100 YEARS Journal of Ecology
British Ecological Society

Journal of Ecology doi: 10.1111/1365-2745.12401

Globally, functional traits are weak predictors of juvenile tree growth, and we do not know why

C. E. Timothy Paine[1]*, Lucy Amissah[2,3], Harald Auge[4,5], Christopher Baraloto[6,7], Martin Baruffol[8], Nils Bourland[9], Helge Bruelheide[5,10], Kasso Daïnou[9], Roland C. de Gouvenain[11], Jean-Louis Doucet[9], Susan Doust[12], Paul V. A. Fine[13], Claire Fortunel[6,14], Josephine Haase[15,16], Karen D. Holl[17], Hervé Jactel[18,19], Xuefei Li[8], Kaoru Kitajima[7,20,21], Julia Koricheva[22], Cristina Martínez-Garza[23], Christian Messier[24], Alain Paquette[25], Christopher Philipson[16], Daniel Piotto[26], Lourens Poorter[2], Juan M. Posada[27], Catherine Potvin[20,28], Kalle Rainio[29], Sabrina E. Russo[30], Mariacarmen Ruiz-Jaen[28], Michael Scherer-Lorenzen[15], Campbell O. Webb[31], S. Joseph Wright[20], Rakan A. Zahawi[32] and Andy Hector[33]

[1]Biological and Environmental Sciences, University of Stirling, Stirling FK9 4LA, UK; [2]Forest Ecology and Forest Management Group, Wageningen University, P.O. Box 47, 6700 AA, Wageningen, The Netherlands; [3]Council for Scientific and Industrial Research-Forestry Research Institute of Ghana, P.O. Box UP63, KNUST, Kumasi, Ghana; [4]Department of Community Ecology, UFZ, Helmholtz Center for Environmental Research, Halle D-06120, Germany; [5]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig D-04103, Germany; [6]INRA, UMR "Ecologie des Forêts de Guyane", Kourou Cedex 97387, French Guiana; [7]International Center for Tropical Botany, Department of Biological Sciences, Florida International University, Miami, FL 33199, USA; [8]Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstr. 190, Zürich CH-8057, Switzerland; [9]Laboratory of Tropical and Subtropical Forest Regions, Unit of Forest and Nature Management, Gembloux Agro-Bio Tech, University of Liège, Liège, Belgium; [10]Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle Wittenberg, Am Kirchtor 1, Halle D-06108, Germany; [11]Department of Biology, Rhode Island College, 600 Mount Pleasant Ave, Providence, RI, USA; [12]Australian Antarctic Division, Channel Highway, Kingston, TAS 7050, Australia; [13]Department of Integrative Biology, University of California, Berkeley, CA, USA; [14]Department of Biology, University of Maryland, College Park, MD, USA; [15]Faculty of Biology, Geobotany, University of Freiburg, Schaenzlestr. 1, Freiburg D-79104, Germany; [16]Ecosystem Management, Institute of Terrestrial Ecosystems, ETH Zurich, Universitätsstr. 16, Zurich CH-8092, Switzerland; [17]Environmental Studies Department, University of California, Santa Cruz, CA 95064, USA; [18]INRA, UMR1202 BIOGECO, Cestas F-33510, France; [19]Univ. Bordeaux, UMR1202 BIOGECO, Talence F-33400, France; [20]Smithsonian Tropical Research Institute, Apartado, Balboa 0843–03092, Panama; [21]Forest Biomaterial Science, Kyoto University, Kitashirakawa Oiwake-cho, Sakyo-ku, Kyoto, Japan; [22]School of Biological Sciences, Royal Holloway University of London, Egham, Surrey TW20 0EX, UK; [23]Universidad Autónoma del Estado de Morelos, Centro de Investigación en Biodiversidad y Conservación, Universidad 1001, Colonia Chamilpa, Cuernavaca, Morelos 62209, Mexico; [24]Center for Forest Research and ISFORT, Université du Québec à Montréal et Université du Québec en Outaouais, PO Box 8888, Centre-Ville Station, Montréal, QC H3C 3P8, Canada; [25]Center for Forest Research, Université du Québec à Montréal, PO Box 8888, Centre-Ville Station, Montréal, QC H3C 3P8, Canada; [26]Universidade Federal do Sul da Bahia, BR 415 Km 39, Ferradas Itabuna-BA 45613-204, Brazil; [27]Biology Program, Faculty of Natural Sciences and Mathematics, Universidad del Rosario, Carrera 24 No. 63C-69, Bogotá 111221, Colombia; [28]Department of Biology, McGill University, 1205 Dr Penfield, Montréal, QC, H3A 1B1, Canada; [29]Section of Ecology, Department of Biology, University of Turku, Turku FI-20014, Finland; [30]School of Biological Sciences, University of Nebraska, 208 Manter Hall, Lincoln, NE 68588, USA; [31]Arnold Arboretum of Harvard University, 1300 Centre Street, Boston, MA 02131, USA; [32]Las Cruces Biological Station, Organization for Tropical Studies, Apartado San Vito de Coto Brus 73-8257, Costa Rica; and [33]Department of Plant Sciences, University of Oxford, Oxford OX1 3RB, UK

Summary

1. Plant functional traits, in particular specific leaf area (SLA), wood density and seed mass, are often good predictors of individual tree growth rates within communities. Individuals and species with high SLA, low wood density and small seeds tend to have faster growth rates.

*Correspondence author: E-mail: c.e.t.paine@stir.ac.uk

2. If community-level relationships between traits and growth have general predictive value, then similar relationships should also be observed in analyses that integrate across taxa, biogeographic regions and environments. Such global consistency would imply that traits could serve as valuable proxies for the complex suite of factors that determine growth rate, and, therefore, could underpin a new generation of robust dynamic vegetation models. Alternatively, growth rates may depend more strongly on the local environment or growth–trait relationships may vary along environmental gradients.

3. We tested these alternative hypotheses using data on 27 352 juvenile trees, representing 278 species from 27 sites on all forested continents, and extensive functional trait data, 38% of which were obtained at the same sites at which growth was assessed. Data on potential evapotranspiration (PET), which summarizes the joint ecological effects of temperature and precipitation, were obtained from a global data base.

4. We estimated size-standardized relative height growth rates (SGR) for all species, then related them to functional traits and PET using mixed-effect models for the fastest growing species and for all species together.

5. Both the mean and 95th percentile SGR were more strongly associated with functional traits than with PET. PET was unrelated to SGR at the global scale. SGR increased with increasing SLA and decreased with increasing wood density and seed mass, but these traits explained only 3.1% of the variation in SGR. SGR–trait relationships were consistently weak across families and biogeographic zones, and over a range of tree statures. Thus, the most widely studied functional traits in plant ecology were poor predictors of tree growth over large scales.

6. *Synthesis.* We conclude that these functional traits alone may be unsuitable for predicting growth of trees over broad scales. Determining the functional traits that predict vital rates under specific environmental conditions may generate more insight than a monolithic global relationship can offer.

Key-words: functional ecology, FunDivEurope, growth, hierarchical models, plant population and community dynamics, relative growth rate, size-standardized growth rate, TreeDivNet

Introduction

Functional traits impact population growth rates via their effects on the vital rates of recruitment, growth, reproduction and survival (Lavorel & Garnier 2002; Violle *et al.* 2007; Adler *et al.* 2014). They have been adopted with enthusiasm by ecologists in part because they reduce the dimensionality inherent in species-rich ecosystems, providing a tractable way to make inferences on community dynamics and ecosystem functioning (McGill *et al.* 2006). The use of functional traits has provided substantial insight into the determinants of community structure, including relative abundances and competitive hierarchies (Kraft, Valencia & Ackerly 2008; Cornwell & Ackerly 2010; Kunstler *et al.* 2012). Making community-level inferences using functional traits is predicated, however, on the assumption that they are strongly associated with the vital rates of individuals.

This assumption has been strongly validated in forested sites, where functional traits, especially wood density, are associated with interspecific variation in the growth rates of trees. Variation in wood density accounted for up to 33% of the variation in relative growth rate (RGR) for the fastest growing juveniles of Panamanian rain forest tree species, though relationships were weaker among adult trees, slower-growing individuals and with other functional traits (Wright *et al.* 2010; Rüger *et al.* 2012). Across Spain, Martínez-Vilalta *et al.* (2010) showed that RGR was inversely related to wood density ($R^2 = 0.35$) using national forest inventory data. At a still larger scale, Poorter *et al.* (2008) showed that wood density explained 11% of the variation in RGR across five neotropical forest sites. Because of the consistency in results among their five sites, Poorter *et al.* (2008) suggested that trait–growth relationships would be similar across rain forests, since all rain forest trees face similar trade-offs.

We tested the hypothesis that the relationships between tree functional traits and RGR that are found within communities are also encountered at a global scale. If traits have a general and consistent relationship with RGR, then significant covariation should be observed in a data set that encompasses global variation in environments and taxa with diverse biogeographic and phylogenetic histories. Such consistency would imply that functional traits can serve as proxies for the complex suite of factors that determine growth rate, given the abiotic and biotic environment, and could thus underpin a new generation of robust dynamic vegetation models (Scheiter, Langan & Higgins 2013; Sakschewski *et al.* in press). Alternatively, at such large scales, growth rates may depend more upon environmental conditions, or upon trait–environment interactions, such that the strength of growth–trait relationships varies along environmental gradients.

