

Changes in species interactions across a 2.5 km elevation gradient: effects on plant migration in response to climate change

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Abstract

Predicted climate change in the Andes will require plant species to migrate upslope to avoid extinction. Central to predictions of species responses to climate change is an understanding of species distributions along environmental gradients. Environmental gradients are frequently modelled as abiotic, but biotic interactions can play important roles in setting species distributions, abundances, and life history traits. Biotic interactions also have the potential to influence species responses to climate change, yet they remain mostly unquantified. An important interaction long studied in tropical forests is postdispersal seed predation which has been shown to affect the population dynamics, community structure, and diversity of plant species in time and space. This paper presents a comparative seed predation study of 24 species of tropical trees across a 2.5 km elevation gradient in the Peruvian Andes and quantifies seed predation variation across the elevational gradient. We then use demographic modelling to assess effects of the observed variation in seed predation on population growth rates in response to observed increasing temperatures in the area. We found marked variation among species in total seed predation depending on the major seed predator of the species and consistent changes in seed predation across the gradient. There was a significant increase in seed survival with increasing elevation, a trend that appears to be driven by regulation of seed predators via top-down forces in the lowlands giving way to bottom-up (productivity) regulation at mid- to high elevations, resulting in a ninefold increase in effective fecundity for trees at high elevations. This potential increase in seed crop size strongly affects modelled plant population growth and seed dispersal distances, increasing population migration potential in the face of climate change. These results also indicate that species interactions can have effects on par with climate in species responses to global change.

Keywords: Andes, climate change, demography, life table response experiment, seed dispersal, seed predation, species interactions, species migration

Received 30 November 2009; revised version received 6 April 2010 and accepted 16 April 2010

Introduction

Changes in species distributions along environmental gradients of temperature and moisture form the foundation for predictions of species responses to global climate change (Thomas *et al.*, 2004; Malcolm *et al.*, 2006; Colwell *et al.*, 2008; Feeley & Silman, 2010). In humid tropical systems, species extinctions are tied to species' abilities to migrate to higher elevations rather than latitudinally, as in temperate systems (Colwell *et al.*, 2008). Recent studies from Earth's highest biodiversity hotspot, the tropical Andes, predict a minimum 4 °C warming (Cramer *et al.*, 2004; Urrutia & Vuille, 2009). Given the adiabatic lapse rate of 5.6 °C km⁻¹, temperature changes of this magnitude require that species must migrate upslope ~700–800 m by 2100 to remain in equilibrium with climate,

with recent studies predicting that migration rates less than equilibrium lead to large-scale extinctions (Silman, 2007; Feeley & Silman, 2009, 2010). Most research on terrestrial species distributions along environmental gradients, both modelling (see Malcolm *et al.*, 2002; Thomas *et al.*, 2004 for overviews) and empirical work (e.g. Ibáñez *et al.*, 2008), focuses on changes in abiotic gradients (Davis *et al.*, 1998). However, biotic interactions are central to plant distributional ecology, and changes in biotic interactions can have profound effects on species distributions (Weltzin *et al.*, 1997; Leathwick & Austin, 2001; Webb & Peart, 2001). Indeed in a major empirical study of plant responses to climate change, a treatment intended to 'control' for seed predators had effects on plant recruitment that equalled or exceeded climate treatments (Ibáñez *et al.*, 2008). This raises acute questions: can species migrate fast enough to remain in equilibrium with climate? Are there biotic interactions that hinder or facilitate migration?

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Biotic interactions that have quantifiable impacts on plant populations can change over environmental gradients, similar to those long-documented in animal studies (e.g. Connell, 1961; Terborgh, 1971). These interactions include competition (Wilson & Keddy, 1986), herbivory by insects (Koptur, 1985; Miller *et al.*, 2006, 2009), mammals (Anderson *et al.*, 2007), insect seed dispersal, (Zelikova *et al.*, 2008), and seed predation (Louda, 1982; Muñoz & Arroyo, 2002; Rey *et al.*, 2002). Postdispersal seed predation is a widely studied and quantitatively important plant-animal interaction that can control population dynamics in time and space (Janzen, 1971; Hulme, 1998; Silman *et al.*, 2003). Seed addition experiments suggest that seed limitation is important in many different terrestrial habitats (Silman, 1996; Hulme, 1998; Svenning & Wright, 2005; but see Crawley, 2000). Seed predators can affect plant populations through changes in population dynamics (Harper, 1977; Crawley, 2000), community structure (Howe & Brown, 1999), and species diversity (Hubbell, 1980). In long-term studies of the population dynamics of tropical trees, Silman *et al.* (2003) and Wyatt & Silman (2004) found that population fluctuations in a major seed predator (white-lipped peccary) controlled recruitment of the two dominant tropical tree species (*Astrocaryum murumuru* and *Iriarteia deltoidea*) in Western Amazonia. Rodents as seed predators have been shown to have considerable impact on plant populations (Price & Jenkins, 1986), and to affect seed recruitment in tropical canopy trees (e.g. De Steven & Putz, 1984; Schupp, 1990). Additionally, seed predation has been shown to interact with other species interactions to radically alter distance- and frequency-dependent recruitment in tropical trees, a central mechanism maintaining diversity in tropical forests (Janzen, 1970; Connell, 1978; Wright & Duber, 2001; Wyatt & Silman, 2004).

