LETTERS

Beyond the fast–slow continuum: demographic dimensions structuring a tropical tree community

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Abstract

Life-history theory posits that trade-offs between demographic rates constrain the range of viable life-history strategies. For coexisting tropical tree species, the best established demographic trade-off is the growth-survival trade-off. However, we know surprisingly little about co-variation of growth and survival with measures of reproduction. We analysed demographic rates from seed to adult of 282 co-occurring tropical tree and shrub species, including measures of reproduction and accounting for ontogeny. Besides the well-established fast–slow continuum, we identified a second major dimension of demographic variation: a trade-off between recruitment and seedling performance vs. growth and survival of larger individuals (≥ 1 cm dbh) corresponding to a 'stature–recruitment' axis. The two demographic dimensions were almost perfectly aligned with two independent trait dimensions (shade tolerance and size). Our results complement recent analyses of plant life-history variation at the global scale and reveal that demographic trade-offs along multiple axes act to structure local communities.

Keywords

Barro Colorado Island, demography, functional traits, growth-survival trade-off, life-history strategies, long-lived pioneer, mortality, seed production, tropical forest, weighted Principal Component Analysis.

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INTRODUCTION

Life-history theory posits that organisms face allocation trade-offs underlying different demographic processes (growth, survival, reproduction) and that the resulting trade-offs among demographic rates constrain the range of viable life-history strategies (e.g. Stearns 1999). Recent analyses of demographic trade-offs in > 600 vascular plant species across biomes identified two major dimensions of demographic variation: the well-established fast–slow continuum and a novel reproductive strategy dimension (Salguero-Gómez *et al.* 2016; Salguero-Gómez 2017). If demographic trade-offs arise from fundamental allocation strategies, they should correspond to allocation strategies expressed at the level of plant organs (Reich 2014), and it is the central tenet of trait-based ecology that functional traits constrain individual performance and population level demographic rates and fitness (Violle *et al.* 2007) and thus enable predictions concerning community assembly and ecosystem dynamics (McGill *et al.* 2006). Indeed, at the global scale, strong links have been found between functional traits and plant life-history strategies

(Adler *et al.* 2014). Within local communities, demographic trade-offs promote species coexistence by reducing fitness differences between species (Loehle 2000). Therefore, demographic trade-offs and their relationships with functional trait spectra also need to be explored within real-world local communities of coexisting species that contain rare species and where all species experience the same climate.

Tropical forests offer a unique possibility to test whether trade-offs identified globally hold within single diverse communities because they harbour hundreds of syntopic species, with up to 900+ tree species in a single hectare (Wilson *et al.* 2012), and because demographic data are becoming increasingly available for tropical tree species from long-term permanent monitoring plots (Anderson-Teixeira *et al.* 2015). Indeed, there is abundant empirical support for the prevalence of the fast–slow continuum of lifestyles for coexisting tropical tree species reflected by the growth-survival trade-off, especially for seedlings and saplings and between growth in high light vs. survival in low light (e.g. Baraloto *et al.* 2005; Gilbert *et al.* 2006; Wright *et al.* 2010; Iida *et al.* 2014). There is also evidence that the demographic fast–slow continuum at the

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individual/population level corresponds to functional traits related to shade tolerance and reflecting the fast–slow continuum at the level of plant organs within a tropical forest community (Wright *et al.* 2010), as well as at the global scale (Adler *et al.* 2014).

However, we know surprisingly little about how measures of reproduction co-vary with growth or survival for coexisting species. We expect per-capita rates of reproduction to be associated with the fast–slow continuum because species with a fast lifestyle and low survival need many recruits to offset mortality and maintain populations (Turner 2001; Muller-Landau 2010; Uriarte *et al.* 2012). However, because larger trees can potentially invest more resources into reproduction and accommodate more flowers and seeds than smaller trees, we argue that recruitment per unit basal area of adult trees is another, and potentially more meaningful, baseline for comparison among species than per-capita rates (Muller-Landau *et al.* 2008). The degree to which species differ in their fecundity or recruitment success relative to the basal area of adult trees indicates their relative allocation of resources to reproduction (vs. growth and survival). However, it is yet unclear how basal-area-weighted fecundity or recruitment rates trade-off with growth and survival.

Theory predicts that body size plays a key role in the evolution of species' life histories in general (Brown & Sibly 2006). Consistent with this, tree stature is an important determinant of tropical tree life histories (Turner 2001). To reach a tall stature, species should be selected for high longevity (i.e. high survival) and fast growth (Loehle 2000; Poorter *et al.* 2008; Wright *et al.* 2010; Rüger *et al.* 2012; Iida *et al.* 2014; Visser *et al.* 2016), at the expense of delayed reproduction (Koons *et al.* 2008) and low recruitment rates (Kohyama 1993; Kohyama *et al.* 2003; King *et al.* 2006; Visser *et al.* 2016). As shade tolerance and tree stature are often independent in tropical tree communities (e.g. Kooyman & Westoby 2009; Wright *et al.* 2010), we expect that a second demographic dimension captures the relationships of demographic rates with maximum size.

