Seedling recruitment factors in low-diversity Hawaiian wet forest: towards global comparisons among tropical forests

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Abstract.   Recruitment limitations determine forest community regeneration patterns. Source limitation and dispersal limitation contribute to overall seed limitation, while environmental conditions and habitat associations influence establishment limitation. Several hypotheses have made contradictory predictions for how the relative importance of these limitations should vary with diversity. However, comparative data have not been available for low-diversity tropical forests. We quantified recruitment limitations using 2.5 yrs of seed rain and seedling distribution data collected within a 4 ha forest dynamics plot in low-diversity native-dominated Hawaiian wet forest. We further quantified seedling irradiance and substrate habitat associations and niche overlap (using Pianka's niche overlap index). Additionally, we compared recruitment limitations and the frequency of seedling habitat associations across forests using the few available published data from sites employing similar field and analytical methods. In Hawaiian wet forest, seed dispersal more strongly limited recruitment than did establishment limitation across species, with 11 of 18 species completely seed limited (i.e., no seeds found). However, the relative importance of limitations varied greatly among species. For the three most abundant species, habitat conditions more strongly limited regeneration than did seed arrival, especially for the dominant canopy species, *Metrosideros polymorpha*, which was not seed limited. Most species were significantly associated with specific ranges of irradiance and/or substrates. Although habitat associations may indicate niche differentiation, Hawaiian species also showed significant niche overlap. Across the three forests compared, community-wide mean seed and establishment limitation values were similar, despite wide variation in diversity. However, recruitment limitations differed strongly among species within forests due to species' life-history differences. While seed limitation in Hawaiian forest was as high as in high-diversity forests, mechanisms may differ; seed limitation in Hawaii may arise from loss of pollinators and dispersers rather than from a high proportion of rare species as occurs in high-diversity forests. The strong habitat associations in Hawaiian forest relative to high-diversity forests supported theoretical expectations that lower species diversity should increase the importance of habitat associations. However, these habitat associations were not linked to niche differentiation in Hawaii. Our findings suggest that high recruitment limitation may facilitate coexistence despite niche overlap in low-diversity Hawaiian forest.

Key words: Center for Tropical Forest Science; *Cheirodendron trigynum*; *Coprosma rhynchocarpa*; dispersal limitation; establishment limitation; habitat association; Hawaii, USA; *Metrosideros polymorpha*; Pianka's niche overlap; regeneration ecology; seed limitation.

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INTRODUCTION

A key objective of ecology is to understand the factors that determine the distributions and abundances of plant species within and across ecosystems. Thus, the relative importance of recruitment limitations is an increasing focus of ecological research (Grubb 1977, Tilman 1994, Hubbell et al. 1999, Chesson 2000, Nathan and Muller-Landau 2000, Muller-Landau et al. 2002, Adler et al. 2007, Clark et al. 2007, Poorter 2007, Myers and Harms 2010). Seedling abundance across the landscape (and its opposite, "seedling limitation") is determined by seed limitation and establishment limitation; in turn, seed limitation arises from source limitation and is determined by adult seed production and dispersal limitation (quantitative definitions in Fig. 1; Nathan and Muller-Landau 2000, Muller-Landau et al. 2002, Terborgh et al. 2011). The relative importance of seed and establishment limitations highlights the fundamental ecology and the general mechanisms for species coexistence within given ecosystems. For example, high seed limitation is an "equalizing" mechanism that may promote species coexistence by allowing species to avoid hierarchical interspecific competition (i.e., "winning-by-forfeit"; Hurtt and Pacala 1995). Alternatively, high establishment limitation reflects niche differentiation and habitat specificity which are "stabilizing" mechanisms for species coexistence (Tilman 1994, Chesson 2000, Muller-Landau et al. 2002, Gravel et al. 2006, Adler et al. 2007, Paine and Harms 2009, Mutshinda and O'Hara 2011).

Ecologists have proposed multiple hypotheses to explain how equalizing and stabilizing mechanisms may differ across ecosystems varying in structure and diversity (summarized in Table 1). However, these hypotheses sometimes lead to contradictory predictions, and their ability to account for patterns across forests have not been examined simultaneously. The paucity of data, especially for low-diversity forest, impedes this work. We considered all the available hypotheses to uncover how regeneration processes may vary with differences in fundamental ecosystem properties. We provide (1) the first explicit test of the relative importance of seed and establishment limitations in low-diversity tropical forest, (2) an examination of the frequency (proportion) of species with habitat associations and niche differentiation in such a system, and (3) a first comparison across tropical forests with differing ecosystem properties using available data from studies that have employed standardized methods. Such studies are enormous logistical undertakings, and this first comparison will motivate future research to test emerging patterns and will provide a framework for refining, synthesizing, and assimilating incoming data.
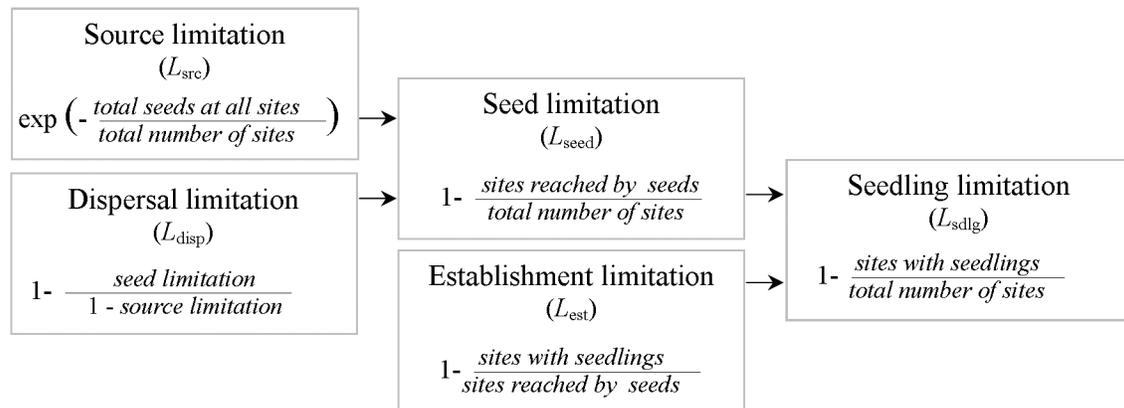

Fig. 1. Components of seedling limitation and their calculations as per Muller-Landau et al. (2002) where seed production determines source limitation (L_{src}), and dispersal limitation (L_{disp}) determines seed availability across sites (seed limitation; L_{seed}). Subsequently, once seeds arrive, habitat characteristics determine establishment limitation (L_{est}). Both seed and establishment limitation contribute to the limitation of seedling distribution across sites (L_{sdlg}).

