General allometric scaling of net primary production agrees with plant adaptive strategy theory and has tipping points

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Summary

1. Allometric scaling of net primary production (NPP) with plant biomass (B) is important to ecological carbon dynamics and energetics. Metabolic theory predicts a nonlinear power law for NPP scaling, based on fractal vascular systems, resulting in a linear model when using log NPP/log B axes that are standard in allometry. Alternatively, two other hypotheses predict nonlinear models for log-transformed data, with potential tipping points. Size-based competition may cause a quadratic curve as larger plants limit NPP by smaller plants. More inclusively, the plant adaptive strategies hypothesis predicts a sigmoidal curve to represent those same competitive effects, plus stress and ruderal adaptations that maintain relatively low NPP in habitats that are abiotically limiting or disturbed.

2. We evaluated all three hypotheses for terrestrial vascular plants, using information theoretic model selection based on the Akaike Information Criterion (AICc). Published data ($N = 709$) were organised in subsets according to reported organisational level and plant growth form. Alternative curves were compared for a general model (using all data) and per subset. Potential tipping points were estimated using segmented regression.

3. The plant adaptive strategies hypothesis was supported in general (AICc weight = 1·00) and via internal consistency for five of six subsets (86% of data). Competition was supported as affecting NPP at greater B, where quadratic and sigmoidal models often coincided. Only non-woody assemblages most plausibly fit a power law model, perhaps related to sparse data at lowest B.

4. *Synthesis.* Adaptive strategies and corresponding environmental conditions appear to constrain terrestrial net primary production scaling relative to metabolic theory's ideal. Moreover, tipping points in general nonlinear net primary production scaling (at c. 38 and 360 g m^{-2} B) indicate thresholds for rapid changes in net primary production given changing B that occurs via changing climate, human appropriation and land use.

Key-words: biomass, competition, CSR theory, metabolic theory, nonlinear allometry, NPP, ruderal, stress-tolerant

Introduction

Net primary production (NPP; g dry mass m^{-2} year^{-1}) is a summary measure of plant growth, which drives energetics and carbon cycling for most of the world's ecosystems, and is the source of many renewable resources and a vital pathway to reduce global atmospheric CO_2 levels. Though sometimes considered an ecosystem property, NPP is also measured for other hierarchical levels of organisation (i.e., populations, communities and biomes). One way to estimate NPP is to use an allometric scaling relationship (hereafter called NPP scaling) where NPP is a function of biomass (B; g dry mass m^{-2}). Allometry is the study of relationships among different measures of organisms, typically using body size as a predictor. Logarithmic transformations are used for multiple reasons, including a theoretical expectation for multiplicative growth and practical compliance with regression assumptions (Kerkhoff & Enquist 2009; Jenkins 2015). A power law has been the sole method to describe NPP scaling and generates a linear model in log-log space (e.g., Kerkhoff & Enquist 2006; Coomes, Lines & Allen 2011; Lin *et al.* 2013; Michaletz *et al.* 2014; Hatton *et al.* 2015; Jenkins 2015).

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Two problems exist for NPP scaling and are addressed here. First, multiple working hypotheses to explain the general NPP scaling shape have not been empirically evaluated. Rather, all NPP scaling research has used a single function, the power law model based on the Metabolic Theory of Ecology (Brown *et al.* 2004a,b), even if coefficients have been predicted to shift due to other factors (e.g., Kerkhoff & Enquist 2006; Coomes, Lines & Allen 2011; Lin *et al.* 2013; Michaletz *et al.* 2014; Hatton *et al.* 2015; Jenkins 2015). As fruitful as this research has been, it is not yet based on strong inference because alternative models – based on alternative hypotheses – have not been compared (Platt 1964; Burnham & Anderson 2002; McGill, Maurer & Weiser 2006). Second, a general NPP scaling model (i.e., across all systems and the full range of NPP and B) does not yet exist. Instead, separate NPP scaling models exist for separate systems (e.g., forest stands, grasslands), all using power laws but reporting model coefficients unique to each data set (Kerkhoff & Enquist 2006; Coomes, Lines & Allen 2011; Lin *et al.* 2013; Michaletz *et al.* 2014; Hatton *et al.* 2015; Jenkins 2015). A general NPP scaling model would be fundamentally valuable for ecology, for which even the existence of a unifying theory and general, predictive models has long been debated (e.g., Hairston 1989; Peters 1991; Lawton 1999; Brown *et al.* 2004b; Dodds 2009).

Three hypotheses help to predict the shape of allometric scaling for NPP and are summarised below in order of increasing complexity. Because two of the hypotheses predict nonlinear NPP scaling, tipping points are also briefly introduced (Scheffer *et al.* 2009; Hughes *et al.* 2013; Reyer *et al.* 2015; van Nes *et al.* 2016).

METABOLIC THEORY OF ECOLOGY

The Metabolic Theory of Ecology (MTE) has been an important basis for allometric NPP scaling, and is based on an *ideal*, fractally structured system (Enquist, Brown & West 1998; West, Brown & Enquist 1999; Niklas & Enquist 2001; Brown *et al.* 2004a; Enquist, West & Brown 2009; West, Enquist & Brown 2009). According to MTE, a power law (NPP = aB^b) is expected for NPP scaling, where a linear model (i.e., log NPP = $a + b$(log B)) describes the relationship in log-log space (Fig. 1; West, Enquist & Brown 2009; Enquist, West & Brown 2009).

