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The enigma of terrestrial primary productivity: measurements, models, scales and the diversity–productivity relationship

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Net primary productivity (NPP) is a variable of primary interest to ecologists, as it is related both to resource availability, potentially affecting biological diversity, and to the dynamics of the carbon cycle. However, there are alarming discrepancies in NPP estimates as well as in the reported form of the relationship between NPP and species richness. Such discrepancies could be due to the different and often simplified assumptions of various global NPP models and the heterogeneity of field NPP measurements that comprise a mix of natural vegetation and plantations. Here we review different global models of NPP and available original sources of NPP field measurements in order to examine how their geographic patterns are affected by various assumptions and data selection, respectively. Then we review studies dealing with diversity–productivity relationships in view of different NPP estimates. We show that although NPP does generally decrease with increasing latitude, geographic NPP patterns considerably differ between individual models as well as between the models and field NPP data. Such inconsistencies might be partially responsible for discrepancies in productivity–richness relationships, although these are also driven by other factors that covary with productivity and affect diversity patterns. To reconcile the discrepancies between various NPP measures, it is necessary to 1) standardize field NPP data, 2) develop scaling techniques that bridge the gap between the scale of field NPP measurements and NPP models, and 3) build global NPP models that account for nutrient limitation (especially concerning phosphorus in the tropics) and are parameterized by field measurements. Also, 4) a better theory needs to be developed to distinguish the effect of productivity from the effects of other environmental variables on diversity patterns. Improving our ability to estimate NPP will help us predict future NPP changes and understand the drivers of species richness patterns.

Environmental productivity is a key variable in ecology, climatology and agriculture. It is considered the main determinant of resource availability, which drives the intensity of intraspecific and interspecific competition (Grime 1973), and thus presumably limits the number of coexisting species (Hutchinson 1959, Wright 1983, Hawkins et al. 2003, Huston 2014). Productivity is usually measured as net primary production (NPP), which is the amount of biomass or carbon produced by primary producers per unit area and time. Biomass production is important for ecosystem services, agriculture and forestry (Haberl et al. 2007), as well as for the global carbon cycle, which in turn affects the water cycle and climate (Clark et al. 2003, Lee et al. 2012). Knowledge of the global distribution of NPP and its underlying processes is thus important not only for understanding biodiversity patterns and potential agricultural yield, but also for predicting global climatic changes and vegetation dynamics.

Surprisingly, there is no clear consensus about global patterns of terrestrial NPP (Huston and Wolverton 2009, Gillman et al. 2015). Traditionally, productivity has been assumed to follow a latitudinal trend, with decreasing NPP from the equator towards the poles and with the highest NPP in tropical rainforests. By contrast, Huston and Wolverton (2009) used field measurements to argue that latitudinal trends in terrestrial NPP follow those observed in the seas, with the highest productivity (at least during the vegetation season) in temperate zones, and not in the tropics. The productivity of tropical forests could be slightly lower than that of temperate forests during the vegetation season due to shorter daylight hours, higher temperatures during the night, leading to higher respiration rates, and stronger nutrient limitation (Huston and Wolverton 2009). However, field measurements of NPP are still highly inconclusive and can be interpreted differently depending on the decision as to which measurements are considered reliable (Clark et al. 2001; below). Productivity models are at the same time based on simplified assumptions and are not always consistent with field data (Huston and Wolverton 2009, Cleveland et al. 2015). The debate, therefore, had yet to be settled.

Productivity is considered one of the major determinants of species richness (Gaston 2000), but the relationship between productivity and species diversity is controversial (Mittelbach et al. 2001, Gillman and Wright 2006, Adler et al. 2011, Grace et al. 2012, Fraser et al. 2015). Productivity

or its surrogates have been shown to closely correlate with species richness at large spatial scales (Wright 1983, Waide et al. 1999, Hawkins et al. 2003, Gillman and Wright 2006, Field et al. 2009), and it is reasonable to assume that productivity limits the amount of available resources within communities and consequently the maximum number of species that can attain viable populations (Hutchinson 1959, Wright 1983, Hurlbert and Stegen 2014). However, various productivity–richness relationships have been reported at smaller scales, including hump-shaped (Grime 1973, Tilman and Pacala 1993, Mittelbach et al. 2001, Fraser et al. 2015) or even negative ones (Šímová et al. 2013). Hump-shaped relationships have been reported more often for grassland ecosystems, where productivity was measured directly at peak biomass during the growing season (Waide et al. 1999, Mittelbach et al. 2001, Gillman and Wright 2006, but see Pärtel et al. 2007, Adler et al. 2011). When productivity was estimated less directly in forest ecosystems (using, for example, stem diameter increments or allometric relationships), the unimodal relationship was not observed (Laanisto et al. 2008). Although the observed variation in productivity–diversity relationships may be due to its scale dependence and various confounding factors (namely collinearity with other factors affecting species richness such as habitat heterogeneity, disturbances or asymmetric competition), it is also possible that it results from the different ways of measuring productivity (Huston 2014).

Here we review the different estimates of net primary productivity and the limits of individual modelling approaches. Then we present an overview of available data on local NPP measurements, explore their biases, and discuss the challenges concerning their utilization and interpretation of their geographic patterns. Further, we discuss the implications of different NPP estimates for the interpretation of the observed relationships between environmental productivity and species diversity, and for predicting future productivity changes. Finally, we present a list of key steps that need to be done in order to improve the quality and reliability of NPP estimates across the globe.

Productivity patterns at large scales: an overview of modelling approaches

NPP cannot be directly measured at large spatial scales. It is possible to measure some variables that to various degrees correlate with productivity (e.g. using remote sensing), but estimates of NPP must then be based on models that assume certain (statistical or causal) relationships between these variables and productivity (Fig. 1). Several classes of models are used to estimate NPP, each with its advantages and limitations.

Climate-based models
The first two important global models independently developed by Rosenzweig (1968) and Lieth (1975) were based on relationships between NPP and climatic variables. Rosenzweig (1968) plotted various NPP measurements from 24 mature natural forest stands against annual actual evapotranspiration (AET, calculated based on monthly temperature, precipitation and latitude or altitude following the Throntwaite method; Thornthwaite 1948). Rosenzweig realized that there was a linear relationship when both AET and NPP were logarithmized, so that AET could be used
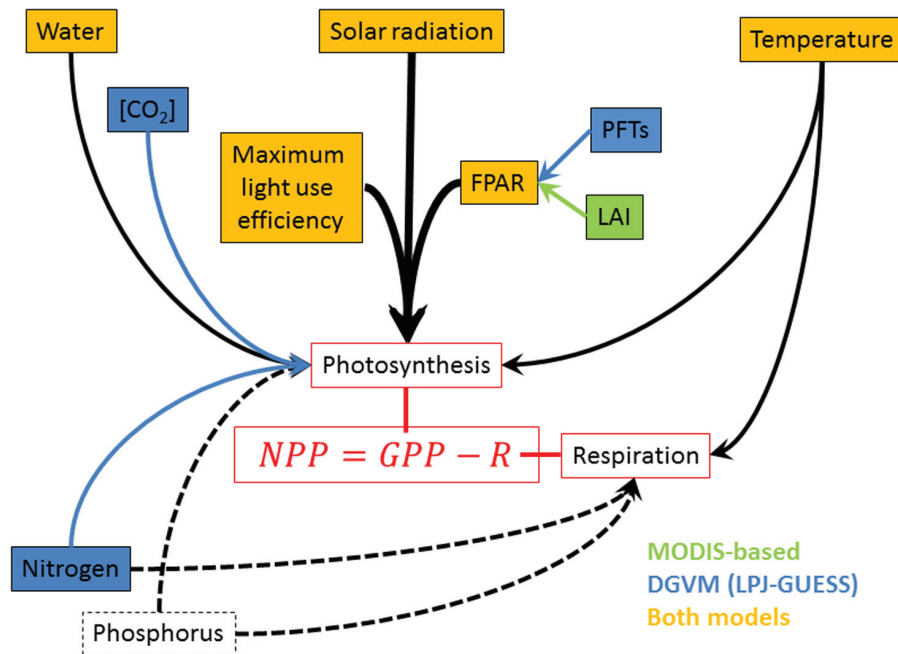

Figure 1. Simplified scheme of causal links between environmental variables and NPP assumed by remote sensing-based and dynamic vegetation models (DGVMs). Variables and links contained within the remote sensing-based models (here the MODIS-based model, Running et al. 2004) are highlighted in green; those used in DGVMs (here the LPJ-GUESS, Sitch et al. 2003) are blue. The variables that are common for both models are yellow with black arrows. Dashed lines indicate links that are likely missing. LUE is light use efficiency, LAI is leaf area index, FPAR is the fraction of photosynthetically active radiation absorbed by plants, and PFTs are plant functional types.

as a surrogate of NPP. Most of these stands, however, were located within the USA, which limited the global applicability of this approach. Lieth (1975) estimated global NPP patterns based on 50 field NPP measurements from different biomes worldwide (although tropical sites were also largely under-sampled). NPP values were paired with annual temperature and precipitation measurements obtained from the closest meteorological stations, and a global NPP map (the so-called Miami model) was generated using multiple regression of log-NPP on log-temperature and log-precipitation. The Miami model became the basis for the later development of more complex climate-based models such as the High-Resolution Biosphere Model (HRBM; Esser 1994). However, the idea of NPP as a simple increasing function of temperature and precipitation does not work in the tropics, where NPP becomes relatively independent of these variables (Clark et al. 2001, Luyssaert et al. 2007). This suggests that other factors limit a further increase of NPP in the tropics. Indeed, other environmental variables, such as nutrient limitation, have been shown to be crucial determinants of field NPP measurements in the tropics (Aragão et al. 2009, Quesada et al. 2009, 2012). Another problem is that the spatial coverage of meteorological stations is rather poor in the tropics (Hijmans et al. 2005), compromising the validity of these models in tropical areas. On the other hand, although other productivity models are currently preferred, the simplicity of climate-based models has an advantage in that they can be used to estimate historical productivity, for which only temperature and precipitation time series are available (Peng et al. 1995, Brovkin et al. 2002, Wang et al. 2005).