We examined three commonly measured functional traits, for which global relationships with the individual tree growth would be expected: specific leaf area (SLA), wood density and seed mass (Grime, Hunt & Grime 1975; Poorter & Remkes 1990; Poorter & van der Werf 1998). RGR should correlate positively with increasing SLA, but negatively with wood density and seed mass, for the following reasons. SLA is a strong determinant of carbon assimilation capacity per unit mass invested in photosynthetic surface area (Rees *et al.* 2010). Wood density governs the translation of assimilated carbon into stem and branch biomass, thereby influencing tree height and crown growth. Denser wood is associated with increased construction costs and decreased hydraulic conductance, both of which can reduce growth rate (Chave *et al.* 2009). Finally, seed mass is inversely related to survival for seedlings, and can thus affect the growth of juvenile plants via life-history correlations, although this effect dissipates when growth rates are compared at a standard size (Turnbull *et al.* 2012).

At a global scale, variation in temperature and precipitation should also affect growth rates. Though rates of photosynthesis and maintenance respiration are strongly temperature dependent (Atkin *et al.* 2005), the primary ecological effect of elevated temperature on growth rates derives from its interaction with low precipitation, increasing drought stress. High evaporative demand may limit photosynthetic carbon assimilation due to stomatal closure to reduce water stress (Keenan *et al.* 2013).

We assessed the relative importance of functional traits and environmental conditions in determining variation in sapling growth rates using a unique global data set of 27 352 individual juvenile trees representing 278 species from sites on all forested continents. Functional trait data were collected for all species, 38% of which were obtained from the same sites at which growth was assessed. Potential evapotranspiration (PET) was obtained for all sites from a global data base. We estimated growth rates at a standardized size using nonlinear hierarchical Bayesian models, which allowed us to account for uncertainty in growth rates. We then assessed the relationships among growth rates, functional traits and PET using mixed-effect models. Functional traits may better predict maximal than mean growth rates (Grime, Hunt & Grime 1975; Ter Steege 2003; Wright *et al.* 2010). Therefore, we also used linear quantile mixed-effect models to examine the growth of the fastest growing species. To further assess the generality of growth–trait relationships, we partitioned the variation in the global relationships among plant families and biogeographic regions.

Materials and methods

STUDY SITES AND GROWTH DATA

We assessed height growth on juvenile trees because less data were available for radial growth and for adults. Furthermore, juveniles are expected to have stronger growth–trait relationships than adults, given their smaller pools of stored reserves. We included only free-standing tree species; palms were also excluded as they do not have secondary growth. Data on tree growth were compiled from 27 sites across six continents. The key criterion for the inclusion of a site in this study was that juvenile trees of known age were grown in a nursery, then planted into mixed-species stands. This ensured a measure of consistency in the age and ontogenetic stage of juveniles within and among sites. The median juvenile was 37 cm tall when transplanted (interquartile range: 7–170 cm).

The core of the data set came from the European sites of TreeDivNet (www.treedivnet.ugent.be), which constitute the experimental platform of FunDivEUROPE (Baeten *et al.* 2013), a consortium of biodiversity–ecosystem functioning studies on woody plants. These sites were complemented by other TreeDivNet sites (Bruelheide *et al.* 2014), reforestation trials and studies designed to test specific ecological hypotheses. The latter two classes of studies were located through literature searches. In sites with multiple diversity treatments, we used only data from the one with the greatest species diversity. These treatments most closely resembled natural conditions, and their use allowed us to avoid interference with ongoing research at each site. Where light availability was manipulated, we used the treatment with the greatest light availability to reduce within-site heterogeneity and to assure positive growth rates. The sites spanned a latitudinal range from 18° S (Queensland, Australia) to 62° N (Satakunta, Finland).

Across our sites, annual rainfall varied between 533 and 4900 mm, and mean annual temperature varied between 5.0 and 27.7 °C. Temperature and precipitation were highly correlated, however, precluding an examination of their individual effects ($r = 0.79$). Therefore, we investigated environmental conditions in terms of potential evapotranspiration (PET), which integrates the effects of temperature and precipitation, and expresses the ability of the atmosphere to remove water through evaporation and transpiration (Allen *et al.* 1998). This climatic metric, though relatively crude, was appropriate for this study, in which the heterogeneity of data sources precludes the investigation of more detailed aspects of the biotic environment. We obtained standardized PET data for each site from the Consortium for Spatial Information's Global Aridity and PET Database (http://www.cgiar-csi.org/data/global-aridity-and-pet-database). PET data were downloaded with 30 arc-second spatial resolution as an annual average over the years 1950–2000. We extracted the PET values for grid cells within 50 km of each study site, then, for analysis, calculated the mean PET for each site.

In total, we studied 278 species and 27 352 individuals, on which 120 150 measurements were made. Because there was substantial variation among sites in terms of light availability, planting density, study duration and species composition, the 39 species that occurred in more than one site were modelled independently, yielding 333 species-site combinations (henceforth referred to as 'species'). Sample sizes varied among sites: 3–48 species and 35–7065 individuals were measured at each site. The median species was represented by 32 individuals (range: 5–2205) and 124 measurements (range: 10–10 716). The median study lasted 49 months (range 11–145). Nomenclature follows that of The Plant List (http://theplantlist.org). See Fig. 1 and Table S1 in Supporting Information for details of each site.

TRAIT DATA

Functional trait data were acquired from many sources. In 14 of the 27 sites, traits were measured on the same species at which growth was assessed, yielding 'local' values of SLA, wood density and seed mass for 192, 121, and 66 species, respectively. Trait data for the remaining species were obtained from publicly available data bases and published studies. The TRY data base of plant traits (Chave *et al.*

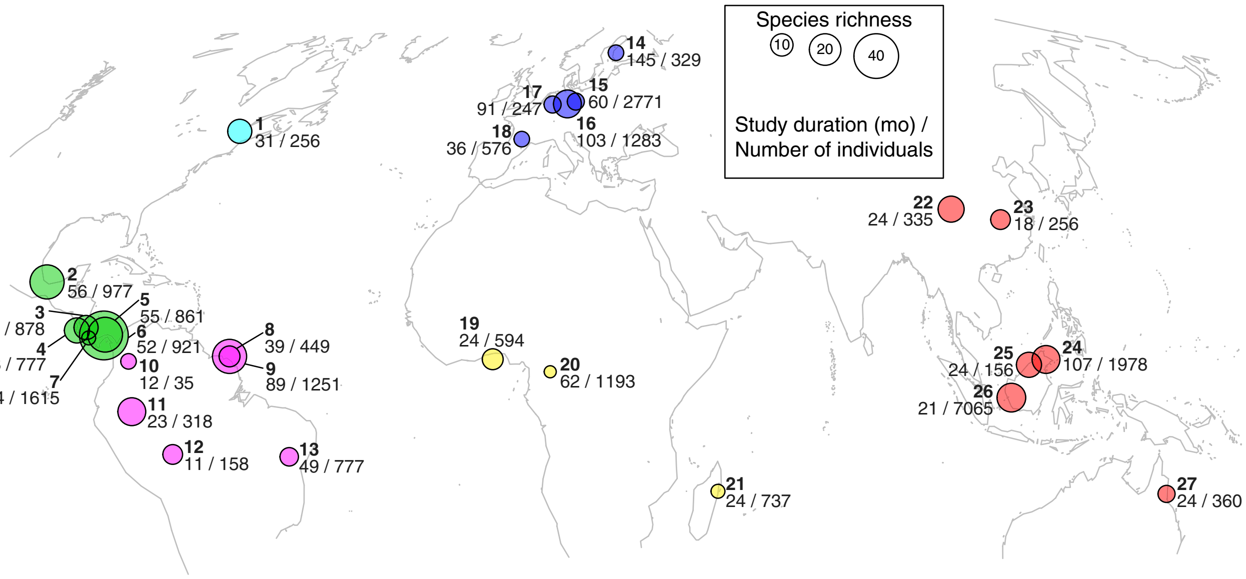

Fig. 1. Map of study sites. Points are coloured by biogeographic region and scaled to the number of species studied at each site. Bold font indicates site numbers, whereas plain text indicates study duration (in months) and the number of individuals monitored for growth at each site. See Table S1 for details.

2009; Kattge *et al.* 2011) and the Kew Seed Information Database (SID, http://data.kew.org/sid) were the primary resources for data on SLA, wood density and seed mass, respectively. Supplemental data were gleaned from literature searches. Species-level data on SLA, wood density and seed mass were available for 91, 96 and 86% of species, respectively. To estimate the functional traits of the remaining species, we first obtained the relevant traits for all congeneric species from the aforementioned primary data sources. Following Gallagher & Leishman (2012), we regressed genus-mean trait values against the observed species-mean trait values and then predicted species-mean trait values from the genus-mean values (R^2: SLA: 15%, WD 73%, SM: 86%).

ANALYSES

Relationships between relative growth rates and functional traits were evaluated in a three-step process.

First, we selected the functional form to predict individual height as a function of time. In 23 sites, juveniles were measured for height four or more times, allowing nonlinear models to be fit. Such models are appropriate because RGR tends to decrease over time, owing to the accumulation of non-photosynthetic biomass and the local depletion of soil resources (Paine *et al.* 2012). We fit linear, exponential, power-law, asymptotic and logistic mixed-effect models for each species-site combination separately, then selected the best function for each one on the basis of Akaike's information criterion (AIC). In the remaining four sites, juveniles were measured three times; their growth was modelled as an exponential function of time. All growth models included individual trees as a random effect.