In part because MTE represents ideal systems and has been controversial (Isaac & Carbone 2010; Glazier 2014, 2015), MTE-based allometric scaling research has rapidly evolved to recognise that multiple predictor variables also apply. However, MTE-based analyses continue to use only the power law model described above (e.g., Kerkhoff & Enquist 2006; Agutter & Tuszynski 2011; Coomes, Lines & Allen 2011; Glazier *et al.* 2011; Lin *et al.* 2013; Michaletz *et al.* 2014; Glazier 2015; Hatton *et al.* 2015; Jenkins 2015). This history is analogous to that for biogeographical species-area relationships. Both subjects initially focused on bivariate power laws, followed by debate on an ideal (or canonical) power law exponent *b*, and then recognition that coefficient *a* and other predictors are important to their respective response variables
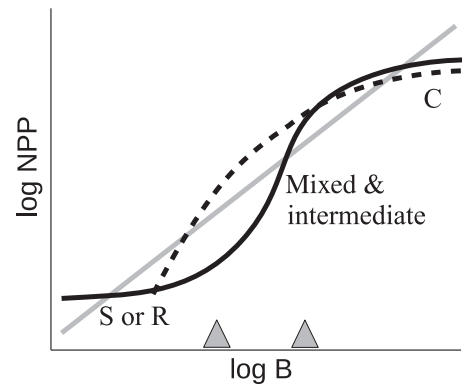

Fig. 1. Three hypothesised net primary production (NPP) scaling models. The metabolic theory of ecology predicts that an ideal system will have a linear model in log-log space (grey line; West, Enquist & Brown 2009; Enquist, West & Brown 2009). The asymmetric size-based competition hypothesis (Kerkhoff & Enquist 2006) is interpreted here as predicting a quadratic function (dashed line), where NPP is constrained at greater B. Universal Adaptive Strategy Theory (Grime & Pierce 2012) is interpreted here as predicting a sigmoidal function (solid black line), where competitive strategies (C) match the upper competition prediction and stress-tolerant (S) or ruderal (R) strategies predict a lower asymptote. In between, a mixture of strategies and their intermediates (e.g., CR) predict steep NPP scaling. Hypothetical tipping points are indicated by triangles.

(Rosenzweig 1995; Lomolino 2000). Moving forward, allometric analyses of animals have recently included other explanatory factors beyond MTE-based theoretical ideals, including size-inefficiency trade-offs and predation risk (Kolokotrones, Van Savage & Fontana 2010; Glazier *et al.* 2011; Glazier 2015). For vegetation-related analyses, factors such as competition, site conditions, and disturbance are recognised to modify MTE-based expectations but that knowledge has not yet translated to general NPP scaling hypotheses that transcend the simple linear model above (Coomes & Allen 2007; Coomes, Lines & Allen 2011; Coomes *et al.* 2012; Lin *et al.* 2013).

COMPETITION

In general, negative biotic interactions (e.g., predation, competition) may constrain realised allometric scaling of metabolism and growth relative to an unfettered MTE ideal (Kerkhoff & Enquist 2006; Coomes, Lines & Allen 2011; Glazier *et al.* 2011; Lin *et al.* 2013). Specifically with regard to NPP, larger plants are predicted to competitively reduce NPP of smaller plants and thus constrain MTE-based NPP scaling (Kerkhoff & Enquist 2006; Coomes & Allen 2007; Coomes, Lines & Allen 2011; Lin *et al.* 2013). If analyses are restricted to a bivariate power law, the effect translates to a greater *a* coefficient and a reduced *b* coefficient (Kerkhoff & Enquist 2006; Lin *et al.* 2013). However, a quadratic equation *in log-log space* (i.e., log NPP = $a + b \log(B) - c(\log B)^2$) may better describe competitive effects because it represents the positive effect of B on NPP expected by MTE (the '+ $b \log(B)$' component) and the competitive effects by larger plants (the '$- c(\log B)^2$' component). A negative *c* coefficient would be

consistent with a downward deflection due to competition, whereas a positive *c* coefficient would represent a concave upward (i.e., U-shaped) curve relative to a power law (e.g., Kolokotrones, Van Savage & Fontana 2010). Importantly, the quadratic model is the next most parsimonious model beyond the linear (in log-log space) power law model of MTE (Kolokotrones, Van Savage & Fontana 2010; Mori *et al.* 2010). Finally, this hypothesis is consistent with evidence that growth rate increases with tree size, but that competition affects systems that vary in productivity (Stephenson *et al.* 2014; Grace *et al.* 2016). As an aside, the competition hypothesis is related to hypotheses for changes in forest structure through time (Tang *et al.* 2014), but the focus here extends beyond forest communities and does not address a temporal sequence for one place. Also, an alternative hypothesis related to hydraulic limitation in larger plants has already been rejected for NPP scaling (Ryan, Phillips & Bond 2006).

Though not recognised in MTE-based work, a quadratic function for NPP scaling has long been theorised for vascular plant growth as part of predator–prey theory applied to grazing systems (Noy-Meir 1975). In that original model, the quadratic arch for green biomass descends to the right as proportionally more B is dedicated to non-grazeable biomass. In the present study, such a decrease is not relevant because accumulated total above-ground B is used (rather than green tissue only), so only the left half of Noy-Meir's (1975) growth curve is applied here. For all of the three reasons mentioned above (two components, parsimony, history), a quadratic curve up to an asymptote was expected here (Fig. 1).

UNIVERSAL ADAPTIVE STRATEGY THEORY

It has been argued that a single selective force (e.g., competition, above) cannot explain the multiple spectra of plant trait variability evident worldwide (Díaz *et al.* 2016). Competition is but one major selection pressure used to explain plant life histories, and both B and NPP arise from those multicausal life histories. Indeed, from the outset, biomass, primary production and limitations to plant growth have been key components of the CSR theory of plant life-history strategies, so named because it is based on the occurrence of suites of plant traits that allow survival under competition for resources (C-selected or 'competitor' strategy), abiotic limitation of metabolism (S-selected or stress-tolerant) or repeated disturbances that are lethal to exposed tissues and select for high reproductive output rather than persistence (R-selected 'ruderals'; Grime 1977; Hodgson *et al.* 1999; Grime 2001; Pierce *et al.* 2016). For example, Grime (1977) begins:

