1
2   Globally, functional traits are weak predictors of juvenile tree growth, and we do not
3 know why

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

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124 **RUNNING TITLE**
125   Functional traits and growth rates

126

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128   FunDivEurope, functional ecology, growth, hierarchical models, Plant population and
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130

131   SUMMARY

132   1. Plant functional traits, in particular specific leaf area (SLA), wood density and seed mass,

133   are often good predictors of individual tree growth rates within communities. Individuals

134   and species with high SLA, low wood density and small seeds tend to have faster growth

135   rates.

136   2. If community-level relationships between traits and growth have general predictive value,

137   then similar relationships should also be observed in analyses that integrate across taxa,

138   biogeographic regions, and environments. Such global consistency would imply that traits

139   could serve as valuable proxies for the complex suite of factors that determine growth rate,

140   and, therefore, could underpin a new generation of robust dynamic vegetation models.

141   Alternatively, growth rates may depend more strongly on the local environment or

142   growth-trait relationships may vary along environmental gradients.

143   3. We tested these alternative hypotheses using data on 27,352 juvenile trees, representing

144   278 species from 27 sites on all forested continents, and extensive functional-trait data,

145   38% of which were obtained at the same sites at which growth was assessed. Data on

146   potential evapotranspiration (PET), which summarises the joint ecological effects of

147   temperature and precipitation, were obtained from a global database.

148   4. We estimated size-standardized relative height growth rates (SGR) for all species, then

149   related them to functional traits and PET using mixed-effect models for the fastest-

150   growing species and for all species together.

151   5. Both the mean and 95th percentile SGR were more strongly associated with functional

152   traits than with PET. PET was unrelated to SGR at the global scale. SGR increased with

153   increasing SLA and decreased with increasing wood density and seed mass, but these

154   traits explained only 3.1% of the variation in SGR. SGR-trait relationships were

155   consistently weak across families and biogeographic zones, and over a range of tree

156   statures. Thus, the most widely studied functional traits in plant ecology were poor

157   predictors of tree growth over large scales.

158   6. *Synthesis.* We conclude that these functional traits alone may be unsuitable for predicting

159   growth of trees over broad scales. Determining the functional traits that predict vital rates

160   under specific environmental conditions may generate more insight than a monolithic

161   global relationship can offer.

162   **INTRODUCTION**

163   Functional traits impact population growth rates via their effects on the vital rates of

164   recruitment, growth, reproduction and survival (Lavorel & Garnier 2002; Violle *et al.* 2007;

165   Adler *et al.* 2014). They have been adopted with enthusiasm by ecologists in part because

166   they reduce the dimensionality inherent in species-rich ecosystems, providing a tractable way

167   to make inferences on community dynamics and ecosystem functioning (McGill *et al.* 2006).

168   The use of functional traits has provided substantial insight into the determinants of

169   community structure, including relative abundances and competitive hierarchies (Kraft,

170   Valencia & Ackerly 2008; Cornwell & Ackerly 2010; Kunstler *et al.* 2012). Making

171   community-level inferences using functional traits is predicated, however, on the assumption

172   that they are strongly associated with the vital rates of individuals.

173   This assumption has been strongly validated in forested sites, where functional traits,

174   especially wood density, are associated with interspecific variation in the growth rates of

175   trees. Variation in wood density accounted for up to 33% of the variation in relative growth

176   rate (RGR) for the fastest-growing juveniles of Panamanian rain-forest tree species, though

177   relationships were weaker among adult trees, slower-growing individuals, and with other

178   functional traits (Wright *et al.* 2010; Rüger *et al.* 2012). Across Spain, Martínez-Vilalta *et al.*

179   (2010) showed that RGR was inversely related to wood density ($R^2 = 0.35$) using national

180   forest inventory data. At a still larger scale, Poorter *et al.* (2008) showed that wood density

181   explained 11% of the variation in RGR across five Neotropical forest sites. Because of the

182   consistency in results among their five sites, Poorter *et al.* (2008) suggested that trait-growth

183   relationships would be similar across rain forests, since all rain forest trees face similar trade-

184   offs.

185   We tested the hypothesis that the relationships between tree functional traits and RGR

186   that are found within communities are also encountered at a global scale. If traits have a

187   general and consistent relationship with RGR, then significant covariation should be observed

188   in a data set that encompasses global variation in environments and taxa with diverse

189   biogeographic and phylogenetic histories. Such consistency would imply that functional traits

190   can serve as proxies for the complex suite of factors that determine growth rate, given the

191   abiotic and biotic environment, and could thus underpin a new generation of robust dynamic

192   vegetation models (Scheiter, Langan & Higgins 2013; Sakschewski *et al.* in press).

