

Density-dependent seedling mortality varies with light availability and species abundance in wet and dry Hawaiian forests

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Summary

1. Conspecific density may contribute to patterns of species assembly through negative density dependence (NDD) as predicted by the Janzen-Connell hypothesis, or through facilitation (positive density dependence; PDD). Conspecific density effects are expected to be more negative in darker and wetter environments due to higher pathogen abundance and more positive in stressful, especially dry, environments (stress-gradient hypothesis). For NDD to contribute to maintaining diversity, it should be apparent at the community-wide scale as a negative correlation between seedling recruitment, growth or survival and conspecific adult abundance (community compensatory trend; CCT).

2. We examined seedling survival in relation to con- and heterospecific adults within 10 m and con- and heterospecific seedlings within 1 m for 13 species within two 4-ha permanent plots located in dry and wet forests in Hawaii. We also examined interactions between conspecific density and light and species' commonness.

3. For all species pooled, adult conspecific effects were positive (PDD) in both dry and wet forests, though they were stronger in the dry forest. In contrast, seedling conspecific effects were negative (NDD), though only significantly so in the wet forest.

4. The strength and direction of density effects varied with understorey light such that seedlings had the highest survival where both adult conspecific density and light were high but the lowest survival where seedling conspecific density and light were high.

5. In the wet forest, the most common species showed positive effects of adult conspecifics, but the less common species showed negative adult conspecific effects. We found mixed evidence for a CCT: seedling survival was positively correlated with basal area, but negatively correlated with tree density (stems ha⁻¹). Thus, it remains unclear whether NDD is a diversity-maintaining mechanism in these forests.

6. *Synthesis.* Overall, we found that positive conspecific effects influenced seedling mortality patterns more than negative interactions did, even in tropical wet forest where NDD is predicted to drive species' abundances. Additionally, the strength and direction of density effects varied with forest type, PAR, and species' abundance, underscoring the need to consider abiotic factors and species' life-history traits in tests of density dependence hypotheses.

Key-words: community compensatory trend, density dependence, determinants of plant community diversity and structure, facilitation, Janzen-Connell hypothesis, regeneration dynamics, seedling ecology, tropical dry forest, tropical wet forest

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Introduction

Ecologists continue to debate the mechanisms that maintain diversity and drive spatial patterns of species abundance, in particular, the extent to which negative versus positive interactions influence the regeneration of forest trees. The Janzen-Connell hypothesis (JCH; Janzen 1970; Connell 1971) posits that negative density dependence (NDD) occurs where predators and pathogens specialize on a given species such that nearby conspecific juveniles suffer due to proximity to adults attracting enemies, which will reduce recruitment where nearby conspecific adult and/or juvenile densities are high. This mechanism may maintain species diversity by decreasing population growth rates for common species, thereby providing an advantage to rare species (Volkov *et al.* 2005) and was proposed as an explanation for how plant species in tropical forests maintain high diversity given low environmental variation. Janzen (1971) further theorized that NDD would be absent in low-diversity forest because they contain too few species to harbour highly specialized predators and pathogens. In particular, he predicted that a common Hawaiian tree species, *Acacia koa* A. Gray, would show low NDD due to few specialized seed predators. Although the majority of studies testing this hypothesis have been conducted in tropical forest, numerous studies show that NDD may be as strong in temperate as in tropical forest (meta-analysis in Comita *et al.* 2014), decoupling the presumed association between NDD and diversity. However, comparing forests that vary in diversity but that also vary in climate obscures the interpretation of whether the JCH is a function of diversity *per se* (e.g., tropical high-diversity versus temperate low-diversity). Alternatively, positive density dependence (PDD) can arise if conspecific density facilitates seedling survival or if habitat preferences lead to clustering of conspecifics. We aimed to examine the broader application of these theories to seedlings within and across forests varying in light and water availability. Thus, we tested for negative and positive effects of conspecific density on tree seedling survival in wet and dry Hawaiian forest and how these might vary with forest type, understorey light, and species' relative abundance at the local (1–25 m) and community (4-ha) scale. We focused our study on seedling survival because density effects are usually strongest at this life stage (Comita *et al.* 2014) and because it is a major bottleneck that determines future population growth and forest composition (Leck, Parker & Simpson 2008).

Patterns of density dependence may shift with local and regional environmental factors (Aiba & Nakashizuka 2007; Comita *et al.* 2009). A recent global meta-analysis of density dependence found a weak correlation between precipitation and density effects, with density effects becoming generally more negative with increasing precipitation across sites; this association was stronger in tropical than temperate locations (Comita *et al.* 2014). This global pattern leads to the prediction that conspecific density dependence would be more negative in wet forest than dry forest. The explanation for this effect may be that seedlings in low light in moist sites suffer higher mortality due to pathogens because pathogens are more abundant or virulent

in these environments (Augspurger 1984b; Goodale *et al.* 2014). In contrast, a different mechanism might lead to *positive* density effects in dry forests, if, as predicted from the 'stress-gradient hypothesis', facilitation increases and competition decreases with higher abiotic stress, as might be found in strongly water-limited environments (Bertness & Callaway 1994; Jia *et al.* 2011). However, shaded locations near adult conspecifics in dry forest may also create refuges for pathogens where NDD would be high. Furthermore, seedlings in dry forest may be more susceptible to pathogens because they are already under stress (Bunker & Carson 2005; Chase 2007; Brooker *et al.* 2008; Fajardo & McIntire 2011; Jia *et al.* 2011). Thus, numerous hypotheses can be generated for the complex interactions of biotic neighbourhood, regional climate, and understorey light conditions, though few density dependence studies explore these interactions.

