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PAPER



Latitude, productivity and species richness

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ABSTRACT

Aim Global patterns in primary productivity in natural ecosystems are important for interpreting ecological processes and patterns of biodiversity. Net primary productivity (NPP) on land has long been thought to be greatest in tropical forests and to decrease towards the poles. However, it has recently been claimed that the NPP of mid-latitude forests is as great as, or even greater than, that of tropical forests and that ecologically relevant productivity peaks at mid-latitudes. Here we evaluate these hypotheses by testing for relationships between latitude and productivity using a range of forest productivity datasets.

Location Global.

Methods We apply ordinary least squares regression and *t*-test analyses to published latitude–productivity data for forests, specifically updated to include an expanded dataset for the previously data-poor tropics, and we evaluate the relationship between the primary productivity of forests and modelled vascular plant species richness.

Results Contrary to the recent claims, we found strong support for a negative relationship between latitude and annual NPP of forests with all datasets, and NPP was significantly greater in tropical forests than in temperate forests. Vascular plant richness was positively correlated with NPP.

Main conclusions NPP of forests increases towards the equator. Given that species richness also increases towards the equator, and that vascular plant richness correlates with NPP, these results are consistent with recent meta-analyses showing that the relationships between productivity and species richness of both plants and animals in natural ecosystems are predominantly positive. These results are congruent with ecological theories that predict a positive relationship between species richness and productivity, and they indicate that there is no need to explain peaked richness–productivity relationships over broad spatial extents, since they do not appear to exist.

Keywords

Competitive exclusion hypothesis, energy–richness hypothesis, forests, integrated evolutionary speed hypothesis, latitudinal gradient, net primary productivity, plants, species richness, water–energy dynamics.

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INTRODUCTION

Global patterns in annual net primary productivity (NPP) in natural ecosystems are important for understanding global carbon dioxide budgets (natural and anthropogenic) and they are fundamental to understanding the functional and evolution-

ary relationships within ecosystems and biomes. Important among these processes are those that may act to maintain or drive biodiversity patterns. Theories that attempt to explain biodiversity patterns by invoking primary productivity include the competitive exclusion hypothesis (Grime, 1973, 1979; Huston, 1979), the energy–richness (or more individuals) hypothesis

(Hutchinson, 1959; Wright, 1983; Wright *et al.*, 1993), the integrated evolutionary speed hypothesis (Rensch, 1959; Rohde, 1992; Gillman & Wright, 2014) and the biological relativity to water–energy dynamics hypothesis (O'Brien, 2006). The first of these hypotheses is based on the assumption that the predominant relationship between productivity and species richness is unimodal (or hump-shaped), whereas the latter three are based on the assumption that the predominant relationship is positive.

Gause's competitive exclusion principle at high productivities is applied by Grime (1979) in his 'hump-backed model' and by Huston (1979) in his 'dynamic equilibrium theory'. These models predict a unimodal relationship between NPP and species richness on the basis that, at low productivity, stress and a lack of resources limit the number of species that can survive. As productivity increases, species richness rises, until at high productivities competitive exclusion again reduces species richness, either because competition is more intense (Grime, 1973; Grime, 1979) or/and because high productivity leads to a decrease in the heterogeneity of limiting resources (Huston, 1979; Tilman, 1982; Tilman & Pacala, 1993). Grime's model was formulated to explain the species diversity of herbaceous plant communities at local scales, whereas Huston's was developed for general application to the maintenance of diversity and has been applied at global scales (e.g. Huston, 2012).

The energy–richness hypothesis suggests that species with small populations are more vulnerable to stochastic events and that persistence depends on species maintaining 'minimum viable populations' (Coleman *et al.*, 1982; Rosenzweig, 1995). Because every individual requires a minimum quantum of energy flux to survive, a species also requires a minimum quantum of energy flux to remain viable. If energy limits the number of coexisting individuals, then environments with higher productivity can sustain more species with minimum viable populations (Wright, 1983).

The integrated evolutionary speed hypothesis (Gillman & Wright, 2014) is an extension of the evolutionary speed hypothesis (Rensch, 1959; Rohde, 1992) and differs from the latter by invoking productivity as the key variable instead of temperature or UV radiation. Under this hypothesis, temperature, water availability and biome area – all key variables determining total NPP – are predicted to be positively associated with evolutionary speed, rate of speciation and ultimately species accumulation and resident biodiversity. Mechanisms that might potentially link productivity to genetic evolution are discussed in Gillman & Wright (2013).

The biological relativity to water–energy dynamics hypothesis (O'Brien, 2006) proposes that the potential rate of evolution and rate of change in the geographical distribution of species should be greatest where the capacity for liquid water–energy dynamics is greatest for the longest time. Thus, it invokes a positive relationship between productivity and species diversity in both ecological and evolutionary time.

Different hypotheses are predicated on different relationship patterns, and therefore it is important to identify the predominant form of these relationships. There has been considerable controversy relating to the form that the species richness–NPP

relationship takes and how it may vary as a function of spatial scales of grain and extent (Whittaker, 2010). However, until recently there has been a general consensus that NPP on land is maximal in the tropics and declines with increasing latitude in parallel with broad-scale patterns of biodiversity (e.g. Leith & Whittaker, 1975; Begon *et al.*, 2005).

Given the theoretical importance of the relationship, remarkably few studies have explicitly tested the relationship between measured NPP and latitude at the global scale. Instead, much of the literature on global patterns of productivity (e.g. Kicklighter *et al.*, 1999) relies on modelled NPP. Plant growth is limited by three primary factors, water, energy and nutrient availability, each of which influences patterns of NPP and varies across broad spatial scales. However, NPP models commonly only account for the water and energy components, with very few analyses accounting for soil nutrient variables (Cramer *et al.*, 1999). Nonetheless, irrespective of the inclusion/exclusion of nutrient data, there is general agreement in relation to global NPP patterns: all models reviewed by Kicklighter *et al.* (1999) show maximum NPP around the equator.

Recently this consensus has been challenged by Huston & Wolverton (2009), who suggest that 'annual aboveground NPP of tropical forests differs little from that of temperate forests, and may in fact be substantially lower' (Huston & Wolverton (2009, p. 360). They also claimed that monthly net primary productivity (MNPP) during the growing season – the portion of NPP that is available to herbivores – is greatest in mid-latitude temperate forests. However, these authors did not undertake any statistical analysis of their data and their claims regarding both the NPP and the MNPP pattern remains untested. Therefore, to test their hypothesis we examine latitude–NPP data from three sources: (1) the Huston & Wolverton (2009) data (hereafter HW data), (2) Oak Ridge National Laboratory, USA database (hereafter ORNL data), and (3) ORNL data combined with a newly expanded dataset of tropical forest NPP.

