Research article

Environmental conditions differently shape leaf, seed and seedling trait composition between and within elevations of tropical montane forests

Maciej K. Barczyk[1,2,3], **Diana Carolina Acosta-Rojas**[1,2], **Carlos Iván Espinosa**[4], **Jürgen Homeier**[5,6], **Boris A. Tinoco**[7], **Andre Velescu**[8], **Wolfgang Wilcke**[8], **Matthias Schleuning**[1] and **Eike Lena Neuschulz**[1]

[1]Senckenberg Biodiversity and Climate Research Centre (SBiK-F), Frankfurt am Main, Germany
[2]Goethe University Frankfurt, Faculty of Biological Sciences, Frankfurt am Main, Germany
[3]Adam Mickiewicz University in Poznań, Forest Biology Center, Poznań, Poland
[4]Universidad Técnica Particular de Loja, Department of Biological Sciences, Loja, Ecuador
[5]HAWK University of Applied Sciences and Arts, Faculty of Resource Management, Göttingen, Germany
[6]University of Göttingen, Plant Ecology and Ecosystems Research, Göttingen, Germany
[7]Universidad del Azuay, Escuela de Biología, Cuenca, Ecuador
[8]Karlsruhe Institute of Technology (KIT), Institute of Geography and Geoecology, Karlsruhe, Germany

Correspondence: Maciej K. Barczyk (maciejkbarczyk@gmail.com)

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

www.oikosjournal.org

Introduction

Investigating variability in plant functional traits contributes to the understanding of demographic processes and the prevalence of ecological strategies in plant communities across environmental gradients (Westoby 1998, Lavorel and Garnier 2002, Moles et al. 2005, Adler et al. 2014, Kraft et al. 2015a). In particular, studies focusing on the composition of plant functional traits in ecological communities can offer insights into processes of community assembly because the functional trait composition varies between and within ecosystems (Díaz and Cabido 2001, Bouchard et al. 2024). Field studies have revealed that environmental filtering along environmental gradients shapes variation in trait values and the dominance of different ecological strategies at distinct locations (Albrecht et al. 2018, Homeier et al. 2021, Pierick et al. 2021, Rosbakh et al. 2022). For instance, mean values of traits such as specific leaf area, seed mass and wood density increase with increasing mean annual temperature at large spatial scales (Bruelheide et al. 2018, Bouchard et al. 2024). While climate and soil conditions explain functional composition of such plant traits globally, microclimatic and local soil conditions can also shape trait variation at small spatial scales due to their effects on plant growth and survival (Lebrija-Trejos et al. 2010, Kraft et al. 2015b, Wieczynski et al. 2019). However, the effects of local scale environmental variation on plant trait composition are yet little known, especially for highly diverse tropical ecosystems.

Several plant species maintain high trait plasticity along the plant life cycle (Visser et al. 2016, Falster et al. 2018) and plant ecological strategies may change over their ontogeny in response to changing environmental conditions (Dayrell et al. 2018). Thus, plant communities respond differently to environmental filtering depending on their stage in the plant life cycle. While species turnover in seedling communities, for instance, can be shaped by biotic pressures and environmental heterogeneity (Barczyk et al. 2023), species turnover in adult trees appears to be more sensitive to soil conditions (Werner and Homeier 2015, Peguero et al. 2023). In consequence, species sorting may differently affect plant communities at early and late life stages (Clarke et al. 2001, Foster et al. 2011, Larson and Funk 2016). Capturing the composition of functional traits that reflect plant growth, reproduction and recruitment strategies can therefore reveal new insights into how plant traits, such as leaf, seed or seedling traits, are filtered along environmental gradients at different plant life stages.

Leaf traits are powerful predictors of changes in the growth strategies of plants, mainly reflected by the leaf economics spectrum (Wright et al. 2004, Díaz et al. 2016, Maynard et al. 2022). The leaf economics spectrum describes the tradeoff between nutrient-rich, 'acquisitive' leaves and long-lived, 'conservative' leaves. Specific leaf area (leaf area per dry mass; SLA) is a key functional trait that reflects the main tradeoffs in investment strategies and variability in resource allocation (Westoby 1998, Wright et al. 2004, Maynard et al. 2022). For instance, species with long-lived, conservative leaves tend to dominate under harsh environmental conditions at high elevations, while species with acquisitive leaves are more abundant in lowland tropical rainforests (Hulshof et al. 2013). In addition, local-scale variation in environmental conditions can lead to changes in community weighted means of leaf functional traits (Schmitt et al. 2020, Báez et al. 2022).

Seed traits capture essential tradeoffs in plant reproductive strategies of adult plants (Westoby 1998, Moles and Westoby 2006, Bolmgren and Eriksson 2010). Primarily, seed mass influences plant fitness through a tradeoff between the costs of seed production and benefits in terms of germination success (Moles and Westoby 2006, Visser et al. 2016, Sales et al. 2021). Consequently, plants may either produce many small seeds or a few large seeds, representing a size–number tradeoff in seed production (Moles et al. 2004, Moles and Westoby 2006). As such, differences in seed mass influence seedling survival and growth (Baraloto et al. 2005, Moles and Westoby 2006, Falster et al. 2018), as well as plant fitness and the fate of future plant generations (Terborgh et al. 2008, Canham and Murphy 2016, Kuprewicz and García-Robledo 2019). While previous studies have focused on studying seed trait composition across large spatial scales (Duivenvoorden and Cuello A 2012, Sales et al. 2021, Bouchard et al. 2024), little is known on differences in seed trait composition at local scales (Rosbakh et al. 2022, Acosta-Rojas et al. 2023a). Generally, canopy properties and soil conditions can trigger variation in seed traits (Acosta-Rojas et al. 2023a), and plants tend to produce larger seeds on fertile soils due to a higher resource allocation into reproduction (Grubb and Coomes 1997, Jager et al. 2015). Identifying the associations between seed mass and environmental conditions can lead to a better understanding of the drivers of seed trait composition across different spatial scales (Saatkamp et al. 2019).

Finally, seedling traits have drawn more attention recently, because they are essential for community assembly at early plant life stages (Auffret et al. 2017, Harrison and LaForgia 2019, Westoby et al. 2022). For instance, the initial seedling height shortly after germination can be a measure of the growth capacity and resistance of young plants (Baraloto et al. 2005). As such, this trait reflects the energy supply provided to a seedling by a seed (Moles et al. 2004, Hu et al. 2017) and, thus, the initial capacity of seedlings to invest into growth (Baraloto et al. 2005, Falster et al. 2018, Umaña et al. 2021a). Initial seedling height can mirror the regeneration strategy of a plant species as seedlings of early- and late-successional species tend to differ in size and growth strategy (Baraloto et al. 2005). Specifically, late-successional species tend to produce larger seeds and seedlings than early-successional species and are more likely to establish in light-limited environments

(Dalling and Hubbell 2002, Wright et al. 2003, Visser et al. 2016, Gibert et al. 2016). In contrast, seedlings of small-seeded and early-successional species are more likely to establish in canopy gaps and can surpass large-seeded species in growth rates under open canopy (Dalling and Hubbell 2002, Baraloto et al. 2005). While local variability in soil and light conditions may affect seedling traits (Umaña et al. 2021a, Song et al. 2021), little is known to what extent initial seedling height is associated with broad- and local-scale environmental variation.