Density dependence may also vary with species abundances within forests. For example, common species may experience stronger effects of NDD because they are more likely to experience high conspecific density (Lin *et al.* 2012). However, less common or rare species have been shown to experience stronger NDD than common species in some circumstances (Hubbell *et al.* 2001; Bunker & Carson 2005; Queenborough *et al.* 2007; Comita *et al.* 2010; Kobe & Vriesendorp 2011; Lin *et al.* 2012), and might contribute to species rarity. When NDD acts at the community scale, overall abundance is correlated with higher *per capita* mortality, resulting in a *community-level compensatory trend* (CCT) that contributes to coexistence by favouring population growth of less common species (Connell, Tracey & Webb 1984; Webb & Peart 1999). A CCT will be apparent as a negative correlation between community-wide species abundance (e.g., basal area or individuals ha⁻¹) and seedling performance (e.g., growth or survival).

Hawaiian dry and wet forests provide a novel ecological study system to test hypotheses for how density dependence interacts with regional and local environmental variables. First, Hawaiian forests are structurally similar to continental tropical forests, but support much lower species diversity due to Hawaii's extreme geographic isolation and young geological age (Ostertag *et al.* 2014). Second, Hawaii Island, where these plots are located, contains extreme climatic variation within a relatively small area, facilitating comparison of density dependence between dry and wet forests. In this study, we tested predictions that density effects would be: (i) negative in the wet and potentially positive in the dry forest; (ii) most negative under lower light; (iii) more negative for the less common species at local (1–25 m) and community-wide (4 ha) scales.

Materials and methods

DATA COLLECTION

We conducted this study in the Laupahoehoe and Palamanui Forest Dynamics Plots (FDPs) which are part of the Hawaii Permanent Plot Network (HIPNET; www.hippnet.hawaii.edu) and the Smithsonian

Tropical Research Institute Center for Tropical Forest Science plot network (CTFS-ForestGEO; www.ctfs.si.edu; Anderson-Teixeira *et al.* 2015). We list relevant characteristics of both FDPs in Table 1. As elsewhere in the tropics, the forests where the plots were established are affected by land use history, but we selected these sites to provide the best available representation of each forest type, although the dry forest contains more invasive species than the wet forest, neither have any evidence of previous fire or logging (Ostertag *et al.* 2014). In each FDP, we established a grid of 64 seedling census stations each comprised of three 1-m² seedling subplots ($n = 192$). For each seedling (defined as native woody species < 1 m height) in seedling subplots, we recorded condition (alive/dead) for 2.5 years in the wet forest (from winter 2008 to summer 2011) and 1.5 years in the dry forest (from winter 2010 to summer 2012). We analysed data for species that were found in $n \geq 3$ subplots, which included 300 individuals of five species in the dry forest and 3148 individuals of eight species in the wet forest (for species names and information see Supporting Information, Table S1A,B). We measured percentage transmitted diffuse photosynthetically active radiation (PAR, %) at each seedling plot using paired LI-COR quantum sensors (LI-COR, Lincoln NE) below and above the forest canopy on uniformly overcast days (Montgomery & Chazdon 2002; Inman-Narahari *et al.* 2014). Further details on plot establishment, diversity, and structure are available in Appendix S1, online at www.hipnet.hawaii.edu and in (Ostertag *et al.* 2014).

DATA ANALYSIS

As an index of adult tree density, we calculated the sum of the basal area of trees ≥ 1 cm stem diameter at standard height (DSH, 1.3 m)

Table 1. Properties of two 4-ha forest dynamics plots on Hawaii Island; errors represent 1 SE from the mean

Property	Palamanui dry forest	Laupahoehoe wet forest
Location	19°44' N, 155°59' W	19°55' N, 155°17' W
Elevation	240 m	1120 m
Mean annual precipitation†	835 mm	3440 mm
Mean annual temperature	20 °C‡	16 °C§
Number of tree species	15	21 (incl. 3 tree ferns)
Number of seedling species	5 ($n = 300$)	8 ($n = 3148$)
Seedling density (seedlings m ⁻²)	0.96 ± 0.23	9.32 ± 1.37
Dominant canopy tree species	<i>Diospyros sandwicensis</i> (Ebenaceae)	<i>Metrosideros polymorpha</i> (Myrtaceae)
Subcanopy dominant	<i>Psydrax odorata</i> (Rubiaceae)	<i>Cibotium</i> spp. (Cibotiaceae)
BA (m ² ·ha ⁻¹)	8.64	67.3
Mean PAR (%)	47 ± 1.8	6.4 ± 0.29
PAR categories		
Low (%)	< 37	< 4
Medium (%)	≥ 37, < 75	≥ 4, < 7
High (%)	≥ 75	≥ 7

†Giambelluca *et al.* (2013).

‡wrc.dri.edu.

§Crews *et al.* (1995).

within 25 m of each seedling plot at 2 m intervals centre divided by the distance of each tree from seedling plot centres ($A = \sum$ (basal area/distance); Comita & Hubbell 2009). This index integrates tree size and distance from focal seedlings. We present results for the effects of density within 10 m as this is a distance found to be important in previous studies of NDD (Comita & Hubbell 2009; Metz, Sousa & Valencia 2010). We calculated this index separately for adult conspecifics (A_{CON}) and adult heterospecifics (A_{HET}). Within each 1 m² subplot, we calculated conspecific seedling densities (S_{CON}) and heterospecific seedling densities (S_{HET}) for each focal seedling. We categorized the two most common species in each forest type as 'most common' and the remaining species as 'less common'. We calculated community-wide tree density as the number of individual trees ≥ 1 cm DSH within each 4 ha FDP (stems ha⁻¹) and the basal area (BA) of these trees as the estimated area of each stem at DSH (m² ha⁻¹).