Differential seed predation on plant species is reported in many studies (e.g. Terborgh *et al.*, 1993; Notman & Gorchov, 2001; Muñoz & Cavieres, 2006; Xiao *et al.*, 2006), and a central question surrounding differential predation is if there are species traits that predict it. One of the largest species differences in tropical forest communities is seed size, which ranges over more than six orders of magnitude. In tropical forests of South America, where seed predators range from small insects (particularly ants; $\sim 10^{-2}$ g) to large bodied mammals such as peccaries and tapirs (10^4 – 10^5 g), this wide variation in seed size can have multiple effects. The physical capability of predators to open seeds of different sizes or the nutritional return on search and handling time (Louda, 1989; Blate *et al.*, 1998) may change the suite of seed predators to which a plant species is exposed. Seed size may also affect predation risk indirectly through differences in germination rate, which in turn affects the period of time a seed is

at risk of predation (Silman, 1996; Baraloto & Forget, 2007). Size-independent effects that affect predation risk include variability in secondary chemistry (Janzen, 1969), caloric content (Kear, 1962), nutritional content (Kelrick *et al.*, 1985; Hulme, 1993), and seed density (Nilsson & Wästljung, 1987).

The few studies that have compared seed predation at different elevations showed that predation varies with elevation due to changes in the activity of ants and birds (Louda, 1982; Muñoz & Arroyo, 2002) or changes in vegetation structure (Rey *et al.*, 2002). The generality of these studies, which encompass a limited elevational range, is further limited by the inclusion of only one to three study species.

Here we report the results of a large-scale field experiment spanning 2500 m in elevation, representing $\sim 14^\circ\text{C}$ change in temperature, to look at seed predation in 24 species of tropical trees distributed along the eastern flank of the Andes and adjacent Amazonian lowlands. We (1) ask whether there are general patterns in seed predation rates by seed predator guilds and (2) quantify variation in seed predation rates with elevation. We then use these data in a life table response experiment (LTRE) to look at the effects of seed predation on species predicted population growth rates and migration potential under scenarios of climate change.

Methods

Study site

The study was performed in the Kosñipata Valley on the southeastern flank of the Peruvian Andes ($13^\circ 06'\text{S}$, $71^\circ 36'\text{E}$). In 2003, a network of 14 1 ha permanent plots was established along an elevation gradient in primary montane forest roughly every 250 m from 800 to 3450 m. Eleven of the permanent plots were used in this study, excluding three that are elevational replicates. Climate along the gradient is perhumid, with annual precipitation ranging from ~ 7 m at the lower end of the gradient to 2.4 m at 3500 m, and mean annual temperatures ranging from 23 to 8.5°C with increasing elevation. All trees ≥ 10 cm dbh [diameter at breast height (1.33 m)] have been tagged and identified to species.

Study species

The 23 native tree species used in this study (Table 1) were chosen to represent a range of seed sizes and elevational ranges (species that grow in low, mid-, and high elevations). A tropical grass, *Zea mays* L., has been demonstrated to be edible by a broad variety of rodents and was used as a control along the gradient. Seeds were collected in July 2008 by searching the permanent plots and the forests at Wayqecha Cloud Forest Research Center (~ 2600 – 3200 m) and Pantiacolla Lodge (~ 400 – 800 m). Seeds were gathered from ripe fruits in

Table 1 Species used in seed predation experiments in order of increasing seed mass