193   Alternatively, at such large scales, growth rates may depend more upon environmental

194   conditions, or upon trait-environment interactions, such that the strength of growth-trait

195   relationships varies along environmental gradients.

196   We examined three commonly measured functional traits, for which global

197   relationships with the individual tree growth would be expected: specific leaf area (SLA),

198   wood density and seed mass (Grime, Hunt & Grime 1975; Poorter & Remkes 1990; Poorter

199   & van der Werf 1998). RGR should correlate positively with increasing SLA, but negatively

200   with wood density and seed mass, for the following reasons. SLA is a strong determinant of

201   carbon assimilation capacity per unit mass invested in photosynthetic surface area (Rees *et al.*

202   2010). Wood density governs the translation of assimilated carbon into stem and branch

203   biomass, thereby influencing tree height and crown growth. Denser wood is associated with

204   increased construction costs and decreased hydraulic conductance, both of which can reduce

205   growth rate (Chave *et al.* 2009). Finally, seed mass is inversely related to survival for

206   seedlings, and can thus affect the growth of juvenile plants via life-history correlations,

207   although this effect dissipates when growth rates are compared at a standard size (Turnbull *et*

208   *al.* 2012).

209   At a global scale, variation in temperature and precipitation should also affect growth

210   rates. Though rates of photosynthesis and maintenance respiration are strongly temperature-

211   dependent (Atkin *et al.* 2005), the primary ecological effect of elevated temperature on

212   growth rates derives from its interaction with low precipitation, increasing drought stress.

213   High evaporative demand may limit photosynthetic carbon assimilation due to stomatal

214   closure to reduce water stress (Keenan *el al*. 2013).

215   We assessed the relative importance of functional traits and environmental conditions

216   in determining variation in sapling growth rates using a unique global dataset of 27,352

217   individual juvenile trees representing 278 species from sites on all forested continents.

218   Functional trait data were collected for all species, 38% of which were obtained from the

219   same sites at which growth was assessed. Potential evapotranspiration (PET) was obtained

220   for all sites from a global database. We estimated growth rates at a standardized size using

221   nonlinear hierarchical Bayesian models, which allowed us to account for uncertainty in

222   growth rates. We then assessed the relationships among growth rates, functional traits and

223   PET using mixed-effect models. Functional traits may better predict maximal than mean

224   growth rates (Grime *et al.* 1975; ter Steege 2003; Wright *et al.* 2010). Therefore, we also used

225   linear quantile mixed-effect models to examine the growth of the fastest-growing species. To

226   further assess the generality of growth-trait relationships, we partitioned the variation in the

227   global relationships among plant families and biogeographic regions.

228

229   **MATERIALS AND METHODS**

230   *Study sites and growth data*

231   We assessed height growth on juvenile trees because less data were available for radial

232   growth and for adults. Furthermore, juveniles are expected to have stronger growth-trait

233   relationships than adults, given their smaller pools of stored reserves. We included only free-

234   standing tree species; palms were also excluded as they do not have secondary growth. Data

235   on tree growth were compiled from 27 sites across six continents. The key criterion for the

236   inclusion of a site in this study was that juvenile trees of known age were grown in a nursery,

237   then planted into mixed-species stands. This ensured a measure of consistency in the age and

238   ontogenetic stage of juveniles within and among sites. The median juvenile was 37 cm tall

239   when transplanted (inter-quartile range: 7-170 cm).

240   The core of the dataset came from the European sites of TreeDivNet

241   (www.treedivnet.ugent.be), which constitute the experimental platform of FunDivEUROPE

242   (Baeten *et al.* 2013), a consortium of biodiversity-ecosystem functioning studies on woody

243   plants. These sites were complemented by other TreeDivNet sites (Bruelheide *et al.* 2014),

244   reforestation trials, and studies designed to test specific ecological hypotheses. The latter two

245   classes of studies were located through literature searches. In sites with multiple diversity

246   treatments, we used only data from the one with the greatest species diversity. These

247   treatments most closely resembled natural conditions, and their use allowed us to avoid

248   interference with on-going research at each site. Where light availability was manipulated, we

249   used the treatment with the greatest light availability to reduce within-site heterogeneity and

250   to assure positive growth rates. The sites spanned a latitudinal range from 18º S (Queensland,

251   Australia) to 62º N (Satakunta, Finland).

252   Across our sites, annual rainfall varied between 533 and 4900 mm, and mean annual

253   temperature between 5.0 and 27.7º C. Temperature and precipitation were highly correlated,