Radiation-based NPP models

These models are based on the finding that productivity of annual crops under well-watered and fertilized conditions linearly increases with the increasing amount of absorbed solar energy (Monteith 1972). This assumption was used in the so-called Chikugo model by Uchijima and Seino (1985). Specifically, they calculated annual NPP as a function of annual net radiation, latent heat of evaporation and annual precipitation, based on theoretical predictions parameterized using NPP field data. Because the model was validated using NPP measurements for Japan, it is not suitable for sites where water is a limiting factor (Zhou and Zhang 1995, Zhou et al. 2002). Given the strong correlation of net radiation with latitude, the Chikugo model revealed a strong latitudinal gradient in productivity which has been shown to correlate well with species richness (Adams and Woodward 1989, Gaston and Blackburn 1995). Nevertheless, net radiation by itself is not a sufficient determinant of NPP even in well-watered regions, as productivity is limited also by the total leaf area absorbing the solar energy (Box et al. 1989, Running et al. 2004), as well as other factors mentioned below.

Remote sensing-based models

With the development of remote-sensing techniques, the normalized difference vegetation index (NDVI) became a widely used estimate of the proportion of solar radiation absorbed by leaves (Box et al. 1989). The NDVI is a measure of 'vegetation greenness' and is calculated as the difference between spectral reflectance measurements in the red and near-infrared wavelength band normalized by their sum.

NDVI integrated over a year became a popular surrogate of annual NPP (Goward and Dye 1987, Box et al. 1989, Lo Seen Chong et al. 1993). However, the NDVI reaches saturation in dense vegetation, leading to similar NDVI values for forests with different NPP (Sánchez-Azofeifa et al. 2009, Lee et al. 2013). Another problem is the presence of clouds, which distorts reflectance measurements and can lead to the underestimation of NPP in some tropical areas with a dense cloud cover (Zhao et al. 2005). Finally, without information about light-use efficiency, pure NDVI is not a sufficient measure of the fraction of photosynthetically active radiation absorbed by leaves (Ruimy et al. 1999, Jenkins et al. 2007). For this reason, Production Efficiency Models (PEMs) were developed, combining the NDVI with empirical estimates of maximum potential light use efficiency and other factors further constraining photosynthesis and respiration such as solar radiation, temperature (Box 1), water availability or atmospheric CO_2 concentration (Cramer et al. 1999, Turner et al. 2002, Jenkins et al. 2007).

Currently the most commonly used remote sensing-based model is the MOD17 NPP model (hereafter referred to as the MODIS-based model), a product of the Moderate Resolution Spectroradiometer (MODIS) sensor (Running et al. 2004). NPP in this model is estimated as GPP minus autotrophic respiration R

$$NPP = GPP{-}R \qquad\qquad (1)$$

where GPP is the daily net photosynthesis rate calculated according to the equation

$$GPP = \varepsilon \times PAR \times FPAR \qquad\qquad (2)$$

Here ε is the conversion efficiency (or the light use efficiency) that transforms photosynthetically active radiation absorbed by leaves into tissue growth; it is a function of biome-specific maximum ε, daily minimum temperature and vapour pressure deficit (Zhao et al. 2005, Zhao and Running 2010). PAR is photosynthetically active radiation (estimated from solar radiation), and $FPAR$ is the fraction of PAR absorbed by plants estimated on the basis of the remotely sensed leaf area index (LAI), which replaces the NDVI (Fig. 1). Autotrophic respiration R has two components: daily maintenance respiration (R_m), calculated as a function of the daily average air temperature, and annual growth respiration (R_g), estimated as a constant proportion of total NPP (see supplementary material in Zhao and Running 2010 for details).

The algorithms of other PEMs are similar, differing mainly in the environmental variables constraining the maximum ε and in the calculation of R, although the models differ also in terms of their time-steps and spatial resolution (see McCallum et al. 2009 for detailed comparison). For instance, ε is assumed to be limited by the minimum temperature and vapour pressure deficit in the MODIS-based model, while the CASA algorithm (Carnegie-Ames-Stanford Approach; Potter et al. 1993) assumes that ε is limited by temperature stress and actual and potential evapotranspiration (see Potter et al. 2012 for details). The CASA is also the only PEM where NPP is modelled directly, without estimating GPP or R. This model has become the basis for the global map of Human Appropriation of Net Primary Productivity (HANPP, Imhoff et al. 2004).

Box 1. The effect of temperature on productivity.

Temperature affects all biological rates (Brown et al. 2004), including photosynthesis and respiration. It is therefore reasonable to assume that it affects NPP as well. The fundamental relationship between biological rates and temperature is given by Boltzmann–Arrhenius equation

$$B \sim e^{-E/(kT)}$$

where B is the metabolic (or any other) rate, T is temperature in kelvins, k is Boltzmann constant, and E is the activation energy of a key biochemical reaction (Brown et al. 2004). It follows that the logarithm of the rates should linearly depend on $(1/kT)$, with the slope of $-E$. However, it is complicated by the fact that different processes can have different E, so that e.g. photosynthesis reveals different temperature-dependence than respiration (Allen et al. 2005). NPP is determined by both processes, so its overall temperature-dependence may not be straightforward. Moreover, some studies found no temperature dependence of primary productivity during the vegetation season (Kerkhoff et al. 2005).

In fact, many NPP models include temperature dependencies in their assumptions. The first climate-based models were based solely on the statistical dependency between measured NPP and temperature, but the later approaches explicitly model such dependencies. Typically (as in the case of the MODIS-based model), the rate of photosynthesis is assumed to be lower at low and high temperatures, i.e. that there is some optimum temperature for photosynthesis, and that respiration is positively temperature-dependent. Most models (especially DGVMs) also account for temperature dependencies of other processes, namely water balance, evapotranspiration or decomposition rate. Also, the models often assume that minimum temperature is more important than mean temperature. Various treatment of temperature in different models naturally leads to different model outputs and various latitudinal trends of modelled NPP.

Importantly, the temperature used in the models is air temperature, because plants are considered to be poikiloterms. Nevertheless, a hypothesis of a limited homeothermy of plants has recently been supported (Michaletz et al. 2015). This finding highlights the need to consider plant tissue temperature, i.e. the temperature where the plant metabolism is taking place. The fact that plant tissue temperature can be independent of air temperature may also be partly responsible for the weak correlation between field NPP measurements and air temperature.

The main advantage of remote sensing-based models is that they rely on directly measured vegetation properties, typically sampled each month or every couple of weeks, which can be averaged over a given time period. They thus provide information about instantaneous NPP for a selected period, not only about annual averages as in the case of the previous category of climate-based models. Another advantage is the relative simplicity of their algorithms, at least in comparison to the dynamic vegetation models discussed below. However, the leaf area index faces similar problems as the NDVI, namely a tendency to reach saturation in dense forests (thus underestimating productivity; Huete et al. 2002) and the uneven availability of data from different regions due to the presence of clouds (Wilson et al. 2014). Additionally, the MODIS-based GPP corresponds much better to field GPP measurements than when comparing MODIS-based NPP and field NPP measurements (Turner et al. 2005, 2006). The difference between the reliability of MODIS-based GPP and NPP values can be interpreted as evidence of other unmeasured factors limiting NPP through their effect on the proportion of GPP allocated to growth vs respiration, such as available nutrients (Malhi 2012).

Potsdam model

The plethora of different NPP models led to several comparative studies published in a series of papers in 'Global Change Biology' in 1999 (see the introductory paper by Cramer and Field 1999) resulting from two workshops held at the Potsdam Institute for Climate Impact Research. The most famous output of these workshops was the model synthesis by Cramer et al. (1999), where the global NPP pattern was obtained by averaging 17 different NPP models (including climate-based models, remote sensing-based models and dynamic vegetation models described below). After removing two outliers (TURC, Ruimy et al. 1996, and HYBRID, Friend et al. 1997), the models largely agreed in their NPP estimates and their geographic trends (Fig. 2a), probably due to the fact that most of them estimated NPP as a function of the same variables, namely solar radiation, water balance and ambient CO_2 concentration (Cramer et al. 1999). Unfortunately, only a few of these models accounted for nutrient limitation, and these models produced lower NPP than those without nutrient constraints (Cramer et al. 1999).

