Basic and Applied Ecology 75 (2024) 44–52

Contents lists available at ScienceDirect

Basic and Applied Ecology

journal homepage: www.elsevier.com/locate/baae

RESEARCH PAPER

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

Maciej K. Barczyk[a,b,*], Diana Carolina Acosta-Rojas[a,b], Carlos Iván Espinosa[c], Matthias Schleuning[a], Eike Lena Neuschulz[a]

[a] Senckenberg Biodiversity and Climate Research Centre, Frankfurt am Main 60325, Germany
[b] Department of Biological Sciences, Goethe-Universität, Frankfurt am Main 60438, Germany
[c] Departamento de Ciencias Biológicas, EcoSs Lab, Universidad Técnica Particular de Loja, Loja 1101608, Ecuador

ARTICLE INFO

Keywords:
Direct seeding
Montane forest
Podocarpus National Park
Seedling establishment
Seed sowing experiment
Tropical forest restoration

ABSTRACT

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

Introduction

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

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

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[*] Corresponding author at: Senckenberg Biodiversity and Climate Research Centre, Frankfurt am Main 60325, Germany.
E-mail address: maciejkbarczyk@gmail.com (M.K. Barczyk).

https://doi.org/10.1016/j.baae.2024.01.005
Received 16 December 2022; Accepted 31 January 2024

et al., 2018; Moreira et al., 2018). For instance, insect herbivory can follow hump-shaped patterns across elevations in tropical mountains (Sam et al., 2020), and leaf damage of plants is more likely to occur in human-altered habitats than inside natural forests (Morante-Filho et al., 2016).

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

Although recent studies have investigated which factors influence seedling recruitment across environmental gradients (García-Hernández et al., 2019; Lin et al., 2017), the effects of abiotic and biotic factors on plant species with different traits have rarely been studied in tropical mountains (Rozendaal et al., 2019; but see Toledo-Aceves et al. 2019). In addition, montane habitats are prone to drastic alterations due to land-use change (Lippok et al., 2013; Sales et al., 2020). Deforestation by humans limits plant recruitment (Gallegos et al., 2016; Granados et al., 2017), yet we lack field experiments that test how seedling recruitment differs among contrasting habitats (Cole et al., 2011; but see de la Peña-Domene et al. 2017, Toledo-Aceves et al. 2019). Ultimately, experiments in forests and human-modified habitats can inform the selection of plant species for forest restoration (Bastin et al., 2019). While previous studies have recommended using late-successional species and seed nucleation to restore tropical montane forests in Costa Rica (Cole et al., 2011; Palma & Laurance, 2015), there is limited information on seedling recruitment in deforested habitats of other tropical mountains (but see Toledo-Aceves et al. 2021).

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

Materials and methods

Study area

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

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

Seed sowing experiment

On each of the 18 plots, we randomly selected three relatively flat subplots of roughly 15 m^2 with no trees, resulting in a total of 54 subplots (Fig. 1). The distance between subplots was a minimum of 20 m. Prior to the sowing experiment, we removed the existing vegetation on these subplots to clear the soil surface for the sowing. All subplots located in the pastures were fenced to avoid trampling by cattle, whereas all forest subplots remained unfenced because of the rarity of large mammals in the forest.