Table 1. Synthesis of hypotheses from the published literature on how recruitment limitations (seed limitation (L_{seed}) and establishment limitation (L_{est})) and/or the frequency of habitat associations would in theory vary with forest ecosystem properties (P1–3) including explicit predictions for how these would differ based on the known properties of the extremely low-diversity Hawaiian forest relative to high-diversity tropical forests (see *Introduction* for further explanation).

| Community property | Predicted effect on L_{seed}, L_{est} and/or the frequency of habitat associations | Source | Prediction for Hawaii v. other high-diversity tropical forests | | |
			Comparison of properties	L_{seed}	L_{est} and frequency of habitat associations
P1: Stem density and/ or basal area	As stem density and/or basal area increases, so does community-wide competition for space and other resources, thereby increasing L_{est} and species habitat associations.	1, 2	Similar structure†	na	Similar
P2: Species diversity	A) As species diversity increases, habitat breadths along resource axes narrow, thereby increasing L_{est} and habitat associations.	3, 4	Lower diversity	na	Lower
	B) As species diversity increases, interspecific interactions among many species become more unpredictable, reducing directional selection for species habitat differentiation, thereby decreasing L_{est} and habitat associations.	4, 5, 6	Lower diversity	na	Higher
P3: Proportion of rare species	A high proportion of rare species leads to high community-wide L_{seed} which decreases direct competition, thereby decreasing L_{est} and habitat associations.	7, 8	Lower proportion of rare species	Lower	Higher

Notes: We found alternative hypotheses with contrasting predictions for the effects of species diversity on recruitment limitations and habitat associations (P2 A and P2 B). Sources are: 1, Pianka (1972); 2, Rusterholz (1981); 3, Ricklefs (2001); 4, Ricklefs (2004); 5, Hubbell (2006); 6, Volkov et al. (2009); 7, Hubbell (2001); 8, Gravel et al. (2006).
  † Structural properties such as basal area, stem density, and biomass.

Hawaiian forest, which has extremely low species diversity due to its isolation and small land area (Carlquist 1985), provides a unique opportunity to test hypotheses for how diversity and structure influence regeneration processes because the structure and climate are similar to those of most other tropical wet forests, while the diversity is very different. Though fewer species occur in Hawaiian forest, they are functionally diverse, from the dominant canopy species *Metrosideros polymorpha* which produces many wind-dispersed seeds (Drake 1992) to species with relatively larger seeds contained in bird-dispersed fruits such as *Coprosma rhynchocarpa*. Based on published theories, we made explicit predictions for how seedling ecology in Hawaiian wet forest may differ from high-diversity tropical forests, all else being equal (Table 1). First, niche differentiation and therefore establishment limitations and habitat associations should be similar among forests with similar structural properties (Table 1, P1; Pianka 1972, Rusterholz 1981). Therefore, because aspects of Hawaiian forest structure, including stem density and basal area, are within the range of those of tropical forests with higher diversity (Midgley and Niklas 2004), we expected to find establishment limitations and habitat associations similar to those found in other tropical forests, based on this property alone. Second, the low species diversity in Hawaiian forest may drive lower establishment limitation and fewer habitat associations if fewer species promotes greater niche breadth (Table 1, P2A; Ricklefs 2001, 2004). Alternatively, one may predict the opposite scenario, that the low species diversity in Hawaiian forest would drive higher establishment limitation and more habitat associations if the relatively few species have highly predictable interspecific interactions and if this results in

greater niche differentiation (Table 1, P2B; Ricklefs 2004, Hubbell 2006, Volkov et al. 2009). Third, because rare species typically have high seed limitation and Hawaiian wet forest has a lower proportion of rare species than other tropical forests (19% of species with ≤1 individual/ha versus 42% averaged for 13 other tropical forests; $t = 6.63$, $P < 0.001$; Losos and Leigh 2004), we predicted that Hawaiian forest should have lower seed limitation than high-diversity tropical forests (Table 1, P3; Hubbell 2001, Gravel et al. 2006).

We addressed key questions for the first time in low-diversity tropical forest by combining two major approaches to seed and seedling ecology. First, we quantified seed availability and seedling distribution using standard seed traps and seedling plots to determine seed and establishment limitations in low-diversity Hawaiian forest. Second, we quantified seedling densities in substrate and light microhabitats to determine habitat associations and niche overlap. We addressed these questions: (1) How influential is seed limitation relative to establishment limitation for seedling recruitment? (2) What are the frequency and strength of species habitat associations for substrate and light? (3) Is there evidence of interspecific niche differentiation (measured as Pianka's niche overlap)? Further, we utilized previous studies to address for the first time (4) how do the relative importance of seed and establishment limitations and the extent of habitat associations vary across tropical forests with a wide range of diversity?

METHODS

Study site

We conducted this study in the Laupahoehoe Forest Dynamics Plot (FDP) of the Hawaii Permanent Plot Network (HIPPNET; www. hippnet.hawaii.edu), a member of the Smithsonian Tropical Research Institute Center for Tropical Forest Science network (CTFS; www. ctfs.si.edu). The 4 ha FDP is located on Hawaii Island (19°55′ N, 155°17′ W) in the Hawaii Experimental Tropical Forest (HETF; www.hetf. us). The FDP was established in 2008 at 1120 m elevation in native-dominated primary tropical lower montane wet forest (Holdridge 1947). Within the FDP, all native woody species ≥1 cm diameter at breast height (DBH) were tagged, mapped, measured and identified following standard CTFS protocols (Condit 1998). The dominant canopy tree species is *Metrosideros polymorpha* and the subcanopy is dominated by tree ferns in the genus *Cibotium*; these species account for 21% and 27% of the stems, respectively (R. Ostertag, *unpublished data*). Mean annual precipitation is 3440 mm (Giambelluca et al. 2012) and the mean annual temperature is 16°C (Juvik and Juvik 1998). Rainfall is largely aseasonal and monthly temperature averages ranged from 14°C to 16°C during 2011 based on the adjacent above-canopy climate tower. Though the 4 ha FDP size in Hawaii is smaller than that of the majority of CTFS FDPs (25 to 50 ha), due to its extremely low species diversity this FDP provides comparable sample sizes for most species and an adequate representation of species diversity for this forest type, based on species accumulation curves (R. Ostertag, *unpublished data*). Further, the HIPPNET FDPs were selected to be highly representative in their species composition, structure, and dynamics and thus to allow elucidation of the processes occurring across larger areas of Hawaiian forest.

