of large seed size in tropical trees and lianas. *Journal of Tropical Ecology*, 13, 617–621. <https://doi.org/10.1017/S0266467400010750>
- Hautier, Y., Tilman, D., Isbell, F., Seabloom, E. W., Borer, E. T., & Reich, P. B. (2015) Anthropogenic environmental changes affect ecosystem stability via biodiversity. *Science*, 348, 336–340. <https://doi.org/10.1126/science.aaa1788>
- Holl, K. D. (1999) Factors limiting tropical rain forest regeneration in abandoned pasture: seed Rain, seed germination, microclimate, and soil. *Biotropica*, 31, 229–242. <https://doi.org/10.1111/j.1744-7429.1999.tb00135.x>
- Holl, K. D. (2012) Restoration of Tropical Forests. In: van Andel, J. & Aronson, J. (Eds), *Restoration Ecology: The New Frontier*. 2nd edition. Chichester: Wiley Blackwell, pp. 103–114.
- Holl, K. D. (Ed) (2023) *Introducción a la Restauración Ecológica*. México DF: CopIt-arXives.
- Holl, K. D., Loik, M. E., Lin, E. H. V., & Samuels, I. A. (2000) Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and

- establishment. *Restoration Ecology*, 8, 339–349. <https://doi.org/10.1046/j.1526-100x.2000.80049.x>
- Homeier, J., Werner, F. A., Gradstein, S. R., Breckle, S. W., & Richter, M. (2008) Potential vegetation and floristic composition of Andean forests in South Ecuador, with a focus on the RBSF. In: Beck, E., Bendix, J., Kottke, I., Makeschin, F., & Mosandl, R. (Eds), *Gradients in a Tropical Mountain Ecosystem of Ecuador*. Heidelberg: Springer Berlin, pp. 87–100.
- Howe, H. F., & Smallwood, J. (1982) Ecology of Seed Dispersal. *Annual Review of Ecology and Systematics*, 13, 201–228.
- Hubbell, S. P. (Ed) (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton: Princeton University Press.
- Jaeger, B. (2017) *Computes R Squared for Mixed (Multilevel) Models (0.1.2)*. Available at: <https://github.com/bcjaeger/r2glmm> [Accessed 16 May 2023]
- Kassambara, A. (2018) *ggpubr: “ggplot2” Based Publication Ready Plots*. Available at: <https://rpkgs.datanovia.com/ggpubr/> [Accessed 16 May 2023]
- Kitajima, K. (2002) Do shade-tolerant tropical tree seedlings depend longer on seed reserves? Functional growth analysis of three Bignoniaceae species. *Functional Ecology*, 16, 433–444. <https://doi.org/10.1046/j.1365-2435.2002.00641.x>
- Körner, C. (Ed) (2003) *Alpine Plant Life*. Berlin: Springer.
- Le Bagousse-Pinguet, Y., Gross, N., Maestre, F. T., Maire, V., Bello, F., Fonseca, C., et al. (2017) Testing the environmental filtering concept in global drylands. *Journal of Ecology*, 105, 1058–1069. <https://doi.org/10.1111/1365-2745.12735>
- Levin, S. A., Muller-Landau, H. C., Nathan, R., & Chave, J. (2003) The ecology and evolution of seed dispersal: a theoretical perspective. *Annual Review of Ecology, Evolution, and Systematics*, 34, 575–604. <https://doi.org/10.1146/annurev.ecolsys.34.011802.132428>
- Magnusson, A., Skaug, H. J., Nielsen, A., Berg, C. W., Kristensen, K., Maechler, M., et al. (2020) Package “glmmTMB”. *Generalized Linear Mixed Models using Template Model Builder*. Available at: <https://cran.r-project.org/web/packages/glmmTMB/index.html> [Accessed 16 May 2023]
- Markl, J. S., Schleuning, M., Forget, P. M., Jordano, P., Lambert, J. E., Traveset, A., et al. (2012) Meta-Analysis of the effects of human disturbance on seed dispersal by animals. *Conservation Biology*, 26, 1072–1081. <https://doi.org/10.1111/j.1523-1739.2012.01927.x>



- Martínez-Garza, C., Flores-Palacios, A., De La Peña-Domene, M., & Howe, H. F. (2009) Seed rain in a tropical agricultural landscape. *Journal of Tropical Ecology*, 25, 541–550. <https://doi.org/10.1017/S0266467409990113>
- Mazón, M., Aguirre, N., Echeverría, C., & Aronson, J. (2019) Monitoring attributes for ecological restoration in Latin America and the Caribbean region. *Restoration Ecology*, 27, 992–999. <https://doi.org/10.1111/rec.12986>
- Meli, P., Holl, K. D., Rey Benayas, J. M., Jones, H. P., Jones, P. C., Montoya, D., et al. (2017) A global review of past land use, climate, and active vs. passive restoration effects on forest recovery. *PLOS ONE*, 12, e0171368. <https://doi.org/10.1371/journal.pone.0171368>
- Moles, A., & Westoby, M. (2002) Seed addition experiments are more likely to increase recruitment in larger-seeded species. *Oikos*, 99, 241–248. <https://doi.org/10.1034/j.1600-0706.2002.990204.x>
- Muscarella, R., & Fleming, T. H. (2007) The role of frugivorous bats in tropical forest succession. *Biological Reviews*, 82, 573–590. <https://doi.org/10.1111/j.1469-185X.2007.00026.x>
- Palma, A. C., Goosem, M., Fensham, R. J., Goosem, S., Preece, N. D., Stevenson, P. et al. (2021) Dispersal and recruitment limitations in secondary forests. *Journal of Vegetation Science*, 32, e12975. <https://doi.org/10.1111/jvs.12975>
- Pandit, R., Scholes, R., Montanarella, L., Brainich, A., Barger, N., ten Brink, B., et al. (2018) Summary for policymakers of the assessment report on land degradation and restoration of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Available at: [https://www.ipbes.net/system/tdf/spm\\_3bi\\_ldr\\_digital.pdf?file=1&type=node&id=28335](https://www.ipbes.net/system/tdf/spm_3bi_ldr_digital.pdf?file=1&type=node&id=28335) [Accessed 16 May 2023]
- Quitíán, M., Santillán, V., Bender, I. M. A., Espinosa, C. I., Homeier, J., Böhning-Gaese, K., et al. (2019) Functional responses of avian frugivores to variation in fruit resources between natural and fragmented forests. *Functional Ecology*, 33, 399–410. <https://doi.org/10.1111/1365-2435.13255>
- Quitíán, M., Santillán, V., Espinosa, C. I., Homeier, J., Böhning-Gaese, K., Schleuning, M., et al. (2018) Elevation-dependent effects of forest fragmentation on plant-bird interaction networks in the tropical Andes. *Ecography*, 41, 1497–1506. <https://doi.org/10.1111/ecog.03247>