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

We sowed seeds of each species in both forest and pasture plots at

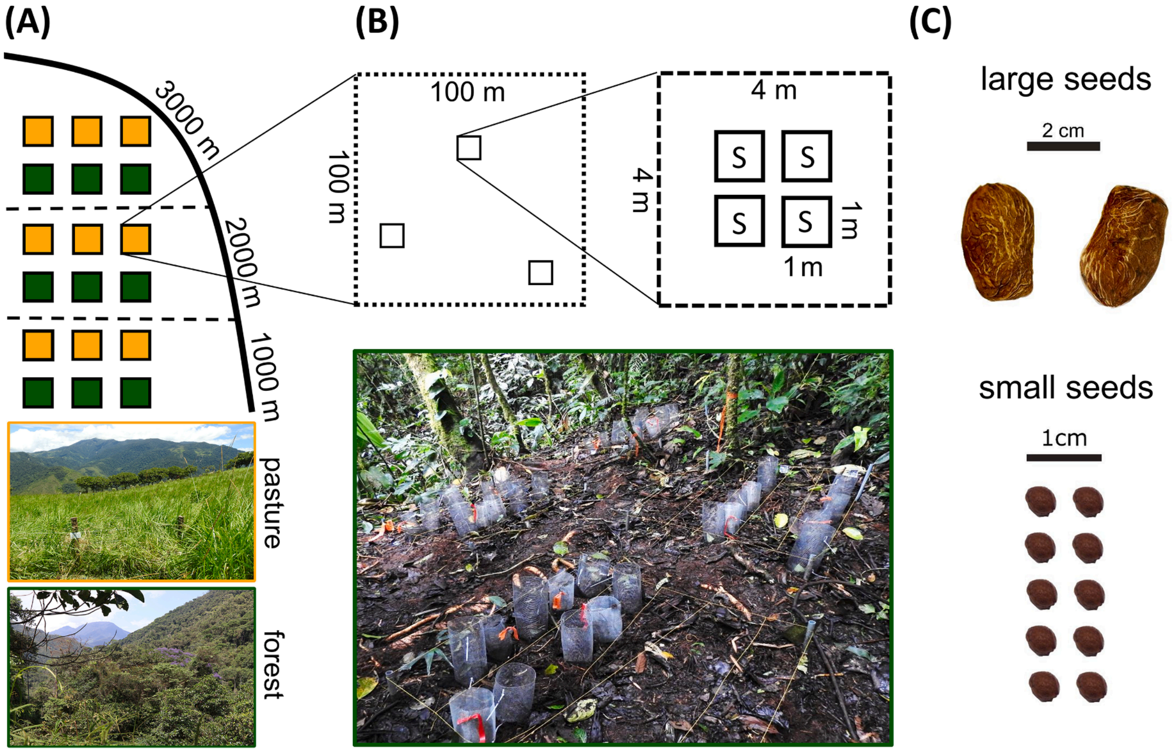

Fig. 1. Design of a seed sowing experiment with five species in the tropical mountains of South Ecuador. (A) Schematic overview of the location of plots ($n = 18$) at three elevations a.s.l. Green squares correspond to primary forest plots, yellow squares indicate pasture plots. Photographs show habitat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

their elevation of origin. We did not transplant seeds outside of the natural occurrence of the study species, because we aimed to compare differences in seedling recruitment across habitats at the respective home elevation. None of the species used for the experiment occurred outside the elevation of origin. Sowing times depended on the time of fruiting and therefore occurred between December 2018 and August 2019 reflecting the natural variation among the study species (i.e., *Ocotea* sp. – December 2018; *H. fendleri* and *C. ducuoides* – February 2019; *H. purpurascens* – June 2019; *T. guianensis* ssp. *subandina* – August 2019).

In each subplot, we set up four quadrates of 1 m^2 to sow seeds and bordered them with strings (sowing units; see Fig. 1B). Because large-seeded and small-seeded species differ in germination rates, we sowed a larger number of seeds for small-seeded than for large-seeded species (Paz & Martínez-Ramos, 2003). We sowed ten small or two large seeds into a 10 × 10 cm patch of mosquito net filled with soil and protected it with a metallic mesh tube that was open at the top to lower seed predation by rodents and birds (Paine & Beck, 2007) and to easily find and handle seedlings at repeated surveys. Insect herbivores were able to access and feed on emerging seedlings. In total, 7214 small and 1248 large seeds were sown (sum = 8462 seeds; see also Appendix A: Table A1 in Supplementary Material). Prior to sowing, all seeds were treated for 1 min in 5 % chlorine bleach solution to clean the seeds of any fungal pathogens (Luna et al., 2014).

Every three months, we recorded and marked each emerging seedling with a plastic cable tie. Depending on the study species and the timing of the sowing experiment, the monitoring period lasted between 10 and 18 months: *Ocotea* sp. – 18 months; *H. fendleri* and *C. ducuoides* – 15 months; *H. purpurascens* – 12 months; *T. guianensis* ssp. *subandina* – 10 months. During each visit, we measured seedling height and recorded traces of herbivory and fungal pathogens. We considered any kind of external damage including bites and leaf mining as traces of herbivory (Muehleisen et al., 2020). Likewise, changes in leaf colour and/or necrotic spots on leaves were considered as traces of fungal pathogens (Benítez-Malvido & Lemus-Albor, 2005). At the end of the experiment, we harvested each seedling to measure its dry biomass. After careful cleaning of the seedlings with water, we cut the stems from the roots to separate below- and aboveground biomass. Roots and stems with leaves were then put into paper bags and dried in the oven at 60 °C for 72 h. After drying the samples, we weighed the aboveground- and belowground dry biomass of each seedling with a high precision analytical balance (KERN & SOHN GmbH, Germany). Based on these two measures, we calculated the ratio between below- and aboveground biomass (i.e., root-to-shoot ratio) for each seedling as a relative measure of below- versus aboveground investment.