254   however, precluding an examination of their individual effects ($r = 0.79$). Therefore, we

255   investigated environmental conditions in terms of potential evapotranspiration (PET), which

256   integrates the effects of temperature and precipitation, and expresses the ability of the

257   atmosphere to remove water through evaporation and transpiration (Allen *et al.* 1998). This

258   climatic metric, though relatively crude, was appropriate for this study, in which the

259   heterogeneity of data sources precludes the investigation of more detailed aspects of the

260   biotic environment. We obtained standardized PET data for each site from the Consortium for

261   Spatial Information's Global Aridity and PET Database (http://www.cgiar-

262   csi.org/data/global-aridity-and-pet-database). PET data were downloaded with 30 arc-second

263   spatial resolution as an annual average over the years 1950-2000. We extracted the PET

264   values for grid cells within 50 km of each study site, then, for analysis, calculated the mean

265   PET for each site.

266   In total, we studied 278 species and 27,352 individuals, on which 120,150

267   measurements were made. Because there was substantial variation among sites in terms of

268   light availability, planting density, study duration and species composition, the 39 species

269   that occurred in more than one site were modelled independently, yielding 333 species-site

270   combinations (henceforth referred to as 'species'). Sample sizes varied among sites: 3 to 48

271   species, and 35 to 7065 individuals were measured at each site. The median species was

272   represented by 32 individuals (range: 5 to 2205) and 124 measurements (range: 10 to 10716).

273   The median study lasted 49 months (range 11 to 145). Nomenclature follows that of The

274   Plant List (http://theplantlist.org). See Figure 1 and Supplementary Table 1 for details of each

275   site.

276

277   *Trait data*

278   Functional trait data were acquired from many sources. In 14 of the 27 sites, traits were

279   measured on the same species at which growth was assessed, yielding 'local' values of SLA,

280   wood density and seed mass for 192, 121, and 66 species, respectively. Trait data for the

281   remaining species were obtained from publicly available databases and published studies.

282   The TRY database of plant traits (Kattge *et al.* 2011), Chave *et al.* (2009) and the Kew Seed

283   Information Database (SID, http://data.kew.org/sid), were the primary resources for data on

284   SLA, wood density and seed mass, respectively. Supplemental data were gleaned from

285   literature searches. Species-level data on SLA, wood density and seed mass were available

286   for 91, 96 and 86% of species, respectively. To estimate the functional traits of the remaining

287   species, we first obtained the relevant traits for all congeneric species from the

288   aforementioned primary data sources. Following Gallagher & Leishman (2012), we regressed

289   genus-mean trait values against the observed species mean trait values, and then predicted

290   species-mean trait values from the genus-mean values (R^2: SLA: 15%, WD 73%, SM: 86%).

291

292   *Analyses*

293   Relationships between relative growth rates and functional traits were evaluated in a three-

294   step process.

295   *First*, we selected the functional form to predict individual height as a function of

296   time. In 23 sites, juveniles were measured for height four or more times, allowing nonlinear

297   models to be fit. Such models are appropriate because RGR tends to decrease over time,

298   owing to the accumulation of non-photosynthetic biomass and the local depletion of soil

299   resources (Paine *et al.* 2012). We fit linear, exponential, power-law, asymptotic and logistic

300   mixed-effect models for each species-site combination separately, then selected the best

301   function for each one on the basis of Akaike's information criterion (AIC). In the remaining

302   four sites, juveniles were measured three times; their growth was modelled as an exponential

303   function of time. All growth models included individual trees as a random effect.

304   *Second*, we predicted the height of each individual tree as a function of time using

305   species-specific Bayesian hierarchical models with the functional forms selected in step one.

306   Parameters were given uninformative priors and were fitted with a Hamiltonian Monte Carlo

307   sampler using the No-U-Turns (NUTS) algorithm, with the constraint that predicted heights

308   always be positive. We implemented these models in stan 2.5 via the package 'rstan' in R

309   3.1.1 (R Core Development Team 2014; Stan Development Team 2014). Four chains were

310   run for each species-specific growth model. All models were run for 20,000 iterations,

311   discarding the first 19,000 as a burn-in period. We used the Rhat statistic, together with a

312   visual inspection of the chains, to assess convergence (Gelman & Rubin 1992). Parameters in

313   all models converged before 1000 iterations (Rhat≈1).

314   These models yielded posterior distributions of growth parameters for each species,

315   from which we calculated posterior distributions of RGR at a standardized height of 100 cm,

316   a height attained by almost all species. We refer to this size-standardized RGR as 'SGR'.

