OPINION

Does climate directly influence NPP globally?

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Abstract

The need for rigorous analyses of climate impacts has never been more crucial. Current textbooks state that climate directly influences ecosystem annual net primary productivity (NPP), emphasizing the urgent need to monitor the impacts of climate change. A recent paper challenged this consensus, arguing, based on an analysis of NPP for 1247 woody plant communities across global climate gradients, that temperature and precipitation have negligible direct effects on NPP and only perhaps have indirect effects by constraining total stand biomass (M_{tot}) and stand age (a). The authors of that study concluded that the length of the growing season (l_{gs}) might have a minor influence on NPP, an effect they considered not to be directly related to climate. In this article, we describe flaws that affected that study's conclusions and present novel analyses to disentangle the effects of stand variables and climate in determining NPP. We re-analyzed the same database to partition the direct and indirect effects of climate on NPP, using three approaches: maximum-likelihood model selection, independent-effects analysis, and structural equation modeling. These new analyses showed that about half of the global variation in NPP could be explained by M_{tot} combined with climate variables and supported strong and direct influences of climate independently of M_{tot}, both for NPP and for net biomass change averaged across the known lifetime of the stands (ABC = average biomass change). We show that l_{gs} is an important climate variable, intrinsically correlated with, and contributing to mean annual temperature and precipitation (T_{ann} and P_{ann}), all important climatic drivers of NPP. Our analyses provide guidance for statistical and mechanistic analyses of climate drivers of ecosystem processes for predictive modeling and provide novel evidence supporting the strong, direct role of climate in determining vegetation productivity at the global scale.

Keywords: carbon, climate change, net primary productivity, production, rainfall

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Introduction

Understanding climate effects is critical to anticipate the impacts of climate change on ecosystem processes, such as carbon storage, which have feedbacks on the climate system. According to current textbooks on physiology and ecology, climate has strong, direct impacts on net primary productivity (NPP) in ecosystems worldwide (Begon et al., 2006; Chapin et al., 2012; Taiz et al., 2015). Many studies have established empirical relationships between NPP and climate within and across ecosystems (e.g., Leith, 1975; Schuur, 2003; Del Grosso et al., 2008). There are well-established trends for the increase of NPP across ecosystems with higher

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temperature and precipitation from tundra to the temperate zone and sometimes from the temperate zone to the tropics (Huston & Wolverton, 2009; Chapin et al., 2012; Gillman et al., 2015), and evidence for the influence of climate change on specific ecosystems is accumulating weekly (e.g., Brienen et al., 2015). Most approaches to examining relationships between NPP and climate across ecosystems considered the total effect of climate variables on NPP, that is, both direct effects and those that are indirect, via differences in stand structure. Thus, the direct effects of climate include its influence on the physiological and environmental determinants of plant growth, which are directly regulated by temperature and water availability, including the kinetics of photosynthetic rates and respiration rates and plant biomass allocation

(Berry & Björkman, 1980; Geider *et al.*, 2001; Huxman *et al.*, 2004; Chapin *et al.*, 2012; Long, 2012; Vila *et al.*, 2013; Coomes *et al.*, 2014; Lichstein *et al.*, 2014). *Indirect* effects of climate on NPP include the influence of climate on the structure of given ecosystems. For example, NPP is strongly influenced by total stand biomass (M_{tot}) (Keeling & Phillips, 2007; Pan *et al.*, 2013), and stands are often larger where rainfall is higher (Pregitzer & Euskirchen, 2004; Keeling & Phillips, 2007; Coomes *et al.*, 2014).

Resolving and disentangling the direct and indirect effects of climate on NPP is clearly important, because direct effects would signify more immediate responses to ongoing climate change. However, a recent paper (Michaletz *et al.*, 2014) has challenged the consensus, arguing, based on a statistical analysis of a global dataset for woody plant-dominated communities, that climate has negligible direct influences on NPP at the global scale. They explained this conclusion as the result of plants' convergence in productivity despite global climate variation due to 'selection to maximize plant growth across climate gradients'. They hypothesized that climate may have indirect effects, although these were not presented or quantified.