Second, we predicted the height of each individual tree as a function of time using species-specific Bayesian hierarchical models with the functional forms selected in step one. Parameters were given uninformative priors and were fitted with a Hamiltonian Monte Carlo sampler using the No-U-Turns (NUTS) algorithm, with the constraint that predicted heights always be positive. We implemented these models in stan 2.5 via the package 'rstan' in R 3.1.1 (R Core Development Team 2014; Stan Development Team 2014). Four chains were run for each species-specific growth model. All models were run for 20 000 iterations, discarding the first 19 000 as a burn-in period. We used the Rhat statistic, together with a visual inspection of the chains, to assess convergence (Gelman & Rubin 1992). Parameters in all models converged before 1000 iterations (Rhat$\approx$1).

These models yielded posterior distributions of growth parameters for each species, from which we calculated posterior distributions of RGR at a standardized height of 100 cm, a height attained by almost all species. We refer to this size-standardized RGR as 'SGR'. Size standardization reduces the potential for bias when making comparisons among species that vary in initial size (Rees *et al.* 2010; Turnbull *et al.* 2012), as was the case here. SGR was calculated as the derivative of the function used to predict height, divided by the standard height (Paine *et al.* 2012). Trait values can vary over ontogeny, and size-standardized trait values can explain variation in SGR (Rees *et al.* 2010), even though species rankings are largely maintained (Poorter 2007). Even so, we did not analyse ontogenetic variation in trait values, because data on ontogenetic variation were not available for most species in the data set.

Third, we predicted SGR as a function of PET and functional traits (SLA, wood density, and seed mass) for all species, and for the fastest growing species (i.e. species in the 95th quantile of growth rates). The former group was analysed with linear mixed-effect models, whereas the latter group was analysed using linear mixed-effect quantile models (Geraci 2014) including additive and interactive effects (Table 1). Because preliminary analyses indicated that SGR varied substantially among sites, we included site-specific intercepts as a random effect in all models. In all models, SGR and seed mass were log-transformed to improve normality. Predictor values were always centred and standardized to unit variance, to allow comparisons among their slope parameters. Thus, intercepts represent the SGR for a species with trait values at the global mean and with PET at the global average. We accounted for uncertainty in our estimates of SGR by weighting each observation by the standard deviation of its posterior distribution obtained in step two. Doing so, we assumed the true SGR values were log-normally distributed with species-specific means and standard deviations. In contrast, in many previous studies,

Table 1. Comparison of (a) all species, (b) fast-growing species and (c) fast-growing individuals. The first two groups were fit using linear mixed-effect models, whereas the latter group was fit using linear quantile mixed-effect models. Models are sorted by increasing Akaike information criterion (AIC). PET: Potential evapotranspiration

	Model	*N* Parameters	ΔAIC
(a) All species	Traits	6	0.0
	PET + Traits	7	1.5
	Intercept-only	10	5.1
	PET	4	6.6
	PET × Traits	10	6.7
(b) Fast-growing species	Traits	6	0.0
	PET + Traits	7	2.9
	PET × Traits	10	14.9
	PET	4	32.6
	Intercept-only	3	72.9
(c) Fast-growing individuals	PET + Traits	7	0.0
	Traits	6	0.1
	PET × Traits	10	5.2
	PET	4	20.6
	Intercept-only	3	20.7

species-mean growth rates have been assessed as point estimates, implying that they were known without error (Reich, Walters & Ellsworth 1992; Poorter & van der Werf 1998; but see Rüger *et al.* 2012). Models were compared on the basis of AIC. For the linear mixed-effect models, pseudo R^2 was obtained with the method of Nakagawa & Schielzeth (2013). We were not able to calculate the variance explained for the fast-growing species, because such methods have not yet been developed for linear quantile mixed-effect models (Geraci 2014).

In addition to the global analyses, we partitioned variance in the SGR–trait relationships among study sites, plant families and biogeographic regions following the approach of Gelman (2005). Our aim was to estimate the variation contributed by each source to global SGR–trait relationships, rather than to test hypotheses. Thus, we built an additional linear mixed-effect model with random intercepts and slopes for sites, families and regions. Our biogeographic regions mostly aligned with continental margins but were adjusted to reduce variation in sample sizes (Fig. 1). To make the sources of variation comparable, we assumed that effects of sites, families and regions on intercepts and slopes were each drawn from separate, independent zero-mean normal distributions. We estimated the variance contributed by each source to SGR and the three SGR–trait relationships through 2000 bootstrap samples of the variance–covariance matrix. Linear mixed-effect models and linear quantile mixed-effect models were implemented in the lme4 and lqmm packages, respectively (Bates *et al.* 2014; Geraci 2014).

Results

Species-mean SLA varied fifteen-fold (3.37–50.38 $m^2 \cdot kg^{-1}$), wood density fivefold (0.16–0.96 $g \cdot cm^{-3}$) and seed mass by six orders of magnitude (0.11–33 333 mg). Functional traits were largely uncorrelated with each other, with coefficients of determination ≤0.06, though there were significantly positive SLA-wood density and seed mass–wood density relationships (Fig. 2). See Table S2 in Supporting Information for details of the studied species and their functional traits.

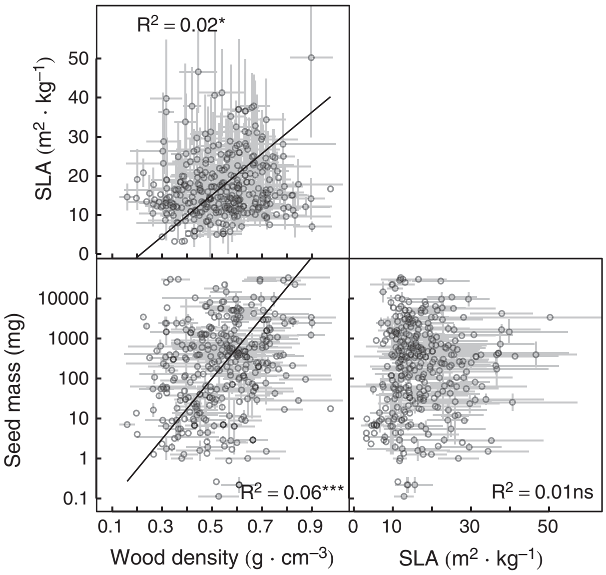

Fig. 2. Correlations among functional traits for the 333 species-site combinations. Note that seed mass is presented on log-transformed axes. Functional traits were largely independent of one another. Fitted lines are derived from standardized major-axis regressions. Error bars indicate one standard error of the mean *: $P \leq 0.05$; ***: $P \leq 0.0001$.

Log-transformed height was best modelled with a logistic or asymptotic function for 210 and 70 species, respectively, whereas the remaining 53 were adequately modelled by exponential functions (Figure S1 in Supporting Information). Thus, growth rates decreased as individual trees increased in size in 84% of the studied species. Species-mean SGR varied among species over four orders of magnitude, from 9.52×10^{-6} $cm \cdot cm^{-1} \cdot day^{-1}$ in *Protium aracouchini* to 0.014 $cm \cdot cm^{-1} \cdot day^{-1}$ in *Phyllanthus salviifolius*, with the median species having a SGR of 1.28×10^{-3} $cm \cdot cm^{-1} \cdot day^{-1}$ (Fig. 3).

Both mean and 95th percentile SGR were more strongly associated with functional traits than with PET. For all species together, as well as fast-growing species, models with traits alone had the lowest AIC values (Table 1). The three functional traits were associated with mean SGR, with each SGR–trait slope differing significantly from zero (95 per cent confidence intervals: SLA, 0.09 – 0.11; WD: −0.11 to −0.09, SM: −0.10 to −0.08; Fig. 3). Judged by their standardized slope coefficients, the three traits were associated with SGR to a similar degree. Thus, a 10 $m^2 \cdot kg^{-1}$ increase in SLA increased SGR by 10.3%, a 0.1 $g \cdot cm^{-3}$ increase in wood density reduced SGR by 5.3% and a one order of magnitude increase in seed mass reduced SGR by 7.3%. Overall, however, functional traits explained only 3.1% of the variation in SGR (marginal pseudo-R^2). Examined independently, SLA, wood density and seed mass explained 0.8%, 1.4% and 1.6% of the variation in SGR, respectively. Far more variance was explained by among-site variation in SGR (conditional pseudo-R^2: 71%).

