Seedling performance trade-offs influencing habitat filtering along a soil nutrient gradient in a tropical forest

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Abstract. Recent studies have provided evidence that trade-offs in biomass allocation, resource-use efficiency, and anti-herbivore defense influence seedling performance and distribution across soil types. Our previous research suggested that soil nutrient availability acted as a filter for understory palm community assembly and species coexistence in a lower montane forest in western Panama. Here, we experimentally tested three potential mechanisms that could be driving this filtering of palm communities along a soil nutrient gradient. We examined seedling performance of 13 understory palm taxa with differing distribution patterns transplanted to five sites, where they were both exposed to and protected from herbivores. We found the strongest evidence for habitat filtering at the lowest-nutrient site, where seedlings of locally occurring species had significant performance advantages over those of locally absent species, regardless of protection from herbivores. When transplanted to the lowest-nutrient site, seedlings of naturally occurring species maintained high above- to belowground biomass ratios, maximized photosynthetic nitrogen-use efficiency, and minimized leaf area loss to herbivores and pathogens. Species from low-fertility sites were therefore able to maintain higher survival and relative growth rates (RGR) at the lowest-nutrient site than species from more fertile sites. Similar patterns were found for a high-nutrient site, where naturally occurring species had higher RGR compared to species from lower-fertility sites. However, the functional traits associated with the differences in performance at high-nutrient sites were less clear, perhaps due to increased light limitation in the understory of these sites. At higher-nutrient sites, protection from herbivores significantly reduced leaf area damage and mortality rates in seedlings, particularly for naturally occurring species. Overall, morphological and physiological traits were more strongly coupled with soil nutrient availability than were leaf damage or seedling performance across the sites. Nonetheless, the coordination of all three trade-offs was related to the strongest performance advantage and, therefore, ecological filtering along the soil nutrient gradient in this lower montane forest.

Key words: anti-herbivore defense; biomass allocation; dispersal limitation; functional traits; growth trade-offs; lower montane tropical forest; niche partitioning; plant–soil interactions; resource-use efficiency; seedling performance; soil nutrients; understory palms.

INTRODUCTION

Habitat filtering, or the selection of species with ecological strategies favored by specific environmental conditions, is a key process influencing community assembly across resource gradients in many ecosystems (Keddy 1992, Kraft et al. 2008, Cornwell and Ackerly 2009). Soil nutrients are essential plant resources, and soil heterogeneity can have a filtering effect on regional species pools to determine local community assembly (Weiher et al. 1998, Andersen et al. 2010b, 2012, Katabuchi et al. 2012). A number of recent studies have found evidence that heterogeneity in soil resources contributes to high species turnover, or β-diversity, in tropical forests (Paoli et al. 2006, John et al. 2007, Baldeck et al. 2013, Condit et al. 2013). Experimental tests of seedling performance in relation to soil type, topography, and/or nutrient availability have identified possible mechanisms by which soils act as filters generating species–soil associations (Fine et al. 2004, Palmiotto et al. 2004, Baltzer et al. 2005, Baraloto et al. 2006, 2007). Plant–soil associations have been shown to arise from trade-offs between growth and biomass allocation, resource-use efficiency, and anti-herbivore defense. However, the extent to which these three trait-based trade-offs simultaneously affect habitat filtering along soil nutrient gradients has not been experimentally examined.

In general, plants growing in high-nutrient soils have high relative growth rates (RGR) associated with high leaf-area ratios (LAR), specific leaf area (SLA), and allocation to aboveground biomass (Poorter and Remkes 1990, Aerts and Chapin 2000, Palmiotto et al. 2004,

Dent and Burslem 2009). Plants from low-nutrient soils, on the other hand, have low RGR, SLA, and foliar N, as well as enhanced allocation belowground (Chapin 1980, Tilman and Wedin 1991, Aerts and Chapin 2000). Thus, trade-offs in allocation to above- and belowground biomass may influence seedling performance across soil gradients (Coomes and Grubb 1998, Palmiotto et al. 2004, Baraloto et al. 2006, Dent and Burslem 2009). For example, in Lambir Hills National Park in Sarawak, Malaysian Borneo, Palmiotto et al. (2004) found that species from relatively nutrient-rich clays developed on shale had higher RGR compared to species from relatively nutrient-poor loams developed on sandstone (Baillie et al. 2006), regardless of the soil type on which they were grown. The authors suggested that this effect was due to higher allocation to aboveground biomass and higher LAR and SLA for the species from the clay soil. However, when species from nutrient-rich clays were grown in nutrient-poor loams, enhanced allocation to roots resulted in a lower RGR compared to their RGR when grown in their native soil. This suggests that species ability to optimize above- to belowground allocation with soil nutrient availability is related to their distribution pattern.

In addition to species differences in trade-offs between growth and biomass allocation, species may differ in resource-use efficiency (RUE), with consequences for their distribution along resource gradients (Chapin 1980, Aerts and Chapin 2000, Baltzer et al. 2005, Baraloto et al. 2007). For example, species from low-nutrient soils frequently have higher leaf longevity, lower foliar nutrient concentrations, and lower maximum photosynthetic rates than species from high-nutrient soils (Chapin 1980, Aerts and Chapin 2000). Collectively, these traits enhance nutrient-use efficiency (NUE) by increasing carbon gain per unit of nutrient uptake. Another potentially limiting soil resource that plants may optimize their resource-use efficiency to is soil water availability. To maximize water-use efficiency (WUE), the amount of carbon gain per unit water loss, species may maintain lower stomatal conductance and/or transpiration rates by increasing concentrations of photosynthetic enzymes to increase photosynthetic rates at a given internal CO_2 concentration (Wright et al. 2001, Baltzer et al. 2005, 2008). Species from drought-prone habitats frequently have higher WUE than species from ever-wet habitats (Wright et al. 2001, Baltzer et al. 2005, 2008, Engelbrecht et al. 2007). For example, in the Sepilok Forest Reserve in Sabah, Malaysian Borneo, Baltzer et al. (2005) have found that species from sandstone soils, which have a low water-holding capacity, have a conservative water-use strategy compared to generalists or species from alluvial soils. This suggests that species physiological constraints are important in determining species distributions across soil hydrological gradients.

In contrast to use-efficiency and allocation-based hypotheses that account for resource-based habitat partitioning, it has also been proposed that species allocating resources to defense at the expense of growth should be favored in low-nutrient environments where biomass is more costly to produce (Coley et al. 1985, 1996, Fine et al. 2004, 2006). For example, Fine et al. (2004) found that differences in allocation to defense determined seedling performance in soils that differed in nutrient availability in the Peruvian Amazon. When protected from herbivores, poorly defended species from a more nutrient-rich clay soil outperformed well-defended species from a nutrient-poor white-sand soil. However, when exposed to herbivores, clay-soil specialists growing on white sand were unable to replace tissue lost to herbivores. In contrast, well-defended white-sand specialists maintained positive growth and lower mortality when growing on white-sand soil. Thus, soil-based habitat associations may be mediated by biotic interactions.

These three field experiments each provide support for a distinct trade-off involved in determining seedling performance and species distribution across contrasting soil types. However, experiments to date have generally examined these trade-offs independently and were limited to comparisons between pairs of strongly contrasting soil types. The present study aimed to build on our existing knowledge of the trade-offs involved in determining soil-based habitat associations by simultaneously examining morphological, physiological, and defense traits involved in promoting seedling growth and survival across a soil nutrient gradient.

Our study focuses on palms, which are commonly reported to show soil-based habitat associations (Clark et al. 1995, Vormisto et al. 2004, Savolainen et al. 2006, Andersen et al. 2010b). Palms (Arecaceae) are a major component of the understory in tropical forests and modify microsite conditions for seedling establishment (Farris-Lopez et al. 2004, Wang and Augspurger 2004). Therefore, understanding palm ecology and processes influencing palm species distributions has direct implications for regeneration within tropical forests. Despite the abundance of studies demonstrating the correlation of palm species to various soil variables, few studies have experimentally examined the mechanistic underpinnings of palm–soil associations (but see Andersen et al. [2010a] and Andersen and Turner [2013]). Given strong ecological preferences, high species diversity, and high population densities, palms are an excellent group with which to test mechanisms influencing habitat partitioning along soil nutrient gradients.