Dynamic global vegetation models

The major disadvantage of the models above is their limited ability to make any predictions about future changes of NPP. For this purpose, more complex models are currently being developed, such as the dynamic global vegetation models (DGVMs). These models simulate changes in ecosystem structure (such as vegetation distribution and phenology) and function (such as biogeochemical cycling, GPP and NPP) under climatic changes in daily, monthly or annual time-steps (Cramer et al. 2001a). Vegetation properties are typically represented by separate vegetation units called plant functional types (PFTs) (Cramer et al. 2001a). The main problem of the PFTs approach is that ecosystems are formed by plant species of various characteristics, so PFTs are not homogeneous units (Van Bodegom et al. 2012, Wullschleger et al. 2014, Pappas et al. 2016). Another serious problem is that the assumed response of PFTs to climate changes is modelled based on experimental evidence or observations obtained in temperate biomes, leading to large uncertainty about low- and high-latitude NPP variation (Clark et al. 2001, Hickler et al. 2008, Dietze 2014). If nutrient
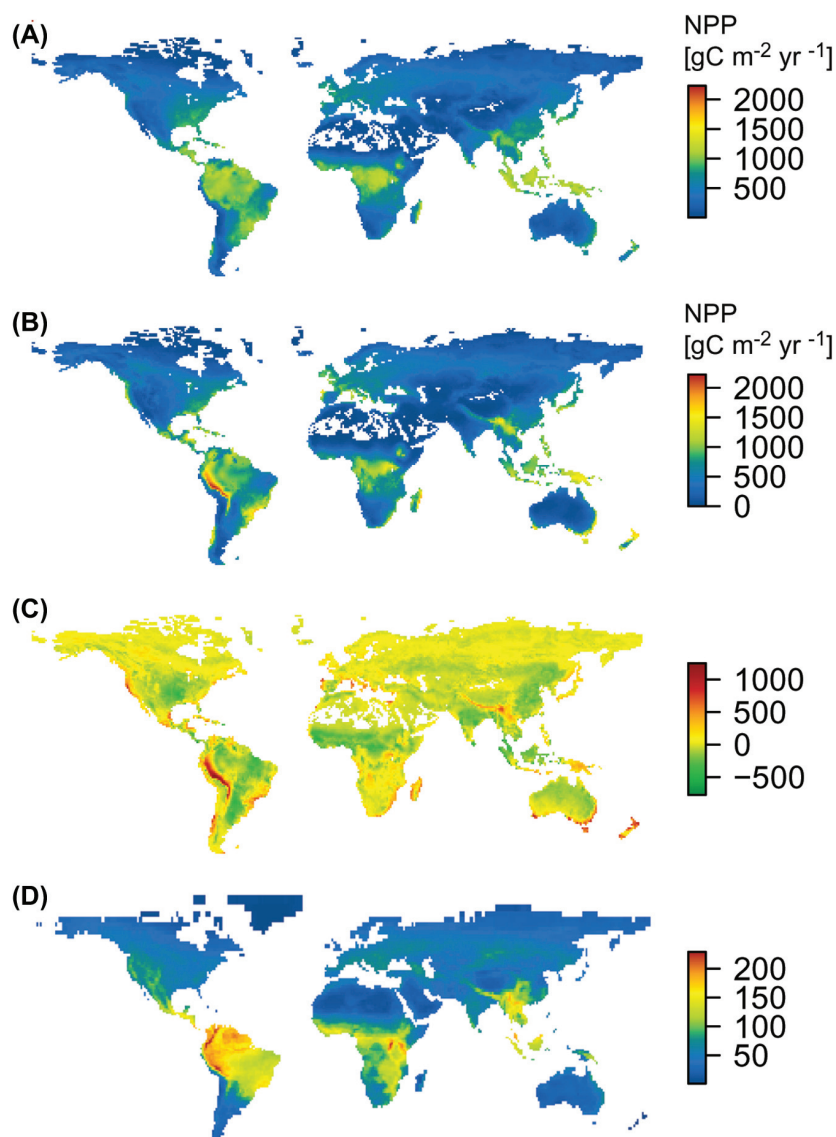
Figure 2. Geographic patterns of annual NPP estimated by (A) the Potsdam model and (B) the MODIS-based model (averaged over years 2000–2012), and the residuals from the MODIS-based model when regressed against the Potsdam model (C), compared to (D) geographic distribution of mammal species richness (taken from <www.iucnredlist.org>). Note that the Potsdam model generates a considerably more pronounced latitudinal gradient of NPP than the MODIS-based model, in which high productivity levels are reached in a few relatively small regions (western slopes of the Andes, Atlantic Forest in Brazil, east-African Rift, foothills of the Himalayas, New Guinea). Interestingly, these regions also represent hotspots of vertebrate species richness.

limitation is included in these models (which is not always the case), it typically only concerns nitrogen (Hickler et al. 2015, Walker et al. 2015), while the role of phosphorus, a key nutrient in the tropics, is largely overlooked (Aragão et al. 2009, Quesada et al. 2009). This also applies to other potentially limiting nutrients such as potassium (Wright et al. 2011, Lloyd et al. 2015). These limitations can be overcome by using continuous plant traits instead of PFTs (Scheiter et al. 2013) and by including information about concentration of soil phosphorus (Yang et al. 2013) or nutrient concentrations in plant tissues (cf. Kattge et al. 2011). However, incorporating the effect of nutrients and continuous plant traits would increase the model complexity (which is already quite high), leading to even greater uncertainties in model outputs (Wieder et al. 2015a).

In summary, different models differ as to their assumptions, but since many of them include temperature or solar irradiation (Box 1, Fig. 1), most of them lead to similar geographic patterns showing the latitudinal productivity gradient. This gradient is partly driven by the effect of temperature variation on the length of the vegetation season, which may be then considered a first-order predictor of annual NPP (Huston and Wolverton 2009). However, even complex models usually fail to include some limiting factors. None of the models explicitly accounts for phosphorus limitation in the tropics, compromising the reliability of most models in the tropical zone. Furthermore, even well-established models, like the Potsdam or the MODIS-based model, produce different geographic patterns of annual NPP (Fig. 2c). It is thus necessary to also consider

field NPP measurements to evaluate geographic trends in NPP.

What do field measurements say about geographic trends in NPP?

Field measurements do not provide a clear picture of geographic trends in NPP. There are several reasons for this. Most field observations come from temperate or boreal regions, while tropical ecosystems are largely undersampled (Clark et al. 2001, Olson et al. 2013), even though this is now changing (Avissar et al. 2002, Malhi et al. 2002, Phillips et al. 2009, Malhi et al. 2015). Different studies were conducted for different reasons (Cannell 1982) and therefore at sites of different ages and successional stages (Vogt et al. 1987, Danilin 1995), which also masks geographic patterns of NPP (Michaletz et al. 2014, Gillman et al. 2015). Study sites are typically selected non-randomly, including natural primary forest stands or managed sites, depending on the focus of the particular study. The studies also vary in the method of estimating standing biomass and biomass increments and in the time period of the sampling. Whereas NPP of herbaceous communities is typically measured using biomass harvest in the peak growing season, forest biomass is estimated based on various site-specific or published allometries, or more direct estimates using litterfall traps or stem increments measured over one year or averaged over multiple years (Cannell 1982, Michaletz et al. 2014). Some NPP estimates include the effect of herbivory, and some include the biomass of fruits, etc. Unfortunately, these methods are often poorly documented, making it difficult to evaluate the quality of field data (Clark et al. 2001).

The largest database containing field NPP data has been compiled by the Global Primary Productivity Data Initiative (GPPDI, Olson et al. 2001, 2013). Curiously enough, studies exploring the latitudinal productivity gradient using these data qualitatively differ in their conclusions. Whereas Olson et al. (2001) and Gillman et al. (2015) report a decrease of NPP from the tropics towards high latitudes, Cramer et al. (2001b) and Huston and Wolverton (2009) report the highest NPP in certain temperate forests and in savannas. Such surprising disagreement among studies that used the same database can be due to three main reasons. One is data grouping. Gillman et al. (2015) averaged forest NPP data that were collected < 100 km apart from each other (and then used these values in OLS regression with latitude as the explanatory variable) whereas Huston and Wolverton (2009) first grouped all forest data points into several latitudinal bins and then plotted mean NPP and its standard deviation against the latitude of the bins. The second reason is data selection. Cramer et al. (2001b) used a smaller dataset than the updated version of Olson et al. (2013). The third reason may lie in data quality. The steep latitudinal decrease of NPP reported by Gillman et al. (2015) was maintained when only a cleaned and well-documented subset of the GPPDI, the so-called class A category (Olson et al. 2001) was used. However, the majority of the GPPDI data belong to the class B category, originating from a mixture of studies focusing on ecosystem NPP, comprising various altitudinal or successional gradients, fertilization treatments or forest cultures

(see primary papers from Cannell 1982, or GPPDI class B data references). Such heterogeneity in the data may mask actual geographic patterns of NPP. Indeed, when young successional forests were excluded, Gillman et al. (2015) found a steeper decrease of NPP from the tropics towards the poles than when they were included.

