DEMOGRAPHY BEYOND THE POPULATION

Functional traits as predictors of vital rates across the life cycle of tropical trees

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Summary

1. The 'functional traits' of species have been heralded as promising predictors for species' demographic rates and life history. Multiple studies have linked plant species' demographic rates to commonly measured traits. However, predictive power is usually low – raising questions about the practical usefulness of traits – and analyses have been limited to size-independent univariate approaches restricted to a particular life stage.

2. Here we directly evaluated the predictive power of multiple traits simultaneously across the entire life cycle of 136 tropical tree species from central Panama. Using a model-averaging approach, we related wood density, seed mass, leaf mass per area and adult stature (maximum diameter) to onset of reproduction, seed production, seedling establishment, and growth and survival at seedling, sapling and adult stages.

3. Three of the four traits analysed here (wood density, seed mass and adult stature) typically explained 20–60% of interspecific variation at a given vital rate and life stage. There were strong shifts in the importance of different traits throughout the life cycle of trees, with seed mass and adult stature being most important early in life, and wood density becoming most important after establishment. Every trait had opposing effects on different vital rates or at different life stages; for example, seed mass was associated with higher seedling establishment and lower initial survival, wood density with higher survival and lower growth, and adult stature with decreased juvenile but increased adult growth and survival.

4. Forest dynamics are driven by the combined effects of all demographic processes across the full life cycle. Application of a multitrait and full-life cycle approach revealed the full role of key traits, and illuminated how trait effects on demography change through the life cycle. The effects of traits on one life stage or vital rate were sometimes offset by opposing effects at another stage, revealing the danger of drawing broad conclusions about functional trait–demography relationships from analysis of a single life stage or vital rate. Robust ecological and evolutionary conclusions about the roles of functional traits rely on an understanding of the relationships of traits to vital rates across all life stages.

Key-words: adult stature, leaf mass per area, model averaging, seed size, tree growth, tree mortality, wood density

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Introduction

Functional biology has raised the possibility that morphological and physiological traits, henceforth functional traits, might be strongly related to interspecific variation in

vital rates and serve as proxies for life history variation (McIntyre *et al.* 1999; Westoby *et al.* 2002; Westoby & Wright 2006). However, the predictive power of functional traits is often very low, raising questions about how 'functional' the selected traits really are (Paine *et al.* 2015). For example, coefficients of determination (R^2) average just 0·08 for predictions of growth and mortality rates of tropical trees (Poorter *et al.* 2008; Wright *et al.* 2010; Iida *et al.* 2014a,b). Such low predictive power strongly limits the potential of traits to serve as proxies for life history variation or inform global vegetation models (Cox *et al.* 2013; Friedlingstein *et al.* 2014).

Previous studies in tropical forest trees have provided an incomplete picture of the role of traits in tree demography. Limitations include restriction of analyses to particular life stages, ignoring size dependence (Poorter *et al.* 2008; Wright *et al.* 2010), and/or consideration of only one trait at a time (Iida *et al.* 2014a,b). First, most previous studies consider a single vital rate and/or life stage, even though traits will generally have different roles and different predictive power for different demographic rates. For instance, seed mass is strongly negatively correlated with seed production (Muller-Landau *et al.* 2008), strongly positively correlated with seedling establishment rates (Moles & Westoby 2006), and has weaker relationships with growth and survival later in life (Wright *et al.* 2010). Secondly, most previous studies ignore the size dependency of demographic rates, focusing instead on mean survival and growth over broad size classes (Poorter *et al.* 2008; Wright *et al.* 2010; but see Iida *et al.* 2014b). This overlooks important interactions between traits and size, as taller trees experience strikingly different resource and competitive conditions (Poorter *et al.* 2005; Hérault *et al.* 2011; Falster, FitzJohn & Westoby 2016). Thirdly, many studies consider only a single trait, thus inherently limiting the total explanatory power of traits (Muller-Landau *et al.* 2008; Iida *et al.* 2014a,b). Many traits will influence plant function simultaneously and each trait can be involved in multiple trade-offs with contradictory effects on vital rates (Marks & Lechowicz 2006). To improve understanding of how traits influence plant demography, we consider size dependence, evaluate trait–demography rela-

tionships across the entire life cycle, and consider multiple traits in a model-averaging framework.

We evaluate to what degree four key traits can explain variation in demography among tropical tree species. The four key traits are adult stature, wood density, seed mass and specific leaf area, which provide largely independent information about plant strategies (Table 1; Westoby *et al.* 2002; Wright *et al.* 2007). In contrast to previous work, our analyses are comprehensive including not only growth and mortality of trees (Poorter *et al.* 2008; Wright *et al.* 2010; Rüger *et al.* 2012; Iida *et al.* 2014a), but also reproductive schedules; seed production; and seedling establishment, growth and mortality. We use a model-averaging approach (Burnham & Anderson 2002; Grueber *et al.* 2011) to simultaneously weigh the effects of all four traits on each vital rate for up to 136 tree and shrub species from Barro Colorado Island, Panama. We aim to quantify (i) which traits explain variation at different life stages; (ii) the predictive power of all traits combined to explain variation in all components of the life cycle; and (iii) the relative effect sizes of each trait at each life stage while mapping out contradictory effects across life stages.

Materials and methods

STUDY SITE

Our data are from the moist tropical forest of the 50-ha Forest Dynamics Plot (FDP) on Barro Colorado Island (BCI; 9°9′ N, 79°51′ W), Panama. Annual rainfall averages 2650 mm (since 1929), with a dry season between January and April, and temperature averages 27 °C (see Leigh 1999, for details).

VITAL RATES

We used five data sets to quantify vital rates for the entire life cycle.

1. *Trees.* In the FDP, all free-standing woody stems ≥1 cm diameter breast height (dbh, measured at 1·3 m) were censused in 1981–1982, 1985 and every 5 years thereafter. In each census, diameters of every stem are measured, and all new individuals are tagged, mapped, and identified to species. These censuses

Table 1. Details on the functional trait data, including units, mean and standard deviation, range, common ecological associations and references

Trait	Mean (SD)	Range	Associations	Sources
Wood density (WD: g cm^{-3})	0·59 (0·14)	0·29, 0·91	Mechanical strength, vulnerability to hydraulic failure, defence against decay, growth–survival trade-off	Chave *et al.* (2009), Anten & Schieving (2010) and Larjavaara & Muller-Landau (2010)
Seed mass (SM: g)	0·06 (8·14)*	4·9e-05, 22·87	Seed production, seed dispersal, seedling tolerance to stress, seedling competitive ability	Westoby *et al.* (2002), Moles & Westoby (2006) and Muller-Landau (2010)
Leaf mass per area (LMA: g m^{-2})	231·84 (314·89)	9·4, 1891·35	Leaf construction cost, photosynthetic capacity, respiration rates, leaf life span, leaf herbivory	Westoby *et al.* (2002), Wright *et al.* (2004) and Osnas *et al.* (2013)
Adult stature (D$_{max}$: mm)	398·97 (334·35)	12, 1775·67	Life history variation	Kohyama (1993) and Westoby *et al.* (2002)

*Geometric mean.

provide information on growth and survival for individuals ≥1 cm dbh (hereafter 'trees'). We analysed data from the 1990 to 2010 censuses, excluding earlier censuses because of small but important differences in measurement methods (Condit et al. 1999; Rüger et al. 2009).