We recently reported several lines of evidence supporting the influence of soil nutrients on understory palm communities in lower montane forests of the Fortuna Forest Reserve, western Panama (Andersen et al. 2010a, b, 2012, Andersen and Turner 2013). We surveyed understory palm species- and trait-based community composition in five 1-ha forest inventory plots across a soil fertility gradient in continuous old-growth forest (Andersen et al. 2010b, 2012). Along the

PLATE 1. Palm seedlings in a field transplant experiment. (A) Paired common gardens at a low nutrient site (Honda) with seedlings growing exposed to (E−) and protected from (E+, background) herbivores. (B) *Chamaedorea palmeriana*, (C) *C. recurvata*, (D) *Reinhardtia gracilis*, (E) *C. tepejilote* with herbivory, (F) *C. woodsoniana* with herbivory. Photo credits: K. M. Andersen.

soil nutrient gradient, there were marked changes in palm community species composition, which were attributed to a combination of spatially limited seed dispersal and changes in soil nitrogen, phosphorus, and base cations (Andersen et al. 2010b). The majority of the 25 understory palm species recorded at Fortuna were associated with intermediate-fertility andesitic soils, whereas low-fertility rhyolitic and high-fertility dacitic soils supported endemic species as well as distinct morphologies of widespread species. Furthermore, morphological and physiological leaf traits of adult palms were strongly correlated with soil nutrient availability (Andersen et al. 2012). In addition, a nitrogen tracer experiment using seedlings of eight palm species with contrasting distributions across the soil fertility gradient found that nitrogen uptake rates corresponded with species–soil associations, further suggesting the importance of physiological traits in determining species distributions (Andersen and Turner 2013). Finally, a nitrogen addition experiment at a low-nitrogen site using seedlings of nine species with contrasting distribution patterns across the soil fertility

gradient found that although foliar nitrogen and physiological leaf traits increased with nitrogen addition, enhanced seedling performance was masked by herbivory, which was related to leaf quality (Andersen et al. 2010a). This suggested that in addition to morphological and physiological traits, susceptibility to herbivores might mediate species distributions. Thus, both seedling experiments and trait-based surveys suggested that niche processes related to soil nutrient availability, and soil nitrogen in particular, generate palm species distribution patterns in the lower montane forests of Fortuna.

Here, we expand our previous research on environmental filtering of understory palm species by experimentally testing three trade-offs involving morphological, physiological, and defense traits of understory palm species that are distributed along a soil nutrient gradient in Fortuna. We use a seedling transplant experiment to test the following hypotheses about how mechanisms influencing seedling performance change with resource availability. If environmental filtering is important in determining species distribution patterns along the soil

Table 1. Environmental conditions at five sites along a soil nutrient gradient at the Fortuna and Palo Seco Forest Reserves in western Panama.

Watershed	Chorro	Honda	Samudio	Palo Seco	Hornito
Site code	CH	HON	SAM	PS	HRN
Environmental variables					
Soil nutrient ranking	lowest	low	intermediate	high	highest
Parent material	rhyolite	rhyolite	andesite	andesite	dacite
Soil variables					
pH (in water)	3.90 ± 0.05	3.84 ± 0.05	4.49 ± 0.09	4.49 ± 0.05	5.10 ± 0.09
Al ($\mu g/cm^3$)	149.6 ± 12.0	712.4 ± 64.9	1059 ± 32.1	1091 ± 36.4	327.1 ± 45.5
Ca ($\mu g/cm^3$)	191.2 ± 27.7	242.4 ± 38.1	335.1 ± 43.8	225.7 ± 33.3	2735 ± 194
K ($\mu g/cm^3$)	37.32 ± 2.81	61.14 ± 5.24	52.66 ± 3.16	46.09 ± 8.23	141.8 ± 10.3
Mg ($\mu g/cm^3$)	76.48 ± 9.60	86.90 ± 12.28	62.97 ± 5.73	58.84 ± 6.67	338.1 ± 29.3
P ($\mu g/cm^3$)	2.83 ± 0.23	3.16 ± 0.49	0.61 ± 0.04	1.20 ± 0.14	6.93 ± 0.95
Zn ($\mu g/cm^3$)	1.08 ± 0.12	1.69 ± 0.16	0.85 ± 0.04	0.93 ± 0.05	4.51 ± 0.52
CEC ($cmol_c/kg$)	20.75 ± 0.99	40.39 ± 3.66	38.38 ± 1.15	30.84 ± 1.18	52.10 ± 2.54
Total bases ($cmol_c/kg$)	10.41 ± 1.10	8.40 ± 1.10	6.33 ± 0.72	3.85 ± 0.51	42.79 ± 3.04
NH_4 ($\mu g/cm^3$)	8.24 ± 1.03	7.40 ± 0.79	1.77 ± 0.32	1.26 ± 0.23	20.70 ± 5.44
NO_3 ($\mu g/cm^3$)	0.30 ± 0.03	0.83 ± 0.10	0.39 ± 0.05	0.99 ± 0.31	0.66 ± 0.08
TIN ($\mu g/cm^3$)	8.55 ± 1.03	8.23 ± 0.83	2.16 ± 0.32	2.25 ± 0.50	21.35 ± 5.47
N:P	2.90 ± 0.28	3.69 ± 0.57	3.69 ± 0.51	1.98 ± 0.30	4.32 ± 0.98
Bulk density (g/cm^3)	0.11	0.18	0.22	0.32	0.11
Light conditions					
Canopy openness (%)	6.32	5.77	6.27	4.85	5.31
Red : far red ratio	0.46 ± 0.02	0.32 ± 0.02	0.44 ± 0.04	0.25 ± 0.04	0.34 ± 0.05
Moisture					
Total 2007 rainfall (m)	4.29	6.06	4.44	6.49	5.08
Dry season rainfall (mm)	263	339	106	384	112
Soil water content (wet season; g/cm^3)	4.34 ± 0.31	2.42 ± 0.10	1.88 ± 0.06	1.18 ± 0.05	2.74 ± 0.17
Soil water content (dry season; g/cm^3)	4.21 ± 0.30	2.24 ± 0.08	1.90 ± 0.06	1.24 ± 0.05	1.97 ± 0.13
Soil water content (g/cm^3)	4.29 ± 0.31	2.34 ± 0.08	1.88 ± 0.06	1.21 ± 0.05	2.42 ± 0.15
Combined PCA axes					
PC1 environmental	−0.61 ± 0.18	−0.55 ± 0.21	−1.34 ± 0.13	−2.01 ± 0.14	4.41 ± 0.51
PC2 environmental	−3.05 ± 0.24	−0.49 ± 0.09	0.42 ± 0.08	2.32 ± 0.17	0.93 ± 0.17
PC3 environmental	−0.02 ± 0.09	−0.08 ± 0.26	0.10 ± 0.17	−0.16 ± 0.17	0.15 ± 0.50

Notes: Soil samples were collected at a depth of 10 cm from the soil surface from each experimental garden ($n = 99$ samples). Exchangeable cations and phosphorus were Mehlich-III extracted, and nitrogen was 2 mol/L KCl extracted. Abbreviations for soil variables are as follows: CEC, cation exchange capacity; TIN, total inorganic nitrogen; N:P, nitrogen to phosphorus ratio. Red : far red was measured above every seedling within each garden ($n = 883$ seedlings) and mean values for each garden were used in the combined principal component analysis. Rainfall, canopy openness, and bulk density values are based on Andersen et al. (2010*b*) measured at adjacent forest inventory plots. All other means are shown ±SE.

nutrient gradient, seedlings of species that are native to a site should have functional trait values that maximize performance compared to seedlings of species that do not naturally occur at that site. At sites with low soil nutrient availability, where the cost of replacing tissue lost to herbivores is the greatest, species with traits that maximize belowground resource acquisition, persistence, and anti-herbivore defense should have higher survival and growth rates. At sites with relatively high soil nutrient availability, where belowground resources are not limiting, species with traits that maximize allocation to aboveground biomass and photosynthetic rates should have higher survival and growth rates. Whereas many trait-based studies have found evidence for habitat filtering across soil resource gradients (Kraft et al. 2008, Cornwell and Ackerly 2009, Andersen et al. 2012), here we use an experimental approach that allows us to explicitly test the potential mechanisms that may be driving this filtering, and thus determining species distribution patterns in tropical forests.