317   Size-standardization reduces the potential for bias when making comparisons among species

318   that vary in initial size (Rees *et al.* 2010; Turnbull *et al.* 2012), as was the case here. SGR

319   was calculated as the derivative of the function used to predict height, divided by the standard

320   height (Paine *et al.* 2012). Trait values can vary over ontogeny, and size-standardized trait

321   values can explain variation in SGR (Rees *et al.* 2010), even though species rankings are

322   largely maintained (Poorter 2007). Even so, we did not analyse ontogenetic variation in trait

323   values, because data on ontogenetic variation were not available for most species in the

324   dataset.

325   *Third*, we predicted SGR as a function of PET and functional traits (SLA, wood

326   density, and seed mass) for all species, and for the fastest-growing species (i.e., species in the

327   95th quantile of growth rates). The former group was analysed with linear mixed-effect

328   models, whereas the latter group was analysed using linear mixed-effect quantile models

329   (Geraci 2014) including additive and interactive effects (Table 1). Because preliminary

330   analyses indicated that SGR varied substantially among sites, we included site-specific

331   intercepts as a random effect in all models. In all models, SGR and seed mass were log-

332   transformed to improve normality. Predictor values were always centred and standardized to

333   unit variance, to allow comparisons among their slope parameters. Thus, intercepts represent

334   the SGR for a species with trait values at the global mean and with PET at the global average.

335   We accounted for uncertainty in our estimates of SGR by weighting each observation by the

336   standard deviation of its posterior distribution obtained in step two. Doing so, we assumed the

337   true SGR values were log-normally distributed with species-specific means and standard

338   deviations. In contrast, in many previous studies, species-mean growth rates have been

339   assessed as point estimates, implying that they were known without error (Reich, Walters &

340   Ellsworth 1992; Poorter & van der Werf 1998; but see Rüger *et al.* 2012). Models were

341   compared on the basis of AIC. For the linear mixed-effect models, pseudo R^2 was obtained

342   with the method of Nakagawa & Schielzeth (2013). We were not able to calculate the

343   variance explained for the fast-growing species, because such methods have not yet been

344   developed for linear quantile mixed-effect models (Geraci 2014).

345   In addition to the global analyses, we partitioned variance in the SGR-trait

346   relationships among study sites, plant families and biogeographic regions following the

347   approach of Gelman (2005). Our aim was to estimate the variation contributed by each source

348   to global SGR-trait relationships, rather than to test hypotheses. Thus, we built an additional

349   linear mixed-effect model with random intercepts and slopes for sites, families and regions.

350   Our biogeographic regions mostly aligned with continental margins but were adjusted to

351   reduce variation in sample sizes (Fig. 1). To make the sources of variation comparable, we

352   assumed that effects of sites, families and regions on intercepts and slopes were each drawn

353   from separate, independent, zero-mean normal distributions. We estimated the variance

354   contributed by each source to SGR and the three SGR-trait relationships through 2000

355   bootstrap samples of the variance-covariance matrix. Linear mixed-effect models and linear

356   quantile mixed-effect models were implemented in the lme4 and lqmm packages,

357   respectively (Bates *et al.* 2014; Geraci 2014).

358

359   **RESULTS**

360   Species-mean SLA varied fifteen-fold (3.37–50.38 $m^2 \cdot kg^{-1}$), wood density five-fold (0.16–

361   0.96 $g \cdot cm^{-3}$), and seed mass by six orders of magnitude (0.11–33,333 mg). Functional traits

362   were largely uncorrelated with each other, with coefficients of determination ≤ 0.06, though

363   there were significantly positive SLA-wood density and seed mass-wood density

364   relationships (Fig. 2). See Supplementary Table 2 for details of the studied species and their

365   functional traits.

366   Log-transformed height was best modelled with a logistic or asymptotic function for

367   210 and 70 species, respectively, whereas the remaining 53 were adequately modelled by

368   exponential functions (Supplementary Figure 1). Thus, growth rates decreased as individual

369   trees increased in size in 84% of the studied species. Species-mean SGR varied among

370   species over four orders of magnitude, from $9.52×10^{-6}$ cm·cm^{-1}·day^{-1} in *Protium aracouchini*

371   to 0.014 cm·cm^{-1}·day^{-1} in *Phyllanthus salviifolius*, with the median species having a SGR of

372    $1.28×10^{-3}$ cm·cm^{-1}·day^{-1} (Fig. 3).