The HW data comprise forest stands of various ages, and therefore some examination of stand age and its relevance to NPP is required. Huston & Wolverton (2009) used data from stands described as mature or more than 100 years old. However, in temperate forests of the Southern Hemisphere conifers may not emerge through the early successional vegetation until 100–150 years after the initiation of succession (Ogden, 1985). Average longevities for many conifers exceed 600 years (Ogden & Stewart, 1995) and they can take 240 years or more to reach medium sizes (Gillman, 2008). In northern temperate forests longevities often exceed 200 years for angiosperms (e.g. Lorimer *et al.*, 2001) and some conifers can reach 3000–4000 years of age (Westing, 1964). Forest successional sequences can thus exhibit on-going compositional change for hundreds of years as stands mature.

Many of the sites for which data are available in temperate latitudes are for young forests relative to average life spans (i.e. < 200 years old). Age-related decline in stand productivity is well documented (Ryan *et al.*, 1997) and young forests that are rebuilding from disturbance tend to have accelerated growth

rates (O'Neill & DeAngelis, 1981; Pregitzer & Euskirchen, 2004). Recent work indicates that while individual trees increase their growth rate with increasing size (Stephenson *et al.*, 2014), stand-level productivity declines with age due to declines in stand densities. Analyses that include many young forest stands are therefore likely to be biased towards higher productivities, particularly in temperate latitudes. We therefore undertook two sets of analyses wherever possible; firstly comprising stands over 100 years old, and secondly only including stands over 200 years old.

There are many sources of potential error in the estimation of forest NPP (see reviews by Clark *et al.*, 2001; Malhi *et al.*, 2011) and it is beyond the scope of this article to attempt to resolve them all. We focus instead on collating available data and examining several alternative datasets of varying properties.

MATERIALS AND METHODS

We examined three sets of latitude–productivity data: aboveground dry weight NPP, from HW data (Ecological Archives M079-012-S2); total NPP, in grams carbon (C) fixed per square metre per year ($\text{g C m}^{-2} \text{ year}^{-1}$), downloaded from ORNL (details available in Olson *et al.*, 2001a); and a newly expanded dataset of tropical forest NPP (detailed below) together with the ORNL data. For ease of comparison, all dry weight NPP data were converted to NPP ($\text{g C m}^{-2} \text{ year}^{-1}$) using the IPCC standard conversion factor of 0.5 (IPCC, 1996).

Two subsets of the HW data were used: the first included forest sites described as mature, or over 100 years old, and the second included only those sites described as mature, or over 200 years old. We omitted three sites described as 'dry forest' on the basis that productivity is depressed in dry forest relative to wet forest. We corrected an internal error for a site located at latitude 64.32° and longitude 100.21°; within their spreadsheet a conversion of units misplaced a decimal point, such that $1.01 \text{ Mg ha}^{-1} \text{ year}^{-1}$ of dry weight leaf litter was converted to $1010 \text{ g m}^{-2} \text{ year}^{-1}$ instead of $101 \text{ g m}^{-2} \text{ year}^{-1}$. The correct total dry weight production for this site is $421 \text{ g m}^{-2} \text{ year}^{-1}$ not $1330 \text{ g m}^{-2} \text{ year}^{-1}$ as reported by Huston & Wolverton (2009), but as noted above we convert these data from grams dry weight to grams carbon. We report aboveground NPP using the HW data because that is what those authors reported.

One problem with NPP data is that many data points are not spatially independent, as clusters of data derive from multiple plots within close proximity within particular forests and landscapes. Sampling intensity within forests also varies by an order of magnitude within the datasets and regression analysis will place greater importance on results from sites with greater sampling intensity. This suggests that regions are more appropriate sampling units than plots. We therefore undertook additional analyses using averaged productivities and latitudes for those sites located < 100 km from each other.

We tested for relationships between latitude and forest NPP using data available from ORNL (<http://www.daac.ornl.gov>) (details available in Olson *et al.*, 2001a,b). These datasets are described as varying in their level of extensiveness and quality assurance. Class A data represent intensively studied or well-

documented study sites and have complete NPP measurements and good documentation (Olson *et al.*, 2001b). Class B data represent more numerous 'extensive' sites with less documentation and site-specific information.

We also analysed Class A and B data combined with our new tropical datasets. Datasets from tropical latitudes are quite literally pivotal in discussions about latitudinal relationships, but have previously been greatly underrepresented in such analyses. The data included here are based on the compilation of the literature in Malhi *et al.* (2011), plus data from new sites in lowland Amazonia reported by Malhi *et al.* (2014), Araujo-Murakami *et al.* (2014), Doughty *et al.* (2014), del Aguila-Pasquel *et al.* (2014), da Costa *et al.* (2014) and Rocha *et al.* (2014). At all the new tropical sites NPP is considered as the sum of canopy litterfall, aboveground wood productivity, belowground wood productivity (usually estimated as a fraction of aboveground wood productivity) and fine root productivity. These terms were measured to standard protocols as described in the original papers. Many of the recent studies also include additional minor components of NPP (e.g. branch turnover, small tree and liana productivity, loss to herbivory); we exclude these terms from the current study to retain consistency with the ORNL dataset where these terms were not measured.

A subset of the HW data contained wood, litter and total NPP, plus the duration of the growing seasons and we were therefore able to test for relationships between latitude and MNPP during growing seasons. The component of MNPP that is available to herbivores within the season of production is mainly the leaf, flower and fruit production, whereas wood production is typically stored for many decades before becoming available to other trophic levels. Therefore, using data for forests more than 100 years old for which growing season length is recorded we tested for a relationship between latitude and litterfall MNPP averaged across the growing season. Because of the usually long delay between growth and trophic transfer, wood production can become trophically available at any time of the year. On average, the wood production can be assumed to be released to the ecosystem over the full year. We therefore added the monthly wood production averaged from the whole year to the monthly litterfall production from the growing season and again tested for a correlation with latitude.

Using each of the datasets listed above we tested for relationships between NPP and absolute latitude using ordinary least squares (OLS) regression. Because OLS regression is considered to be robust to violations of the assumption of normality unless other assumptions (e.g. homoscedasticity) are also violated, residuals were inspected against fitted values and using normal Q–Q plots, but normality tests were not conducted. We tested for linear relationships between NPP and latitude, and to detect quadratic relationships we also tested for second-order polynomial relationships. *P*-values reported for quadratic relationships are for the quadratic term in the model. We also compared average NPP of tropical forest (sites of latitudes < 23.5°) with average NPP of temperate forest (between latitudes 23.5° and 50°). Mean productivity differences were tested using Welsh