Materials and Methods

Study sites and species

The study was conducted at five sites in continuous old-growth forest spanning the Fortuna Forest Reserve in Chiriqui Province and the Palo Seco Forest Reserve in Bocas del Toro in the highlands (800 to 1400 m above sea level) of western Panama, henceforth Fortuna (Table 1). Rainfall is high in this area (>4 m mean annual precipitation), but dry season rainfall decreases from the Caribbean to Pacific slopes (Cavelier et al. 1996). Soil surveys, light conditions, and rainfall were previously assessed in 1-ha forest inventory plots and reported in Andersen et al. (2010*b*). The soil nutrient gradient arises from differences in extractable inorganic nitrogen (N), phosphorus (P), and base cations, forming a gradient of soil nutrient availability over a span of 13 km (Table 1; Andersen et al. 2010*b*). For simplicity, we refer to the five sites based on their relative soil nutrient availability based on Andersen et al. (2010*b*): (1) lowest (Chorro; soils formed in rhyolitic tuff), (2) low (Honda;

TABLE 2. List of species, grouped by soil associations, and relative abundance (%) at each site in the study based on Andersen et al. (2010b).

Species and soil association	Authority	Species code	Growth habit	Transplant date	Relative abundance (%) at each site				
					CH	HON	SAM	PS	HRN
Rhyolitic									
Chamaedorea palmeriana	Hodel and Uhl	CPA	acualescent	January 2006	6	10	11	0	0
Chamaedorea cf. *pinnatifrons*	cf. *pinnatifrons*	CPILG	aerial	January 2006	15	1	1	0	0
Chamaedorea recurvata	Hodel	CRE	aerial	January 2006	24	4	1	0	0
Andesitic									
Chamaedorea deckeriana	(Klotzsch) Hemsl.	CD	aerial	January 2006	0	0	0	12	0
Chamaedorea pinnatifrons	(Jacq.) Oerst.	CPI	aerial	January 2006	15	1	2	10	18
Chamaedorea robertii	Hodel and Uhl	CRO	acualescent	January 2006	0	5	17	6	0
Chamaedorea scheryi	L. H. Bailey	CSC	acualescent	April 2006	0	<1	1	1	0
Chamaedorea sullivaniorum	Hodel and Uhl	CSU	acualescent	August 2006	0	0	0	3	0
Chamaedorea tepejilote	Liebm.	CT	aerial	January 2006	0	0	0	2	0
Geonoma cuneata var. *gracilis*	(H. Wendl. ex Spruce) Skov	GCU	acualescent	January 2006	0	41	49	51	57
Reinhardtia gracilis	(H. Wendl.) Drude ex Dammer	RG	aerial	August 2006	0	0	0	3	0
Dacitic									
Chamaedorea woodsoniana	L. H. Bailey	CW	aerial	January 2006	0	<1	<1	1	6
Lowland									
Geonoma congesta	H. Wendl. ex Spruce	GCO	aerial	August 2006	0	0	0	0	0

Notes: Nomenclature is based on Henderson, Galeano, and Bernal (1995). *Chamaedorea* cf. *pinnatifrons* morphotaxa is based on seed size and shape, and relative abundance is based on half of the value reported for *C. pinnatifrons*. Nutrient (Mehlich III extractable base cations and phosphorus) and inorganic nitrogen availability (2 mol/L KCl extractable) increases from rhyolitic (CH, HON) to andesitic (SAM, PS) to dacitic (HRN) soils.

rhyolitic tuff), (3) intermediate (Samudio; andesitic), (4) high (Palo Seco; andesitic), and (5) highest (Hornito; dacitic; Table 1). In April 2007, we measured light availability directly above each seedling (height 10–50 cm) as red : far red (R:FR) ratios (Skye Instruments SKR 110, Skye Instruments, Llandrindon Wells, UK), which have been shown to effectively measure light conditions with high quantitative and qualitative sensitivity across a range of canopy conditions in tropical forests (Capers and Chazdon 2004). In addition, we measured soil nutrient availability and soil moisture for each experimental garden and calculated multivariate resource availability for each garden using principal component analysis (see supplementary materials for detailed methods). Light availability and soil water content followed the opposite pattern as soil nutrient availability across the sites, generally decreasing in availability from rhyolitc to andesitic to dacitic sites (Table 1 and Appendix A: Table A1, Fig. A1). Soil cations and phosphorus content positively loaded on the environment PC1 axis. However, principal component axis 2 (PC2 environment) best represented the shift from soil nutrient to light limitation across the sites, with light positively and soil variables negatively loading on PC2 environment.

Within the Arecoideae subfamily, we chose 13 focal palm taxa: nine species associated with andesitic soils, one species and one morphospecies associated with rhyolitic soils, one species associated with dacitic soils, and one species common in lowland forest (Table 2). Of the taxa included, *Chamaedorea pinnatifrons* (see Plate 1) is one of the most widespread, with notable morphometric variation among populations (Hodel 1992, Henderson et al. 1995, Henderson 2005). In our area, the *C.* cf. *pinnatifrons* collected from rhyolitic soils had larger, round seeds compared with populations found on andesitic or dacitic soils (K. M. Andersen, *unpublished data*). We included *C.* cf. *pinnatifrons* collected from rhyolitic soils and *C. pinnatifrons* collected on andesitic or dacitic soils as separate taxa to compare the seedling performance between the two distinct morphotypes.

Transplant experiment

Seeds from the 13 focal taxa were collected from May to August 2005 from at least 10 individuals per species in Fortuna (see Plate 1). *Geonoma congesta* seeds were collected from the Caribbean lowland forests of the Panama Canal area, cleaned and transported to Fortuna. Seeds were germinated in a growing house at the Smithsonian Tropical Research Institute Fortuna Field Station at 1000 m above sea level. To control for any differences in mycorrhizal communities among the sites, germination substrate was a 50:50 mix of washed sand and soil collected from the location where the seedlings would later be transplanted. Light conditions

were adjusted to 3% light with shadecloth. Mean time to germination varied from 3 to 6 months among the species, with an additional 1 to 3 months before the first leaf was fully expanded (K. M. Andersen, *unpublished data*). Seedlings with at least one leaf were transplanted to common gardens at five sites across the Fortuna soil nutrient gradient from February to August 2006 (Table 2). Variation in initial transplant dates was due to differences in mean time to germination and leaf expansion rates. Species with an incomplete set of replicates at the initial transplant date due to intraspecific variation in leaf expansion rates and replicates lost to herbivory in the first months were replaced from April to August 2006. There was no indication of transplant shock for seedlings at any of the sites (Appendix B: Fig. B1) and soil water content in the gardens remained above 1 g water/cm^3 soil throughout the experiment. Five seedlings per species per soil type were selected at random and harvested at the time of transplant to record initial biomass and leaf area for relative growth rate calculations.