- R Core Team. (Eds) (2021). A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.
- Ratcliffe, S., Wirth, C., Jucker, T., van der Plas, F., Scherer-Lorenzen, M., Verheyen, K., et al. (2017) Biodiversity and ecosystem functioning relations in European forests depend on environmental context. *Ecology Letters*, 20, 1414–1426. <https://doi.org/10.1111/ele.12849>
- Reid, J. (2015) Indicators of success should be sensitive to compositional failures: reply to Suganuma and Durigan. *Restoration Ecology*, 23, 519–520. <https://doi.org/10.1111/rec.12254>
- Reid, J., Wilson, S. J., Bloomfield, G. S., Cattau, M. E., Fagan, M. E., Holl, K. D., et al. (2017). How long do restored ecosystems persist? *Annals of the Missouri Botanical Garden*, 102, 258–265. <https://doi.org/10.3417/2017002>
- Ricketts, T. (2001) The matrix matters: effective isolation in fragmented landscapes. *The American Naturalist*, 158, 87–99.
- Russo, S. E., & Augspurger, C. K. (2004) Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. *Ecology Letters*, 7, 1058–1067. <https://doi.org/10.1111/j.1461-0248.2004.00668.x>
- Saavedra, F., Hensen, I., & Schleuning, M. (2015) Deforested habitats lack seeds of late-successional and large-seeded plant species in tropical montane forests. *Applied Vegetation Science*, 18, 603–612. <https://doi.org/10.1111/avsc.12184>
- San-José, M., Arroyo-Rodríguez, V., Jordano, P., Meave, J. A., & Martínez-Ramos, M. (2019) The scale of landscape effect on seed dispersal depends on both response variables and landscape predictor. *Landscape Ecology*, 34, 1069–1080. <https://doi.org/10.1007/s10980-019-00821-y>
- San-José, M., Arroyo-Rodríguez, V., & Meave, J. A. (2020) Regional context and dispersal mode drive the impact of landscape structure on seed dispersal. *Ecological Applications*, 30, e02033. <https://doi.org/10.1002/eap.2033>
- Schupp, E. W., Milleron, T., & Russo, S. E. (2002) Dissemination limitation and the origin and maintenance of species-rich tropical forests. In: Levey, D. J., Silva, W. R., & Galetti, M. (Eds) *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. Wallingford: CABI Publishing, pp 19–33.
- Šímová, I., Violle, C., Kraft, N. J. B., Storch, D., Svenning, J.-C., Boyle, B., et al. (2015) Shifts in trait means and variances in North American tree assemblages: species

- richness patterns are loosely related to the functional space. *Ecography*, 38, 649–658. <https://doi.org/10.1111/ecog.00867>
- Stevenson, P. (2001) The relationship between fruit production and primate abundance in Neotropical communities. *Biological Journal of the Linnean Society*, 72, 161–178. <https://doi.org/10.1006/bijl.2000.0497>
- Swenson, N. G., & Enquist, B. J. (2009) Opposing assembly mechanisms in a Neotropical dry forest: implications for phylogenetic and functional community ecology. *Ecology*, 90, 2161–2170. <https://doi.org/10.1890/08-1025.1>
- Tabarelli, M., Peres, C., & Melo, F. (2012) The ‘few winners and many losers’ paradigm revisited: emerging prospects for tropical forest biodiversity. *Biological Conservation*, 155, 136–140. <https://doi.org/10.1016/j.biocon.2012.06.020>
- Terborgh, J., Huanca Nuñez, N., Alvarez Loayza, P., & Cornejo Valverde, F. (2017) Gaps contribute tree diversity to a tropical floodplain forest. *Ecology*, 98, 2895–2903. <https://doi.org/10.1002/ecy.1991>
- Tovar, C., Melcher, I., Kusumoto, B., Cuesta, F., Cleef, A., Meneses, R. I., Halloy, S., Llambí, L. D., Beck, S., Muriel, P., Jaramillo, R., Jácome, J., & Carilla, J. (2020) Plant dispersal strategies of high tropical alpine communities across the Andes. *Journal of Ecology*, 108, 1910–1922. <https://doi.org/10.1111/1365-2745.13416>
- United Nations Environment Programme and Food and Agriculture Organization of the United Nations. (Eds) (2021) Principles for ecosystem restoration to guide the United Nations Decade 2021–2030. Rome: FAO.
- Vancutsem, C., Achard, F., Pekel, J.-F., Vieilledent, G., Carboni, S., Simonetti, D., et al. (2021) Long-term (1990–2019) monitoring of forest cover changes in the humid tropics. *Science Advances*, 7, eabe1603. <https://doi.org/10.1126/sciadv.abe1603>
- Wickham, H. (Eds) (2016) ggplot2: Elegant Graphics for Data Analysis, 1st edition. New York: Springer-Verlag.
- Wijdeven, S. M. J., & Kuzee, M. E. (2000) Seed availability as a limiting factor in forest recovery processes in Costa Rica. *Restoration Ecology*, 8, 414–424. <https://doi.org/10.1046/j.1526-100x.2000.80056.x>
- Wright, J. S. (2002) Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia*, 130, 1–14. <https://doi.org/10.1007/s004420100809>

Zimmerman, J. K., Pascarella, J. B., & Aide, T. M. (2000) Barriers to forest regeneration in an abandoned pasture in Puerto Rico. *Restoration Ecology*, 8, 350–360. <https://doi.org/10.1046/j.1526-100x.2000.80050.x>