2. *Seed rain*. Seed rain has been recorded in 200 0·5-m^2 seed traps since January 1987 (Wright et al. 2005). Traps are located in a stratified random manner along trails within the FDP. All reproductive parts (seeds, flowers, fruits and capsules) are identified to species and counted weekly (presence is recorded for flowers). We used seed data from 1993 to 2012, as these years correspond to records of newly recruiting seedlings (data set 3, below).

3. *Small seedlings*. All seedlings and small saplings <1 cm dbh (with no limits on height) were censused annually in 600 1-m^2 seedling plots from 1994 through 2012. These plots are located 2 m from three sides of each of the 200 seed traps (Wright et al. 2005).

4. *Large seedlings*. Free-standing woody plants ≥20 cm in height and <1 cm dbh were censused in 20 000 1-m^2 seedling plots each year from 2001 through 2013, with the exceptions of 2005, 2007 and 2010 (Comita et al. 2007; Comita & Hubbell 2009). These plots are located in a 5-m grid across the FDP. In each census, the status (i.e. alive/dead) of previously tagged seedlings is checked, all individuals are measured for height (except in 2002, when only new recruits were measured), and new individuals are tagged and identified to species. In analyses of growth and survival all census intervals which include missing years were dropped (i.e. no intervals of >1 year are included for data set 4).

5. *Reproductive status*. We assessed the reproductive status of 13 358 individual trees to quantify size-dependent probabilities of reproduction. For each species, a size-stratified sample of trees was randomly selected and visited during species-specific reproductive seasons. Reproductive status (fertile or sterile) was evaluated from the ground using binoculars. For eight dioecious species, we evaluated sex expression of all individuals within the FDP. Data were collected between January 1995 and January 1996 for 31 species (Wright et al. 2005), between 2005 and 2007 for 51 wind dispersed species, and between April 2011 and September 2014 for 81 species.

TRAIT DATA

Trait data include seed mass (SM), leaf mass per area (LMA), adult size (D_{max}) and wood density (WD; Table 1; Wright et al. 2010). SM refers to endosperm and embryo dry mass determined after dissecting diaspores to isolate the endosperm and embryo. LMA was determined for shade leaves collected from the upper canopy of the six smallest individuals of each species in the FDP. We could not use sun-exposed leaves as a basis of comparison because most FDP species are treelets that complete their entire life cycle in the shaded understorey (King, Wright & Connell 2006). D_{max} is the mean dbh of the six largest individuals in the FDP (2005 census) and an additional 150 ha of mapped tree plots located within 30 km and mostly within 10 km of BCI. D_{max} is well correlated with maximum tree height ($r = 0.95$ on a log–log scale). Species-specific WD was estimated from tree cores collected within 15 km of BCI, and was calculated as oven-dried (60 °C) mass divided by fresh volume (technically wood specific gravity). Further details can be found in Wright et al. (2010). The four traits are largely independent of one another, with coefficients of determination (R^2 values) of 0·00068, 0·0056, 0·017, 0·052, 0·12 and 0·13 for LMA-D_{max}, SM-WD, WD-D_{max}, SM-D_{max}, LMA-SM and LMA-WD relationships, respectively (Wright et al. 2010).

We normalized trait values to enable model averaging, and facilitate comparison of effect sizes among traits with very different levels of interspecific variation (Grueber et al. 2011), using all 136 species evaluated here. Species-level trait values were normalized, with SM and D_{max} first log-transformed, by subtracting mean trait values and then dividing by the standard deviation of the trait values (Table 1).

STUDY SPECIES

For each life stage and vital rate, we analysed all species with trait data and sufficient demographic data to ensure reasonable precision of species-specific vital rate estimates. Table 2 gives exact selection criteria and the number of species in each analysis. Table S1 (Supporting information) gives the identities of the species in each analysis. Figure S1 shows the distribution of trait values across all species within each analysis.

FITTING TRAIT-BASED MODELS FOR VITAL RATES

We evaluated relationships between size-dependent vital rates and traits, including trait–size interactions, using generalized linear mixed models (GLMMs), with species and individual included as random effects. The most complex full model had the following form:

Table 2. Species selection criteria and sample sizes for each analysis

Analysis	Selection criteria	Number of species	Years
Reproduction (mm dbh)	Reproductive status assessed for >20 trees. Species with too wide confidence intervals were excluded after visual inspection of fit	60 (8891)	1995–2014
Seed production	Species had at least 30 seeds captured in traps, and must have been included in the reproductive analysis to estimate reproductive basal area	38 (NA)	1993–2010
Seedling establishment	30 or more seedling recruits observed between 1995 and 2011, with >30 seeds observed for the fruiting years corresponding to 1995–2011 seedling recruitment (taking account of species-specific germination delays)	68 (NA)	1994–2011
Seedling survival (mm height)	>100 individuals in data set	80 (93 082)	2001–2013
Seedling growth (mm height)	>100 individuals in data set	80 (75 990)	2001–2013
Tree survival (mm dbh)	>100 individuals in data set	117 (267 469)	1990–2010
Tree growth (mm^2 basal area)	>100 individuals in data set	117 (214 373)	1990–2010

Each vital rate under the column 'Analysis' is defined in the text, with corresponding units for size given in parenthesis when the analysis was carried out on individual data. Under 'Number of species', the total number of species in each analysis is given with the total number of individuals between parentheses. This value is 'NA' when the corresponding analysis concerns species-level data. The column 'Years' gives the time span of data used in each analysis. A total of 136 unique species were included across all analyses.

$$y \sim \beta_o + \beta_1 s + \sum_{i=1}^{4} \left(\beta_{i+1} T_i + \beta_{i+5} T_i s \right) + \varepsilon_{\mathrm{sp}} + \varepsilon_{\mathrm{ind}} + \varepsilon_{\mathrm{residual}}$$

$$\mathrm{eqn1}$$

where y is growth, (logit) survival or (logit) reproductive fraction; and s is size in mm height, dbh or mm^2 basal area for analyses of seedlings, reproductive size or tree survival, and growth, respectively. Trait effects including their interactions with size are given by the expression in parentheses, where T_i represents trait i (corresponding to SM, WD, LMA or D_{max}). The random effects of species and individuals are denoted by $\varepsilon_{\mathrm{sp}}$ and $\varepsilon_{\mathrm{ind}}$, respectively, and $\varepsilon_{\mathrm{residual}}$ is the residual error. For each size-dependent vital rate, we fit 82 possible models including eqn. 1 and all subsets involving different combinations of the trait and trait by size effects (Table S2).