To test for density dependence, we modelled individual seedling survival as a function of con- and heterospecific adult and seedling density using generalized linear mixed-effects models (GLMM; see Appendix S1 for further details of analysis methods). We analysed seedling survival as the probability of survival of each individual within the first year after tagging. To test for the effects of forest type, PAR, and species abundance (most versus less common), we included these factors as interaction terms with each of the four density variables (S_{CON} , S_{HET} , A_{CON} and A_{HET}) in separate GLMM analyses. We tested the effect of each factor on the patterns of density dependence by determining the significance of the interaction terms between density variables and each factor. To identify a community compensatory trend (CCT), we used GLMM analysis to test correlations between seedling survival and tree density (stems ha⁻¹) and BA at the community-wide (i.e., 4-ha plot) scale (Chen *et al.* 2010; Lin *et al.* 2012).

We conducted all analyses using R 3.1.1 (R Core Team, 2014). We fitted GLMM models using the *glmer* function in the LME4 package version 1.1-7 (Bates *et al.* 2014) and obtained predicted effects from GLMM models using the LSMEANS package version 2.05 (Lenth 2014).

Results

DENSITY DEPENDENCE IN DRY AND WET HAWAIIAN FORESTS

The dry and wet forests differed in several striking ways relating to microclimate and canopy tree and understorey seedling abundance and composition (Table 1). First, PAR was more than sevenfold higher in dry than in wet forest ($t_{201} = 22$, $P < 0.001$; Table 1). Second, the mean plot-wide BA of adults that were also found as seedlings was 5.4-fold greater in wet versus dry forest (Table 1). Third, none of the species found as seedlings in the dry forests were also found as seedlings in the wet forest (Table S1A,B). Fourth, seedling density (seedlings m⁻²) was nearly 10-fold higher in the wet than the dry forest ($t_{202} = -6.03$, $P < 0.001$; Table 1). Finally, seedling heights at the initial survey were on average almost fourfold greater in dry than in wet forest ($t_{310} = 8.81$, $P < 0.001$; Table S1A,B).

Despite major differences between the dry and wet forests with respect to environmental conditions, species composition, and adult and seedling density, overall seedling survival

did not differ between dry and wet forests when averaged across species ($t_{13,1} = -1.65$, $P = 0.124$) or individuals ($t_{366} = -1.81$, $P = 0.071$; Table S1A,B). Mean survival for each species ranged from 0 to 100% in both forest types (Table S1A,B), and species differences were significant only in the wet forest (dry forest $P = 0.701$; wet forest $P < 0.001$).

We found evidence for both negative and positive density dependence (NDD and PDD, respectively) and these effects varied with forest type. Adult conspecific density (A_{CON}) was positively correlated with overall seedling survival in both forest types (Figs 1a and S1). The effect size (log odds ratio; LOR) of A_{CON} was 10-fold larger in dry than in wet forest (dry forest: LOR = 1.70 ± 0.38 SE, $P < 0.001$; wet forest: LOR = 0.15 ± 0.05 SE, $P < 0.001$, $A_{CON} \times$ forest plot interaction $P < 0.001$). Predicted seedling survival increased by an average of 9.1% vs. 5.0% for every 10% increase in A_{CON} in the dry versus the wet forest, respectively. Seedling survival was negatively correlated with seedling conspecific density (S_{CON}) in both forests (although in dry forest large variances made this effect not significant), and effects differed between wet and dry forests (Figs 1b and S1; dry forest: LOR = -0.20 ± 0.25 SE, $P = 0.410$; wet forest: LOR = 0.26 ± 0.06 SE, $P < 0.001$, $S_{CON} \times$ forest plot interaction $P < 0.001$). In contrast, heterospecific adult density (A_{HET}) effects were negative in both forests (Fig. S1; dry forest: LOR = -0.39 ± 0.17 SE, $P = 0.024$; wet forest: LOR = -0.25 ± 0.09 SE, $P = 0.005$; $A_{HET} \times$ forest plot interaction $P = 0.001$). Seedling survival was not correlated with heterospecific seedling density (S_{HET}) in either forest (Fig. S1). Conspecific density generally had stronger effects than heterospecific density in Hawaiian forest (Fig. S1), indicating that conspecific density effects differed from interspecific competition.

The effects of adult con- and heterospecific density varied with spatial scale within each forest (Fig. S2). In both forests, the effect sizes of adult density steadily increased with distance. Indeed, the effects of conspecific adults became more strongly positive, whereas those for heterospecific adults

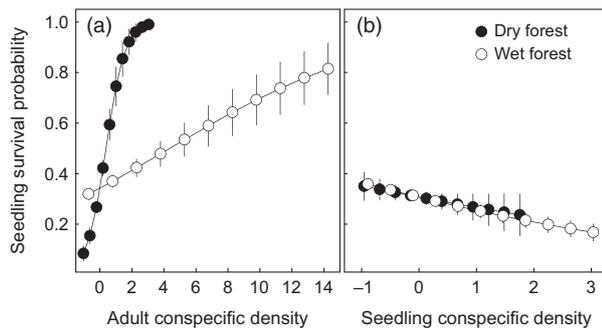


Fig. 1. Seedling survival probability as a function of (a) adult conspecific density within 10 m (A_{CON}), and (b) seedling conspecific density within 1-m² seedling subplots (S_{CON}) in Palamanui dry forest and Laupahoe wet forest; lines represent predicted survival from GLMM analysis (parameters summarized in Figure S1); error bars represent SE; note different x-axis scales; all density \times forest interaction terms $P < 0.001$.

became more strongly negative with distance. Conspecific adult (A_{CON}) effects were significant from 3 to 25 m in the dry forest and from 7 to 25 m in the wet forest and heterospecific adult (A_{HET}) effects were significant from 9 to 25 m in the dry forest and from 7 to 25 m in the wet forest. As with the density dependence effects presented within 10 m, effect sizes for conspecifics were much larger for the dry than the wet forest.