Our examination of their statistical analysis revealed serious flaws that resulted in erroneous conclusions. We conducted new analyses of the same database, to resolve and disentangle the effects of climate and stand variables on NPP using three approaches – maximum-likelihood model selection, independent-effects analysis, and structural equation modeling – all of which point to the opposite conclusion: there are direct and very large effects of climate on world vegetation productivity at a range of timescales. This debate is important for analyses to resolve the influence of climate on ecosystem processes.

## Analyses of global NPP by Michaletz *et al.* and their pitfalls

Michaletz *et al.* rejected a direct role for climate in determining NPP based on four analyses, each of which contained flaws (Table 1). To clarify the analyses, we present a synthetic schema of the linkages among stand variables, climatic variables, and ecological rates (Fig. 1), based on standard understanding and definitions of terms (Chapin *et al.*, 2012; Malhi *et al.*, 2015). Climate variables may have direct effects on gross primary productivity (GPP) and/or on autotrophic (i.e., plant) respiration (R_a) and therefore on NPP, where NPP = GPP−R_a. In addition, a higher stand biomass (M_{tot}) will tend to increase GPP, R_a, and NPP, and changes in stand age (a) might also influence NPP and its components. Because climate variables can also set

constraints on M_{tot}, there may be *indirect* effects of climate variables on NPP, via M_{tot} and (by association) a. Subtracting from NPP the biomass losses due to plant mortality followed by decomposition and heterotrophic respiration (R_h) result in the net biomass change (NBC = NPP−R_h), which in turn drives changes in M_{tot}. The NBC is equivalent to, or translatable to the 'net ecosystem production' (NEP), the change of organic matter or carbon mass in the ecosystem (Fernandez-Martinez *et al.*, 2014). The NBC is determined fundamentally by NPP for stands that are increasing in biomass, although in disturbed or declining stands, NBC can be negative, when R_h exceeds NPP. The stand age-averaged biomass change (ABC) is the average of NBC over the entire known age of the stand, which can also be determined as M_{tot}/a.

In their first analysis, Michaletz *et al.* tested the correlations of NPP with its primary drivers in Fig. 1, that is, with stand and climate variables. Michaletz *et al.* noted the apparently strong correlation between NPP and mean annual temperature (T_{ann}) and mean annual precipitation (P_{ann}) in their database – correlations similar in strength to that between NPP and stand biomass (M_{tot}; replotted in Fig. 2b–d; see Appendix S1). In our analyses, NPP indeed correlated with all the climate variables in the Michaletz *et al.* database, including also the length of growing season (l_{gs}), and growing season temperature and precipitation (T_{gs} and P_{gs}, respectively; Fig. 2a, and b and c insets). Michaletz *et al.* argued that NPP was also strongly associated with stand age (a), although they presented a different kind of evidence for this: they plotted NPP vs. M_{tot} relationships for four stand age classes. They found that younger stands had higher NPP than older stands at a given M_{tot} (replotted in our Fig. 2d), which they attributed to stand age-related decline in NPP at the global scale. However, this conclusion arose from a spurious graphical analysis (see Appendix S2). When we applied the same test for correlation of NPP with a that Michaletz *et al.* performed for the other variables (Fig. 2a–c), we found a very weak negative relationship of NPP to a ($R^2 = 0.05$; $P < 0.001$; Fig. 3a). Indeed, NPP was statistically independent of a for stands > 35 years ($R^2 = 0.004$; $P = 0.08$; $n = 972$) or > 50 years ($R^2 = 0.002$; $P = 0.28$; $n = 676$; Fig. 3b), which is when pronounced declines in growth occur in most natural woody ecosystems (Gower *et al.*, 1996; Weiner & Thomas, 2001; Pregitzer & Euskirchen, 2004; He *et al.*, 2012). Stand age-related growth reductions are ecosystem specific, and the sampling by Michaletz *et al.* of ecosystems of different ages in the database could not resolve this. Our analyses suggest that the apparently higher NPP of stands < 50 years in this database was instead explained by a sampling bias, as these young stands were sampled in