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

Here, we present a cross-scale comparison of plant traits at different plant life stages (i.e. adult trees, seeds and seedlings) in relation to environmental conditions at local and regional scales. Specifically, we tested how the trait composition of leaves, seeds and seedlings was associated with environmental conditions across and within elevations in highly diverse tropical montane forests. We calculated community weighted means of key traits assigned to each plant life stage (i.e. specific leaf area, seed mass and initial seedling height) and related them to broad-scale environmental variation across elevations and to variation in local-scale environmental factors (i.e. soil and light conditions) within elevations. First, we expected consistent differences in trait composition across elevations, reflected by decreasing trait means due to the prevalence of conservative strategies under the harsh climatic conditions at high elevations (Duivenvoorden and Cuello A 2012, Homeier et al. 2021, Umaña et al. 2021a). Second, we expected that trait variation within elevations is associated with local soil and light conditions. In particular, we expected that specific leaf area would be positively associated with favourable soil conditions, due to a high allocation of resources into acquisitive leaves (Jager et al. 2015, Homeier et al. 2021, Pierick et al. 2021). Similarly, we expected seed mass to increase under favourable soil conditions, because plants growing on fertile soils are more likely to allocate resources into their seeds (Grubb and Coomes 1997, Pérez-Ramos et al. 2014, Jager et al. 2015). Finally, we expected initial seedling height to increase under open canopy, because of less light limitation (Baraloto et al. 2005, Song et al. 2021, Umaña et al. 2021a).

Material and methods

Study design

This study was carried out in the Podocarpus National Park and San Francisco Reserve, located between the Amazon Basin and the main ridge of the Eastern Andes in southern Ecuador. The protected area of the Podocarpus National Park spans over 1400 km^2 and covers an elevational gradient of more than 2000 m (ca 900–3600 m a.s.l.). The area is characterized by mostly intact evergreen montane forests, hosting numerous endemic and undescribed plant species (Homeier et al. 2008, Kessler and Kluge 2008). The mean annual temperature ranges between 20°C at 1000 m a.s.l., 15.5°C at 2000 m a.s.l. and 10°C at 3000 m a.s.l. (Bendix et al. 2008). The mean annual precipitation also varies strongly among elevations: 2432 mm at 1000 m, 2330 mm at 2000 m and 4522 mm at 3000 m (Santillán et al. 2018, Wilcke et al. 2019).

Our research was conducted on nine 1-ha plots (three at each elevation; Fig. 1a) in the frame of the DFG Research Unit 2730 (RESPECT) that established these plots along an elevational gradient ranging from 1000 to 3000 m a.s.l. in old-growth forests (Bendix et al. 2021). The lowest study plots were located in evergreen premontane forest along the Bombuscaro River (1000 m a.s.l., 04°06′S, 78°58′W). The plots at mid elevations were placed in lower montane forest in the San Francisco Reserve (2000 m a.s.l., 03°58′S, 79°04′W). The high elevation plots were located in upper evergreen tropical montane forest in Cajanuma (3000 m a.s.l., 04°06′S, 79°10′W). All plots had a minimum pairwise distance of 100 m (Bendix et al. 2021). While climatic conditions (temperature and precipitation) differ strongly across elevations (Supporting information), local microhabitat conditions (in particular, soil moisture and canopy conditions) also vary strongly among and within plots at the same elevation (Barczyk et al. 2023).

Within each plot, we established several subplots to study the variability in leaf, seed and seedling trait composition. Subplots were differently sized given the different life stages corresponding to each of these traits. To measure leaf traits of adult trees, we divided each 1-ha plot into 25 subplots of 400 m^2 (tree census; framed with green colour in Fig. 1b). In total, this resulted in 225 subplots, where leaf measurements were taken on a total number of 418 individual trees (75 subplots per elevation). To capture variability in seed trait composition, we established 18 seed traps (0.6 × 0.6 m; seed trap area = 0.36 m^2) per plot to capture seed rain, regularly distributed across the plots (seed traps; yellow dots in Fig. 1b). In total, we captured seed rain in 162 seed traps across the elevations (54 traps per elevation). Finally, we set up nine regularly distributed 1-m^2 subplots (1 × 1 m) per plot, to monitor recruiting seedlings (recruitment census; blue quadrates in Fig. 1b). In total, we recorded seedling recruitment at 81 subplots (27 subplots per elevation). Hence, we were able to study variability in the respective traits representing different plant life stages with a coherent study design capturing changes in trait composition within and across elevations.

(a)

(b)