Two vital rates, seed production and seedling establishment, were measured and analysed at species level, and we related these to traits directly using generalized linear models (GLMs) without size effects. Here too, we evaluated a suite of models including all subsets of SM, LMA, D_{max} and WD (16 models per vital rate; Tables S3 and S4). Details of model fitting for each vital rate follow.

Reproduction

The size-dependent probability of reproduction was evaluated with a logistic GLMM (eqn. 1 with binomial error) using data set 5.

Seed production

Species-specific seed production (f_{seeds}, seeds per year per m^2 of reproductive basal area) was quantified as the mean flux of seeds arriving (seeds per year per m^2 of trap area) divided by mean reproductive basal area density (m^2 of reproductive basal area per m^2 of plot area). We used seed trap and tree census data from 1993 through 2012. Reproductive basal area was calculated from the tree census data in combination with the fitted logistic models for size-dependent probability of reproduction. The logistic models predicted each individual's reproductive probability as a function of its size. We then weighted each individual's basal area by its reproductive probability to calculate total reproductive basal area. Total reproductive basal area was interpolated between FDP censuses to calculate annual values of f_{seeds}, which were then averaged over years to obtain a single mean value for each species. These simple estimates of seed production were qualitatively similar to more sophisticated estimates obtained using inverse modelling (Text S1, Fig. S2). We chose to use the simple estimates because they were available for more species. Estimates of f_{seeds} were then related to traits using linear regression.

Seedling establishment

Species-specific mean seed to seedling establishment probabilities were calculated as the mean flux of newly recruiting seedlings per year per m^2 in seedling plots in years 1995 to 2012 (data set 3) divided by the mean flux of seeds arriving per year per m^2 in seed traps for the corresponding fruiting years after accounting for germination delays (Wright *et al.* 2005; data set 2). Seedling establishment rates were related to traits using GLMs (i.e. logit transform).

Growth

Growth was modelled as height growth for seedlings (mm per year) and basal area growth for trees (mm^2 per year) using LMMs (eqn 1). We used basal area growth because general additive models (GAMs) showed that basal area growth was generally linearly

related to size (mm^2 basal area). Growth rates were calculated as the difference in sizes divided by the time in years between censuses (data sets 1, 3 and 4). For data set 1, we excluded individuals marked as 'resprout', 'buttressed', 'leaning' and 'broken above 1·3 m' in each census, as well as those with growth rates more than four 4 standard deviations from the mean. These are likely measurement errors (Rüger *et al.* 2011).

Survival

The size-dependent (mm height and mm dbh for seedlings and trees, respectively) probability of survival was evaluated with a logistic GLMM (eqn 1 with binomial error) using data sets 1, 3 and 4.

We used model averaging to calculate average parameters (Burnham & Anderson 2002). All models were assigned a weight based on their AIC score and fitted parameters were averaged over the full set of models using these weights to obtain a final average model. The final average model provides a basis to compare effect sizes. Model averaging is superior to selecting the best model because models with similar fits are not ignored (Burnham & Anderson 2002; Whittingham *et al.* 2006; Bolker *et al.* 2009). For this reason, model averaging provides a more robust basis for inference and prediction, reducing bias in estimation of effect sizes, especially in cases where multiple variables influence the response variable (Grueber *et al.* 2011). This contrasts with stepwise multiple regression, which is seen as poorly suited to disentangle contributions of multiple traits to vital rates (Wittingham *et al.* 2006). We averaged parameters over all models having AIC weights >0 using the 'zero method' in which parameters are assigned the value zero where absent from models. This is a conservative approach to model averaging (i.e. leading to lower effect sizes) and is recommended when comparing effect sizes among variables (Burnham & Anderson 2002; Grueber *et al.* 2011). Confidence intervals for each weighted parameter were estimated following Buckland, Burnham & Augustin (1997).

We evaluated model fits to the full data sets, including variation among individuals, using marginal and conditional R^2 values developed for mixed-effects models (Nakagawa & Schielzeth 2013). These R^2 values provide information on how well the trait-based hierarchical models (the GLMMs) explain individual-level variation in vital rates over all species in the community. To evaluate linearity, we plotted model residuals against size for each model (Fig. S3). Residuals deviated from linearity for seedlings taller than 2·5 m and for trees with dbh >50 cm in the growth and survival analyses. To ensure linearity, we therefore excluded trees with dbh >50 cm and seedlings taller than 2·5 m (corresponding to 0·41% and 0·47% of the data, respectively). Nonlinearity was not detected in our reproduction analysis. All analyses were performed in R 3.1.1 (R-core 2014), making use of the LME4 package for mixed-effects models (Bates *et al.* 2015). An example R-code is provided for model averaging (Appendix S2).

THE POWER OF TRAITS TO EXPLAIN INTERSPECIFIC VARIATION

We performed a second set of analyses to estimate the contributions of traits to explaining *interspecific* variation in demographic rates at particular sizes, and thereby to enable more direct comparisons of our results with earlier studies based on species-level estimates of vital rates (Poorter *et al.* 2008; Wright *et al.* 2010; Iida *et al.* 2012). We first calculated trait-based predictions for each species and each vital rate based on the fitted average models. We then compared these predictions with observed mean

vital rates and calculated associated R^2 values. For seed production and seedling establishment, these comparisons used observed species-specific mean rates. For size-dependent vital rates (growth, survival, reproduction), we estimated species-specific moving averages using generalized additive models (GAMs; example code in Appendix S2), which make no prior assumptions on the functional shape of the relationship (Figs S4–S8). We then estimated size-specific R^2 values in three steps: (i) species-specific mean rates were given from GAM predictions for each vital rate at size points ranging from 0 to 1·5 m height for seedlings and from 1 to 25 cm dbh for trees (at these size ranges, analyses always included 15 or more species); (ii) demographic rates for these sizes were predicted using only fixed effects from each averaged trait models; and (iii) we calculated R^2 values for correlations between trait-based and GAM estimated mean rates at each size. To evaluate the predictive power of individual single traits, we repeated the calculation of R^2 values for single-trait average models for every trait, where single-trait models were based on averaging over models including only size, the single focal trait and/or the trait–size interaction as predictors. Single-trait models represent the best-case scenario, in terms of R^2, when using a single trait.

SEPARATE ANALYSES AT EVERY SIZE

Out of an abundance of caution, we performed a final analysis to guard against the possibility that underlying assumptions of linear relationships with size or the random effects structure in the mixed-effects model may unduly influence results. The (G)LMMs allow only linear relationships between vital rates and size, and might misstate the influence of predictors if there are underlying nonlinearities with size. Additionally, to improve computational feasibility, we included only random species intercepts, but ignored random slopes with size, which potentially may impact effect sizes (Schielzeth & Forstmeier 2009). To address these concerns, we evaluated relationships between traits and species-specific vital rates separately for each size. We fit GLMs (sets of 16 models, as shown in Tables S3 and S4) to species mean rates (estimated from the GAMs) for seedlings between 0 and 1·5 m tall and trees between 1 and 25 cm dbh. We then compared effect sizes and R^2 values with the mixed-effect models (eqn 1). This analysis allows for varying intercepts, slopes and functional shapes between size and vital rates for each species. However, the analysis is also far less parsimonious and weights all species equally regardless of sample size and hence is likely to overestimate the strength of trait–vital rate relationships. When results are qualitatively similar this indicates no major problems with our assumptions. In this case, our initial analyses (eqn 1) are less biased for inference and yield the greatest predictive accuracy (Gelman 2006).