Additional demographic trade-offs may also occur between performance (growth or survival) at different resource levels (e.g. light-gradient partitioning, Latham 1992) or at different sizes or ontogenetic stages (size-gradient partitioning, Lusk 2004; Baraloto *et al.* 2005). However, most often, species seem to maintain their rank order in growth and survival across gradients of gap size or light availability (Gilbert *et al.* 2006; Kitajima & Poorter 2008; Rüger *et al.* 2011; Sterck *et al.* 2013) and across different size classes (Zhu *et al.* 2018). Thus, we expect survival and growth rates generally to be aligned across ontogenetic stages or light levels.

To evaluate demographic trade-offs and their relationships with functional trait spectra, we assembled trait data and demographic rates from seed to adult for 282 coexisting tree and shrub species at Barro Colorado Island (BCI), Panama. We accounted for tree size and light availability by assigning trees to one of four canopy layers based on the number of tree crowns above them (Bohlman & Pacala 2012) and estimated growth and survival rates for each species and canopy layer. For subsets of species, we also included data on seedling growth and survival (Wright *et al.* 2005; Comita *et al.* 2007). As measures of reproduction, we included the number of sapling recruits as well as the number of seedling recruits and seed numbers for subsets of the species.

Our objectives are twofold. First, we aim to establish the demographic spectrum of coexisting tropical tree species including multiple trade-offs between survival, growth and reproduction using an unprecedented amount of demographic field data and accounting for ontogenetic variation and resource availability. A novel weighted PCA (wPCA) allowed us to incorporate uncertainty associated with small sample sizes of rare species, which is a crucial feature for application in hyperdiverse systems (Delchambre 2014). Second, we aim to elucidate relationships between independent dimensions in functional traits and independent dimensions in demographic rates to explore coordination of adaptive strategies at the organ and individual/population level.

We hypothesised that the most important dimension of demographic variation for coexisting plant species in tropical forests is driven by a trade-off between growth and survival rates, in all canopy layers and ontogenetic stages, consistent with the well-documented fast–slow continuum of lifestyles (Stearns 1999). Because light is a key limiting resource in tropical forests, we expected this demographic dimension to be aligned with functional traits that are specifically related to species' shade tolerance. We further hypothesised that a second demographic dimension captures the relationships of demographic rates with tree stature.

We indeed found a two-dimensional spectrum of life-history strategies that explained two-thirds of demographic variation for the 282 species. In addition to the fast–slow continuum, our results revealed a second demographic trade-off between recruitment and seedling performance vs. growth and survival of larger individuals (≥ 1 cm dbh). The demographic space spanned by these trade-offs was almost perfectly aligned with a trait spectrum created by a shade tolerance and a size dimension. This is consistent with the scaling of fundamental plant strategies from organs to individuals and populations.

METHODS

Demographic rates of trees ≥ 1 cm dbh

We analysed data from a 50-ha forest census plot on BCI, Panama (9.15° N, 79.85° W). BCI is a 1567-ha island in the Panama Canal covered with tropical lowland moist forest. The climate on BCI is warm throughout the year (27.1 °C mean annual temperature), but rainfall is seasonal with 90% of the 2600 mm annual total falling during the wet season from May to December. In the 50-ha plot, all free-standing woody stems ≥ 1 cm diameter at breast height (dbh) were mapped, identified to species and measured in 1981–1983, 1985 and every 5 years thereafter (www.forestgeo.si.edu; Hubbell & Foster 1983; Condit 1998). Here we used the first seven censuses and determined survival and annual dbh growth rate (mm year^{-1}) for each individual tree (excluding palms and hemiepiphytes). Details on handling of growth outliers or dbh measurement problems are given in the Supplement.

To account for differences in tree size and light availability, trees were assigned to one of four canopy layers. To do this, the 50-ha plot was divided into 31.25 × 31.25 m subplots

(Bohlman & Pacala 2012). Within each subplot, trees were sorted by size and assigned to the top canopy layer (layer 1) until the cumulative area of their crowns exceeded the subplot area (Bohlman & Pacala 2012). Smaller trees were successively assigned to lower canopy layers in the same way (see Supplement for additional details). The canopy layers captured observed differences between trees in terms of size and light availability in a subset of the data for which individual-level estimates of light availability were available (Table S1 in the Supplement). We used crown observations from aerial photographs to assess uncertainty in canopy layer assignments (Bohlman & Pacala 2012). As an example, trees classified as being in the top canopy layer were assigned probabilities of 81 and 19% of actually being in canopy layer 1 or 2, respectively. These probabilities were used to weight the contribution of trees to the estimation of demographic rates in the different canopy layers (see below).

We pooled growth and survival observations from the six census intervals. Ignoring repeated measurements of the same individuals did not bias our results (Fig. S1). To reduce computation time, we drew random samples of 100 observations for growth and 1000 observations for survival per species and canopy layer when there were more observations available. In total, 56 015 and 331 218 observations were used to estimate growth and survival rates, respectively, for 282 species.