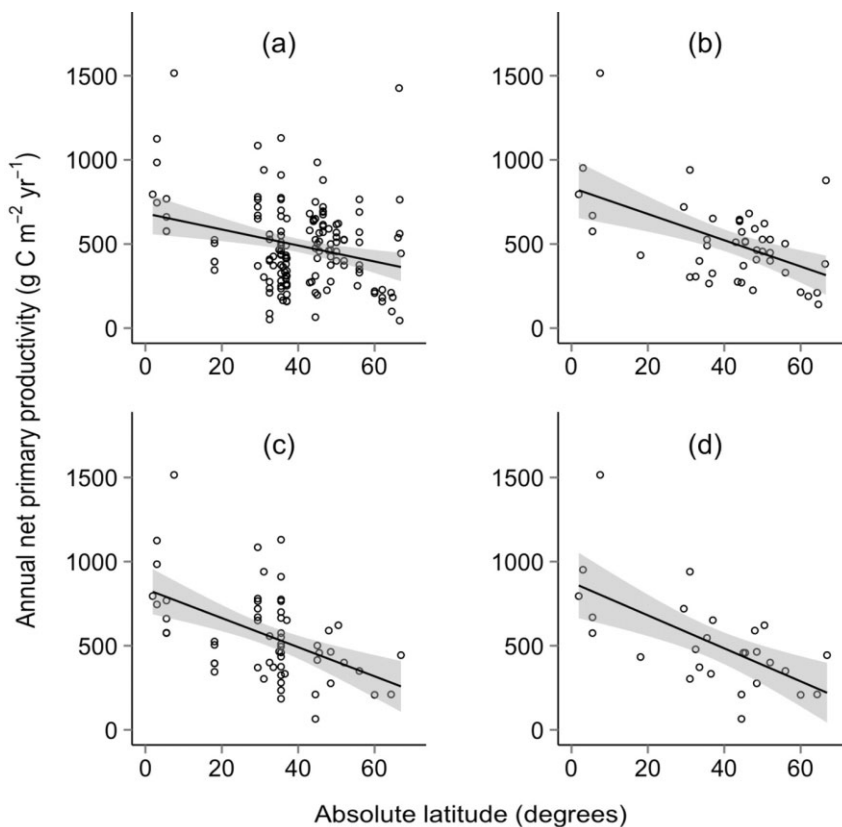


Figure 1 The relationships between latitude and aboveground net primary productivity obtained from the data of Huston & Wolverton (2009): (a) stands over 100 years old ($n = 146$, $R^2 = 0.072$, $P = 0.001$); (b) stands over 100 years old using averages for sites within 100 km of each other ($n = 45$, $R^2 = 0.277$, $P = 0.0002$); (c) stands over 200 years old ($n = 60$, $R^2 = 0.247$, $P = 5.42 \times 10^{-5}$); and (d) stands over 200 years old, using averages for sites within 100 km of each other ($n = 27$, $R^2 = 0.398$, $P = 0.0004$). Grey shading shows 95% confidence intervals of the regression lines.

two-sample *t*-tests. All data were normal (tested with the Anderson–Darling test).

In addition, we tested the relationship between species richness and NPP using a global map of total vascular plant richness in hexagonal grids of 7800 km² (Kreft & Jetz, 2007; Ellis *et al.*, 2012). Although this map involved interpolations of species richness using measured values and a predictive model, the model used does not include NPP as a predictor, and their modelled species richness correlates strongly with measured species richness (Kreft & Jetz, 2007). The Kreft & Jetz (2007) model does not include field measurements of accumulated biomass and therefore values of species richness predicted by this model can safely be regressed against directly measured NPP. We rasterized the Ellis *et al.* (2012) map of species richness and extracted point estimates for species richness at each of our NPP estimate locations, with interpolation from surrounding values using the Spatial Analyst function ‘extract values to points’ in ArcGIS 10.0. Regression analyses and tests of means were performed in R 3.0.2. All data are published but summaries are available from the corresponding author.

RESULTS

Latitude and annual net primary productivity

A weak negative linear relationship between aboveground NPP and latitude was found for forests over 100 years old using the HW data ($n = 146$, $R^2 = 0.072$, $P = 0.001$) (Fig. 1a). A quadratic

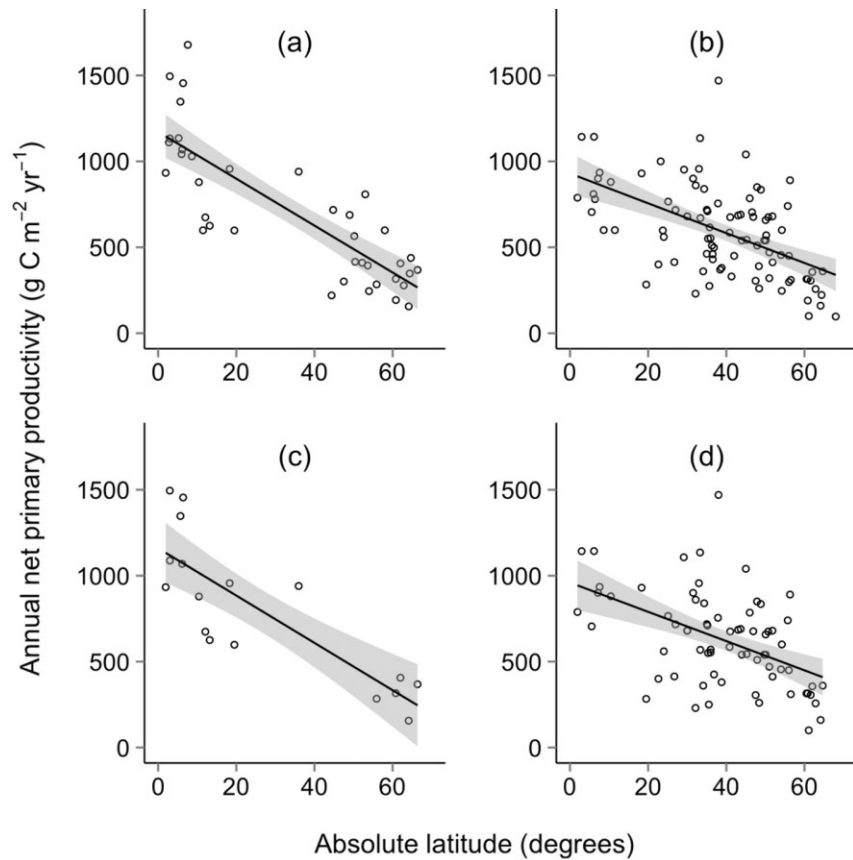
relationship was also statistically significant ($R^2 = 0.100$, $P = 0.008$), but the relationship was a negative decelerating curve not a hump-shaped curve. Mean NPP was greater for tropical sites (708 g C m⁻² year⁻¹) than for temperate sites (475 g C m⁻² year⁻¹) (d.f. = 14.78, $t = 2.618$, $P = 0.0196$).

When NPP data for forests over 100 years old were averaged from sites within 100 km of each other to improve the independence of data and reduce the influence of uneven sampling intensity a clearer negative linear relationship was obtained ($n = 45$, $R^2 = 0.277$, $P = 0.0002$) (Fig. 1b). A test for a quadratic relationship yielded a non-significant result ($P = 0.253$).