Seed rain and seedling demography censuses

We quantified seed rain and seedling abundances for 2.5 yrs, from September 2009 to January 2012 for seed rain and from December 2008 to June 2011 for seedlings. Within the 160 × 160 m central area of the 4 ha Laupahoehoe FDP, we established a grid of 64 seed and seedling census stations. Following standard CTFS seedling plot protocols (Wright et al. 2005), each census station comprised one 0.5 m² seed trap with a fine mesh bag suspended approximately 80 cm above the ground ($N = 64$) and three 1 × 1 m seedling plots within 2 m of each seed trap ($N = 192$; Fig. 2). The arrangement and density of census stations facilitated thorough seed collection from adult trees throughout the 4 ha FDP, with all traps evenly spaced at 20 m intervals. We excluded the outer 20 m of the FDP to reduce seed input from unmapped trees. Given the small FDP size, the density of census stations in this study was high, providing ample sampling intensity and relatively detailed spatial information. For example, the proportion of the total FDP area covered by our seed and seedling plots were
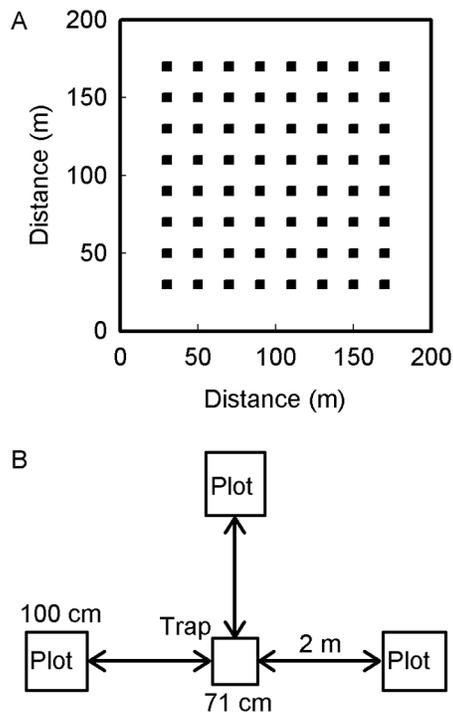
Fig. 2. (A) Schematic of census station locations within the 4 ha forest dynamics FDP in Hawaiian wet forest, and (B) diagram of a census station with three 1 m^2 seedling plots within 2 m of a 0.5 m^2 seed trap.

ten- and four-fold higher, respectively, than for the system in the 50 ha Barro Colorado Island (BCI) FDP (Wright et al. 2005). This design provided sufficient spatial replication to accurately represent the FDP, just as the FDP size allowed it to adequately represent Hawaiian rainforest (see previous section).

In each seedling plot, we censused and measured stem height for all native woody species < 1 cm DBH (hereafter referred to as "seedlings"). For each seedling we recorded species, location, size, and rooting substrate (i.e., soil, root mat, rock, log, or tree fern). We included tree ferns as a rooting substrate because many trees establish epiphytically in Hawaiian forests (Drake and Pratt 2001). Each species was in a different genus, so hereafter we refer to species by their genus names (see Table 2 for complete names). The mean ± SE for seedling height across all censuses was 8.8 ± 0.27 cm, with all individuals <2.6 m.

We measured irradiance and substrate to allow

estimation of habitat associations. We determined the percentage cover of each substrate type (categories listed above) in the 160 × 160 m central area of the 4 ha FDP using 20 m long point-intercept line transects ($N = 32$) located in a random stratified design. Substrate data were collected every 10 cm along each transect. To characterize the seedling light environment, we measured understory and above canopy photosynthetically active radiation (PAR, μmol photons·m^{-2}·s^{-1}) and determined transmitted PAR (TPAR as understory PAR/above canopy PAR; Anderson 1964, Nicotra and Chazdon 1994). We used mean TPAR values from four measurements (in December 2009, July 2010, December 2010, and June 2011) to represent average light levels for each seedling plot in summer and winter. For each measurement, we recorded two consecutive 15 s average PAR measurements using a 1 m long line quantum sensor (LI-191, LI-COR, Lincoln, NE, USA) positioned 1 m above the center of each seedling plot and above-canopy PAR measurements logged at 1 minute intervals from a point quantum sensor (LI-190; LI-COR) mounted on a climate tower adjacent to the FDP. We determined TPAR on uniformly overcast days to focus on the diffuse irradiance transmitted to the seedlings. Diffuse TPAR measured on overcast days correlates well with mean total daily PAR and long-term mean PAR in the understory (Anderson 1964, Parent and Messier 1996, Tobin and Reich 2009). Further, diffuse irradiance better represents the light available to understory plants and that to which they are acclimated, due to its deeper penetration into the forest canopy versus direct irradiance (Alton et al. 2007, Urban et al. 2007, Tobin and Reich 2009). As confirmation of the validity of sampling on overcast days, we assessed the proportion of diffuse total above-canopy PAR using a BF3 "Sunshine Sensor" (Delta-T Devices Ltd, Cambridge, UK; Wood et al. 2003) mounted on an above-canopy climate tower adjacent to the FDP. Our approach was validated, as the mean ± SE for the proportion of diffuse to total PAR was 91 ± 0.01% during the TPAR measurements.

Analysis

Our analyses focused on seedling recruitment limitations and habitat associations. We quantified recruitment limitation factors across the FDP

Table 2. Species found in seedling plots and/or seed traps in Laupahoehoe FDP; minimum, mean, and maximum heights with number of individuals found (N), and recruitment limitations calculated over 2.5 yrs; limitation formulas in Fig. 1; detailed species data in Appendix: Table A1.

Species	Code	Height (cm)	N	Source	Dispersal	Seed	Estab	Seedling
Acacia koa	AK	1.0–**28.0**–188	10	0	0.42	0.42	0.81	0.89
Broussaisia arguta	BA	1.0–**15.0**–82.0	8	1.00		1.00		0.95
Cheirodendron trigynum	CT	0.5–**4.5**–240	1496	0	0	0	0.19	0.20
Clermontia parviflora	CP	12.0–**43.0**–104	3	1.00		1.00		0.95
Coprosma rhynchocarpa	CR	0.5–**8.0**–243	370	0	0.11	0.11	0.14	0.28
Hedyotis hillebrandii	HH	**36.0**	1	1.00		1.00		0.98
Ilex anomala	IA	0.5–**33.0**–186	16	1.00		1.00		0.81
Leptecophylla tameiameiae	LT	2.0–**6.0**–14.0	3	1.00		1.00		0.97
Metrosideros polymorpha	MP	0.5–**3.5**–256	1494	0	0	0	0.14	0.14
Myrsine lessertiana	ML	5.5–**16.0**–28.0	3	0.13	0.95	0.95	0.33	0.97
Perrottetia sandwicensis	PS	2.0–**5.8**–14.0	4	0.48	0.70	0.84	0.70	0.95
Vaccinium calycinum	VC	0.50–**23.0**–175	118	0	0.87	0.88		0.59

Notes: Empty cells indicate that the value could not be calculated from the data. The three most common species appear in bold. Nomenclature follows Wagner et al. (1999) and Stevens (2001 onwards). Sample sizes: seedling plots $N = 192$ and seed traps $N = 64$. Estab, establishment.

after Muller-Landau et al. (2002; see Fig. 1 for logic and formulas). We calculated seed limitation (L_{seed}) and its two subcomponents, source and dispersal limitations (L_{src} and L_{disp}), from seed trap data; and calculated seedling and establishment limitations (L_{sdlg} and L_{est}) from seedling plot census data. We calculated these factors for each species represented in the seedling plots. We excluded *Vaccinium* from seedling and establishment limitation calculations because we could not reliably distinguish true seedlings from vegetative clones. Limitation values range from 0 to 1, with a higher value indicating stronger limitation. The L_{src} formulation used (Fig. 1) assumes that seeds have equal probability of arriving everywhere, and thus are randomly (stochastically) distributed. An alternative equation for L_{src} assumes a uniform or hyper-dispersed distribution of seeds such that seeds are evenly distributed to all sites (Muller-Landau et al. 2002). For our data, both formulas provided similar results and therefore we present results based only on the former. We regressed each variable (L_{seed} and L_{est}) on L_{sdlg} both separately and combined, and regressed seed limitation subcomponents (L_{src}, L_{disp}) on L_{seed} to determine which most closely predicted seed limitation. We conducted analyses using R version 2.15.0 (R Development Core Team 2012).