We estimated average annual dbh growth (g) and survival rates (s) for each species (j) in the four canopy layers (k) with a Bayesian model using the software package RSTAN (Stan Development Team 2016, see Supplement for model specifications). Because assignment to canopy layers was probabilistic, each individual contributed information to the average growth rate of the species of several canopy layers ($g_{j,k}$). The likelihood of observed growth rate of individual i of species j ($obs_{i,j}$) is

$$p(obs_{i,j}|p_i, g_j, \sigma_j) = \sum_{k=1}^{4} p_{i,k} \cdot Lognormal(obs_{i,j}|g_{j,k}, \sigma_{j,k})$$

with p being a vector of probabilities that individual i is in each of the four canopy layers. Likewise, the likelihood of individual i of species j to have survived or died ($alive_{i,j}$) is

$$p(alive_{i,j}|p_i, s_j) = \sum_{k=1}^{4} p_{i,k} \cdot Bernoulli(alive_{i,j}|surv_{i,k})$$

with $surv_{i,k} = s_{j,k}^{t_i}$, i.e. the annual survival rate of species j in layer k ($s_{j,k}$) to the power of the number of years elapsed between the censuses for individual i (t_i). Across species, log-transformed growth rates and survival rates per layer were assumed to follow normal and beta distributions respectively. Parameter estimates for species were increasingly subject to shrinkage towards the mean of these community-level distributions (and associated with large uncertainty) with decreasing sample size. Of the 282 species, 114 species lacked information for at least one canopy layer.

To quantify sapling recruitment, we estimated the average number of recruits over the 1 cm dbh threshold in the entire plot as the mean of a Poisson distribution (λ_j) based on the number of recruits per species in each of the six 5-year census intervals ($r_{j,int}$)

$$p(r_{j,int}|\lambda_j) = Poisson(r_{j,int}|\lambda_j)$$

We divided recruitment rates (λ_j) by the basal area of reproductive trees because fecundity is commonly assumed to be a linear function of a tree's basal area (Muller-Landau *et al.* 2008). The threshold size where 50% of the individuals are reproductive was estimated as $0.5 \times dbh_{max}$, which was found to be in good agreement with observed reproductive size thresholds in a study of 136 BCI tree species ($r^2 = 0.81$, Visser *et al.* 2016). For 13 species with observed $dbh_{max} > 2$ m, we set the reproductive size threshold to 1 m. This definition of the reproductive size threshold did not affect the results (Fig. S2). We also determined per-capita sapling recruitment rates by dividing λ_j by the average abundance (≥ 1 cm dbh) of the species.

We used credible intervals of parameter estimates to assign weights in a weighted PCA (see below). Weights were calculated for each species j based on the width of the 95% credible interval (wCI) of parameter i as $weight_{i,j} = 1-(wCI_{i,j}/max(wCI_i))$. Thus, species with a 95%CI one quarter as wide as the species with largest uncertainty, were assigned a weight of 0.75. Maximum weights were > 0.9 for all parameters. The species with the largest uncertainty (widest CI) was assigned a small weight of 1.0e–6. In analogy to the coefficient of variation, we calculated weights for recruitment rates based on $wCI(\lambda_j)/\lambda_j$, rather than on $wCI(\lambda_j)$, because the CI is wider for species with many recruits, but relative uncertainty is lower.

Seedling demographic rates

We estimated seedling demographic rates from censuses in 2003, 2004, 2006, 2008, 2009, 2011, 2012 and 2013 that recorded the height and fate of each seedling (≥ 20 cm height) in 20 000 1 m² seedling plots evenly spaced across the 50-ha plot (Comita *et al.* 2007). To minimise differences in growth and survival due to size differences, we only included seedlings > 30 cm and < 100 cm tall. For survival, we included 33 414 observations from 1-year census intervals. For growth, we included all census intervals and calculated annual height growth rate for 76 178 individuals. We computed an average species height growth rate and survival rate with a Bayesian model and calculated weights as above (see Supplement for additional details).

Seed production and seedling recruits

Seed rain has been recorded weekly in 200 0.5-m² seed traps within the 50-ha plot since January 1987, with new seedling recruits (< 1 cm dbh, no minimum size cutoff) censused annually since 1994 in three 1-m² seedling plots adjacent to each seed trap (Wright *et al.* 2005). Using seed and seedling data from 1994 to 2012, we fit the average annual number of seeds and seedling recruits as the mean of a Poisson distribution (λ_j) and scaled them relative to the basal area of reproductive trees and abundance as above. We calculated weights based on $wCI(\lambda_j)/\lambda_j$ as above.

Multivariate analyses

We performed a weighted PCA (wPCA) on nine demographic characteristics (growth and survival rates ≥ 1 cm dbh in four

canopy layers, sapling recruitment) plus seedling growth and survival, seed number and seedling recruitment for subsets of the species. We adopted a method from astrophysics (Delchambre 2014; see Supplement) that allows for weighting of each demographic parameter of each species separately. Thus, the wPCA approach has the benefit of allowing all species to contribute information, weighted by the uncertainty of the data. The rarest of species would, individually, have a negligible impact on the results because their small sample sizes result in high uncertainty in demographic rates and consequently low weights in the wPCA. However, given the large number of rare species within tropical tree communities, including them is critical for capturing variation within the community. A bias could arise if some species were only represented in some of the canopy layers (which is more likely for rare species), so we checked the robustness of results by performing the wPCA on a subset of (relatively abundant) species with observations in all canopy layers (all weights > 0.4). We also checked the effect of phylogenetic relatedness on wPCA results by re-running the analysis on random subsets of 131 phylogenetically overdispersed species (≤ 3 species per family) and by performing phylogenetic PCA (see Supplement). Demographic rates were transformed to ensure normality (see Supplement). Meaningful principal components were determined by the broken stick criterion (Legendre & Legendre 2012).