We reviewed the class B data (downloaded on 28 February 2014 from <https://daac.ornl.gov>) in order to explore the extent to which the presence of forest plantations or fertilization/irrigation treatments affected the previously reported latitudinal NPP trend. Since global data of non-forest field NPP are very scarce (1093 of forest data points vs 177 non-forest data points in class B), we included data only from biomes classified as forests or those dominated by woody species (deciduous broadleaved, deciduous needle-leaved, evergreen broadleaved, evergreen needle-leaved, Mediterranean, mixed forest and savanna). We focused only on sites with known aboveground net primary productivity (ANPP), not including combined aboveground and belowground measurements (total net primary productivity, TNPP). We searched for primary studies using references associated with the selected data points in order to locate information about each study site. If the reference was missing, we matched the data with data points reported by Cannell (1982) based on the coordinates, elevation and data description. When we were unable to find the primary source, sites having the term 'plantation' in their data description or those where focal species were apparently exotic for a given site (e.g. *Pinus radiata* in New Zealand) were regarded as plantations. We divided the data into 1) natural habitats, 2) plantations or experimentally fertilized/irrigated sites and 3) sites with undetermined status (it was impossible to confidently find the primary reference, or it was unclear whether
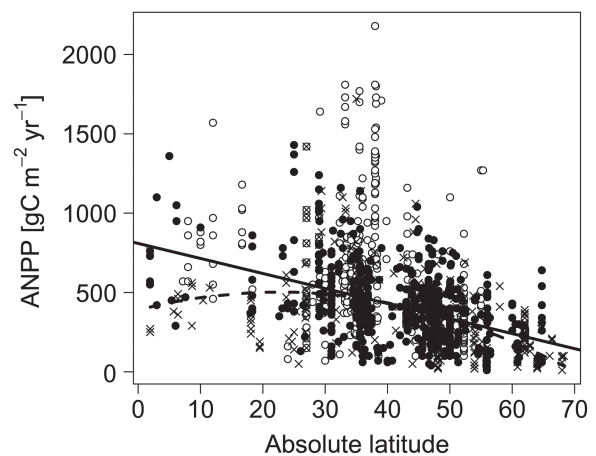

Figure 3. The relationship between forest aboveground net primary production (ANPP) and absolute latitude for class B data from GPPDI (Olson et al. 2013). Plantations or forests under fertilization/irrigation experiments are represented by white circles and the dashed line (polynomial fit, $r^2 = 0.07$, $p < 0.001$) whereas natural vegetation is represented by black circles and the solid line (linear fit, $r^2 = 0.2$, $p < 0.001$). For natural stands, the quadratic term of productivity was not significant and the AIC of the linear model was lower than the AIC of the quadratic model. For plantations, both the terms were significant, the quadratic model having a better fit according to the AIC. Data points with unclear classification are represented by crosses.

the forest was planted or not). There were 492 sites of natural vegetation, 309 sites of plantations or human-modified forests and 292 forests with unknown status.

Natural habitats and plantations show very different geographic trends of NPP. Natural stands exhibit a linear decrease of ANPP with latitude (Fig. 3). Plantations or fertilized plots, by contrast, show a unimodal relationship, temperate areas reaching the highest values (Fig. 3). Therefore, contrary to some previous studies (Huston and Wolverton 2009, Huston 2014), field measurements of NPP for natural vegetation follow a latitudinal gradient with the highest NPP in the tropics. The fact that NPP of forest plantations is highest in the temperate zone is in accord with the findings of Huston and Wolverton (2009) that agricultural NPP is highest in temperate biomes. In principle, it is still possible that natural temperate forests would also be very productive had they not been destroyed and converted into fields and plantations (Huston and Wolverton 2009). However, large values of NPP in temperate plantations may be simply due to the fact that studies measuring NPP of forest plantations were mostly conducted in temperate biomes, so there was a higher chance of finding extremely high values. Another explanation is that plantations correspond to early successional stages and comprise selected trees that are able to gain high biomass in a short time. The lower productivity of tropical plantations, on the other hand, can follow from the loss of nutrients and soil structure with the clearing of the original biomass.

Do field data match global NPP models?

Regardless of whether GPPDI data or local measurements recently taken in the tropics are used, the geographic trends based on field measurements often disagree with the predictions of global NPP models (Fig. 4; Clark et al. 2001, Zaks et al. 2007, Cleveland et al. 2015). It seems that models in which productivity is assumed to be tightly related to temperature have a tendency to predict higher tropical NPP than suggested by field measurements (Zaks et al. 2007), while remote sensing-based models tend to underestimate tropical NPP due to the abovementioned effect of NDVI or LAI saturation (Ruimy et al. 1994, Turner et al. 2005, 2006). Although both field data and models agree on the general decrease of NPP from the equator towards the poles, the discrepancy between modelled and measured NPP values within individual climatic zones is quite high (Ni 2003, Potter et al. 2012, Cleveland et al. 2015). One reason may reside in the scale of sampling. Field data are sampled at much finer scales than those used in models, so they do not represent random samples covering the whole landscape. Field measurements can be comparable to the predictions of global NPP models (and could be eventually used for parameterizing them) only when they are collected by a systematic stratified design, and are therefore representative of the given region.

Another factor potentially responsible for the discrepancy between field NPP measurements and the models is nutrient availability, which naturally affects field measurements but is not accounted for in the models. For instance, the strong decrease in locally measured values of NPP from the western to the eastern Amazon, most likely reflecting the gradient
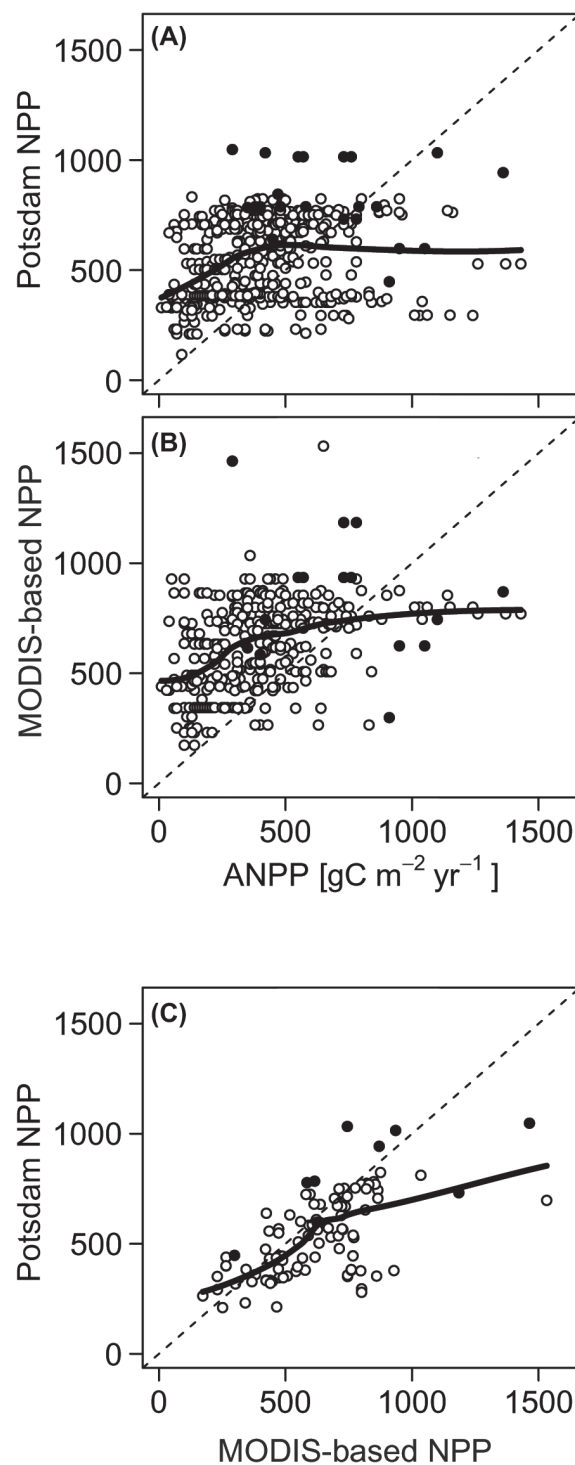
Figure 4. The relationship between annual net above-ground primary production (ANPP) obtained from GPPDI restricted for natural forest stands, and NPP estimated by the (A) Potsdam model and (B) the MODIS-based model, extracted from the same locations as the data points. (C) comparison between the two models. Black circles represent tropical sites (absolute latitude < 23.4) whereas white circles represent temperate and boreal sites (absolute latitude > 23.4); dashed is the identity line. The higher number of data points in panel (A) and (B) is due to the multiple plots with different ANPP reported for the same location. The trend line is fitted as a loess (local polynomial regression) curve. Note that the Potsdam model predicts higher NPP for most tropical sites and that none of the models provides a good prediction of the field NPP measurements.

of nutrients, did not appear in the NPP models (Cleveland et al. 2015). Similarly, the progressive temporal increase in NPP predicted by some models disagrees with long-term experiments and observations, and this disagreement is largest for models that do not account for the nutrient limitation (Hickler et al. 2015). It would thus be necessary, besides overcoming the abovementioned scale gap, to include also data on soil nutrients in order to provide more reliable NPP estimates for large spatial scales.

How is species richness related to productivity?

The lack of a consensus regarding NPP estimates may partially explain the inconsistency in the reported relationships between species richness and productivity. In fact, many studies have regarded climatic variables, including evapotranspiration, remote-sensing-based layers like the NDVI and various NPP models, as more or less equivalent (Hawkins et al. 2003, Field et al. 2009, Cusens et al. 2012), since all of them are positively related to each other. All these variables correlate well with species richness at large spatial scales, and although some previous studies have reported curvilinear or hump-shaped relationships between productivity and species richness even at large spatial scales (Mittelbach et al. 2001), recent studies agree that large-scale species richness of higher taxa increases monotonically, and often almost linearly, with most of these variables (Francis and Currie 2003, Currie et al. 2004, Storch et al. 2006, Keil et al. 2008).

The problem is that although productivity has been postulated to be a major determinant of diversity on land (Wright 1983, Currie 1991, Gaston 2000), its covariation with other variables impedes the separation of its effect from the effects of other factors. Indeed, although the MODIS-based or Potsdam NPP models provide good predictions of species richness patterns at large scales (Buckley and Jetz 2007, Qian 2010, Goetz et al. 2014, McBride et al. 2014), temperature or AET often perform better (Table 1; Phillips et al. 2010, Šímová et al. 2011, Belmaker and Jetz 2011, Jetz and Fine 2012). It is thus possible that effects other than productivity are causally responsible for variation in species richness (Currie et al. 2004, Storch 2012), although the observed comparatively weaker effect of NPP could also be

due to the abovementioned problems surrounding its proper estimation.