Species	Family	Mass (g)	Elevation range (m)
<i>Hesperomeles ferruginea</i>	Rosaceae	0.005 ± 0.002	2400–3800
<i>Heliocarpus americanus</i>	Malvaceae	0.007 ± 0.003	0–2110
<i>Solanum</i> sp.	Solanaceae	0.010 ± 0.009	0–3900
<i>Myrica pubescens</i>	Myricaceae	0.013 ± 0.005	2000–3400
<i>Hyeronima oblonga</i>	Euphorbiaceae	0.02 ± 0.01	265–2445
<i>Turpinia occidentalis</i>	Rosaceae	0.04 ± 0.02	95–2787
<i>Rinorea</i> sp.	Violaceae	0.05 ± 0.02	50–840
<i>Guatteria duodecima</i>	Annonaceae	0.12 ± 0.06	150–1321
<i>Zea mays</i>	Poaceae	0.17 ± 0.02	20–3500
<i>Virola sebifera</i>	Fabaceae	0.23 ± 0.11	36–1330
<i>Tapirira guianensis</i>	Anacardiaceae	0.29 ± 0.05	50–1778
<i>Myrcia</i> sp.	Myrtaceae	0.30 ± 0.08	50–2700
<i>Symplocos psiloclada</i>	Symplocaceae	0.33 ± 0.12	3463–3874
<i>Mollinedia</i> sp.	Monimiaceae	0.35 ± 0.10	120–2500
<i>Ormosia</i> sp.	Fabaceae	0.40 ± 0.06	0–2269
<i>Meliosma vasquezii</i>	Sabiaceae	0.46 ± 0.04	130–1605
<i>Wettinia</i> sp.	Areaceae	0.53 ± 0.09	80–1940
<i>Prunus detrita</i>	Rosaceae	0.60 ± 0.11	111–636
<i>Guarea pterorhachis</i>	Meliaceae	0.60 ± 0.29	100–1100
<i>Protium</i> sp.	Burseraceae	0.65 ± 0.11	16–1550
<i>Matisia malacocalyx</i>	Malvaceae	1.24 ± 0.32	118–1126
<i>Coussarea ecuadorensis</i>	Rubiaceae	1.45 ± 0.15	352–1576
<i>Dictyocaryum lamarkianum</i>	Areaceae	3.02 ± 0.84	500–2076
<i>Iriarteia deltoidea</i>	Areaceae	3.56 ± 0.62	88–815

Mass (g) is the mean measurement of 10 seeds ± SD. Elevational ranges were calculated from vouchers in the Global Biodiversity Information Facility database. Ranges are for the species when available or genus otherwise.

the canopy or from beneath parent trees. Voucher samples were collected from parent trees to confirm identification of species used. Only mature seeds with no visible signs of damage were used in experiments, and all fleshy pulp was removed from seeds manually. Elevational ranges (Table 1) were derived from plant collections data housed in the Global Biodiversity Information Facility (GBIF; <http://www.data.gbif.org>). Ranges are for species when seeds were identified to species, otherwise, ranges represent the elevational range of the genus.

Seed predation experiments

Experimental sites were established in August and September 2008. Seed sites were located adjacent to previously installed fruit and seed traps, with 25 seed sites on a 20 m grid across each of eleven 1 ha plots (Fig. 1). Three species, *I. deltoidea*, *Dictyocaryum lamarkianum*, and *Z. mays*, had three replicate seeds at each site, increasing the sample size. A single seed of the remaining 21 species was used, giving a total of 30 seeds placed at each site (Fig. 1c). Seeds were placed in a 5 × 6 array with 10 cm separating each seed. A total of 8250 seeds were placed: 750 at each elevation, 275 of each species (825 of *I. deltoidea*, *D. lamarkianum*, and *Z. mays*) and 25 seeds of each species at each elevation (75 of *I. deltoidea*, *D. lamarkianum*, and *Z. mays*).

All seeds were surrounded by an 8 cm high mesh screen inserted 3 cm into the dirt. The screen delineated an area in which to search for seeds during recensuses and to prevent them

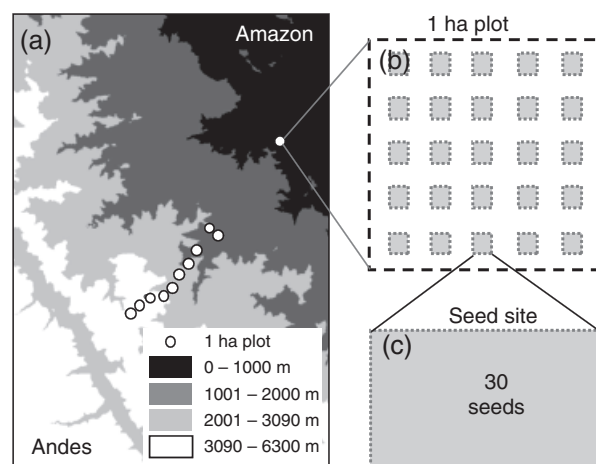


Fig. 1 Experimental design – (a) eleven 1 ha plots across an elevational gradient from 1000 to 3450 m, each with (b) 25 seed sites with (c) 30 seeds at each seed site (a single seed of 21 species plus three seeds each of *Iriarteia deltoidea*, *Dictyocaryum lamarkianum*, and *Zea mays*).

from washing away in high rainfall and was not adequate to exclude potential seed predators. Predation experiments were recensused 1, 3, and 10 weeks from the date of installation. Here we present results from the 10-week census as the conclusions

drawn from failure time analysis of each census period were not different (Hillyer, 2009). Seeds were marked as absent if they could not be located within the bounds of the mesh fence. Seeds that remained were recorded as being intact, bitten, mouldy, with larva, or germinating.