> The external factors limiting plant *biomass* in any habitat may be classified into two categories. The first, which henceforth will be described as stress, consists of conditions that restrict *production*, e.g., shortages of light, water, or mineral nutrients and suboptimal temperatures. The second, referred to here as disturbance, is associated with the partial or total destruction of the plant *biomass*. . . .[emphases added here]

With similar patterns evident throughout a wide range of organisms, CSR theory was recently generalised throughout the tree of life as a universal adaptive strategy theory (UAST; Grime & Pierce 2012), with 'CSR theory' recognised as a subset of the theory for plants. This reflects, in part, the widespread and historic recognition of three main endpoints of adaptive specialisation in animals (e.g. Greenslade 1972; Southwood 1977; see Grime & Pierce (2012) for review), but UAST extends this beyond the few major eukaryotic groups previously considered. Expectations for NPP and B continue in updated CSR plant strategy theory and UAST (Grime 2001; Grime & Pierce 2012), though most attention in CSR/UAST research has addressed morphological traits related to biomass allocation (e.g., Grime *et al.* 1997; Hodgson *et al.* 1999; Cerabolini *et al.* 2010a). Here, we focus on general NPP- and biomass-related predictions from CSR theory/UAST.

According to CSR theory (Grime 1977, 2001; Hodgson *et al.* 1999), competitive strategists attain larger B in order to pre-empt and acquire more resources than other plants. Thus, the competition hypothesis (explained above) is nested within the more complex hypothesis arising from CSR theory. The two hypotheses may not be discernible for a subset that represents a portion of the entire data range (e.g., forest trees, predicted to be affected by competition at large B), but should be discernible in a more general data set.

Stress-tolerant strategists grow conservatively, resulting in relatively low annual NPP, and maintain relatively low above-ground B and NPP as a result of adaptations to habitats in which resource availability or environmental extremes limit metabolic performance (Grime 1977; Pierce, Vianelli & Cerabolini 2005; Mokany, Raison & Prokushkin 2006). Some stress-tolerant plant species can gradually accrue large B over a long life span. Thus, stress-tolerant adaptations should contribute to relatively low NPP values across a range of B values, with a relatively low slope.

Ruderal strategists are adapted for habitats with abundant resources but frequent disturbance events (e.g., fire, grazing) that create brief temporal opportunities for growth. In those conditions, fitness favours rapid reproduction and dispersal over accrual of large above-ground biomass, though relatively high densities may also generate substantial NPP per unit area. Ruderal strategists may thus contribute to both the lower asymptote and the central region of an NPP scaling curve, a phenomenon already observed for herbaceous communities in Europe (Cerabolini *et al.* 2016).

Consistent with the above expectations derived from CSR theory and UAST (Grime 1977; Grime & Pierce 2012), we hypothesised that NPP scaling should follow a sigmoidal curve (Fig. 1). Here, we use a simple logistic function (log NPP = $a/(1 + \exp((b - \log B)/c))$ that has minimal NPP = 0, a maximal NPP (*a*), an inflection point (*b*) and a shape coefficient (*c*; Pinheiro & Bates 2006). Specifically, stress-tolerant adaptations should maintain relatively low NPP across lower values of B to form the lower asymptote (i.e., low-sloped 'tail') of a sigmoidal curve. Low-NPP ecosystems may also be dominated by ruderal strategies because

adaptation to disturbance involves investment in seed production rather than vegetative growth. For example, low-biomass desert or xeric grassland communities are dominated by stress-tolerant (S) or ruderal (R) species depending on the local prevalence of either abiotic limitations to growth or disturbance, respectively (Kelemen *et al.* 2013). At moderate B, equivalent to the steeply increasing phase of the sigmoidal NPP curve (Fig. 1), evidence from other grassland ecosystems indicates a mixture of CSR strategies, including numerous ruderal strategists (Cerabolini *et al.* 2016). Finally, competitive strategists should generate maximal NPP at greater B to form the upper asymptote of the sigmoidal curve (Grime 1977). The competitive hypothesis clearly applies to forests (Kerkhoff & Enquist 2006), but grassland communities can also be dominated by C-selected species, which prevent the establishment of subordinate species adapted for other strategies (Kelemen *et al.* 2013; Cerabolini *et al.* 2016).

Based on the above, CSR strategies should modify the power law expected by MTE to cause sigmoidal NPP scaling, but the three 'phases' of a sigmoidal function should not be expected to match the three strategies. Instead, the three strategies may intermingle in the function, but with relatively more S and R towards low B and relatively more C at high B. The current work did not explore the placement of CSR categories in the NPP scaling data, principally because available NPP and B data refer to ecosystem-level measurements for which the precise mix of local plant strategies has not been determined. Plant species have been characterised for CSR traits (e.g., Hodgson *et al.* 1999; Cerabolini *et al.* 2010a; Pierce *et al.* 2013), and in a small number of local cases CSR strategies have been explicitly linked to ecosystem properties such as biomass (Cerabolini *et al.* 2010b, 2016), but the combination of CSR, NPP and B data has not yet accrued. Indeed, life-history strategies apply best to species, which comprised only 25% of all data analysed here. Here, we first test the hypothesis that general NPP scaling across broad scales of NPP and B should be sigmoidal as a net result of myriad CSR strategies summarised above. Given support for that hypothesis, studies to amass detailed CSR strategies and associated NPP and B are then justified.