Results

Our analyses included 136 different species, with 38 to 117 species for each vital rate (Table 2). The full range of trait values observed among BCI trees was well represented for each vital rate (Fig. S1). The species included a wide range of growth forms (shrubs to understorey and canopy trees), seed dispersal mechanisms (ballistic, wind, mammals and/or birds), and relative abundances [from 13·5% (*Faramea occidentalis*) to 0·29% (*Hampea appendiculata*) of all stems in the FDP]. WD, SM, LMA and D_{max} varied by 0·5, 5·7, 2·3 and 2·2 orders of magnitude, respectively (Table 1).

SEED PRODUCTION

The average model for seed production was based on nine models with nonzero weights (weights above 0·001; Table S3), included all four traits and explained 65% of interspecific variation (Table 3). Seed production was negatively related to SM (slope −1·13; Table 3, Fig. 1a) with all other traits having approximately 7–50 times smaller effect sizes (Table 3, Fig. 1a).

SEEDLING ESTABLISHMENT

The average model for seedling establishment was based on four models with nonzero weights (weights above 0·001; Table S4), included all four traits and explained 66% of interspecific variation (Table 3). Seedling establishment increased with seed mass (slope 1·32; Table 3, Fig. 1b) and decreased with D_{max} (slope −1·06; Table 3, Fig. 1b). LMA and WD hardly influenced seedling establishment rates (Table 3, Fig. 1b).

SEEDLING GROWTH RATES

The average model for seedling growth rates was based on nine models with nonzero weights (weights above 0·001; Table S5). It included all four size–trait interactions and explained 10% of the individual-level variation, with the fixed effects of size, traits and their interactions explaining only 1% of the individual growth variation (Table 3). Seedling growth rates decreased with SM and WD, with smaller effects for larger seedlings (Table 3, Fig. 2a,b). LMA and D_{max} hardly influenced seedling growth rates (Fig. 2c,d).

SEEDLING SURVIVAL RATES

The full model, including all size–trait interactions, contained 100% of the weight for seedling survival (Table S6). This model explained 25% of the individual-level variation in seedling survival, with the fixed effects of size, traits and their interactions explaining 16% of the individual variation (Table 3). Seedling survival increased with WD and decreased with D_{max}, and these effects diminished with seedling size (Fig. 2f,h). The direction of relationships between seedling survival and SM and LMA changed with seedling size (Fig. 2e,g). For small seedlings, survival was greater for species with smaller seeds and larger LMA. For larger seedlings, survival was greater for species with larger seeds and smaller LMA.

TREE GROWTH RATES

The full model, including all size–trait interactions, also contained 100% of the weight for tree growth rates (Table S7). This model explained 66% of the individual-level variation in tree growth, with the fixed effects of size, traits and their interactions explaining 26% of the individual variation (Table 3). Tree growth rates decreased with

Table 3. Coefficients (and standard errors) from the full averaged model for each of the evaluated vital rates (columns)

	Seed production	Seedling establishment	Seedling growth	Tree growth	Seedling survival	Tree survival	Reproduction
Intercept	**−2·95 (0·0781)**	**−3·21 (0·0816)**	**42 (2·07)**	**108 (8·7)**	**1·31 (0·0582)**	**2·19 (0·0663)**	**−3·71 (0·0939)**
SM	**−1·13 (0·0618)**	**1·32 (0·0866)**	**−11·1 (2·31)**	**−22·5 (9·5)**	−0·22 (0·065)	**0·387 (0·0722)**	**−0·226 (0·0724)**
WD	0·0152 (0·0312)	0·0137 (0·0349)	**−13 (2·2)**	**−70·4 (9·79)**	**0·451 (0·0607)**	**0·536 (0·0748)**	0·123 (0·0693)
LMA	−0·166 (0·0844)	−0·00413 (0·035)	−0·0605 (2·32)	−2·19 (9·41)	**0·204 (0·0665)**	**0·249 (0·0724)**	**−0·281 (0·0875)**
D_{max}	−0·0247 (0·0448)	**−1·06 (0·0826)**	0·434 (1·96)	**36·6 (9·97)**	**−0·348 (0·0578)**	**−0·297 (0·0758)**	**−0·386 (0·11)**
Size			**−0·0124 (0·000477)**	**0·00934 (7·63e-05)**	**0·00116 (2·34e-05)**	**−0·00282 (0·000116)**	**0·0174 (0·000224)**
Size : SM			**0·00479 (0·000332)**	**−0·00031 (3·14e-05)**	**0·000458 (2·1e-05)**	**−0·000976 (9·73e-05)**	**0·000675 (5·99e-05)**
Size : WD			**0·00496 (0·000596)**	**0·000858 (4·83e-05)**	8·65e-06 (1·52e-05)	**−0·00121 (0·000107)**	−0·000109 (7·53e-05)
Size : LMA			**0·00112 (0·000772)**	**−0·000946 (5·03e-05)**	**−0·000529 (3·04e-05)**	**−0·000642 (0·000104)**	−0·000143 (9·62e-05)
Size : Dmax			−1·98e-05 (2·29e-05)	**0·00255 (9·66e-05)**	**0·000272 (2·25e-05)**	**0·00581 (0·000161)**	**−0·000877 (0·000197)**
R^2_{size}			0·0015	0·1676	0·0321	1e-04	0·1775
R^2_{fixed}			0·0084	0·2591	0·1581	0·0654	0·2469
$R^2_{species}$			0·0776	0·4015	0·2507	0·187	0·5063
$R^2_{individual}$			0·0343	0·5172	0·1581	0·0654	0·3451
R^2_{full}	0·65	0·66	0·1035	0·6595	0·2507	0·187	0·6045