Seed mortality was calculated from the number of seeds that were bitten or absent, with the assumption that seed removal equalled predation. Vander Wall *et al.* (2005) outline the objections to this assumption, with the main objection being that seed removal can function as secondary dispersal, not predation, as removed seeds are sometimes cached and remain viable. However, a literature review shows that <10% of all seeds removed are secondarily dispersed, and that within these, survival and germination from cached seeds is low (as seed predators return to eat the cached seeds) for both temperate and tropical species: *Quercus* spp., 1.5–2.5% (Jensen & Nielsen, 1986); *Fagus grandifolia*, 0–4% (Jensen, 1982); *Gustavia superba*, 0.75–10% (Forget, 1992); *Dipteryx panamensis*, 0–2% (Forget, 1993). Additionally, the mortality of seedlings germinating from cached seeds is high (Forget, 1993; Vander Wall, 1994). Finally, if seed removal is an overestimate of actual seed predation, this overestimation is made across all elevations.

The majority of seed predators are thought to be rodents, but birds and insects, particularly ants, consume seeds as well. Trophic structure of the animal community changes strongly across the gradient. Rodent diversity declines around 1000 m accompanied by a sharp decrease in predator diversity (Solari *et al.*, 2006). Long-term and extensive bird surveys also show a decrease of bird diversity along the elevation gradient (Terborgh *et al.*, 1984; Walker *et al.*, 2006). Ant abundance decreases with elevation, with ants abundant at low elevations and becoming rare above 1500–2000 m (Webb, 2008).

Predation risk was modelled with Cox proportional hazard regression (Cox, 1972) using JMP v. 3.2.2 (SAS Institute Inc., Cary, NC, USA, 1989–2007). A proportional hazards failure time model was used because treatments were thought to increase the risk during times of hazard, but not the timing of the hazard itself (Fox, 2001). Locally weighted scatter plot smoothing (LOESS), a nonparametric regression technique, was used to estimate expected survival rates across elevation for groups of species. LOESS does not require the specification of a function (like linear or logistic regression) to fit a model, so it is useful for modelling processes for which there are no theoretical expectations (Cleveland & Devlin, 1988).

LTRE

Large variations in life history parameters do not necessarily translate into large effects on population growth rates (e.g. Leslie, 1945; Caswell, 2001; Brodie *et al.*, 2009), particularly in life stages with relatively low elasticities. A standard method to test for the importance of life history phenomena on population growth rates is a LTRE (Caswell, 2001; Brodie *et al.*, 2009). To test for the importance of observed variation in seed predation rates, we conducted a LTRE using observed variation in predation rates across the elevation gradient and assessing the effects on representative life histories of a variety of tropical tree species. The literature was searched for demographic studies of tropical trees that published complete

transition matrices. Of the 19 studies found that published life tables for tropical trees, all but five studies were excluded because analyses did not consider a seed to seedling transition stage. The five species chosen provide a range of life history strategies, from the fast-growing, small-seeded pioneer species *Cecropia obtusifolia* (Cecropiaceae; Alvarez-Buylla, 1994), through mature forest species such as *Pentaclethra macroloba* (Fabaceae; Hartshorn, 1975), *Podococcus barteri* (Arecaceae; Bullock, 1980), and *Brosimum alicastrum* (Moraceae; Peters, 1991), to the large-seeded, mature forest species *A. mexicanum* (Arecaceae; Piñero *et al.*, 1984). The seed to seedling transition of each matrix was replaced with (1) seed survival rates from seed predation experiments for each elevation and then (2) with seed survival rates of small-seeded species only. All other parameters in the transition matrix were kept constant with elevation. The per capita intrinsic rate of increase (r) was then calculated for each version of the matrix using PopTools (Hood, 2009). The percent change in r over elevation was calculated using the r at 1750 m for all species and the r at 1000 m as the minimum for small-seeded species.

Results

Seed predation

Seed predation shows consistent changes with elevation (Fig. 2a), and there were large and significant differences in seed survival among species across the entire gradient (species main effect, $P = 0.0004$, Table 2; Fig. 3). The relationship between seed survival and elevation varied significantly among species (species by elevation interaction, $P = 0.007$, Table 2; Fig. 3), with species responses falling into two major patterns of seed predation changes with elevation. The five smallest seeded species (<0.025 g) all showed a discernable, step-like increase in survival rate around 1750 m, with 100% mortality below 1750 m, and survival gradually increasing above (Fig. 2b). Species with larger seed sizes have minimum seed survival at 1750 m, with strongly increasing survival above and a small increase in survival at the lowest elevation studied (Fig. 2c). *Z. mays* had lower and less variable seed survival than native tree species but still displayed a unimodal response to elevation (Fig. 3).