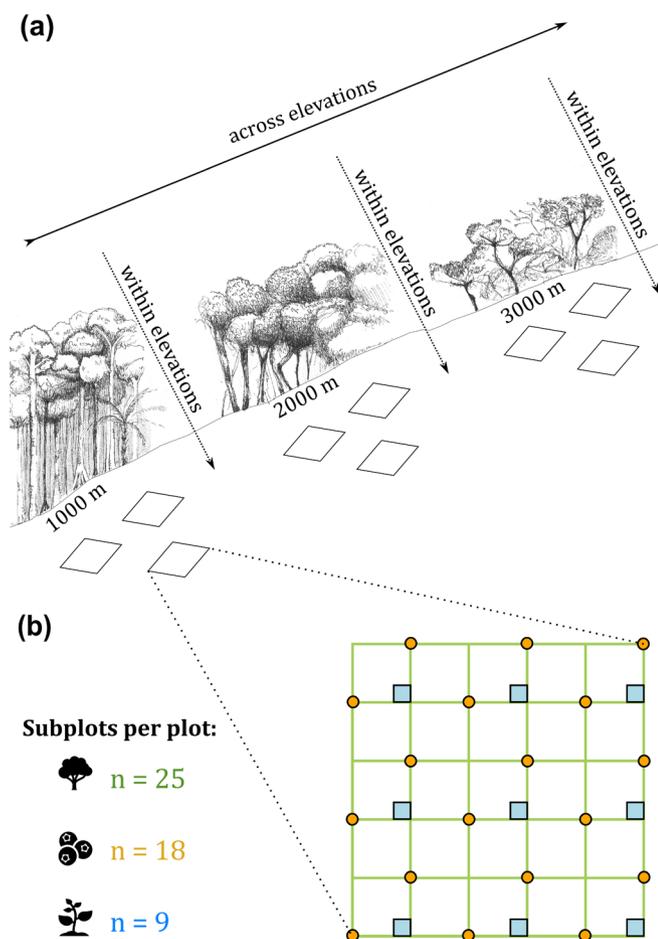**Subplots per plot:**

🌳 n = 25

🌱 n = 18

🌿 n = 9

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

Environmental conditions

To quantify environmental conditions within elevations, we measured the soil C/N ratio and canopy openness. We measured these two environmental factors because they are proxies for two crucial resources for plants: nutrients and light (Wright et al. 2003, Umaña et al. 2021b). In 2018, we collected 418 representative samples from the mineral soil (0–10 cm soil depth) across the nine study plots (Velescu et al. 2022). The samples were taken close to those tree individuals ($n = 418$) that had been selected for leaf trait measurements, and covered a total number of 167 out of 225 tree census plots. The soil samples were taken with a soil auger at five locations close to each tree and bulked to a composite sample. They were dried at 40°C, sieved to <2 mm and an aliquot was milled in a planetary ball mill. We determined total carbon (C) and nitrogen (N) concentrations by elemental analysis via thermal combustion at 1020°C, catalytic reduction and detection by thermal conductivity after chromatographic separation of CO_2 and N_2 (Flash 2000 HT Plus, Thermo Scientific). Because soils were free of carbonates and were moderately to strongly acidic, all C was assumed to be organic C. Based on C and N concentrations in the soils, mass-related soil C/N ratios were calculated to approximate the organic matter turnover in the soils and the availability of nutrients to plants. High soil C/N ratios indicate slow turnover of organic matter, resulting in low N availability to plants (Post et al. 1985, Wilcke et al. 2020). Values of soil C/N ratios were averaged for each tree census subplot ($n = 225$). We then averaged these mean C/N values and assigned them to the spatially closest seed trap ($n = 162$) and recruitment census subplot ($n = 81$). Thus, soil C/N ratios were assigned to each individual census (trees, seeds and seedlings) accounting for the different subplots of each life stage (Supporting information).

In October 2019, we visited all study plots to take hemispherical photos and to estimate light conditions. We photographed the canopy 0.7 m above ground at each recruitment census subplot ($n = 81$). Photos were taken with a digital camera fitted with a fish-eye converter lens. All photos were taken in the mornings with overcast sky. The hemispherical photos were analysed in Gap Light Analyzer ver. 2.0 (1999, SFU/IES, Canada/USA). For each photograph representing one subplot, we calculated canopy openness, defined as the percentage of open canopy in relation to full canopy cover (0–100%). Values of canopy openness were matched to the corresponding recruitment census ($n = 81$) and were then assigned to the spatially closest seed trap and tree census at the subplot level (Supporting information). Canopy openness was only weakly correlated with soil C/N ratio (Pearson's $r = 0.44$, $p < 0.01$, $n = 67$ subplots).

Specific leaf area

The tree inventory included all woody stems with a diameter at breast height (DBH) ≥ 10 cm and was conducted on the 25 tree census subplots inside each 1-ha plot ($n = 225$ subplots in total; Fig. 1). All trees were labelled and herbarium specimens were collected for taxonomic identification. The abundance of each species was defined at the subplot level as the total number of individual stems of a respective species encountered at each subplot. Trait measurements were done on a representative subset of 52 species representing different successional stages and plant families (32 plant families in total). The preselection of species was made by choosing the abundant tree species in the study plots at each elevation which covered different ecological strategies from early-successional pioneers to late-successional tree species and from understory species to tall canopy trees (Homeier et al. 2021). The preselected species represented a substantial part of the community and accounted for about 41% of total basal area within the 1-ha plot at 1000 m a.s.l., 50% at 2000 m a.s.l. and 32% at 3000 m a.s.l.; Homeier et al. 2021). All individual trees of the preselected species in the tree census subplots were marked with a plastic tag. From 5–10 randomly selected

individuals of these species (n = 418 in total), we collected 20 young and undamaged sun leaves attached to two to three branches cut by a pruning tool from the top of the tree crown under as much sun exposure as possible. The entire branches were kept in sealed polyethylene bags with water-soaked tissues prior to measurements. Subsequently, all leaves were dried at 60°C for 3–4 days to measure leaf dry mass.

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

Seed mass

To capture seed rain, we installed a total of 162 seed traps (trap area 0.6 × 0.6 m = 0.36 m², 1.5 mm nylon mesh; Fig. 1). The traps were placed about 1 m above the ground and the content was emptied every 15 days between January 2019 and January 2020. The material collected in the traps was separated into fruits and seeds. In most cases, the dispersal units matched seeds in a strict botanical sense, however some diaspores were comprised of seeds and the surrounding fruit structure. Seeds with a length < 1 mm were discarded, as these could not be captured by the nylon mesh. We identified the dispersed seeds to the lowest possible taxonomic level using reference plant material from the forest or from herbariums, field guides and the help of botanical experts (Acosta-Rojas et al. 2023a). Based on these samples, we obtained the abundance of all species and morphospecies at each seed trap pooled over repeated censuses. All seeds were dried at 60°C for 3–4 days and then weighted with a high precision analytical balance (precision 0.0001 g).

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

Initial seedling height

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

Initial seedling height is a good proxy of a plant's capacity to establish and grow, because it reflects the net energy provision of seeds to seedlings (Moles and Westoby 2004, Baraloto et al. 2005). At each visit, we measured initial seedling height [cm] for each recently established seedling (within the last four months; Baraloto et al. 2005). Precisely, the height of each seedling was measured as a distance between the stem base and the terminal bud using manual callipers enabling a precision of 1 mm. To validate that initial seedling height is associated with the growth strategy of seedlings, we related initial seedling height with the relative growth rate over four-months intervals for a subset of seedlings in the dataset (n = 220 seedling individuals from 83 species). For these seedlings, we calculated the relative growth rate (RGR) as described in Baraloto et al. (2005) with the Eq. 1:

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

Initial seedling height was negatively related to RGR within and across species (linear mixed model (LMM) with a random term of species identity: estimate = −0.11, SE = 0.01, p < 0.001) indicating that seedlings with a small initial height were fast growing, whereas initially large seedlings were slow growing (Supporting information). This close correlation suggests that initial seedling height reflects different growth strategies at the seedling stage (Adler et al. 2014, Reich 2014, Falster et al. 2018).

Community-weighted means of traits

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

and seed trap, we calculated the community-weighted means with Eq. 2:

$$CWM = \sum_{i=1}^{n} trait_i \times abundance_i$$

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

In order to test for covariation in the composition of different types of traits, we correlated the trait values of leaves, seeds and seedlings at the subplot level using the spatial matching of environmental conditions (n = 81, Supporting information). Community-weighted means of specific leaf area were weakly correlated with seed mass (Pearson's r = 0.34, p < 0.05) and initial seedling height (Pearson's r = 0.43, p < 0.05). In contrast, no significant correlation was detected between the community-weighted means of seed mass and initial seedling height (Pearson's r = 0.11, p = 0.061).

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

Statistical analyses

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

We performed LMMs to test how community-weighted means of leaf, seed and seedlings varied across and within elevations. The first model tested how the composition of leaf, seed and seedling traits changed across elevations by testing the interaction effects between life stage and elevation. The second model tested how trait composition was related

to environmental variation (i.e. soil C/N ratio and canopy openness) within elevations. To simplify the interpretation of model estimates, we removed the intercepts and main effects of the environmental predictor variables from these models as described in Schielzeth (2010). This model formulation allowed us to test for the trait-specific trends in the variation of leaf, seed and seedling traits across and within elevations. In addition, all models included a random factor of plot identity (n = 9 plots) to control for unmeasured variability among plots. All analyses were conducted in R ver. 4.2.3 (www.r-project.org) and the associated packages 'ggplot2' (Wickham 2016), 'lme4' (Bates et al. 2015), 'lmerTest' (Kuznetsova et al. 2017), 'MuMIn' (Bartoń 2023) and 'tidyverse' (Wickham 2011).