The negative linear relationships were stronger and latitude accounted for a greater proportion of the variability in NPP among forests described as mature or over 200 years old, both using the raw data and using data averaged from sites located within 100 km of each other ($n = 60$, $R^2 = 0.247$, $P = 5.42 \times 10^{-5}$; $n = 27$, $R^2 = 0.398$, $P = 0.0004$, respectively) (Fig. 1c,d). Tests for quadratic relationships produced negative decelerating curves, in contrast to hump-shaped curves, but were not statistically significant ($P = 0.722$ and $P = 0.429$, respectively).

A negative linear relationship between latitude and total NPP was found using the ORNL Class A data averaged from sites within 100 km of each other ($n = 38$, $R^2 = 0.683$, $P < 1.62 \times 10^{-10}$) (Fig. 2a). There was no evidence of a quadratic relationship ($P = 0.279$). Results were similar when all sites were treated as independent data ($n = 50$, linear $R^2 = 0.647$, $P < 2.00 \times 10^{-12}$). Mean NPP for Class A data was greater for tropical sites

Figure 2 The relationships between latitude and total net primary productivity obtained using the Oak Ridge National Laboratory data (Olson *et al.*, 2001b). (a) Class A data from intensively studied or well-documented study sites averaged from sites within 100 km of each other ($n = 38$, linear $R^2 = 0.683$, $P = 1.62 \times 10^{-10}$). (b) Class B data are from more numerous 'extensive' sites with less documentation and site-specific information available – data are averaged from sites within 100 km of each other ($n = 93$, linear $R^2 = 0.295$, $P = 2.20 \times 10^{-8}$). (c) Class A data excluding sites > 1000 m a.s.l. and with annual precipitation < 500 mm ($n = 17$, linear $R^2 = 0.690$, $P = 3.61 \times 10^{-5}$). (d) Class B data excluding sites > 1000 m a.s.l. and with < 500 mm annual precipitation ($n = 71$, linear $R^2 = 0.250$, $P = 1.04 \times 10^{-5}$). Quadratic relationships were not significant in any of these analyses. Grey shading shows 95% confidence intervals of the regression lines.



(1044 g C m⁻² year⁻¹) than for temperate sites (573 g C m⁻² year⁻¹) (d.f. = 6.9, $t = 3.02$, $P = 0.0199$).

Similarly, Class B data from ORNL produced a negative linear relationship between latitude and NPP ($n = 93$, linear, $R^2 = 0.295$, $P = 2.2 \times 10^{-8}$) (Fig. 2b) and no evidence of a quadratic relationship. Results were similar when all sites were treated as independent data ($n = 154$, linear, $R^2 = 0.243$, $P = 8.05 \times 10^{-11}$). Mean NPP using Class B data was greater for tropical sites (793 g C m⁻² year⁻¹) than for temperate sites (629 g C m⁻² year⁻¹) (d.f. = 22.8, $t = 2.28$, $P = 0.0326$).

Because both elevation and precipitation can potentially influence productivity we reran the regression analyses for latitude versus productivity excluding all sites > 1000 m a.s.l. or with precipitation < 500 mm year⁻¹, or for which one of these variables was not recorded. Results were not materially different from the original analysis (Class A data, $n = 17$, linear, $R^2 = 0.670$, $P = 3.61 \times 10^{-5}$) (Class B data, $n = 71$, linear, $R^2 = 0.250$, $P = 1.04 \times 10^{-5}$) (Fig. 2c,d). Results were also similar when only aboveground NNP was analysed (see Appendix S1 in Supporting Information).

Adding the new tropical data to Class A ORNL data for sites < 1000 m a.s.l and with precipitation > 500 mm year⁻¹ improved sampling intensity for tropical latitudes. Regression analysis produced a similar, negative linear relationship ($n = 24$, $R^2 = 0.685$, $P = 6.06 \times 10^{-7}$) (Fig. 3a). Adding the new tropical data to Class B ORNL data produced a higher mean productivity for tropical sites (1035 g C m⁻² year⁻¹) than for temperate sites

(678 g C m⁻² year⁻¹) (d.f. = 31.1, $t = 4.65$, $P = 5.87 \times 10^{-5}$) and a negative linear relationship between latitude and productivity ($n = 71$, linear, $R^2 = 0.442$, $P = 2.66 \times 10^{-10}$) (Fig. 3b).

Growing season MNPP

We found no evidence of a relationship between latitude and litterfall MNPP averaged across the growing season (Fig. 4a). Similarly, when monthly wood production averaged from the whole year was added to monthly litterfall production from the growing season and again tested for a correlation with latitude, neither linear nor quadratic relationships were statistically significant (Fig. 4b).

Species richness and annual net primary productivity

We also tested the relationship between species richness of vascular plants as determined by Ellis *et al.* (2012) for 7800-km² cells using Kreft & Jetz's (2007) vascular plant species richness model, and both NPP and latitude. A positive linear relationship was found between NPP and species richness for both datasets (Class A data, $n = 24$, linear $R^2 = 0.592$, $P = 1.11 \times 10^{-5}$; Class B data, $n = 71$, linear $R^2 = 0.347$, $P = 6.68 \times 10^{-8}$), although residuals are non-normal and heteroscedastic for the Class B data, and so these particular results should be interpreted with caution (Fig. 5a,b).

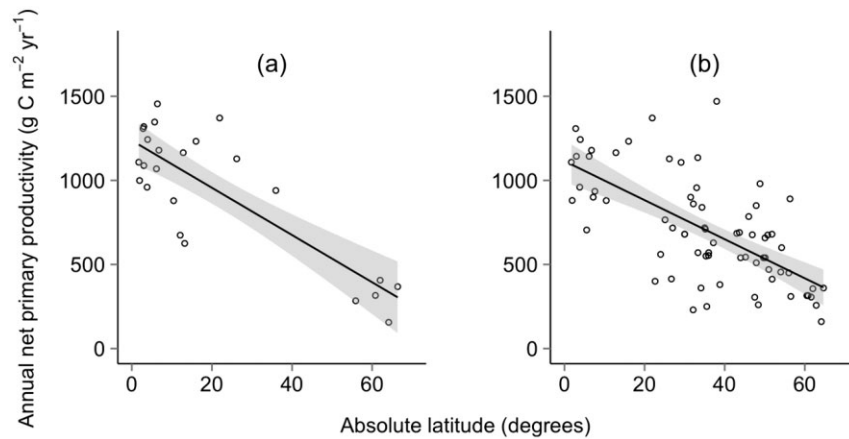


Figure 3 The relationships between latitude and total net primary productivity. (a) New tropical data combined with Class A data from Oak Ridge National Laboratory (ORNL) (Olson *et al.*, 2001b) with data averaged from sites within 100 km of each other ($n = 24$, linear $R^2 = 0.684$, $P = 6.06 \times 10^{-7}$). (b) New tropical data combined with Class B data from ORNL (Olson *et al.*, 2001b) with data averaged from sites within 100 km of each other ($n = 71$, linear $R^2 = 0.592$, $P = 1.11 \times 10^{-3}$). All data are from sites < 1000 m a.s.l. and with annual precipitation > 500 mm. Quadratic relationships were not significant in either of these analyses. Grey shading shows 95% confidence intervals of the regression lines.