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

Abiotic factors

We buried several data loggers at the depth of sown seeds (ca. 2 cm deep) to measure surface temperature. Surface temperature was recorded at all 54 subplots using iButton data loggers (Maxim/Dallas Semiconductor Corp., Texas, U.S.A) every 4 h throughout an entire year (June 2019 – June 2020). We calculated two measures related to surface temperature: mean daily mean surface temperature and mean daily maximum surface temperature. We decided to use mean daily maximum surface temperature values for the three driest months (September–November 2019) in the analyses, as extreme temperatures increase seedling mortality by drought stress (Holl, 1999). Average soil moisture was measured at all subplots twice during two seasons: dry (i.e., less rainy) season (October 2019) and rainy season (May-June 2020) using a tensiometer (SM150 Kit, Delta-T Devices Ltd., UK). We used soil moisture records from the dry season in the analyses, assuming that low soil moisture would increase drought stress in combination with high temperatures. Both abiotic variables were non-correlated at the subplot level (Pearson's $r < 0.15$, $p > 0.05$). Summary statistics (mean and SD) of both abiotic variables are given in the Appendix A: Table A2.

Biotic factors

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

Statistical analysis

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

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

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

Results

Over the entire experimental period, a total of 913 seedlings established out of 8462 sown seeds across habitat types and elevations. Overall, 370 seedlings established out of 1248 large seeds (29.6 %), and 543 seedlings established out of 7214 small seeds (7.5 %). After the one-year-period after sowing, seedling establishment and recruitment success differed between species (Appendix A: Fig. A2). The variation in seedling establishment of the three small-seeded species ranged between 0 and 0.40 (shown as a proportion, $n = 32$ subplots at mid and high elevations; see Fig. 1). Recruitment success of the three small-seeded species varied between 0 and 0.30. Similarly, seedling establishment of the two large-seeded species varied between 0.03 and 0.75, and their recruitment success ranged between 0 and 0.50 ($n = 36$ subplots at low and mid elevations). Although seedling establishment and recruitment success of the small-seeded species varied greatly, *Ocotea* sp. and *Tapirira guianensis* ssp. *subandina* (large-seeded species) established and recruited on average better than *Clusia ducuoides, Hedyosmum purpurascens* and *Hieronyma fendleri* (small-seeded species, Appendix A: Table A3).

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

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

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

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

Surface temperature was the most important explanatory variable in the models (Table 3) and interacted with seed size in the effects on