373   Both mean and 95th percentile SGR were more strongly associated with functional

374   traits than with PET. For all species together, as well as fast-growing species, models with

375   traits alone had the lowest AIC values (Table 1). The three functional traits were associated

376   with mean SGR, with each SGR-trait slope differing significantly from zero (95 per cent

377   confidence intervals: SLA, 0.09 – 0.11; WD: -0.11 – -0.09, SM: -0.10 – -0.08; Fig. 3). Judged

378   by their standardized slope coefficients, the three traits were associated with SGR to a similar

379   degree. Thus, a 10 m^2·kg^{-1} increase in SLA increased SGR by 10.3%, a 0.1 g·cm^{-3} increase in

380   wood density reduced SGR by 5.3%, and a one order of magnitude increase in seed mass

381   reduced SGR by 7.3%. Overall, however, functional traits explained only 3.1% of the

382   variation in SGR (marginal pseudo-R^2). Examined independently, SLA, wood density and

383   seed mass explained 0.8%, 1.4% and 1.6% of the variation in SGR, respectively. Far more

384   variance was explained by among-site variation in SGR (conditional pseudo-R^2: 71%).

385   When the fastest-growing species were analysed (i.e., species in the 95th percentile of

386   growth rates), seed mass was significantly negatively related to SGR (P < 0.0001), whereas

387   SLA and wood density had no effect (SLA: P = 0.42, wood density: P = 0.072; Fig. 3A-C).

388   Accordingly, comparing standardized slope coefficients from the quantile mixed-effect model,

389   seed mass affected the SGR of fast-growing species more strongly than did SLA or wood

390   density (seed mass = -0.17, SLA = -0.01, wood density = -0.13). For these species, a one

391   order of magnitude increase in seed mass reduced SGR by 19.2%.

392   We partitioned the variation in SGR and the SGR-trait relationships among sites,

393   plant families and biogeographic regions (Fig. 4). SGR varied among families, but families

394   did not differ in their SGR-trait relationships (parametric bootstrap likelihood ratio test: P =

395   0.45). There was no evidence of variation in SGR or SGR-trait relationships among

396   biogeographic regions (P ≥ 0.31). Therefore, sites were the dominant source of variation in

397   SGR, with relatively minor contributions from families and regions.

398   We assessed the generality of growth-trait relationships in four additional ways. First,

399   we assessed them using only those sites in which study designs were most similar. This

400   evaluated the possibility that global growth-trait relationships were obscured by among-site

401   variation in experimental design (Supplementary Table 1). To do so, we considered the

402   global sites of TreeDivNet, and the European sites of that network (nine and five sites,

403   respectively). Growth-trait relationships in the global TreeDivNet sites were of a similar

404   magnitude to those in the global dataset (standardized slope coefficients: SLA: -0.15, WD: -

405   0.14, SM: -0.14; Supplementary Figure 2). In the European TreeDivNet sites, there were

406   significant interactions between functional traits and PET, such that increasing PET

407   strengthened SGR-trait effects (Supplementary Figure 2), despite the shorter gradients of PET

408   and traits in this geographically restricted subset of the data. Surprisingly, in both analyses,

409   increasing SLA was associated with reduced growth rates.

410   Competitive interactions could intensify as juveniles grow, for example, affecting

411   SGR-trait relationships. We examined, therefore, whether the strength of growth-trait

412   relationships varied with the size at which growth rates were measured. We repeated the

413   linear mixed-effect analyses using SGR estimated at heights of 200, 300, and 500 cm,

414   including only the species that attained those heights. Models that included additive effects of

415   PET and functional traits were preferred when SGR was estimated at these heights.

416   Nevertheless, we infer that PET only marginally affected growth rates, because more-

417   parsimonious trait-only models fit the data equivalently well, regardless of the size at which

418   growth was assessed (ΔAIC: 2.5, 0.8 and 1.2, respectively). Seed mass was the only

419   significant predictor of growth at heights above 100 cm (Supplementary Figure 3). The slope

420   of the growth-seed mass relationships remained largely consistent as juveniles grew. Thus,

421   growth trait relationships became no stronger as juveniles increased in size.