We established ten blocks of paired herbivore exclosure (E+) and control (E−) treatment gardens at each of five sites along the soil gradient in a split-plot design. Blocks were arranged 5–20 m from the border of 1-ha forest inventory plots with at least 10 m separating the blocks and <1 m between the paired treatment gardens. One seedling per taxon was randomly assigned a 25 × 25 cm position within each 1 × 1 m garden, to yield 1300 transplanted seedlings. Exclosure gardens were completely covered by nylon netting (1-mm mesh) to exclude both insect and vertebrate herbivores (E+). Plastic chicken wire with 1-inch (2.5-cm) mesh was used to reinforce the roofs of exclosure gardens, preventing damage to the netting from falling canopy debris. Control gardens had only a netting roof to control for light interception (E−). Leaf litter and debris were cleared from the roofs intermittently and at each census, and netting was changed when it became stained or damaged. Seedlings were monitored in censuses every two months until October 2007 (15–21 months) for survival, growth, and herbivore damage. We report data for survival through the end of the experiment and harvest data for growth and leaf damage.

During the first two weeks of September 2007, we measured gas exchange on the youngest fully mature leaf of seedlings within at least five E+ gardens per site for a total of 4–9 individuals per species at each site using a portable gas exchange system (LI-6400, Li-Cor, Lincoln, Nebraska, USA). Additional gardens were measured at the low-nutrient Chorro site to improve estimation of low gas exchange rates. Maximum photosynthetic rates (A_{max}) were measured at saturating light levels (400 μmol·m^{-2}·s^{-1}). The cuvette was maintained at near-ambient conditions (~75% relative humidity, 20–25°C, and 400 ppm CO_2). Gas exchange was only measured when the leaf was fully induced and stable readings were observed using the graphics of the LI-6400 program.

Leaves that gas exchange was measured on were collected the following month at the time of the harvest, ground, and analyzed for foliar N and P concentrations and natural abundance of N stable isotopes (δ^{15}N). For foliar P concentration, individual leaf samples were homogenized by species within site ($n = 65$ samples) and analyzed by ignition (550°C, 1 h) and extraction in 1 mol/L H_2SO_4 with detection by molybdate colorimetry using a Lachat Quikchem 8500 (Hach, Loveland, Colorado, USA). Foliar N concentration and δ^{15}N were analyzed for each seedling with gas exchange measurements ($n = 349$) using an elemental analyzer (Flash HT) with a continuous flow interface (ConFlo III) and a Delta-V Advantage isotope ratio mass spectrometer (Thermo Scientific, Bremen, Germany). Foliar δ^{15}N values are related to rates of N cycling and the δ^{15}N abundance of the soil (Pardo and Nadelhoffer 2010, Andersen et al. 2012), as well as physiological traits such as nitrogen uptake rates (Andersen and Turner 2013). Photosynthetic nutrient-use efficiency (PNUE) quantifies the μmol carbon gained per unit N invested in leaf material and was measured as A_{max} over foliar N content.

In October 2007, we harvested eight paired gardens per site to measure biomass allocation patterns, foliar nutrients, and leaf area damage. Seedlings were separated into root, shoot, and leaf components and weighed. Leaf toughness was measured as fracture toughness using a 516-1000MRP push-pull gauge "penetrometer" (Chatillon/Amtek, Largo, Florida, USA). Leaves were scanned prior to drying to measure leaf area and leaf area damage using ImageJ (Rasband 2009). Leaf area damage was calculated as the percentage of total leaf area missing. Leaves recorded as 100% damaged from herbivory or pathogens in field censuses were included in the leaf area damage calculations. Harvest data were used to calculate the following growth and morphological parameters: relative growth rate (mg·g^{-1}·d^{-1}), leaf area ratio (LAR), specific leaf area (SLA; cm^2/g), leaf mass ratio (LMR), and root mass ratio (RMR). These morphological variables are functionally important for resource use and acquisition, and ultimately, seedling performance. Leaf area ratio and SLA are leaf traits related to the amount of leaf area available for light interception. Leaf mass ratio and RMR are ratios defining carbon allocation to above- and belowground biomass.

Data analysis

We examined whether seedlings of locally occurring species perform better than locally absent species ("home-site advantage") and whether these performance advantages were related to seedling functional traits across the soil fertility gradient. For survival, relative growth rate, and percentage of leaf area damaged, we calculated the average values by garden for naturally occurring and locally absent species at each site. By pooling data by species presence/absence, we achieved
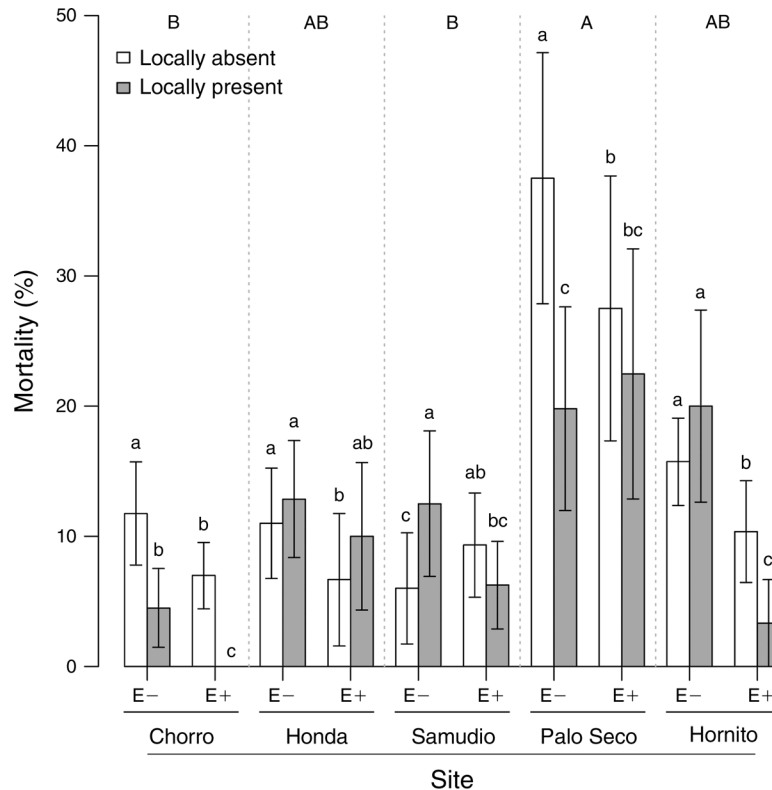
Fig. 1. Mortality of seedlings of species naturally occurring or naturally absent from five sites along a soil nutrient gradient when protected from (E+) or exposed to (E−) herbivores. Bars represent mean values (±SE) of the species origin groups. Different capital letters represent differences in mortality among the sites ($P < 0.05$) and different lower-case letters represent differences in mortality among origin and herbivore exclosure combinations within each site ($P < 0.05$).

equal sample sizes across the gardens and sites and met the statistical assumptions of models. To examine the effects of site, herbivore exclosure treatment, and species distribution patterns mortality (%) and leaf area damage (%), we used generalized linear mixed models fit by Laplace approximation with a Poisson error distribution and log-link function (Bolker et al. 2008), using the glmer function in the R package lme4 (Bates et al. 2013). Full models included site, the binary species presence/absence variable, and herbivore exclosure treatment as fixed effects and herbivore exclosure garden within block within site as nested random effects to account for the split-plot experimental design. Reduced models were used to assess the effects of species presence/absence and herbivore exclosure treatments for each site separately with the nested random effects of herbivore exclosure treatment within block. To compare mortality and leaf damage among treatment combinations within site, we conducted multiple comparison tests using Tukey contrasts in the multcomp package in R (Hothorn et al. 2008). In addition, we examined seedling survival curves using Kaplan-Meier estimators for species growing in exposed and protected gardens at each site in the survival package in R (Therneau 2013; Appendix B: Fig. B1).