Bold face indicates confidence intervals not including zero ($a < 0.05$). The measure of size was height (mm) for seedlings, dbh (mm) for survival and reproduction, and basal area for growth (mm²). Complete lists of evaluated models with AIC values and AIC weights are given in Tables S4–S9. With the exception of seed production and seedling establishment, the R^2 values in the table are specific to mixed-effects models (Nakagawa & Schielzeth 2013), and reflect the fit of the model including fixed effects of size only ('R^2_{size}'), fixed effects of size and traits ('R^2_{fixed}'), fixed and species random effects ('$R^2_{species}$'), fixed and individual random effects ('$R^2_{individual}$'), and the full mixed model ('R^2_{full}'). Trait variables were normalized prior to model fits.
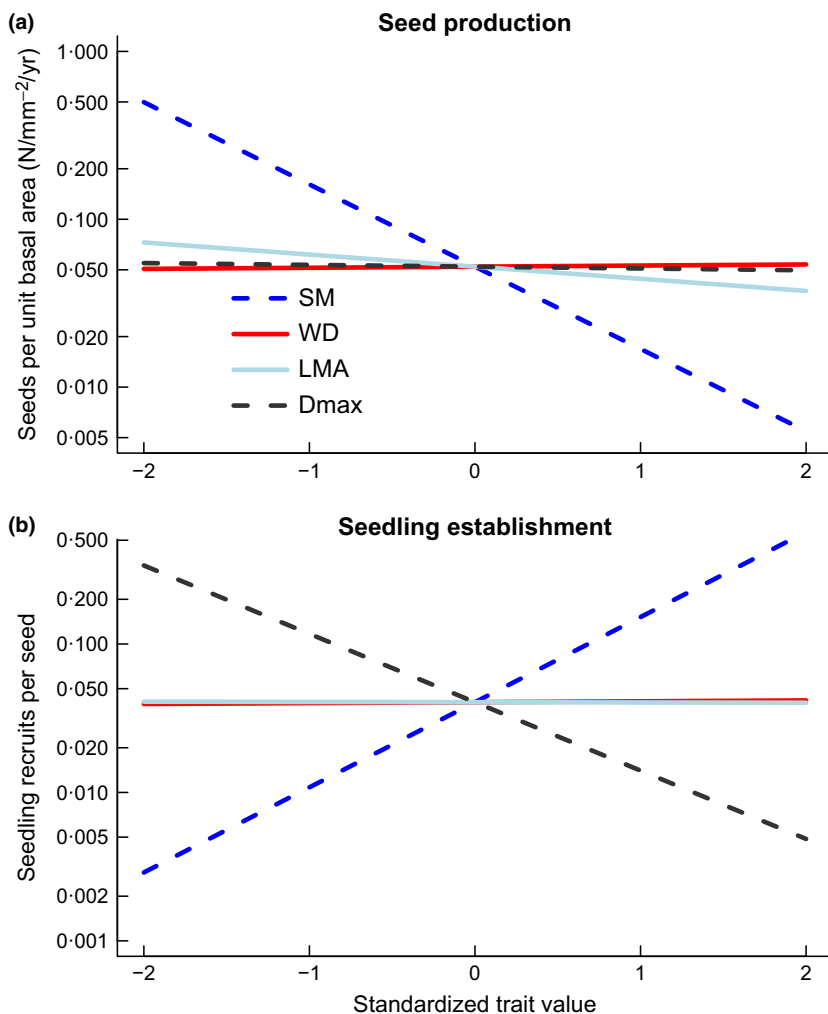
Fig. 1. Fitted effects of deviations in seed mass (SM), wood density (WD), leaf mass per area (LMA) and maximum stature (D_{max}) from their mean values on seed production (a), and the rate of seedling establishment (b) when other traits are held at their mean values. Predictions are plotted against standardized trait values (standard deviations from the mean). Observed trait value means and standard deviations are given in Table 1. Panels a and b show that traits can have opposing effects not only between life stages (SM in a and b) but also between different traits within a single life stage (D_{max} and SM in Panel b).

WD and increased with D_{max} (Table 3, Fig. 2j,l). The effect of WD decreased with tree size (Fig. 2j), and the effect of D_{max} increased with tree size (Table 3, Fig. 2l). SM and LMA had much smaller effects on tree growth rates (Fig. 2I,k).

TREE SURVIVAL RATES

The full model, including all size–trait interactions, contained 99·7% of the weight for tree survival rates (Table S8). The average model explained 19% of the individual-level variation in seedling survival, with the fixed effects of size, traits and their interactions explaining 7% of the individual variation (Table 3). Tree survival was strongly influenced by D_{max}, and was generally larger for species with larger D_{max} (Fig. 2p). Tree survival was also greater for species with larger SM, WD and LMA over nearly the full range of tree sizes, with the exception of the very largest individuals (Fig. 2m–o).

REPRODUCTION

Nine models with nonzero weights contributed to the average model for reproduction (Table S9), which included all size–trait interactions and explained 60% of the individual-level variation, with the fixed effects of size, traits and their interactions explaining 25% of the variation (Table 3 and Table S9). D_{max} had the largest effect on reproductive status, with larger-statured species becoming reproductive at larger sizes than smaller-statured species (Fig. 2t). The threshold size at which 50% of individuals are reproductive is well predicted by the following simple equation: $R_{50} = \frac{1}{2}D_{max}$ ($R^2 = 0.81$; Fig. S9).

THE POWER OF TRAITS TO EXPLAIN INTERSPECIFIC VARIATION

Figure 3 summarizes the proportion of *interspecific* variation in vital rates explained by D_{max}, LMA, SM and WD throughout tree life cycles on BCI. These proportions are consistently higher than the proportions explained by traits and size in the GLMMs (Table 3) because the latter includes additional variation among individuals. The R^2 values for each trait separately are presented in Tables S10–12.