422   Within-site variation in environmental conditions could retard the growth of some

423   individuals. For example, photo-inhibition may have reduced growth rates for shade-tolerant

424   species planted into sunny sites (Loik & Holl 2001), even as shading from faster-growing

425   neighbours may have reduced growth rates for some individuals in others (Tobner *et al.*

426   2013). We evaluated this possibility by modelling the growth of the fastest-growing

427   individuals (i.e., individuals in the 95th percentile of growth rates for each species) with an

428   additional set of mixed-effect models. A functional trait-only model fit the data more

429   parsimoniously and almost equivalently well as a model including PET (Table 1). Though all

430   three functional traits significantly affected the growth of the fastest-growing individuals, the

431   standardized slope coefficients were no greater in magnitude than in the model for all species

432   (SLA: 0.09, WD: -0.12, SM: -0.12; Fig. 3D-F). Nor did this model explain substantially more

433   variance in growth rates (marginal pseudo-R^2, SLA: 0.7%, wood density: 1.6%, seed mass:

434   2.2%). Thus, even for the fastest-growing individuals in each species, functional traits

435   remained poor predictors of growth.

436   Finally, not all functional trait values were available for all species at the sites where

437   saplings were measured. Intra-specific trait variation, however, can be substantial (Albert *et*

438   *al.* 2010). By including trait data drawn from databases and the literature, we may have

439   introduced variation which obscured the global growth-trait relationships. We tested this

440   possibility by evaluating whether the slopes of the growth-trait relationships differed between

441   the set of species with locally measured traits and the set with trait data obtained from other

442   sources. The three traits were measured locally on differing subsets of species. SLA, wood

443   density and seed mass were locally available for 192, 121 and 66 species, respectively. Thus,

444   we built a mixed-effect model for each trait to test if the slope of the growth-trait relationship

445   depended on the origin of the trait data. They did not (parametric bootstrap likelihood ratio

446   tests: $P \geq 0.88$). These models were similarly poor at explaining the variation in SGR (Pseudo

447    $R^2 \leq 2.3\%$). Therefore, we do not believe that the weakness in the global growth-trait

448   relationships is attributable to intra-specific trait variation.

449

450   **DISCUSSION**

451   At a global scale, among-species variation in sapling growth was positively associated with

452   SLA, and negatively with wood density and seed mass. Even so, they were surprisingly weak,

453   and did not strengthen when we analysed more homogeneous geographic subsets, juveniles

454   of larger stature, fast-growing individuals, or locally collected functional trait data. Due to

455   their significant negative covariation, we conclude that the relationships between functional

456   traits and sapling growth are globally consistent. On the other hand, growth and growth-trait

457   relationships were independent of global variation in potential evapotranspiration. We discuss

458   why traits are reasonable predictors of performance at local, but not global scales, and the

459   implication of our results for trait-based global vegetation modelling.

460

461   *Why are global growth-trait relationships so weak?*

462   Previous studies have found stronger relationships between growth and the traits we studied,

463   especially when plants were grown under controlled conditions (Grime *et al.* 1975; Poorter &

464   van der Werf 1998). Combinations of functional traits explained up to 40-60% of the

465   variation in diameter growth for field-grown trees assessed at single sites (Wright *et al.* 2010;

466   Rüger *et al.* 2012), and slightly less at regional scales (Poorter *et al.* 2008; Martínez-Vilalta *et*

467   *al.* 2010). In contrast, we found that the three functional traits explained little variation in

468   growth at the global scale. This broad result is made robust by the use of a) a substantial

469   dataset of global scope, b) data-collection methods that were standardized across globally

470   distributed study sites, c) an analysis through which uncertainty was propagated and d)

471   estimates of relative growth rate that were made at standardized sizes.

472   The discrepancy between previous studies and the current, global one might be

473   explained by the fact that an individual's growth rate is not only affected by its functional

474   traits, but also by the environmental conditions it experiences and the suitability of its traits to

475   its environment. Environmental conditions entered our analyses as the fixed effect of PET,

476   which summarized the joint influence of temperature and precipitation, and the random effect

477   of site, which accounted for unmeasured sources of variation in SGR among sites.

478   Surprisingly, PET affected neither SGR nor global SGR-trait relationships, although among-

479   site variation in SGR was substantial. This may have occurred because we selected study

480   sites with similar experimental designs and relatively high-light conditions; 59% of species

481   were planted into sites with ≥ 50% sunlight, and 70% were planted with ≥ 25% sunlight

482   (Supplementary Table 1). Simultaneously, we found weak relationships between SGR and

483   functional traits. Together, these observations suggest that growth rates were strongly

484   affected by unmeasured within-site variation in environmental conditions. We tested this by

485   evaluating the relationships among growth, traits and PET for the fastest-growing individuals

486   of each species, and surprisingly, found that relationships were no stronger than in the overall

487   analysis (Fig. 3D-F). This indicates that functional traits were poor predictors of growth even

488   for individuals that did not experience adverse environmental conditions. The discrepancy

489   could also have arisen if there were substantial variation in growth-trait relationships among

490   sites, but after testing with an additional set of models that allowed for varying growth-trait

491   relationships in each site, we found no support for the suggestion that growth-trait

492   relationships vary among sites (parametric bootstrap likelihood ration tests: $P \geq 0.75$),

493   confirming the minor variance in slopes explained by sites in the variance-partitioning

494   analysis (Fig. 4).