Table 1 Summary of the four analyses of Michaletz et al. (2014) aiming to disentangle the effects of climate variables (mean annual and growing season temperature and precipitation, and the length of the growing season; T_{ann}, T_{gs}, P_{ann}, P_{gs}, and l_{gs}, respectively) and stand variables (stand biomass and age, M_{tot} and a, respectively) on net primary productivity (NPP) across ecosystems globally, with their conclusions, the pitfalls we describe, and the corrected conclusions

| Analysis	Conclusion of Michaletz et al.	Pitfall	Corrected conclusion
1. Testing correlations of NPP with stand and climate variables.	NPP was apparently positively correlated with M_{tot} and climate variables, and negatively related to a.	Spurious test for association of NPP with a rather than standard correlation test as for other variables.	NPP was correlated with M_{tot} and climate variables, but not importantly with a in this dataset.
2. Testing correlations of NPP normalized by growing season length (NPP/l_{gs}) with other climate variables.	NPP/l_{gs} was considered to represent NPP "more instantaneously", and it was not correlated with other climate variables, suggesting that the correlations of NPP with climate variables were 'spurious'.	The l_{gs} is a primary climate variable, and controlling out the effect of climate removes the ability to resolve the correlation with other climate variables.	The strong relationships between NPP and l_{gs}, T_{gs} and T_{ann}, P_{gs} and P_{ann} all imply a strong influence of climate on NPP.
3. Applying a multiplicative power law model (Eqn M3) to predict NPP as a function of stand and climate variables, then comparing this model with a simpler model without climate variables, and finally using partial correlation analysis to attempt to disentangle the importance of predictor variables in Eqn (M3).	The Eqn (M3) fitted the data well, although a simpler model without climate variables apparently fitted even better, and the partial correlations showed that NPP was closely related only to M_{tot} and a, and weakly to individual climate variables when all the other variables were controlled, suggesting that 'age and biomass together explained most of the variation in NPP' without any direct influence of climate on NPP.	Equation (M3) included a hidden circular term: by including M_{tot} and a as multiplicative factors, they effectively included stand age-averaged biomass change (ABC) as a predictor of NPP. However, ABC is a downstream variable mechanistically and statistically correlated with NPP and thus also influenced by (and correlated with) climate variables (Figs 1 and 4). The comparison of the full model with the simpler model without climate variables was erroneous. The use of partial correlation analysis was inappropriate for that purpose.	Even using Eqn (M3), maximum-likelihood model selection showed that climate variables have importance in determining NPP, more so after removing the circularity from the model. Independent-effects analysis showed that climate had approximately the same influence on NPP as M_{tot}.