INTERACTION OF DENSITY DEPENDENCE WITH UNDERSTOREY LIGHT

Seedling density dependence interacted with understorey with light within forests. The effects of PAR as a continuous variable showed strong positive effects in relation to A_{CON} in both the dry (PAR LOR = 3.20 ± 0.73 SE, $P < 0.001$) and the wet forest (PAR LOR = 3.78 ± 1.04 SE, $P < 0.001$). However, PAR as continuous variable showed no significant effect in relation to S_{CON} in the dry forest ($P > 0.05$) and it had a strong negative effect in the wet forest (log odds ratio = -3.73 ± 1.12 SE, $P < 0.001$). When examined as a categorical variable, A_{CON} effects were most strongly positive in high PAR (Figs 2a,b and S3) whereas S_{CON} effects were most negative in high PAR (Figs 2c,d and S3).

DENSITY DEPENDENCE, SPECIES ABUNDANCE AND COMMUNITY COMPENSATORY TRENDS

The effects of A_{CON} differed between the two most common species and the remaining less common species in the wet forest: seedling survival in relation to A_{CON} showed PDD for the more common species and NDD for the less common species (Figs 3 and S1). The effects of S_{CON} also tended to be more negative for the less common than for the more common species in the wet forest. In the dry forest, A_{CON} effects did not differ substantially with species commonness; the overall trends for S_{CON} differed with commonness, but mean effects were not significant (Fig. S1).

When seedling survival was analysed as a function of species abundance at the community-wide scale (4-ha plot), we found mixed evidence for a community compensatory trend (CCT) in both forests. For all species pooled within each forest, seedling survival decreased weakly with increased community-wide tree density (stems ha⁻¹), whereas it increased with strongly basal area (BA) (Table 2). When we repeated the analysis on the most common and the less common species separately, we found similar results (not shown).

Discussion

DENSITY DEPENDENCE IN HAWAIIAN FOREST

We found strong evidence of both positive and negative density-dependent seedling survival in dry and wet Hawaiian forest. Additionally, we found evidence that the magnitude and direction of these patterns varied with forest type, light and species abundance. Our results support earlier studies showing

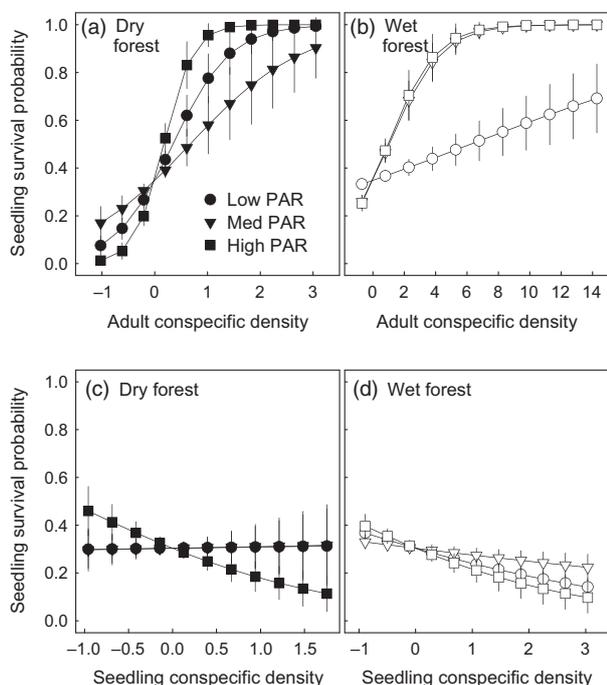


Fig. 2. Seedling survival as a function of adult conspecific density (A_{CON}) seedling conspecific (S_{CON}) at high, medium and low transmitted photosynthetically active radiation (PAR; category ranges in Table 1) in Palamanui dry forest (a, c) and Laupahoe wet forest (b and d); lines represent predicted values from GLMM analysis on categorical variables (parameters summarized in Figure S3); error bars represent SE; note different x-axis scales.

that density dependent effects are not limited to high diversity tropical forests (Comita *et al.* 2014), and extend the generality of seedling density dependence to low diversity tropical forest. Our results show that the effects of density on seedling survival interact significantly with climate, abiotic environment and species characteristics.

COMPARISON BETWEEN DRY AND WET FORESTS

Overall, the effects of adult density on seedling survival were stronger in the dry than in the wet forest; the positive density dependence (PDD) in relation to adult conspecifics was nearly twofold higher in the dry than in the wet forest. The PDD in both forests may be accounted for by similar preferences of conspecific adults and seedlings for habitats that support higher survival and/or by facilitation whereby conspecific adults modify local environments to favour conspecific seedling survivorship. In the wet forest, the PDD may arise from similar preferences of adults and seedlings of given species (e.g., topographic associations), or the sharing of beneficial biotic interactions (e.g., mycorrhizas), whereas in the dry forest, adult conspecifics additionally would facilitate seedling survival through shading, which lowers heat and water stress (Sack 2004; Semchenko *et al.* 2012), and many seedlings establish in pockets of organic soil that form around large adult trees (pers. obs.). The greater PDD in the dry forest was generally consistent with the stress gradient hypothesis, which predicts increased facilitation in stressful habitats (Bertness & Callaway