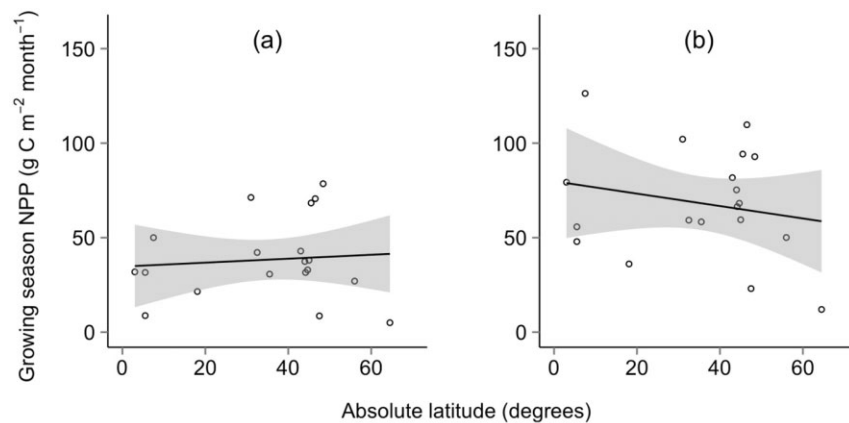


Figure 4 Relationships between latitude and monthly net primary productivity (MNPP) during the growing season for forest over 100 years old. (a) MNPP of litter during the growing season ($n = 19$, linear $R^2 = 0.0080$, $P = 0.715$; quadratic $R^2 = 0.207$, $P = 0.0625$). (b) Litter MNPP during the growing season plus wood MNPP averaged over 12 months ($n = 19$, linear $R^2 = 0.0434$, $P = 0.392$; quadratic $R^2 = 0.164$, $P = 0.324$). This assumes leaf, flower and fruit production is available for herbivores during the growing season but that trophic availability of wood productivity is not restricted to the growing season. Data from Huston & Wolverton (2009). The fitted lines are included for visual assistance only and do not represent significant fits. Grey shading shows 95% confidence intervals of the regression lines.

DISCUSSION

We consistently found negative relationships between latitude and NPP within forests from all the datasets we analysed and annual tropical forest productivity was significantly higher than temperate forest productivity. These results contradict the hypothesis by Huston & Wolverton (2009) that productivity in temperate regions is as high as or higher than productivity in equatorial regions and confirms the previously held view that forest productivity as a first-order pattern declines with latitude (e.g. Leith & Whittaker, 1975). We found that this relationship is stronger when only old-growth forests (> 200 years) are

included in analyses, suggesting that forest age should be taken into account when measuring patterns of productivity. These results are consistent with strong evidence of negative latitudinal gradients in both leaf-litter production and seed production (Keeling & Phillips, 2007; Moles *et al.*, 2009).

In tropical forest, where species richness and the diversity of tree architecture are each high and where the range of wood densities is wider than that in temperate zones, assumptions about relationships between basal area and total tree biomass will often be subject to greater error (Clark *et al.*, 2001; Chave *et al.*, 2006; Swenson & Enquist, 2007). Under-recording of productivity is also a source of error in the estimation of forest

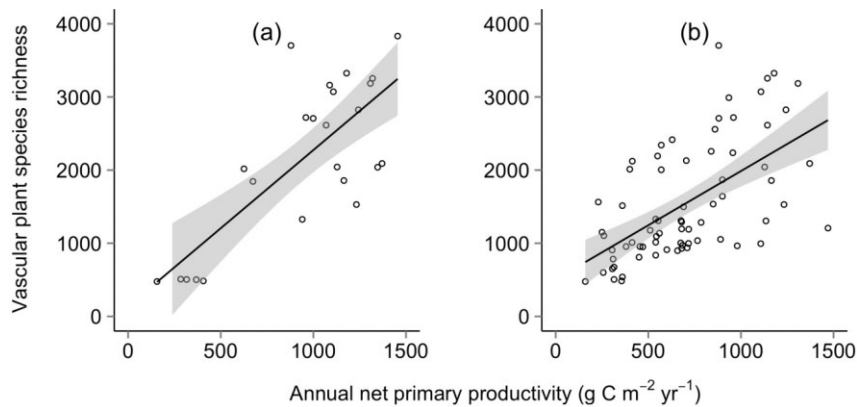


Figure 5 The relationships between vascular plant species richness and net primary productivity (NPP) using data derived from Ellis *et al.*'s (2012) map of angiosperm species richness and Oak Ridge National Laboratory NPP data (Olson *et al.*, 2001b). (a) Class A NPP data from intensively studied or well-documented study sites averaged from sites < 100 km from each other regressed with species richness for the 7800-km² cells centred on each site's coordinates ($n = 24$, linear $R^2 = 0.793$, $P < 5.48 \times 10^{-9}$). (b) Class B NPP data from more numerous 'extensive' sites with less documentation and site-specific information available: data are averaged from sites < 100 km from each other regressed with species richness for the 7800-km² cells centred on each site's coordinates ($n = 71$, linear $R^2 = 0.347$, $P = 6.68 \times 10^{-8}$). Grey shading shows 95% confidence intervals of the regression lines.

NPP (Malhi *et al.*, 2009). Productivity that often goes unrecorded includes loss to leaf and fruit herbivory (Metcalf *et al.*, 2014), decomposition of litter before collection and suspension of litterfall in understorey vegetation such as palms, and productivity of epiphytes, lianas and small trees. Turnover of fine roots in forests declines with latitude (Gill & Jackson, 2000) and along elevational gradients in the tropics (Girardin *et al.*, 2013) but is often underestimated. Such methodological issues can amount to substantial underestimation of NPP, particularly in lowland tropical forests, and therefore would suggest that our results are conservative relative to this type of error. Indeed, for consistency in our analyses we subtracted productivity due to herbivory, small trees and branch turnover from new tropical datasets where some of these additional terms were estimated, as these were generally not included in earlier studies.

Given that species richness also declines with latitude (Hillebrand, 2004) and modelled vascular plant richness correlates with NPP (Fig. 5), our results are consistent with previous studies showing that positive relationships between productivity and species richness predominate. Synthetic analyses of available datasets demonstrate that the predominant form of association between species richness and productivity across a wide range of grains and extents of analysis for plants and animals is positive (Gillman & Wright, 2006, 2010; Cusens *et al.*, 2012) (Fig. 6). Across continental-to-global extents positive relationships were the only relationship observed for plants (Gillman & Wright, 2006) and positive relationships were observed in approximately 90% of studies on animals (Cusens *et al.*, 2012). These synthetic assessments used strict selection criteria designed to ensure that member studies represented were robust tests of the productivity–species richness relationship (Gillman & Wright, 2010).