Mortality also varied significantly with elevation (elevation main effect, $P < 0.0001$, Table 2). The average survival (1 – mortality) of all species showed a unimodal response to elevation (Fig. 2a). Minimum seed survival was at 1750 m (6%) with seed survival increasing nine-fold between 1750 and 3450 m, [Pr(survive) 0.06–0.56; Fig. 2a]. Seed survival was also higher at 1000 m than at mid-elevations (Fig. 2a).

Demography

When population growth rates were simulated using the survival probabilities for large-seeded species

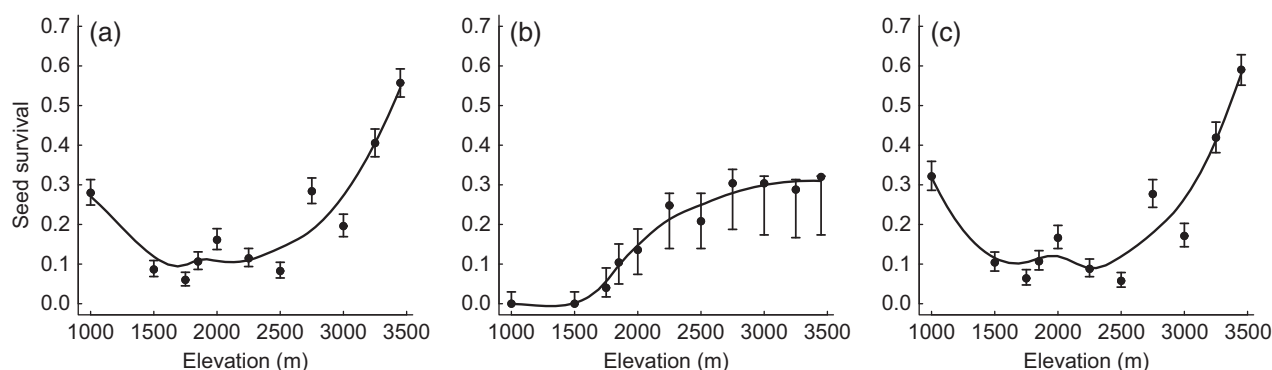


Fig. 2 Seed survival of (a) all species across the elevational gradient ($N_{\text{elevation}} = 750$), (b) small-seeded species (<0.025 g, $N_{\text{elevation}} = 125$) and (c) large-seeded species ($N_{\text{elevation}} = 625$). Points are fit with a nonparametric regression function using locally weighted scatter plot smoothing. Error bars are binomial confidence intervals.

Table 2 Summary of Cox proportional hazard model for seed mortality

Source	df	C^2	P
Elevation	1	438.18	<0.0001
Species	23	52.7	0.0004
Species \times Elevation interaction	23	43.06	0.007

across the gradient, all species showed large increases in r from 1750 to 3450 m (Fig. 4a). The smallest observed change among all species is a doubling of per capita rates of increase in response to changes in predation rate (Fig. 4b). The large-seeded palm *A. mexicanum* shows an eightfold increase in r across the elevational gradient (Fig. 4b). LTREs using survival patterns from small-seeded species showed a distinct pattern, with per capita rates of increase remaining constant and low until 1500 m, and rapidly increasing above this, reaching a maximum at ca. 2000 m (Fig. 5a). In species modelled with small seed sizes, increased seed survival leads to changes in r ranging from 50 to almost 600% (Fig. 5b).

Discussion

This study assessed seed predation rates across an elevation gradient running from the Amazonian lowlands to Andean tree line using 24 species with elevation ranges varying over 2.5 km and seeds ranging in size over four orders of magnitude. Overall, seeds experienced lower predation at higher elevations (Fig. 2a), a change that has quantifiable impacts on the potential population growth of trees. The conclusions of this study highlight the importance of taking gradients of biotic interactions into account when considering species distributions and migration.

Seed survival in all species changed significantly across the elevational gradient, but they changed in

differing ways (Fig. 3), showing that seed traits are important in influencing the interaction between plants and seed predators. One of the traits that varies greatly among species is seed size, and when species are divided into small (<0.025 g)- and large (>0.04)-seeded species survival is still highest at higher elevations, but the pattern is markedly different. The survival of the five smallest species at the lowest elevations is lower than the survival of large species, with small-seeded species showing a stepwise increase in survival at mid-elevations (Fig. 2b), while large-seeded species showed a consistent, increasing trend in seed survival with increasing elevation above 1750 m (Fig. 2c). We attribute this to the fact that seeds of all sizes faced predation from rodents, but only small seeds faced additional predation from ants, which have been shown to be voracious predators of small seeds (e.g. Mittelbach & Gross, 1984). Ant abundance as measured along this elevation gradient decreases markedly above 1500 m (Webb, 2008), corresponding to the step-like increase in increasing survival of small seeds.