TIPPING POINTS

Unlike the NPP scaling hypothesis based on metabolic theory, the hypotheses based on UAST and competition (summarised above) predict nonlinear scaling curves (Fig. 1), which make tipping points possible (Scheffer 2009; Scheffer *et al.* 2009; Brook *et al.* 2013; Hughes *et al.* 2013; Reyer *et al.* 2015; van Nes *et al.* 2016). If present, a tipping point is important because it is 'a threshold in conditions at which a small change in conditions leads to a strong change in the state of a system' (Reyer *et al.* 2015, p. 6). The hypothesised, nonlinear NPP scaling curves (Fig. 1) are consistent with a general definition of tipping points (Reyer *et al.* 2015; van Nes *et al.* 2016) and are not to be confused with more extreme, Z-shaped curves that would indicate abrupt and irreversible changes between alternative stable states (Beisner, Haydon &

Cuddington 2003). Instead, tipping points on quadratic or sigmoidal curves indicate reversible changes (or 'non-catastrophic thresholds'; Scheffer *et al.* 2009). For example, a shift from right to left on the sigmoidal NPP scaling curve (Fig. 1) through a tipping point represents a regime shift from a relatively high B and NPP system towards a lower B and NPP system (e.g., deforestation; Asner *et al.* 2004). Conversely, reforestation (e.g., Cunningham *et al.* 2015) is a positive B shift through that tipping point. Thus, tipping points in a general NPP scaling model may inform global afforestation goals and harvest limits that are important to carbon cycling and human appropriation of NPP (Imhoff *et al.* 2004; Haberl, Erb & Krausmann 2014).

GENERAL APPROACH AND LIMITS

Here, we tested for a general NPP scaling relationship based on hypotheses described above and that derive from fundamental principles (i.e., photosynthesis in vascularised tissues, size-based competition, adaptive life history strategies). The three alternative hypotheses described above prescribed alternative allometric curve shapes, and a regression model for each curve shape was selected for parsimony (i.e., fewest coefficients, simplicity) and historical precedent. It is possible that some other regression models could fit data better, but such models would need to be well justified by hypotheses, and we know of only the three evaluated here. Information theoretic model selection (Burnham & Anderson 2002) was ideal for this hypothesis-testing framework and was used here.

Analyses included hierarchical levels of organisation (i.e., species' populations, assemblages (i.e., taxonomically based subsets of communities; Fauth *et al.* 1996), ecosystems and biomes) for a number of reasons: NPP scaling data are reported for these levels; an objective was to evaluate internal consistency for a general model (i.e., is each subset consistent with the general model?); and effects of this variety needed to be addressed in analyses. We expected differences among hierarchical levels because life-history strategies apply more clearly to species and assemblages (Grime 1977) than to integrative ecosystems, which then may not adhere well to a particular curve. In addition, populations and assemblages were subdivided as woody and non-woody, because those growth forms differ markedly in structure and function (e.g., metabolically inactive xylem in woody tissues; Díaz *et al.* 2016). We expected that some subsets may be truncated (e.g., include only relatively large B), which could affect hypothesised model fits. Because the competition hypothesis can be considered a part of CSR theory and should be especially important at large B, sigmoidal and quadratic curves at larger B values may resemble each other and both be interpreted as being caused by competition (Fig. 1). However, we expected a general model (i.e., using the entire range of B data) to be sigmoidal because competition is not the only important process, especially in habitats where plant species occupy the same habitat but are not in direct contact (for examples see

Grime & Pierce 2012). In stressful or disturbed habitats, CSR theory predicts that plant growth differs from other habitats where competition is more important.

Materials and methods

DATA ACQUISITION AND HANDLING

Paired and independently estimated above-ground NPP and B data for vascular plants and systems dominated by them were extracted from data provided in Jenkins (2015; data available from http://www.esapubs.org/archive/ecos/C006/012/suppl-1.php). Those data were compiled from peer-reviewed journal publications and books. In all data sets used here, NPP and B were verified to be independently estimated. Multiple data sets or values within compilations were excluded if NPP was calculated with an assumed or estimated P/B or 'estimative ratio' (Whittaker & Marks 1975).

All data were expressed in units of dry mass as g m^{-2} year^{-1} for NPP and g m^{-2} for B. Obtained data were originally reported for different hierarchical levels of organisation, which were retained here and included in analyses because we expected those levels to affect patterns. Specifically, a population represents a single species in a location; an assemblage represents a taxonomically based set of species in a location (e.g., grasses); an ecosystem represents all primary producers in a location (e.g., forest); and a biome represents a regional set of ecosystems in a particular climate. Species and assemblages were also divided into woody or non-woody sets according to their growth form, so that six subsets were generated for analyses. Data values for one subset were not used in another subset.

Two important data sources for grasslands (Scurlock, Johnson & Olson 2002) and forests (Keeling & Phillips 2007) required decisions during data handling. Scurlock, Johnson & Olson (2002) provided grassland data based on four methods to estimate B and NPP; we used B data based on their 'method 2' (peak above-ground live + standing dead matter) to best match the recommended method 5 to estimate NPP (Scurlock, Johnson & Olson 2002), which uses related live and standing dead matter, and where timing of annual cycles was based on trough–peak cycles of biomass (Singh, Lauenroth & Steinhorst 1975). This choice of method is also supported by the fact that inclusion of dead matter greatly improved the utility of biomass as a predictor of species richness in a global study, at least for herbaceous ecosystems (Fraser *et al.* 2015), probably because dead matter produced extensively by dominant species plays a key role in limiting the ability of subordinates to establish and thus contribute to ecosystem properties (Stevens *et al.* 2004). The inverse of relationships evaluated here (i.e., the B/NPP relationship) was reported for many forest data sets (Keeling & Phillips 2007). Forest NPP studies are often based on increment data alone (i.e., changes in above-ground standing biomass), and lack substantial NPP due to litterfall, tropical litterfall decomposition, volatile organic compounds, and herbivory. These additional contributors to NPP are especially important in tropical forests (Keeling & Phillips 2007); following their recommendation, we used their standardised data.

STATISTICAL ANALYSES

Linear and quadratic models (described above) were computed using generalised least squares regressions (gls in the *nlme* package of R v. 3.2.2; R Core Team 2015). Generalised least squares models provided leniency on assumptions of normality and homoscedasticity.