To examine the effects of species presence/absence, herbivore exclosure treatment, and site on relative growth rates, we used linear mixed models using the lmer function in the R package lme4 and estimated parameters and probability values using Monte Carlo Markov chain (MCMC) simulation methods using the pvals.fnc function in the R package language (Baaven 2013). To specifically test the effect of species distribution patterns, we fit site-specific models with species presence/absence as a fixed effect, and species within herbivore exclosure treatment within block as a nested random effect. Protection from herbivores did not significantly affect RGR and subsequent models were conducted on pooled values across the exclosure treatments for each block.

To test for the effects of site and species distribution on seedling functional trait variables (morphological, physiological, and defense traits), we used linear mixed models with site and species presence/absence as fixed effects, and with block within site as a nested random effect and controlled for species identity using a variance function (Pinheiro and Bates 2000) in the R package nlme. For consistency across the trait variables, we only included data from the herbivore exclosure treatments that were protected from herbivores (E+). In addition, we explored the relationships among traits and shifts in
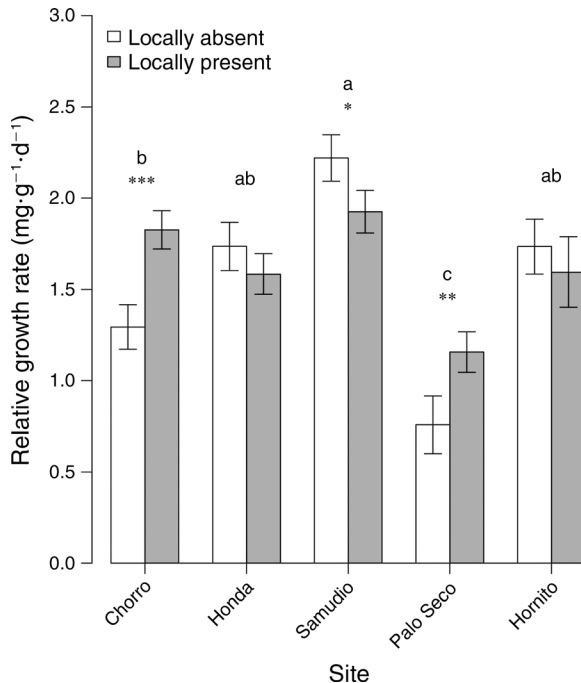
FIG. 2. Relative growth rates of seedlings transplanted to five sites across a soil nutrient gradient. Shaded bars represent mean values (±SE) of species that naturally occur at the site (present) and white bars represent means of species that are not naturally occurring at the site (absent). Different letters above the bars represent significant differences in growth among sites and asterisks represent significant differences between species that are present and absent from the site.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

trait values among sites using a principal component analyses (see Appendix A for full details and results). To calculate multivariate trait values, we included only the key functional traits identified in the linear mixed models. We examined the correlation between resource availability, defined by PC2 environment, and the multivariate trait values and seedling performance. To examine which traits or combination of traits were important in determining seedling performance, we conducted Pearson correlation tests between multivariate traits and individual functional traits, growth, survival, and leaf damage. All data were analyzed using R (R Development Core Team 2013, version 3.0.0).

RESULTS

Seedling performance

Mortality rates.—Seedling mortality rates were generally lower for poorer-nutrient sites compared to higher-nutrient sites (Fig. 1, Appendix C: Fig. C1). Seedling

mortality rates were positively correlated with the multivariate trait PC2 axis (Appendix C: Fig. C2), which represented shifts in leaf quality (Appendix A: Table A2). Mortality was highest at Palo Seco (high-nutrient site; 26.8% ± 4.6%, mean ± SE) and lowest at Chorro (lowest-nutrient site; 5.8% ± 1.5%), with the other sites ranging from 8.5% ± 2.2% at Samudio (intermediate-nutrient site) and 12.35% ± 2.5% at Hornito (highest-nutrient site). Overall, mortality was higher when seedlings were exposed to herbivores (15.2% ± 2.0%) than when protected from herbivores (10.3% ± 1.9%; $z = 9.60$, $P < 0.0001$). In addition, there was a significant home-site advantage ($z = 6.27$, $P < 0.0001$), with lower mortality rates for seedlings of locally occurring species (11.2% ± 1.9%) than for seedlings of locally absent species (14.3% ± 2.0%). However, the magnitude of effects of protection from herbivores and home-site advantage were site dependent (Fig.1). Mortality rates were lower for seedlings protected from herbivores compared to seedlings exposed to herbivores at Chorro (lowest-nutrient site; $z = 5.93$, $P < 0.0001$) and Hornito (highest-nutrient site; $z = 3.26$, $P < 0.01$). In addition, protection from herbivores reduced mortality rates compared to seedlings exposed to herbivores for locally absent species at Honda (low-nutrient site; $z = 3.61$, $P < 0.001$) and Palo Seco (high-nutrient site; $z = 3.91$, $P < 0.0001$) and for locally occurring species at Samudio (intermediate-nutrient site; $z = 4.45$, $P < 0.0001$). There was a home-site advantage in terms of lower mortality rates at Chorro ($z = 8.54$, $P < 0.0001$) and Palo Seco ($z = 7.32$, $P < 0.0001$), as well as for seedlings protected from herbivores at Hornito ($z = 5.74$, $P < 0.0001$). In contrast, locally occurring species had higher mortality rates at Honda ($z = 2.43$, $P < 0.05$) and when exposed to herbivores at Samudio ($z = 4.61$, $P < 0.0001$).

Relative growth rates.—Overall, RGR differed significantly among sites, but there was not a consistent home-site advantage (Fig. 2, Appendix C: Fig. C1). Relative growth rates were negatively correlated with the multivariate trait PC1 axis (Appendix C: Fig. C2), which represented a shift from a conservative to productive ecological strategy (Appendix A: Table A2). The two intermediate-nutrient sites, Samudio and Palo Seco, had the highest (2.23 mg·g⁻¹·d⁻¹ ± 0.08) and the lowest (1.07 mg·g⁻¹·d⁻¹ ± 0.07) RGR, respectively. Seedlings of species naturally occurring at Chorro ($t = 5.13$, $P < 0.001$) and Palo Seco ($t = 3.20$, $P < 0.01$) had higher RGR than species that were locally absent at these sites. Seedlings of species naturally occurring at Samudio had lower RGR than locally absent species ($t = 2.63$, $P < 0.05$). There was no difference in RGR between seedlings of locally occurring and locally absent species at Honda or at Hornito.

FIG. 3. Biomass allocation and leaf traits (mean ± SE) of seedlings growing at five sites across a soil nutrient gradient. (A) Root mass ratio (RMR), (B) leaf area ratio (LAR), (C) foliar nitrogen concentration, (D) foliar phosphorus content, (E) foliar δ¹⁵N values, (F) mass-based photosynthetic capacity (A_{mass}), (G) photosynthetic nitrogen use efficiency, and (H) leaf fracture toughness. Sites are ranked and listed in order of increasing soil nitrogen and bars are shaded by species natural presence/absence at