Productivity is expected to limit the number of species either through limiting the total number of individuals (the More Individuals Hypothesis; Wright 1983, Srivastava and Lawton 1998), or the total niche space at a given site (Schemske 2002, Chase and Leibold 2003). However, the evidence for such hypotheses is limited. It seems that species richness variation does not follow the variation in the total number of individuals (Currie et al. 2004, Šímová et al. 2011, 2013, Storch 2012). It is also often independent of diversity in functional traits that presumably represents the niche space size (Ricklefs 2012, Lamanna et al. 2014, Šímová et al. 2015). The effects of temperature-dependent diversification rates (Rohde 1992, Allen et al. 2002, Brown 2014, Gillman and Wright 2014) or historically determined climatic tolerances of species (Latham and Ricklefs 1993, Wiens and Donoghue 2004) have therefore been regarded as more important large-scale diversity determinants (Currie et al. 2004). If this is the case, productivity correlates with diversity only due to its covariation with other factors that are causally linked to diversity, including temperature and long-term environmental stability (e.g. the age and historical extent of individual biomes, Jetz and Fine 2012).

The lack of a clear relationship between local species richness and productivity also casts doubt on the role of productivity in determining diversity at the community level. Biomass production estimated from the NDVI or from allometric equations is a poorer predictor of local species richness of woody plants than minimum temperature or precipitation (Šímová et al. 2011), and neither biomass nor the number of individuals seem to be responsible for variation in the diversity of herbaceous vegetation (Šímová et al. 2013). Furthermore, productivity–diversity (or biomass–diversity) relationships of herbaceous vegetation are extremely variable (Gillman and Wright 2006, Adler et al. 2011, Fridley et al. 2012, Fraser et al. 2015), even though there are theoretical reasons to expect low species richness under very low and very high levels of productivity (Grime 1973, Tilman and Pacala 1993, Huston 2014). However, most of these examples concern the patterns of diversity of autotrophs, i.e. the trophic level that is itself responsible for productivity patterns. Productivity in this case does not represent the inflow of resources into a community of a given taxon, which could then be reflected (according to the More Individuals Hypothesis) in the number of individuals and species. Indeed, plant communities may be productive even if biomass production is realized by a few large individuals or a monospecific stand of a highly productive species. Local species richness of heterotrophs, by contrast, seems to follow NPP quite closely (Hurlbert 2004, Pautasso and Gaston 2005). The local productivity–diversity relationship thus depends not only on the used measure of productivity, but also on the trophic level considered (Groner and Novoplansky 2003).

Additionally, even if productivity positively affects species richness, it is questionable whether annual or seasonal NPP is more ecologically relevant for the diversity at higher trophic levels. Huston and Wolverton (2009) argue that when correcting for growing season length, NPP of the temperate zone is higher than tropical NPP (Körner 2006), and

Table 1. Summary statistics of species richness variation explained by various productivity measures or surrogates reported by Field et al. (2009), with additional data obtained from Cusens (2011). Only the continental extent (Cusens 2011) or the extent > 1000 km (Field et al. 2009) were considered. The number of studies is represented by n; AET is actual evapotranspiration, Temp represents temperature-related variables (mean annual or seasonal temperature or potential evapotranspiration), Prec represents precipitation-related variables (annual or seasonal precipitation or rainfall). NPP is represented by various models such as the Miami model (Lieth 1975), Chikugo (Uchijima and Seino 1985), Potsdam (Cramer et al. 1999) and CASA (Potter et al. 1993).

	n	Mean r^2	Standard deviation of r^2
AET	24	0.63	0.16
NPP	23	0.57	0.22
Temp	21	0.69	0.16
Prec	34	0.42	0.22
NDVI	8	0.38	0.15

they consider this 'corrected' NPP as ecologically more relevant than annual NPP. Seasonal NPP is certainly a more proper estimate of available resources for some taxa such as migratory birds (Hurlbert and Haskell 2003). Its relevance to species richness of other organisms is, however, neither theoretically founded nor empirically supported (Gillman et al. 2015). Current theory assumes that productivity promotes species richness by affecting the persistence of species with viable populations (Storch 2012), and this persistence probably depends even more on productivity levels in the low-productivity season (e.g. winter). However, this may be taxon-specific, depending on the food type, dormancy and life-history strategies, so it is still impossible to generalize.

Although it is clear that productivity is not the single determinant of species richness, and also probably not the most important one (Storch 2012), it is still possible that productivity limits the maximum number of species within regions or communities. In extreme environments, the total number of species must be limited by the maximum total number of individuals, which is at the same time tightly related to the total biomass. Or, using the words of E. Hutchinson (1959): "If the fundamental productivity of an area is limited by a short growing season to such a degree that the total biomass is less than under more favourable conditions, then the rarer species in a community may be so rare that they do not exist." However, when productivity reaches a certain level, other factors affecting species richness can prevail. The crucial factors driving diversity may vary in productive areas, explaining the inconsistency of the diversity–productivity patterns at high NPP levels. Still, if some NPP models explain species richness patterns better than other NPP estimates, focusing on the particular factors assumed to play a role in respective NPP models might prove useful. For instance, in the New World, MODIS-based NPP is highest in the foothills of the Andes (Zhao and Running 2010, Cleveland et al. 2015, Fig. 2b), probably due to the sensitivity of the MOD17 algorithm to variation in minimum temperature (Cleveland et al. 2015). The observation that species richness of mammals or birds also peaks in these regions (Storch et al. 2006, Ceballos and Ehrlich 2006, Hawkins et al. 2012; Fig. 2d) may thus reflect the dependence of species richness on minimum temperature without a necessary link to productivity. Alternatively, however, NPP can really be higher at higher elevations due to lower temperature-dependent respiration rates, and species richness patterns may be productivity-dependent. Such an effect could also potentially explain the lower species richness in humid tropical lowlands such as the centre of the Amazon basin or the Congo basin (Storch et al. 2006).

Generally, it is reasonable to assume that productivity limits species richness, but the limitation is probably strong only under low productivity levels. When productivity increases, other factors, such as long-term environmental stability or climate-dependent diversification rate, likely become more important for species richness. Therefore, there is no 'true relationship' between productivity and species richness, as the apparent relationship observed under higher NPP levels is likely driven by its covariation (or lack thereof) with other diversity-determining factors. To support this conclusion, we would need to employ tools that separate the effect of productivity from those of other factors. These tools would

have to include more accurate productivity measures and a proper theory that would allow to distinguish the effect of productivity from the effects of temperature and history/ stability (Storch 2012). Such a theory would need to explicitly address the dynamic links between resource levels, the total number of individuals and the number of species, as well as simultaneous effects of environment-dependent colonization/speciation and extinction rates on species richness. Furthermore, the role of productivity in the species richness patterns of autotrophs vs heterotrophs needs to be clarified, as does the relevance of growing season NPP compared to that of annual NPP.

Can we predict future changes of productivity patterns?

The uncertainties in DGVMs outputs have resulted in strongly divergent scenarios of future NPP changes. Many models predict a future increase of NPP (Cramer et al. 2001a, Hemming et al. 2013), namely in the humid tropics (Hemming et al. 2013, Zhang et al. 2015), while other models suggest a future decrease of tropical NPP (Goll et al. 2012, Wieder et al. 2015b). This disagreement is mostly due to the oversensitivity of some models to CO_2 concentrations (Rammig et al. 2010, Hickler et al. 2015), while neglecting other limiting factors (Fatichi et al. 2014, Smith et al. 2015). Experimental evidence shows that increasing CO_2 concentrations enhance photosynthesis, leading to higher productivity of C3 plants, particularly trees (Long et al. 2004, Ainsworth and Long 2005). Most models thus predict an increase in the rates of these processes in the near future (Rammig et al. 2010, Cox et al. 2013, Huntingford et al. 2013). The CO_2 fertilization effect is also assumed to enhance plant water use efficiency by reducing stomatal openings and consequently reducing plant transpiration rates (Drake et al. 1997, Kruijt et al. 2008), which would further increase NPP (Zhang et al. 2015). These predictions have been supported by evidence of recently increasing standing biomass and forest production (Pan et al. 2013), although this increase was not as strong as predicted by the models (Hickler et al. 2015, Smith et al. 2015). Moreover, CO_2 fertilization experiments were typically conducted in the temperate zone, especially in agricultural ecosystems, while experiments or observations from tropical and high-latitude ecosystems are missing (Long et al. 2004, Leakey et al. 2012).

In tropical forests, increasing CO_2 levels seem to lead mostly to allocation of biomass to more labile tissues such as fine roots and shoots (DeLucia et al. 2005, De Kauwe et al. 2014) and to elevated growth rates of short-lived species and shade-tolerant species such as lianas (Phillips et al. 2002, Körner 2006). This results in faster carbon turnover rates (Phillips and Gentry 1994, Körner 2006, Phillips et al. 2009). These effects can be a consequence of a lack of phosphorus, which limits the total amount of carbon that can be allocated to woody tissues (Hickler et al. 2015). Indeed, DGVMs incorporating the phosphorus cycle predict future NPP decreases (Goll et al. 2012, Wang et al. 2015, Wieder et al. 2015b). Moreover, models of future NPP changes only include potential NPP, without accounting for land use changes.

Box 2. How to improve NPP measurements and predictions?