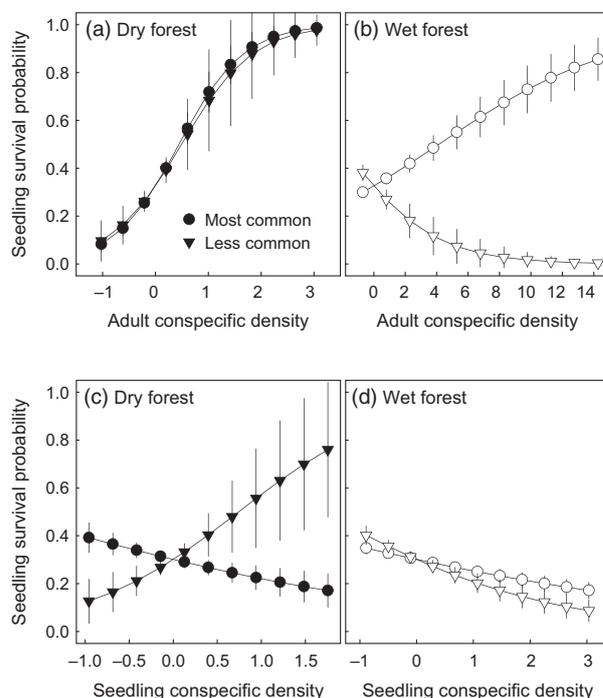


Fig. 3. Survival of most common and less common seedlings as a function of adult conspecific density within 10 m (A_{CON}), and seedling conspecific density within 1-m² seedling subplots (S_{CON}) in Palamanui dry forest (a, c) and Laupahoe wet forest (b and d); lines represent predicted values from GLMM analysis (parameters summarized in Figure S1); error bars represent SE; note different x-axis scales.

Table 2. Relationships between seedling survival and community-wide (4-ha plot) species abundance measured as tree density (stems ha⁻¹) and basal area (m² ha⁻¹) in dry forest (Palamanui) and wet forest (Laupahoe) modelled using GLMM analysis with all species pooled; effects reported as log odds ratios where negative values represent a negative relationship among variables

Tree abundance metric	Dry forest			Wet forest		
	Log odds ratio	SE	P	Log odds ratio	SE	P
Tree density	-0.766	0.187	< 0.001	-0.309	0.05	< 0.001
Basal area	2.308	0.491	< 0.001	0.734	0.065	< 0.001

1994; Jia *et al.* 2011), and/or may reflect a greater pathogen-induced mortality counteracting the PDD in wet than in the shady, moist wet forest (Augsburger 1984a,b; Coley & Barone 1996). Notably, in contrast with conspecifics, adult heterospecifics had consistently negative effects. Our results differ from a tropical dry forest study in India of 1–10 cm diameter trees that showed strongly negative density-dependent survival in relation to adult conspecifics (John *et al.* 2002).

Seedling–seedling interactions supported our prediction that density dependence would be more negative in the wet than the dry forest. Our results differ from those of recent studies

in a seasonal tropical rainforest showing that local-scale negative density dependence is stronger in dry than wet seasons (Lin *et al.* 2012), but consistent with a recent meta-analysis showing higher NDD with increasing precipitation (Comita *et al.* 2014). Further study is needed to determine whether these patterns result from increased predators and pathogens in wet versus dry forest, or from higher intraspecific competition in wet forest where overall seedling density was also higher. There may also be unexplored factors unique to Hawaii due to their isolation or changes due to human influence (e.g., loss of dispersers and introduced predators and pathogens), highlighting the importance of conducting replicate studies in a variety of ecosystems.

INTERACTIONS BETWEEN PLANT DENSITY AND PAR

Photosynthetically active radiation (PAR) influenced seedling responses to conspecific density in complex ways. Seedlings survived best where both PAR and A_{CON} were highest in both forests, whereas S_{CON} negatively affected seedling survival in high PAR. Higher PDD in high PAR suggests that fungal pathogens are important mechanisms of density-dependent mortality (Connell, Tracey & Webb 1984) because seedlings have lower pathogen-induced mortality in higher irradiance (Augspurger 1984a,b). Negative responses to seedling density in high PAR could be due to intraspecific competition, which would be consistent with the stress-gradient hypothesis that competition increases in high resource environments (Bertness & Callaway 1994; Jia *et al.* 2011). Sites with higher light also tended to have higher overall seedling density, especially in the wet forest, which may intensify competition (Inman-Narahari *et al.* 2013). However, the negative correlation between seedling survival and density contrasts with earlier studies showing that small seedlings scarcely interact in tropical rainforests (Paine *et al.* 2008). Thus, increasing PAR intensified density dependence within both forests, though differently in relation to adult versus seedling effects. Our findings differ from those of Comita *et al.* (2009), who tested the interaction between adult conspecific density dependence and canopy openness, and found no significant interaction between these variables. However, we tested the effects of density in relation to PAR, a more direct measure of plant available light than canopy openness, which may account for the differences in results.