By contrast, we note that some meta-analyses of the species richness–productivity relationship have reported unimodal

relationships to be common, even at large spatial scales (Mittelbach *et al.*, 2001), and have suggested that there may be latitudinal variation in their frequency (Pärtel *et al.*, 2007; Laanisto *et al.*, 2008). However, these particular meta-analyses have received criticism on several grounds (Whittaker, 2010) and re-analyses of their data have presented results that contrast with their findings. In particular, many of the reported unimodal relationships are not unimodal when properly assessed. For example, studies testing for relationships using GLIM regression or the MOS test have been found to erroneously detect unimodal relationships that do not exist (Whittaker & Heegaard, 2003; Gillman & Wright, 2006; Cusens *et al.*, 2012). Similarly, Murtaugh (2003) demonstrated using simulations that over 99% of MOS tests were positive for a unimodal relationship despite his data having been drawn from distributions that were not unimodal. In previous work (Gillman & Wright, 2006; Whittaker, 2010) it has been shown that many unimodal relationships that have been reported are likely to be artefacts due to variables that are confounded with the surrogate used for productivity, such as when rainfall is confounded with increasing elevation. Unimodal relationships can also be an artefact of inappropriate plot size. In some cases examined, plot sizes were deemed to be so small that in productive sites they were not large enough to accommodate more than a single individual – in such instances no meaningful measure of species richness can be obtained. Finally, many reported unimodal relationships have been artefacts of farming activity where intensive grazing, mowing or the application of fertilizers has made inferences about evolutionary and ecological relationships between productivity and species assemblages inappropriate. For example, Adler *et al.* (2011) found that productivity across the globe is a poor predictor of species richness sampled using 1-m² plots in grassland. However, when they removed sites of anthropogenic origin they found a positive linear effect ($P = 0.013$), which

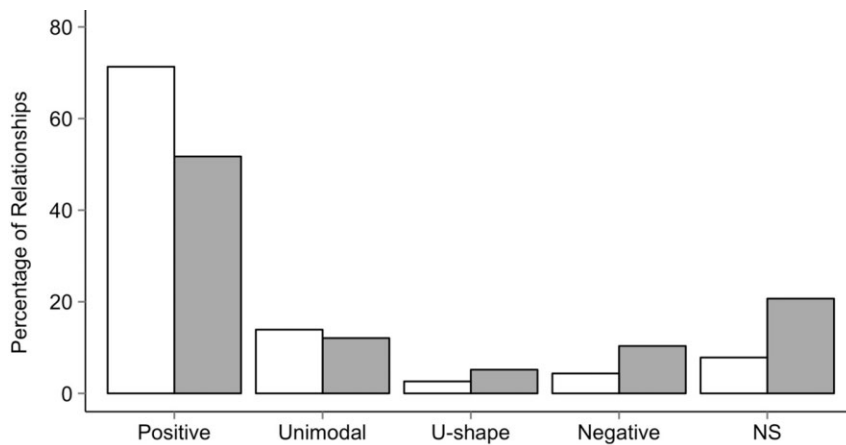


Figure 6 Productivity–animal species richness relationships (empty bars) ($n = 115$) and productivity–plant species richness relationships (solid bars) ($n = 58$). Datasets were drawn from the literature and screened according to pre-set criteria designed to ensure member studies represented unbiased and valid tests of the productivity–species richness relationship. Data from Gillman & Wright (2010) and Cusens *et al.* (2012). See those papers for analyses of the productivity–species richness relationship broken down by sampling grain and extent. NS, not significant.

although weak and probably inconsequential (Grace *et al.*, 2014) is nonetheless consistent with the predominately positive relationships reported in the synthetic reviews by Gillman and colleagues (Gillman & Wright, 2006, 2010; Cusens *et al.*, 2012). If data are to be used for making inferences about evolutionary processes they need to be obtained from systems that are not fundamentally altered or degraded by human activities.

Seasonal forests between latitudes of 10° and 30° tend to be relatively water-limited due to Hadley cell atmospheric circulation patterns (Lomolino *et al.*, 2010). Depressed productivity at these latitudes can be seen in Figs 1 & 2. These results are consistent with known water-limiting effects on both productivity and species richness at latitudes intermediate between the equatorial regions (0 – 10°) and the mid-latitudes in which temperate deciduous forests occur (Hawkins *et al.*, 2003; Whittaker *et al.*, 2007).

Our results have important implications for species richness theories that attempt to explain geographical gradients of diversity as a function of productivity or factors that are correlated with productivity (such geographical gradients include the latitudinal diversity gradient, which is complicated by pronounced gradients in water availability). Our findings are consistent with the energy–richness hypothesis (Wright, 1983), the integrated evolutionary speed hypothesis (Gillman & Wright, 2014) and the hypothesis of biological relativity to water–energy dynamics (O’Brien, 2006). By contrast, theories that attempt to explain diversity as a unimodal function of productivity (e.g. Huston, 2012) are inconsistent with our results. While unimodal plant species richness–productivity relationships are sometimes observed at fine scales, they occur much less often than positive relationships and do not appear to scale up to coarser scales of analysis, and hence cannot provide an explanation for the grand clines of diversity.

The significance of short-term NPP rates in forest ecosystems

Although more sampling may ultimately demonstrate a different pattern, we found no evidence of a latitudinal trend in average monthly litterfall productivity over the growing season.

When monthly wood production, averaged across 12 months, was added to growing season monthly litter production and regressed against latitude the relationship was again non-significant, thereby failing to support the mid-latitude peak hypothesis (Huston, 2012). Furthermore, we don’t believe there has been adequate theoretical justification of the concept that average monthly productivity during the growing season is more important than annual productivity.

CONCLUSION

The claim by Huston & Wolverton (2009) that NPP in temperate latitudes is as high or higher than at tropical latitudes is not supported by the data. We instead found a negative relationship between latitude and NPP of forest stands and that productivity of forests is greatest in tropical regions. Because diversity also declines towards the poles and modelled coarse-scale vascular plant richness correlates with NPP, our findings are consistent with the predominantly positive relationships between productivity and species richness that have been found at both large and small spatial scales using statistically and ecologically stringent meta-analytical techniques (Gillman & Wright, 2006; Cusens *et al.*, 2012). These results are consistent with theories that predict a positive relationship between species richness and productivity, such as the energy–richness hypothesis (Wright, 1983), the integrated evolutionary speed hypothesis (Gillman & Wright, 2014) and the biological relativity to water–energy dynamics hypothesis (O’Brien, 2006). However, each of these hypotheses has specific predictions that require in-depth testing in the future (e.g. Currie *et al.*, 2004).

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REFERENCES

- Adler, P.B., Seabloom, E.W., Borer, E.T. *et al.* (2011) Productivity is a poor predictor of plant species richness. *Science*, **333**, 1750–1753.

