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Scale-dependent relationships between tree species richness and ecosystem function in forests

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Summary

1. The relationship between species richness and ecosystem function, as measured by productivity or biomass, is of long-standing theoretical and practical interest in ecology. This is especially true for forests, which represent a majority of global biomass, productivity and biodiversity.

2. Here, we conduct an analysis of relationships between tree species richness, biomass and productivity in 25 forest plots of area 8–50 ha from across the world. The data were collected using standardized protocols, obviating the need to correct for methodological differences that plague many studies on this topic.

3. We found that at very small spatial grains (0.04 ha) species richness was generally positively related to productivity and biomass within plots, with a doubling of species richness corresponding to an average 48% increase in productivity and 53% increase in biomass. At larger spatial grains (0.25 ha, 1 ha), results were mixed, with negative relationships becoming more common. The results were qualitatively similar but much weaker when we controlled for stem density: at the 0.04 ha spatial grain, a doubling of species richness corresponded to a 5% increase in productivity and 7% increase in biomass. Productivity and biomass were themselves almost always positively related at all spatial grains.

4. *Synthesis.* This is the first cross-site study of the effect of tree species richness on forest biomass and productivity that systematically varies spatial grain within a controlled methodology. The scale-dependent results are consistent with theoretical models in which sampling effects and niche complementarity dominate at small scales, while environmental gradients drive patterns at large scales. Our study shows that the relationship of tree species richness with biomass and productivity changes qualitatively when moving from scales typical of forest surveys (0.04 ha) to slightly larger scales (0.25 and 1 ha). This needs to be recognized in forest conservation policy and management.

Key-words: biodiversity, biomass, complementarity, determinants of plant community diversity and structure, productivity, sampling effects, species diversity, trees

Introduction

Research into the relationship between species richness and ecosystem function is motivated by both a basic interest in understanding ecological communities (Pianka 1966; Odum 1969; Tilman *et al.* 1997) and a practical need to conserve and manage ecosystem services (Schwartz *et al.* 2000; Srivastava & Vellend 2005). Ecosystem functions are classified as stocks, fluxes or stabilizing functions (Pacala & Kinzig 2002; Srivastava & Vellend 2005). Woody productivity (a flux) and biomass carbon storage (a stock) are two key ecosystem functions in forests (Pacala & Kinzig 2002). Forest carbon storage is of particular concern because globally forests hold more carbon than the atmosphere (Pan *et al.* 2011), and management of these carbon stores is an important tool for mitigating global climate change. In total, forests account for approximately 60% of terrestrial productivity and 85% of biomass (Randolph *et al.* 2005) and tropical forests alone account for more than 50% of terrestrial species diversity (Wilson 1988).

Many studies of species richness and ecosystem function have focused on productivity (Tilman *et al.* 1997; Loreau *et al.* 2001). Theory predicts positive effects of species richness on productivity through niche complementarity, facilitation and sampling effects (Abrams 1995; Tilman 1999; Fridley 2001; Loreau *et al.* 2001; Flombaum & Sala 2008). Niche complementarity occurs because niches, such as differences in resource-use or enemy-defence strategies, lead to increases in a species' performance as local abundance of conspecifics decreases and thus to better overall community-level performance, that is, higher productivity, when there are more species and fewer individuals per species (Janzen 1970; Connell 1971; Comita *et al.* 2010; Mangan *et al.* 2010). Facilitation occurs when species enhance one another's performances (Hooper 1998). Sampling effects arise because species richness varies randomly across quadrats, and quadrats with high species richness are more likely, by chance, to contain particular high-yield species. These sampling effects are also referred to as selection effects (Turnbull *et al.* 2012), because they assume that the high-yield species contribute disproportionately in mixtures.

The predicted positive relationships between richness and productivity are broadly supported by small-scale empirical

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studies that manipulate species richness in herbaceous communities (Tilman *et al.* 1997; Hooper 1998; Symstad *et al.* 1998; Loreau *et al.* 2001), but observational studies have produced mixed results. Early observational studies pointed to a hump-shaped relationship in which species richness peaks at intermediate productivity and declines towards extreme high or low productivity (Grime 1979; Loreau *et al.* 2001; Mittelbach *et al.* 2001; Rahbek 2005; Mittelbach 2010). But subsequent studies have cast doubt on the generality of the hump-shaped relationship, with positive, negative, flat and even *U*-shaped relationships being observed (Mittelbach 2010; Whittaker 2010). Theoretical explanations for hump-shaped productivity–richness patterns (Abrams 1995; Rosenzweig & Abramsky 1998; Aarssen 2001) generally assume that productivity acts as a proxy for environmental conditions and that environmental conditions drive species richness. One proposed mechanism for declines in species richness at high productivity is that in high-resource environments, there is less environmental heterogeneity and hence fewer niches (Rosenzweig & Abramsky 1998). Alternatively, the 'species pool' hypothesis explains the overall unimodal pattern by postulating that fewer species are adapted to extreme low- or high-productivity environments, because of a mid-domain effect (Aarssen 2004) or because low- and high-productivity areas have been less common over geological time (Schamp, Aarssen & Lee 2003). Although the hump-shaped productivity–richness pattern has a long history of theoretical and empirical support, its general applicability remains a matter of debate (Whittaker 2010; Adler *et al.* 2011; Fridley *et al.* 2012).