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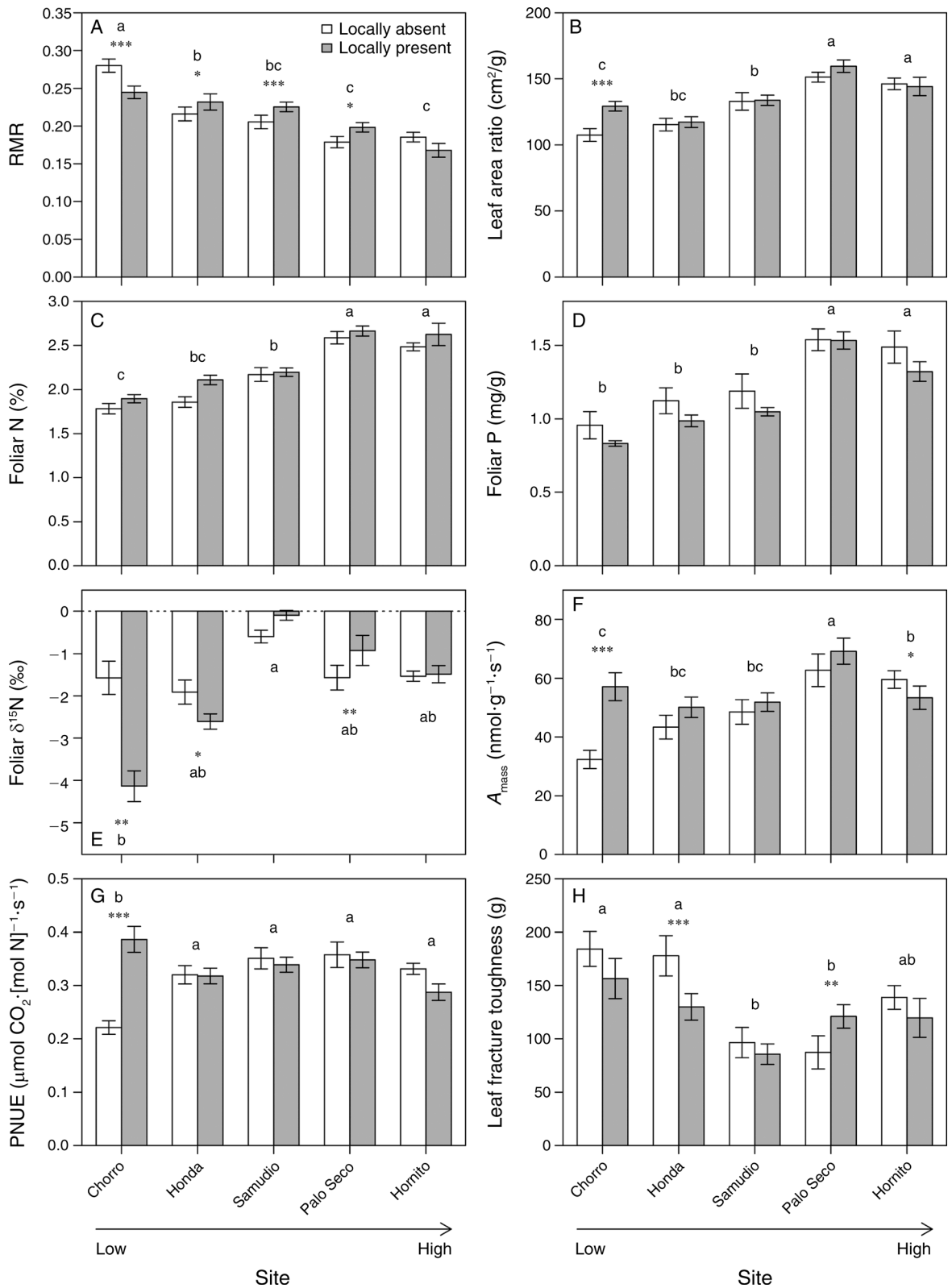
that site. Different letters above the bars indicate significantly different trait means among the sites ($P < 0.05$) and asterisks represent significant differences between species that are present and absent from a site. Mixed models for all traits were run on seedlings in protected herbivore treatment only for consistency in sample sizes.
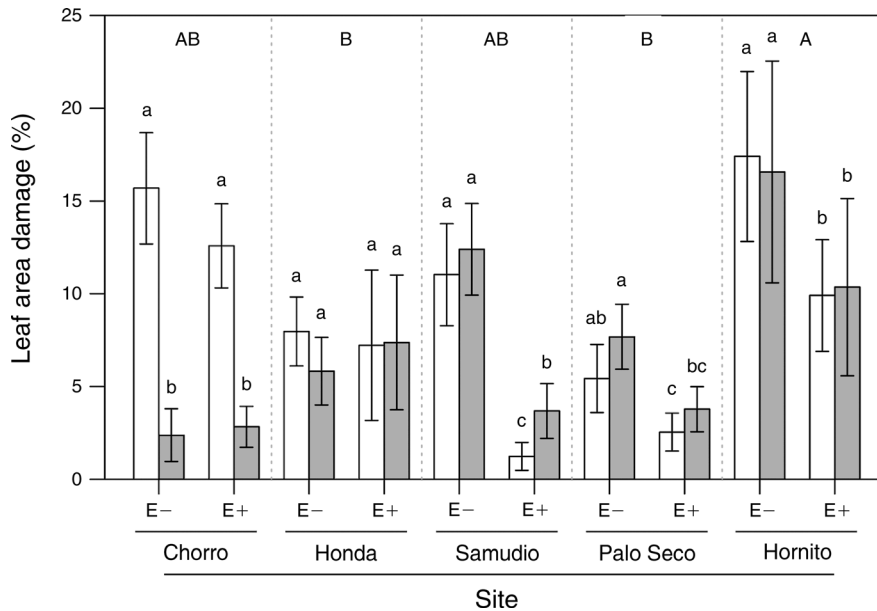
* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Fig. 4. Effect of the herbivore exclosure treatment on leaf damage of seedlings growing at five sites differing in soil nutrient availability; leaf area damage per plant (mean ± SE) for seedlings of species locally absent and present when exposed to (E−) and protected from (E+) herbivores. Sites are listed in order of increasing soil nutrient availability and bars are shaded by species natural presence/absence at that site. Capital letters represent differences among sites ($P < 0.05$), and lower-case letters represent differences among treatment combinations within a site ($P < 0.05$).

Seedling traits

Biomass allocation.—Biomass allocation was strongly related to soil nutrient availability, with increasing aboveground and decreasing belowground investment as soil nutrient availability increased (Fig. 3A, B). This biomass allocation trade-off was captured in the seedling trait principal components analysis with RMR loading negatively and LAR and SLA loading positively along the trait PC1 axis (Appendix A: Table A2, Fig. A2). Furthermore, seedlings of species naturally occurring at the Chorro site were able to maintain relatively high leaf area ratios, whereas seedlings of locally absent species showed a greater increase in investment to belowground biomass at the cost of aboveground biomass (Fig. 3A, B). At intermediate-nutrient sites, seedlings of naturally occurring species had higher root mass ratios than locally absent species; however, leaf area ratio was not related to species distribution patterns. At the highest-nutrient site, there was no difference in biomass allocation with species distribution pattern, but root mass ratios were low and leaf area ratios were high compared to lower-nutrient sites. In contrast, SLA did not differ with site or species home-site association.

Resource-use efficiency.—Photosynthetic rates and foliar nitrogen and phosphorus all increased with increasing soil nutrient availability among the sites (Fig. 3) and along the trait PC1 axis (Appendix A: Table A2, Fig. A2). Foliar nutrients and photosynthetic rate increased and photosynthetic nutrient-use efficiency rates decreased along the trait PC2 axis. There were no differences between locally occurring

and absent species for foliar nitrogen or phosphorus concentrations at any site (Fig. 3C, D). At low-nutrient sites, locally occurring species had $\delta^{15}N$ values that were significantly lower (more depleted) than locally absent species, whereas at Palo Seco this pattern was reversed, and there were no differences between species occurrence groups at Samudio or Hornito (Fig. 3E). Despite overall lower photosynthetic rates at the lowest-nutrient site, species naturally occurring at the lowest-nutrient site were able to maintain relatively high photosynthetic levels compared to locally absent species (Fig. 3F). Thus, photosynthetic N-use efficiency was significantly higher for locally occurring species than locally absent species at the lowest-nutrient site (Fig. 3G).

Herbivory and defense.—Leaf fracture toughness was generally higher at lower-nutrient sites compared to higher-nutrient sites (Fig. 3H) and was negatively correlated with the trait PC1 axis (Appendix A: Table A2, Fig. A2). However, species that naturally occurred at the low-nutrient Honda site had lower leaf fracture toughness than locally absent species, whereas species that naturally occurred at the high fertility Palo Seco site had higher leaf fracture toughness than locally absent species. There was no difference in leaf fracture toughness with home-site association at Chorro, Samudio, or Hornito.