When the fastest growing species were analysed (i.e. species in the 95th percentile of growth rates), seed mass was significantly negatively related to SGR ($P < 0.0001$), whereas SLA and wood density had no effect (SLA: $P = 0.42$, wood

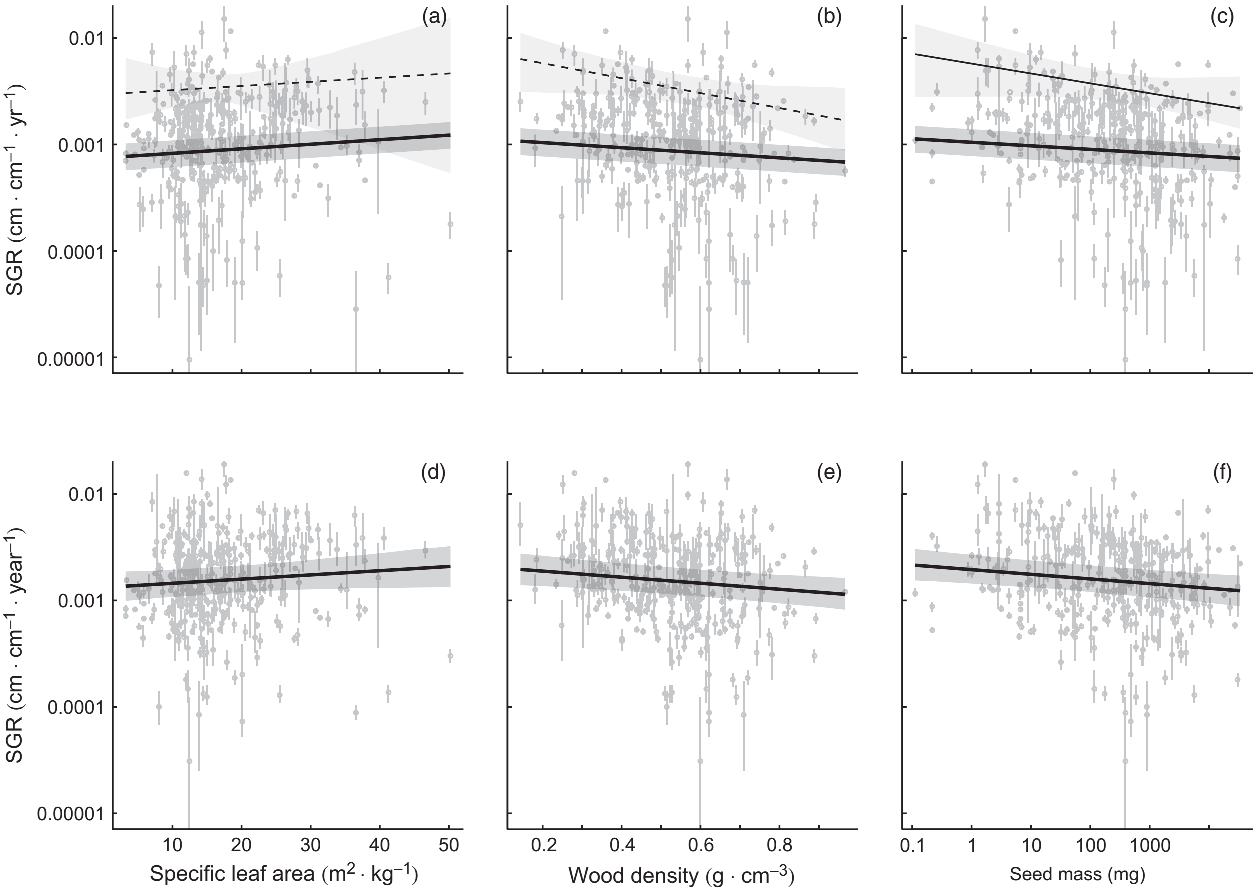

Fig. 3. Global relationships between size-standardized relative growth rate (SGR) and SLA, wood density, and seed mass. In a–c), points represent mean SGR for each species, whereas in d–f), points represent the 95th percentile of growth rates of individuals in each species. Thick regression lines and darker shading show overall relationships fitted with a weighted linear mixed-effects model, whereas thinner lines and lighter shading show relationships for fast-growing species, which were fitted with a weighted linear 95th quantile mixed-effects model. Solid lines represent significant relationships ($\alpha \leq 0.05$), whereas dashed lines indicate non-significant ones. Relationships are shown with 95% confidence intervals. In all models, weights are the inverse of the credible intervals around species-specific growth rates, which are indicated by error bars.

density: $P = 0.072$; Fig. 3a–c). Accordingly, comparing standardized slope coefficients from the quantile mixed-effect model, seed mass affected the SGR of fast-growing species more strongly than did SLA or wood density (seed mass = −0.17, SLA = −0.01, wood density = −0.13). For these species, a one order of magnitude increase in seed mass reduced SGR by 19.2%.

We partitioned the variation in SGR and the SGR–trait relationships among sites, plant families and biogeographic regions (Fig. 4). SGR varied among families, but families did not differ in their SGR–trait relationships (parametric bootstrap likelihood ratio test: $P = 0.45$). There was no evidence of variation in SGR or SGR–trait relationships among biogeographic regions ($P \geq 0.31$). Therefore, sites were the dominant source of variation in SGR, with relatively minor contributions from families and regions.

We assessed the generality of growth–trait relationships in four additional ways. First, we assessed them using only those sites in which study designs were most similar. This evaluated the possibility that global growth–trait relationships were obscured by among-site variation in experimental design (Table S1). To do so, we considered the global sites of TreeDivNet, and the European sites of that network (nine and five sites, respectively). Growth–trait relationships in the global TreeDivNet sites were of a similar magnitude to those in the global data set (standardized slope coefficients: SLA: −0.15, WD: −0.14, SM: −0.14; Figure S2 in Supporting Information). In the European TreeDivNet sites, there were significant interactions between functional traits and PET, such that increasing PET strengthened SGR–trait effects (Figure S2), despite the shorter gradients of PET and traits in this geographically restricted subset of the data. Surprisingly, in both analyses, increasing SLA was associated with reduced growth rates.

Competitive interactions could intensify as juveniles grow, for example, affecting SGR–trait relationships. We examined, therefore, whether the strength of growth–trait relationships varied with the size at which growth rates were measured. We repeated the linear mixed-effect analyses using SGR estimated at heights of 200, 300 and 500 cm, including only the species that attained those heights. Models that included additive effects of PET and functional traits were preferred when SGR was estimated at these heights. Nevertheless, we infer that PET only marginally affected growth rates, because more

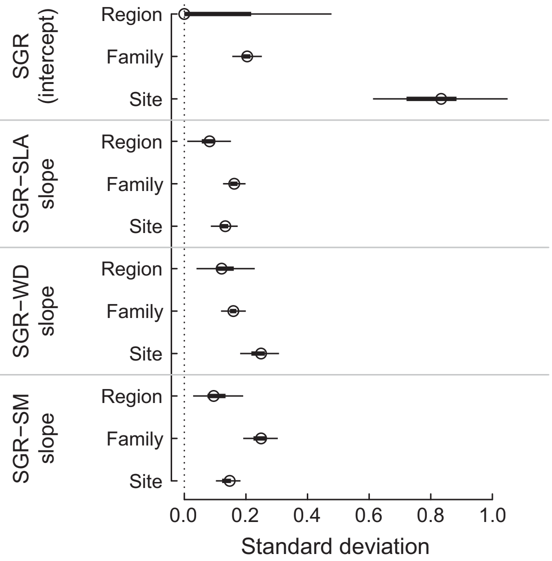

Fig. 4. A summary of the variance contributed to the global growth–trait relationships by study sites, plant families and biogeographic regions. Variation in SGR was greater among study sites than among families or regions, whereas SGR–trait relationships were relatively consistent among sites, families and regions. Points, thick bars and thin bars show means, 50% confidence intervals and 95% confidence intervals of the finite-population standard deviations, respectively. The point estimates are not always at the centre of the intervals because all variance components must be non-negative (Gelman 2005).

parsimonious trait-only models fit the data equivalently well, regardless of the size at which growth was assessed (ΔAIC: 2.5, 0.8 and 1.2, respectively). Seed mass was the only significant predictor of growth at heights above 100 cm (Figure S3 in Supporting Information). The slope of the growth–seed mass relationships remained largely consistent as juveniles grew. Thus, growth–trait relationships became no stronger as juveniles increased in size.

Within-site variation in environmental conditions could retard the growth of some individuals. For example, photoinhibition may have reduced growth rates for shade-tolerant species planted into sunny sites (Loik & Holl 2001), even as shading from faster-growing neighbours may have reduced growth rates for some individuals in others (Tobner *et al.* 2013). We evaluated this possibility by modelling the growth of the fastest growing individuals (i.e. individuals in the 95th percentile of growth rates for each species) with an additional set of mixed-effect models. A functional trait-only model fit the data more parsimoniously and almost equivalently well as a model including PET (Table 1). Though all three functional traits significantly affected the growth of the fastest growing individuals, the standardized slope coefficients were no greater in magnitude than in the model for all species (SLA: 0.09, WD: −0.12, SM: −0.12; Fig. 3d–f). Nor did this model explain substantially more variance in growth rates (marginal pseudo-R^2, SLA: 0.7%, wood density: 1.6%, seed mass: 2.2%). Thus, even for the fastest growing individuals in each species, functional traits remained poor predictors of growth.

Finally, not all functional trait values were available for all species at the sites where saplings were measured. Intraspecific trait variation, however, can be substantial (Albert *et al.* 2010). By including trait data drawn from data bases and the literature, we may have introduced variation that obscured the global growth–trait relationships. We tested this possibility by evaluating whether the slopes of the growth–trait relationships differed between the set of species with locally measured traits and the set with trait data obtained from other sources. The three traits were measured locally on differing subsets of species. SLA, wood density and seed mass were locally available for 192, 121 and 66 species, respectively. Thus, we built a mixed-effect model for each trait to test if the slope of the growth–trait relationship depended on the origin of the trait data. They did not (parametric bootstrap likelihood ratio tests: $P \geq 0.88$). These models were similarly poor at explaining the variation in SGR (Pseudo $R^2 \leq 2.3\%$). Therefore, we do not believe that the weakness in the global growth–trait relationships is attributable to intraspecific trait variation.