The pattern of seed survival along the elevation gradient for large-seeded species is likely driven by elevational variation in seed predator abundance and community structure as well. Although there are no quantitative studies of mammal communities across tropical Andean elevation gradients, measurements from the study area show that both rodent species diversity and the plant productivity supporting rodent communities decrease dramatically above 1500 m (rodents: Solari *et al.*, 2006; productivity: Girardin *et al.*, 2010). We suggest that in tandem these factors decrease the abundance of rodents, increasing seed survival with elevation. The result that large seeds also have higher survival at the lowest elevation may be due to plot-to-plot variation, or it may reflect a change in the importance of factors regulating of rodent communities from productivity ('bottom-up') at higher elevations to predation ('top-down') at the

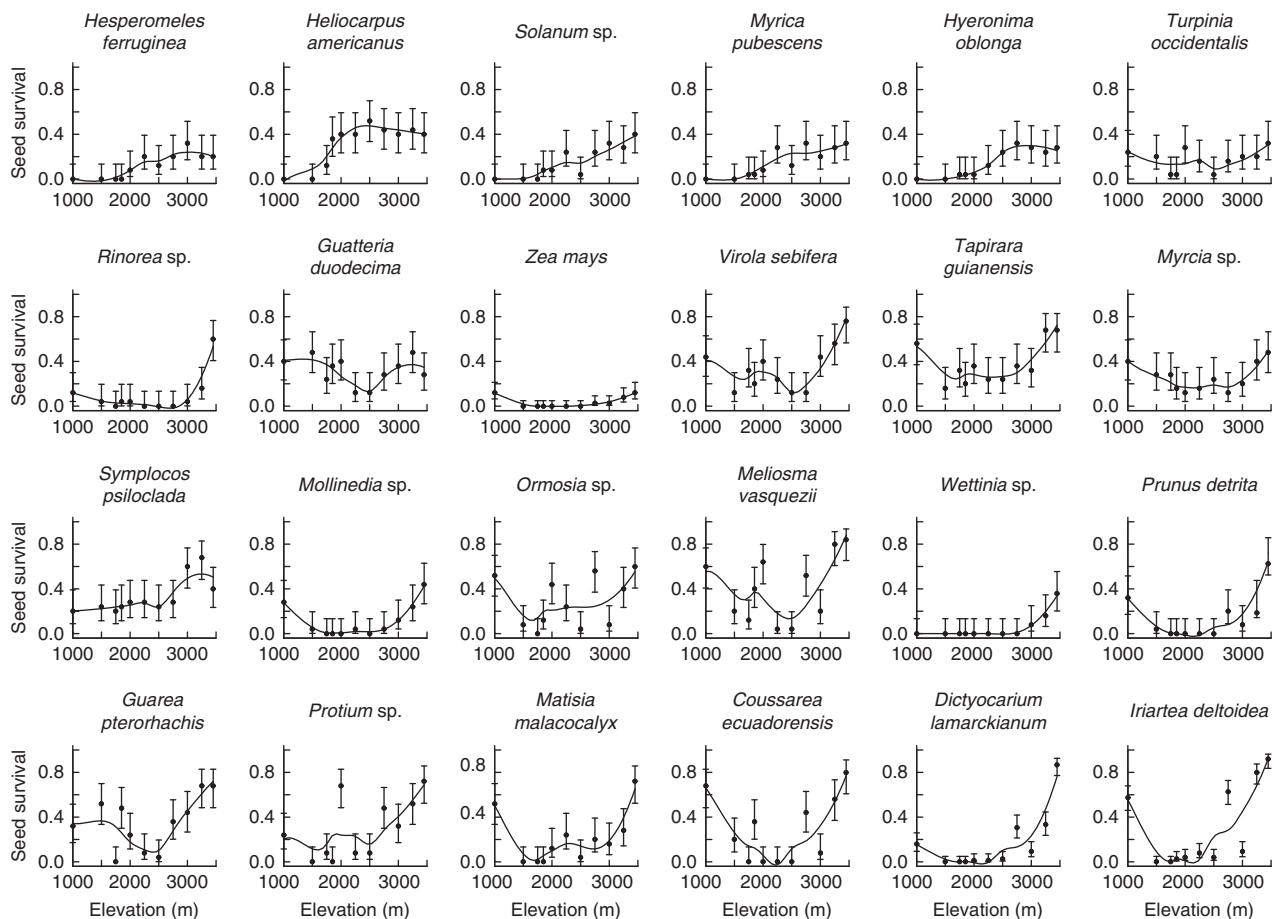


Fig. 3 Seed survival of individual species across the elevational gradient. Species are ordered by increasing seed mass. Each point represents the number of seeds surviving out of 25 seeds (75 seeds for *Iriartea deltoidea*, *Dictyocaryum lamarkianum*, and *Zea mays*) placed at each elevation. Points are fit with a nonparametric regression function using locally weighted scatter plot smoothing. Error bars are binomial confidence intervals.

lowest elevations. In adjacent areas of lowland Amazonia, a wide suite of avian and mammalian predators has been found to keep vertebrate seed predator populations low enough to permit increased seed survival (e.g. Silman *et al.*, 2003; Terborgh *et al.*, 2008).