## **Supporting information**

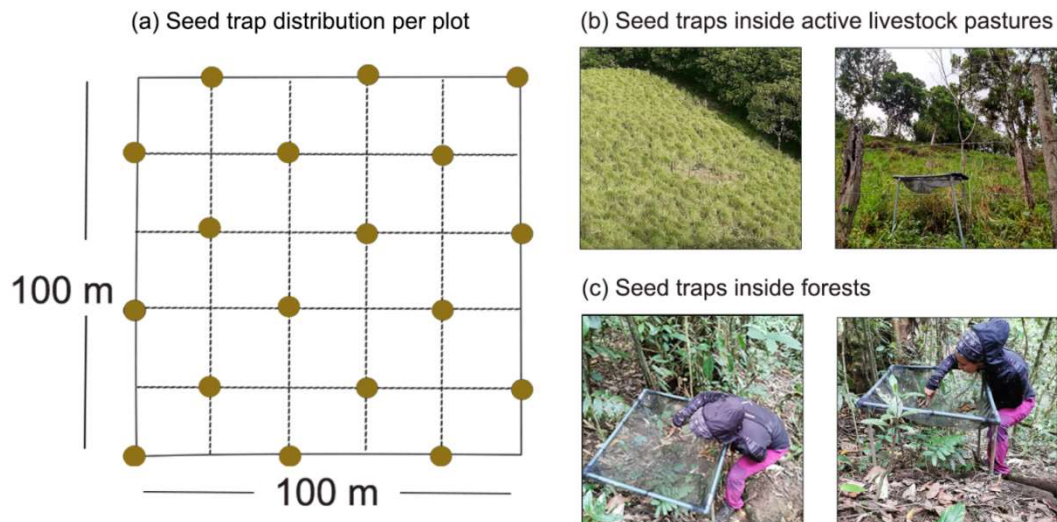
**Appendix S1.** Distances among pasture plots and forests along the elevational gradient in the tropical montane forests of southern Ecuador. Nine pasture plots were located at three elevations (1000, 2000 and 3000 m a.s.l.). Given are plot ID, the minimum distance from the plot center to the forest edge, to the closest conserved forest, and to the closest reference plot in the forest located at the same elevation.

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<b>Elevation</b>	<b>Plot ID</b>	<b>Distance to the forest edge (m)</b>	<b>Distance to the closest conserved forest (m)</b>	<b>Distance to the closest reference plot in the forests (m)</b>
1000 m a.s.l.	BO1P	96.0	511.0	7796.0
	BO2P	141.0	506.0	6755.0
	BO3P	183.6	456.0	6722.0
2000 m a.s.l.	SF1P	209.0	550.0	788.0
	SF2P	110.0	636.0	960.0
	SF3P	387.0	846.0	1063.0
3000 m a.s.l.	CA1P	247.0	455.0	2215.0
	CA2P	174.0	443.0	2071.0
	CA3P	103.0	325.0	1974.0

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**Appendix S2.** Scheme of study design inside 18 1-ha plots installed in forests and active livestock pastures along an elevational gradient in southern Ecuador: (a) Distribution of seed traps inside each plot (each trap is marked with a brown circle). (b) Seed traps were fenced by wire cable to avoid trap damaging by cattle. (c) Seed rain sampling inside forest plots.



**Appendix S3.** Seed dispersal mode and number of seeds collected per species/morphospecies in the tropical montane forests of southern Ecuador. Seeds were collected along an elevational gradient at 1000, 2000 and 3000 m a.s.l in two habitat types: forests (F) and active livestock pastures (P). The amount of seeds corresponds to the overall number of seeds collected in the 324 traps over the three months period. Taxonomic identity is indicated by family and species/morphospecies. Seed dispersal modes correspond to either endozoochorous (E) or non-endozoochorous (NE) species.

Family	Species/morphospecies	Elevation	Habitat	Seed dispersal mode	Amount of seeds
ACANTHACEAE	<i>Mendoncia gracilis</i>	1000	F	NE	3
ACTINIDACEAE	<i>Saurauia sp1</i>	1000	F	E	73
ACTINIDACEAE	<i>Saurauia sp2</i>	1000	F	E	474
ALZATEACEAE	<i>Alzatea verticillata</i>	2000	F	NE	16403
AMARANTHACEAE	<i>Amaranthaceae sp</i>	2000	F	E	1
ANACARDIACEAE	<i>Tapirira guianensis subandina</i>	2000	F	E	16
ANNONACEAE	<i>Guatteria pastaza</i>	1000	F	E	19
APIACEAE	<i>Daucus sp</i>	2000, 3000	P	NE	30
APOCYNACEAE	<i>Apocynaceae sp1</i>	1000	P	NE	25
APOCYNACEAE	<i>Apocynaceae sp2</i>	3000	P	NE	1
APOCYNACEAE	<i>Apocynaceae sp3</i>	2000	P	NE	349
AQUIFOLIACEAE	<i>Ilex laurina</i>	3000	P	NE	6
AQUIFOLIACEAE	<i>Ilex sp</i>	2000	F	NE	7
ARALIACEAE	<i>Araliaceae</i>	1000	P	E	5
ARECACEAE	<i>Arecaceae sp1</i>	1000	F	E	1

ARECACEAE	<i>Arecaceae sp2</i>	1000	P	E	6
ASTERACEAE	<i>Critoniopsis sp</i>	1000	F	NE	69
ASTERACEAE	<i>Asteraceae sp1</i>	1000	P	NE	437
ASTERACEAE	<i>Asteraceae sp2</i>	3000	F	NE	8
ASTERACEAE	<i>Asteraceae sp3</i>	2000	F	NE	93
ASTERACEAE	<i>Asteraceae sp4</i>	2000	P	NE	449
ASTERACEAE	<i>Asteraceae sp5</i>	1000	P	NE	655
ASTERACEAE	<i>Asteraceae sp6</i>	3000	F	NE	94
ASTERACEAE	<i>Asteraceae sp7</i>	3000	P	NE	20
ASTERACEAE	<i>Asteraceae sp8</i>	2000	F	NE	4
ASTERACEAE	<i>Asteraceae sp9</i>	2000	P	NE	65
ASTERACEAE	<i>Asteraceae sp10</i>	1000	F	NE	32
ASTERACEAE	<i>Asteraceae sp11</i>	2000	F	NE	41
ASTERACEAE	<i>Asteraceae sp12</i>	2000	P	NE	39
ASTERACEAE	<i>Asteraceae sp13</i>	3000	F	NE	37
ASTERACEAE	<i>Asteraceae sp14</i>	2000	F	NE	17
ASTERACEAE	<i>Asteraceae sp15</i>	2000	P	NE	8
ASTERACEAE	<i>Bidens sp1</i>	1000	P	NE	127
ASTERACEAE	<i>Bidens sp2</i>	1000	F, P	NE	438
ASTERACEAE	<i>Bidens pilosa</i>	3000	P	NE	355
ASTERACEAE	<i>Bidens sp3</i>	2000	P	NE	147
BIGNONIACEAE	<i>Bignoniaceae sp1</i>	2000	P	NE	49
BIGNONIACEAE	<i>Bignoniaceae sp2</i>	2000	P	NE	1
BIGNONIACEAE	<i>Handroanthus chrysanthus</i>	2000	F	NE	57
BURSERACEAE	<i>Protium sp</i>	1000	F	NE	5
CANNABACEAE	<i>Celtis iguanea</i>	1000	F	E	4
CELASTRACEAE	<i>Celastraceae sp</i>	3000	P	E	2
CHLORANTHACEAE	<i>Hedyosmum purpurascens</i>	3000	F, P	E	17
CHLORANTHACEAE	<i>Hedyosmum sp</i>	3000	F	E	15