4. Same as analysis 3, but predicting NPP/l_{gs} using Eqn (M4).	As for analysis 3, but for NPP/l_{gs}.	This analysis combined the errors and pitfalls described above for analyses 2 and 3.	As for analysis 3, but climate explains NPP/l_{gs} more weakly than NPP, as normalizing by l_{gs} already removes much of the effect of climate.
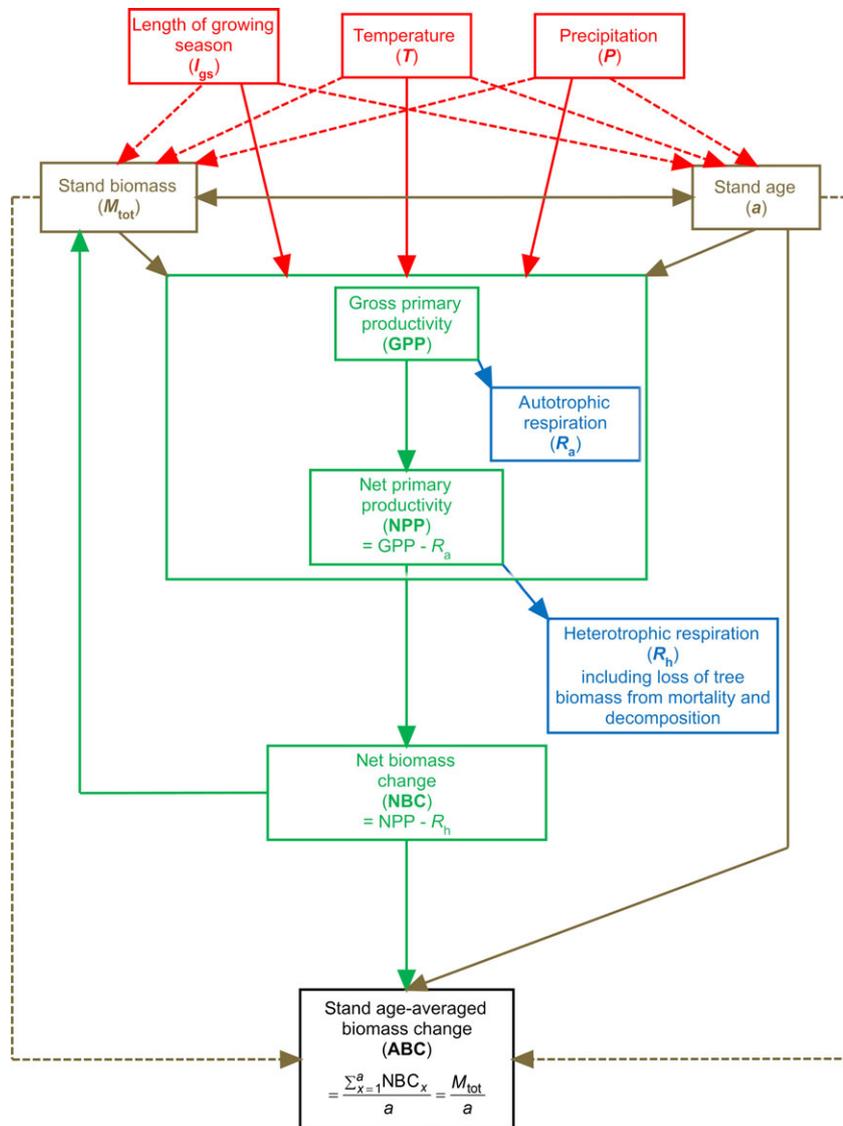
Fig. 1 Synthetic schematic of the linkages among climatic variables, stand variables, and production and loss rates (in red, brown, green, black, and blue, respectively). Climate variables may have direct effects on gross primary productivity (GPP) and/or autotrophic respiration (R_a) and therefore net primary productivity (NPP). In addition, a higher stand biomass (M_{tot}) will tend to increase GPP, R_a, and NPP and changes in stand age (a) might also influence NPP and its components. Because climate variables can also set constraints on M_{tot}, there also may be indirect effects of climate on NPP, via M_{tot} and (by association) a. Subtracting from NPP the biomass losses due to heterotrophic respiration (R_h) gives in the net biomass change in the system (NBC), which in turn drives changes in M_{tot}. (We note that the mortality of trees, followed by their decomposition, is accounted for in R_h). The stand age-averaged biomass change (ABC) is the average of NBC over the known age of the stand developed from bare ground and can also be calculated as M_{tot}/a. One important implication is that if M_{tot} and a are used in combination to predict NPP, as done by Michaletz *et al.*, a circularity arises, because ABC = M_{tot}/a, and thus, one is predicting NPP not from primary drivers, but from ABC, which is downstream variable mechanistically driven by (and statistically associated with) NPP. Such an analysis loses resolution to detect climate influences on NPP. Note that this formulation focuses on the processes determining NPP within a given ecosystem; variation among ecosystems in NPP (i.e., in a global analysis) should be driven by the same factors, although other sources of variation play a key role, for example, differences in the pool of species and their traits. Additionally, climate, M_{tot} and a may also have potential influences on R_h (not shown). Our analyses disentangled the direct vs. indirect effects of climate on NPP and showed substantial direct as well as indirect effects of climate on NPP.