495   Our choice of growth metric may have affected our inference of the strength of the

496   growth-trait relationships. Ideally, growth would be assessed as whole-plant biomass, rather

497   than as stem height. This was not feasible in the current study, as it would have required

498   species-specific allometries or destructive harvests, which were not available for most species

499   in our dataset. Growth can also be measured as girth, which is often strongly correlated with

500   height (Martínez-Garza, Bongers & Poorter 2013). For trees <140 cm, however, there is little

501   consensus on the point at which girth should be measured. Moreover, height growth can be

502   evaluated much more precisely than radial growth because small plants grow more in height

503   than in diameter, and height growth is more ecologically relevant, as it determines an

504   individual's position in the vertical light profile of the forest, and thus, its access to light.

505   Using stem height may have introduced some noise into the analysis, owing to interspecific

506   variation in biomass allocation to height. We believe, however, that it is unlikely to have been

507   sufficient to generate the globally weak trait-growth relationships we observed.

508   Altogether, it is unclear why global relationships among functional traits, PET and

509   growth are so weak. Thus, evaluating the joint effects of environmental conditions and

510   functional traits on growth rates remains an important topic of study (Rüger *et al*. 2012).

511

512   *Toward better predictions of growth*

513   To better manage and conserve ecological communities, we must improve our ability to

514   predict their dynamics (Clark *et al.* 2001). The most promising models to do so are rooted in

515   demography (Boulangeat *et al.* 2012), but obtaining demographic data is challenging,

516   especially in species-rich communities where many species are rare. The ability to accurately

517   predict vital rates, and thus demography, from data that are relatively easily obtained would

518   allow a step change in ecological forecasting (Adler *et al.* 2014). The relative ease of

519   collecting functional trait data and the potential of functional traits to yield insight into

520   population and community structure (Kraft *et al.* 2008; Cornwell & Ackerly 2010; Kunstler

521   *et al.* 2012), suggest that integrating them into dynamic vegetation models would increase

522   their reliability (Scheiter *et al.* 2013; Sakschewski *et al.* in press). Our results, however,

523   indicate that the functional traits most commonly investigated in plant ecology are poor

524   predictors of growth at large scales. Though organ-specific functional traits are easily

525   measured, they integrate many physiological processes, are intricately interrelated, and can be

526   highly plastic (Russo *et al.* 2010; Paine *et al.* 2011; Pérez-Harguindeguy *et al.* 2013).

527   Moreover, functional integration occurs at the individual level, not at the level of organs

528   (Craine *et al.* 2012). Thus, many combinations of trait values can yield similar growth rates

529   (Marks & Lechowicz 2006). Integrated measures, such as whole-plant carbon use efficiency,

530   may be more effective (Enquist *et al.* 2007).

531   Is it feasible to predict plant community dynamics over broad scales? It has been

532   suggested that 'hard' functional traits, such as photosynthetic or respiration rates, would be

533   better predictors of vital rates than 'soft' traits such as SLA, wood density and seed mass

534   (Lavorel & Garnier 2002). This is unlikely under field conditions, however, because the

535   physiological bases of hard traits make them overly sensitive to heterogeneity in

536   environmental conditions. Contrastingly, experimental measurements of whole-plant

537   tolerance to low resource availability may predict vital rates, and thus community dynamics,

538   over broader scales than can organ-specific functional traits (Craine *et al.* 2012). As data on

539   species' physiological tolerance to low resource availability become more widely available,

540   they should allow broader-scale predictions of community structure and dynamics

541   (Engelbrecht *et al.* 2007). We suggest that future studies focus on determining which

542   functional traits predict the vital rates of individuals under various environmental conditions,

543   and at what spatial scales (Martínez-Garza *et al.* 2005), rather than seeking monolithic global

544   relationships. Regardless of the approach, improving techniques to predict the dynamics of

545   ecological communities remains a vital task, given the urgent need for their management and

546   conservation.