The predictions for relationships between richness and productivity outlined above lead directly to similar predictions for richness–biomass relationships, insofar as higher forest productivity is associated with higher standing biomass. In annual herbaceous communities, above-ground biomass is essentially synonymous with productivity, and the two terms are often used interchangeably. In forests, however, productivity and biomass are distinct (Rosenzweig & Abramsky 1998): although at local scales higher productivity enables faster biomass accumulation over forest succession and higher eventual old-growth biomass (Bonan *et al.* 2003), productivity and biomass and are not significantly associated at global scales (Keeling & Phillips 2007). Therefore, biomass and productivity should be treated separately in analyses of species richness and ecosystem function in forests.

Relatively few studies on the relationship of species richness to biomass and productivity have been conducted in forests. Those that do have generally been limited to small spatial grains (i.e. small size of the sampling unit or quadrat; typically < 0.1 ha) and local to regional spatial extents (Vilà *et al.* 2007; Ruiz-Jaen & Potvin 2010; Paquette & Messier 2011) and generally have found positive relationships. Richness–productivity relationships in forests have also been incorporated in meta-analyses that include other ecosystem types (e.g. Mittelbach *et al.* 2001), but methodological differences between individual studies that comprise the meta-analyses have confounded attempts to draw general conclusions (Whittaker 2010): different studies use different spatial extents, spatial grains, census methodologies and measures of productivity (including rainfall, biomass and other surrogate variables) and focus on different taxonomic groups (including both plants and animals).

For this study, we utilized a global data set of large-scale forest plots to investigate how the relationship of tree species richness to forest biomass and productivity varies across a range of spatial grains within sites and to test whether the observed patterns are general across sites. Our approach of using a standardized global data set allowed us to overcome the limitations of many previous cross-site studies (usually meta-analyses) that address the topic of species richness, productivity and biomass. We predicted that richness and function (the latter measured by productivity and biomass) would be positively related at most sites and that productivity would be strongly positively related to biomass at all sites. We also predicted that successional processes associated with treefall gaps (Schnitzer & Carson 2001) might lead to negative relationships at small spatial grains at some sites, because areas that have recently been in gaps typically have many small stems, high species richness and low biomass, while areas with mature trees have fewer, larger stems, lower species richness and higher biomass (Condit *et al.* 1996; Aarssen, Laird & Piter 2003).

Materials and methods

SITE SELECTION

We compared relationships between tree species richness, annual above-ground coarse woody dry productivity (CWP) and above-ground dry woody biomass (AGB) across 25 forest plots in the global network coordinated by the Center for Tropical Forest Science/Smithsonian Institution Global Earth Observatories (CTFS/SIGEO) (http://www.sigeo.si.edu/). The plots spanned temperate and tropical regions across five continents (Table 1; Fig. 1). Twelve of the plots were censused two or more times (at intervals of 4–10 year; Table 1), in which case we used two consecutive censuses for CWP estimates (see below) and the first of these censuses for AGB and richness estimates. For single-census plots, we analysed only AGB and richness. The forest plots have similar spatial extents (8–50 ha; Table 1) and censuses of individual stems at each site followed the standard CTFS/SIGEO protocols (Condit 1998).

DATA COLLECTION

The data for each plot were trimmed, if necessary, to fit within a rectangular region with edges that were even multiples of 100 m (Table 1). This guaranteed that the plot could be evenly divided into 1 ha quadrats and that the same total area could be used for analyses at all spatial grains. Sections of the plot outside the rectangular region were discarded. We then subdivided the plot into nonoverlapping quadrats at three spatial grains: 20 × 20 m (0.04 ha), 50 × 50 m (0.25 ha) and 100 × 100 m (1 ha).

Species richness for each quadrat at each spatial grain was calculated by summing the number of tree species with at least 1 stem ≥ 10 cm DBH in the quadrat. We used species richness rather than

Table 1. Study sites (ordered by distance from the equator; further details at http://www.ctfs.si.edu/)

Site name	Short name	Latitude	Longitude	Rainfall (mm year^{-1})	Area used (ha)	Census years used
Yasuni	yas	0.69°S	76.40°W	3081	25	1996, 2003
Pasoh	pas	2.98°N	102.31°E	1788	50	2000, 2005
Amacayacu	ama	3.81°S	70.27°W	3200	25	2011
Lambir	lam	4.19°N	114.02°E	2664	50	1992, 1997
Korup	kor	5.07°N	8.85°E	5272	50	1998, 2008
Sinharaja	sin	6.40°N	80.40°E	5012	25	1995, 2001
Barro Colorado Island	bci	9.15°N	79.85°W	2551	50	2005, 2010
Mudumalai	mud	11.60°N	76.53°E	1249	50	1996, 2000
Huai Kha Khaeng	hkk	15.63°N	99.22°E	1476	50	1993, 1999
Palanan	pal	17.04°N	122.39°E	3380	16	1998, 2004
Luquillo	luq	18.33°N	65.82°W	3548	15	2005
Xishuangbanna	xis	21.61°N	101.57°E	1532	20	2007
Dinghushan	dhs	23.16°N	112.51°E	1985	20	2005, 2010
Lienhuachih	lie	23.91°N	120.88°E	2285	25	2008
Fushan	fus	24.76°N	121.56°E	4271	25	2004, 2009
Ilha do Cardoso	PEI	25.10°S	47.96°W	2261	9	2004
Gutianshan	gut	29.25°N	118.12°E	1964	24	2005
Yosemite	yos	37.76°N	119.82°W	1061	24	2010
SCBI	scb	38.89°N	78.15°W	1976	24	2008
SERC	SER	38.89°N	76.56°W	1080	16	2011
Dongling	don	39.96°N	115.41°E	568	20	2010
Changbai	cha	42.38°N	128.08°E	700	25	2004, 2009
Haliburton	hal	45.29°N	78.64°W	1050	8	2009
Wabikon	wab	45.55°N	88.80°W	780	24	2008
Wytham Woods	wyt	51.77°N	1.34°W	726	18	2010