We explored the correspondence in eight traits with demographic dimensions: maximum height, wood density, seed mass, leaf mass per area (LMA), leaf dry matter content (LDMC), leaf phosphorous (Leaf P) and nitrogen (Leaf N) concentrations, and leaf area. Traits were mostly collected in the 50-ha plot or close by and are described in the Supplement and in Wright *et al.* (2010). Maximum height, seed mass, LMA and leaf area were log-transformed. There were 188 species with complete trait information. First, we related traits independently to both demographic dimensions simultaneously (function 'envfit', R-package 'VEGAN') searching for the direction of most rapid change in traits in demographic space.

In addition, we tested whether trait dimensions were significantly related to demographic dimensions using Procrustes analysis (function 'pro', R-package 'VEGAN', Peres-Neto & Jackson 2001) which compares two ordinations of the same objects (here species) with each other. Trait dimensions were determined as the first two principal components of a standard PCA including all eight traits. Demographic dimensions are the first two principal components of the wPCA. All analyses were carried out in R version 3.3.2 (R Development Core Team 2016).

RESULTS

Demographic dimensions

We first performed the wPCA for demographic rates of trees ≥ 1 cm dbh (282 species) including per-basal area (Fig. 1a) or per-capita recruitment rates (Fig. 1b). The first two principal components explained a larger proportion of the variance than predicted by the broken stick model (Legendre & Legendre 2012) and we limit our interpretation to them. The first dimension (wPCA axis 1, 37% explained demographic variation when per-basal area recruitment rates were included) represented a trade-off between growth and survival rates in all canopy layers, i.e. the general fast–slow continuum of life-history strategies (Figs. 1a,b and 2, Tables S2,S3). Understory survival (layers 3 and 4) and growth in layers 2–4 contributed most strongly to the trade-off. Demographic rates in the top canopy layer (layer 1) contributed less as they had lower weights on average because fewer individuals were present here, and many species were absent (Table S1). Per-basal area sapling recruitment rates were unrelated to the first dimension, whereas high per-capita recruitment rates were associated with a fast lifestyle.

As expected, gap-dependent pioneer species, such as *Trema micrantha* (Cannabaceae), *Cecropia insignis* and *C. obtusifolia* (Urticaceae), *Zanthoxylum ekmanii* (Rutaceae), *Hampea appendiculata* and *Ochroma pyramidale* (both Malvaceae), were associated with fast lifestyles (Fig. 1a, S3). They can grow > 10 mm year^{-1} in dbh and 15 to 30% of their understory individuals die each year. The species with the slowest life histories included *Capparidastrum frondosum* (Capparaceae), *Talisia* spp. (Sapindaceae), *Swartzia simplex* var. *grandiflora* (Fabaceae) and *Ouratea lucens* (Ochnaceae). Most of their individuals grow < 0.5 mm year^{-1} and understory survival exceeds 99%.

The second dimension (28% explained variation) distinguished species that have above-average growth and survival in all canopy layers but suffer low recruitment, especially in terms of per-basal area recruitment rates, from species that grow and survive poorly but have many recruits. This second axis describes a continuum from long-lived pioneers (positive extreme) to 'short-lived breeders' (negative extreme). The most extreme long-lived pioneers were *Cavanillesia platanifolia* (Malvaceae), *Hura crepitans* (Euphorbiaceae) and *Anacardium excelsum* (Anacardiaceae). In the canopy, they grow > 5 mm year^{-1} on average and survival is > 99%. They have < 0.2 sapling recruits per m² of adult basal area. The short-lived breeders included many shrubs of the genera *Piper* (e.g. *P. cordulatum*, *P. perlasense*, Piperaceae) and *Psychotria* (e.g. *P. horizontalis*, *P. marginata*, Rubiaceae). They grow < 1 mm year^{-1}, survival tends to be < 95%, but they have several thousand recruits per m² of adult basal area.

The overall demographic strategies remained similar when performing the wPCA only including tall species (maximum height > 18 m) or short-statured species (maximum height ≤ 18 m, Fig. 2). They were also robust to possible pseudo-replication associated with phylogenetically related species (Fig. S4) and phylogenetic correction (Tables S4–S7).