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

Results

We measured specific leaf area on 418 individual trees of 52 plant species (20 species at 1000 m, 20 species at 2000 m and 12 at 3000 m) at 164 subplots (i.e. subplots without the respective plant species had to be discarded from the analysis). Specific leaf area varied between 26 (*Clusia elliptica* at 3000 m) and 241 cm^2 g^{-1} (*Mollia gracilis* at 1000 m).

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

Changes in trait composition across elevations

Community-weighted means of all plant traits decreased with increasing elevation (Table 1). Mean specific leaf area of adult trees decreased from about 116 cm^2 g^{-1} at 1000 m to 56 cm^2 g^{-1} at 3000 m a.s.l. (Fig. 2a). Mean seed mass decreased from 0.100 g at 1000 m to 0.016 g at 3000 m a.s.l. (Fig. 2b). Mean initial seedling height showed a similar trend and decreased from 5.8 cm at 1000 m to 3.5 cm at 3000 m a.s.l. (Fig. 2c). The decreases in specific leaf area, seed mass and initial

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

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

seedling height with increasing elevation were highly significant (Table 1). The analysis restricted to the subplots directly sampled for both environmental and trait variables showed qualitatively identical patterns (Supporting information).

Changes in trait composition within elevations

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

Discussion

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

Changes in trait composition across elevations

We found that elevation had consistent effects on the trait composition of different plant life stages, likely because broad-scale environmental filtering of the trait composition of plant communities increased with increasing elevation. Previous
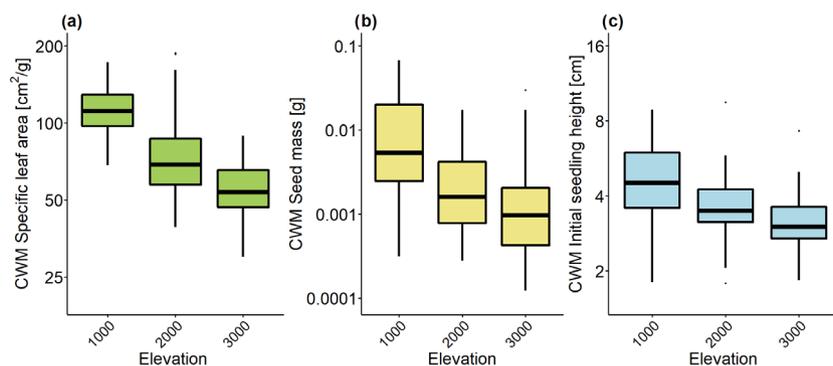

Figure 2. Community-weighted means of leaf, seed and seedling traits across elevations. Shown are: (a) specific leaf area of adult trees; (b) seed mass captured in seed rain; (c) initial seedling height of recruiting seedlings. Community-weighted means are based on trait values and abundances recorded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

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

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

studies identified temperature as a major environmental driver causing shifts in species and trait composition across elevational gradients (Nottingham et al. 2018, Homeier et al. 2021, Acosta-Rojas et al. 2023a). Community-weighted means of specific leaf area were decreasing with increasing elevation. This is in line with previous studies on the composition of other leaf traits across elevational gradients in tropical montane and lowland forests (Hulshof et al. 2013, Schmitt et al.

2020, Homeier et al. 2021). Trees growing at high elevations have been shown to invest more into the production of conservative leaves (i.e. leaves with small specific leaf area), which are more resistant and long-lasting to stand harsh climatic conditions (Westoby 1998, Hulshof et al. 2013). Similarly, previous studies have demonstrated that community-weighted means of seed mass decrease in tropical and temperate mountains along steep environmental gradients because
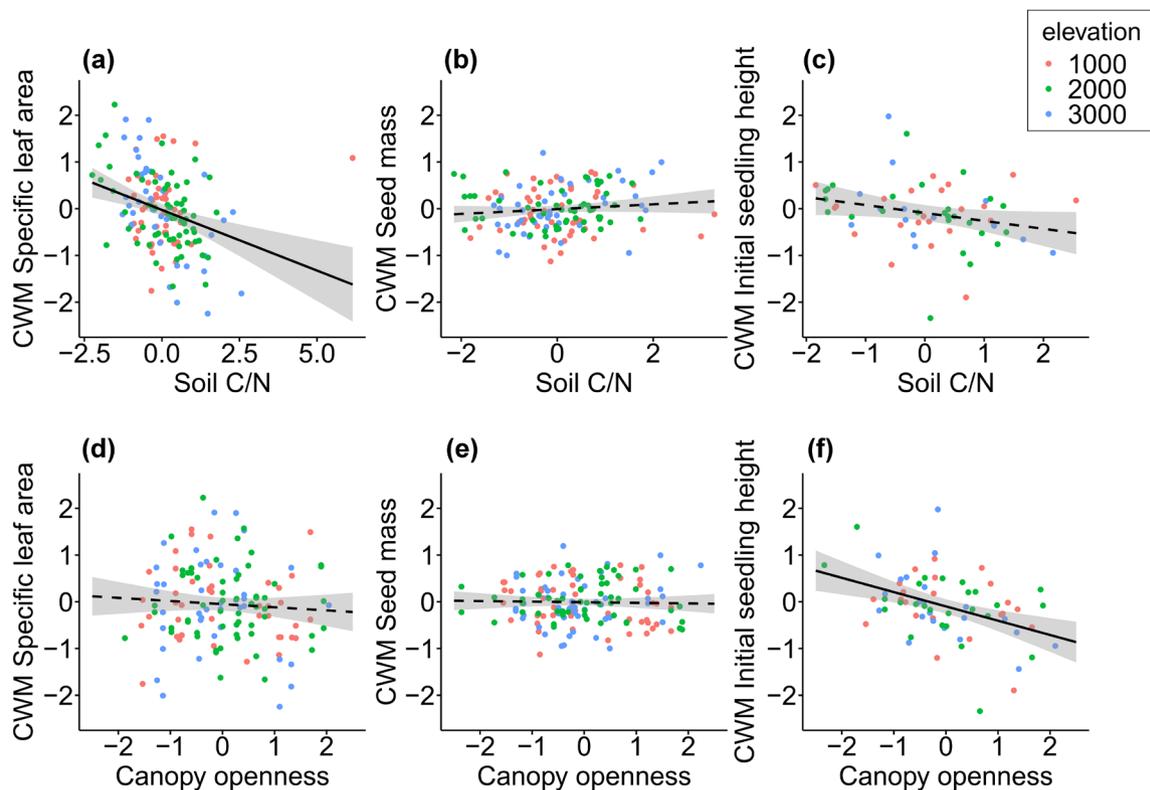