Effects on demography

Changes in seed predation rates translate directly into increases in effective fecundity of trees, meaning that individuals in populations along the advancing front of upwardly migrating trees will have many more seeds available for establishment than counterparts at lower elevations (Fig. 2a). For example, the increase in seed survival at high elevations means that a tree growing in our highest cloud forest plot at 3450 m could potentially have nine times as many seeds available for establishment as a conspecific growing in cloud forest at 2000 m.

While these changes in fecundity can affect the migration potential of trees, because seed-to-seedling

transitions have low elasticities (Pfister, 1998), it is not a foregone conclusion that increases in seed survival would affect population growth rates. However, the results of the LTRE showed that the percent changes in survival caused by the changes in biotic interactions across the gradient is so large (Fig. 4b) that it overwhelms the low proportional effect of changes in seed predation on population growth rate (Fig. 4a). In this study, modifying population transition matrices to reflect higher effective fecundity had the *minimum* effect of doubling the per capita rate of increase and can cause even greater changes in some species. While the absolute magnitude of change was greatest in the pioneer species *Cecropia*, the large-seeded, late successional palm *Astrocaryum* showed the largest increase in population growth in response to observed predation rates, with populations at higher elevations having an $8 \times$ proportional change in r (Fig. 4a,b). In the LTRE for small seeds, *C. obtusifolia*, known to suffer high rates of ant predation (Myster, 1997), showed a 400% increase

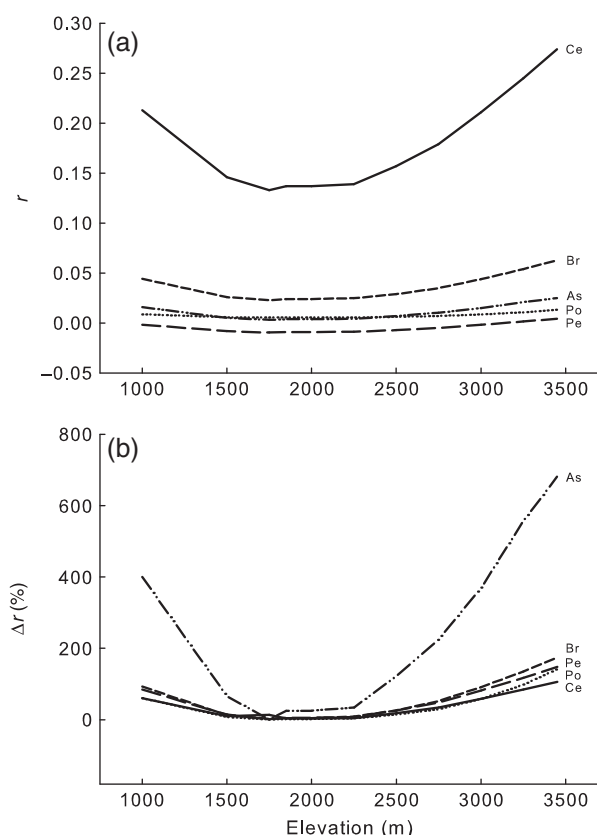


Fig. 4 Results from life table response simulations for five species of tropical trees under observed seed predation rates across the elevation gradient. (a) Per capita intrinsic rate of population increase (r) vs. elevation. (b) Percent change in r vs. elevation. As, *Astrocaryum*; Br, *Brosimum*; Ce, *Cecropia*; Pe, *Pentaclethra*; Po, *Podococcus*.

in r corresponding to the loss of its primary seed predator. This indicates that during upward migration small-seeded species from low elevations will escape a major recruitment filter with the effect of accelerating migration upwards in response to increasing temperature.

As climate changes, individuals at the edge of their tolerable ranges will no longer be at the physiological stress point, but will rather be closer to their optimum. Therefore, the vital rates and true fecundity of trees should not change if species track their climatic niches, but seed predation pressure will depend on the upward migration rates of seed predators. It is expected that predation pressure will be lower at the advancing front of tree population migration until seed predator communities (which are limited by productivity) come to be in equilibrium with the changes in vegetation community. Tree species that are slow to migrate and lag behind migrating seed predators may face increased predation pressure at higher elevations. Ants, whose range may be controlled by cloud base or other abiotic factors, may simultaneously follow tree migration, dis-