DENSITY DEPENDENCE FOR MOST COMMON VERSUS LESS COMMON SPECIES

In the wet forest, conspecific adult density correlated with higher seedling survival (PDD) for the most common species and lower seedling survival (NDD) for the less common species. While other researchers have also found stronger NDD for rare versus common species in both tropical (Queenborough *et al.* 2007; Comita *et al.* 2010; Kobe & Vriesendorp 2011; Lin *et al.* 2012) and temperate (Johnson *et al.* 2012) regions, Condit, Hubbell & Foster (1992) found stronger NDD for the more common tropical species. For the most

common species, high seedling densities near conspecifics may overwhelm predator and pathogen effects (i.e., a high proportion of seedlings succumb to predators and pathogens, but very high starting populations allow enough individuals to persist that higher overall densities remain near conspecifics), resulting in an overall positive association with conspecific adult density when density-dependent mortality is not overcompensating (Freckleton & Lewis 2006). However, it may be that variation among species in the direction and/or strength of density dependence varies not with large-scale abundance *per se*, but rather with local abundance (i.e., clustering) and/or functional characteristics of the tree species (e.g., life-form, seed type, leaf traits and associated pathogens/predators). For example, Connell, Tracey & Webb (1984) found NDD for understorey trees and shrubs, but not for canopy trees. In our study, the less common species (which had higher NDD) were smaller-stemmed understorey trees and shrubs and the most common species included the dominant canopy tree.

The less common understorey species comprise the majority of diversity in Hawaii and other ecosystems, and density-dependent effects on these species may be important drivers of forest diversity (Wright 2002). Thus, negative density dependence may contribute to diversity not only by reducing dominance of the most common species (Connell, Tracey & Webb 1984), but also by contributing to the rarity of a large number of less common species. For the most common species, the lack of negative density dependence may explain how the dominant species in these forests can achieve such high abundance, due to their greater survival across a wide range of locations without constraint by abundance of conspecifics.

COMMUNITY COMPENSATORY TRENDS

We found equivocal evidence for a community compensatory trend (CCT) in Hawaiian forest: seedling survival correlated negatively with community-wide density (stems ha^{-1}) of adult trees, but correlated positively with basal area. The finding of a strong positive community-wide recruitment trend with basal area was consistent with our local-scale findings of a positive correlation between seedling survival and adult conspecific density within 10 m (PDD). It is also consistent with our result that the less common species experienced NDD at the local scale if the more common species are generally favoured. We considered that the discrepancy between the effects of community-wide tree density and basal area was caused by the most dominant canopy tree in each forest having both high basal area and strong PDD, whereas the less common species tend to be smaller-stemmed trees for which the number of stems may be a better metric than basal area for quantifying density. However, removal of the large tree species from the analysis produced similar results to those with all species included. A CCT is considered evidence that negative density dependence promotes community-wide coexistence (Connell, Tracey & Webb 1984; Webb & Peart 1999). However, it is not clear if CCTs are the result of negative

density dependence or of other inherent factors controlling the survival rate or the population size of a given species. For example, a species may experience strong negative density dependence at the local scale, and yet still have an overall higher survival rate than another species that suffers high non-density-dependent mortality. Additionally, CCT theory assumes that all species have equivalent carrying capacities, ignoring that some species may be less common due to limited availability of preferred habitats such as gaps. Other studies have also reported mixed results (Queenborough *et al.* 2007; Comita *et al.* 2009; Chen *et al.* 2010; Metz, Sousa & Valencia 2010; Lin *et al.* 2012). For example, Comita *et al.* (2009) found a positive correlation between seedling survival and community-wide adult abundance (number of individuals) and a negative correlation between seedling survival and community-wide basal area – the opposite of our results. Given that the positive correlation with basal area were much stronger than the negative correlations with tree density, we expect that other mechanisms, such as niche differentiation or neutral processes, may be more important for maintaining the diversity of these forests.

CONSERVATION IMPLICATIONS

The results of our study have important implications for restoration and conservation in Hawaiian forests. Our results indicate that seedling density, light availability, and forest type should be considered when planting species for forest restoration. For example, dry forest restoration may be more successful if seedlings are planted near adult conspecifics, but where conspecific seedling density is low, especially in high light. In wet forest, planting the most common species near adult conspecifics may be beneficial, but less common (and possibly rare species) may survive better when spaced further from adult and other juvenile conspecifics.

Tropical dry forest is the most endangered ecosystem globally (Janzen 1988; Gillespie *et al.* 2011) and understanding regeneration dynamics, particularly the role of density dependence, is essential to the long-term conservation of this forest type. We found only two published studies on density dependence in tropical dry forest (John *et al.* 2002; Sullivan 2003), and these reported weak community-level NDD for trees ≥ 1 cm diameter at breast height (DBH; John *et al.* 2002) and density-dependent herbivory for *Tabebuia ochracea* saplings (Sullivan 2003). The study sites received higher mean annual rainfall (1230 mm at Mudumalai John *et al.* 2002) and 2076 mm at Guanacaste (Sullivan 2003), than the 835 mm at our Palamanui site. In addition, neither study investigated seedlings, the life stage for trees when NDD is typically highest (Silva Matos, Freckleton & Watkinson 1999; Bagchi *et al.* 2010; Metz, Sousa & Valencia 2010; Fine & Mesones 2011; Luo *et al.* 2012). This study is an important first step for understanding how mechanisms known to be important for maintaining diversity in other forests types may also operate in tropical dry forest.

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Data accessibility

Data deposited in the Dryad repository: <http://dx.doi.org/10.5061/dryad.6vd61> (Inman-Narahari *et al.* 2016).