CLETHRACEAE	<i>Clethra revoluta</i>	2000, 3000	F	NE	147
CLUSIACEAE	<i>Clusia ducuoides</i>	2000	F	E	1
CLUSIACEAE	<i>Clusia sp</i>	3000	F	E	9
CLUSIACEAE	<i>Clusiaceae sp</i>	3000	F	E	10
COMBRETACEAE	<i>Terminalia sp</i>	1000	P	NE	192
CUNNONIACEAE	<i>Weinmania pubescens</i>	3000	F	NE	41
ERICACEAE	<i>Ericaceae sp1</i>	1000	F	E	50
ERICACEAE	<i>Ericaceae sp2</i>	1000	P	E	632
ERICACEAE	<i>Ericaceae sp3</i>	2000	F	E	1241
ERICACEAE	<i>Ericaceae sp4</i>	2000	P	E	6
ERICACEAE	<i>Ericaceae sp5</i>	1000	F	E	1371
ERICACEAE	<i>Ericaceae sp6</i>	2000	F	E	7
EUPHORBIACEAE	<i>Alchornea lojaensis</i>	2000	F	E	2
EUPHORBIACEAE	<i>Alchornea sp1</i>	2000	F	E	6
EUPHORBIACEAE	<i>Alchornea sp2</i>	1000	P	E	19
EUPHORBIACEAE	<i>Alchornea sp3</i>	1000	F	E	1
EUPHORBIACEAE	<i>Hieronyma sp</i>	3000	P	E	2
EUPHORBIACEAE	<i>Sapium sp1</i>	1000	F	E	1
EUPHORBIACEAE	<i>Sapium sp2</i>	2000	F	E	3
FABACEAE	<i>Fabaceae sp1</i>	1000	P	E	1
FABACEAE	<i>Fabaceae sp2</i>	1000	P	E	7
FABACEAE	<i>Fabaceae sp3</i>	1000	P	E	9
HYPERICACEAE	<i>Vismia cavanillesiana</i>	2000	F	E	49
LAURACEAE	<i>Ocotea calophylla</i>	3000	F	E	1
LAURACEAE	<i>Persea sp1</i>	2000	F	E	1
LAURACEAE	<i>Persea sp2</i>	2000	F	E	5
LAURACEAE	<i>Lauraceae sp1</i>	1000	F	E	1
LAURACEAE	<i>Lauraceae sp2</i>	1000	F	E	1
LAURACEAE	<i>Persea ferruginea</i>	3000	F	E	2

MALPIGUIACEAE	<i>Banisteriopsis sp</i>	2000	P	NE	1
MALVACEAE	<i>Mollia sp</i>	1000	F	NE	93
MELASTOMATAACEAE	<i>Meriania sp1</i>	2000	F	NE	3566
MELASTOMATAACEAE	<i>Melastomataceae sp1</i>	1000	F	E	94
MELASTOMATAACEAE	<i>Melastomataceae sp2</i>	1000	P	E	75
MELASTOMATAACEAE	<i>Melastomataceae sp3</i>	3000	F	E	86
MELASTOMATAACEAE	<i>Melastomataceae sp4</i>	3000	P	E	17
MELASTOMATAACEAE	<i>Melastomataceae sp5</i>	1000	F	E	27
MELASTOMATAACEAE	<i>Melastomataceae sp6</i>	3000	F	E	52
MELASTOMATAACEAE	<i>Melastomataceae sp7</i>	2000	F	E	95
MELASTOMATAACEAE	<i>Melastomataceae sp8</i>	3000	F	E	3536
MELASTOMATAACEAE	<i>Melastomataceae sp9</i>	2000	F	E	1606
MELASTOMATAACEAE	<i>Melastomataceae sp10</i>	2000	F	E	8
MELASTOMATAACEAE	<i>Melastomataceae sp11</i>	3000	F	E	54
MELASTOMATAACEAE	<i>Meriania tomentosa</i>	3000	F	NE	101
MELASTOMATAACEAE	<i>Meriania sp2</i>	3000	F	NE	160
MELASTOMATAACEAE	<i>Meriania sp3</i>	3000	F	NE	200
MELASTOMATAACEAE	<i>Meriania sp4</i>	3000	F	NE	10380
MELASTOMATAACEAE	<i>Meriania sp5</i>	3000	F	NE	1064
MELASTOMATAACEAE	<i>Meriania sp6</i>	3000	F	NE	3241
MELASTOMATAACEAE	<i>Meriania sp7</i>	3000	F	NE	113
MELASTOMATAACEAE	<i>Miconia punctata</i>	1000	F	E	39
MELASTOMATAACEAE	<i>Miconia aff. punctata</i>	2000	F	E	2
MELASTOMATAACEAE	<i>Miconia sp</i>	3000	F	E	3210
MELIACEAE	<i>Cedrela odorata</i>	2000	P	NE	14
MELIACEAE	<i>Guarea macrophylla</i>	1000	F	E	12
MENISPERMACEAE	<i>Odontocarya sp</i>	1000	F	E	8
MORACEAE	<i>Ficus sp1</i>	1000	F	E	14946
MORACEAE	<i>Ficus sp2</i>	2000	F	E	770