SEPARATE ANALYSES AT EVERY SIZE

Traits had qualitatively similar influences on vital rates (Fig. S10) and explained similar proportions of interspecific
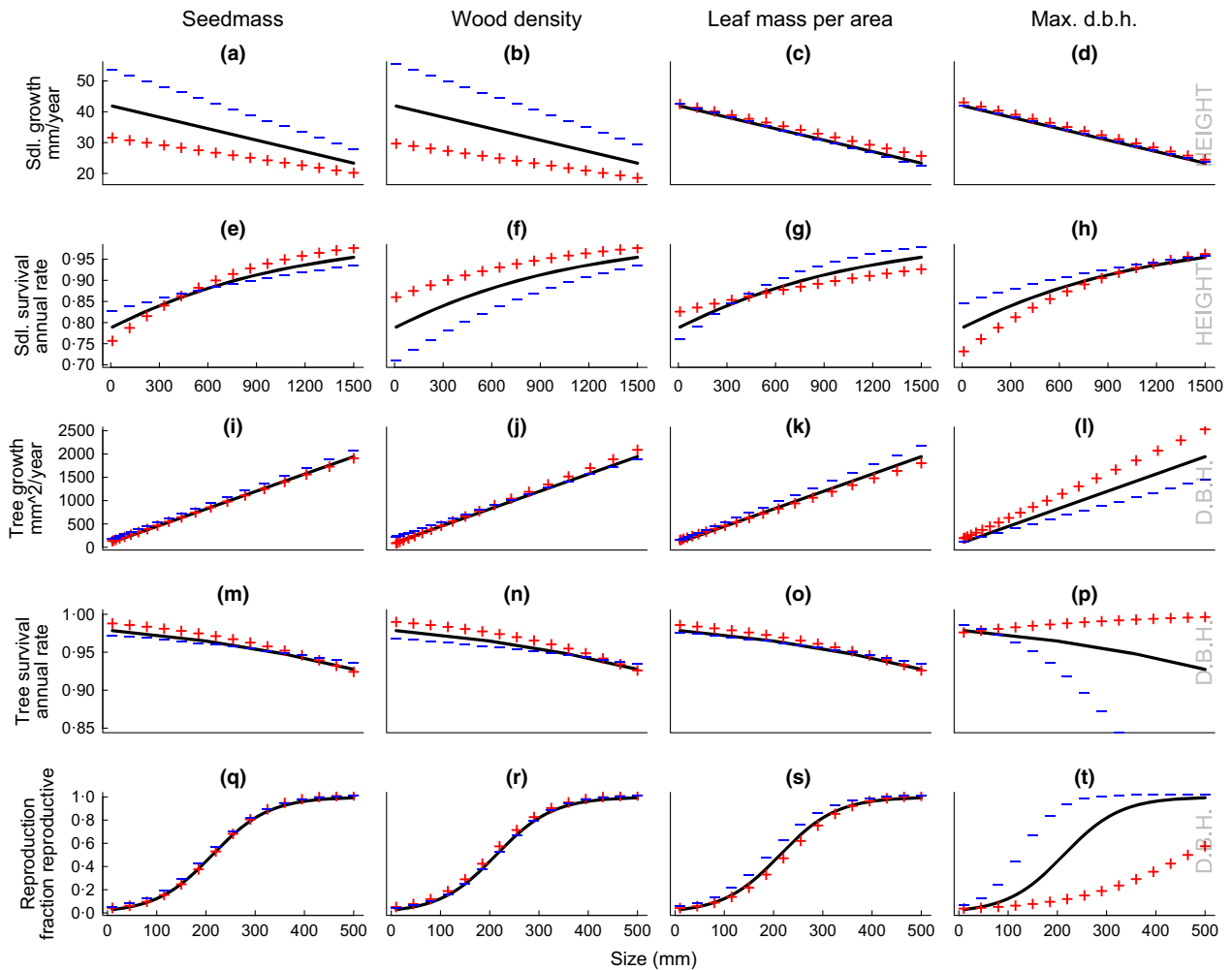
Fig. 2. Fitted effects of each trait (columns) on size-dependent vital rates (rows) in the averaged models. The black lines present the vital rate–size relationships with all traits set to their mean values. The red plus signs and blue minus lines present the same relationships with one trait set to its mean plus or minus one standard deviation, respectively, and the three remaining traits set to their mean values. The trait whose value varies among the blue, black and red lines is named at the top of each column. Observed trait value means and standard deviations are given in Table 1. Grey text at the right outermost column gives the corresponding measure of size (in mm) for each row of panels. The figure shows that the effect sizes corresponding to different traits differ greatly throughout the life cycle of trees among species, as shown by the + and − lines from the top to the bottom of the graph.

variation (Fig. S11) in analyses that fit separate models for every size and in our main analyses.

Discussion

We systematically quantified trait–demography relationships across the entire life cycle of multiple co-occurring species of tropical trees for the first time while incorporating individual-level, size-dependent variation in growth, survival and reproduction (Table 3, Fig. 2). Full models, including random effects for individuals and species, explained 10–25% of the overall variation for seedling growth, seedling survival and tree survival (Table 3). Factors missing from our models clearly affect these three vital rates. Likely candidates include abiotic and biotic environmental variation associated with soils, local competitive effects and plant pests. The full models performed much

better for tree growth rates and reproductive status, explaining 66% and 60% of overall variation, respectively. The fixed effects of size, wood density (WD), seed mass (SM), leaf mass per area (LMA), adult size (D_{max}) and interactions between size and traits explained 1–26% of the variation observed over all individuals of all species for the five size-dependent vital rates (Table 3). Our trait-based average models explained between 4% and 65% of *interspecific* variation in mean size-specific demographic rates, depending on the size and demographic rate, with more variation explained for small than for large size classes (Fig. 3). In comparison with previous studies of species-level trait–demography relationships among tropical trees (Poorter *et al.* 2008; Wright *et al.* 2010; Iida *et al.* 2012, 2014a), our analyses provide clear improvements in predictive power and new insights into how effects vary with size.
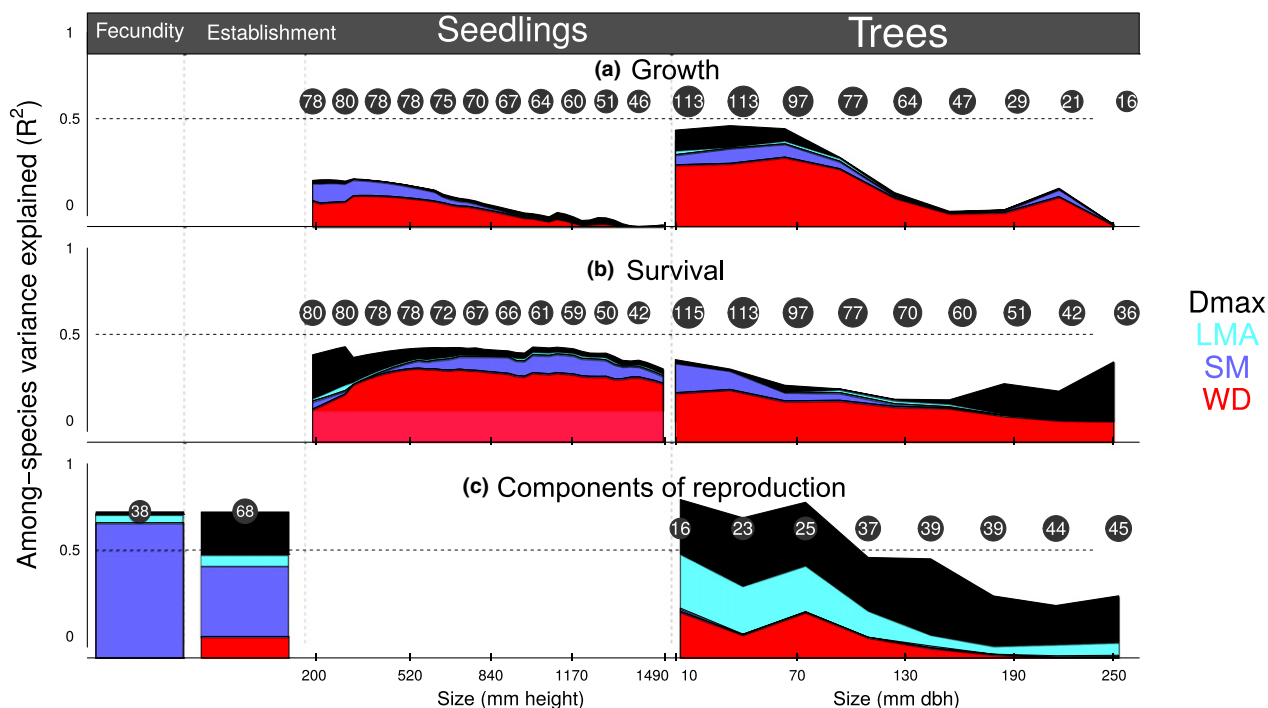
Fig. 3. The proportion of interspecific variation in various demographic rates explained by the four functional traits throughout the life cycle, as measured by R^2 values. The rows show results for (top to bottom) size-dependent growth, size-dependent survival, and vital rates associated with reproduction. The R^2 value at the upper edge of the stacked colours represents the proportion of the total variation among species explained by the fixed effect terms in the full averaged model (i.e. including traits D_{max}, LMA, SM and WD), where the observed values for each species are based on species-specific GAMs. The relative importance of different traits is indicated by the relative height of each colour band as a proportion of the total, with height scaled to the R^2 values for averaged models including only one trait (i.e. including only D_{max}, LMA, SM or WD; Tables S10–12). The number of species included in the analyses varies with size; for reference, the numbers of species included at various sizes are shown in solid circles above each graph. Variation in vital rates explained among species shows that seed mass is initially influential but diminishes in importance with wood density becoming more important.