The sigmoidal model was computed using nls in the basic *stats* package of R and the SSlogis function, which is self-starting and iteratively solves for the three coefficients (log NPP = a/(1 + exp ((b − log B)/c))). This logistic function has the same number of coefficients as the competition model (three) and is more parsimonious than other logistic functions, including a cubic function, which might be thought as a next parsimonious step but has four terms (intercept and three coefficients). In all models, log$_{10}$ (NPP) was the response variable, and log$_{10}$ (B) was the predictor variable. Analyses compared the three models using information theoretic model selection, based on corrected Akaike information criterion (AICc) and weights (w_i; Burnham & Anderson 2002). In model comparisons, we emphasised w_i, which indicates the probability that a model is the most plausible among those listed. Model coefficients and their significance (i.e., *P*-values) were recorded but significance was not used in model selection. Residual standard errors (also known as standard deviations of residuals) were used as accessory information to compare models; smaller values indicate a stronger fit. Model selection was conducted with the *bbmle* package in R.

The three alternative models were compared for each of the six subsets to evaluate internal consistency for an overall model, where generality would be most simply indicated with a consistent answer among levels (i.e., similar model selection and coefficients). We expected subsets to differ in their most plausible models because data differed widely. Also, a sigmoidal and quadratic model might both be plausible for a subset and support the competitive portion of the adaptive strategies hypothesis.

The three alternative models were also evaluated for a general model using all data, model selection (as above), and using mixed-effect models to represent subsets as random effects. This approach focused on general NPP scaling pattern as the fixed effect of interest while accounting for variance among hierarchical levels (identified in prior analyses). The mixed-effect models were computed using lme (in the *nlme* package of R) for linear and quadratic models, and nlme with the SSlogis function for the sigmoidal model, where subsets were random grouping factors.

Tipping points were evaluated for each subset and overall with segmented regression, using the *segmented* package in R. Tipping points are indicated well by segmented regression, even where strongly curved sigmoidal curves were not evaluated (Toms & Lesperance 2003; Vanacker *et al.* 2015). Segmented regression fits separate linear models into data with a designated maximum number of possible break points that join the linear segments. If a sigmoidal model was clearly most plausible, up to two possible break points were evaluated. If a quadratic model was plausible, one possible break point was evaluated. If a linear model was plausible, no tipping point analysis was warranted. Starting values were selected based on the range of B values. Tipping points were estimated with 5000 maximum iterations and reported with 95% confidence intervals (CIs). Preliminary runs showed that tipping point estimates were sensitive to number of iterations, where results based on default iterations (50) were quite variable, but ≤5000 iterations repeatedly attained values very similar to 10 000 iterations.

Results

A total of 709 pairs of above-ground NPP and B data values were compiled from the literature. Data ranged almost 6 orders of magnitude for NPP and B. Woody plants dominated the collected data: 71% of population and assemblage data

values included woody plants. Also, most of the ecosystem and biome data included woody shrubs and forests. Not surprisingly, non-woody taxa tended to have lower B while trees and forests tended to have greater B, though ranges overlapped.

The UAST (sigmoidal) and competition (quadratic) models were supported in five of six subsets (Table 1, Fig. 2). The sigmoidal model of NPP scaling was most plausible for woody populations ($N = 114$; $w_i = 0.94$; Fig. 2a). Non-woody populations ($N = 59$) were plausibly represented by both the sigmoidal and quadratic models ($w_i = 0.51$ and 0.44, respectively), which were similar in fit, related to the relatively narrow range of B values (Fig. 2b).

Woody assemblages were plausibly represented by only the sigmoidal model ($N = 282$, $w_i = 1.0$; Fig. 2c). Non-woody assemblages were the exception here, and were best represented by the linear model ($N = 100$, $w_i = 0.74$, Fig. 2d). We considered this result to be affected by one extremely low value and sparse data at low B (Fig. 2d). Ecosystem NPP scaling was better represented by the sigmoidal model ($N = 106$, $w_i = 0.63$) than by the quadratic ($w_i = 0.37$), though the truncated data set did not include an apparent lower asymptote (Fig. 2e). Finally, NPP scaling of biomes was similarly represented by the quadratic and sigmoidal

curves ($N = 48$; $w_i = 0.52$ and 0.33, respectively), with very similar fits (Fig. 2f).

Tipping points calculated for each subset ranged from 1·5 to 4·4 (Table 2). Two tipping points were obtained for woody species and assemblages, consistent with their plausible sigmoidal curves (Table 2; Fig. 2). Non-woody species, ecosystems and biomes were represented plausibly by both sigmoidal and quadratic models, so only one tipping point was calculated for each (Table 2).

General NPP scaling was plausibly represented by only the UAST-based sigmoidal model ($w_i = 1.0$). The quadratic and linear models were implausible (both $w_i < 0.001$; Table 1). In other words, the sigmoidal model was >1000 times more likely to be the most plausible, general model. Two tipping points (1·58, 2·56; Table 2) were detected for the general pattern (Fig. 3). The two general tipping points back-transform to 38 and 360 g m^{-2} as approximate transitions between the lower asymptote, steeply increasing segment and the upper asymptote of NPP scaling (Fig. 3).

In summary, the UAST-based sigmoidal model for general NPP scaling was well supported and mostly supported internally, given quadratic and/or sigmoidal models were most plausible for five of six subsets that represented 86% of data values.