When including seedling demographic rates of 198 species, seedling growth and survival consistently formed part of the fast–slow continuum (axis 1, 38%, Fig. 1c,d). The second dimension was dominated by a trade-off between tree performance (≥ 1 cm dbh) vs. seedling performance and recruit numbers (axis 2, 25%). Including the number of seeds and first-year seedling recruits for 74 species did not alter the overall demographic dimensions (Fig. 1e,f). Consistent with previous results, per-basal area seed and seedling numbers were mostly associated with the second dimension (axis 2, 25%), with long-lived pioneers having low numbers of seeds,
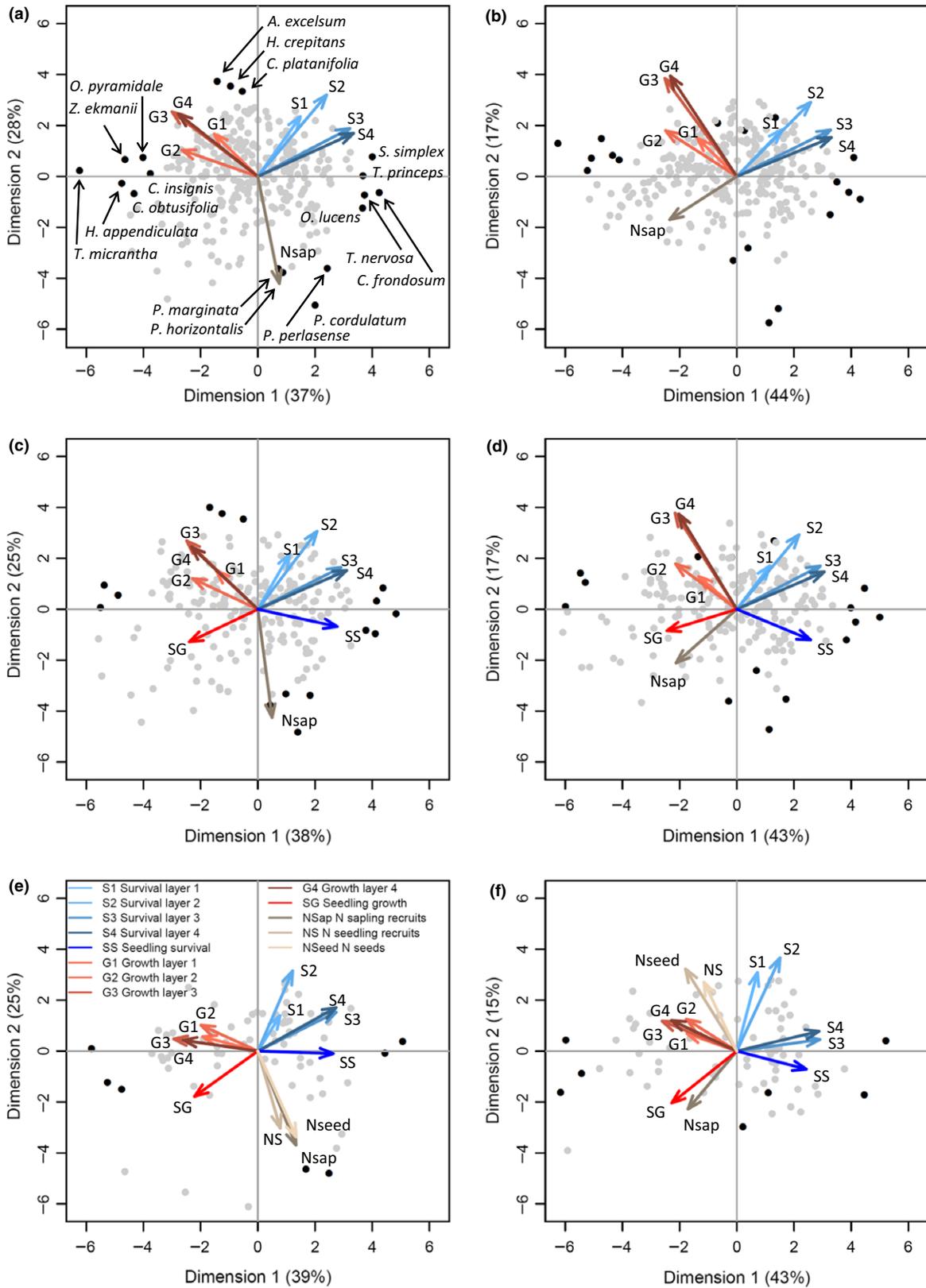
Figure 1 Demographic variation of tropical trees and shrubs at BCI, Panama, is characterised by the growth-survival trade-off (1st dimension) and a trade-off extending from long-lived pioneers to short-lived breeder syndromes ('stature–recruitment axis', 2nd dimension). Shown are wPCA loadings of annual dbh growth and survival rates of individuals ≥ 1 cm dbh in four canopy layers and the number of sapling recruits (a,b 282 species), additionally annual seedling height growth and survival (c,d 198 species), and additionally the number of seeds and seedling recruits (e,f 74 species). Measures of reproduction are per-basal area rates in a, c and e, and per-capita rates in b, d and f.
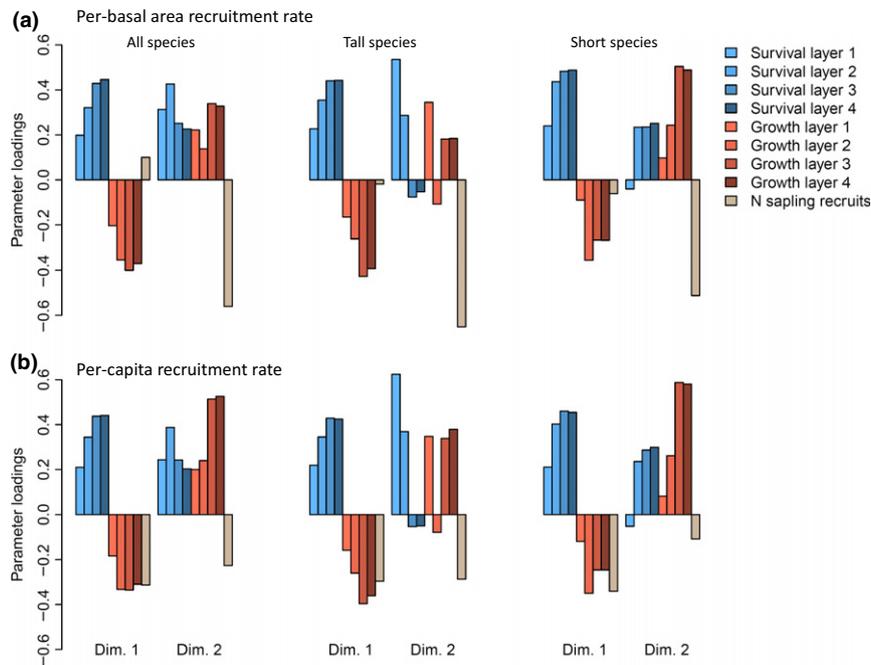
Figure 2 The two most important demographic dimensions are consistent for all species (282 species, left), tall species (maximum height > 18 m, 117 species, middle) and short species (maximum height ≤ 18 m, 155 species, right). Shown are wPCA loadings of annual survival and dbh growth rates of individuals ≥ 1 cm dbh in four canopy layers and the number of sapling recruits for tree and shrub species at BCI, Panama. Recruitment rates are per-basal area rates (a) and per-capita rates (b).