some other measure of diversity (e.g. Shannon's index) because richness is easily interpreted and most relevant to theoretical richness–function mechanisms (e.g. niche complementarity and sampling effects). We included only trees ≥ 10 cm DBH because trees of this size contribute the vast majority of CWP and AGB. (For CWP, trees ≥ 10 cm DBH constitute 91.3 ± 3.8% (mean ± standard deviation) of the CWP of all trees ≥ 1 cm DBH at the 12 sites at which CWP was calculated, all of which had data on stems ≥ 1 cm DBH. For AGB, trees ≥ 10 cm DBH constitute 96.3 ± 2.9% of the AGB of all trees ≥ 1 cm DBH at the 19 sites for which data on stems ≥1 cm DBH were available.)

The AGB of each individual stem (including all stems ≥10 cm DBH on multistemmed individuals) was estimated from DBH and allometric regressions. At some sites, we were able to use site-specific or species-specific allometric regressions; at other sites, we used generic allometric equations (Chave *et al.* 2005; Table S1, in Supporting Information). Total AGB for each quadrat at each spatial grain was calculated by summing AGB for all stems in a quadrat. Although errors associated with allometric equations can be large (Chave *et al.* 2004), they should in general lead to fairly consistent under- or over-estimates of AGB within sites, meaning that the resulting within-site relationships between richness and AGB should be robust.

The CWP for each quadrat was calculated as the sum of AGB growth for surviving stems and AGB of new stems divided by the length of the census interval in years. In six of the plots, individual stems on multistemmed trees had not been tagged and recorded consistently, so we could estimate change in AGB only at the tree level. For these plots, CWP was therefore underestimated (because the data do not reveal cases in which a stem on a multistemmed tree died and was replaced by a different stem during the census interval). In all plots, negative CWP estimates for stems or trees that apparently shrunk were replaced with zero CWP, because individual tree CWP, by definition, cannot be negative.

STATISTICAL ANALYSIS

All variables were log-transformed prior to analysis. Statistical analyses were performed in the software R version 2.15.0 (http://www.r-project.org/). At each site and for each spatial grain, we used generalized least-squares models with a maximum likelihood fitting method (nlme package in R) to fit richness–CWP (independent–dependent variable), richness–AGB and CWP–AGB relationships among quadrats. We used generalized least-squares models because we needed to account for spatial autocorrelation among quadrats, and generalized least-squares is a reliable method for doing so (Beale *et al.* 2010). We used a maximum likelihood method rather than a restricted maximum likelihood method because we wanted to compare the separate models with Akaike Information Criterion (AIC) and because we did not need to estimate variance components (Zuur *et al.* 2009). We fitted linear models with and without spherical autocorrelation structure, and for each combination of site, scale and variables, we selected the model with the lowest AIC (Tables S2 and S3 in Supporting Information). Effect size was measured as the slope of a relationship on log-log axes, so that if $y = Ax^b$, then b is the effect size, and an effect size of zero indicates no effect of the variable x on the variable y. The mean effect size across sites for each relationship was calculated as a variance-weighted mean of the site effects, and confidence intervals on the mean effect size were estimated by bootstrapping over sites.

Our method of fitting individual site models with generalized least-squares is exactly equivalent to fitting a single mixed-effects model for all of the data with 'site' as a fixed effect. A different approach would be to treat 'site' as a random effect: this would minimize the overall error in the mean effect size but would lead to biased site effects because of shrinkage (individual site observations are pulled towards the mean). We did not fit such a random-effects model because we wanted unbiased site effects and because the resulting estimate of the mean effect size is unlikely to be substantially different from the fixed-effects model. Moreover, existing *R* implementations of mixed-effects models do not allow different strengths of spatial autocorrelation at different effect levels (i.e. at different sites).

In the richness–CWP and richness–AGB regressions, we treated richness as the independent variable, because we assumed that the causal effects of richness on CWP and AGB (due to niche complementarity and sampling effects) would be stronger than those in the reverse direction (due to environmental gradients) at the small spatial extents considered (at larger spatial extents than those considered here, it would make more sense to treat richness as the dependent variable). In the CWP–AGB regressions, we treated CWP as the independent variable, because we assumed that CWP directly affects AGB more than *vice versa*. In any case, these are predominantly issues of interpretation: the qualitative results of all our analyses change little if the dependent and independent variables are switched (results not shown).