References

- Aiba, M. & Nakashizuka, T. (2007) Variation in juvenile survival and related physiological traits among *Dipterocarp* species co-existing in a Bornean forest. *Journal of Vegetation Science*, **18**, 379–388.
- Anderson-Teixeira, K.J., Davies, S.J., Bennett, A.C., Gonzalez-Akre, E.B., Muller-Landau, H.C., Wright, S.J. *et al.* (2015) CTFS-ForestGEO: a world-wide network monitoring forests in an era of global change. *Global Change Biology*, **21**, 529–549.
- Augsburger, C.K. (1984a) Light requirements of neotropical tree seedlings – a comparative-study of growth and survival. *Journal of Ecology*, **72**, 777–795.
- Augsburger, C.K. (1984b) Seedling survival of tropical tree species – interactions of dispersal distance, light-gaps, and pathogens. *Ecology*, **65**, 1705–1712.
- Bagchi, R., Swinfield, T., Gallery, R.E., Lewis, O.T., Gripenberg, S., Narayan, L. & Freckleton, R.P. (2010) Testing the Janzen-Connell mechanism: pathogens cause overcompensating density dependence in a tropical tree. *Ecology Letters*, **13**, 1262–1269.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014) *lme4: linear mixed-effects models using Eigen and S4*. R package version 1.1-7 available at <http://CRAN.R-project.org/package=lme4>.
- Bertness, M.D. & Callaway, R. (1994) Positive interactions in communities. *Trends in Ecology & Evolution*, **9**, 191–193.
- Brooker, R.W., Maestre, F.T., Callaway, R.M., Lortie, C.L., Cavieres, L.A., Kunstler, G. *et al.* (2008) Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology*, **96**, 18–34.
- Bunker, D.E. & Carson, W.P. (2005) Drought stress and tropical forest woody seedlings: effect on community structure and composition. *Journal of Ecology*, **93**, 794–806.
- Chase, J.M. (2007) Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences*, **104**, 17430–17434.
- Chen, L., Mi, X., Comita, L.S., Zhang, L., Ren, H. & Ma, K. (2010) Community-level consequences of density dependence and habitat association in a subtropical broad-leaved forest. *Ecology Letters*, **13**, 695–704.
- Coley, P.D. & Barone, J.A. (1996) Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics*, **27**, 305–335.
- Comita, L.S. & Hubbell, S.P. (2009) Local neighborhood and species' shade tolerance influence survival in a diverse seedling bank. *Ecology*, **90**, 328–334.
- Comita, L.S., Uriarte, M., Thompson, J., Jonckheere, I., Canham, C.D. & Zimmerman, J.K. (2009) Abiotic and biotic drivers of seedling survival in a hurricane-impacted tropical forest. *Journal of Ecology*, **97**, 1346–1359.
- Comita, L.S., Muller-Landau, H.C., Aguilar, S. & Hubbell, S.P. (2010) Asymmetric density dependence shapes species abundances in a tropical tree community. *Science*, **329**, 330–332.