- del Aguila-Pasquel, J., Doughty, C.E., Metcalfe, D.B., Silva-Espejo, J.E., Girardin, C.A.J., Gutierrez, J.A.C., Navarro-Aguilar, G.E., Quesada, C.A., Hidalgo, C.G., Huaymacari, J.M.R., Halladay, K., del Castillo Torres, D., Phillips, O. & Malhi, Y. (2014) The seasonal cycle of productivity, metabolism and carbon dynamics in a wet aseasonal forest in north-west Amazonia (Iquitos, Peru). *Plant Ecology and Diversity*, **7**, 71–83.
- Araujo-Murakami, A., Doughty, C.E., Metcalfe, D.B., Silva-Espejo, J.E., Arroyo, L., Heredia, J.P., Flores, M., Sibling, R., Mendizabal, L.M., Pardo-Toledo, E., Vega, M., Moreno, L., Rojas-Landivar, V.D., Halladay, K., Girardin, C.A.J., Killeen, T.J. & Malhi, Y. (2014) The productivity, allocation and cycling of carbon in forests at the dry margin of the Amazon forest in Bolivia. *Plant Ecology and Diversity*, **7**, 55–69. doi: 10.1080/17550874.2013.798364.
- Begon, M., Townsend, C.R. & Harper, J.L. (2005) *Ecology: from individuals to ecosystems*, 4th edn. Blackwell Publishing, Oxford.
- Chave, J., Muller-Landau, H.C., Baker, T.R., Easdale, T.A., ter Steege, H. & Webb, C.O. (2006) Regional and phylogenetic variation of wood density across 2456 Neotropical tree species. *Ecological Applications*, **16**, 2356–2367.
- Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R. & Ni, J. (2001) Measuring net primary production in forests: concepts and field methods. *Ecological Applications*, **11**, 356–370.
- Coleman, B.D., Mares, M.A., Willig, M.R. & Hsieh, Y.H. (1982) Randomness, area, and species richness. *Ecology*, **63**, 1121–1133.
- da Costa, A.C.L., Metcalfe, D.B., Doughty, C.E., de Oliveira, A.A.R., Neto, G.F.C., da Costa, M.C., de Athaydes Silva Junior, J., Aragão, L.E.O.C., Almeida, S., Galbraith, D.R., Rowland, L.M., Meir, P. & Malhi, Y. (2014) Ecosystem respiration and net primary productivity after 8–10 years of experimental through-fall reduction in an eastern Amazon forest. *Plant Ecology and Diversity*, **7**, 7–24. doi: 10.1080/17550874.2013.798366.
- Cramer, W., Kicklighter, D.W., Bondeau, A., Iii, B.M., Churkina, G., Nemry, B., Ruimy, A. & Schloss, A.L. (1999) Comparing global models of terrestrial net primary productivity (NPP): overview and key results. *Global Change Biology*, **5**, 1–15.
- Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guegan, J., Hawkins, B.A., Kaufman, D.M., Kerr, J.T., Oberdorff, T., O'Brien, E.M. & Turner, J.R.G. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, **7**, 1121–1134.
- Cusens, J., Wright, S.D., McBride, P.D. & Gillman, L.N. (2012) What is the form of the productivity–animal-species-richness relationship? A critical review and meta-analysis. *Ecology*, **93**, 2241–2252.
- Doughty, C.E., Metcalfe, D.B., da Costa, M.C., de Oliveira, A.A.R., Neto, G.F.C., Silva, J.A., Aragão, L.E.O.C., Almeida, S.A., Quesada, C.A., Girardin, C.A.J., Halladay, K., da Costa, A.C.L. & Malhi, Y. (2014) The production, allocation and cycling of carbon in a forest on fertile terra preta soil in eastern Amazonia compared with a forest on adjacent infertile soil. *Plant Ecology & Diversity*, **7**, 41–53. doi: 10.1080/17550874.2013.798367.
- Ellis, E.C., Antill, E.C. & Kreft, H. (2012) All is not loss: plant biodiversity in the Anthropocene. *PLoS ONE*, **7**, e30535.
- Gill, R.A. & Jackson, R.B. (2000) Global patterns of root turnover for terrestrial ecosystems. *New Phytologist*, **147**, 13–31.
- Gillman, L.N. (2008) Assessment of sustainable forest management in New Zealand indigenous forest. *New Zealand Geographer*, **64**, 57–67.
- Gillman, L.N. & Wright, S.D. (2006) The influence of productivity on the species richness of plants: a critical assessment. *Ecology*, **87**, 1234–1243.
- Gillman, L.N. & Wright, S.D. (2010) Mega mistakes in meta-analyses: devil in the detail. *Ecology*, **91**, 2550–2552.
- Gillman, L.N. & Wright, S.D. (2013) Patterns of evolutionary speed: in search of a causal mechanism. *Diversity*, **5**, 811–823.
- Gillman, L.N. & Wright, S.D. (2014) Species richness and evolutionary speed: the influence of temperature, water and area. *Journal of Biogeography*, **41**, 39–51.
- Girardin, C.A.J., Aragão, L.E.O.C., Malhi, Y., Huaraca Huasco, W., Metcalfe, D.B., Durand, L., Mamani, M., Silva-Espejo, J.E. & Whittaker, R.J. (2013) Fine root dynamics along an elevational gradient in tropical Amazonian and Andean forests. *Global Biogeochemical Cycles*, **27**, 252–264.
- Grace, J.B., Adler, P.B., Harpole, W.S., Borer, E.T. & Seabloom, E.W. (2014) Causal networks clarify productivity–richness interactions, bivariate plots do not. *Functional Ecology*, **28**, 787–798.
- Grime, J.P. (1973) Competitive exclusion in herbaceous vegetation. *Nature*, **242**, 344–347.
- Grime, J.P. (1979) *Plant strategies and vegetation processes*. John Wiley and Sons, Chichester.
- Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guegan, J., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105–3117.
- Hillebrand, H. (2004) On the generality of the latitudinal diversity gradient. *The American Naturalist*, **163**, 192–211.
- Huston, M.A. (1979) A general hypothesis of species diversity. *The American Naturalist*, **113**, 81–101.
- Huston, M.A. (2012) Precipitation, soils, NPP, and biodiversity: resurrection of Albrecht's curve. *Ecological Monographs*, **82**, 277–296.
- Huston, M.A. & Wolverton, S. (2009) The global distribution of net primary production: resolving the paradox. *Ecological Monographs*, **79**, 343–377.
- Hutchinson, G.E. (1959) Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist*, **93**, 145–159.
- IPCC (1996) Revised 1996 guidelines for national greenhouse gas inventories. Intergovernmental Panel on Climate Change.
- Keeling, H.C. & Phillips, O.L. (2007) The global relationship between forest productivity and biomass. *Global Ecology and Biogeography*, **16**, 618–631.