To test for possible unimodal relationships usually characteristic of data sets across broader environmental gradients, we repeated the above richness–CWP and richness–AGB analyses with the independent and dependent variables switched and with quadratic models included. Relationships were considered significantly unimodal only if the turning point of the quadratic model was within the range of the data [as judged by the Mitchell-Olds and Shaw test (Mitchell-Olds & Shaw 1987; Mittelbach *et al.* 2001)], and the quadratic model had the lowest AIC. By these criteria, only nine of 111 model comparisons resulted in a significant unimodal relationship, and all but two of these showed an increasing trend over the range of the data. This is consistent with the absence of theoretical support for unimodal relationships at local spatial scales (Fridley *et al.* 2012). We did not consider unimodal relationships further.

EFFECTS OF STEM DENSITY

To control for the possible confounding effects of number of stems per quadrat on the results, we repeated the original analysis after first removing the effect of stem density on CWP and AGB with locally weighted polynomial (LOESS) regressions (function loess in *R* with span = 1 and degree = 2). The original generalized least-squares regressions were then repeated but with the residuals of these LOESS regressions replacing CWP and AGB as the dependent variables (Fig. 3 and Tables S3.1–S3.6 in Supporting Information) and with no intercept term because the residuals of the LOESS regressions have zero mean. This two-stage regression method was used because it is more conservative than, for example, a standard multiple linear regression. It is conservative because it attributes as much variation in CWP or AGB as possible to stem density (within the constraints of what a LOESS regression can fit) rather than to species richness. The regression of the LOESS residuals on species richness then provides a conservatively biased estimate of the effect of species richness on CWP or AGB, which we use as a lower bound on the true effect size alongside the upper bound from the original analysis (which did not consider the effects of stem density at all).

Results

At the smallest spatial grain (0.04 ha), productivity and biomass were both positively related to species richness within most forest plots (Fig. 2a,b). The mean effect size across our forest plots was $b = 0.566$ (95% confidence interval = [0.426, 0.717]) for productivity and 0.613 [0.480, 0.755] for biomass, meaning that a doubling of species richness corresponds to an average 48% $(=2^b–1)$ increase in productivity and 53% increase in biomass.

Results at the larger spatial grains (0.25 and 1 ha) were qualitatively different: relationships between richness and productivity were weak and often negative (Fig. 2c,e; mean effect size –0.096 [–0.309, 0.091] at 0.25 ha and –0.415 [–1.090, 0.068] at 0.1 ha), as were relationships between richness and biomass (Fig. 2d,f; mean effect size 0.059 [–0.218, 0.337] at 0.25 ha and –0.357 [–1.031, 0.255] at 1 ha). Individual results for each site are presented in the Supporting Information (Figs S1–S6 and Tables S2.1–S2.6 in Supporting Information).

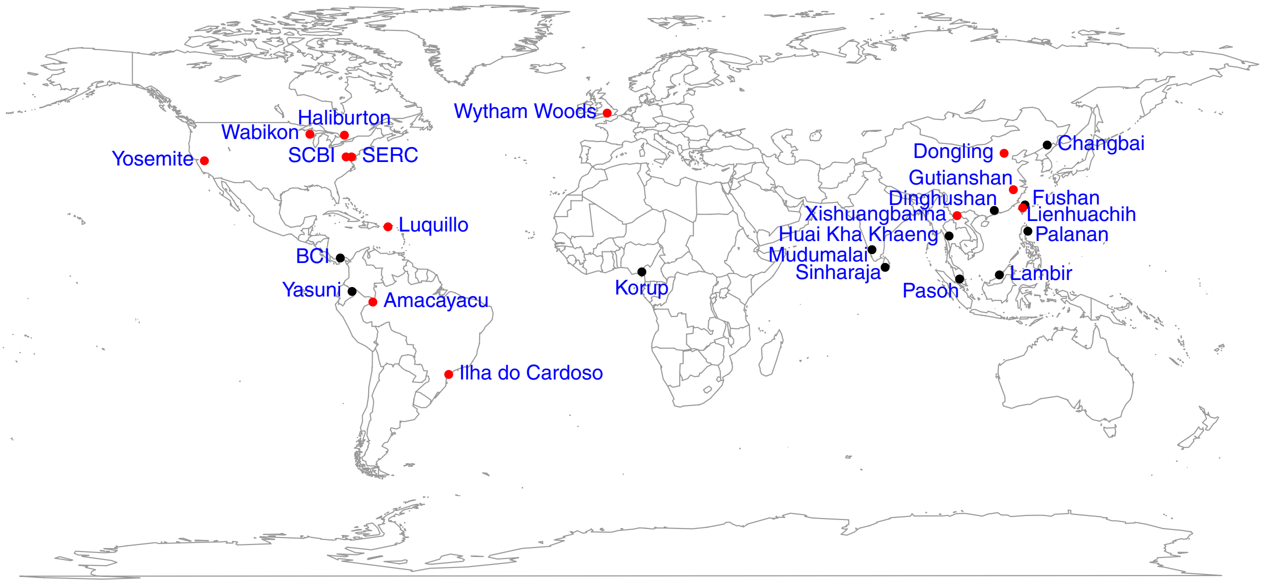

Fig. 1. Locations of the study sites. Black points indicate sites at which both above-ground dry biomass and coarse woody productivity were estimated. Red points indicate sites at which only above-ground dry biomass was estimated.