Figure 3. Relationships between community-weighted means of leaf, seed and seedlings traits and soil and light conditions within elevations. Specific leaf area (a, d); seed mass (b, e); and initial seedling height (c, f) in relation to soil C/N ratio (a–c) and canopy openness (d–f). Each point represents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

of less favourable climatic conditions and stronger abiotic filtering at high elevations (Duivenvoorden and Cuello A 2012, Rosbakh et al. 2022). The decline in seed mass with increasing elevation could also be related to the lower diversity of large seed-dispersing animals and thus, a lower proportion of endozoochorous species at high elevations in the study area (Quitián et al. 2018, Acosta-Rojas et al. 2023a). Further studies at different locations would be required to confirm this pattern, given mixed evidences for the relationship between mean seed mass and seed disperser size (Forget et al. 2007, Bolmgren and Eriksson 2010, Sales et al. 2021). We further found a significant decrease in community-weighted means of initial seedling height across elevations. To the best of our knowledge, a reduction in mean initial seedling height at high elevations has not been reported so far. The decrease in initial seedling height across elevations may be related to the decrease in mean seed mass with increasing elevation, given the covariation between initial seedling height and seed mass reported in previous studies (Moles et al. 2004, Baraloto et al. 2005). Furthermore, this suggests that late successional species producing large seedlings are more prevalent at lower elevations corresponding to the structural changes from taller, more densely covered lower montane to the more open upper montane forests (Homeier et al. 2010, Arellano et al. 2016). Further exploration of differences in initial seedling height across environmental gradients could inform whether this trait can be a general predictor of seedling survival, related to the plant economics spectrum (Reich 2014, Winkler et al. 2024). Overall, we found that environmental variation across elevations leads to consistent changes in the mean trait values of leaves, seeds and seedlings, suggesting similar shifts in resource allocation patterns across different plant life stages at large spatial scales (Lasky et al. 2014, Visser et al. 2016, Umaña et al. 2021b). Generally, plants were forced to invest into less 'expensive' plant organs (e.g. less acquisitive leaves, smaller seeds and seedlings) under harsher environmental conditions at high elevations. Similar patterns have been described for multiple leaf and root traits in association with a decrease in mean temperature in the same study area (Homeier et al. 2021, Pierick et al. 2024).

Changes in trait composition within elevations

We detected pronounced differences in trait–environment associations within elevations. In contrast to our expectation, only specific leaf area, but not seed mass and initial seedling height, was related to variation in soil C/N ratios. Within elevations, specific leaf area was negatively associated with increasing C/N ratio. Previous studies found similar trends and showed that trees growing on more fertile soils (e.g. low C/N ratio) tend to produce acquisitive leaves (i.e. large specific leaf area) (Hodgson et al. 2011, Hulshof et al. 2013, Schmitt et al. 2020, Homeier et al. 2021). This is because plants growing on fertile soils invest more into growth by producing acquisitive leaves with high photosynthetic capacity to compete for light and accelerate reproduction (Apaza-Quevedo et al. 2015, Falster et al. 2018, Homeier et al.

2021). Both inter- and intra-specific shifts from plants with acquisitive to conservative leaves have been reported along environmental gradients as a consequence of this tradeoff (Schmitt et al. 2020). In line with that, recent studies from tropical forests demonstrated that soil fertility is a main driver of plant community assembly, because leaf traits are crucial to mediate species sorting in tropical tree communities (Dantas de Paula et al. 2021, Peguero et al. 2023).

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

We found that initial seedling height, but not specific leaf area and seed mass, was related to variation in canopy openness within elevations. Previous studies from other tropical forests have shown that canopy openness fosters seedling growth, as light is a limiting factor for seedling growth in the forest understorey (Baraloto et al. 2005, Song et al. 2021, Umaña et al. 2021a). In our study, we found that seedlings growing under open canopy tended to be smaller than seedlings growing under dense canopy cover. This relationship likely reflects different ecological strategies of plants under different light conditions. Late-successional plant species are usually equipped with large seeds which yield large seedlings (Dalling and Hubbell 2002, Saavedra et al. 2015). Consequently, large-seeded species can better cope with biotic and abiotic pressures at the seedling stage, and prevail over small-seeded species in the shaded understory (Wright et al. 2003, Baraloto et al. 2005). In fact, shade-tolerant late-successional species are more likely to establish under a dense canopy than early-successional species (Dalling and Hubbell 2002, Falster et al. 2018, Umaña et al. 2021a), but grow more slowly than the small-sized seedlings of early-successional species (Baraloto et al. 2005, Supporting information). Overall, our findings imply that community assembly of plants at the initial stage is highly dependent on light conditions at the local scale. It also suggests that initial seedling height is a valuable functional trait that can reflect differences in growth rates and the prevailing successional strategy in different environmental contexts.

Seed mass was not significantly associated with canopy openness. A study on seed rain from the same area recently demonstrated that canopy openness was negatively related to seed rain richness within elevations (Acosta-Rojas et al. 2023a). Hence, local light conditions may influence species richness in seed rain, but were unrelated to mean seed mass

at the community level. A very interesting finding of our study is that canopy openness affected the composition of seed and seedling traits differently although the two traits are correlated (Baraloto et al. 2005). This finding depicts differences in filtering mechanisms and species sorting at adult and seedling stage. The upcoming seedling communities appear to be characterised by a different trait composition than the established adult plant communities, indicating high dynamics in the trait composition of tropical plant communities. Disequilibrium dynamics in trait–environment associations may be particularly strong in tropical montane forests that undergo rapid small-scale changes in light conditions, due to frequent natural disturbances (Dislich and Huth 2012).

In our study, we investigated trait–environment associations across different plant life stages and spatial scales by focussing on one representative trait for each plant stage (Westoby 1998, Moles and Westoby 2006, Falster et al. 2018). Previous studies have proposed to use multiple traits in studying trait–environment associations in order to increase the power and accuracy of analyses of trait–environment associations (Bruelheide et al. 2018, Saatkamp et al. 2019, Maynard et al. 2022, Rosbakh et al. 2022). Given the close correlations between traits describing the main axes of the plant economics spectrum (e.g. for leaf traits, specific leaf area and leaf thickness), we are confident that our trait selection allowed us to describe the main axes of variation for leaf, seed and seedling traits. Nevertheless, we encourage future studies to measure multiple traits across plant life stages despite the challenges related to obtaining these traits.

Conclusions

We found trait-specific variation in the functional composition of plant communities with regard to variation in soil and light conditions within elevations, although large-scale patterns in trait composition of leaves, seeds and seedling were consistent across elevations. At small spatial scales, leaf trait variation was primarily governed by variation in soil conditions, whereas variation in seedling size depended on changing light conditions. In contrast, the functional composition in terms of seed size seems to be shaped by factors unmeasured in our study or may be in disequilibrium with current abiotic conditions. Our study of plant traits across the plant life cycle shows that plant responses to environmental conditions are contingent on their life stage. The variable responses of plants at different life stages are related to scale-dependent effects of environmental filtering on plant communities which is likely to contribute to the exceptionally high plant diversity in the Andean tropical mountains.

Author contributions

Maciej K. Barczyk: Conceptualization (equal); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (equal); Writing – original draft (lead). **Diana Carolina Acosta-Rojas**: Conceptualization (equal); Data curation (supporting); Investigation (equal); Methodology (equal); Writing – review and editing (supporting). **Carlos Iván Espinosa**: Funding acquisition (supporting); Investigation (supporting); Methodology (supporting); Writing – review and editing (supporting). **Jürgen Homeier**: Data curation (supporting); Funding acquisition (supporting); Investigation (equal); Methodology (supporting); Writing – review and editing (supporting). **Boris A. Tinoco**: Writing – review and editing (supporting). **Andre Velescu**: Data curation (supporting); Funding acquisition (supporting); Investigation (equal); Methodology (supporting); Writing – review and editing (supporting). **Wolfgang Wilcke**: Funding acquisition (supporting); Investigation (supporting); Methodology (supporting); Writing – review and editing (supporting). **Matthias Schleuning**: Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Supervision (equal); Writing – review and editing (equal). **Eike Lena Neuschulz**: Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Supervision (equal); Writing – review and editing (equal).