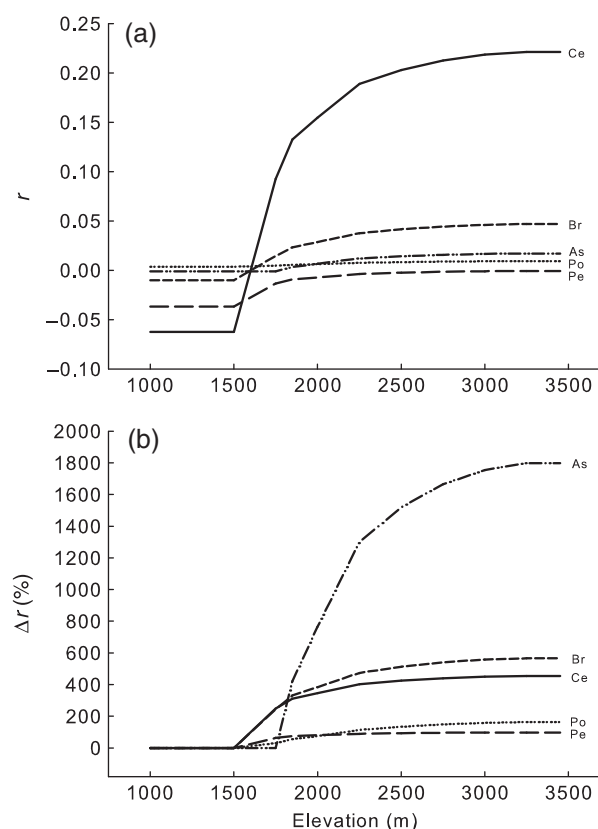


Fig. 5 Results from life table response simulations for five species of tropical trees under observed seed predation rates for small-seeded species across the elevation gradient. (a) Per capita intrinsic rate of population increase (r) vs. elevation. (b) Percent change in r vs. elevation. As, *Astrocaryum*; Br, *Brosimum*; Ce, *Cecropia*; Pe, *Pentaclethra*; Po, *Podococcus*.

proportionately increasing the predation pressure on small-seeded species. This disequilibrium between the migrating plant community and seed predator community can assist or hinder plants in migrating upslope in response to changing climate.

Dispersal

Maximum dispersal distance has been shown to be directly related to fecundity (Clark *et al.*, 1999; Jiang & Zhang, 2008). In this study, the increases in effective fecundity will lead to increases in maximum seed dispersal distances, with positive implications for plant migration. In a simple simulation using realistic, fat-tailed dispersal kernels (2Dt distribution) maximum dispersal distance increases linearly with seed crop size; for every 100 seeds added to fecundity the maximum dispersal distance increases a median of ~220 m (Appendix S1). The observed $9 \times$ increase in effective fecundity across the elevation gradient in this study equals a $\sim 15 \times$ increase in modelled maximum dis-

persal distance. This result shows that trees colonizing areas upslope of their current distribution will have markedly increased maximum dispersal distance, and suggests accelerating rates of migration as species move upslope in this system (e.g. Clark *et al.*, 1999; Jiang & Zhang, 2008).

Conclusions

Climate changes predicted for the tropical Andes in the current century – the change in the abiotic environmental gradient – will require that trees migrate ~ 800 m in elevation in order to remain in equilibrium with climate; $10\text{--}30\times$ faster than the rate of migration observed for trees on the east Andean slope in the paleorecord (Bush *et al.*, 2004). Furthermore, future population sizes and extinction scenarios for Andean trees depend critically on their migration abilities, with plants unable to remain in equilibrium with climate experiencing large losses in population size and elevated extinction probabilities.

Here we demonstrate that there is a biotic environmental gradient of species interactions on the east Andean slope that strongly affects seed survival rates for species, causing survival probabilities for most species to increase ninefold across the ranges of elevation that Andean species will need to migrate to remain in equilibrium with climate. We show that this increase in seed survival will translate into increases in per capita rates of increase in tree populations of up to $8\times$ across the gradient, and that decreases in seed predation lead to effective increases in fecundity, translating into greater dispersal distances in species relying on secondary seed dispersal. The resulting increases in population growth rate and dispersal distances due to decreasing postdispersal seed predation shows that the gradient in biotic interaction acts as a positive force aiding plant migration in response to climate change.

Acknowledgements

We thank SERNANP – Manu and the personnel of Manu National Park for supporting this work, and M. N. R. Quisipupanqui and J. D. Salazar for exceptional help in the field. Pantiacolla Tours, The Amazon Conservation Association, and the Cock-of-the-Rock Lodge provided logistical support throughout the project. Support came from the Gordon and Betty Moore Foundation's Andes to Amazon initiative and NSF DEB-0237684 and NSF BCS-0216607. This paper is a contribution of the Andes Biodiversity and Ecosystem Research Group.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Maximum seed dispersal distances versus effective fecundity (seed crop escaping predation) for a population of 1000 trees simulated using a 2Dt distribution. Lines represent 10th, 50th (median) and 90th percentiles. Average dispersal distance remains nearly constant with fecundity, ranging from 3 m–7 m, with median dispersal distance being constant at 1 m.

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