moister, warmer climates with 1–2 month longer growing seasons on average than the older stands (Appendix S2). Thus, while both climate and M_{tot} were strong predictors of NPP, a strong influence of a on NPP at the global scale was not supported by our analysis.
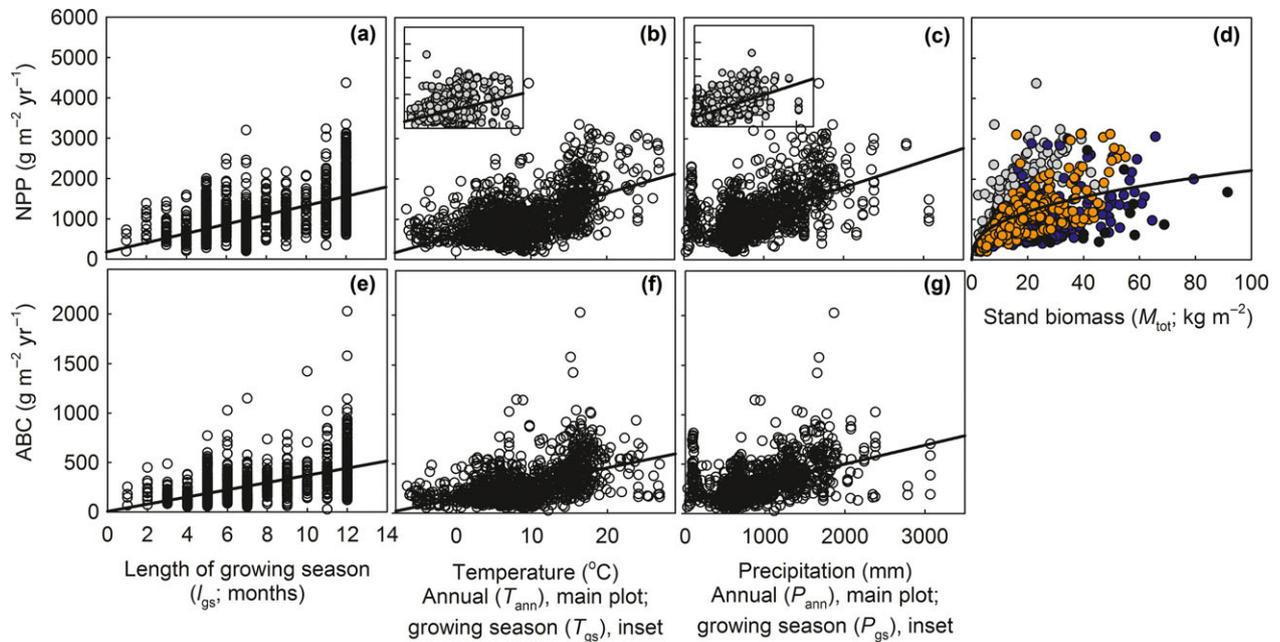
Fig. 2 Correlations of net primary productivity (NPP) and stand age-averaged biomass change (ABC = M_{tot} divided by stand age, a) with climate variables and stand biomass (M_{tot}), from the global database compiled by Michaletz *et al.* (2014). Main panels B, C, and D are replotted from Michaletz *et al.* (2014), and additional plots represent our novel analyses. Notably, ABC is highly correlated with NPP (Fig. 4) and shows the same correlations with climate variables. Climate variables are (a) and (e) length of growing season (l_{gs}; R^2 = 0.31 and 0.28, respectively; $P < 0.001$; (b) and (f) mean annual temperature (T_{ann}; R^2 = 0.30 and 0.24, respectively; $P < 0.001$) and inset with gray symbols, growing season mean temperature (T_{gs}; R^2 = 0.12; $P < 0.001$); (c) and (g) mean annual precipitation (P_{ann}; R^2 = 0.28 and 0.22, respectively; $P < 0.001$) and inset with gray symbols, growing season mean precipitation (P_{gs}; R^2 = 0.29; $P < 0.001$); and (d) M_{tot} (power law fitted; R^2 = 0.31; $P < 0.001$); black, blue, orange, and gray points represent, respectively, stands 0–50, 51–100, 101–200, and ≥201 years old. Lines are fitted by least squares regression; for all relationships but those with M_{tot}, the correlations were stronger with untransformed than log-transformed data, but remained significant in either form.
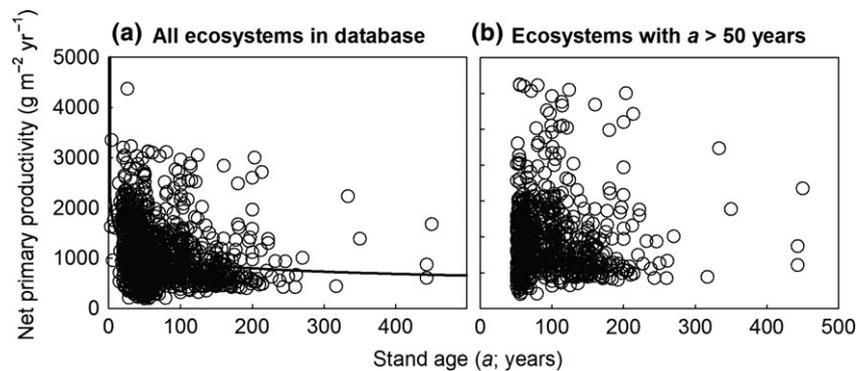
Fig. 3 Plots of net primary productivity (NPP) against stand age from the global database compiled by Michaletz *et al.* (2014), for (a) all 1247 woody dominated ecosystems in the database (R^2 = 0.05; power law fitted, given its higher correlation than linear; $P < 0.001$) and (b) for stands >50 years of age. R^2 = 0.002; $P = 0.28$; $n = 676$).