WOOD DENSITY

Higher WD is associated with higher resistance to hydraulic failure and to decay and with higher structural strength for a given diameter, but at the cost of slower diameter growth rates (reviewed by Chave *et al.* 2009). Previous studies concur that wood density (WD) is the single trait best able to predict growth and survival among tropical tree species, with coefficients of determination (R^2) averaging 0·093 (±0·077 SD) and 0·076 (±0·079 SD) for relationships with growth and survival, respectively (using the maximum R^2 values reported in Poorter *et al.* 2008; Wright *et al.* 2010; Iida *et al.* 2014a,b). Our size-specific coefficients of determination, which were always greater for wood density than for other traits for analyses of growth and survival (Table 3), are consistent with this conclusion. Wood density had progressively less predictive power for the survival and growth of larger trees, which is consistent with previous comparisons of broad sizes classes (Poorter *et al.* 2008; Wright *et al.* 2010). The benefits and costs associated with variation in WD affect basal area growth and survival directly, but have negligible effects on reproduction, seed production and seedling establishment (Fig. 3).

In interpreting the relationship of WD to growth and survival at constant diameter or constant height in this and other studies, it is important to keep in mind that these relationships are dependent upon the size (and growth) currency used as the basis for comparison. The same 'size' in diameter or height is associated with larger biomass in higher WD species, and the same biomass growth translates to less diameter, basal area, and height growth in higher WD species (Larjavaara & Muller-Landau 2010). Relationships of growth with WD may weaken or even disappear when growth is expressed on the basis of biomass instead of diameter (Rüger *et al.* 2012). Thus, the strong relationships of growth with WD might in part be seen as an artefact of our choice of currency, much as mass-normalized leaf traits show stronger interrelationships than area-normalized leaf traits (Osnas *et al.* 2013). Similarly, the use of height and diameter as measures of size might introduce bias towards positive relationships between survival and WD, because the same 'size' in diameter or height is associated with larger biomass in higher WD species, and survival increases with biomass on BCI (Muller-Landau *et al.* 2006). Future analyses should evaluate how much variation in growth and survival is explained by WD when these currency effects are eliminated.

SEED MASS

Previous studies and our analyses (Fig. 3) concur that seed mass (SM) explains minimal variation in growth and survival among tropical trees (R^2 averages 0.002 ± 0.0022 SD and 0.101 ± 0.041 SD, respectively; Fig. 3; Poorter *et al.* 2008; Wright *et al.* 2010). This is unsurprising because seed reserves and direct effects of seed size are exhausted well before the large minimum sizes (≥ 1 cm dbh) used to delimit trees. Those relationships with SM that remain at these large sizes reflect indirect effects, whose unknown causation must involve unrecognized correlations among traits and life histories.

SM has much stronger effects at the earliest stages of regeneration. SM was strongly negatively related to seed production and strongly positively related to seedling establishment on BCI (Fig. 1). This is consistent with the well documented trade-off between seed quantity and per-seed investment (Henery & Westoby 2001; Muller-Landau 2010). SM also influenced seedling performance. Small-seeded species consistently grew faster than large-seeded species, although this effect diminished with seedling size (Fig. 2a). Small-seeded species also had lower survival rates than large-seeded species, but only at larger seedling sizes. Among the smallest seedlings, small-seeded species actually had higher survival rates than large-seeded species (Fig. 2e). Environmental variation associated with germination sites likely confounds all of these relationships (Lichstein *et al.* 2010; Muller-Landau 2010). Small-seeded species tend to establish in the least stressful locations, and those locations improve subsequent performance. Large-seeded species are able to establish in more competitive environments, which limit subsequent performance. On a population level, this causes smaller-seeded species to have lower establishment rates, because appropriate resource-rich sites are infrequent, and larger growth and survival rates than larger-seeded species that establish widely in less favourable environments. Clearly, observed vital rates are influenced not only by species traits, but by the habitats in which individuals are found (i.e. environmental filtering; Lasky *et al.* 2013). We discuss this issue in more detail below.

LEAF MASS PER AREA

Previous studies and our results concur that LMA explains minimal variation in growth and survival among tropical trees (R^2 averages 0.08 ± 0.025 SD and 0.11 ± 0.071 SD, respectively; Fig. 3, this study; Poorter *et al.* 2008; Wright *et al.* 2010; Iida *et al.* 2014b). LMA is thought to be a minor factor affecting carbon gain in larger trees where crown architecture determines light interception (Sterck & Bongers 2001). Surprisingly, LMA was also vanishingly unimportant for seedling establishment, growth and survival (Figs 1b, 2c,g and 3). LMA had non-negligible correlations only with reproductive status, with species with lower LMA tending to reproduce at smaller sizes (Figs 2 and 3). This relationship between LMA and reproductive status provides another example, as with seed mass, of an indirect effect, whose unknown causation must involve unrecognized correlations among traits and life histories.

There are at least two possible reasons for the negligible relationships of LMA with seedling growth and survival (Figs 2c,g and 3). First, our LMA values are for saplings (≥ 1 cm dbh), and seedling LMA values may differ. Previous studies show that leaf traits at juvenile and adult stages are generally strongly correlated (Iida *et al.* 2014a); however, as LMA measurements for recently established seedlings remain rare, we cannot discount ontogenetic changes in LMA between seedlings and saplings (Spasojevic *et al.* 2014). LMA values determined for seedlings might yet yield stronger relationships between LMA and seedling performance. A second possible cause of weak relationships between LMA and growth and survival applies to both seedlings and trees. Costs and benefits associated with LMA variation might balance, yielding similar growth and survival rates on a population level. Low LMA species tend to have low construction costs and large leaf turnover rates, whereas high LMA species tend to have larger construction costs and lower leaf turnover rates (Wright *et al.* 2004). This may result in similar net carbon gain over time, minimizing potential relationships between LMA and demographic rates.