Data availability statement

The raw data have been stored at the data warehouse of the RESPECT Project website www.tropicalmountainforest.org.

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.5mkkwh7f6 (Barczyk et al. 2024) and https://doi.org/10.5061/dryad.6hdr7sr4v (Acosta-Rojas et al. 2023b).

Supporting information

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

References

Acosta-Rojas, D. C., Barczyk, M., Espinosa, C. I., Gusmán, J., Peña, J., Neuschulz, E. L., Schleuning, M. and Homeier, J. 2021. Field guide of animal-dispersed plants: fruits and seeds in and around Podocarpus National Park. – INABIO 1: 16.

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

Acosta-Rojas, D. C. et al. 2023b. Climate and microhabitat shape the prevalence of endozoochory in the seed rain of tropical montane forests [Dataset]. Dryad. https://doi.org/10.5061/dryad.6hdr7sr4v

Adler, P. B., Salguero-Gómez, R., Compagnoni, A., Hsu, J. S., Ray-Mukherjee, J., Mbeau-Ache, C. and Franco, M. 2014. Functional traits explain variation in plant life history strategies. – Proc. Natl Acad. Sci. USA 111: 740–745.

Albrecht, J., Classen, A., Vollstädt, M. G. R., Mayr, A., Mollel, N. P., Schellenberger Costa, D., Dulle, H. I., Fischer, M., Hemp, A., Howell, K. M., Kleyer, M., Nauss, T., Peters, M. K., Tschapka, M., Steffan-Dewenter, I., Böhning-Gaese, K. and Schleuning, M. 2018. Plant and animal functional diversity drive mutualistic network assembly across an elevational gradient. – Nat. Commun. 9: 3177.

Andersen, K. M., Corre, M. D., Turner, B. L. and Dalling, J. W. 2010. Plant–soil associations in a lower montane tropical forest: physiological acclimation and herbivore-mediated responses to nitrogen addition: seedling responses to nitrogen addition in a tropical montane forest. – Funct. Ecol. 24: 1171–1180.

Apaza-Quevedo, A., Lippok, D., Hensen, I., Schleuning, M. and Both, S. 2015. Elevation, topography, and edge effects drive functional composition of woody plant species in tropical montane forests. – Biotropica 47: 449–458.

Arellano, G., Jørgensen, P. M., Fuentes, A. F., Loza, M. I., Torrez, V. and Macía, M. J. 2016. Oligarchic patterns in tropical forests: role of the spatial extent, environmental heterogeneity and diversity. – J. Biogeogr. 43: 616–626.

Auffret, A. G., Rico, Y., Bullock, J. M., Hooftman, D. A. P., Pakeman, R. J., Soons, M. B., Suárez-Esteban, A., Traveset, A., Wagner, H. H. and Cousins, S. A. O. 2017. Plant functional connectivity – integrating landscape structure and effective dispersal. – J. Ecol. 105: 1648–1656.

Báez, S., Fadrique, B., Feeley, K. and Homeier, J. 2022. Changes in tree functional composition across topographic gradients and through time in a tropical montane forest. – PLoS One 17: e0263508.

Baraloto, C., Forget, P.-M. and Goldberg, D. E. 2005. Seed mass, seedling size and Neotropical tree seedling establishment. – J. Ecol. 93: 1156–1166.

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

Barczyk, M. K., Acosta-Rojas, D. C., Espinosa, C. I., Homeier, J., Tinoco, B. A., Velescu, A., Wilcke, W., Schleuning, M. and Neuschulz, E. L. 2024. Data from: Environmental conditions differently shape leaf, seed and seedling trait composition between and within elevations of tropical montane forests. – Dryad Digital Repository, https://doi.org/10.5061/dryad.5mkkwh7f6.

Bartoń, K. 2023. Mumin: multi-model inference (1.47.0). – https://cran.rstudio.com/web/packages/MuMIn/index.html.

Bates, D., Mächler, M., Bolker, B. and Walker, S. 2015. Fitting linear mixed-effects models using lme4. – J. Stat. Softw. 67: 1–48.

Bendix, J., Rollenbeck, R., Richter, M., Fabian, P. and Emck, P. 2008. Climate. – In: Beck, E., Bendix, J., Kottke, I., Makeschin, F. and Mosandl, R. (eds), Gradients in a tropical mountain ecosystem of Ecuador. – Ecological studies, vol. 198. Springer-Verlag, pp. 87–100.

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. and Farwig, N. 2021. A research framework for projecting ecosystem change in highly diverse tropical mountain ecosystems. – Oecologia 195: 589–600.

Bolmgren, K. and Eriksson, O. 2010. Seed mass and the evolution of fleshy fruits in angiosperms. – Oikos 119: 707–718.

Bouchard, E. et al. 2024. Global patterns and environmental drivers of forest functional composition. – Global Ecol. Biogeogr. 33: 303–324.

Bruelheide, H. et al. 2018. Global trait–environment relationships of plant communities. – Nat. Ecol. Evol. 2: 1906–1917.

Canham, C. D. and Murphy, L. 2016. The demography of tree species response to climate: seedling recruitment and survival. – Ecosphere 7: e01424.

Clarke, P. J., Kerrigan, R. A. and Westphal, C. J. 2001. Dispersal potential and early growth in 14 tropical mangroves: do early life history traits correlate with patterns of adult distribution? – J. Ecol. 89: 648–659.

Dalling, J. W. and Hubbell, S. P. 2002. Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. – J. Ecol. 90: 557–568.

Dantas de Paula, M., Forrest, M., Langan, L., Bendix, J., Homeier, J., Velescu, A., Wilcke, W. and Hickler, T. 2021. Nutrient cycling drives plant community trait assembly and ecosystem functioning in a tropical mountain Biodiversity Hotspot. – New Phytol. 232: 551–566.

Dayrell, R. L. C., Arruda, A. J., Pierce, S., Negreiros, D., Meyer, P. B., Lambers, H. and Silveira, F. A. O. 2018. Ontogenetic shifts in plant ecological strategies. – Funct. Ecol. 32: 2730–2741.

Díaz, S. and Cabido, M. 2001. Vive la différence: plant functional diversity matters to ecosystem processes. – Trends Ecol. Evol. 16: 646–655.

Díaz, S. et al. 2016. The global spectrum of plant form and function. – Nature 529: 167–171.

Dislich, C. and Huth, A. 2012. Modelling the impact of shallow landslides on forest structure in tropical montane forests. – Ecol. Modell. 239: 40–53.

Duivenvoorden, J. F. and Cuello A, N. L. 2012. Functional trait state diversity of Andean forests in Venezuela changes with altitude. – J. Veg. Sci. 23: 1105–1113.