Second, Michaletz *et al.* argued that the correlations of NPP with climate variables should be discounted, based on a novel interpretation of l_{gs}. They calculated the variable NPP/l_{gs} as a 'more instantaneous' version of NPP and found only weak relationships of NPP/l_{gs} with growing season temperature (T_{gs}) and precipitation (P_{gs}; R^2 = 0.026 and 0.017, respectively; $P \leq 0.001$),

and concluded from this analysis that there is a negligible direct effect of climate on NPP. They further argued that the strong correlation of NPP with T_{ann} found in their first analysis (Fig. 2b), and in previous studies, was spurious, arising only as an artifact of the correlation of T_{ann} with l_{gs}. Michaletz *et al.* thus considered the influence of l_{gs} *not* to be a direct climatic effect and

featured this conclusion in their Abstract. In our view, this is a misclassification of l_{gs}, and by controlling out the effect of l_{gs} on NPP, Michaletz et al. removed much of the influence of climate on NPP before testing its correlations with other climate variables. A clear understanding of l_{gs} as a primary climate variable is essential, because it is an important driver not only of NPP, as shown in many previous studies, and as we found for the Michaletz et al. database (Fig. 1a), but it is also a major determinant of the geographical distribution of biomes (Walter, 1985; Chapin et al., 2012). Indeed, l_{gs} can be considered as a climate variable by its calculation and also geophysically, mathematically, and biologically. l_{gs} was calculated from climate data (as the number of months with mean minimum temperature greater than 0.6 °C and a moisture index > 0.08, considered as thresholds of air temperature and precipitation for woody plant growth). Geophysically, l_{gs} and T_{gs} are intrinsically correlated across locations globally, shifting downward with latitude and altitude and increasing with continentality. The same is true of l_{gs} and P_{gs} but to a lesser extent given that the intrinsic correlations of P_{gs} with latitude, altitude, and continentality are to some extent decoupled by winds and ocean currents that influence rainfall independently of latitude and altitude. Mathematically, l_{gs} is a fundamental climatic component of T_{ann} and P_{ann}:

$$T_{ann} = l_{gs} \times T_{gs} + (1 - l_{gs}) \times T_{ngs} \qquad (1)$$

$$P_{ann} = l_{gs} \times P_{gs} + (1 - l_{gs}) \times P_{ngs} \qquad (2)$$

where in this formulation, l_{gs} is expressed as a fraction of the 12 months of the year, and T_{ngs} and P_{ngs} the temperature and precipitation, respectively, of the nongrowing season. Simplifying further,