seedlings and sapling recruits. However, in terms of per-capita rates, long-lived pioneers had many seeds and recruits per-capita, but few sapling recruits (Fig. 1f). All findings were robust to excluding species not present in all canopy layers from the analysis (Figs. S5 and S6).

Correspondence between trait and demographic dimensions

Demographic dimensions were most strongly related to maximum height (r^2 = 57%), wood density (33%) and seed mass (27%, Table 1, Fig. 3a). Wood density was only related to the first demographic dimension, maximum height mostly to the second demographic dimension and seed mass to both dimensions (Fig. 3a). Two significant principal components explained 35 and 20% of variation among traits (Table S8). The first component had large positive loadings for LMA and LDMC, moderately positive loadings of wood density and negative loadings of Leaf P and Leaf N (Table S8). We interpret this dimension as 'shade tolerance'. The second component had large positive loadings for maximum height, seed mass and leaf area, and describes a 'size' dimension. These two trait dimensions were significantly related to demographic dimensions. The correlation between the two ordinations was 0.53 (Significance assessed by permutation tests = 0.001). Trait dimensions corresponded so closely with demographic dimensions that their offset is barely visible (Fig. 3b).

DISCUSSION

We performed a comprehensive assessment of demographic trade-offs for 282 coexisting tropical tree and shrub species by

Table 1 Fitted trait vectors in the demographic ordination space (Fig. 1a) for 188 species with complete trait information

Traits	Dimension 1	Dimension 2	r^2
Maximum height	−0.22	0.98	0.57***
Wood density	1.00	−0.05	0.33***
Seed mass	0.61	0.79	0.27***
LMA	1.00	0.01	0.07**
LDMC	0.89	0.45	0.11***
Leaf P	−0.74	0.67	0.15***
Leaf N	−0.96	0.28	0.05*
Leaf area	−0.49	0.87	0.07**

The second and third columns are direction cosines. Significance levels are based on random permutations of the data (*P < 0.05, **P < 0.01, ***P < 0.001). Demographic dimension 1 describes the growth-survival trade-off. Dimension 2 describes a trade-off extending from long-lived pioneers to short-lived breeder syndromes. Traits are leaf mass per area (LMA), leaf dry matter content (LDMC), leaf phosphorous concentration (Leaf P) and leaf nitrogen concentration (Leaf N).

including demographic rates from seed to adult and all species – even rare ones – through a weighted PCA that incorporated uncertainty in demographic rates. As expected, the most important dimension of demographic variation was a fast–slow continuum of lifestyles (Reich 2014), created by a trade-off between fast growth and high per-capita recruitment rates vs. high survival (e.g. Turner 2001; Wright *et al.* 2010; Uriarte *et al.* 2012). This demographic dimension captured a moderate proportion of the demographic diversity (37%). Growth and survival rates from seedling to adult and across the four canopy layers were consistently aligned with this axis of

(a)