Table 1. Model selection parameters and coefficients for compared model sets. Sigmoidal model: log NPP = $a/(1 + \exp((b - \log B)/c))$. Quadratic model: log NPP = $a + b \log B - c (\log B)^2$. Linear model: log NPP = $a + b \log B$. Models per set are sorted in ascending order of ΔAICc, and coefficients are listed only for plausible models. Lower values of residual standard errors (RSEs) indicate a better fit

Models	ΔAICc	w_i	a	b	c	RSE
General model ($N = 709$)						
Sigmoidal	0	1·00	3·34***	2·18***	0·70***	0·29
Quadratic	42·8	<0·001				
Linear	112·8	<0·001				
Subsets						
Woody species ($N = 115$)						
Sigmoidal	0	0·94	3·38***	2·53***	0·70***	0·34
Quadratic	6·1	0·04				
Linear	8·8	0·01				
Non-woody species ($N = 60$)						
Sigmoidal	0	0·51	3·20***	1·66***	0·47***	0·46
Quadratic	0·3	0·44	−2·06	3·01***	0·44*	0·45
Linear	4·6	0·05				
Woody assemblages ($N = 283$)						
Sigmoidal	0	1	3·42***	2·27***	0·89***	0·22
Quadratic	21·4	<0·001				
Linear	65·7	<0·001				
Non-woody assemblages ($N = 101$)						
Linear	0	0·74	0·02	0·92***		0·21
Quadratic	2·1	0·26				
Sigmoidal	13·7	<0·001				
Ecosystems ($N = 107$)						
Sigmoidal	0	0·63	3·36***	2·30***	0·64***	0·31
Quadratic	1·1	0·37	−2·84***	2·64***	0·28***	0·30
Linear	31·6	<0·001				
Biomes ($N = 48$)						
Quadratic	0	0·52	−1·22*	1·53***	0·12*	0·33
Sigmoidal	0·9	0·33	3·40***	2·49***	0·80***	0·34
Linear	2·4	0·15				

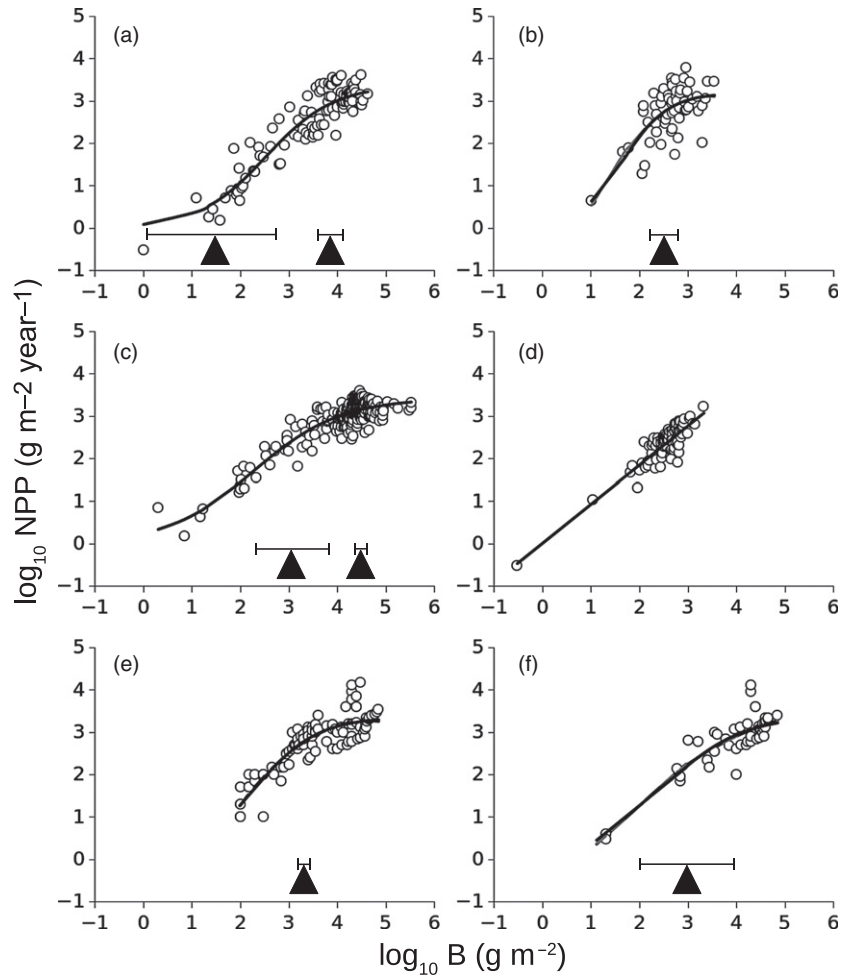*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Fig. 2. Net primary production (NPP) as a function of plant biomass (B) for hierarchical levels of organisation and plant forms. In each case, the most plausible model (Table 1) is shown as a solid black line, and if applicable, a secondary plausible model is shown as a grey line (often barely visible behind the black line). (a) Woody and (b) non-woody populations, (c) woody assemblages, (e) ecosystems, and (f) biomes were most plausibly fit by sigmoidal and/or quadratic models. Only (d) non-woody assemblages were most plausibly fit by a linear model. Triangles indicate tipping points (±95% confidence intervals) identified by segmented regression (see Table 2).

Table 2. Tipping points per analysis, where values are $\log_{10}$ (B; g m^{-2}). Values were obtained using segmented regression, where ≤2 tipping points were possible if only a sigmoidal model was plausible and ≤1 point was possible if a quadratic model was plausible

Data set	Tipping points (95% CI)
Woody populations	1·465 (±1·373); 3·877 (±0·267)
Non-woody populations	2·597 (±0·330)
Woody assemblages	3·042 (±0·753); 4·459 (±0·114)
Non-woody assemblages	–
Ecosystems	3·255 (±0·214)
Biomes	3·007 (±0·950)
General model	1·580 (±0·289); 2·557 (±0·091)

Fig. 3. General model for net primary production (NPP) scaling. The sigmoidal mixed-effect model included hierarchical levels as random effects. Triangles indicate tipping points (+95% confidence intervals) identified by segmented regression (Table 2).