$$T_{ann} = l_{gs}(T_{gs} - T_{ngs}) + T_{ngs} \qquad (1a)$$

$$P_{ann} = l_{gs}(P_{gs} - P_{ngs}) + P_{ngs} \qquad (2a)$$

Thus, l_{gs} is a component of T_{ann} and P_{ann} and, because it is also an intrinsic geophysical correlate of their other components, T_{gs} and P_{gs}, with which it is multiplied, the effects of l_{gs} on T_{ann} and P_{ann} are quantitatively very strong. All terms in these equations, including l_{gs}, are biological climatic drivers too, being determinants of the amount of energy available annually to the ecosystem for metabolism. Indeed, l_{gs} is defined as an interface of biology with climate: the window of time that permits plant growth. l_{gs} represents a tighter constraint with much less wiggle room for plants to compensate by adaptation or acclimation than T_{gs} or P_{gs}. While species can acclimate or adapt to some extent to mitigate against lower T_{gs} or P_{gs}, producing species variation in responses to T_{gs} or P_{gs}, a community cannot mitigate a shorter l_{gs} as readily, given its definition as the days above the minimum threshold for all plant growth. A shorter l_{gs} will certainly narrow the growing window for most or all species. For all these reasons, l_{gs} captures more of the influence of climate on NPP than the other factors in Eqns (1) and (2), in the database of Michaletz et al., and in previous studies of drivers of NPP and the limits of biome distributions globally (Begon et al., 2006; Chapin et al., 2012). Consequently, in our view, the weak correlation of NPP/l_{gs} with T_{gs} or P_{gs} does not imply that the correlation of NPP with T_{ann} or with P_{ann} was spurious, as Michaletz et al. argued. Controlling for l_{gs} before testing the relationship of NPP to other climate variables removed a major climate variable which was a correlate of the other climate variables and thus does not test the influence of climate 'more directly'. Rather, the strong relationships between NPP and l_{gs}, T_{gs}, T_{ann}, P_{gs}, and P_{ann} all imply a strong influence of climate on NPP.

For their third and fourth analyses, Michaletz et al. introduced a multiplicative model, which they derived from metabolic scaling theory, with which, they argued, NPP can be strongly predicted without the need for any climate variables. They described NPP as a multiplicative function of the variables at the top of Fig. 1, that is, M_{tot} and a, precipitation (P_{ann} or P_{gs}), temperature (T_{ann} or T_{gs}) and l_{gs}, and constants and fitted parameters (eqn 3 of Michaletz et al., 2014, here referred to as Eqn M3):

$$\ln(NPP) = \alpha\ln(M_{tot}) + \alpha_a \ln(a) - \frac{E}{kT} + \alpha_P \ln(P) \\ + \alpha_{l_{gs}} \ln(l_{gs}) + \beta_{0,1} \qquad (M3)$$

Michaletz et al. found this model had a high R^2 of 0.77, which they attributed to the strong explanatory power of M_{tot} and a, and a negligible influence of climate. However, we found that the high R^2 of Eqn (M3) arose due to a hidden circularity from the use of both M_{tot} and a as multiplicative predictors. Equation (M3) can be rewritten as:

$$\ln(NPP) = -\alpha_a \ln(ABC) + (\alpha + \alpha_a) \ln(M_{tot}) - \frac{E}{kT} \\ + \alpha_P \ln(P) + \alpha_{l_{gs}} \ln(l_{gs}) + \beta_{0,1} \\ (M3a)$$

(see Appendix S3). Thus, Eqn (M3) effectively uses the stand age-averaged biomass change (ABC) as a predictor variable, because ABC = M_{tot}/a (Fig. 1). Yet, ABC is mechanistically determined by NPP and statistically correlated with NPP (Figs 1 and 4; R^2 = 0.71; $P < 0.001$; see Appendix S4). Thus, Eqn (M3) predicts NPP from ABC which is its intrinsic correlate (note that the fitted parameter α_a takes a negative value, so the relationship
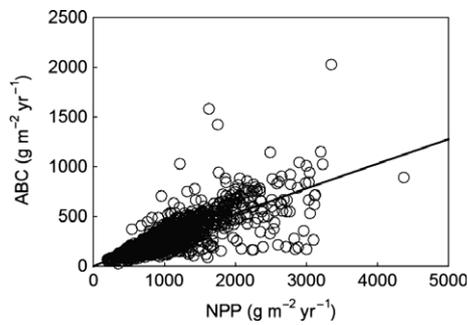
Fig. 4 Correlation of net primary productivity (NPP) with stand age-averaged biomass change (ABC = M_{tot} divided by stand age, a) for the database of 1247 woody plant-dominated ecosystems compiled by Michaletz *et al.* (2014). $R^2 = 0.71$ for power law fit; $P < 0.001$.

of predicted NPP to ABC is positive). Indeed, of all factors in Eqn (M3a), ABC is the strongest driver – the R^2 value was 0.71 for predicting NPP from ABC, close to that for the full model. Further, we found that ABC was itself strongly correlated with climate variables (Fig. 2e–g), supporting climate effects not only on NPP, but also on biomass accumulation averaged across the known lifetime of stands worldwide.