To test for habitat associations, we conducted randomized χ^2 goodness-of-fit tests on the distribution of each species across habitat cate-gories using Monte-Carlo randomization with 1000 iterations, similar to Webb and Peart (2000). In preliminary tests using Moran's I analysis (Fortin and Dale 2005), we found that spatial autocorrelation existed for irradiance within, but not across, census stations. We accounted for this, and for possible spatial autocorrelation of substrate, by employing a randomization analysis that tests for habitat associations independent of space, similar to that used by previous authors (e.g., Webb and Peart 2000, Harms et al. 2001). Analyses conducted comparing this approach with standard contingency tests and torus-translation randomization methods show that the full randomization method we used was the most conservative of the three (Harms et al. 2001). We used this more conservative test as it could be applied to our habitat data that we collected at the seedling plot scale (for irradiance) or individual seedling scale (for substrate). We tested actual distributions for each species against expected distributions based on relative abundance of substrates within the FDP measured using random transects (as described above). For light habitat, we tested actual distributions against the proportion of seedling plots in each light category. For the analysis of light habitat associations, we transformed TPAR into a categorical variable based on inter-quartile ranges (low TPAR, <4%; low-median TPAR, ≥4–6%; median-high TPAR, ≥6–8%; high TPAR, ≥8%; Valencia et al. 2004). As an indication of

the degree of habitat association, we used the unsquared χ^2 values as a simple index to examine the degree of deviations from the expected frequencies in each habitat as: (observed frequency – expected frequency)/expected frequency (Agresti 2007). For this metric, zero indicates no difference from random distributions, positive values represent positive associations, and negative values represent negative associations with the value of the number representing the magnitude of the deviation.

Habitat associations for given species suggest the importance of niche processes, but they do not necessarily indicate habitat differentiation *among* species. To test whether substrate and TPAR habitat associations differed among seedling species, we calculated Pianka's niche overlap index (Pianka's *O*) for each pairwise combination of species with adequate sample sizes (total 15 pairs) and compared actual niche overlap values with randomly generated simulations (1000 iterations) to obtain p-values using the bootstrap procedure in the 'pgirmess' package in R (Pianka 1973, Gotelli and Entsminger 2000, Cavender-Bares et al. 2004, Giraudoux 2009). Pianka's *O* measures the relative frequency of shared microhabitat utilization by species pairs; values range from 0 (no overlap) to 1 (total overlap). This approach is commonly used for analysis of habitat use by animals (e.g., Glen and Dickman 2008, Hadi et al. 2012) and may also be effectively applied to vegetation, as the index behaves similarly to other commonly used niche overlap measures (Potts et al. 2004, Rödder and Engler 2011, Wilson and Stubbs 2012). Habitat association and niche overlap analyses were conducted for the six species found in at least four of the seedling plots.

Comparisons of habitat associations and limitation indices among tropical forests

To examine the hypotheses listed in Table 1, we compared limitation indices and the proportion of species with habitat associations across forests varying in diversity. We restricted our comparisons to forest plots that used similar seedling and seed measurement experimental designs (i.e., 1 m^2 seedling plots and 0.5 m^2 seed traps). We compared our mean values for L_{seed}, L_{src}, L_{disp}, and L_{est} with published means from four studies in two other tropical forests: Nouragues, French

Guiana (Bongers et al. 2001, Norden et al. 2009) and BCI, Panama (Dalling et al. 2002, Muller-Landau et al. 2002, Losos and Leigh 2004) and we further compared our data for mean L_{src} with that of a temperate plot located in Changbai, China (Li et al. 2012). We compiled results on the proportion of species with habitat associations in four published studies of three forests located in Gunung Palung, Borneo (Webb 1997, Webb and Peart 2000), Yasuniì, Ecuador (Queenborough et al. 2007, Metz 2012), and BCI, Panama (Comita et al. 2007). Differences in light availability across microhabitats directly represent the availability of above-ground resources (Denslow 1980) while variations in substrate or topography are likely to affect plants through availability of below-ground resources such as soil nutrients and water (Clark et al. 1999). Thus, we separately examined the proportion of species associated with above-ground habitat factors (e.g., light) and below-ground habitat factors (e.g., substrate, topography, and physiography as proxies for soil water and nutrient resources).

RESULTS

Importance of seed and establishment limitations in low-diversity Hawaiian wet forest

Over 2.5 yrs, nearly 50,000 *Metrosideros* seeds and >36,000 seeds of six other species arrived in seed traps, including seeds for seven of the 12 species for which we found seedlings in seedling plots. All limitations were highly variable among species in Hawaiian forest (Table 2). Of 18 tree species found within the FDP, all but four species had almost complete L_{src} and high L_{disp} (i.e., only dispersing seeds into <5% of traps) and high L_{sdlg} values (i.e., seedlings recruited in <10% of seedling plots). For those species, mean values ± SE for L_{src} and L_{disp} were 0.47 ± 0.14 and 0.44 ± 0.16, respectively. This indicates that, on average, species produced too few seeds to distribute them into half the traps, and dispersed seeds into fewer than half the traps. These limitations resulted in a mean for L_{seed} of 0.68 ± 0.12 ($N =$ 12). By contrast, the three most common species, *Metrosideros*, *Cheirodendron* and *Coprosma* (in order of commonness) had low to zero L_{seed}, L_{src}, and L_{disp}.

Establishment limitation was as important as seed limitation for the most common species in

Hawaiian forest. Indeed, L_{est} was equal to or higher than L_{seed} for four of the six species for which L_{est} could be calculated (Table 2). When averaged across species, L_{est} was statistically similar to L_{seed} (0.39 ± 0.12 and 0.38 ± 0.17, respectively; paired t-test $t = 0.022$, $P = 0.98$). Overall recruitment success differed strongly among species, and the three most common tree species comprised 95% of all seedlings. Species could be divided into two distinct groups: three species with low-to-moderate overall L_{sdlg} (range 0.19–0.23), and 15 species with high L_{sdlg} (range 0.59–1). Across species, L_{sdlg} was more strongly related to L_{seed} than L_{est} ($R^2 = 0.80$ versus 0.64; $F_{1,10} = 40$ and $F_{1,4} = 7.2$; $P < 0.001$ and 0.055, respectively) and L_{seed} was more strongly related to L_{disp} than L_{src} ($R^2 = 0.99$ versus 0.55; $F_{1,5} = 345$ and $F_{1,10} = 12$; $P < 0.001$ and 0.005, respectively), based on linear regression analysis.