Discussion

GENERAL NPP SCALING IS SIGMOIDAL, CONSISTENT WITH UAST

Results support the hypothesis that general terrestrial NPP scaling is constrained by adaptive life-history strategies to a sigmoidal curve. Unlike prior NPP scaling work, this conclusion was obtained by model selection, where an MTE-based power mod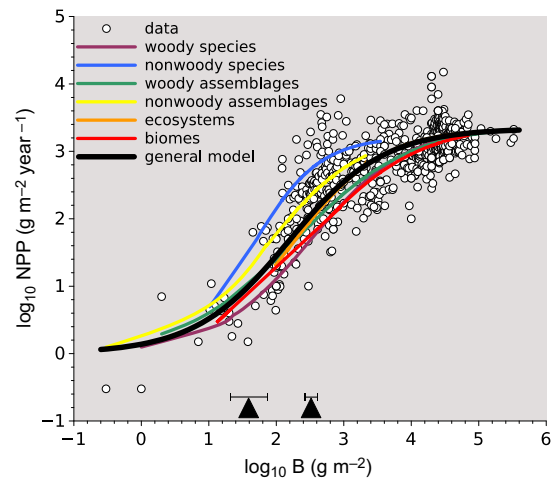el for an ideal system was compared to two alternative models based on alternative hypotheses. The general NPP scaling curve and curves for most subsets include tipping points, which have important implications for carbon

cycling and sustainable human appropriation of NPP (Haberl, Erb & Krausmann 2014). In contrast to most NPP scaling research (e.g., Kerkhoff & Enquist 2006; Lin *et al.* 2013; Michaletz *et al.* 2014; Hatton *et al.* 2015; Jenkins 2015), a strong inference approach based on information-theoretic model selection was used here to evaluate three alternative hypotheses (Platt 1964; Burnham & Anderson 2002; McGill, Maurer & Weiser 2006). This approach was consistent with a shift in focus from the value of the power law exponent (e.g., Enquist, Brown & West 1998; West, Brown & Enquist 1999; Niklas & Enquist 2001; Brown *et al.* 2004a; West, Enquist & Brown 2009) towards factors in empirical systems that impinge on ideal conditions hypothesised by MTE (e.g., Coomes & Allen 2007; Coomes, Lines & Allen 2011; Coomes *et al.* 2012, 2014). The MTE-based power law model (linear in log-log space) can represent NPP scaling well *for specific systems* and remains useful to predict NPP from B for a data set or to test the MTE (e.g., Kerkhoff & Enquist 2006; Michaletz *et al.* 2014; Hatton *et al.* 2015; Jenkins 2015). But the main goal here was to evaluate *general* NPP scaling, where analyses ranged from species to biomes and traversed c. 6 orders of magnitude for B and NPP. This range was exceeded by several orders of magnitude analyses of separate systems (e.g., forests), typical of most other analyses (e.g., Kerkhoff & Enquist 2006; Michaletz *et al.* 2014; Hatton *et al.* 2015; Jenkins 2015).

General NPP scaling was plausibly predicted only by a UAST-based sigmoidal model, which predicted NPP responses to B within about one order of magnitude. Nonlinear NPP scaling functions were also most plausible in five of six hierarchical levels. As a result, we infer that vascular plant adaptations and their environments cascade up to regulate terrestrial NPP (Grime 1977; Lin *et al.* 2013). Patterns described here should be general to terrestrial systems dominated by vascular plants for two reasons. Over 700 data values used here represent global systems, ranging from species to biomes. Also, mechanisms underlying UAST (i.e., adaptations to competition, stress and disturbance) for NPP scaling are fundamental and should apply generally (Grime & Pierce 2012).

Results here support the hypothesis that asymmetric size-based competition by larger plants deflects the MTE-based power law at greater values of B (Grime 1977; Kerkhoff & Enquist 2006; Coomes, Lines & Allen 2011). This hypothesis is consistent with CSR theory and UAST, though to our knowledge this work is the first to relate the shape of NPP scaling to CSR plant adaptive strategies (Grime 1977; Grime & Pierce 2012). Inter- and intra-specific competition are important in forests and other systems (Lonsdale 1990; Grime 2001; Coomes & Allen 2007; Enquist, West & Brown 2009; Grace *et al.* 2016; Kunstler *et al.* 2016). Given infrequent disturbance and suitable conditions, large trees dominate B and NPP in forests with dense canopies, leaving relatively little contribution of subcanopy and ground-layer vegetation (Fahey *et al.* 2010). Conversely, frequent disturbance and/or unsuitable conditions greatly affect forest NPP and carbon flux (Coomes *et al.* 2012).

At the other end of the biomass spectrum, stress-tolerant strategies in particular (and the extreme environmental conditions that select for them) are supported as regulators of NPP scaling. The lower asymptote in the sigmoidal curve is consistent with stress-tolerant adaptations that maintain existing B and dedicate limited resources to growth, and thus have relatively low NPP (Grime & Pierce 2012). Ruderal strategies may also be consistent with this range of the NPP scaling model because resources are often allocated to abundant but small seeds rather than growth and thus standing biomass (Grime & Pierce 2012; Díaz *et al.* 2016). Indeed, Cerabolini *et al.* (2016) found that many herbaceous communities in northern Italy characterised by extremely low B were dominated by R-selected species. However, relatively few data were available for low-B compared to high-B systems for the present study. Model coefficients and the lower tipping point location may shift with additional low-B data, but a sigmoidal model should remain most plausible given that >700 data values were used here. It may be expected that facilitation affects NPP scaling at low B, but facilitation is actually more evident at moderate B levels and should not alter the lower asymptote appreciably (Michalet *et al.* 2006). Also, we do not expect a sigmoidal model with inclusion of below-ground data because above-ground B equals or exceeds below-ground B in habitats that select for stress tolerance (Hadley & Szarek 1981; Yang *et al.* 2010). However, data here represent only above-ground NPP and B, and so it would be valuable to test observed relationships with whole-plant data, should enough accrue.