MORACEAE	<i>Ficus sp3</i>	1000	F	E	2
MORACEAE	<i>Ficus sp4</i>	2000	F	E	1
MORACEAE	<i>Naucleopsis francisci</i>	2000	F	E	1
MYRICACEAE	<i>Morella pubescens</i>	2000, 3000	F, P	E	5
PASSIFLORACEAE	<i>Passifloraceae sp</i>	2000	P	E	24
PENTAPHYLACACEAE	<i>Ternstroenia macrocarpa</i>	3000	F	E	34
PHYLLANTHACEAE	<i>Hieronyma sp</i>	2000	F	E	2
PHYLLANTHACEAE	<i>Hieronyma fendleri</i>	2000	F	E	80
PIPERACEAE	<i>Piperaceae sp</i>	2000	F	E	33943
POACEAE	<i>Axonopus sp</i>	2000, 3000	P	NE	1286
POACEAE	<i>Chusquea falcata</i>	2000	F	E	316
POACEAE	<i>Holcus lanatus</i>	1000	P	NE	14
POACEAE	<i>Melinis sp</i>	1000, 3000	F, P	NE	631
POACEAE	<i>Panicum sp</i>	1000	P	NE	178
POACEAE	<i>Paspalum sp1</i>	1000	P	NE	40
POACEAE	<i>Poaceae sp1</i>	1000	F	NE	50
POACEAE	<i>Poaceae sp10</i>	2000	P	NE	15
POACEAE	<i>Poaceae sp11</i>	1000	P	NE	3
POACEAE	<i>Poaceae sp12</i>	2000	P	NE	19
POACEAE	<i>Poaceae sp13</i>	1000	P	NE	1
POACEAE	<i>Poaceae sp14</i>	1000	P	NE	6
POACEAE	<i>Poaceae sp2</i>	3000	P	NE	587
POACEAE	<i>Poaceae sp3</i>	2000	F	NE	721
POACEAE	<i>Poaceae sp5</i>	1000	P	NE	18
POACEAE	<i>Poaceae sp6</i>	3000	P	NE	428
POACEAE	<i>Poaceae sp7</i>	2000	P	NE	6
POACEAE	<i>Poaceae sp8</i>	1000	P	NE	8
POACEAE	<i>Poaceae sp9</i>	2000	P	NE	4178
POACEAE	<i>Setaria sphacelata</i>	1000, 2000, 3000	P	NE	9087

POACEAE	<i>Valeriana sp</i>	2000	F	NE	1
POLYGONACEAE	<i>Muehlenbeckia tamnifolia</i>	3000	F	E	3
POLYGONACEAE	<i>Triplaris sp</i>	1000	F	NE	1
PRIMULACEAE	<i>Myrsine coriacea</i>	1000	P	E	5
PRIMULACEAE	<i>Myrsine sp</i>	1000	F	E	1
PRIMULACEAE	<i>Primulaceae sp</i>	3000	F	E	7
ROSACEAE	<i>Prunus sp</i>	1000	F	E	1
ROSACEAE	<i>Rubus sp</i>	1000, 2000	P	E	3
RUBIACEAE	<i>Rubiaceae sp</i>	3000	F	E	6
RUBIACEAE	<i>Guettarda sp1</i>	1000	F	E	1
RUBIACEAE	<i>Faramea sp</i>	2000	F	E	3
RUBIACEAE	<i>Guettarda sp2</i>	2000	F	E	2
RUBIACEAE	<i>Ladenbergia oblongifolia</i>	1000	F	NE	66
RUBIACEAE	<i>Rubiaceae sp1</i>	3000	F	E	4
RUBIACEAE	<i>Rubiaceae sp2</i>	3000	P	E	2
RUBIACEAE	<i>Rubiaceae sp3</i>	2000	F	E	26
RUBIACEAE	<i>Matayba inelegans</i>	2000	F	E	16
SIPARUNACEAE	<i>Siparuna muricata</i>	3000	F	E	8
SOLANACEAE	<i>Solanaceae sp1</i>	1000	F	E	1
SOLANACEAE	<i>Solanaceae sp2</i>	1000	P	E	1
SOLANACEAE	<i>Solanaceae sp3</i>	2000	P	E	27
SYMPLOCACEAE	<i>Symplocaceae sp1</i>	3000	F	E	2
SYMPLOCACEAE	<i>Symplocaceae sp2</i>	3000	F	E	1
SYMPLOCACEAE	<i>Symplocaceae sp3</i>	3000	F	E	1
UNDETERMINED	MB026	1000	F	NE	4
UNDETERMINED	MB028	1000	F	E	10
UNDETERMINED	MB039	1000	F	E	1
UNDETERMINED	MB042	1000	F	E	1
UNDETERMINED	MB045	1000	F	E	1

UNDETERMINED	MB059	1000	F	E	2
UNDETERMINED	MB072	1000	F	E	1
UNDETERMINED	MB089	1000	F	E	1
UNDETERMINED	MB155	1000	F	E	12
UNDETERMINED	MB157	1000	F	E	3
UNDETERMINED	MB170	1000	F	E	3
UNDETERMINED	MB177	1000	F	E	2
UNDETERMINED	MB187	1000	F	E	4
UNDETERMINED	MB197	1000	F	E	1
UNDETERMINED	MB206	1000	F	E	2
UNDETERMINED	MB208	1000	F	E	2
UNDETERMINED	MB218	1000	F	E	2
UNDETERMINED	MB228	1000	F	E	1
UNDETERMINED	MB231	1000	F	E	1
UNDETERMINED	MB240	1000	F	E	2
UNDETERMINED	MB241	1000	F	E	1
UNDETERMINED	MBOP_001	1000	P	E	21
UNDETERMINED	MBOP_003	1000	P	E	1
UNDETERMINED	MBOP_004	1000	P	E	12
UNDETERMINED	MBOP_005	1000	P	E	1
UNDETERMINED	MBOP_006	1000	P	E	7
UNDETERMINED	MBOP_007	1000	P	E	4
UNDETERMINED	MBOP_008	1000	P	E	1
UNDETERMINED	MBOP_010	1000	P	NE	25
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UNDETERMINED	MBOP_015	1000	P	E	4
UNDETERMINED	MBOP_016	1000	P	E	2

UNDETERMINED	MBOP_017	1000	P	E	1
UNDETERMINED	MBOP_020	1000	P	E	5
UNDETERMINED	MBOP_021	1000	P	NE	1
UNDETERMINED	MC012	3000	F	NE	326
UNDETERMINED	MC041	3000	F	E	1
UNDETERMINED	MC045	3000	F	E	3
UNDETERMINED	MC079	3000	F	E	1
UNDETERMINED	MC106	3000	F	E	1
UNDETERMINED	MC108	3000	F	E	20
UNDETERMINED	MC119	3000	F	E	107
UNDETERMINED	MC120	3000	F	E	1
UNDETERMINED	MC121	3000	F	E	3
UNDETERMINED	MC127	3000	F	E	1
UNDETERMINED	MC149	3000	F	E	1
UNDETERMINED	MC154	3000	F	E	1
UNDETERMINED	MCAP_001	3000	P	E	6
UNDETERMINED	MCAP_002	3000	P	E	13
UNDETERMINED	MCAP_003	3000	P	E	6
UNDETERMINED	MCAP_004	3000	P	E	2
UNDETERMINED	MCAP_005	3000	P	E	1
UNDETERMINED	MCAP_007	3000	P	E	2
UNDETERMINED	MCAP_010	3000	P	E	2
UNDETERMINED	MCAP_011	3000	P	E	5
UNDETERMINED	MCAP_012	3000	P	E	2
UNDETERMINED	MCAP_013	3000	P	E	1
UNDETERMINED	MCAP_014	3000	P	E	6
UNDETERMINED	MCAP_016	3000	P	E	2
UNDETERMINED	MCAP_017	3000	P	E	1
UNDETERMINED	MCAP_019	3000	P	E	2