Strong habitat associations in Hawaiian wet forest

Species distributions were linked with habitat. Of the six species analyzed, five showed significant associations with substrate type and three with TPAR category. The strength of associations varied across species as indicated by the degree of deviations from the expected frequencies in each habitat, which ranged from −1.0 to 5.6 for substrate (indicating none to >65 times as many seedlings as expected) and −1.0 to 1.1 for TPAR (indicating none to >2 times as many seedling as expected; Fig. 3). All species were positively associated with tree ferns and negatively associated with soil. All species were positively associated with at least two substrates, and in particular, *Metrosideros* was positively associated with all substrates except soil (Fig. 3). All species except *Ilex* were positively associated with high irradiance and negatively associated with low irradiance (Fig. 3). Seedling habitat associations did not reflect commonness of substrates but did reflect commonness of understory irradiance environments. For example, few seedlings were found on soil (7%), though it was the most common substrate, accounting for almost half the substrate cover in the plot (46%). Instead, nearly half of the seedlings occurred on tree ferns (45%), although the tree fern substrate comprised only 9% of estimated cover. For TPAR, species appeared to be relatively evenly distributed
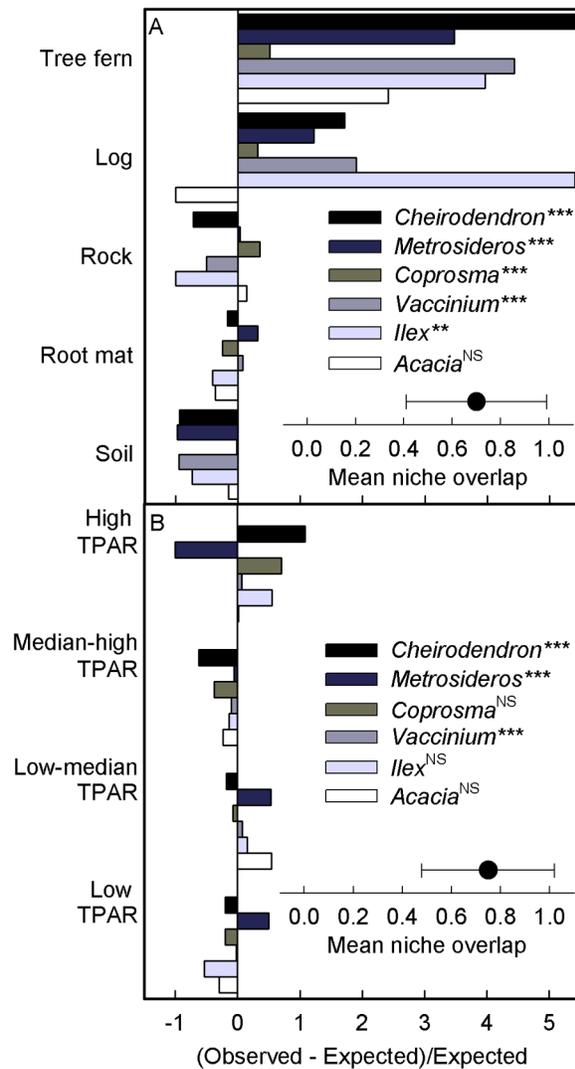

Fig. 3. Degree and direction of habitat associations with (A) substrate and (B) percent transmitted photosynthetically active radiation (TPAR) for Hawaiian wet forest seedlings displayed as the ratio of (observed − expected)/expected such that distributions not different from null expectations equal zero; positive values indicate positive associations and negative values indicate negative associations based on χ^2 randomization tests (** $P < 0.01$, *** $P < 0.001$, [NS] not significant) with inset figures indicate Pianka's niche overlap averaged over all 15 pairwise combinations of species (see Appendix: Fig. A1 for means for each species pair). Species sorted in decreasing order of abundance.

across the range of irradiance levels most commonly encountered in seedling plots, with most species showing preferences for low-median TPAR and high TPAR (32% and 30% of seedlings, respectively).

Significant niche overlap in Hawaiian wet forest

Although all species were significantly associated with at least one habitat category, analysis of Pianka's O showed that species' habitat distributions across substrate and TPAR categories overlapped more than expected by random chance. Bootstrapped mean Pianka's O values among 15 species pairs were similar for substrate and TPAR, indicating that species overlapped similarly in their abundances in substrate and light categories. For substrate, they ranged from 0.45 to 0.94 (mean, 0.70 and 95% CI, 0.29) and for TPAR, they ranged from 0.44 to 0.88 (mean, 0.75 and 95% CI, 0.27; Fig. 3 and Appendix: Fig. A1).

Comparisons of habitat associations and limitation indices among tropical forests

Seedling recruitment factors were remarkably similar when averaged across species and comparing forest sites overall. Across forests varying strongly in diversity, mean values for L_{sdlg} and L_{seed} were similar while L_{est} was higher for BCI than for Laupahoehoe, and lowest for Nouragues. Thus, the low-diversity site was intermediate in L_{est} to two high-diversity sites. When we examined the two components of L_{seed}, we found that L_{src} in Laupahoehoe was intermediate and mean L_{disp} was similar across forests varying in diversity (Fig. 4). However, limitation indices varied considerably among species within each of the forests compared.

We found a higher proportion of species with habitat associations in Hawaii than reported in previous studies of other tropical forests (Table 3), except for a recent study in Yasuni, Ecuador (Metz 2012). In the Laupahoehoe FDP, 57% of seedling species were associated with TPAR and 86% were associated with substrate, compared with an overall average of 30% ± 10 (SE) of species with habitat associations in other studies. When habitats associated with above- or below-ground resources were considered separately (e.g., light as an above-ground resource versus substrate and topography as below-ground resources), there was the first indication of a potential inverse relationship between the frequency of seedling light habitat associations and diversity across the three forests compared (Table 3). By contrast, though Laupahoehoe had higher associations than the other FDPs, there was no apparent trend for decreasing habitat associations with increased diversity for below-ground resources (e.g., topography and substrate; Table 3).

Discussion

Strong importance of seed and establishment limitation in low-diversity Hawaiian wet forest

Although both L_{seed} and L_{est} were high for most of the Hawaiian forest species, L_{seed} was most important for defining seedling regeneration patterns. Fourteen of 18 species found in the FDP were highly seed limited while the four most common seedling species had low L_{seed}. Indeed, across species, L_{sdlg} was driven by low seed availability and dispersal rates, and L_{est} influenced seedling distribution to a lesser extent. Although L_{src} was widespread and probably limits the regeneration of most species, L_{disp} better predicted seedling distributions, suggesting that seed dispersal, rather than seed production, was the primary determinant of differences in seedling recruitment for the majority of species. We note that species varied substantially in dispersal mode from *Metrosideros* with abundant wind dispersed seeds versus *Ilex* with larger animal dispersed fruits.