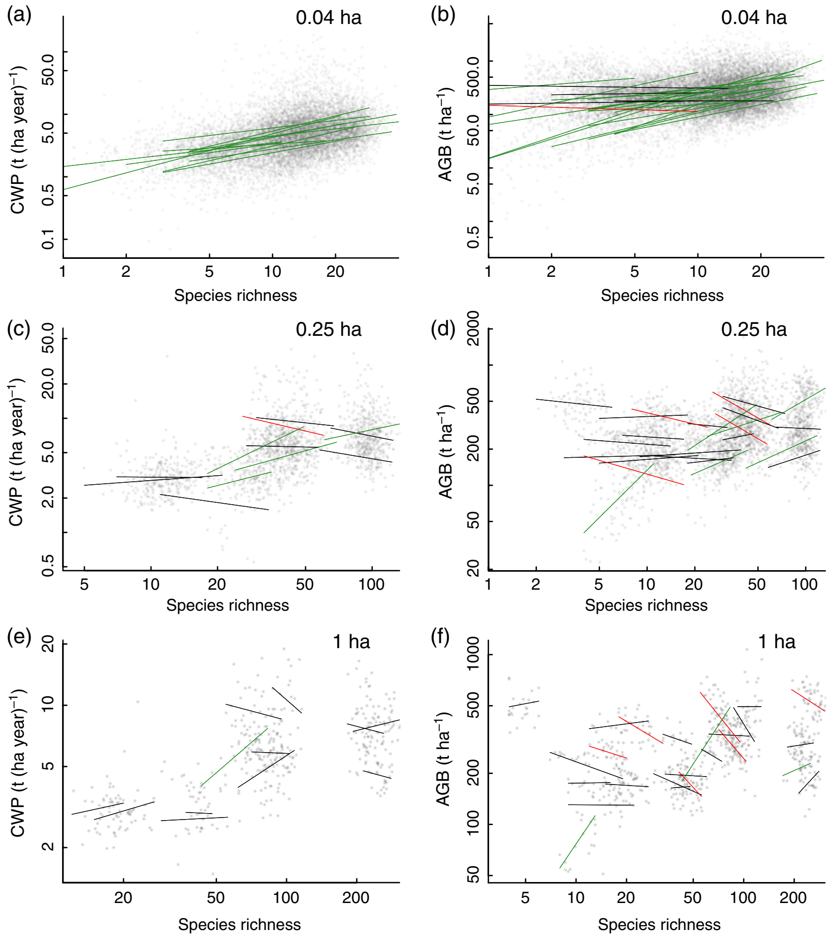

Fig. 2. Observed relationships of tree species richness to coarse woody productivity (CWP; panels a, c, e) and above-ground biomass (AGB; panels b, d, f) at the study sites at three spatial grains (0.04 ha, 0.25 ha, 1 ha). Points show the quadrat data (number of points for each site = site area/spatial grain; see Table 1), lines show regressions for individual sites, with green indicating positive slopes, red negative slopes and black slopes not significantly different from zero. Axis scales are logarithmic.

The results of the analysis controlling for stem density were qualitatively similar to the main results, but the positive relationships were generally weakened (Fig. 3). The weaker positive relationships at the 0.04 ha grain were evident in the much smaller mean effect sizes, 0.067 [–0.019, 0.146] for productivity and 0.098 [0.016, 0.179] for biomass, meaning that a doubling of species richness corresponds to an average 5% increase in productivity and 7% increase in biomass (Fig. 3a,b). Controlling for stem density moved the mean effect size in a negative direction at the 0.25 ha spatial grain but not the 1 ha spatial grain for both the richness–productivity (–0.220 [–0.541, 0.049] at 0.25 ha and –0.317 [–0.767, 0.040] at 1 ha) and richness–biomass (–0.214 [–0.437, 0.001] at 0.25 ha and –0.327 [–0.915, 0.227] at 1 ha) relationships. The relationship of stem density itself to biomass and productivity was generally positive but saturating at the 0.04 ha spatial grain and variable at the larger spatial grains (Figs S7–S12 in Supporting Information).

The productivity–biomass relationships were generally positive, and in contrast to the results involving species richness, the effect sizes were fairly robust to increasing spatial grain and to the inclusion of stem density in the model (Fig. 4). The effect sizes before controlling for stem density were 0.371 [0.244, 0.485], 0.322 [0.218, 0.432] and 0.409 [0.210, 0.638] at the 0.04, 0.25 and 1 ha spatial scales, respectively, and 0.251 [0.138, 0.352], 0.273 [0.171, 0.377] and 0.350 [0.177, 0.552] after controlling for stem density (Fig. 4).