Discussion

At a global scale, among-species variation in sapling growth was positively associated with SLA, and negatively with wood density and seed mass. Even so, they were surprisingly weak, and did not strengthen when we analysed more homogeneous geographic subsets, juveniles of larger stature, fast-growing individuals or locally collected functional trait data. Due to their significant negative covariation, we conclude that the relationships between functional traits and sapling growth are globally consistent. On the other hand, growth and growth–trait relationships were independent of global variation in potential evapotranspiration. We discuss why traits are reasonable predictors of performance at local, but not global scales, and the implication of our results for trait-based global vegetation modelling.

WHY ARE GLOBAL GROWTH–TRAIT RELATIONSHIPS SO WEAK?

Previous studies have found stronger relationships between growth and the traits we studied, especially when plants were grown under controlled conditions (Grime, Hunt & Grime 1975; Poorter & van der Werf 1998). Combinations of functional traits explained up to 40–60% of the variation in diameter growth for field-grown trees assessed at single sites (Wright *et al.* 2010; Rüger *et al.* 2012), and slightly less at regional scales (Poorter *et al.* 2008; Martínez-Vilalta *et al.* 2010). In contrast, we found that the three functional traits explained little variation in growth at the global scale. This broad result is made robust by the use of (i) a substantial data set of global scope, (ii) data-collection methods that were standardized across globally distributed study sites, (iii) an analysis through which uncertainty was propagated and (iv) estimates of relative growth rate that were made at standardized sizes.

The discrepancy between previous studies and the current, global one might be explained by the fact that an individual's growth rate is not only affected by its functional traits, but also by the environmental conditions it experiences and the suitability of its traits to its environment. Environmental conditions entered our analyses as the fixed effect of PET, which summarized the joint influence of temperature and precipitation, and the random effect of site, which accounted for unmeasured sources of variation in SGR among sites. Surprisingly, PET affected neither SGR nor global SGR-trait relationships, although among-site variation in SGR was substantial. This may have occurred because we selected study sites with similar experimental designs and relatively high-light conditions; 59% of species were planted into sites with ≥50% sunlight, and 70% were planted with ≥25% sunlight (Table S1). Simultaneously, we found weak relationships between SGR and functional traits. Together, these observations suggest that growth rates were strongly affected by unmeasured within-site variation in environmental conditions. We tested this by evaluating the relationships among growth, traits and PET for the fastest growing individuals of each species and, surprisingly, found that relationships were no stronger than in the overall analysis (Fig. 3d–f). This indicates that functional traits were poor predictors of growth even for individuals that did not experience adverse environmental conditions. The discrepancy could also have arisen if there were substantial variation in growth–trait relationships among sites, but after testing with an additional set of models that allowed for varying growth–trait relationships in each site, we found no support for the suggestion that growth–trait relationships vary among sites (parametric bootstrap likelihood ration tests: $P \geq 0.75$), confirming the minor variance in slopes explained by sites in the variance-partitioning analysis (Fig. 4).

Our choice of growth metric may have affected our inference of the strength of the growth–trait relationships. Ideally, growth would be assessed as whole-plant biomass, rather than as stem height. This was not feasible in the current study, as it would have required species-specific allometries or destructive harvests, which were not available for most species in our data set. Growth can also be measured as girth, which is often strongly correlated with height (Martínez-Garza, Bongers & Poorter 2013). For trees < 140 cm, however, there is little consensus on the point at which girth should be measured. Moreover, height growth can be evaluated much more precisely than radial growth because small plants grow more in height than in diameter, and height growth is more ecologically relevant, as it determines an individual's position in the vertical light profile of the forest, and thus, its access to light. Using stem height may have introduced some noise into the analysis, owing to interspecific variation in biomass allocation to height. We believe, however, that it is unlikely to have been sufficient to generate the globally weak trait–growth relationships we observed.

Altogether, it is unclear why global relationships among functional traits, PET and growth are so weak. Thus, evaluating the joint effects of environmental conditions and functional traits on growth rates remains an important topic of study (Rüger *et al.* 2012).

TOWARDS BETTER PREDICTIONS OF GROWTH

To better manage and conserve ecological communities, we must improve our ability to predict their dynamics (Clark *et al.* 2001). The most promising models to do so are rooted in demography (Boulangeat *et al.* 2012), but obtaining demographic data is challenging, especially in species-rich communities where many species are rare. The ability to accurately predict vital rates, and thus demography, from data that are relatively easily obtained would allow a step change in ecological forecasting (Adler *et al.* 2014). The relative ease of collecting functional trait data and the potential of functional traits to yield insight into population and community structure (Kraft, Valencia & Ackerly 2008; Cornwell & Ackerly 2010; Kunstler *et al.* 2012) suggest that integrating them into dynamic vegetation models would increase their reliability (Scheiter, Langan & Higgins 2013; Sakschewski *et al.* in press). Our results, however, indicate that the functional traits most commonly investigated in plant ecology are poor predictors of growth at large scales. Though organ-specific functional traits are easily measured, they integrate many physiological processes, are intricately interrelated, and can be highly plastic (Russo *et al.* 2010; Paine *et al.* 2011; Pérez-Harguindeguy *et al.* 2013). Moreover, functional integration occurs at the individual level, not at the level of organs (Craine et al. 2012). Thus, many combinations of trait values can yield similar growth rates (Marks & Lechowicz 2006). Integrated measures, such as whole-plant carbon use efficiency, may be more effective (Enquist *et al.* 2007).

Is it feasible to predict plant community dynamics over broad scales? It has been suggested that 'hard' functional traits, such as photosynthetic or respiration rates, would be better predictors of vital rates than 'soft' traits such as SLA, wood density and seed mass (Lavorel & Garnier 2002). This is unlikely under field conditions, however, because the physiological bases of hard traits make them overly sensitive to heterogeneity in environmental conditions. Contrastingly, experimental measurements of whole-plant tolerance to low resource availability may predict vital rates, and thus community dynamics, over broader scales than can organ-specific functional traits (Craine *et al.* 2012). As data on species' physiological tolerance to low resource availability become more widely available, they should allow broader-scale predictions of community structure and dynamics (Engelbrecht *et al.* 2007). We suggest that future studies focus on determining which functional traits predict the vital rates of individuals under various environmental conditions, and at what spatial scales (Martínez-Garza *et al.* 2005), rather than seeking monolithic global relationships. Regardless of the approach, improving techniques to predict the dynamics of ecological communities remains a vital task, given the urgent need for their management and conservation.

Acknowledgements

We thank the multitudes involved in planting, measuring and maintenance of the study sites, and collecting growth and trait data. Jens Kattge, manager of the TRY global trait data base, and Kyle Dexter contributed additional trait data. Statistical advice from Marco Geraci, Sophia Ratcliffe, Nadja Rüger and Christian Wirth strengthened the analysis. This research was funded by Swiss National Science grant number 121967 to A.H. and by the European Union Seventh Framework Program (FP7/2007–2013) under grant agreements n° 265171 (project FunDivEUROPE) and n° 226299 (project BACCARA).

Author contributions

CETP and AH conceived the analysis. CETP performed analyses and wrote the first draft of the manuscript. All authors contributed data and contributed substantially to revisions.

Data accessibility

All growth and functional trait data used in this study are archived at the DRYAD online data base under doi:10.5061/dryad.h9083.

In addition to the data collected for this study, functional trait data were obtained from the following sources.

Agyeman, V.K., Kyereh, B., Swaine, M.D. & Thompson, J. (2010) Species differences in seedling growth and leaf water response to light quality. *Ghana Journal of Forestry*, **26**, 101–123.

Agyeman, V.K., Swaine, M.D. & Thompson, J. (1999) Responses of tropical forest tree seedlings to irradiance and the derivation of a light response index. *Journal of Ecology*, **87**, 815–827.

Anonymous. (2000) *Seeds of Woody Plants in China*. China Forestry Publishing House.

Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L.L., Di Fiore, A., Erwin, T.L., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Lloyd, J., Monteagudo, A., Neill, D. A., Patiño, S., Pitman, N.C.A., Silva, J.N.M. & Martínez, R.V. (2004) Variation in wood density determines spatial patterns in Amazonian forest biomass. *Global Change Biology*, **10**, 545–562.

Baraloto, C. & Forget, P.-M. (2007) Seed size, seedling morphology, and response to deep shade and damage in neotropical rain forest trees. *American Journal of Botany*, **94**, 901–911.

Baraloto, C., Goldberg, D.E. & Bonal, D. (2005) Performance trade-offs among tropical tree seedlings in contrasting microhabitats. *Ecology*, **86**, 2461–2472.

Blaser, J., Rajoelison, G., Tsza, G., Rajemison, M., Rabevohitra, R., Randrianjafy, H., Razafindrianilana, N., Rakotovao, G. & Comtet, S. (1993) *Choix des Essences Pour la Sylviculture À Madagascar*.

Bloor, J.M.G. (2003) Light responses of shade-tolerant tropical tree species in north-east Queensland: a comparison of forest- and shadehouse-grown seedlings. *Journal of Tropical Ecology*, **2**, 163–170.

Bloor, J.M.G. & Grubb, P.J. (2004) Morphological plasticity of shade-tolerant tropical rainforest tree seedlings exposed to light changes. *Functional Ecology*, **18**, 337–348.