Leaf area damage of seedlings generally increased with increasing soil nutrient availability among the sites, particularly for seedlings of naturally occurring species exposed to herbivores, except for the notably low

Fig. 5. Conceptual model of seedling responses to above- and belowground resource availability. As soil nutrient availability increases (solid line), light levels decrease (dotted line) due to increasing canopy cover at higher-nutrient sites. Seedling functional traits are strongly influenced by soil nutrient availability, but higher leaf quality results in higher leaf damage and mortality. Realized relative growth rate decreases as soil nutrient availability increases and light becomes more limiting. Thus, optimal seedling performance (dashed line) is expected at intermediate sites where soils and light levels are co-limiting. Traits listed in roman type are those traits that directly respond to changes in soil fertility and affect the traits listed in italics, which indirectly respond to changes in soil fertility.
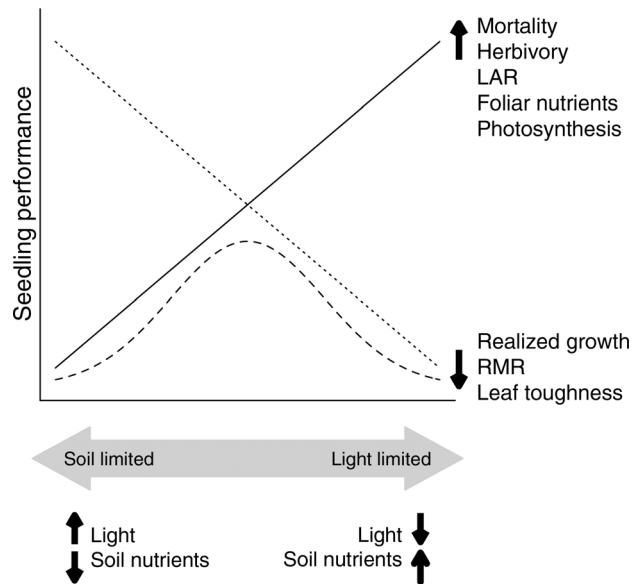
damage at Palo Seco (Fig. 4). Leaf area damage per seedling differed significantly with site, exposure to herbivores, and home-site association (Fig. 4). Leaf damage was highest at the highest-nutrient site, Hornito (13.6% ± 2.32%) and lowest at Palo Seco (4.9% ± 0.8%). The overall mean for leaf area damage was lower for seedlings of locally occurring species (7.3% ± 1.0%) compared to seedlings of locally absent species (9.1% ± 1.0%; $z = 4.02$, $P < 0.0001$). Seedlings exposed to herbivores had higher leaf area damage (10.2% ± 1.1%) compared to seedlings protected from herbivores (6.2% ± 0.9%; $z = 8.90$, $P < 0.0001$). In addition, the magnitude and interaction of these effects differed among sites (Fig. 4).

Effect of resource gradients on seedling traits and performance

Our results indicate that rather than three separate trade-offs, morphological, physiological, and defense traits showed parallel shifts that were strongly related to the environmental gradient across our sites. Root mass ratio and leaf toughness decrease as LAR, foliar nutrients, and photosynthetic rates increase along the trait PC1 axis and explain over 40% in the variation among species and sites (Appendix A: Fig. A2). Trait PC1 was positively related to environmental PC2 axis (Pearson $r = 0.83$, $P < 0.0001$; Appendix C: Fig. C1), which represents the shift from low soil nutrient and high light availability to high soil nutrient availability and low light availability across the sites (Appendix A: Table A1, Fig. A1). The trait PC2 axis explained an additional 18% of the variation among seedlings (Appendix A: Fig. A2), primarily associated with SLA (Appendix A, Table A2) and within-site variation rather than among-site variation (Appendix C: Fig. C1). Mortality rate increased (Pearson $r = 0.32$, $P < 0.05$) along the resource gradient (Fig. 5, Appendix C: Fig.

C1). Relative growth rate was not related to the environmental PC2 axis, but was positively related to R:FR values (Pearson $r = 0.33$, $P < 0.01$; Fig. 5). Despite the shift from conservative to productive trait strategies, RGR decreases (Pearson $r = -0.35$, $P < 0.01$) and mortality increases with trait PC1 values (Pearson $r = 0.29$, $P < 0.05$; Appendix C: Fig. C2).

DISCUSSION

Previous field experiments have demonstrated, separately, the importance of biomass allocation, resource-use efficiency, and herbivores in determining seedling performance across contrasting soil types in tropical forests (Fine et al. 2004, Palmiotto et al. 2004, Baltzer et al. 2005). Here, we simultaneously examined the role of these three mechanisms in determining soil-based resource partitioning among understory palm species in a lower montane forest in western Panama. We found evidence for all three mechanisms in determining environmental filtering, based on shifts in most morphological, physiological, and defense-related parameters measured across the soil fertility gradient. Furthermore, our results showed that key functional trait values differed with species distribution patterns across the sites and, therefore, with the performance of seedlings transplanted across the soil nutrient gradient (Appendix C: Fig. C2). Our results suggested that, at least at low-nutrient sites, seedling performance advantages of locally occurring species over locally absent species were achieved by the coordination of morphological, physiological, and defense traits, and thus, a convergence in a whole-plant strategy. These results were consistent with the stress-gradient hypothesis that predicted stronger filtering in habitats with low soil resource levels compared to habitats with more benign soil resource levels (Weiher and Keddy 1995, Swenson 2011).

One of the most striking patterns we found was the strong influence of soil nutrient availability on palm seedling functional traits. Most species were able to optimize their trait values, and thus, overall plant strategy to the resource availability of the transplant site (Appendix C: Fig. C1). However, the shift toward more productive trait values with increasing soil nutrient availability did not result in increased performance (Appendix C: Fig. C2). Rather, realized growth performance decreased and mortality increased along the resource gradient. Baraloto et al. (2005) suggested that light availability might play a more important role than edaphic factors in determining growth performance of tropical seedlings and, therefore, habitat filtering in some tropical forests. Thus, as soil nutrient availability increased, growth became increasingly limited by decreasing light availability. However, as leaf quality increased with increasing nutrient availability, metabolic costs and leaf area lost to herbivory also increased. Under low-light conditions in the understory of high-nutrient sites, seedlings were unable to achieve high potential productivity or replace tissue lost to herbivores. Together, these constraints might explain the overall high seedling performance observed at the intermediate-nutrient fertility site, where neither soil nutrients nor light strongly limited seedling performance (Fig. 5). In the next section, we discuss how these interacting constraints were mediated by species distribution patterns across sites.

Species distribution in relation to seedling performance

We predicted that if environmental filtering was important in determining species distribution patterns across the soil nutrient gradient, then naturally occurring species would perform better than locally absent species. Overall, seedling performance differed between naturally occurring and locally absent species, but the strength and direction of that difference depended on site. In two of the five sites, we found a home-site advantage in growth and survival rates. At the lowest-nutrient site, seedlings of naturally occurring species were able to allocate greater resources to leaves and maintain higher photosynthetic rates, nutrient-use efficiency, and lower leaf area damage compared to species restricted to higher nutrient soils. This translated to both higher growth and survival for the species naturally occurring at low-nutrient sites. Other studies have shown that low-nutrient soil specialists have conservative functional trait values, but do not necessarily show home-soil performance advantages (Palmiotto et al. 2004, Baltzer et al. 2005, Russo et al. 2005, Brenes-Arguedas et al. 2008). The only other field experiment that has shown clear evidence for seedling performance advantages based on soil nutrient availability included white-sand species in the Peruvian Amazon (Fine et al. 2004, 2006). There, white-sand specialists had higher growth and survival on white-sand soils compared to clay-soil species, but only when exposed to herbivores.