Falster, D. S., Duursma, R. A. and FitzJohn, R. G. 2018. How functional traits influence plant growth and shade tolerance across the life cycle. – Proc. Natl Acad. Sci. USA 115: E6789–E6798.

Forget, P. M., Dennis, A. J., Mazer, S. J., Jansen, P. A., Kitamura, S., Lambert, J. E. and Westcott, D. A. 2007. Seed allometry and disperser assemblages in tropical rain forests: a comparison of four floras on different continents. In A. J. Dennis, R. J. Green, E. W. Schupp and D. A. Westcott (eds), Seed dispersal: theory and its application in a changing world (pp. 5–36). CABI.

Foster, B. L., Questad, E. J., Collins, C. D., Murphy, C. A., Dickson, T. L. and Smith, V. H. 2011. Seed availability constrains plant species sorting along a soil fertility gradient: seed availability constrains plant sorting. – J. Ecol. 99: 473–481.

Gibert, A., Gray, E. F., Westoby, M., Wright, I. J. and Falster, D. S. 2016. On the link between functional traits and growth rate:

meta-analysis shows effects change with plant size, as predicted. – J. Ecol. 104: 1488–1503.

Grubb, P. J. and Coomes, D. A. 1997. Seed mass and nutrient content in nutrient-starved tropical rainforest in Venezuela. – Seed Sci. Res. 7: 269–280.

Harrison, S. and LaForgia, M. 2019. Seedling traits predict drought-induced mortality linked to diversity loss. – Proc. Natl Acad. Sci. USA 116: 5576–5581.

Hodgson, J. G. et al. 2011. Is leaf dry matter content a better predictor of soil fertility than specific leaf area? – Ann. Bot. 108: 1337–1345.

Homeier, J., Werner, F. A., Gradstein, S. R., Breckle, S. W. and 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. and Kottke I. , Makeschin , F. andMosandl , R. (eds), Gradients in a tropical mountain ecosystem of Ecuador, Ecological studies, Vol. 221. Springer-Verlag, pp. 87–100.

Homeier, J., Breckle, S.-W., Günter, S., Rollenbeck, R. T. and Leuschner, C. 2010. Tree diversity, forest structure and productivity along altitudinal and topographical gradients in a species-rich Ecuadorian montane rain forest: Ecuadorian montane forest diversity and structure. – Biotropica 42: 140–148.

Homeier, J., Seeler, T., Pierick, K. and Leuschner, C. 2021. Leaf trait variation in species-rich tropical Andean forests. – Sci. Rep. 11: 9993.

Hu, J. and Riveros-Iregui, D. A. 2016. Life in the clouds: are tropical montane cloud forests responding to changes in climate? – Oecologia 180: 1061–1073.

Hu, X. W., Zhang, R., Wu, Y. P. and Baskin, C. C. 2017. Seedling tolerance to cotyledon removal varies with seed size: a case of five legume species. – Ecol. Evol. 7: 5948–5955.

Hulshof, C. M., Violle, C., Spasojevic, M. J., McGill, B., Damschen, E., Harrison, S. and Enquist, B. J. 2013. Intra-specific and inter-specific variation in specific leaf area reveal the importance of abiotic and biotic drivers of species diversity across elevation and latitude. – J. Veg. Sci. 24: 921–931.

Jager, M. M., Richardson, S. J., Bellingham, P. J., Clearwater, M. J. and Laughlin, D. C. 2015. Soil fertility induces coordinated responses of multiple independent functional traits. – J. Ecol. 103: 374–385.

Kessler, M. and Kluge, J. 2008. Diversity and endemism in tropical montane forests - From patterns to processes. – In: Gradstein, S. R., Homeier, J. and Ganser, D. (eds), The tropical mountain forest – patterns and processes in a biodiversity hotspot. Biodiversity and ecology series 2. Göttingen Centre for Biodiversity, pp. 35–50.

Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., Levine, J. M. and Fox, J. M. 2015a. Plant functional traits and the multidimensional nature of species coexistence. – Proc. Natl Acad. Sci. USA 112: 797–802.

Kraft, N. J. B., Godoy, O. and Levine, J. M. 2015b. Community assembly, coexistence and the environmental filtering metaphor. – Funct. Ecol. 29: 592–599.

Kuprewicz, E. K. and García-Robledo, C. 2019. Deciphering seed dispersal decisions: size, not tannin content, drives seed fate and survival in a tropical forest. – Ecosphere 10: e02551.

Kuznetsova, A., Brockhoff, P. B. and Christensen, R. H. B. 2017. lmerTest package: tests in linear mixed effects models. – J. Stat. Softw. 82: 1–26.

Larson, J. E. and Funk, J. L. 2016. Regeneration: an overlooked aspect of trait-based plant community assembly models. – J. Ecol. 104: 1284–1298.

Lasky, J. R., Uriarte, M., Boukili, V. K. and Chazdon, R. L. 2014. Trait-mediated assembly processes predict successional changes in community diversity of tropical forests. – Proc. Natl Acad. Sci. USA 111: 5616–5621.

Lavorel, S. and Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail: plant response and effect groups. – Funct. Ecol. 16: 545–556.

Lebrija-Trejos, E., Pérez-García, E. A., Meave, J. A., Bongers, F. and Poorter, L. 2010. Functional traits and environmental filtering drive community assembly in a species-rich tropical system. – Ecology 91: 386–398.

Maynard, D. S. et al. 2022. Global relationships in tree functional traits. – Nat. Commun. 13: 3185.

Moles, A. T. and Westoby, M. 2004. What do seedlings die from and what are the implications for evolution of seed size? – Oikos 106: 193–199.

Moles, A. T. and Westoby, M. 2006. Seed size and plant strategy across the whole life cycle. – Oikos 113: 91–105.

Moles, A. T., Falster, D. S., Leishman, M. R. and 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.

Moles, A. T., Ackerly, D. D., Webb, C. O., Tweddle, J. C., Dickie, J. B., Pitman, A. J. and Westoby, M. 2005. Factors that shape seed mass evolution. – Proc. Natl Acad. Sci. USA 102: 10540–10544.

Nottingham, A. T., Fierer, N., Turner, B. L., Whitaker, J., Ostle, N. J., McNamara, N. P., Bardgett, R. D., Leff, J. W., Salinas, N., Silman, M. R., Kruuk, L. E. B. and Meir, P. 2018. Microbes follow Humboldt: temperature drives plant and soil microbial diversity patterns from the Amazon to the Andes. – Ecology 99: 2455–2466.

Peguero, G., Coello, F., Sardans, J., Asensio, D., Grau, O., Llusià, J., Ogaya, R., Urbina, I., Van Langenhove, L., Verryckt, L. T., Stahl, C., Bréchet, L., Courtois, E. A., Chave, J., Hérault, B., Janssens, I. A. and Peñuelas, J. 2023. Nutrient-based species selection is a prevalent driver of community assembly and functional trait space in tropical forests. – J. Ecol. 111: 1218–1230.

Pérez-Ramos, I. M., Aponte, C., García, L. V., Padilla-Díaz, C. M. and Marañón, T. 2014. Why is seed production so variable among individuals? A ten-year study with oaks reveals the importance of soil environment. – PLoS One 9: e115371.