Calvo-Alvarado, J.C., McDowell, N.G. & Waring, R.H. (2008) Allometric relationships predicting foliar biomass and leaf area:sapwood area ratio from tree height in five Costa Rican rain forest species. *Tree Physiology*, **28**, 1601–8.

Carvalho, P.E.R. (2003) *Espécies Arbóreas Brasileiras*. Embrapa Informação Tecnológica Brasília.

Chave, J., *et al.* (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**, 351–66. doi:10.1111/j.1461-0248.2009.01285.x.

Choong, M.F., Lucas, P.W., Ong, J.S.Y., Pereira, B., Tan, H.T.W. & Turner, I.M. (1992) Leaf fracture toughness and sclerophylly: their correlations and ecological implications. *New Phytologist*, **121**, 597–610.

Clark, D. & Clark, D.B. (1992) Life history diversity of canopy and emergent trees in a neotropical rain forest. *Ecological Monographs*, **62**, 315–344.

Coll, L., Potvin, C., Messier, C. & Delagrange, S. (2008) Root architecture and allocation patterns of eight native tropical species with different successional status used in open-grown mixed plantations in Panama. *Trees*, **22**, 585–596.

Cornelissen, J., Diez, P. & Hunt, R. (1996) Seedling growth, allocation and leaf attributes in a wide range of woody plant species and types. *Journal of Ecology*, **84**, 755–765.

Cornwell, W.K., Cornelissen, J.H.C., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.E., *et al.* (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology Letters*, **11**, 1065–1071.

Díaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A., *et al.* (2004) The plant traits that drive ecosystems: Evidence from three continents. *Journal of Vegetation Science*, **15**, 295.

Doucet, J.-L., Kouadio, Y.L., Monticelli, D. & Lejeune, P. (2009) Enrichment of logging gaps with moabi (Baillonella toxisperma Pierre) in a Central African rain forest. *Forest Ecology and Management*, **258**, 2407–2415.

Doust, S.J. (2011) Seed Removal and Predation as Factors Affecting Seed Availability of Tree Species in Degraded Habitats and Restoration Plantings in Rainforest Areas of Queensland, Australia. *Restoration Ecology*, **19**, 617–626.

Doust, S.J., Erskine, P.D. & Lamb, D. (2008) Restoring rainforest species by direct seeding: tree seedling establishment and growth performance on degraded land in the wet tropics of Australia. *Forest Ecology and Management*, **256**, 1178–1188.

Falster, D.S. & Westoby, M. (2005) Alternative height strategies among 45 dicot rain forest species from tropical Queensland, Australia. *Journal of Ecology*, **93**, 521–535.

Freschet, G.T., Cornelissen, J.H.C., van Logtestijn, R.S.P. & Aerts, R. (2010) Evidence of the "plant economics spectrum" in a subarctic flora. *Journal of Ecology*, **98**, 362–373.

Fyllas, N.M., Patiño, S., Baker, T.R., Nardoto, G.B., Martinelli, L.A., Quesada, C.A., *et al.* (2009) Basin-wide variations in foliar properties of Amazonian forest: phylogeny, soils and climate. *Biogeosciences*, **6**, 2677–2708.

Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., *et al.* (2007) Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. *Annals of Botany*, **99**, 967–985.

Gerhardt, K. & Friedriksson, D. (1995) Biomass allocation by broad-leaf mahogany seedlings, Swietenia macrophylla (King), in abandoned pasture and secondary dry forest in Guanacaste, Costa Rica. *Biotropica*, **27**, 174–182.

Gonzalez, E.J. (1993) Effect of seed size on germination and seedling vigor of Virola koschnyi Warb. *Forest Ecology and Management*, **57**, 275–281.

González-Rodríguez, V., Villar, R. & Navarro-Cerrillo, R.M. (2011) Maternal influences on seed mass effect and initial seedling growth in four Quercus species. *Acta Oecologica*, **37**, 1–9.

de Gouvenain, R.C., Kobe, R.K. & Silander, J.A. (2007) Partitioning of understorey light and dry-season soil moisture gradients among seedlings of four rain-forest tree species in Madagascar. *Journal of Tropical Ecology*, **23**, 569–579.

Hector, A., Philipson, C.D., Saner, P., Chamagne, J., Dzulkifli, D., O'Brien, M., Snaddon, J.L., Ulok, P., Weilenmann, M., Reynolds, G. & Godfray, H.C.J. (2011) The Sabah Biodiversity Experiment: a long-term test of the role of tree diversity in restoring tropical forest structure and functioning.. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **366**, 3303–15.

Hidayat, S. & Simpson, W.T. (1994) *Use of Green Moisture Content and Basic Specific Gravity to Group Tropical Woods for Kiln Drying*. US Dept. of Agriculture, Forest Service, Forest Products Laboratory,

Holl, K.D., Zahawi, R. A., Cole, R.J., Ostertag, R. & Cordell, S. (2011) Planting seedlings in tree islands versus plantations as a large-scale tropical forest restoration strategy. *Restoration Ecology*, **19**, 470–479.

Kattge, J. *et al.* (2011) TRY Plant Trait Database. http://try-db.org

Kattge, J., Knorr, W., Raddatz, T. & Wirth, C. (2009) Quantifying photosynthetic capacity and its relationship to leaf nitrogen content for global-scale terrestrial biosphere models. *Global Change Biology*, **15**, 976–991.

Kitajima, K., Cordero, R. A & Wright, S.J. (2013) Leaf life span spectrum of tropical woody seedlings: effects of light and ontogeny and consequences for survival. *Annals of Botany*, **112**, 685–699.

Kitajima, K., Llorens, A.-M., Stefanescu, C., Timchenko, M.V., Lucas, P.W. & Wright, S.J. (2012) How cellulose-based leaf toughness and lamina density contribute to long leaf lifespans of shade-tolerant species. *New Phytologist*, **195**, 640–52.

Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., *et al.* (2008) The LEDA Traitbase: a database of life-history traits of the Northwest European flora. *Journal of Ecology*, **96**, 1266–1274.

Kurokawa, H., Kitahashi, Y., Koike, T., Lai, J. & Nakashizuka, T. (2004) Allocation to defense or growth in dipterocarp forest seedlings in Borneo. *Oecologia*, **140**, 261–70.

Lavinsky, A.O., Souza Sant'Ana, C., Mielke, M.S., Almeida, A.-A.F., Gomes, F.P., França, S. & Costa Silva, D. (2007) Effects of light availability and soil flooding on growth and photosynthetic characteristics of Genipa americana L. seedlings. *New Forests*, **34**, 41–50.

Lee, H.S., Davies, S.J., LaFrankie, J.V., Tan, S., Yamakura, T., Itoh, A., Ohkubo, T. & Ashton, P.S. (2002) Floristic and structural diversity of mixed dipterocarp forest in Lambir Hills National Park, Sarawak, Malaysia. *Journal of Tropical Forest Science*, **14**, 379–400.

Lehto, T. & Grace, J. (1994) Carbon balance of tropical tree seedlings: a comparison of two species. *New Phytologist*, **127**, 455–463.

Li, X. (2011) *Light-Use Strategies and Biomass Accumulation of Woody Species in a Subtropical Forest in Southwest China*. University of Zurich.

Markesteijn, L. & Poorter, L. (2009) Seedling root morphology and biomass allocation of 62 tropical tree species in relation to drought- and shade-tolerance. *Journal of Ecology*, **97**, 311–325.

Medlyn, B.E., Badeck, F.W., DePury, D.G.G., Barton, C.V.M., Broadmeadow, M., Ceulemans, R., *et al.* (1999) Effects of elevated [CO2] on photosynthesis in European forest species: a meta-analysis of model parameters. *Plant, Cell & Environment*, **22**, 1475–1495.

Messier, J., McGill, B.J. & Lechowicz, M.J. (2010) How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters*, **13**, 838–848.

Niinemets, Ü. (2001) Global-scale climatic controls of leaf dry mass per area, density, and thickness in trees and shrubs. *Ecology*, **82**, 453–469.

Ogaya, R. & Peñuelas, J. (2003) Comparative field study of Quercus ilex and Phillyrea latifolia: photosynthetic response to experimental drought conditions. *Environmental and Experimental Botany*, **50**, 137–148.

Okubo, S., Tomatsu, A., Muhamad, D., Harashina, K. & Takeuchi, K. (2012) Leaf functional traits and functional diversity of multistoried agroforests in West Java, Indonesia. *Agriculture, Ecosystems & Environment*, **149**, 91–99.

Onoda, Y., Westoby, M., Adler, P.B., Choong, A.M.F., Clissold, F.J., Cornelissen, J.H.C., *et al.* (2011) Global patterns of leaf mechanical properties. *Ecology Letters*, **14**, 301–312.

Ordoñez, J.C., van Bodegom, P.M., Witte, J.-P.M., Bartholomeus, R.P., van Hal, J.R. & Aerts, R. (2010) Plant strategies in relation to resource supply in mesic to wet environments: does theory mirror nature? *The American Naturalist*, **175**, 225–239.

Osunkoya, O., Ash, J. & Hopkins, M. (1994) Influence of seed size and seedling ecological attributes on shade-tolerance of rain-forest tree species in northern Queensland. *Journal of Ecology*, **82**, 149–163.

Otani, T. & Shibata, E. (2000) Seed dispersal and predation by Yakushima macaques, Macaca fuscata yakui, in a warm temperate forest of Yakushima Island, southern Japan. *Ecological Research*, **15**, 133–144.