(b)
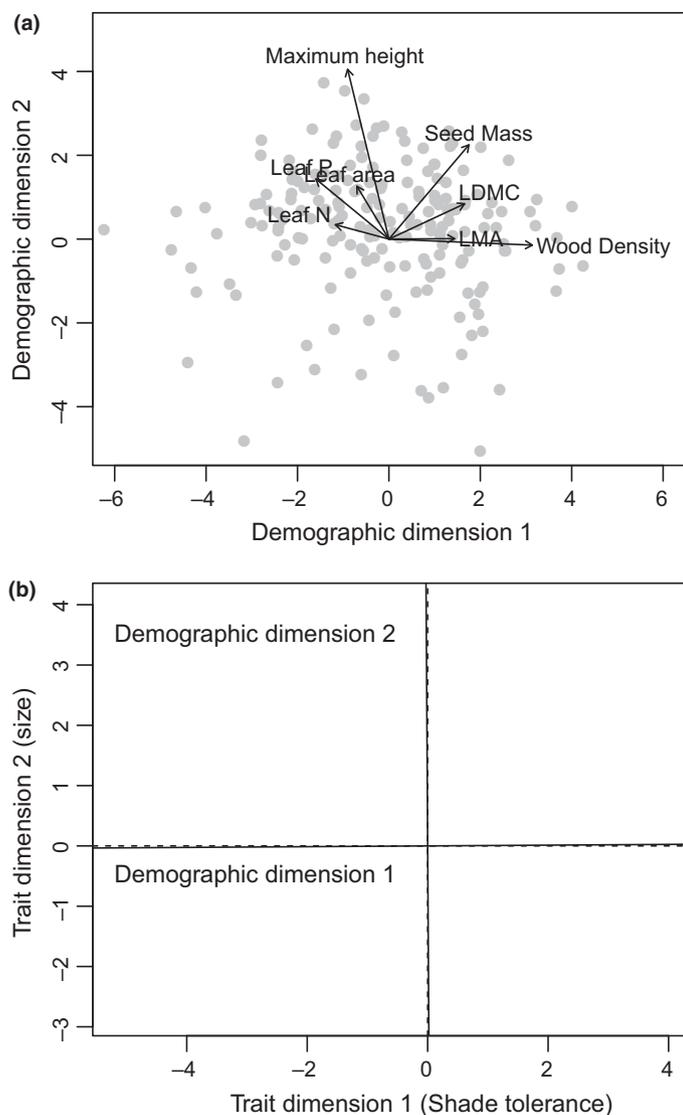
Figure 3 Correspondence between functional traits and demographic dimensions in 188 tree and shrub species at BCI, Panama, with complete trait information. (a) Trait vectors fitted onto the demographic ordination produced by the wPCA. Arrows point in the direction of most rapid change of traits in demographic space. Traits are the same as in Table 1. (b) Procrustes analysis comparing the ordination of species in trait space (dashed lines) vs. demographic space (solid lines). Both ordinations overlap so closely that their offset is barely visible.

life-history variation. Our results thus confirm the generality of the growth-survival trade-off (Welden *et al.* 1991; Kitajima 1994; Gilbert *et al.* 2006; Iida *et al.* 2014; Philipson *et al.* 2014).

This demographic fast–slow continuum was aligned with a trait dimension that describes the fast–slow continuum at leaf level, created by a trade-off between leaf traits maximising short-term carbon gain vs. long-term leaf persistence (high leaf N and P vs. high LMA and LDMC, Poorter & Bongers 2006; Sterck *et al.* 2006; Reich 2014; Lasky *et al.* 2015). However, even if wood density was not loading strongly on this trait dimension, it was the single best predictor of a species' position along the demographic fast–slow continuum, whereas

the predictive power of individual leaf traits was low (e.g. Poorter *et al.* 2008; Wright *et al.* 2010; Rüger *et al.* 2012; Visser *et al.* 2016).

Basal area-corrected measures of reproductive effort or success – the number of seeds, seedling or sapling recruits – were largely independent from the fast–slow continuum and defined the second dimension. They were associated with high seedling performance (growth and survival) and traded off against growth and survival at the tree (≥ 1 cm dbh) stage. This means that species that bias resource allocation towards growth and survival ≥ 1 cm dbh, allocate disproportionately few resources to reproduction and seedling performance and vice versa. Thus, the second dimension describes a continuum extending from 'long-lived pioneers' (fast growth and high survival when ≥ 1 cm dbh but poor seedling performance, low recruitment) to 'short-lived breeders' (opposite characteristics). Interestingly, in terms of per-capita reproductive rates, the long-lived pioneers have many seeds and seedlings, but due to the low seedling performance, only few of them make it to the sapling stage.

This demographic dimension was aligned with a 'size dimension' in functional traits (high maximum height, seed mass and leaf area, cf. Díaz *et al.* 2016), with adult stature being the best predictor. Thus, tall species tend to maximise canopy performance at the expense of recruitment rates, whereas short species tend to maximise recruitment and seedling performance at the expense of performance ≥ 1 cm dbh (King *et al.* 2006; Visser *et al.* 2016). We call this a 'stature–recruitment axis' in line with the prediction of the forest architecture hypothesis that small species can coexist with tall species through higher recruitment rates (Kohyama 1993).

The demographic strategy of long-lived pioneers has been described before (e.g. Ford & Ishii 2001). Conspicuous examples from temperate forests include Douglas fir (*Pseudotsuga menziesii*, Ishii & Ford 2002) and giant sequoia (*Sequoiadendron giganteum*, York *et al.* 2011). These are tall canopy or emergent tree species – often wind-dispersed – that depend on large-scale disturbances to regenerate, and then grow quickly into the canopy and survive there as giant trees for several centuries (e.g. York *et al.* 2011). Long-lived pioneers maintain their populations by building up a 'demographic storage', i.e. by conserving existing seed sources that are placed above the main canopy and can thus supply distant disturbed areas with seeds via wind or animal dispersal (6 and 13 out of the 20 most extreme long-lived pioneers in our study respectively; Wright *et al.* 2016). In contrast, tropical short-lived pioneers form seed banks (Dalling *et al.* 1997) and shade-tolerant species form seedling banks to exploit the limited opportunities for successful establishment (Comita *et al.* 2007).