547

556
557   **DATA ACCESSIBILITY**
558   All growth and functional trait data used in this study are archived at the DRYAD online
559   database under doi:10.5061/dryad.h9083.
560   In addition to the data collected for this study, functional trait data were obtained from the
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899

900   **TABLES**

901   **Table 1** Comparison of A) all species, B) fast-growing individuals in all species, and c) fast-

902   growing species. The first two groups were fit using linear mixed-effect models, whereas the

903   latter group was fit using linear quantile mixed-effect models. Models are sorted by

904   increasing Akaike Information Criterion (AIC). PET: Potential evapotranspiration

	Model	N Parameters	ΔAIC
All species	Traits	6	0.0
	PET + Traits	7	1.5
	Intercept-only	10	5.1
	PET	4	6.6
	PET x Traits	10	6.7
Fast-growing species	Traits	6	0.0
	PET + Traits	7	1.9
	PET x Traits	10	14.9
	PET	4	32.6
	Intercept-only	3	72.9
Fast-growing individuals	PET + Traits	7	0.0
	Traits	6	0.1
	PET x Traits	10	5.2
	PET	4	20.6
	Intercept-only	3	20.7

905   **FIGURES**

906   **Figure 1**   Map of study sites. Points are coloured by biogeographic region and scaled to

907   the number of species studied at each site. Bold font indicates site numbers, whereas plain

908   text indicates study duration (in months) and the number of individuals monitored for growth

909   at each site. See Supplementary Table 1 for details.

910

911   **Figure 2**   Correlations among functional traits for the 333 species-site combinations.

912   Note that seed mass is presented on log-transformed axes. Functional traits were largely

913   independent of one another. Fitted lines are derived from standardized major-axis

914   regressions. Error bars indicate one standard error of the mean.

915

916   **Figure 3**   Global relationships between size-standardized relative growth rate (SGR) and

917   SLA, wood density, and seed mass. In A-C), points represent mean SGR for each species,

918   whereas in D-F), points represent the 95th percentile of growth rates of individuals in each

919   species. Thick regression lines and darker shading show overall relationships fitted with a

920   weighted linear mixed-effects model, whereas thinner lines and lighter shading show

921   relationships for fast-growing species, which were fitted with a weighted linear 95th quantile

922   mixed-effects model. Solid lines represent significant relationships ($\alpha \leq 0.05$), whereas

923   dashed lines indicate non-significant ones. Relationships are shown with 95% confidence

924   intervals. In all models, weights are the inverse of the credible intervals around species-

925   specific growth rates, which are indicated by error bars.

926

927   **Figure 4**   A summary of the variance contributed to the global growth-trait relationships

928   by study sites, plant families and biogeographic regions. Variation in SGR was greater among

929   study sites than among families or regions, whereas SGR-trait relationships were relatively

930   consistent among sites, families and regions. Points, thick bars and thin bars show means,

931   50% confidence intervals and 95% confidence intervals of the finite-population standard

932   deviations, respectively. The point estimates are not always at the centre of the intervals

933   because all variance components must be nonnegative (Gelman 2005).

934

935   **SUPPLEMENTARY MATERIAL**

936   **Supplementary Table 1**   Summary data on each experimental site.

937   **Supplementary Table 2**   Summary data on each species-site combination.

938   **Supplementary Figures**

939   **1)**   Predicted growth of each of the 333 species-site combination over time. Points

940   indicate observed sizes of individuals, heavy black lines indicate species-mean

941   growth, and thin grey lines indicate growth of repeatedly-observed individuals. The

942   colour of the associated confidence envelopes indicates the fitted functional form

943   green: asymptotic; red: exponential; blue: logistic. Note that height is log-transformed

944   and that scales vary among panels.

945   **2)**   Relationships between size-standardized relative growth rate (SGR) and SLA, wood

946   density, and seed mass in the worldwide TreeDivNet sites (Top row, panels A-C) and

947   the European TreeDivNet sites (Bottom row, panels D-F). A trait-only model fit the

948   former data best, whereas the latter were best fit by a model that included a trait-PET

949   interaction. In all panels, relationships are weighted by the inverse of the credible

950   intervals around species-specific growth rates, which are indicated by error bars. SGR

951   was log-transformed for analysis and back-transformed for presentation.

952   **3)**   Relationships between size-standardized relative growth rate (SGR) and SLA, wood

953   density, and seed mass in the global dataset. SGR was estimated at standardized

954   heights of 200 cm (Top row, panels A-C), 300 cm (Middle row, panels D-F) and 500

955   cm (Bottom row, panels G-I). A trait-only model fit all three sets of data best. In all

956   panels, relationships are weighted by the inverse of the credible intervals around

957   species-specific growth rates, which are indicated by error bars. SGR was log-

958   transformed for analysis and back-transformed for presentation.

959