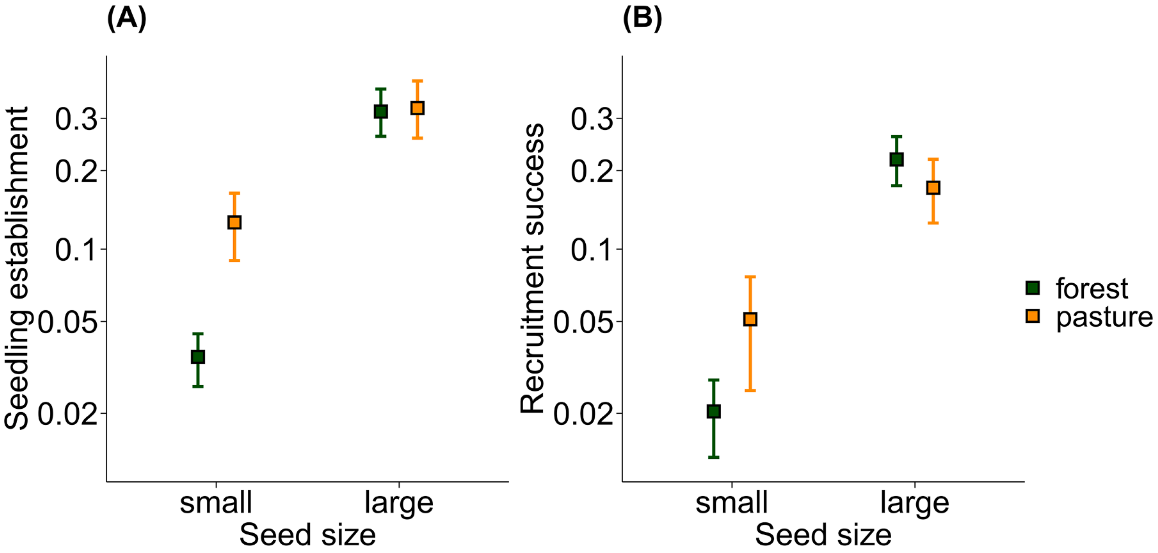

Fig. 2. Seed size-dependent seedling establishment and recruitment success in two habitat types (green: forest, yellow: pasture) in the tropical mountains of South Ecuador. (A) Seedling establishment of three small- and two large-seeded species, shown as the proportion of seedlings established from seeds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

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

	Estimate	*Std. Error*	*z*	*p*	*R^2m*	*R^2c*
(A) Seedling establishment					0.40	0.90
(Intercept)	-0.74	0.54	-1.38	0.168		
Seed size (small)	-2.67	0.64	-4.18	**<0.001**		
Habitat (pasture)	-0.65	0.40	-1.63	0.104		
Seed size (small) x habitat (pasture)	2.08	0.26	8.12	**<0.001**		
(B) Recruitment success					0.33	0.85
(Intercept)	-1.40	0.60	-2.35	**0.019**		
Seed size (small)	-2.52	0.73	-3.46	**<0.001**		
Habitat (pasture)	-0.92	0.39	-2.36	**0.018**		
Seed size (small) x habitat (pasture)	2.01	0.35	5.69	**<0.001**		

seedling establishment and recruitment success. Seedling establishment and recruitment success of large-seeded species decreased with increasing temperature, whereas small-seeded species were more likely to establish at high temperatures (Appendix A: Fig. A3). According to the model (Table 3), an increase by one standard deviation unit of surface temperature (~ 5 °C) corresponded to a decrease in the odds of establishment and recruitment of large-seeded species by about 40 %. For small-seeded species, an increase by one standard deviation unit of surface temperature corresponded to an increase of the odds by about 60 % and 70 %, respectively. For example, the proportion of seedlings established from large seeds was predicted to decrease from 0.59 at 10 °C to 0.08 at 30 °C. In contrast, the model predicted an increase in the seedling establishment of small-seeded species from 0.03 at 10 °C to around 0.22 at 30 °C. In addition, the recruitment success of small-seeded species increased with increasing soil moisture (Table 3B). According to the model predictions, recruitment success of small-seeded species was expected to increase from 0.06 at 10 °C and 50 % soil moisture to 0.43 at 30 °C and 100 % soil moisture. The abiotic variables explained about 30 % of the variation in seedling establishment and recruitment success (Table 3). Neither seedling establishment nor recruitment were significantly related to insect herbivory incidence. Below- and aboveground biomass of seedlings were unrelated to abiotic or biotic variables, whereas root-to-shoot ratio was positively associated with surface temperature for both small- and large-seeded species (effect of surface temperature on root-to-shoot ratio: estimate (standard deviation units) = 0.08, t value = 5.23, $p < 0.001$)

Discussion

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

Habitat type and seedling recruitment

We found that seedlings of large-seeded species were more likely to establish than small-seeded species, but only in the forest habitat. Consequently, seed size seems to be a driving factor for differences in the regeneration process between natural and deforested habitats of tropical montane forests. A general advantage of large-seeded species to recruit has been detected in many tropical forests (Dalling & Hubbell, 2002;