Pierick, K., Leuschner, C. and Homeier, J. 2021. Topography as a factor driving small-scale variation in tree fine root traits and root functional diversity in a species-rich tropical montane forest. – New Phytol. 230: 129–138.

Pierick, K., Link, R. M., Leuschner, C. and Homeier, J. 2023. Elevational trends of tree fine root traits in species-rich tropical Andean forests. – Oikos 2023: e08975.

Pierick, K., Leuschner, C., Link, R. M., Báez, S., Velescu, A., Wilcke, W. and Homeier, J. 2024. Above- and belowground strategies of tropical montane tree species are coordinated and driven by small-scale nitrogen availability. – Funct. Ecol. 38: 1364–1377.

Post, W. M., Pastor, J., Zinke, P. J. and Stangenberger, A. G. 1985. Global patterns of soil nitrogen storage. – Nature 317: 613–616.

Quitián, M., Santillán, V., Espinosa, C. I., Homeier, J., Böhning-Gaese, K., Schleuning, M. and Neuschulz, E. L. 2018. Elevation-dependent effects of forest fragmentation on plant–bird interaction networks in the tropical Andes. – Ecography 41: 1497–1506.

Reich, P. B. 2014. The world-wide 'fast–slow' plant economics spectrum: a traits manifesto. – J. Ecol. 102: 275–301.

Rosbakh, S., Chalmandrier, L., Phartyal, S. and Poschlod, P. 2022. Inferring community assembly processes from functional seed trait variation along elevation gradient. – J. Ecol. 110: 2374–2387.

Saatkamp, A. et al. 2019. A research agenda for seed-trait functional ecology. – New Phytol. 221: 1764–1775.

Saavedra, F., Hensen, I. and Schleuning, M. 2015. Deforested habitats lack seeds of late-successional and large-seeded plant species in tropical montane forests. – Appl. Veg. Sci. 18: 603–612.

Sales, L. P., Kissling, W. D., Galetti, M., Naimi, B. and Pires, M. 2021. Climate change reshapes the eco-evolutionary dynamics of a Neotropical seed dispersal system. – Global Ecol. Biogeogr. 30: 1129–1138.

Santillán, V., Quitián, M., Tinoco, B. A., Zárate, E., Schleuning, M., Böhning-Gaese, K. and Neuschulz, E. L. 2018. Spatio-temporal variation in bird assemblages is associated with fluctuations in temperature and precipitation along a tropical elevational gradient. – PLoS One 13: e0196179.

Schielzeth, H. 2010. Simple means to improve the interpretability of regression coefficients: interpretation of regression coefficients. – Methods Ecol. Evol. 1: 103–113.

Schmitt, S., Hérault, B., Ducouret, É., Baranger, A., Tysklind, N., Heuertz, M., Marcon, É., Cazal, S. O. and Derroire, G. 2020. Topography consistently drives intra- and inter-specific leaf trait variation within tree species complexes in a Neotropical forest. – Oikos 129: 1521–1530.

Song, X., Yang, J., Cao, M., Lin, L., Sun, Z., Wen, H. and Swenson, N. G. 2021. Traits mediate a tradeoff in seedling growth response to light and conspecific density in a diverse subtropical forest. – J. Ecol. 109: 703–713.

Terborgh, J., Nuñez-Iturri, G., Pitman, N. C. A., Valverde, F. H. C., Alvarez, P., Swamy, V., Pringle, E. G. and Paine, C. E. T. 2008. Tree recruitment in an empty forest. – Ecology 89: 1757–1768.

Umaña, M. N., Arellano, G., Swenson, N. G. and Zambrano, J. 2021a. Tree seedling trait optimization and growth in response to local-scale soil and light variability. – Ecology 102: e03252.

Umaña, M. N., Lin, L., Swenson, N. G. and Zhang, C. 2021b. Tradeoffs in above- and below-ground biomass allocation influencing seedling growth in a tropical forest. – J. Ecol. 109: 1184–1193.

Velescu, A., Fabian, T. and Wilcke, W. 2022. Soil chemical properties associated with PFT tree species in the Core Plots at 1000, 2000 and 300 m a.s.l. (dataset). – http://www.tropicalmountainforest.org/data_pre.do?citid=1948.

Visser, M. D., Bruijning, M., Wright, S. J., Muller-Landau, H. C., Jongejans, E., Comita, L. S. and Kroon, H. 2016. Functional traits as predictors of vital rates across the life cycle of tropical trees. – Funct. Ecol. 30: 168–180.

Vollstädt, M. G. R., Ferger, S. W., Hemp, A., Howell, K. M., Töpfer, T., Böhning-Gaese, K. and Schleuning, M. 2017. Direct and indirect effects of climate, human disturbance and plant traits on avian functional diversity. – Global Ecol. Biogeogr. 26: 963–972.

Wang, B. C. and Smith, T. B. 2002. Closing the seed dispersal loop. – Trends Ecol. Evol. 17: 379–386.

Werner, F. A. and Homeier, J. 2015. Is tropical montane forest heterogeneity promoted by a resource-driven feedback cycle? Evidence from nutrient relations, herbivory and litter decomposition along a topographical gradient. – Funct. Ecol. 29: 430–440.

Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. – Plant Soil 199: 213–227.

Westoby, M., Schrader, J. and Falster, D. 2022. Trait ecology of startup plants. – New Phytol. 235: 842–847.

Wickham, H. 2011. The split-apply-combine strategy for data analysis. – J. Stat. Softw. 40: 1–29.

Wickham, H. 2016. ggplot2: elegant graphics for data analysis. – https://ggplot2-book.org/.

Wieczynski, D. J., Boyle, B., Buzzard, V., Duran, S. M., Henderson, A. N., Hulshof, C. M., Kerkhoff, A. J., McCarthy, M. C., Michaletz, S. T., Swenson, N. G., Asner, G. P., Bentley, L. P., Enquist, B. J. and Savage, V. M. 2019. Climate shapes and shifts functional biodiversity in forests worldwide. – Proc. Natl Acad. Sci. USA 116: 587–592.

Wilcke, W., Velescu, A., Leimer, S., Bigalke, M., Boy, J. and Valarezo, C. 2019. Temporal trends of phosphorus cycling in a tropical montane forest in Ecuador during 14 years. – J. Geophys. Res. Biogeosci. 124: 1370–1386.

Wilcke, W., Velescu, A., Leimer, S., Blotevogel, S., Alvarez, P. and Valarezo, C. 2020. Total organic carbon concentrations in ecosystem solutions of a remote tropical montane forest respond to global environmental change. – Global Change Biol. 26: 6989–7005.

Winkler, D. E., Garbowski, M., Kožić, K., Ladouceur, E., Larson, J., Martin, S., Rosche, C., Roscher, C., Slate, M. L. and Korell, L. 2024. Facilitating comparable research in seedling functional ecology. – Methods Ecol. Evol. 15: 464–476.

Wright, S. J., Muller-Landau, H. C., Condit, R. and Hubbell, S. P. 2003. Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. – Ecology 84: 3174–3185.

Wright, I. J. et al. 2004. The worldwide leaf economics spectrum. – Nature 428: 821–827.