- Comita, L.S., Queenborough, S.A., Murphy, S.J., Eck, J.L., Xu, K., Krishnadas, M., Beckman, N. & Zhu, Y. (2014) Testing predictions of the Janzen-Connell hypothesis: a meta-analysis of experimental evidence for distance and density-dependent seed and seedling survival. *Journal of Ecology*, **102**, 845–856.
- Condit, R., Hubbell, S.P. & Foster, R.B. (1992) Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a neotropical forest. *The American Naturalist*, **140**, 261–286.
- Connell, J.H. (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. *Dynamics of Populations* (eds P.J.D. Boer & G. Gradwell), pp. 298–312. Centre for Agricultural Publishing and Documentation, Wageningen, The Netherlands.
- Connell, J.H., Tracey, J.G. & Webb, L.J. (1984) Compensatory recruitment, growth, and mortality as factors maintaining rain-forest tree diversity. *Ecological Monographs*, **54**, 141–164.
- Crews, T.E., Kitayama, K., Fownes, J.H., Riley, R.H., Herbert, D.A., Mueller-Dombois, D. & Vitousek, P.M. (1995) Changes in soil phosphorus fractions and ecosystem dynamics across a long chronosequence in Hawaii. *Ecology*, **76**, 1407–1424.
- Fajardo, A. & McIntire, E.J.B. (2011) Under strong niche overlap conspecifics do not compete but help each other to survive: facilitation at the intraspecific level. *Journal of Ecology*, **99**, 642–650.
- Fine, P.V.A. & Mesones, I. (2011) The role of natural enemies in the germination and establishment of *Pachira* (Malvaceae) trees in the Peruvian Amazon. *Biotropica*, **43**, 265–269.
- Freckleton, R.P. & Lewis, O.T. (2006) Pathogens, density dependence and the coexistence of tropical trees. *Proceedings of the Royal Society of London B: Biological Sciences*, **273**, 2909–2916.
- Giambelluca, T.W., Chen, Q., Frazier, A.G., Price, J.P., Chen, Y.-L., Chu, P.-S., Eischeid, J.K. & Delpart, D.M. (2013) Online Rainfall Atlas of Hawai'i. *Bulletin of the American Meteorological Society*, **94**, 313–316.
- Gillespie, T.W., Keppel, G., Pau, S., Price, J.P., Jaffré, T., Meyer, J.-Y. & O'Neill, K. (2011) Floristic composition and natural history characteristics of dry forests in the Pacific. *Pacific Science*, **65**, 127–141.
- Goodale, U.M., Berlyn, G.P., Gregoire, T.G., Tennakoon, K.U. & Ashton, M.S. (2014) Differences in survival and growth among tropical rain forest pioneer tree seedlings in relation to canopy openness and herbivory. *Biotropica*, **46**, 183–193.
- Hubbell, S.P., Ahumada, J.A., Condit, R. & Foster, R.B. (2001) Local neighborhood effects on long-term survival of individual trees in a neotropical forest. *Ecological Research*, **16**, 859–875.
- Inman-Narahari, F., Ostertag, R., Cordell, S., Giardina, C. P., Nelson-Kaula, K. & Sack, L. (2013) Seedling recruitment factors in low-diversity Hawaiian wet forest: towards global comparisons among tropical forests. *Ecosphere*, **4**, 1–19.
- Inman-Narahari, F., Ostertag, R., Asner, G.P., Cordell, S., Hubbell, S.P. & Sack, L. (2014) Trade-offs in seedling growth and survival within and across tropical forest microhabitats. *Ecology and Evolution*, **4**, 3755–3767.
- Inman-Narahari, F., Ostertag, R., Hubbell, S., Giardina, C., Sack, L. & Cordell, S. (2016) Data from: Density-dependent seedling mortality varies with light availability and species abundance in wet and dry Hawaiian forests. *Dryad Digital Repository*, doi:10.5061/dryad.6vd61.
- Janzen, D. (1970) Herbivores and the number of tree species in tropical forests. *The American Naturalist*, **104**, 501–528.
- Janzen, D.H. (1971) Seed predation by animals. *Annual Review of Ecology and Systematics*, **2**, 465–492.
- Janzen, D. (1988) Tropical dry forests, the most endangered major tropical ecosystem. *Biodiversity* (ed E.O. Wilson), pp. 130–137. National Academy Press, Washington, DC, USA.
- Jia, X., Dai, X.-F., Shen, Z.-X., Zhang, J.-Y. & Wang, G.-X. (2011) Facilitation can maintain clustered spatial pattern of plant populations during density-dependent mortality: insights from a zone-of-influence model. *Oikos*, **120**, 472–480.
- John, R., Dattaraja, H., Suresh, H. & Sukumar, R. (2002) Density-dependence in common tree species in a tropical dry forest in Mudumalai, southern India. *Journal of Vegetation Science*, **13**, 45–56.
- Johnson, D.J., Beaulieu, W.T., Bever, J.D. & Clay, K. (2012) Conspecific negative density dependence and forest diversity. *Science*, **336**, 904–907.
- Kobe, R.K. & Vriesendorp, C.F. (2011) Conspecific density dependence in seedlings varies with species shade tolerance in a wet tropical forest. *Ecology Letters*, **14**, 503–510.
- Leck, M.A., Parker, V.T. & Simpson, R.L. (2008) *Seedling Ecology and Evolution*. Cambridge University Press, Cambridge, UK.
- Lenth, R. V. (2014) lsmeans: least-squares means. R package version 2.05 available at <http://CRAN.R-project.org/package=lsmeans>.
- Lin, L., Comita, L.S., Zheng, Z. & Cao, M. (2012) Seasonal differentiation in density-dependent seedling survival in a tropical rain forest. *Journal of Ecology*, **100**, 905–914.
- Luo, Z., Mi, X., Chen, X., Ye, Z. & Ding, B. (2012) Density dependence is not very prevalent in a heterogeneous subtropical forest. *Oikos*, **121**, 1239–1250.
- Metz, M., Sousa, W. & Valencia, R. (2010) Widespread density-dependent seedling mortality promotes species coexistence in a highly diverse Amazonian rainforest. *Ecology*, **91**, 3675–3685.
- Montgomery, R.A. & Chazdon, R.L. (2002) Light gradient partitioning by tropical tree seedlings in the absence of canopy gaps. *Oecologia*, **131**, 165–174.
- Ostertag, R., Inman-Narahari, F., Cordell, S., Giardina, C.P. & Sack, L. (2014) Forest structure in low-diversity tropical forests: a study of Hawaiian wet and dry forests. *PLoS ONE*, **9**, e103268.
- Paine, C.E.T., Harms, K.E., Schnitzer, S.A. & Carson, W.P. (2008) Weak competition among tropical tree seedlings: implications for species coexistence. *Biotropica*, **40**, 432–440.
- Queenborough, S.A., Burslem, D., Garwood, N.C. & Valencia, R. (2007) Neighborhood and community interactions determine the spatial pattern of tropical tree seedling survival. *Ecology*, **88**, 2248–2258.
- R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, available at <http://www.R-project.org>.
- Sack, L. (2004) Responses of temperate woody seedlings to shade and drought: do trade-offs limit potential niche differentiation? *Oikos*, **107**, 110–127.
- Semchenko, M., Lepik, M., Götzenberger, L. & Zobel, K. (2012) Positive effect of shade on plant growth: amelioration of stress or active regulation of growth rate? *Journal of Ecology*, **100**, 459–466.
- Silva Matos, D.M., Freckleton, R.P. & Watkinson, A.R. (1999) The role of density dependence in the population dynamics of a tropical palm. *Ecology*, **80**, 2635–2650.
- Sullivan, J.J. (2003) Density-dependent shoot-borer herbivory increases the age of first reproduction and mortality of neotropical tree saplings. *Oecologia*, **136**, 96–106.
- Volkov, I., Banavar, J.R., He, F.L., Hubbell, S.P. & Maritan, A. (2005) Density dependence explains tree species abundance and diversity in tropical forests. *Nature*, **438**, 658–661.
- Webb, C.O. & Peart, D.R. (1999) Seedling density dependence promotes coexistence of Bornean rain forest trees. *Ecology*, **80**, 2006–2017.
- Wright, S.J. (2002) Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia*, **130**, 1–14.

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Supporting Information

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

Appendix S1. Detailed methods.

Table S1. (A and B) Seedling species attributes.

Figure S1. Effect sizes and SEs for density variables in dry and wet forest, for all species, the most common species, and the less common species.

Figure S2. Analysis of density effects on seedling survival over 3–25 m in dry and wet forest plots.

Figure S3. Effect sizes and SEs for density variables in dry and wet forest in low, medium, and high PAR.