Here, we found a home-site advantage at the lowest-nutrient site both when seedlings were exposed to and protected from herbivores, suggesting that species from the lowest-nutrient site had multiple mechanistic adaptations to poor soils that mediate habitat filtering regardless of pest pressure. Similarly, Stropp (2011) found higher seedling survival of white-sand species growing on white-sand soils in Brazil, regardless of exposure to herbivores, and related the contrast with the Fine et al. (2004) study to relative differences in soil nutrient availability between the soil pairs in the two studies.

Although our findings strongly support home-site advantages and adaptations to soil conditions at the lowest-nutrient site, the evidence that local species hold any advantage is less clear at higher-nutrient sites. We hypothesized that at higher-nutrient sites, functional traits that maximized productivity would be related to enhanced seedling performance. In accordance, morphological and physiological traits followed predicted trends with increasing soil nutrient availability. However, at the high-nutrient Palo Seco site, seedling performance was surprisingly low, despite a home-site advantage. Furthermore, naturally occurring species had higher root mass ratios and leaf fracture toughness than locally absent species, both traits associated with greater persistence rather than productivity (Chapin 1980, Coley et al. 1985). This suggests that the home-site advantage at Palo Seco may not be directly driven by soil nutrients. Soil nutrient gradients are often confounded by other resource gradients, such as light availability (Wilson and Tilman 1993, Palmiotto et al. 2004, Schreeg et al. 2005, Coomes et al. 2009) and soil moisture (Wright et al. 2001, Baltzer et al. 2005, Engelbrecht et al. 2007, Brenes-Arguedas et al. 2008). Light levels and quality at seedling height (10–50 cm) were relatively low at Palo Seco compared to the other sites in the study (Table 1), primarily due to the very high density of understory palms (Andersen et al. 2010b). Therefore, there may be a shift in the resources limiting seedling performance from soil nutrient limitation at the low soil nutrient availability sites toward light limitation at the higher soil fertility sites. Negative correlations between the intensity of competition for below- and aboveground resources have been found in grasslands (Wilson and Tilman 1993) as well as in tropical forests (Baltzer et al. 2005, Brenes-Arguedas et al. 2011), and might explain the performance advantage of the locally occurring species at the high-nutrient Palo Seco site, despite their more conservative trait strategies.

Seedling performance of locally absent species was higher than naturally occurring species only at the intermediate fertility site, Samudio. Locally occurring species at Samudio included a mixture of species associated with andesitic and rhyolitic soils. Locally absent species were primarily associated with andesitic soils, but had a distribution constrained to the Caribbean side of the Continental Divide. The andesitic

species that were locally absent at Samudio had a performance advantage over locally occurring species, suggesting that niche processes do not restrict locally absent species from this site. This corroborates our previous findings that spatially limited seed dispersal may also play a role in determining species distribution patterns across the soil nutrient gradient (Andersen et al. 2010b). Alternative explanations for the absence of home-site performance advantages include other trade-offs such as the tolerance–fecundity trade-off (Muller-Landau 2010) or stochastic processes such as dispersal limitation, ecological drift, and historical contingency in tropical forest community assembly (Hubbell 2001, Condit et al. 2002, Ricklefs 2004). For example, the absence of *Inga* species (Fabaceae) from sites with favorable soil conditions in Peru corresponded with geographic areas separating genetically divergent populations (Dexter et al. 2012). Thus, historical seed dispersal patterns and secondary contact between historical isolated floras explained species absences at sites with preferred soil conditions.

Trait-based mechanisms related to environmental filtering

Biomass allocation.—Trade-offs between above- and belowground biomass have been related to seedling performance across gradients of soil nutrient availability, whereby plants increase investment in belowground biomass with decreasing soil nutrient availability (Chapin 1980, Tilman and Wedin 1991, Coomes and Grubb 1998, Palmiotto et al. 2004). Here, we found a strong shift in biomass allocation to increased root biomass as site nutrient availability decreased, with the highest RMR at the lowest-nutrient site (Chorro). Furthermore, seedlings of the locally absent species at Chorro had a greater shift in investment toward root biomass at the expense of leaf biomass compared to naturally occurring species. This shift in investment toward belowground biomass was also found for seedlings growing in understory light conditions in a field transplant experiment in Sarawak, Malaysia, where three of six species increased fine root mass ratios in low-nutrient soils compared to higher-nutrient soils (Palmiotto et al. 2004).

Shifts in biomass allocation across the soil nutrient gradient paralleled those for foliar nitrogen and phosphorus, suggesting that soil nutrient availability may drive shifts in both physiological and morphological traits. Interestingly, an experiment examining the effect of nitrogen addition on seedling performance for a subset of the palm species included here showed no changes in biomass allocation following nitrogen addition (Andersen et al. 2010a). This suggests that strong shifts in biomass allocation with site fertility rankings might be related to nitrogen co-limitation or limitation by other plant nutrients, such as soil phosphorus (Tanner et al. 1998), which followed similar patterns to nitrogen across the sites examined here. A recent study showed that tree species distribution patterns were driven in part by soil phosphorus availability across a tropical lowland forest (Condit et al. 2013). A phosphorus addition experiment would be necessary to determine the role of phosphorus in driving the biomass allocation patterns we found in the understory palm seedlings.

Physiological traits and resource-use efficiency.—In accordance with plant economic theory (Chapin 1980, Bloom et al. 1985, Aerts and Chapin 2000), foliar nutrient content and photosynthetic rate increased across the soil nutrient gradient. Photosynthetic rates are strongly correlated with foliar N concentrations due to the large proportion of leaf N invested in photosynthetic machinery (Field and Mooney 1986, Evans 1989, Reich et al. 1994). Differences in photosynthetic capacity and foliar nitrogen concentrations also resulted in strong differences in PNUE among sites. At the lowest-nutrient site, naturally occurring species had significantly higher PNUE values than species that did not naturally occur at that site. Seedlings of naturally occurring species at the lowest-nutrient site were able to maintain higher photosynthetic rates than locally absent species, despite similar foliar nitrogen concentrations. Andersen and Turner (2013) showed that understory palm species naturally occurring at the low-nutrient site had lower nitrogen uptake rates compared to understory palms occurring at the same higher-nutrient sites as the current study. Together, this suggests that physiological adaptations are important filters for species occurring at the lowest-nutrient site.

Growth–defense trade-off.—We hypothesized that if palm–soil associations were driven by a trade-off between allocation to growth and anti-herbivore defenses, then species investing heavily in anti-herbivore defenses would have an increasing advantage over poorly defended species as soil nutrients decrease. At the lowest-nutrient site, naturally occurring species had significantly lower leaf area damage compared to locally absent species. Our previous research with understory palms showed that leaf damage was positively correlated with foliar nitrogen and leaf quality traits of seedlings (Andersen et al. 2010a). However, in the current study, we found no differences in foliar N or leaf fracture toughness between seedlings of locally occurring and locally absent species at the lowest-nutrient site. Nonetheless, the greater leaf area damage of locally absent species at the lowest-nutrient sites may have contributed to the lower growth rates compared to naturally occurring species at the lowest-nutrient site, supporting the growth–defense hypothesis (Coley et al. 1985, Fine et al. 2004) in contributing to species distribution patterns along the soil nutrient gradient.

Different coordinated sets of trade-offs appear to influence palm seedling performance and environmental filtering along the soil nutrient gradient in this lower montane forest. The clearest evidence for soil-based habitat partitioning is for the lowest-nutrient site, where locally occurring species have a suite of morphological,

physiological, and anti-herbivore defense adaptations that give them a performance advantage. However, at higher-nutrient sites, there may be a shift toward light limitation on seedling performance, and spatially limited seed dispersal may also be important in determining species distribution patterns. Our study is one of the first to examine multiple mechanisms for niche partitioning along a soil nutrient gradient in a tropical forest. Our results indicate that both niche processes and dispersal limitation influence species distribution patterns along soil nutrient gradients and contribute to the high levels of beta diversity of understory palms, and thus, shifts in community-wide structure in this lower montane forest.

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–C are available online: http://dx.doi.org/10.1890/13-1688.1.sm