Palow, D.T., Nolting, K. & Kitajima, K. (2012) Functional trait divergence of juveniles and adults of nine Inga species with contrasting soil preference in a tropical rain forest (ed. L Sack). *Functional Ecology*, **26**, 1144–1152.

Paoli, G.D., Peart, D.R., Leighton, M. & Samsoedin, I. (2001) An Ecological and Economic Assessment of the Nontimber Forest Product Gaharu Wood in Gunung Palung National Park, West Kalimantan, Indonesia. *Conservation Biology*, **15**, 1721–1732.

Paquette, A. & Messier, C. (2011) The effect of biodiversity on tree productivity: from temperate to boreal forests. *Global Ecology and Biogeography*, **20**, 170–180.

Paulus, B.C., Kanowski, J., Gadek, P. A & Hyde, K.D. (2006) Diversity and distribution of saprobic microfungi in leaf litter of an Australian tropical rainforest. *Mycological Research*, **110**, 1441–54.

Penuelas, J., Sardans, J., Llusià, J., Owen, S.M., Carnicer, J., Giambelluca, T.W., *et al.* (2010) Faster returns on "leaf economics" and different biogeochemical niche in invasive compared with native plant species. *Global Change Biology*, **16**, 2171–2185.

Piotto, D. (2008) A meta-analysis comparing tree growth in monocultures and mixed plantations. *Forest Ecology and Management*, **255**, 781–786.

Piotto, D., Montagnini, F., Ugalde, L. & Kanninen, M. (2003) Performance of forest plantations in small and medium-sized farms in the Atlantic lowlands of Costa Rica. *Forest Ecology and Management*, **175**, 195–204.

Piotto, D., Viquez, E., Montagnini, F. & Kanninen, M. (2004) Pure and mixed forest plantations with native species of the dry tropics of Costa Rica: a comparison of growth and productivity. *Forest Ecology and Management*, **190**, 359–372.

Poorter, L. (1998) *Seedling Growth of Bolivian Rain Forest Tree Species in Relation to Light and Water Availability*. Utrecht University.

Poorter, L. & Bongers, F. (2006) Leaf traits are good predictors of plant performance across 53 rain forest species. *Ecology*, **87**, 1733–1743.

Poorter, H., Niinemets, Ü., Poorter, L., Wright, I.J. & Villar, R. (2009) Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist*, **182**, 565–588.

Poschlod, P., Kleyer, M., Jackel, A.-K., Dannemann, A. & Tackenberg, O. (2003) BIOPOP — A database of plant traits and internet application for nature conservation. *Folia Geobotanica*, **38**, 263–271.

Potvin, C. & Gotelli, N.J. (2008) Biodiversity enhances individual performance but does not affect survivorship in tropical trees. *Ecology Letters*, **11**, 217–23.

Quero, J. & Villar, R. (2007) Seed-mass effects in four Mediterranean Quercus species (Fagaceae) growing in contrasting light environments. *American Journal of Botany*, **94**, 1795–1803.

Quested, H.M., Cornelissen, J.H.C., Press, M.C., Callaghan, T.V., Aerts, R., Trosien, F., *et al.* (2003) Decomposition of sub-arctic plants with differing nitrogen economies: a functional role for hemiparasites. *Ecology*, **84**, 3209–3221.

Reich, P.B., Tjoelker, M.G., Pregitzer, K.S., Wright, I.J., Oleksyn, J. & Machado, J.L. (2008) Scaling of respiration to nitrogen in leaves, stems and roots of higher land plants. *Ecology Letters*, **11**, 793–801.

Royal Botanic Gardens Kew. (2014) Seed Information Database (SID). Version 7.1. http://data.kew.org/sid

Russo, S.E., Davies, S.J., King, D. A. & Tan, S. (2005) Soil-related performance variation and distributions of tree species in a Bornean rain forest. *Journal of Ecology*, **93**, 879–889.

Sales-Come, R. & Hölscher, D. (2010) Variability and grouping of leaf traits in multi-species reforestation (Leyte, Philippines). *Forest Ecology and Management*, **260**, 846–855.

Salinas, N., Malhi, Y., Meir, P., Silman, M.R., Roman Cuesta, R., Huaman, J., Salinas, D., Huaman, V., Gibaja, A, Mamani, M. & Farfan, F. (2011) The sensitivity of tropical leaf litter decomposition to temperature: results from a large-scale leaf translocation experiment along an elevation gradient in Peruvian forests. *New Phytologist*, **189**, 967–77.

Sautu, A., Baskin, J.M., Baskin, C.C. & Condit, R.S. (2006) Studies on the seed biology of 100 native species of trees in a seasonal moist tropical forest, Panama, Central America. *Forest Ecology and Management*, **234**, 245–263.

Scherer-Lorenzen, M., Potvin, C., Koricheva, J., Schmid, B., Hector, A., Bornik, Z., Reynolds, G. & Schulze, E.-D. (2005) The design of experimental tree plantations for functional biodiversity research. *Forest Diversity and Function: Temperate and Boreal Systems* (eds M. Scherer-Lorenzen, C. Körner & E.-D. Schulze), pp. 347–376. Springer Verlag, Berlin, Heidelberg.

Scherer-Lorenzen, M., Schulze, E., Don, A., Schumacher, J. & Weller, E. (2007) Exploring the functional significance of forest diversity: a new long-term experiment with temperate tree species (BIOTREE). *Perspectives in Plant Ecology, Evolution and Systematics*, **9**, 53–70.

Shipley, B. (2002) Trade-offs between net assimilation rate and specific leaf area in determining relative growth rate: relationship with daily irradiance. *Functional Ecology*, **16**, 682–689.

Souza, R. & Válio, I. (2003) Leaf optical properties as affected by shade in saplings of six tropical tree species differing in successional status. *Brazilian Journal of Plant Physiology*, **15**, 49–54.

Turner, I.M. & Tan, H.T.W. (1991) Habitat-related variation in tree leaf form in four tropical forest types on Pulau Ubin, Singapore. *Journal of Vegetation Science*, **2**, 691–698.

Veenendaal, E.M., Swaine, M.D., Lecha, R.T., Walsh, M.F., Abebrese, I.K. & Owusu-Afriyie, K. (1996) Responses of West African forest tree seedlings to irradiance and soil fertility. *Functional Ecology*, **10**, 501–511.

Vincent, G. (2006) Leaf life span plasticity in tropical seedlings grown under contrasting light regimes. *Annals of Botany*, **97**, 245–55.

Wagner, F. (2011) *La Réponse Des Forêts Tropicales Humides Aux Variations Climatiques*. Université des Antilles et de la Guyane.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., *et al.* (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.

Young, J.A. & Young, C.G. (1992) *Seeds of Woody Plants in North America*. Dioscorides Press.

Yumoto, T. & Noma, N. (1998) Cheek-pouch dispersal of seeds by Japanese monkeys (Macaca fuscata yakui) on Yakushima Island, Japan. *Primates*, **39**, 325–338.

References

Adler, P.B., Salguero-Gómez, R., Compagnoni, A., Hsu, J.S., Ray-Mukherjee, J., Mbeau-Ache, C. & Franco, M. (2014) Functional traits explain variation in plant life history strategies. *Proceedings of the National Academy of Sciences of the United States of America*, **111**, 740–745.

Albert, C.H., Thuiller, W., Yoccoz, N.G., Soudant, A., Boucher, F., Saccone, P. & Lavorel, S. (2010) Intraspecific functional variability: extent, structure and sources of variation. *Journal of Ecology*, **98**, 604–613.

Allen, R.G., Pereira, L.S., Raes, D., Smith, M. & Ab, W. (1998) Crop evapotranspiration - Guidelines for computing crop water requirements - FAO Irrigation and drainage paper 56 By., 1–15.

Atkin, O.K., Bruhn, D., Hurry, V.M. & Tjoelker, M.G. (2005) Evans Review No. 2 - The hot and the cold: unravelling the variable response of plant respiration to temperature. *Functional Plant Biology*, **32**, 87–105.

Baeten, L., Verheyen, K., Wirth, C., Bruelheide, H., Bussotti, F., Finér, L. *et al.* (2013) A novel comparative research platform designed to determine the functional significance of tree species diversity in European forests. *Perspectives in Plant Ecology, Evolution and Systematics*, **15**, 281–291.

Bates, D.M., Maechler, M., Bolker, B.M. & Walker, S. (2014) lme4: Linear mixed-effects models using Eigen and S4.

Boulangeat, I., Philippe, P., Abdulhak, S., Douzet, R., Garraud, L., Lavergne, S., Lavorel, S., Van Es, J., Vittoz, P. & Thuiller, W. (2012) Improving plant functional groups for dynamic models of biodiversity: at the crossroads between functional and community ecology. *Global Change Biology*, **18**, 3464–3475.

Bruelheide, H., Nadrowski, K., Assmann, T., Bauhus, J., Both, S., Buscot, F. *et al.* (2014) Designing forest biodiversity experiments: general considerations illustrated by a new large experiment in subtropical China. *Methods in Ecology and Evolution*, **5**, 74–89.

Chave, J., Coomes, D.A., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**, 351–366.

Clark, J.S., Carpenter, S.R., Barber, M., Collins, S.L., Dobson, A., Foley, J.A., Lodge, D.M., Pascual, M.A., Pielke, R.J. & Pizer, W. (2001) Ecological forecasts: an emerging imperative. *Science*, **293**, 657–660.