The following recommendations are applicable for improving NPP estimates:

- Global NPP models should incorporate nutrient limitation, especially by phosphorus for tropical sites.
- Field data should clearly distinguish plantations and artificially fertilized sites from natural vegetation.
- Field data should be standardized with regard to different methods of biomass estimation and the successional stage.
- Up-scaling techniques should be developed that would take local measurements as the basis for the large-scale estimates. This can be done by combining remote sensing with maps of local environmental variables (Zheng et al. 2003, Avitabile et al. 2016) and a stratified design of field NPP measurements.
- Plant functional traits that are related to biomass production (such as plant height or specific leaf area; West et al. 2009, Enquist et al. 2009, 2015) should be utilized to provide independent estimates of biomass production.
- Species responses should be modelled based on plant functional traits without relying on simplified plant functional types (Van Bodegom et al. 2012, Wullschleger et al. 2014). However, this might prove problematic, as the responses of different plants (that have different traits) to environmental gradients and climate change is still largely unknown.
- Human land use should become routinely used in global NPP models, particularly in models that predict future NPP.
- More attention should be paid to non-forest vegetation, which has been largely underrepresented in all large-scale studies dealing with productivity.

In summary, current productivity models cannot reliably predict future changes in NPP, because they are unable to account simultaneously for multiple limiting factors that can vary geographically. In order to better parameterize the models, experiments simultaneously manipulating the levels of CO_2 and nutrients should be conducted across different biomes. To make the predictions realistic, much more attention should also be paid to land-use changes (such as deforestation in the tropics) and their feedback on to the carbon cycle and biomass production (Spracklen et al. 2012, Wieder et al. 2015b).

Conclusion and synthesis

Although there have been arguments that terrestrial productivity should not decrease monotonically from the equator towards the poles and should instead reach maximum values in the temperate zones (Huston and Wolverton 2009, Huston 2012), field NPP measurements as well as most models indicate the existence of a monotonically decreasing latitudinal productivity gradient. Still, the model outputs considerably differ from each other and also from field measurements. Both field measurements and NPP models have specific problems, stemming mostly from the underrepresentation of the tropical zone in terms of the lack of field measurements and insufficient accounting of the limiting factors in the tropics. In order to draw a proper picture of geographic NPP variation and predict future NPP changes, it is necessary to refine both the models and the field measurements (Box 2). In particular, we encourage future studies to focus on the gap between the scale of field NPP measurements and that of the models. One way to bridge this gap would be to parameterize remote sensing-based NPP models by local NPP measurement, including data on soil parameters. Such a procedure will necessarily include a robust stratified sampling scheme for obtaining field NPP measurements that would also cover non-forest sites as well as various disturbed habitats.

Fortunately, the large-scale relationship between productivity and species diversity is not particularly sensitive to the exact way NPP is estimated, as the NPP model outputs are mostly correlated with each other and reveal a latitudinal gradient that is similar to the diversity gradient. The covariance of NPP with many other variables, including temperature and actual evapotranspiration, at the same time poses a problem, as it is difficult to distinguish the pure effect of productivity (i.e. resource input into the community) from the effect of temperature and history (environmental stability), which could have affected species richness via different processes. So far, none of the NPP estimates are accurate enough to unequivocally distinguish the importance of productivity from the importance of other effects. To address this issue, it is necessary to develop a proper theory that would encompass the effect of productivity simultaneously with the other factors potentially affecting species richness, namely temperature (which potentially affects speciation rates as well as species coexistence) and environmental variability/stability (which, besides productivity-dependent population sizes, affects population extinction rates). Additionally, it is necessary to refine the methods of measuring all these variables (including NPP) in a way that will allow us to distinguish the roles of the abovementioned factors.

References

Adams, J. M. and Woodward, F. I. 1989. Patterns in tree species richness as a test of the glacial extinction hypothesis. – Nature 339: 699–701.

Adler, P. B. et al. 2011. Productivity is a poor predictor of plant species richness. – Science 333: 1750–1753.

Ainsworth, E. A. and Long, S. P. 2005. What have we learned from 15 years of free-air CO_2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO_2. – New Phytol. 165: 351–372.

Allen, A. P. et al. 2002. Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. – Science 297: 1545–1548.

Allen, A. P. et al. 2005. Linking the global carbon cycle to individual metabolism. – Funct. Ecol. 19: 202–213.

Aragão, L. et al. 2009. Above-and below-ground net primary productivity across ten Amazonian forests on contrasting soils. – Biogeosciences 6: 2759–2778.

Avissar, R. et al. 2002. The large-scale biosphere–atmosphere experiment in Amazonia (LBA): insights and future research needs. – J. Geophys. Res. Atmospheres 107: 7499–7518.

Avitabile, V. et al. 2016. An integrated pan-tropical biomass map using multiple reference datasets. – Global Change Biol. 22: 1406–1420.

Belmaker, J. and Jetz, W. 2011. Cross-scale variation in species richness–environment associations. – Global Ecol. Biogeogr. 20: 464–474.

Box, E. O. et al. 1989. Accuracy of the AVHRR vegetation index as a predictor of biomass, primary productivity and net CO_2 flux. – Vegetatio 80: 71–89.

Brovkin, V. et al. 2002. Carbon cycle, vegetation, and climate dynamics in the Holocene: Experiments with the CLIMBER-2 model. – Global Biogeochem. Cycles 16: 1139.

Brown, J. H. 2014. Why are there so many species in the tropics? – J. Biogeogr. 41: 8–22.

Brown, J. H. et al. 2004. Toward a metabolic theory of ecology. – Ecology 85: 1771–1789.

Buckley, L. B. and Jetz, W. 2007. Environmental and historical constraints on global patterns of amphibian richness. – Proc. R. Soc. B 274: 1167–1173.

Cannell, M. G. R. 1982. World forest biomass and primary production data. – Academic Press.

Ceballos, G. and Ehrlich, P. R. 2006. Global mammal distributions, biodiversity hotspots, and conservation. – Proc. Natl Acad. Sci. USA 103: 19374–19379.

Chase, J. M. and Leibold, M. A. 2003. Ecological niches: linking classical and contemporary approaches. – Univ. of Chicago Press.

Clark, D. A. et al. 2001. Net primary production in tropical forests: an evaluation and synthesis of existing field data. – Ecol. Appl. 11: 371–384.

Clark, D. A. et al. 2003. Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. – Proc. Natl Acad. Sci. USA 100: 5852–5857.

Cleveland, C. C. et al. 2015. A comparison of plot-based, satellite and Earth system model estimates of tropical forest net primary production. – Global Biogeochem. Cycles 29: 626–644.

Cox, P. M. et al. 2013. Sensitivity of tropical carbon to climate change constrained by carbon dioxide variability. – Nature 494: 341–344.

Cramer, W. and Field, C. B. 1999. Comparing global models of terrestrial net primary productivity (NPP): introduction. – Global Change Biol. 5: 3–4.

Cramer, W. et al. 1999. Comparing global models of terrestrial net primary productivity (NPP): overview and key results. – Global Change Biol. 5: 1–15.

Cramer, W. et al. 2001a. Global response of terrestrial ecosystem structure and function to CO_2 and climate change: results from six dynamic global vegetation models. – Global Change Biol. 7: 357–373.

Cramer, W. et al. 2001b. Determining present patterns of global productivity. – In: Roy, J. et al. (eds), Terrestrial global productivity. Academic Press, pp. 429–448.

Currie, D. J. 1991. Energy and large-scale patterns of animal- and plant-species richness. – Am. Nat. 137: 27–49.

Currie, D. J. et al. 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. – Ecol. Lett. 7: 1121–1134.

Cusens, J. 2011. What is the relationship between productivity and animal species richness? A critical review and meta-analysis. – PhD thesis, Auckland Univ. of Technology.

Cusens, J. et al. 2012. What is the form of the productivity–animal-species-richness relationship? A critical review and meta-analysis. – Ecology 93: 2241–2252.

Danilin, I. 1995. Structure and biomass of larch stands regenerating naturally after clearcut logging. – Water. Air Soil Pollut. 82: 125–131.

De Kauwe, M. G. et al. 2014. Where does the carbon go? A model–data intercomparison of vegetation carbon allocation and turnover processes at two temperate forest free-air CO_2 enrichment sites. – New Phytol. 203: 883–899.

DeLucia, E. H. et al. 2005. Contrasting responses of forest ecosystems to rising atmospheric CO_2: implications for the global C cycle. – Global Biogeochem. Cycles 19: GB3006.

Dietze, M. C. 2014. Gaps in knowledge and data driving uncertainty in models of photosynthesis. – Photosynth. Res. 119: 3–14.

Drake, B. G. et al. 1997. M: a consequence of rising atmospheric CO_2? – Annu. Rev. Plant Physiol. Plant Mol. Biol. 48: 609–639.

Enquist, B. J. et al. 2009. Extensions and evaluations of a general quantitative theory of forest structure and dynamics. – Proc. Natl Acad. Sci. USA 106: 7046–7051.

Enquist, B. J. et al. 2015. Scaling from traits to ecosystems: developing a general trait driver theory via integrating trait-based and metabolic scaling theories. – Adv. Ecol. Res. 52: 249–318.

Esser, G. 1994. High resolution biosphere model: documentation. Model version 3.00. 00. – <http://ecobas.org/www-server/rem/mdb/hrbm.html>.

Fatichi, S. et al. 2014. Moving beyond photosynthesis: from carbon source to sink-driven vegetation modeling. – New Phytol. 201: 1086–1095.

Field, R. et al. 2009. Spatial species-richness gradients across scales: a meta-analysis. – J. Biogeogr. 36: 132–147.

Francis, A. P. and Currie, D. J. 2003. A globally consistent richness-climate relationship for angiosperms. – Am. Nat. 161: 523–536.

Fraser, L. H. et al. 2015. Worldwide evidence of a unimodal relationship between productivity and plant species richness. – Science 349: 302–305.

Fridley, J. D. et al. 2012. Comment on 'Productivity is a poor predictor of plant species richness'. – Science 335: 1441–1441.