ADULT STATURE

Previous studies and our results concur that larger-statured species have larger growth and survival rates among tropical trees (Fig. 2l,p) R^2 values average 0.11 ± 0.039 SD and 0.2 ± 0.066 SD, respectively (using the maximum of reported R^2 values; Fig. 3; Poorter *et al.* 2008; Wright *et al.* 2010; Iida *et al.* 2014a,b). This led to the conclusion that smaller-statured species have lower survival and growth rates as they may have less access to light (Poorter *et al.* 2008; Wright *et al.* 2010; Iida *et al.* 2014a). We see opposing effects on seedlings, however, with taller species at an inherent disadvantage in early life (King, Wright & Connell 2006). Seedling establishment and survival decreased with increasing adult stature (Figs 1b and 2h). These opposing relationships between maximum size and performance between life stages are a condition for coexistence in the 'forest architecture hypothesis'. Large-statured species will out-compete smaller species, if not handicapped during establishment (Kohyama 1993). The handicap observed among large-statured species during establishment might be related to a trade-off between allocation to traits and architectures that enable survival in the forest understorey vs. rapid vertical growth towards the canopy (for a more detailed discussion see Kohyama *et al.* 2003; Poorter *et al.* 2005).

D_{max} was the single most influential trait explaining interspecific variation in reproductive size thresholds (cf. Fig. 2q–s vs. 2t). Species that grow larger only begin to reproduce at larger sizes. The threshold size for reproduction

also increased for taller species in a Malaysian forest (Thomas 1996; Davies & Ashton 1999). For BCI trees, the simple equation $R_{50} = ½D_{max}$ explains 81% of interspecific variation in reproductive size thresholds (Fig. S9). That is, at the time individuals attain half of their species' maximum observed diameter, they have a 50% probability of being reproductive. This is consistent with expectations from game theory models (reviewed by Falster & Westoby 2003), which predict that to maximize reproductive output individuals should first invest heavily in growth, and then only after reaching an optimal size start to invest in reproduction. Extending this, we would expect large-statured species to become reproductive only when they attain a position in the forest canopy (Thomas 1996; Zuidema & Boot 2002), while smaller understorey species will likely reproduce when they obtain optimal crown depth (Kohyama *et al.* 2003) or foliage cover. However, whether this optimal size on average corresponds to the $½D_{max}$ size threshold reported here remains to be tested.

TRAITS AS QUANTITATIVE PREDICTORS OF TREE DEMOGRAPHY

Westoby (1998) suggested that specific leaf area (the inverse of LMA), seed mass and adult stature are three readily measurable traits that represent important dimensions of variation in plant ecology. Our results suggest that, at least for tropical forests, a more promising combination would be adult stature, seed mass and wood density. In our study system, adult stature, seed mass and wood density (but not LMA) each explained substantial interspecific variation in particular vital rates or particular life stages (Fig. 3). Nevertheless, a large proportion of interspecific and individual variation remained unexplained (Table 3 and Fig. 3). Why is the explained variation not higher, and what are the implications for the functional trait research agenda?

Variance partitioning suggests that a considerable fraction of the unexplained interindividual variation is due to species effects not captured by the functional traits included in this study. Variance partitioning quantifies the unexplained variation and, thus, the potential for additional factors to explain variation at each grouping level. Mixed-effects models allow variance partitioning (Bolker *et al.* 2009), and we calculated conditional R^2 values to quantify variation explained at the individual and species levels (Nakagawa & Schielzeth 2013). The addition of species random effects increased conditional R^2 values on average by a factor of 3·2 (compare R^2_{fixed} with $R^2_{species}$ in Table 3). This demonstrates that substantial unexplained interspecific variation remains, variation that might potentially be explained by additional traits. However, species–environment associations might also contribute to unexplained interspecific variation (Messier, McGill & Lechowicz 2010; Lasky *et al.* 2013).

Variation in plant performance among individuals depends strongly on local environment as well as on species traits and their interaction (Uriarte *et al.* 2016). Local environmental variation includes both abiotic factors such as soil nutrients (Condit *et al.* 2013) and water availability (Comita & Engelbrecht 2009), and biotic factors such as local competitive neighbourhoods (Uriarte *et al.* 2004). Such environmental variation is not explicitly included in our models, and thus contributes to variation among individuals captured here by individual-level random effects. Environmental variation can also confound interspecific comparisons of vital rates (Lichstein *et al.* 2010; McMahon, Metcalf & Woodall 2011; Baraloto *et al.* 2012). For example, in closed canopy tropical forests, small-seeded species only establish successfully in relatively high light microsites and higher light levels then contribute to higher initial growth and survival rates (Fig. 2a,e). Inclusion of more information on key environmental covariates for each individual would make it possible to control for any systematic differences in environments among species, and thereby better estimate the true effects of traits on performance (Paine *et al.* 2011; Lasky *et al.* 2014). Other sources of variation will remain stochastic and unpredictable. These include negative height growth due to stem breakage for seedlings (e.g. from falling branches), which happens regularly on BCI (Paciorek *et al.* 2000).

Our full-life cycle approach shows that individual traits can have opposing effects on different vital rates. This raises the possibility that effects at one life stage or vital rate may be offset by opposite effects at another life stage or vital rate. Robust ecological and evolutionary conclusions, based on findings at single life stages or vital rates, will therefore depend on how effect sizes translate to net effects over the full life cycle. Trait-based models that map full-life cycle demographic patterns across trait axes (Figs 1 and 2) may help resolve full-life cycle effects. For instance, when an empirical study finds an effect of increased seed production – which comes at the cost of reduced seed size – trait-based models can be used to calculate whether a net positive effect on seedling recruitment can be expected. A trait-based framework may even be used in a population modelling context (*sensu* Visser *et al.* 2011; Merow *et al.* 2014), to calculate expected net effects when information on the whole life cycle is lacking. In this context, a full-life cycle trait-based approach may add value to ecological research by enabling robust assessments of relationships between traits and population fitness.

The holy grail of the functional traits research agenda is the identification of easily measured traits that are good predictors of life history and demographic performance, and the parameterization of associated models for inferring life history and demography from these traits. With increasing amounts of vital rate variation across species explained, researchers start daring to ask the exciting question of whether trait-based vital rate models can be used to interpolate vital rates for species for which they have trait information but lack demographic data. Such interpolations would increase the number of species that can be included in Earth system models and community-wide studies. How certain do we have to be about these interpolations for the

resulting multispecies analyses to be trustworthy? Our analyses still show a large proportion of unexplained interspecific variation, implying that trait-based models should be used with caution. Nevertheless, we have shown that a single individual measurement (size) and three species-level traits (D_{max}, SM and WD) explained on average 41% of interspecific variation in vital rates (mean R^2 ranged between 0·11 and 0·66; Fig. 3), despite unquantified environmental effects on vital rates. This is quite remarkable and represents a substantial improvement over earlier studies. Functional biology may yet improve understanding of tropical forest dynamics.

Acknowledgements

Data accessibility

Previously archived BCI data set is available from Dryad (datadryad.org) or the Smithsonian DSpace repository (repository.si.edu). Data sets 1, 2, 3 and 5 are achieved at DSpace with DOIs 10.5479/data.bci.20130603, 10.5479/si.data.201511251137, 10.5479/si.data.201511251134 and 10.5479/si.data.201511251100, respectively, while data set 4 is archived at Dryad http://dx.doi.org/10.5061/dryad.fm654 (Visser *et al.* 2016).

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Supporting Information

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

Appendix S1. Including Tables S1–S12, Figures S1–S11 and Text S1.

Appendix S2. R-code example for model averaging.