We show that the 'stature–recruitment axis' is an important dimension of demographic variation (28% of demographic variation) that is orthogonal to the well-known fast–slow continuum. We also describe the other extreme of this strategy axis, which we call 'short-lived breeders'. 'Short-lived breeders' are often understory shrubs with slow growth, low survival, but high recruitment rates. Small shrub species often start reproducing below the 1 cm dbh threshold, and thus their 'sapling recruits' are often fully reproductive and their adult basal area is likely to be underestimated. Also, many of

these species already approach their maximum dbh shortly after passing the 1 cm dbh threshold and may experience elevated mortality due to senescence (pers. obs.) which is also underpinned by their higher seedling survival. This suggests a possible bias with unrealistically high estimates for recruitment and low estimates for survival for some 'short-lived breeders'. For this reason, we excluded shrub and understory tree species from the analysis and repeated the wPCA. The same two demographic dimensions emerged (Fig. 2). This confirms the robustness of our results to potential biases caused by unrealistic estimates for the smallest shrub species.

The endpoints of the two dimensions loosely correspond to traditional classifications of tropical tree species that assign species according to their shade tolerance (pioneer-climax axis) and maximum size into four groups, i.e. 'small pioneer' (fast growth, low survival), 'canopy' (slow growth, high survival), 'large pioneer' (fast growth, high survival), 'understory' (slow growth, low survival; Turner 2001 based on Lieberman et al. 1990 and Favrichon 1994). However, while Turner (2001) equates shade tolerance with growth and maximum size with longevity (i.e. survival), our results show that growth and survival are in fact related to both shade tolerance and maximum size. Moreover, we incorporate measures of reproduction into this classification scheme and back it up with extensive demographic data. Thus our classification scheme may lead to an improved understanding of forest dynamics and support forest management. In particular, long-lived pioneers play an important role in forest succession, carbon storage and timber production (e.g. Grau et al. 1997; De Ridder et al. 2013), and their management could benefit from greater insight into their life histories.

Our discovery of two important demographic dimensions among coexisting tropical tree species also agrees with findings of global analyses of demographic characteristics from matrix models for > 600 plant species covering all vascular plant life forms (Salguero-Gómez et al. 2016; Salguero-Gómez 2017). However, there are also several differences. First, the second dimension in these global analyses (reproductive strategy continuum) is dominated by the number of recruits produced during an individual's lifespan and the degree of iteroparity (spread of reproduction throughout an individual's lifespan). Unfortunately, we have no information about these life-history characteristics, but Tachigali versicolor, the one monocarpic (i.e. semelparous) species in the plot, is almost located at the centre of the second dimension (score –0.14).

Second, in the analyses of Salguero-Gómez et al. (2016) and Salguero-Gómez (2017), (progressive) growth and measures of longevity were mostly related to the first dimension (fast–slow continuum), but not to the second dimension. In our case, growth and survival are related to both dimensions, and together with per-basal area recruitment rates evenly 'partition' the two-dimensional demographic plane, i.e. their 'arrows' are separated by about 120° respectively (Fig. 1a). This is consistent with a three-way trade-off between acquisition, maintenance and regeneration (Grime & Pierce 2012). Most importantly, however, we focus on a community of co-occurring species making our results relevant to questions of community ecology, such as species coexistence and community dynamics. This might also explain why the demographic

syndromes we identified do not correspond to the C-S-R strategy scheme (Grime & Pierce 2012), which was developed for species experiencing different degrees of disturbance.

We found a surprisingly strong correspondence between the orientation of the first two dimensions capturing the largest proportion of between-species variation in functional traits and demographic rates, respectively (Fig. 3b). This indicates that fundamental plant strategies scale up from organ to individual and population scales and lends unprecedented support to the hope of trait-based ecology that functional traits enable predictions concerning community assembly and ecosystem dynamics (McGill et al. 2006). Moreover, among the tree species at BCI, wood density and adult stature are two nearly independent dimensions of plant economics and architecture ($r = -0.1$, cf. Wright et al. 2010) and the strongest predictors of the two independent demographic dimensions identified in this study. Thus, we second Visser et al. (2016) in advocating the use of a WH(S) scheme (wood, height, seed), rather than the LHS scheme (leaf, height, seed) proposed by Westoby (1998), to capture and predict differences in demographic strategies of tropical trees. These traits are easily measurable and can be used as proxies for demographic rates, which are much more labour-intensive and time-consuming to collect. Thus, they offer a promising route to 'diversify' dynamic global vegetation models using trait-based demographic strategies (e.g. Purves & Pacala 2008). This may greatly improve predictions of forest dynamics, which is one of the major sources of uncertainty in climate predictions (Purves & Pacala 2008). However, the relationships between functional trait dimensions and demographic dimensions established here for one tropical forest might not hold across forests with different climates, disturbance regimes or floristic compositions. Thus, an enhanced understanding of the importance of the fast–slow continuum vs. the stature–recruitment axis – and their relationships with functional traits – in a global context is urgently needed.

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DATA ACCESSIBILITY STATEMENT

Previously archived BCI data sets are available from Dryad (datadryad.org) or the Smithsonian DSpace repository (repository.si.edu). Tree censuses (≥1 cm dbh), seed rain, and seedling establishment data are achieved at DSpace with DOIs 10.5479/data.bci.20130603, 10.5479/si.data.201511251137, 10.5479/si.data.201511251134, respectively, while seedling census data is archived at Dryad https://dx.doi.org/10.5061/dryad.fm654 (Visser *et al.* 2016).

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