Cross-site comparisons of mean productivity, mean biomass and mean 1 ha species richness showed that all three variables were positively correlated across sites with no strong evidence of unimodal relationships (Figs S13–S15 and Table S4 in Supporting Information), although the number of data points (sites) was low, and therefore, the statistical power to resolve cross-site patterns was also low.

Discussion

Our results highlight the fundamental role of scale (Waide *et al.* 1999; Mittelbach *et al.* 2001; Rahbek 2005) in determining the observed relationship between species richness and ecosystem function in forests. Previous studies on this topic in forests have found positive relationships between species richness and ecosystem function (as measured by productivity or biomass; Vilà *et al.* 2007; Ruiz-Jaen & Potvin 2010; Paquette & Messier 2011; Zhang, Chen & Reich 2012), but our analyses show that mean effect sizes may become zero or even negative at spatial grains larger than those that have typically been considered before (< 0.1 ha). Moreover, a proportion of the positive effect at small spatial grains may be attributable to local variation in stem density rather than classic species sampling effects, niche complementarity and

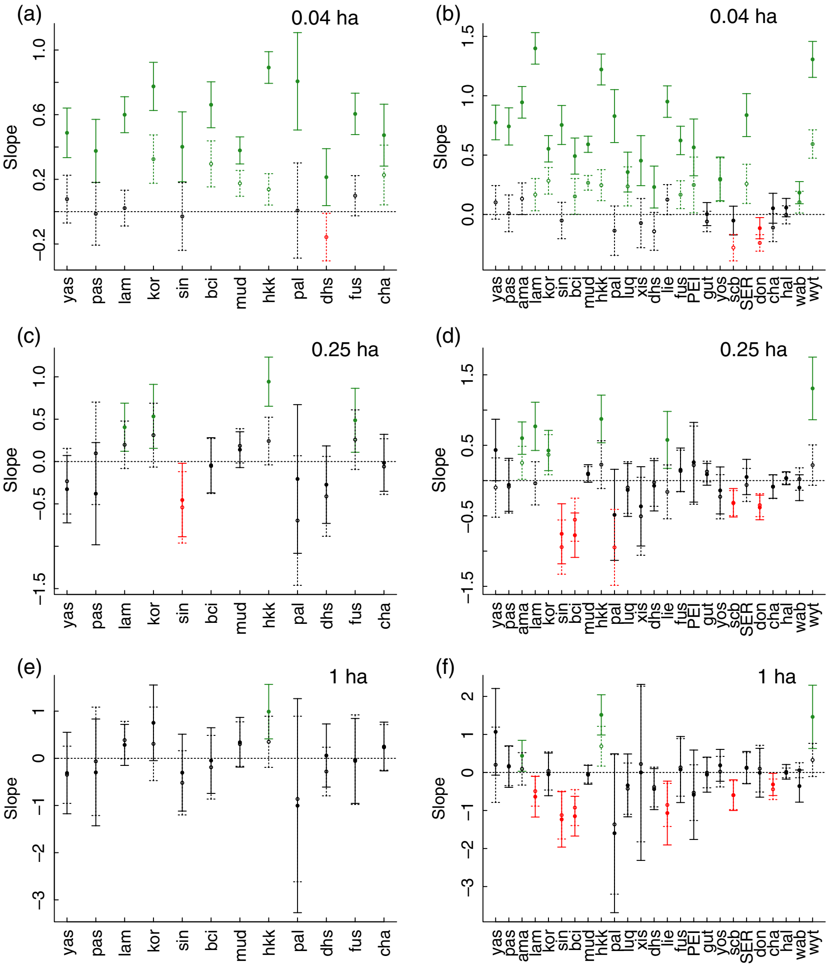

Fig. 3. Strength of observed relationships of tree species richness with coarse woody productivity (CWP; panels a, c, e) and above-ground biomass (AGB; panels b, d, f) at the study sites at three spatial grains (0.04 ha, 0.25 ha, 1 ha). Horizontal axes show site name abbreviations (Table 1). Closed circles with solid whiskers show upper bounds on effect sizes, corresponding to slopes of log CWP or log AGB on log richness and 95% confidence intervals (Fig. 2, Fig. S1–S6). Open circles with dashed whiskers show lower bounds on effect sizes, corresponding to slopes and confidence intervals from the analyses controlling for stem density. Green and red indicate statistically significantly positive and negative slopes.

facilitation. While the small-scale positive effects of species richness on biomass and productivity in forests remain of ecological interest, one clearly cannot easily generalize these effects to larger spatial grains or to scales relevant to conservation and forestry: at some sites, species richness is even significantly negatively related to biomass at large spatial grains.

As noted above, the frequent positive relationships between species richness and ecosystem function in our sites, especially at small spatial grains (Fig. 2a,b, Fig. 3a,b), are consistent with other studies from forests (Vilà *et al.* 2007; Ruiz-Jaen & Potvin 2010; Paquette & Messier 2011; Zhang, Chen & Reich 2012; Gamfeldt *et al.* 2013) and contrast with a recent global study of herbaceous plant communities that found no consistent patterns between productivity and species richness (Adler *et al.* 2011). The positive relationships are also consistent with ecological theory on sampling effects, niche complementarity and facilitation (Fridley 2001). Mechanistically, the sampling effect arises in conjunction with a selection effect, in the sense that some quadrats may, by chance, have been colonized by more species, and quadrats with more species are more likely to contain individual species that are more productive, sets of species that show ecological complementarity, or both, and so are able to utilize available resources more fully, leading to overall higher productivity. Other factors being equal, higher productivity should lead to higher biomass, as seen here (Fig. 4), so this mechanism also provides an explanation for the observed positive relationships between richness and biomass. Theory also suggests that these sampling effects should be strongest at the smallest scales: it is in small quadrats, where there are fewer stems, that chance colonization plays the greatest role.