The relative importance of L_{seed} versus L_{est} was associated with species' relative abundances. One striking finding was that two species, *Metrosideros* and *Cheirodendron*, had zero seed limitation, a phenomenon not previously reported for any studies of comparable duration (Dalling and Hubbell 2002, Muller-Landau et al. 2002, Norden et al. 2009). In other forests, such a phenomenon might be observed after masting years (Metz et al. 2008), but the biology of *Metrosideros* is apparently distinctive in showing this kind of output, each year saturating the landscape with a large number of tiny seeds (Drake 1992). The other species, *Cheirodendron*, is a ubiquitous midstory tree that produces abundant bird-dispersed fruits. However, aside from these exceptionally successful species, most of the tree species recorded in the FDP were completely
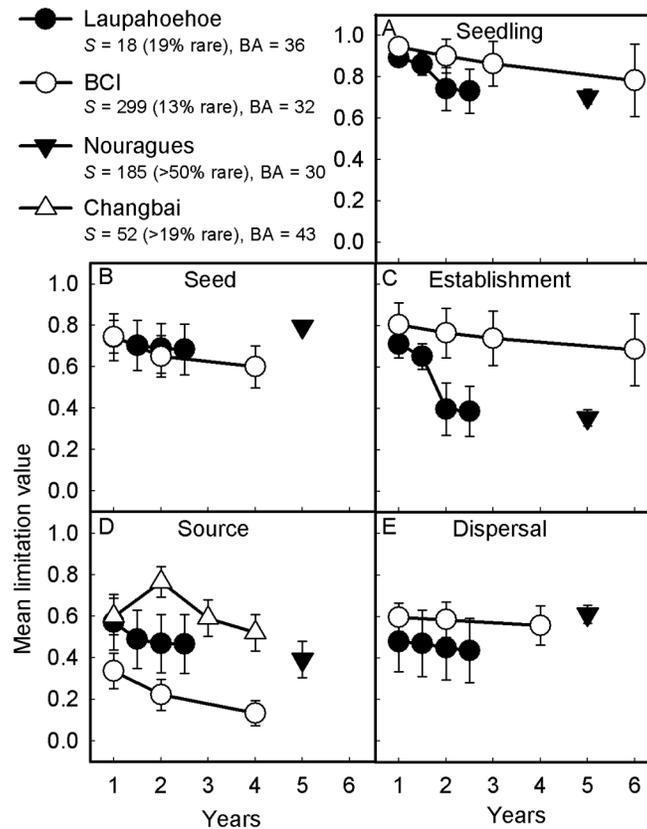
Fig. 4. Seedling recruitment limitation components (as described in Fig. 1) for three forest sites (A) seedling limitation, (B) seed limitation, (C) establishment limitation, (D) source limitation, and (E) dispersal limitation; with the mean ± SE across all species for all time intervals reported; the number of freestanding woody species ≥1 cm DBH within each FDP (S); and the basal area in $m^2 \cdot ha^{-1}$ (BA) from Bongers et al. (2001), Losos and Leigh (2004), and Chave et al. (2008). The number of species included in average ranges for each site (N) are: Laupahoehoe, Hawaii $N = 6$–12 as in Table 2; BCI, Panama $N = 15$ for seed, source, and dispersal limitations (Dalling et al. 2002) including two from Muller-Landau et al. (2002), and $N = 4$ for seedling and establishment limitations (Muller-Landau et al. 2002); Nouragues, French Guiana $N = 14$ (only 5 yr averages were reported; Norden et al. 2009); Changbai, China $N = 25$ (temperate forest; Li et al. 2012).

seed limited ($L_{seed} = 1$), including five of the species with seedlings found in seedling plots. Consequently, L_{seed} may scale up to determine the relative abundances not only of seedlings, but also of canopy trees, which in turn determines L_{seed}, possibly establishing a positive feedback mechanism. Such tantalizing linkages between seed, seedling, and tree abundance require further confirmation because interpretations of the relative importance of recruitment limitations can be affected by study length and type. For example, L_{seed} has been found to be lower for longer field studies (Muller-Landau et al. 2002) and for experimental studies (Clark et al. 2007).

Additionally, L_{est} may be underestimated for rare species or those with extremely patchy distributions. Nevertheless, the negative linkage of L_{seed} with species abundance is strong at the scale of our study and confirms expectations from theory and other forests (Muller-Landau et al. 2002, Losos and Leigh 2004, Gravel et al. 2006).

Strong habitat associations and niche overlap for seedlings in low-diversity Hawaiian forest

In Hawaiian wet forest, most species were strongly associated with specific ranges of irradiance and/or substrate types. However, all species were positively associated with more

Table 3. Extent of habitat associations (percentage of species) in tropical forests with the number of species tested in parentheses, plot location and size, and the analysis used to test significance of habitat associations.

Habitat variable	Site	S	Habitat associations (%)	Analysis	Source
Aboveground					
Light	Laupahoehoe, Hawaii	18	57 (7)	χ^2 randomization	1
	Gunung Palung, Borneo	325	17 (45)	Logistic regression	2
	Yasunìì, Ecuador	1114	13 (15)	Logistic regression	3
Belowground					
Substrate	Laupahoehoe, Hawaii	18	86 (7)	χ^2 randomization	1
Topography	BCI, Panama	299	24 (80)	Torus translation	4
Physiography	Gunung Palung, Borneo	325	23 (22)	χ^2 randomization	2
Topography	Yasunìì, Ecuador	1114	71 (83)†	Torus translation	5

Notes: Differences in light across microhabitats directly represents availability of above-ground resources (Denslow 1980) while variation in substrate or topography are likely to affect plants through availability of below-ground resources such as soil nutrients and water (Clark et al. 1999), thus we grouped studies by whether above- or below-ground habitat variables were assessed and then sorted the studies in ascending order of species richness (S). Basal area of Gunung Palung is 43 $m^2 \cdot ha^{-1}$ (Webb 1997); and Yasunìì is 33 $m^2 \cdot ha^{-1}$ (Losos and Leigh 2004). The Gunung Palung site is comprised of 28 0.6 ha plots, while BCI and Yasunìì sites are each 50 ha FDPs. Sources: 1, this study; 2, Webb and Peart (2000); 3, Queenborough et al. (2007); 4, Comita et al. (2007); 5, Metz (2012).

† Averaged over 8 yrs of data collection.

than one habitat category, and species' habitat associations overlapped substantially. Our results are consistent with studies in high-diversity forests in which new recruits had weak habitat specificity (Kanagaraj et al. 2011) or in which a number of tree species shared preferred habitats (Webb and Peart 2000). The co-occurrence of strong habitat associations and high niche overlap found here for seedling species may be a typical pattern and should be further examined across forests and life-stages. More generally, we note that niche differentiation is often inferred from the existence of habitat associations (Hutchinson 1957, Whittaker 1965, Tilman 1987, Chesson 2000, Wright 2002, Yamada et al. 2006, Chen et al. 2010, Chuyong et al. 2011). However, given the potential commonness of overlapping habitat preferences we suggest caution in treating these as equivalent since they may often be decoupled.