Friend, A. D. et al. 1997. A process-based, terrestrial biosphere model of ecosystem dynamics (Hybrid v3. 0). – Ecol. Model. 95: 249–287.

Gaston, K. J. 2000. Global patterns in biodiversity. – Nature 405: 220–227.

Gaston, K. J. and Blackburn, T. M. 1995. Mapping biodiversity using surrogates for species richness: macro-scales and new world birds. – Proc. R. Soc. B 262: 335–341.

Gillman, L. N. and Wright, S. D. 2006. The influence of productivity on the species richness of plants: a critical assessment. – Ecology 87: 1234–1243.

Gillman, L. N. and Wright, S. D. 2014. Species richness and evolutionary speed: the influence of temperature, water and area. – J. Biogeogr. 41: 39–51.

Gillman, L. N. et al. 2015. Latitude, productivity and species richness. – Glob. Ecol. Biogeogr. 24: 107–117.

Goetz, S. J. et al. 2014. The relative importance of climate and vegetation properties on patterns of North American breeding bird species richness. – Environ. Res. Lett. 9: 34013.

Goll, D. S. et al. 2012. Nutrient limitation reduces land carbon uptake in simulations with a model of combined carbon,

nitrogen and phosphorus cycling. – Biogeosciences 9: 3547–3569.

Goward, S. N. and Dye, D. G. 1987. Evaluating North American net primary productivity with satellite observations. – Adv. Space Res. 7: 165–174.

Grace, J. B. et al. 2012. Response to comments on 'Productivity is a poor predictor of plant species richness'. – Science 335: 1441–1441.

Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. – Nature 242: 344–347.

Groner, E. and Novoplansky, A. 2003. Reconsidering diversity–productivity relationships: directness of productivity estimates matters. – Ecol. Lett. 6: 695–699.

Haberl, H. et al. 2007. Quantifying and mapping the human appropriation of net primary production in earth's terrestrial ecosystems. – Proc. Natl Acad. Sci. USA 104: 12942–12947.

Hawkins, B. A. et al. 2003. Energy, water, and broad-scale geographic patterns of species richness. – Ecology 84: 3105–3117.

Hawkins, B. A. et al. 2012. Different evolutionary histories underlie congruent species richness gradients of birds and mammals. – J. Biogeogr. 39: 825–841.

Hemming, D. et al. 2013. Sensitivity and uncertainty of modelled terrestrial net primary productivity to doubled CO_2 and associated climate change for a relatively large perturbed physics ensemble. – Agricult. For. Meteorol. 170: 79–88.

Hickler, T. et al. 2008. CO_2 fertilization in temperate FACE experiments not representative of boreal and tropical forests. – Global Change Biol. 14: 1531–1542.

Hickler, T. et al. 2015. Modelling CO_2 impacts on forest productivity. – Curr. For. Rep. 1: 69–80.

Hijmans, R. J. et al. 2005. Very high resolution interpolated climate surfaces for global land areas. – Int. J. Climatol. 25: 1965–1978.

Huete, A. et al. 2002. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. – Remote Sens. Environ. 83: 195–213.

Huntingford, C. et al. 2013. Simulated resilience of tropical rainforests to CO_2-induced climate change. – Nat. Geosci. 6: 268–273.

Hurlbert, A. H. 2004. Species–energy relationships and habitat complexity in bird communities. – Ecol. Lett. 7: 714–720.

Hurlbert, A. H. and Haskell, J. P. 2003. The effect of energy and seasonality on avian species richness and community composition. – Am. Nat. 161: 83–97.

Hurlbert, A. H. and Stegen, J. C. 2014. When should species richness be energy limited, and how would we know? – Ecol. Lett. 17: 401–413.

Huston, M. A. 2012. Precipitation, soils, NPP, and biodiversity: resurrection of Albrecht's curve. – Ecol. Monogr. 82: 277–296.

Huston, M. A. 2014. Disturbance, productivity, and species diversity: empiricism vs logic in ecological theory. – Ecology 95: 2382–2396.

Huston, M. A. and Wolverton, S. 2009. The global distribution of net primary production: resolving the paradox. – Ecol. Monogr. 79: 343–377.

Hutchinson, G. E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? – Am. Nat. 93: 145–159.

Imhoff, M. L. et al. 2004. Global patterns in human consumption of net primary production. – Nature 429: 870–873.

Jenkins, J. P. et al. 2007. Refining light-use efficiency calculations for a deciduous forest canopy using simultaneous tower-based carbon flux and radiometric measurements. – Agricult. For. Meteorol. 143: 64–79.

Jetz, W. and Fine, P. V. A. 2012. Global gradients in vertebrate diversity predicted by historical area–productivity dynamics and contemporary environment. – PLoS Biol. 10: e1001292.

Kattge, J. et al. 2011. TRY – a global database of plant traits. – Global Change Biol. 17: 2905–2935.

Keil, P. et al. 2008. Water-energy and the geographical species richness pattern of European and North African dragonflies (Odonata). – Insect Conserv. Divers. 1: 142–150.

Kerkhoff, A. J. et al. 2005. Plant allometry, stoichiometry and the temperature-dependence of primary productivity. – Global Ecol. Biogeogr. 14: 585–598.

Körner, C. 2006. Plant CO_2 responses: an issue of definition, time and resource supply. – New Phytol. 172: 393–411.

Kruijt, B. et al. 2008. Effects of rising atmospheric CO_2 on evapotranspiration and soil moisture: a practical approach for the Netherlands. – J. Hydrol. 349: 257–267.

Laanisto, L. et al. 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 Ecol. Biogeogr. 17: 320–326.

Lamanna, C. et al. 2014. Functional trait space and the latitudinal diversity gradient. – Proc. Natl Acad. Sci. USA 111: 13745–13750.

Latham, R. E. and Ricklefs, R. E. 1993. Global patterns of tree species richness in moist forests: energy-diversity theory does not account for variation in species richness. – Oikos 67: 325–333.

Leakey, A. D. B. et al. 2012. A multi-biome gap in understanding of crop and ecosystem responses to elevated CO_2. – Curr. Opin. Plant Biol. 15: 228–236.

Lee, J.-E. et al. 2012. Reduction of tropical land region precipitation variability via transpiration. – Geophys. Res. Lett. 39: L19704.

Lee, J.-E. et al. 2013. Forest productivity and water stress in Amazonia: observations from GOSAT chlorophyll fluorescence. – Proc. R. Soc. B 280: 20130171.

Lieth, H. 1975. Modeling the primary productivity of the world. – In: Lieth, H. and Whittaker, R. H. (eds), Primary productivity of the biosphere. Springer, pp. 237–263.

Lloyd, J. et al. 2015. Edaphic, structural and physiological contrasts across Amazon Basin forest–savanna ecotones suggest a role for potassium as a key modulator of tropical woody vegetation structure and function. – Biogeosciences 12: 6529–6571.

Lo Seen Chong, D. et al. 1993. Relating the global vegetation index to net primary productivity and actual evapotranspiration over Africa. – Int. J. Remote Sens. 14: 1517–1546.

Long, S. P. et al. 2004. Rising atmospheric carbon dioxide: plants FACE the future. – Annu. Rev. Plant Biol. 55: 591–628.

Luyssaert, S. et al. 2007. CO_2 balance of boreal, temperate, and tropical forests derived from a global database. – Global Change Biol. 13: 2509–2537.

Malhi, Y. 2012. The productivity, metabolism and carbon cycle of tropical forest vegetation. – J. Ecol. 100: 65–75.

Malhi, Y. et al. 2002. Forests, carbon and global climate. – Phil. Trans. R. Soc. Lond. Math. Phys. Eng. Sci. 360: 1567–1591.

Malhi, Y. et al. 2015. The linkages between photosynthesis, productivity, growth and biomass in lowland Amazonian forests. – Global Change Biol. 21: 2283–2295.

McBride, P. D. et al. 2014. Revisiting spatial scale in the productivity–species richness relationship: fundamental issues and global change implications. – AoB Plants 6: plu057.

McCallum, I. et al. 2009. Satellite-based terrestrial production efficiency modeling. – Carbon Balance Manage. 4: 8.

Michaletz, S. T. et al. 2014. Convergence of terrestrial plant production across global climate gradients. – Nature 215: 39–43.

Michaletz, S. T. et al. 2015. Plant thermoregulation: energetics, trait–environment interactions, and carbon economics. – Trends Ecol. Evol. 30: 714–724.

Mittelbach, G. G. et al. 2001. What is the observed relationship between species richness and productivity? – Ecology 82: 2381–2396.

Monteith, J. L. 1972. Solar radiation and productivity in tropical ecosystems. – J. Appl. Ecol. 9: 747–766.

Ni, J. 2003. Net primary productivity in forests of China: scaling-up of national inventory data and comparison with model predictions. – For. Ecol. Manage. 176: 485–495.

Olson, R. J. et al. 2001. Global and regional ecosystem modeling: databases of model drivers and validation measurements. – ORNL Tech. Memo. TM-2001196 Oak Ridge Natl. Lab. Oak Ridge Tenn.

Olson, R. J. et al. 2013. NPP Multi-Biome: Global Primary Production Data Initiative Products, R2. Data Set. – <www.daac.ornl.gov>.

Pan, Y. et al. 2013. The structure, distribution, and biomass of the world's forests. – Annu. Rev. Ecol. Evol. Syst. 44: 593–622.

Pappas, C. et al. 2016. Modeling terrestrial carbon and water dynamics across climatic gradients: does plant trait diversity matter? – New Phytol. 209: 137–151.