- Kicklighter, D.W., Bondeau, A., Schloss, A.L., Kaduk, J. & McGuire, A.D. (1999) Comparing global models of terrestrial net primary productivity (NPP): global pattern and differentiation by major biome. *Global Change Biology*, **5**, 16–24.
- Kreft, H. & Jetz, W. (2007) Global patterns and determinants of vascular plant diversity. *Proceedings of the National Academy of Sciences USA*, **104**, 5925–5930.
- Laanisto, L., Urbas, P. & Pärtel, M. (2008) Why does the unimodal species richness–productivity relationship not apply to woody species: a lack of clonality or a legacy of tropical evolutionary history? *Global Ecology and Biogeography*, **17**, 320–326.
- Leith, H. & Whittaker, R.H. (1975) *Primary productivity of the biosphere*. Springer-Verlag, New York.
- Lomolino, M.V., Riddle, B.R., Whittaker, R.J. & Brown, J.H. (2010) *Biogeography*, 4th edn. Sinauer Associates, Sunderland, MA.
- Lorimer, C.G., Dahir, S.E. & Nordheim, E.V. (2001) Tree mortality rates and longevity in mature and old-growth hemlock-hardwood forests. *Journal of Ecology*, **89**, 960–971.
- Malhi, Y., Aragão, L.E.O., Metcalfe, D.B., Paiva, R., Quesada, C.A., Almeida, S., Anderson, L., Brando, P., Chambers, J.Q., da Costa, A.C.L., Hutyra, L., Oliveira, P., Patino, S., Pyle, E.H., Robertson, A.L. & Teixeira, L.M. (2009) Comprehensive assessment of carbon productivity, allocation and storage in three Amazonian forests. *Global Change Biology*, **15**, 1255–1274.
- Malhi, Y., Doughty, C. & Galbraith, D. (2011) The allocation of ecosystem net primary productivity in tropical forests. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**, 3225–3245.
- Malhi, Y., Amézquita, F.F., Doughty, C.E. *et al.* (2014) The productivity, metabolism and carbon cycle of two lowland tropical forest plots in south-western Amazonia, Peru. *Plant Ecology and Diversity*, **7**, 85–105.
- Metcalfe, D.B., Asner, G.P., Martin, R.E. *et al.* (2014) Herbivory makes major contributions to ecosystem carbon and nutrient cycling in tropical forests. *Ecology Letters*, **17**, 324–332.
- Mittelbach, G.G., Steiner, C.F., Scheiner, S.M., Gross, K.L., Reynolds, H.L., Waide, R.B., Willig, M.R., Dodson, S.I. & Gough, L. (2001) What is the observed relationship between species richness and productivity? *Ecology*, **82**, 2381–2396.
- Moles, A.T., Wright, I.J., Pitman, A.J., Murray, B.R. & Westoby, M. (2009) Is there a latitudinal gradient in seed production? *Ecography*, **32**, 78–82.
- Murtaugh, P.A. (2003) On detecting hump-shaped relationships in ecology: a bootstrap test for monotonicity. *Environmetrics*, **14**, 611–616.
- O'Brien, E.M. (2006) Biological relativity to water–energy dynamics. *Journal of Biogeography*, **33**, 1868–1888.
- O'Neill, R.V. & DeAngelis, D.L. (1981) Comparative productivity and biomass relations of forest ecosystems. *Dynamic properties of forest ecosystems* (ed. by D. Reichle), pp. 411–449. Cambridge University Press, Cambridge.
- Ogden, J. (1985) An introduction to plant demography with special reference to New Zealand trees. *New Zealand Journal of Botany*, **23**, 751–772.
- Ogden, J. & Stewart, G.H. (1995) Community dynamics of the New Zealand conifers. *Ecology of the southern conifers* (ed. by N.J. Enright and R.S. Hill), pp. 81–119. Melbourne University Press, Melbourne.
- Olson, R.J., Johnson, K.R., Zheng, D.L. & Scurlock, J.M.O. (2001a) *Global and regional ecosystem modeling: databases of model drivers and validation measurements*. Oak Ridge National Laboratory, Oak Ridge, TN.
- Olson, R.J., Scurlock, J.M.O., Prince, S.D., Zhang, D.L. & Johnson, K.R. (2001b) *NPP multi-biome: global primary production data initiative products*. Oak Ridge National Laboratory, Oak Ridge, TN.
- Pärtel, M., Laanisto, L. & Zobel, M. (2007) Contrasting plant productivity–diversity relationships across latitude: the role of evolutionary history. *Ecology*, **88**, 1091–1097.
- Pregitzer, K.S. & Euskirchen, E.S. (2004) Carbon cycling and storage in world forests: biome pattern related to forest age. *Global Change Biology*, **10**, 2052–2077.
- Rensch, B. (1959) *Evolution above the species level*. Methuen, London.
- Rocha, W., Metcalfe, D.B., Doughty, C.E., Brando, P., Silvério, D., Halladay, K., Nepstad, D.C., Balch, J.K. & Malhi, Y. (2014) Ecosystem productivity and carbon cycling in intact and annually burnt forest at the dry southern limit of the Amazon rainforest (Mato Grosso, Brazil). *Plant Ecology and Diversity*, **7**, 25–40.
- Rohde, K. (1992) Latitudinal gradients in species diversity: the search for the primary cause. *Oikos*, **65**, 514–527.
- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.
- Ryan, M.G., Binkley, D. & Fownes, J.H. (1997) Age-related decline in forest productivity: pattern and process. *Advances in Ecological Research*, **27**, 213–262.
- Stephenson, N.L., Das, A.J., Condit, R. *et al.* (2014) Rate of tree carbon accumulation increases continuously with tree size. *Nature*, **507**, 90–93.
- Swenson, N.G. & Enquist, B.J. (2007) Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. *American Journal of Botany*, **94**, 451–459.
- Tilman, D. (1982) *Resource competition and community structure*. Princeton University Press, Princeton, NJ.
- Tilman, D. & Pacala, S. (1993) The maintenance of species richness in plant communities. *Species diversity in ecological communities: historical and geographical perspectives* (ed. by R.E. Ricklefs and D. Schluter), pp. 13–25. University of Chicago Press, Chicago, IL.
- Westing, A.H. (1964) The longevity and aging of trees. *The Gerontologist*, **4**, 10–15.
- Whittaker, R.J. (2010) Meta-analyses and mega-mistakes: calling time on meta-analysis of the species richness–productivity relationship. *Ecology*, **91**, 2522–2533.

- Whittaker, R.J. & Heegaard, E. (2003) What is the observed relationship between species richness and productivity? Comment. *Ecology*, **84**, 3384–3390.
- Whittaker, R.J., Nogués-Bravo, D. & Araújo, M.B. (2007) Geographical gradients of species richness: a test of the water–energy conjecture of Hawkins *et al.* (2003) using European data for five taxa. *Global Ecology and Biogeography*, **16**, 76–89.
- Wright, D.H. (1983) Species–energy theory: an extension of species–area theory. *Oikos*, **41**, 496–506.
- Wright, D.H., Currie, D.J. & Maurer, B.D. (1993) Energy supply and patterns of species richness on local and regional scales. *Species diversity in ecological communities* (ed. by R.E. Ricklefs and D. Schluter), pp. 66–74. University of Chicago Press, Chicago.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Aboveground net primary productivity–latitude analysis using Oak Ridge National Laboratory data.