An alternative explanation for the positive relationships of species richness to biomass and productivity is simply that all three variables are positively related to stem density, and that stem density varies locally within a forest plot. This mechanism is of less biological interest than the classic species sampling effects, niche complementarity and facilitation discussed above, although the different mechanisms are by no means mutually exclusive. Our estimates of the effects of species richness on biomass and productivity after controlling for stem density should be considered as lower bounds on the true effect sizes, because our method of controlling for stem density conservatively apportions all covariance between stem density and biomass/productivity to the former. This lower bound would coincide with the true effect size if variation in stem density were the major determinant of richness, productivity and biomass, as might be the case if competition were weak and there were considerable random variation in stem density. The original analysis excluding the effect of stem

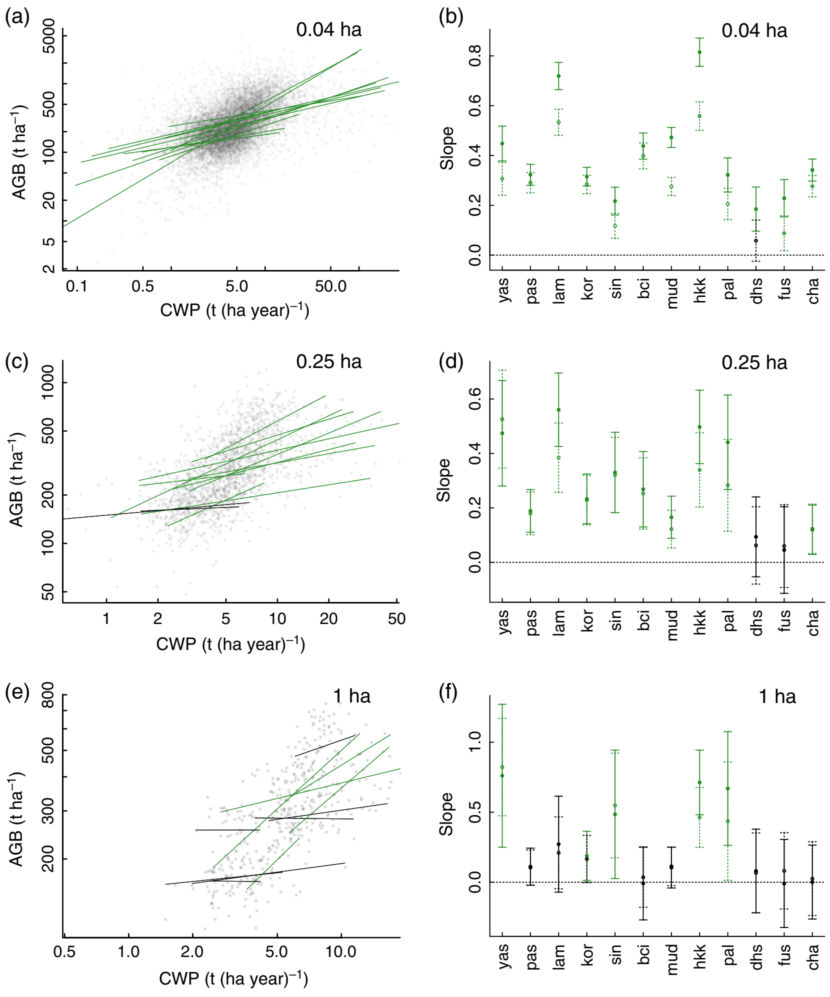

Fig. 4. Panels a, c, e: observed relationships between coarse woody productivity (CWP) and above-ground biomass (AGB) at the study sites at three spatial grains (0.04 ha, 0.25 ha, 1 ha). Points show individual quadrat data, and lines show fitted models (green = statistically significantly positive). Axis scales are logarithmic. Panels b, d, f: strengths of relationships with closed circles showing slopes from panels a, c, e, and solid whiskers showing 95% confidence intervals, and open circles with dashed whiskers showing slopes and confidence intervals from the analysis controlling for stem density. Site name abbreviations on horizontal axes are given in Table 1.

density (Fig. 2) gives an upper bound on the true effect size that would be accurate if species richness were directly determined by productivity, biomass and stem density, as might be the case if niche structure were very strong. In the absence of a mechanistic model, it is difficult to say whether the true effect of species richness on productivity and biomass is closer to the lower or upper bound, but this should be a priority for future research.