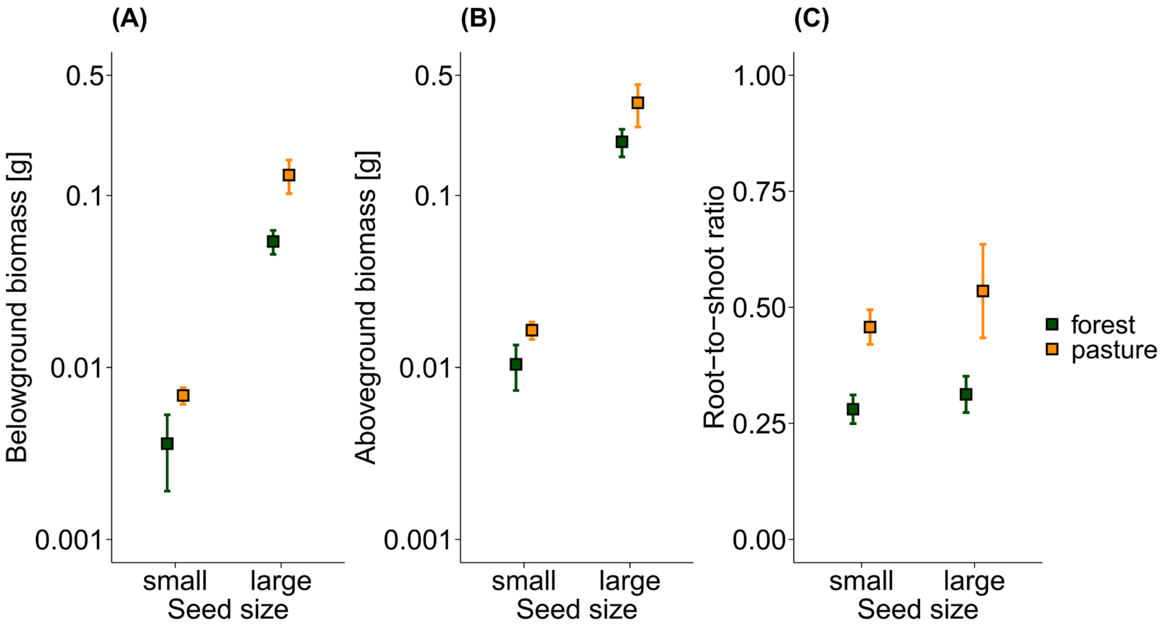

Fig. 3. (A) Belowground biomass, (B) aboveground biomass and (C) root-to-shoot ratio in seedlings of three small- and two large-seeded species in two habitat types (green: forest, yellow: pasture) in the tropical mountains of South Ecuador at the end of the experiment. Biomass variables (A and B) are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

Table 2

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

	Estimate	*Std. Error*	*df*	*t*	*p*	*R^2m*	*R^2c*
(A) Log_{10} belowground biomass						0.71	0.75
(Intercept)	-1.47	0.08	6.57	-18.98	**<0.001**		
Seed size (small)	-1.34	0.08	3.51	-16.27	**<0.001**		
Habitat (pasture)	0.47	0.08	13.07	5.70	**<0.001**		
(B) Log_{10} aboveground biomass						0.72	0.79
(Intercept)	-0.9	0.11	3.3	-7.91	**0.003**		
Seed size (small)	-1.26	0.14	2.81	-8.98	**0.003**		
Habitat (pasture)	0.21	0.07	12.05	3.15	**0.008**		
C) Root-to-shoot ratio						0.17	0.39
(Intercept)	0.32	0.08	3.28	4.11	**0.022**		
Seed size (small)	-0.08	0.10	2.79	-0.80	0.485		
Habitat (pasture)	0.24	0.04	10.98	5.43	**<0.001**		

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

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

Abiotic and biotic factors and seedling recruitment

Surface temperature was the main factor mediating recruitment differences of seedlings belonging to small- and large-seeded species across forest and pasture habitats (Table 3). We found that seedling

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

	Estimate	*Std. Error*	*z*	*p*	R^2m	R^2c
(A) Seedling establishment					0.34	0.91
(Intercept)	-0.85	0.69	-1.22	0.221		
Seed size (small)	-1.75	0.88	-2.00	**0.046**		
Max. temperature	-0.56	0.21	-2.70	**0.007**		
Seed size (small) x Max. temperature	1.02	0.18	5.60	**<0.001**		
(B) Recruitment success					0.35	0.86
(Intercept)	-1.61	0.68	-2.37	**0.018**		
Seed size (small)	-1.69	0.87	-1.95	0.051		
Max. temperature	-0.49	0.21	-2.28	**0.022**		
Soil moisture	-0.04	0.15	-0.29	0.772		
Seed size (small) x Max. temperature	0.99	0.22	4.58	**<0.001**		
Seed size (small) x Soil moisture	0.38	0.15	2.47	**0.014**		