There are several possible explanations for the substantial niche overlap at the scale observed in low-diversity Hawaiian forest. A first explanation may relate to the specifics of the forest community in which we conducted the study. For example, the strong association of Hawaiian forest seedlings with tree ferns resulted in significant overlap in species' substrate preference. This important role of tree ferns for seedling establishment has previously been indicated for other forests in Hawaii and New Zealand (Scowcroft 1992, Coomes et al. 2005, Gaxiola et al. 2008, Cole et al. 2012). Tree ferns are a significant component of Hawaiian wet forests

(Kitayama et al. 1997). Their trunks are composed of adventitious roots which trap organic matter; therefore this substrate may increase plant water and nutrient availability (not measured in our study). Further, the Hawaiian forest might have a particularly limited range of acceptable substrates because of invasive feral pig-disturbance to soil (Drake 1992, LePage et al. 2000, Baltzer and Thomas 2010) and tree ferns can provide a refuge from soil disturbance caused by invasive pigs (Cole et al. 2012). High native and non-native swine densities are common in many forests, including other FDPs, and are known to significantly affect native tree regeneration (Barrios-Garcia and Ballari 2012). Though we observed feral pig activity in some seedling plots, we did not directly investigate the linkage between pig presence and substrate. According to the principle of competitive exclusion, specialization on tree ferns could lead to reduced diversity over time. Experimental assessment of growth and survival on tree ferns versus soil would be extremely valuable to determine how different substrates affect recruitment to larger size classes.

Other explanations for the high niche overlap observed in Hawaiian forest may be derived from the unique properties of these forests. Hubbell (2006) predicted that a low-diversity system should have more predictable pairwise interspecific interactions between few species and thus particularly strong niche differentiation. Although the forest we studied has only 18 tree

species, diversity might still be too high for the effect predicted by Hubbell (2006) to be apparent. Additional cross-site studies would be necessary to identify a low-diversity threshold that might lead to strong niche differentiation by that mechanism. Another explanation is that species may require more time to evolve niche differences than has been available in the assembly of the Hawaiian forest community. However, given that the majority of native Hawaiian species radiated from ancestral colonists into endemic species (Carlquist 1985, Price and Clague 2002, Givnish et al. 2009), it seems reasonable to expect that there has been adequate time for habitat niche differentiation in response to interspecific competition and habitat heterogeneity to also occur (Lankau 2011).

Another explanation may relate to the particular limitations of our study design. Plants respond to many resources and we might have found niche differentiation had we measured species associations with, for example, soil moisture or nutrients (Baltzer et al. 2005, Baraloto et al. 2006, Baraloto et al. 2007, Comita and Engelbrecht 2009). Indeed, while light adaptation is generally a major axis of variation among species in most forests (Augspurger 1984, Denslow 1987, Poorter 1999, Hubbell 2006), plants tend to show the strongest differentiation in relative performance at very low irradiances (Kobe 1999), and the Laupahoehoe FDP had relatively high understory irradiance (6.4% transmitted irradiance versus 0.01–3.0% in other evergreen rainforests; Coomes and Grubb 2000). Further, although niche differences are expected to be apparent at the seedling stage (Grubb 1977), we might find more evidence of niche differences in larger size classes which reflect cumulative survival responses to environmental conditions (Comita et al. 2007). Future studies can provide valuable insight into regeneration and community assembly processes by disentangling and elucidating these mechanisms.

Finally, there is a strong likelihood that the high niche overlap we observed is related to the high seed limitation of most species, and on average, of the entire community. Theories propose that all limitations on recruitment, especially L_{seed}, should equalize interspecific interactions and enable species coexistence in the absence of niche differences (Tilman 1994,

Hurtt and Pacala 1995, Chesson 2000, Hubbell 2005). Thus, our results may be taken as one case in support of strong recruitment limitations permitting coexistence without strong niche differentiation among most species in low-diversity forest.

Comparisons of habitat associations and limitation indices among tropical forests

Our results were partially aligned with theoretical expectations for how recruitment limitations and the frequency of habitat associations may vary across forests varying in diversity and structure (Table 1). Our comparisons provided some evidence in support of the prediction that habitat associations would be higher in forests with low species diversity (Table 1, P2B). This effect may have overwhelmed the tendency for a similar importance of habitat for establishment in forests with similar overall structure (Table 1, P1). However, the low diversity of Hawaiian forest was not a complete explanation for even the greater light habitat associations because the predicted mechanism for increased associations in low-diversity forest was increased niche differentiation due to highly predictable interspecific interactions among relatively few species (Hubbell 2006), whereas instead we found high niche overlap. The strong variation in seedling recruitment limitations among species within each FDP, rather than among FDPs, implies that variation in species' life-history characteristics may influence the relative importance of recruitment limitations more so than variation in ecosystem characteristics. Thus, regeneration limitations appear analogous to species traits such as leaf structure and processes such as litter decomposition, in that they may vary more among species within an ecosystem than across ecosystems (Sack and Holbrook 2006, Cornwell et al. 2008).

A high frequency of habitat associations in low-diversity forest was also predicted by a lower proportion of rare species in low-diversity forest (Table 1, P3). The hypothesized mechanism for that effect was that a lower L_{seed} would increase the potential for species competitive interactions and therefore increase the relative importance of habitat differentiation. Instead, the available data showed that L_{seed} did not co-vary with diversity among forests (Fig. 4). Thus, P3

could not be accepted as the explanation for the strong habitat associations in Hawaiian forest. Indeed, mean L_{seed} in Hawaiian forests was similar to mean values from other tropical forests, while L_{est} was lower, which was contrary to this prediction (Fig. 4). We note that the BCI and Laupahoehoe FDPs had a similar proportion of rare species, and thus based on species rarity we would not have expected dramatic differences to arise between these two forests. Further, Nouragues has an extremely high proportion of rare species (>50%; Bongers et al. 2001) but mean L_{seed} across species was only slightly higher than in Hawaiian forest. We note that the relative abundance of pollinators, dispersers, and seed predators in Hawaii versus other forests is unknown, and that these factors may act in concert with diversity and species rarity to equalize L_{seed} among forests.

Seedling habitat niche overlap might have been similar among forests, but we were unable to evaluate this because seedling niche overlap was not analyzed in the other studies in our comparison group. We note that a greater proportion of species with significant habitat associations does not necessarily indicate greater differentiation among species in their preferred habitats. Indeed, a number of recent studies found that habitat associations overlap among species within high-diversity forests, which may be expected given the large number of species and relatively few habitat categories typically examined. For instance, at BCI all but one of 30 species with significant positive associations were associated with more than one habitat at the seedling stage (Comita et al. 2007). Queenborough (2007) concluded that strict habitat partitioning alone could not account for the coexistence of the 16 Myristicaceae species examined in Yasuniì, despite evidence of habitat associations. Potts et al. (2004) examined tree elevational distributions using an index of niche overlap comparable to ours, and found overlaps ranging from 0.62 ± 0.07 to 0.70 ± 0.05 SE; only slightly lower than the average Pianka's O among species pairs in the Laupahoehoe FDP (0.73 ± 0.04). This suggests that niche overlap in high-diversity forests could be as extensive as in low-diversity forest. Conversely, experimental studies in tropical forests have indicated substantial species differences in seedling resource responses

(Augspurger 1984, Kobe 1999, Givnish et al. 2004, Baraloto et al. 2005). Our findings point to the need for controlled cross-site studies with detailed environmental measurements and the application of consistent methods to evaluate the degree of niche overlap among species.