The several negative relationships observed between species richness and biomass at the 0.25 ha and 1 ha spatial grains (Figs 2d,f and 3d,f) were unexpected and inconsistent with sampling effects and niche complementarity and indicate that different processes are operating at larger scales. One possible mechanism underlying the negative relationships is the successional process following disturbance (Horn 1974): disturbed patches of forests have lower biomass (though usually not lower productivity) and are also likely to have higher species richness, first because they contain more stems and secondly because they may contain a mix of early- and late-successional species; in older patches, a few high-biomass individuals of late-successional species may dominate. This successional effect should become weaker or even disappear after controlling for stem number, because trees of all size classes have similar (though not identical) species richness for a given number of individuals (Condit *et al.* 1996). In contrast, the negative relationships in our analysis persisted when stem number was controlled (Fig. 3d,f). Furthermore, the most obvious disturbances in these forests are those associated with treefall gaps, which occur mostly at scales smaller than our smallest spatial grain (Schnitzer & Carson 2001), a scale at which we observed mostly positive relationships between richness and biomass. Thus, successional mechanisms alone seem insufficient to explain the observed negative relationships.

We propose instead that the negative relationships between species richness and biomass arise from the effects of environmental variables. For example, productivity and biomass may increase with soil fertility but plant species richness may peak at intermediate soil fertility (Grime 1979). This would lead to classic unimodal relationships of species richness to productivity and biomass at large spatial extents that spanned the entire productivity gradient, but positive or negative monotonic relationships at the scale of a forest plot (Loreau *et al.* 2001). This idea could feasibly be tested with data from smaller plots over larger spatial extents in the same regions as our study sites (e.g. Condit *et al.* 2002). More generally, environmental effects could play a role in explaining site differences even without large-scale unimodality. The mix of negative and positive relationships could be attributable to variation in the species pool between regions (e.g. owing to different regional abundances of rich and poor soils) and hence variation in the relationship between species richness and environmental variables (Schamp, Aarssen & Lee 2003; Rahbek 2005).

Previous studies on the species richness–productivity relationship have used various surrogates for productivity, including biomass (Whittaker 2010). Our results provide a clear empirical demonstration of why this may not always be valid: although biomass and productivity are generally positively correlated within our sites (Fig. 4), their relationships to species richness may differ. For example, at the largest spatial grain, a few sites showed significantly negative relationships between species richness and biomass (Fig. 3f), but no relationship between species richness and productivity (Fig. 3e). In forests, at least, biomass and productivity should be treated as separate ecosystem functions.

In view of our results showing scale-dependent relationships of species richness to productivity and biomass, we recommend that models be developed to integrate large-scale environmental information with small-scale sampling effects, niche complementarity and stem density effects. The development of such models should be informed by empirical investigations into the pattern and scale of environmental factors that drive local variation in richness, productivity and biomass in forests. Ultimately, such research should reproduce relationships between richness, productivity and biomass in forests across a range of spatial scales, thus demonstrating a more general understanding of these relationships and providing practical guidance for forestry and conservation endeavours.

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Supporting Information

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

Figure S1. Observed relationships between species richness and coarse woody productivity (CWP) at the study sites at the 0.04 ha spatial scale (as for Fig. 2a but with each site on a separate panel).

Figure S2. Observed relationships between species richness and coarse woody productivity (CWP) at the study sites at the 0.25 ha spatial scale (as for Fig. 2c but with each site on a separate panel).

Figure S3. Observed relationships between species richness and coarse woody productivity (CWP) at the study sites at the 1.0 ha spatial scale (as for Fig. 2e but with each site on a separate panel).

Figure S4. Observed relationships between species richness and aboveground biomass (AGB) at the study sites at the 0.04 ha spatial scale (as for Fig. 2b but with each site on a separate panel).

Figure S5. Observed relationships between species richness and aboveground biomass (AGB) at the study sites at the 0.25 ha spatial scale (as for Fig. 2d but with each site on a separate panel).

Figure S6. Observed relationships between species richness and aboveground biomass (AGB) at the study sites at the 1.0 ha spatial scale (as for Fig. 2f but with each site on a separate panel).

Figure S7. LOESS regressions of coarse woody productivity (CWP) versus stem density at the 0.04 ha spatial scale.

Figure S8. LOESS regressions of coarse woody productivity (CWP) versus stem density at the 0.25 ha spatial scale.

Figure S9. LOESS regressions of coarse woody productivity (CWP) versus stem density at the 1.0 ha spatial scale.

Figure S10. LOESS regressions of aboveground biomass (AGB) versus stem density at the 0.04 ha spatial scale.

Figure S11. LOESS regressions of aboveground biomass (AGB) versus stem density at the 0.25 ha spatial scale.

Figure S12. LOESS regressions of aboveground biomass (AGB) versus stem density at the 1.0 ha spatial scale.

Figure S13. Cross-site relationship of productivity to 1 ha species richness.

Figure S14. Cross-site relationship of biomass to 1 ha species richness.

Figure S15. Cross-site relationship of biomass to productivity.

Table S1 Methods used to estimate productivity and biomass at each site.

Table S2 Numerical output from the fits of the generalized least-squares models of productivity and biomass on species richness.

Table S3 Numerical output from the fits of the generalized least-squares models of productivity and biomass on species richness in the analysis controlling for stem density.

Table S4. Summary data for species richness, biomass and productivity of 1 ha quadrats at each site.