UNDETERMINED	MSF034	2000	F	E	4
UNDETERMINED	MSF042	2000	P	E	30
UNDETERMINED	MSF048	2000	F	E	47
UNDETERMINED	MSF069	2000	F	E	1
UNDETERMINED	MSF112	2000	F	E	1
UNDETERMINED	MSF128	2000	F	E	5
UNDETERMINED	MSF140	2000	F	E	25
UNDETERMINED	MSF150	2000	F	E	700
UNDETERMINED	MSF155	2000	F	E	4
UNDETERMINED	MSF157	2000	F	E	1
UNDETERMINED	MSF159	2000	F	E	1
UNDETERMINED	MSF171	2000	F	E	55
UNDETERMINED	MSF173	2000	F	E	1
UNDETERMINED	MSF175	2000	F	E	4
UNDETERMINED	MSFP_002	2000	P	E	12
UNDETERMINED	MSFP_004	2000	P	E	1
UNDETERMINED	MSFP_009	2000	P	E	2
UNDETERMINED	MSFP_010	2000	P	E	2
UNDETERMINED	MSFP_012	2000	P	E	23
UNDETERMINED	MSFP_013	2000	P	E	5
UNDETERMINED	MSFP_015	2000	P	E	91
UNDETERMINED	MSFP_017	2000	P	E	5
UNDETERMINED	MSFP_018	2000	P	E	15
UNDETERMINED	MSFP_019	2000	P	E	1
UNDETERMINED	MSFP_020	2000	P	E	1
UNDETERMINED	MSFP_021	2000	P	E	6
UNDETERMINED	MSFP_024	2000	P	NE	1
UNDETERMINED	MSFP_025	2000	P	NE	29
UNDETERMINED	MSFP_027	2000	P	NE	1

UNDETERMINED	MSFP_029	2000	P	NE	120
UNDETERMINED	MSFP_030	2000	P	E	20
UNDETERMINED	MSFP_033	2000	P	NE	12
UNDETERMINED	MSFP_035	2000	P	E	91
UNDETERMINED	MSFP_036	2000	P	E	15
URTICACEAE	<i>Cecropia angustifolia</i>	1000	P	E	3
VIOLACEAE	<i>Leonia crassa</i>	1000	F	E	1
ZYGOPHYLLACEAE	<i>Bulnesia sp</i>	3000	F	NE	1

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#### **Appendix S4.** Abstract in Spanish

### **Reducción sistemática de la lluvia de semillas de especies endozoócoras y de semillas grandes en los pastos en comparación con los bosques de las montañas tropicales**

**Preguntas:** (a) ¿Cómo cambian la biomasa y la riqueza de la lluvia de semillas de bosques tropicales maduros a los pastos a diferentes elevaciones? (b) ¿Cambian la masa de semillas y el modo de dispersión de semillas de bosques a pastizales en estas elevaciones? (c) ¿Qué implicaciones tienen estos cambios para la recuperación de zonas deforestadas en las montañas tropicales?

**Ubicación:** bosques montanos maduros y pastizales de ganadería a lo largo de un gradiente elevacional (1000 a 3000 m s.n.m.), localizados en el Parque Nacional Podocarpus, Reserva San Francisco y tierras agrícolas circundantes, Andes del sur de Ecuador.

**Ubicación:** bosques montanos maduros y pastizales de ganadería a lo largo de un gradiente elevacional (1000 a 3000 m s.n.m.), localizados en el Parque Nacional Podocarpus, Reserva San Francisco y tierras agrícolas circundantes, en los Andes del sur de Ecuador.

**Resultados:** los bosques recibieron una mayor biomasa de lluvia de semillas que los pastos, pero sólo en la elevación más baja. La riqueza en la lluvia de semillas no difirió entre tipos de hábitat. La media ponderada por la comunidad de la masa de semillas y la proporción de especies endozoócoras disminuyeron de los bosques a los pastos y tendieron a disminuir con el aumento de la elevación.

**Conclusiones:** aunque la biomasa y la riqueza de la lluvia de semillas fueron en general similares entre bosques y pastos, las semillas grandes y las especies endozoócoras estuvieron peor representadas en la lluvia de semillas de los pastos en comparación con la de los bosques. Nuestros hallazgos sugieren que la lluvia de semillas en los pastos procedía de fuentes de semillas alternativas más que de los bosques maduros más cercanos. Nosotros demostramos que la biomasa y la riqueza de la lluvia de semillas

pueden ser insuficientes para cuantificar el potencial de restauración de zonas deforestadas. Es importante disponer de información adicional sobre rasgos clave de las semillas, como su masa y modo de dispersión, para optimizar los esfuerzos de restauración en las montañas tropicales.

## A4: Curriculum Vitae

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### Education

**2018 - present. PhD student in Biological Sciences**

Goethe University Frankfurt and Senckenberg Biodiversity and Climate Research Centre (BiK-F), Frankfurt am Main, Germany.

Advisor: PD Dr. Matthias Scheluning.

Dissertation title: “Plant functional diversity and seed rain along land-use and elevational gradients in southern Ecuador”

**2017. M.Sc. in Protected Areas, Natural Resources and Biodiversity.**

Universidad de Murcia, Murcia, Spain.

Advisor: Dr. Pilar de la Rúa Tarín.

Master thesis: “Mutualistic networks of seed dispersal in the arborescent matorral with *Zyziphus* (habitat type 5220)”

**2015. M.Sc. in Biological Sciences.**

Universidad de los Andes, Bogotá, Colombia.

Advisor: Dr. Pablo Stevenson.

Master thesis: “Seed dispersal quality by woolly monkeys (*Atelidae*: *Lagothrix lagotricha lugens*): Effects of gut treatment on seed germination”

**2010. B.S., Biology**

Universidad del Valle, Cali, Colombia.

Advisor: Dr. Alba Marina Torres González.

Bachelor thesis: “Frugivory and seed dispersal by Colombian chachalaca (*Ortalis columbiana*, Aves: Cracidae)”

### Scholarships and grants

- In 2022, GRADE Completion Scholarship. Goethe University - DAAD, Germany.