Cornwell, W.K. & Ackerly, D.D. (2010) A link between plant traits and abundance: evidence from coastal California woody plants. *Journal of Ecology*, **98**, 814–821.

Craine, J.M., Engelbrecht, B.M.J., Lusk, C.H., McDowell, N.G. & Poorter, H. (2012) Resource limitation, tolerance, and the future of ecological plant classification. *Frontiers in Plant Science*, **3**, 246.

Engelbrecht, B.M.J., Comita, L.S., Condit, R.S., Kursar, T.A., Tyree, M.T., Turner, B.L. & Hubbell, S.P. (2007) Drought sensitivity shapes species distribution patterns in tropical forests. *Nature*, **447**, 80–82.

Enquist, B.J., Kerkhoff, A.J., Stark, S.C., Swenson, N., McCarthy, M.C. & Price, C.A. (2007) A general integrative model for scaling plant growth, carbon flux, and functional trait spectra. *Nature*, **449**, 218–222.

Gallagher, R. & Leishman, M. (2012) Contrasting patterns of trait-based community assembly in lianas and trees from temperate Australia. *Oikos*, **121**, 2026–2035.

Gelman, A. (2005) Analysis of variance? Why it is more important than ever. *The Annals of Statistics*, **33**, 1–53.

Gelman, A. & Rubin, D. (1992) Inference from Iterative Simulation Using Multiple Sequences. *Statistical Science*, **7**, 457–511.

Geraci, M. (2014) lqmm: Linear quantile mixed models.

Grime, J.P., Hunt, R. & Grime, A.J.P. (1975) Relative growth-rate: its range and adaptive significance in a local flora. *Journal of Ecology*, **63**, 393–422.

Kattge, J., Diaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Bönisch, G., Garnier, E., Westoby, M., Reich, P.B. & Wright, I.J. (2011) TRY–a global database of plant traits. *Global Change Biology*, **17**, 2905–2935.

Keenan, T.F., Hollinger, D.Y., Bohrer, G., Dragoni, D., Munger, J.W., Schmid, H.P. & Richardson, A.D. (2013) Increase in forest water-use efficiency as atmospheric carbon dioxide concentrations rise. *Nature*, **499**, 324–327.

Kraft, N.J.B., Valencia, R. & Ackerly, D.D. (2008) Functional traits and niche-based tree community assembly in an Amazonian forest. *Science*, **322**, 580–582.

Kunstler, G., Lavergne, S., Courbaud, B., Thuiller, W., Vieilledent, G., Zimmermann, N.E., Kattge, J., Coomes, D.A. & Grover, J. (2012) Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: implications for forest community assembly. *Ecology Letters*, **15**, 831–840.

Lavorel, S. & Garnier, E. (2002) Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*, **16**, 545–556.

Loik, M.E. & Holl, K.D. (2001) Photosynthetic responses of tree seedlings in grass and under shrubs in early-successional tropical old fields, Costa Rica. *Oecologia*, **127**, 40–50.

Marks, C.O. & Lechowicz, M.J. (2006) Alternative designs and the evolution of functional diversity. *The American Naturalist*, **167**, 55.

Martínez-Garza, C., Bongers, F. & Poorter, L. (2013) Are functional traits good predictors of species performance in restoration plantings in tropical abandoned pastures? *Forest Ecology and Management*, **303**, 35–45.

Martínez-Garza, C., Pena, V., Ricker, M., Peña, V., Campos, A. & Howe, H.F. (2005) Restoring tropical biodiversity: leaf traits predict growth and survival of late-successional trees in early-successional environments. *Forest Ecology and Management*, **217**, 365–379.

Martínez-Vilalta, J., Mencuccini, M., Vayreda, J. & Retana, J. (2010) Interspecific variation in functional traits, not climatic differences among species ranges, determines demographic rates across 44 temperate and Mediterranean tree species. *Journal of Ecology*, **98**, 1462–1475.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006) Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, **21**, 178–185.

Nakagawa, S. & Schielzeth, H. (2013) A general and simple method for obtaining R2 from generalized linear mixed-effects models (ed. RB O'Hara). *Methods in Ecology and Evolution*, **4**, 133–142.

Paine, C.E.T., Baraloto, C., Bruno, H., Chave, J. & Hérault, B. (2011) Functional traits of individual trees reveal ecological constraints on community assembly in tropical rain forests. *Oikos*, **120**, 720–727.

Paine, C.E.T., Marthews, T.R., Vogt, D.R., Purves, D., Rees, M., Hector, A. & Turnbull, L.A.A. (2012) How to fit nonlinear plant growth models and calculate growth rates: an update for ecologists. *Methods in Ecology and Evolution*, **3**, 245–256.

Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S. & Poorter, H. (2013) New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, **61**, 167–234.

Poorter, L. (2007) Are species adapted to their regeneration niche, adult niche, or both? *American Naturalist*, **169**, 433–442.

Poorter, H. & Remkes, C. (1990) Leaf area ratio and net assimilation rate of 24 wild species differing in relative growth rate. *Oecologia*, **83**, 553–559.

Poorter, H. & van der Werf, A. (1998) Inherent variation in plant growth. *Physiological mechanisms and ecological consequences* (eds H. Lambers, H. Poorter & M.M.I. Van Vuuren), pp. 309–336. Backhuys, Leiden.

Poorter, L., Wright, S.J., Paz, H., Ackerly, D.D., Condit, R.S., Ibarra-Manriquez, G. *et al.* (2008) Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. *Ecology*, **89**, 1908–1920.

R Core Development Team. (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rees, M., Osborne, C.P., Woodward, F.I., Hulme, S.P., Turnbull, L.A. & Taylor, S.H. (2010) Partitioning the components of relative growth rate: how important is plant size variation? *The American Naturalist*, **176**, E152–E161.

Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1992) Leaf life span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs*, **62**, 365–392.

Rüger, N., Wirth, C., Wright, S.J. & Condit, R.S. (2012) Functional traits explain light and size response of growth rates in tropical tree species. *Ecology*, **93**, 2626–2636.

Russo, S.E., Jenkins, K.L., Wiser, S.K., Uriarte, M., Duncan, R.P. & Coomes, D.A. (2010) Interspecific relationships among growth, mortality and xylem traits of woody species from New Zealand. *Functional Ecology*, **24**, 253–262.

Sakschewski, B., von Bloh, W., Boit, A., Rammig, A., Kattge, J., Poorter, L. & Thonicke, K. (in press) Leaf and stem economics spectra drive diversity of functional plant traits in a dynamic global vegetation model. *Global Change Biology*, doi: 10.1111/gcb.12870.

Scheiter, S., Langan, L. & Higgins, S. (2013) Next-generation dynamic global vegetation models: learning from community ecology. *New Phytologist*, **198**, 957–969.

Stan Development Team. (2014) *Stan Modeling Language User's Guide and Reference Manual*.

Ter Steege, H. (2003) *Long-Term Changes in Tropical Tree Diversity*.

Tobner, C.M., Paquette, A., Reich, P.B., Gravel, D. & Messier, C. (2013) Advancing biodiversity-ecosystem functioning science using high-density tree-based experiments over functional diversity gradients. *Oecologia*, **174**, 609–621.

Turnbull, L.A., Philipson, C.D., Purves, D.W., Atkinson, R.L., Cunniff, J., Goodenough, A. *et al.* (2012) Plant growth rates and seed size: a re-evaluation. *Ecology*, **93**, 1283–1289.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the concept of trait be functional!. *Oikos*, **116**, 882–892.

Wright, S.J., Kitajima, K., Kraft, N.J.B., Reich, P.B., Wright, I.J., Bunker, D.E. *et al.* (2010) Functional traits and the growth-mortality trade-off in tropical trees. *Ecology*, **91**, 3664–3674.

Received 23 August 2014; accepted 20 March 2015
Handling Editor: David Gibson

Supporting Information

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

Table S1. Summary data on each experimental site.

Table S2. Summary data on each species-site combination.

Figure S1. Predicted growth of each of the 333 species-site combination over time. Points indicate observed sizes of individuals, heavy black lines indicate species-mean growth, and thin grey lines indicate growth of repeatedly observed individuals. The colour of the associated confidence envelopes indicates the fitted functional form green: asymptotic; red: exponential; blue: logistic. Note that height is log-transformed and that scales vary among panels.

Figure S2. Relationships between size-standardized relative growth rate (SGR) and SLA, wood density, and seed mass in the world-wide TreeDivNet sites (Top row, panels A–C) and the European TreeDivNet sites (Bottom row, panels D–F). A trait-only model fit the former data best, whereas the latter were best fit by a model that included a trait–PET interaction. In all panels, relationships are weighted by the inverse of the credible intervals around species-specific growth rates, which are indicated by error bars. SGR was log-transformed for analysis and back-transformed for presentation.

Figure S3. Relationships between size-standardized relative growth rate (SGR) and SLA, wood density, and seed mass in the global data set. SGR was estimated at standardized heights of 200 cm (Top row, panels A–C), 300 cm (Middle row, panels D–F) and 500 cm (Bottom row, panels G–I). A trait-only model fit all three sets of data best. In all panels, relationships are weighted by the inverse of the credible intervals around species-specific growth rates, which are indicated by error bars. SGR was log-transformed for analysis and back-transformed for presentation.