In between the lower and upper asymptotes, strategy mixtures and intermediates were supported as contributing to steep NPP scaling at moderate B. All hierarchical subsets contributed to this range, but non-woody species and assemblages had especially steep slopes (compare curves in Fig. 3), consistent with high productivity per unit area and unit biomass of wetland and grassland systems. These non-woody systems fit expectations for broadly R-selected strategies (encompassing intermediates such as CR, SR) that include modest dimensions, rapid growth of individual plants when conditions permit and spatially dense populations (Grime 1977; Hodgson *et al.* 1999; Grime & Pierce 2012; Díaz *et al.* 2016). But we note that woody systems were mixed throughout the data (Fig. 2); C, S or R regions of the sigmoidal curve were not simply predicted by a woody/non-woody dichotomy. Clearly, a next step would be to obtain NPP and B data for CSR categorisations of many plant species (across a wide range of plant sizes and life-history strategies) to independently test the patterns reported here. Tests here were more general and only 25% of NPP scaling data were for species, but a detailed CSR-based inquiry into NPP scaling is now well justified. As global CSR data become available, empirical investigation of these NPP scaling relationships will reconnect to initial CSR theory (Grime 1977).

NON-CATASTROPHIC TIPPING POINTS

General NPP scaling has non-catastrophic tipping points (Brook *et al.* 2013; Hughes *et al.* 2013). This departs from

MTE-based linear expectations (on a log-log scale) of NPP scaling, with important implications. We emphasise that prior work on MTE-based NPP scaling often used data covering a more restricted range and did not statistically compare power law models against hypothesised alternatives. Questions of tipping points or thresholds are not relevant if only linear models are used, but are now relevant given the sigmoidal model of general NPP scaling.

Tipping points in NPP scaling mark transitions in the response of NPP given changes in B that occur by human land use, disturbance, succession, climate change, etc. Changes in NPP are critical to ecosystem energetics, carbon cycling and indirectly important to other ecological conditions (e.g., soil erosion, biodiversity, sustainable resource availability). Systems just above a tipping point should exhibit strong reductions in NPP responses if they are reduced in B below the tipping point. Eighty-three per cent of data points exceeded the upper tipping point of 360 g dry mass m^{-2} and represented various grasslands, wetlands and forested systems. Thus, a considerable research base exists to understand NPP responses to changes in B in these most productive systems. For purposes of maximising carbon sequestration, c. 360 g dry mass m^{-2} is a threshold to avoid in land use (e.g., urbanisation, agriculture, deforestation) and a goal to attain in restoration, wherever possible. We also note a boundary for a safe operating zone (i.e., a zone above a threshold) would exceed this 360 g dry mass m^{-2} threshold (Hughes *et al.* 2013). Below the 360 g dry mass m^{-2} threshold, NPP falls with an increasingly steep slope as B is reduced (e.g., due to deforestation or increasing aridity).

Conversely, the lower tipping point of the general model (38 g dry mass m^{-2}) denotes a shift to a marked increase in NPP with modest increases in B. Increased B may occur with succession or climate change (e.g., warming, greater precipitation), and is likely to include compositional change. Given climate change, systems near 0·04 g m^{-2} and that are released from limiting conditions (e.g., increased precipitation or less frequent disturbance) are most likely to rapidly increase productivity. For purposes of carbon sequestration, some of those systems are non-woody and may not store carbon as living biomass, but rather store it in soils or as detrital flux (e.g., coastal wetlands). And of course NPP tipping points cannot detail specific changes in community structure, which are also vitally important to ecology and conservation.

FUTURE DIRECTIONS

The general sigmoidal model ($\log_{10}$ (NPP) = 3·54/(1 + exp (($2·18 - \log_{10}$ B)/0·70)) helps to link energetics and carbon cycling to adaptive life-history strategies. Though CSR theory was originally phrased in terms of production and biomass (see Dr. Grime's quote above), CSR and the more general UAST (Grime & Pierce 2012) is indicated here as a basis to predict global biomass production and carbon cycling. This reconnection of recently separated disciplines should be fruitful for ecology. Model refinements might include other factors, such as palatability, decomposition

rates and flammability of plant biomass among CSR strategies. The predicted placement of species' or community CSR categories in the general model could also be tested. Future work should also explore NPP scaling and CSR strategies in aquatic and marine ecosystems (beyond wetlands included here). Research results in lakes and coastal lagoons are consistent with life-history traits that denote C-, S- and R-strategists (e.g., Reynolds 1984, 1991; Weithoff, Walz & Gaedke 2001; Bonilla *et al.* 2005), but CSR strategies are not yet widely applied to phytoplankton. Potential studies on the relationship between NPP and life-history strategies in plankton are complicated by extensive temporal and spatial variability (Weithoff, Walz & Gaedke 2001) compared to relatively static terrestrial vegetation. However, such studies are required to test the hypothesis that NPP scaling reported here reflects a truly universal principal operating for all primary producers.

The general model should also help predict terrestrial NPP-driven carbon sequestration rates as a function of changing biomass, important to climate change and human resource demands (Cao & Woodward 1998). As such, results here may also inform projections of sustainable human population size. Human population growth is modelled demographically, based on numerous assumptions and thus uncertainty (e.g., Cohen 1995; Pimm 2001). An alternative approach is based on classic predator–prey theory that informed threshold theory (Noy-Meir 1975; May 1977; Scheffer 2009), and relates NPP scaling to human appropriation of NPP, which is already quantified in detail and is fundamental to human population growth (Haberl, Erb & Krausmann 2014). The general NPP scaling model thus represents one-half of that potential approach to represent a fundamental limit to future appropriation of NPP and conservation of remaining biodiversity (Wilson 2016) as we approach 11 billion people by century's end.

Author's contributions

D.G.J. conceived the ideas, collected and analysed data; D.G.J. and S.P. co-wrote the manuscript. Both authors contributed critically to the drafts and gave final approval for publication.

Acknowledgements

Data accessibility

All data are available from Jenkins (2015) at https://doi.org/10.1890/es14-00409.1

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