- In 2019, grant for equal opportunity measures. RESPECT Research Unit 2730 funded by DFG, Germany. (5000 €).
- In 2016, scholarship by practical formation. Autoridad Portuaria de Cartagena and Universidad de Murcia, Spain.
- In 2014, grant MMBF Primate Action Fund. Margot Marsh Biodiversity Foundation – CI. (2350 USD).
- In 2013, financial assistance. Course on Ecology of Neotropical Primates. Deutsches Primatenzentrum, Peru.
- In 2013, grant “Proyecto Semilla”. Biological Sciences Department, Universidad de los Andes. (2.000.000 COP).
- In 2012, financial assistance. Course on Tropical Ecology and Conservation, Organization for Tropical Studies OTS – Universidad de Costa Rica, Costa Rica.
- In 2011, scholarship by young researcher. Departamento Administrativo de Ciencia, Tecnología e Innovación – COLCIENCIAS, Colombia.

### Courses

- *Summer course on Molecular Evolutionary Ecology in Biodiversity*, German Centre for Integrative Biodiversity Research (iDiv), Leipzig, Germany, 2022.
- *Methodological aspects of functional seed ecology*, Seed Ecology VI Symposium - University of Regensburg, Regensburg, Germany, 2019.
- *Ecology of Neotropical Primates*, Deutsches Primatenzentrum, Iquitos, Peru, 2013.
- *Tropical Forest and Climate Change: The importance of carbon cycle*. Colombian Association of Botany, Ibagué, Colombia, 2013.
- *Basic course on Geographical Information Systems*, Universidad del Valle, Cali, Colombia, 2013.
- *Course on Tropical Ecology and Conservation*. Organization for Tropical Studies OTS – Universidad de Costa Rica, Costa Rica, 2012.
- *Course on Ecophysiology of Tropical Plants*, Colombian Association of Botany, Cali, Colombia, 2011.
- *Heritage Interpretation Workshop*, Secretary of Municipal Education of Cali and Centre of Education for Conservation of Cali Zoo, Cali, Colombia, 2010.

### Publications

1. Barczyk, M., Acosta-Rojas, D. C., Espinosa, C. I., Schleuning, M. & Neuschulz, E. L. (2023). Biotic stress and environmental heterogeneity shape beta-diversity of seedling communities in tropical montane forests. *Ecography*, e06538.
2. Acosta-Rojas, D. C., Barczyk, M., Espinosa, C. I., Tinoco, B., 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.
3. Acosta-Rojas, D. C., Jiménez-Franco, M. V., Zapata-Pérez, V. M., De la Rúa, P., & Martínez-López, V. (2019). An integrative approach to discern the seed dispersal role of frugivorous guilds in a Mediterranean semiarid priority habitat. *PeerJ*, 7, e7609.
4. Fonseca, M. L., Cruz, D. M., Acosta-Rojas, D.C., Páez, E. J, & Stevenson, P. R. (2019). Influence of Arthropod and Fruit Abundance on the Dietary Composition

- of Highland Colombian Woolly Monkeys (*Lagothrix lagotricha lugens*). *Folia Primatologica*, 90(4), 240-257.
5. Cruz-Tejada, D. M., Acosta-Rojas, D. C., & Stevenson, P. R. (2018). Are seeds able to germinate before fruit color ripening? Evidence from six Neotropical bird-dispersed plant species. *Ecosphere*, 9(6), e02174.
  6. Stevenson, P. R., Cardona, L. M., Acosta-Rojas, D. C., Henao-Díaz, F., & Cárdenas, S. (2017). Diet of oilbirds (*Steatornis caripensis*) in Cueva de los Guácharos National Park (Colombia): temporal variation in fruit consumption, dispersal, and seed morphology. *Ornitología Neotropical*, 28, 295-307.
  7. Farji-Brener, A., F. Chinchilla, M. N. Umaña, M. Ocasio-Torres, A. Chautamellizo, Acosta-Rojas, D.C., S. Marinero, M. de Torres Curth & S. Amador-Vargas. (2015). Branching angles reflect a tradeoff between reducing trail maintenance costs or travel distances in leaf-cutting ants. *Ecology* (96)2, 510-527
  8. Acosta-Rojas, D.C., M.C. Muñoz, A.M. Torres & G. Corredor. (2012). Dieta y dispersión de semillas: ¿Afecta la guacharaca colombiana (*Ortalis columbiana*) la germinación de las semillas consumidas? *Ornitología Neotropical* 23, 439-453.

### Other knowledge transfer publications

1. Acosta-Rojas, D.C., Barczyk, M., Espinosa, C.I., Gusmán, J., Peña, J., Neuschulz, E.L., Schleuning, M., & J. Homeier. (2021) *Guía de campo de plantas dispersadas por animales: frutos y semillas en el Parque Nacional Podocarpus y sus cercanías/ Field guide of animal-dispersed plants: fruits and seeds in and around Podocarpus National Park*. Publicación n.º 16, Serie de publicaciones del Instituto Nacional de Biodiversidad - INABIO, 116 p, Quito-Ecuador.
2. Acosta-Rojas, D.C., Barczyk, M., Espinosa, C.I., Tinoco, B., Neuschulz, E.L. & M. Schleuning. (2020) Reproductive traits of fleshy-fruited plants along a tropical elevation gradient. *Tabebuia Bulletin* 8:30-44.
3. Acosta-Rojas, D.C., Barczyk, M., Neuschulz, E.L. & M. Schleuning. (2020) Seed diversity: from field sampling to identification. *Tabebuia Bulletin* 7:17-31.
4. Barczyk, M., Acosta-Rojas, D.C., Schleuning, M., & E.L. Neuschulz (2019) Studying plant regeneration processes in Podocarpus National Park - a gift from the Andean bear. *Tabebuia Bulletin* 6:17-21.

### Symposium participation

- *Oral presentation.* Acosta-Rojas, D.C., Barczyk, M., Espinosa, C.I., Tinoco, B., Neuschulz, E.L. & M. Schleuning. *Climate and microhabitat effects on the importance of endozoochory along an elevational gradient in Southern Ecuador*. VII Seed Ecology Conference, Gijón, Spain, from September 5 to 10, 2022.
- *Oral presentation.* Acosta-Rojas, D.C., Barczyk, M., Espinosa, C.I., Tinoco, B., Neuschulz, E.L. & M. Schleuning. *Climate and microhabitat effects on the importance of endozoochory along an elevational gradient in Southern Ecuador*. European Conference of Tropical Ecology, Montpellier, France, from June 7 to 9, 2022.
- *Oral presentation.* Acosta-Rojas, D.C., Barczyk, M., Espinosa, C.I., Tinoco, B., Neuschulz, E.L. & M. Schleuning. *Plant trait association with biotic and abiotic gradients on an animal-dispersed plant metacommunity in tropical mountains*.