establishment and recruitment success decreased with surface temperature but only for seedlings of the two large-seeded species sown at the lower elevations. Surface temperatures were generally higher in pastures than in forests (Appendix A: Table A2), suggesting that this difference was mainly responsible for the lower recruitment of seedlings belonging to the two large-seeded species in pastures. This corresponds with the outcome of a recent study from Northern Peru which showed that maximum temperatures inside montane forests tend to be around 4 °C lower compared to outside forests (Newell, 2022). Another study from the slopes of the Peruvian Andes has reported that solar irradiation limited seedling establishment of two *Polylepis* species, possibly due to increased soil temperature during a dry season (Morales et al., 2018). In other studies from tropical mountains, high temperature and seasonal drought in pastures have been identified as a limiting factor for seedling recruitment (de la Peña-Domene et al., 2017; Martínez-Garza et al., 2013). Intriguingly, we found that the three small-seeded species sown at mid and high elevations recruited better than large-seeded species at high surface temperatures and under high soil moisture. Seedlings of small-seeded species were apparently more resistant to extreme temperatures compared to large-seeded species, especially if a high soil moisture was maintained. A reason for this could be related to a lower exposure of these seedlings to high surface temperatures, as small seedlings may be better covered by surrounding vegetation than large ones. In addition, higher allocation into roots may have helped these seedlings to survive drought events in pastures. Previous studies identified species-specific differences in drought resistance across tropical seedlings (Kupers et al., 2019; Slot & Poorter, 2007). Such inter-specific differences may be linked to distinct ecological strategies of plant species corresponding to differences in shade tolerance (Kupers et al., 2019).

In our study, seedling establishment and recruitment success were unrelated to herbivory incidence despite an overall high incidence of biotic pressures on seedlings in both forest and pasture habitats. Attacks of insect herbivores and fungal pathogens are especially frequent if large mammals are rare (Williams et al., 2021). Other studies along rainfall gradients showed that seedlings from wet tropical forests experience relatively low damage from insect herbivores (Muehleisen et al., 2020), but are more likely to suffer from fungal diseases (Spear et al., 2015). In the wet tropical mountains of South Ecuador, effects of insect herbivory and fungal pathogens on seedling recruitment seemed to be less important for establishment and recruitment variables than the effects of the pronounced temperature differences between habitat types. Our findings do not rule out that biotic pressures can limit seedling recruitment in the studied ecosystems, but the variation in recruitment among species and habitat types seems to be primarily driven by abiotic effects. Future experiments with multiple species may help to gain a more complete understanding about the importance of biotic effects on seedling recruitment in tropical montane ecosystems (Pizano et al., 2014).

Implications for restoration

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

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

Second, we show that seed addition to pasture habitats enables recruitment of small-seeded and, to a lesser extent, of large-seeded species. This measure appears to be particularly important, because previous studies have shown that pastures often lack seeds, especially of late-successional and large-seeded plant species dispersed by animals (de la Peña-Domene et al., 2017; Saavedra et al., 2015). Forest restoration therefore requires active seed addition to facilitate the reforestation of pastures into forest ecosystems (Cole et al., 2010; Holl et al., 2017). Long-term monitoring of seedling establishment and survival followed after seed addition may further help to improve restoration efforts.

Data availability statement

The data used in this study are available at the website of the RESPECT project: www.tropicalmountainforest.org

Funding

This work was funded by the German Research Foundation (DFG) in the frame of the RESPECT research platform: Environmental changes in biodiversity hotspot ecosystems of South Ecuador: RESPonse and feedback effECTs (FOR2730).

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Eike Lena Neuschulz and Matthias Schleuning report that financial support was provided by the German Research Foundation.

Acknowledgments

We thank the Maldonado Macas Family, Kenji Watanabe, Samantha Solís-Oberg, Weronika Gajda-Barczyk, Julia Barczyk, Wioleta Oleś, Diego Iñiguez Quishpe, Milton Ortega Montaño and Wilson Ortega Montaño for their help completing the fieldwork. We thank the Ministerio del Ambiente and the Instituto Nacional de Biodiversidad de Ecuador for granting research permits and the foundation "Nature and Culture International" for providing research facilities. Special thanks go to Felix Matt, Robert Vera, and Mathias Templin for logistical support. Finally, we would like to thank four anonymous reviewers who provided insightful and comprehensive feedback on earlier versions of this manuscript.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2024.01.005.

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