Comparison of seedling recruitment factors and habitat associations across forests is essential to test the generalizability of hypotheses regarding tropical forest regeneration patterns and coexistence. Thus, we argue that the comparative approach outlined in our study is valuable as a first approximation despite the lack of standardized methods across sites and few available data. We note that differences among forest sites in the number and type of species selected, the size of the plot, study duration, and/or analytical methods (for habitat association analysis) might be expected to influence comparisons. Encouragingly, our analyses found that differences among sites appeared largely robust to most of those factors. While limitation factors showed clear temporal trends, we found that site ranks among forests for limitation indices remained similar over time (Fig. 4). We do not expect that our finding of especially strong habitat associations in Laupahoehoe is due to differences in analyses since the randomization tests we employed are more conservative than torus-translation tests which found fewer associated species (Harms et al. 2001). In addition, Metz (2012) analyzed the habitat distributions of 21–110 species over an eight year period and the proportion of species with habitat associations varied by only 11% (from 66–76%) across years and did not appear to be affected by the number of species sampled. Thus, we doubt that these results are an artifact of the study duration or the number species sampled. Finally, we do not expect that differences in plot sizes drove the seedling recruitment patterns we discovered across forests; we found no obvious trend between plot size and either limitations or habitat associations (Table 3 and Fig. 4). For example, the smallest plot had the highest proportion of habitat associations for below-ground resources, followed by two 50 ha FDPs which differed by 47% (Table 3). In addition, our 4 ha FDP had L_{src} values intermediate to a 25 ha and 50 ha FDP. Thus, we propose that the variation among forests in recruitment limitations and habitat associations involves some uncertainty, but that the overall

patterns we found should be robust. Further, these first comparisons made with the available data provide a framework and stimulus to motivate further studies that can incorporate standardization of methods across a wider range of forest sites.

Conclusions and future work

To our knowledge this is the first study in low-diversity tropical forest to examine the extent of habitat associations and niche differentiation and the relative importance of seed and establishment limitations to community assembly processes. We answered three key questions for low-diversity Hawaiian wet forest and determined whether these answers were consistent with expectations from previous theory. Further, using the available published data, we examined how recruitment limitations and habitat associations vary among tropical forests. This study provides a critical first test of hypotheses linking recruitment limitations to ecosystem properties, leading to novel insights into how recruitment limitations and habitat associations vary with diversity within and among across tropical forests.

While many abiotic and biotic factors contribute to forest regeneration dynamics, this study showed that L_{seed} powerfully influenced regeneration patterns for less common species in a low-diversity forest. Further, both high-diversity and low-diversity tropical forests appeared to have similar seed limitation values when averaged across species. This was true despite substantial variation in L_{seed} among species within forests, and the dominance in Hawaiian wet forest of a species with zero seed limitation (*Metrosideros polymorpha*). The strong influence of L_{seed} across tropical forests likely contributes to species coexistence as a factor that leads to reduced competition, consistent with hypotheses of the maintenance of coexistence for species that overlap in habitat distributions, as found in Hawaiian forest. The degree to which the equalizing influence of strong L_{seed} may enable species to overlap in their preferred habitats in high-diversity forests, as indicated here for Hawaiian forest, requires further investigation.

Our results are an important step towards explicitly linking species diversity with recruitment limitations and habitat associations. Comparisons across tropical forests provide insight into how well current hypotheses from coexistence theory predict differences among ecosystems, but suggest that forest-specific mechanisms for recruitment limitations and habitat associations must be further investigated to explain these general patterns. As the first study to attempt to synthesize and extend current theories toward testable predictions for low-diversity forest, our findings open the discussion for further research and point to the necessity of future studies on recruitment limitations to better understand forest composition and dynamics across a wide range of forests.

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SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. Life history information for species found in seedling plots and/or seed traps in Hawaiian wet forest: life forms (C: canopy tree, M: midstory tree, S: shrub); adult tree relative abundance (RA) was calculated as number of individuals of species$_i$/number of individuals of all species.

Species	Auth.	Family	Life form	Propagule type	Seed size (mm)	Dispersal syndrome	RA
Acacia koa	A. Gray	Fabaceae	C	Pod	8.7	Gravity	1.58
Broussaisia arguta	Gaudich.	Hydrangeaceae	S	Fruit	1	Bird	3.04
Cheirodendron trigynum	(Gaudich.) A. Heller	Araliaceae	M	Fruit	4	Bird	37.2
Clermontia parviflora	Gaudich. ex A. Gray	Campanulaceae	S	Fruit	0.7	Bird	0.21
Coprosma rhynchocarpa	A. Gray	Rubiaceae	M	Fruit	5.3	Bird	10.9
Hedyotis hillebrandii	(Fos.) Wagner & Herbst	Rubiaceae	S	Fruit	1.5	Bird	0.49
Ilex anomala	Hook. & Arn.	Aquifoliaceae	M	Fruit	2	Bird	10.8
Leptecophylla tameiameiae	(Cham. & Schltdl.) C. M. Weiller	Ericaceae	S	Fruit	3.5	Bird	0.02
Metrosideros polymorpha	(H. Lév.) H. St. John	Myrtaceae	C	Capsule	1.65	Wind	29.5
Myrsine lessertiana	A. DC.	Myrsinaceae	M	Fruit	4	Bird	2.65
Perrottetia sandwicensis	A. Gray	Celastraceae	M	Fruit	1.2	Bird	0.39
Vaccinium calycinum	Sm.	Ericaceae	S	Fruit	0.75	Bird	2.86

Notes: Nomenclature follows Wagner et al. (1999) and Stevens (2001–). Seed lengths are from the Bishop Museum Hawaii Ethnobotany Online Database (http://173.201.252.229/ethnobotanydb/ethnobotany.php). The three most common species appear in bold.
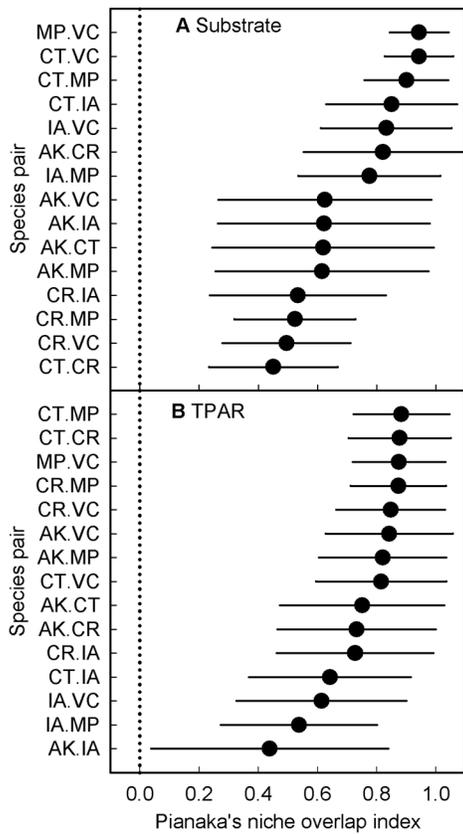
Fig. A1. Light and substrate niche overlap for 15 pairwise combinations of Hawaiian wet forest seedling species with adequate sample sizes; circles represent bootstrapped means (1000 iterations) and error bars represent 95% CIs; all values with CIs not overlapping zero represent significant niche overlap for that species pair; sorted in order of highest to lowest niche overlap; species codes as in Table 2.