Pärtel, M. et al. 2007. Contrasting plant productivity-diversity relationships across latitude: the role of evolutionary history. – Ecology 88: 1091–1097.

Pautasso, M. and Gaston, K. J. 2005. Resources and global avian assemblage structure in forests. – Ecol. Lett. 8: 282–289.

Peng, C. H. et al. 1995. The variation of terrestrial carbon storage at 6000 yr bp in Europe: reconstruction from pollen data using two empirical biosphere models. – J. Biogeogr. 22: 863–873.

Phillips, O. L. and Gentry, A. H. 1994. Increasing turnover through time in tropical forests. – Science 263: 954–958.

Phillips, O. L. et al. 2002. Increasing dominance of large lianas in Amazonian forests. – Nature 418: 770–774.

Phillips, O. L. et al. 2009. Drought sensitivity of the Amazon rainforest. – Science 323: 1344–1347.

Phillips, L. B. et al. 2010. Applying species–energy theory to conservation: a case study for North American birds. – Ecol. Appl. 20: 2007–2023.

Potter, C. S. et al. 1993. Terrestrial ecosystem production: a process model based on global satellite and surface data. – Global Biogeochem. Cycles 7: 811–841.

Potter, C. et al. 2012. Net primary production of terrestrial ecosystems from 2000 to 2009. – Clim. Change 115: 365–378.

Qian, H. 2010. Environment–richness relationships for mammals, birds, reptiles, and amphibians at global and regional scales. – Ecol. Res. 25: 629–637.

Quesada, C. A. et al. 2009. Regional and large-scale patterns in Amazon forest structure and function are mediated by variations in soil physical and chemical properties. – Biogeosci. Discuss. 6: 3993–4057.

Quesada, C. A. et al. 2012. Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. – Biogeosciences 9: 2203–2246.

Rammig, A. et al. 2010. Estimating the risk of Amazonian forest dieback. – New Phytol. 187: 694–706.

Ricklefs, R. E. 2012. Species richness and morphological diversity of passerine birds. – Proc. Natl Acad. Sci. USA 109: 14482–14487.

Rohde, K. 1992. Latitudinal gradients in species diversity: the search for the primary cause. – Oikos: 514–527.

Rosenzweig, M. L. 1968. Net primary productivity of terrestrial communities: prediction from climatological data. – Am. Nat. 102: 67–74.

Ruimy, A. et al. 1994. Methodology for the estimation of terrestrial net primary production from remotely sensed data. – J. Geophys. Res. Atmospheres 99: 5263–5283.

Ruimy, A. et al. 1996. TURC: A diagnostic model of continental gross primary productivity and net primary productivity. – Global Biogeochem. Cycles 10: 269–285.

Ruimy, A. et al. 1999. Comparing global models of terrestrial net primary productivity (NPP): analysis of differences in light absorption and light-use efficiency. – Global Change Biol. 5: 56–64.

Running, S. W. et al. 2004. A continuous satellite-derived measure of global terrestrial primary production. – BioScience 54: 547–560.

Sánchez-Azofeifa, G. A. et al. 2009. Differences in leaf traits, leaf internal structure, and spectral reflectance between two communities of lianas and trees: implications for remote sensing in tropical environments. – Remote Sens. Environ. 113: 2076–2088.

Scheiter, S. et al. 2013. Next-generation dynamic global vegetation models: learning from community ecology. – New Phytol. 198: 957–969.

Schemske, D. W. 2002. Ecological and evolutionary perspectives on the origins of tropical diversity. – In: Chazdon, R. L. and Whitmore, T. C. (eds), Foundations of tropical forest biology: classic papers with commentaries. Univ. of Chicago Press, pp. 163–173.

Šímová, I. et al. 2011. Global species–energy relationship in forest plots: role of abundance, temperature and species climatic tolerances. – Global Ecol. Biogeogr. 20: 842–856.

Šímová, I. et al. 2013. Relationship between species richness and productivity in plants: the role of sampling effect, heterogeneity and species pool. – J. Ecol. 101: 161–170.

Šímová, I. et al. 2015. Shifts in trait means and variances in North American tree assemblages: species richness patterns are loosely related to the functional space. – Ecography 38: 649–658.

Sitch, S. et al. 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. – Global Change Biol. 9: 161–185.

Smith, K. W. et al. 2015. Large divergence of satellite and Earth system model estimates of global terrestrial CO_2 fertilization. – Nat. Clim. Change 6: 306–310.

Spracklen, D. V. et al. 2012. Observations of increased tropical rainfall preceded by air passage over forests. – Nature 489: 282–285.

Srivastava, D. S. and Lawton, J. H. 1998. Why more productive sites have more species: an experimental test of theory using tree-hole communities. – Am. Nat. 152: 510–529.

Storch, D. 2012. Biodiversity and its energetic and thermal controls. – In: Sibly, R. M. et al. (eds), Metabolic ecology. John Wiley & Sons, pp. 120–131.

Storch, D. et al. 2006. Energy, range dynamics and global species richness patterns: reconciling mid-domain effects and environmental determinants of avian diversity. – Ecol. Lett. 9: 1308–1320.

Thornthwaite, C. W. 1948. An approach toward a rational classification of climate. – Geogr. Rev. 38: 55–94.

Tilman, D. and Pacala, S. 1993. The maintenance of species richness in plant communities. – Species Divers. Ecol. Commun. 13–25.

Turner, D. P. et al. 2002. Effects of spatial variability in light use efficiency on satellite-based NPP monitoring. – Remote Sens. Environ. 80: 397–405.

Turner, D. P. et al. 2005. Site-level evaluation of satellite-based global terrestrial gross primary production and net primary production monitoring. – Glob. Change Biol. 11: 666–684.

Turner, D. P. et al. 2006. Evaluation of MODIS NPP and GPP products across multiple biomes. – Remote Sens. Environ. 102: 282–292.

Uchijima, Z. and Seino, H. 1985. Agroclimatic evaluation of net primary productivity of natural vegetation. (1) Chikugo model for evaluating net primary productivity. – J. Agr. Met. 40: 343–352.

Van Bodegom, P. M. et al. 2012. Going beyond limitations of plant functional types when predicting global ecosystem–atmosphere

fluxes: exploring the merits of traits-based approaches. – Global Ecol. Biogeogr. 21: 625–636.

Vogt, K. A. et al. 1987. Conifer and angiosperm fine-root biomass in relation to stand age and site productivity in Douglas-fir forests. – J. Ecol. 75: 857–870.

Waide, R. B. et al. 1999. The relationship between productivity and species richness. – Annu. Rev. Ecol. Syst. 30: 257–300.

Walker, A. P. et al. 2015. Predicting long-term carbon sequestration in response to CO_2 enrichment: how and why do current ecosystem models differ? – Glob. Biogeochem. Cycles 29: 476–495.

Wang, Y. et al. 2005. Holocene climate and carbon cycle dynamics: experiments with the "green" McGill paleoclimate model. – Global Biogeochem. Cycles 19: GB3022.

Wang, Y.-P. et al. 2015. Nitrogen and phosphorous limitation reduces the effects of land use change on land carbon uptake or emission. – Environ. Res. Lett. 10: 14001.

West, G. B. et al. 2009. A general quantitative theory of forest structure and dynamics. – Proc. Natl Acad. Sci. USA 106: 7040–7045.

Wieder, W. R. et al. 2015a. Effects of model structural uncertainty on carbon cycle projections: biological nitrogen fixation as a case study. – Environ. Res. Lett. 10: 44016.

Wieder, W. R. et al. 2015b. Future productivity and carbon storage limited by terrestrial nutrient availability. – Nat. Geosci. 8: 441–444.

Wiens, J. J. and Donoghue, M. J. 2004. Historical biogeography, ecology and species richness. – Trends Ecol. Evol. 19: 639–644.

Wilson, A. M. et al. 2014. Systematic land cover bias in collection 5 MODIS cloud mask and derived products – a global overview. – Remote Sens. Environ. 141: 149–154.

Wright, D. H. 1983. Species-energy theory: an extension of species-area theory. – Oikos: 496–506.

Wright, S. J. et al. 2011. Potassium, phosphorus, or nitrogen limit root allocation, tree growth, or litter production in a lowland tropical forest. – Ecology 92: 1616–1625.

Wullschleger, S. D. et al. 2014. Plant functional types in Earth system models: past experiences and future directions for application of dynamic vegetation models in high-latitude ecosystems. – Ann. Bot. 114: 1–16.

Yang, X. et al. 2013. The distribution of soil phosphorus for global biogeochemical modeling. – Biogeosciences 10: 2525–2537.

Zaks, D. P. M. et al. 2007. From Miami to Madison: investigating the relationship between climate and terrestrial net primary production. – Global Biogeochem. Cycles 21: GB3004.

Zhang, K. et al. 2015. The fate of Amazonian ecosystems over the coming century arising from changes in climate, atmospheric CO_2, and land use. – Global Change Biol. 21: 2569–2587.

Zhao, M. and Running, S. W. 2010. Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. – Science 329: 940–943.

Zhao, M. et al. 2005. Improvements of the MODIS terrestrial gross and net primary production global data set. – Remote Sens. Environ. 95: 164–176.

Zheng, D. et al. 2003. Terrestrial net primary production estimates for 0.5° grid cells from field observations – a contribution to global biogeochemical modeling. – Global Change Biol. 9: 46–64.

Zhou, G. and Zhang, X. 1995. A natural vegetation NPP model. – Acta Phytoecol. Sin. 19: 193–200.

Zhou, G. et al. 2002. Estimating biomass and net primary production from forest inventory data: a case study of China's Larix forests. – For. Ecol. Manage. 169: 149–157.