- Virtual Meeting of the Association for Tropical Biology And Conservation, from July 21 to 23, 2021.
- *Poster.* Acosta-Rojas, D.C., Barczyk, M., Espinosa, C.I., Tinoco, B., Neuschulz, E.L. & M. Schleuning. *Plant functional diversity and seed rain along land-use and elevational gradient in Southern Ecuador*. VI Seed Ecology Symposium, Regensburg, Germany, from July 28 to August 2, 2019.
  - *Oral presentation.* Acosta-Rojas, D.C., Henao-Díaz, L.F. & S. Madriñán. *Reconstruction of character state of aril in legumes: Was Edred John Corner right?* VIII Botanical Colombian Congress, Manizales, Colombia, from August 2 to 6, 2015.
  - *Oral presentation.* Acosta-Rojas, D.C., Cruz-Tejada, D.M., Páez-Crespo, E.J. & P. Stevenson. *Can Woolly monkeys (*Lagothrix lagotricha lugens*) directly affect seed germination at Cueva de los Guácharos National Park, Colombia?* 6th International Symposium – Workshop on Frugivores and Seed Dispersal. University of Kwazulu-Natal, Drakensberg, South Africa, from June 21 to 26, 2015.
  - *Oral presentation.* Henao-Díaz, L.F., Cárdenas-Hoyos, S., Acosta-Rojas, D.C., & P. Stevenson. *Diet and seed dispersal by Oilbird *Steatornis caripensis* in Cueva de los Guácharos National Park*. IV Zoological Colombian Congress, Cartagena, Colombia, from December 1 to 5, 2014.
  - *Oral presentation.* Acosta-Rojas, D.C., Cruz-Tejada, D.M., Páez-Crespo, E.J. & P. Stevenson. *Can Woolly monkeys (*Lagothrix lagotricha lugens*) directly affect seed germination in subandean tropical forest?* IV Zoological Colombian Congress, Cartagena, Colombia, from December 1 to 5, 2014.
  - *Oral presentation.* Acosta-Rojas, D.C. & A.M. Torres. *Do arilated seeds require to be ingested by frugivorous to germinate?: The case of *Cupania latifolia**. XLVII National Congress of Biological Sciences, Cali, Colombia, from October 9 to 13, 2012.
  - *Poster.* Acosta-Rojas, D.C. & C.A. Arango-Díaz. *Germinative dynamic of three melastomatacean species of a tropical dry forest on Valle del Cauca – Colombia*. VI Botanical Colombian Congress, Cali, Colombia, from August 11 to 15, 2011.
  - *Oral presentation.* Acosta-Rojas, D.C., M.C. Muñoz, A.M. Torres & G.A. Corredor. *Frugivory and seed dispersal by Colombian chachalacas (*Ortalis columbiana*, Aves: Cracidae)*. III Zoological Colombian Congress, Medellín, Colombia, from November 21 to 26, 2010.
  - *Poster.* Acosta-Rojas, D.C. & C.A. Arango-Díaz. *Pollination, nectar production and floral visitors of *Caesalpinia pulcherrima* (Fabaceae) in a suburban area of Cali – Colombia*. V Botanical Colombian Congress, San Juan de Pasto, Colombia, from April 19 to 24, 2009.

**Professional skills:** almost 10 years of field work experience working mainly in tropical ecosystems (Colombia and Ecuador) but also in Mediterranean habitats (Spain). I have worked in suburban and remote areas hiking through study areas collecting and identifying plants, measuring nectar production, sampling animal droppings and recording behavioral data of birds and primates. I also have experience in setting up vegetation plots, seed traps, and seeding experiments. In the laboratory, I have measured functional traits of plants, with special attention to fruits and seeds. I have conducted greenhouse and incubator germination tests, as well as seed viability tests with tetrazolium salts and electrical conductivity. I also have experience in the development of molecular analysis (DNA barcoding). In addition, I have extensive

experience in teaching different audiences, coordinating multidisciplinary work teams, managing biological collections and databases, using photo and video editing software (Adobe Photoshop, Adobe Premier, Inkscape), geographic information systems (QGIS and R), and performing statistical analysis (R software).

**Academic teaching:** at Universidad de La Salle (Colombia, 2023), I taught the course “Data analysis in restoration ecology for tropical ecosystems under Global Change”. At Senckenberg Biodiversity and Climate Research Centre (Germany, 2021 and 2022), I assisted in teaching activities related to statistics and paper discussions for the master module of “Community ecology, movement ecology, and macroecology”. At the Colombian Primatological Association (Colombia, 2016), I taught the module “Collection and analysis of fecal samples with ecological, physiological and molecular approaches”. At Universidad Militar Nueva Granada (Colombia, 2016) I taught two courses about (1) population biology and (2) systematics and plant taxonomy. At Universidad de Los Andes (Colombia, 2012-2015), I was a teaching assistant for the courses of (1) biology for psychologists and (2) general ecology.

### **Participation in initiatives of public awareness of sciences**

- October 2016 – July 2017. Environmental educator. Project “Jardín 2.0”. Turismo Botánico. Spain
- June 2013 – June 2015. Environmental educator. Project “Woolly monkeys: sowers of life” Universidad de los Andes Colombia
- February 2010 – December 2010. Coordinator of Science Club. Cali Zoo. Colombia
- January 2009 – December 2009. TV presenter of Science Club section, TV show “Exploradores por Naturaleza”, Colombia.
- October 2006 – 2009. Environmental Educator. Cali Zoo. Colombia

### **Academic services**

- Media Committee. Colombian Primatological Association (2019-2022).
- Member of the Board of Directors and Coordinator of APC-CPBIOL Agreement. Colombian Primatological Association (2015 – 2018).
- Scientific Committee. VI Botanical Colombian Congress. Colombian Association of Botany, Cali, Colombia, from August 11 to 15, 2011.
- Organizing Committee. II Symposium of the Colombian Network of Evolutionary Biology. Universidad del Valle – Universidad Icesi, Cali, Colombia, from October 15 to 17, 2009.

**Peer-Review Services For Scientific Journals:** Referee for *Frontiers in Ecology and Evolution*, *Biotropica*, *South African Journal of Botany*, *Ornitología Neotropical*, *Ecotropica*, and *Revista de Investigación Agraria y Ambiental*.