In our view, the inclusion of the a term in Eqn (M3) led to the flawed analysis of Michaletz *et al.*, because M_{tot} and a together led to inserting ABC, a variable that is logically downstream of NPP, mechanistically determined by NPP, and correlated with NPP (Figs 1 and 4) into the predictive model for NPP, although a actually had no added value as a predictor (Appendices S2 and S3). Although Michaletz *et al.* intended the inclusion of a in the model to account for age-related NPP decline in older stands, such a role for a was not supported in the database (Fig. 3a, b). Further, age-related declines in NPP represent a stand-specific trajectory, highly variable among species within and across ecosystems (Gower *et al.*, 1996; Weiner & Thomas, 2001; Pregitzer & Euskirchen, 2004; He *et al.*, 2012). The multiplicative a term in Eqn (M3) with its single exponent fitted across all ecosystems instead represents a 'general' age-related decline for all ecosystems, which was redundant, being already modeled in Eqn (M3) as α, the fitted coefficient for M_{tot}; a smaller α reflects a greater age-related decline across all ecosystems.

Michaletz *et al.* next argued that climate variables were not important because they found that a simpler model without climate variables, $\ln(NPP) = \alpha \ln(M_{tot}) + \alpha_a \ln(a) + \beta_{0,1}$, had nearly the same R^2 value as the full model. They named this version, without climate variables as a 'general scaling function' to predict NPP worldwide as a multiplicative power law function of M_{tot} and a, given their conclusion that only these two variables mattered (their Fig. 3). However, rather than establishing that M_{tot} and a are primary drivers of NPP, this function simply predicts NPP from ABC, that is, from M_{tot}/a, which is circular given that ABC is intrinsically correlated with, and mechanistically downstream of NPP (Figs 1 and 4). Additionally, Michaletz *et al.* stated that this simpler version without climate variables was selected with greater likelihood in a model comparison over Eqn (M3), which included climate variables; they reported AIC values of −1768 vs. 140. Such a strong discrepancy in AIC values suggests an error, and indeed, we were unable to replicate this result with their data. In our analyses of the database using maximum-likelihood model comparisons, models including climate variables were always better supported, with lower AIC values, than models with M_{tot} and a alone (see section, "Rigorous approaches to testing the direct and indirect influences of climate on NPP"). Michaletz *et al.* also conducted a partial correlation analysis considering the relationship of NPP to each variable in eqn $M3$ while controlling for all of the others and found that NPP was closely related only to M_{tot} and a, and weakly related to all individual climate variables (including l_{gs}) when all the other variables were controlled. From this analysis, they concluded that 'age and biomass together explained most of the variation in NPP'. That was a counterintuitive conclusion, because NPP was correlated as strongly with climate variables as with M_{tot} and much more strongly than with a (Fig. 2a–d). Indeed, the partial correlation analysis conducted by Michaletz *et al.* was inappropriate for resolving the influence of climate variables. As Murray & Conner (2009) pointed out, 'partial correlations are not designed to partition the variance shared between multiple correlated predictors and the dependent variables'. More specifically, in this global database, the climate variables T_{ann}, T_{gs}, P_{ann}, P_{gs}, and l_{gs} were positively intercorrelated ($R^2 = 0.073$–0.90; $P < 0.001$), so partialing out any one or more climate variables cancels the influence of others and removes the ability to resolve their influence in a partial correlation analysis (Zar, 1999). Additionally, partialing out both M_{tot} and a together removes much of the variation because the two define ABC, an intrinsic correlate of NPP (Fig. 4), which is also correlated with the climate variables (Fig. 2e–g). Finally, the apparent importance of a in this partial correlation analysis also arose from that circularity – when controlling out M_{tot}, a becomes an important predictor of NPP due to a statistical artifact (see Appendix S2). Such a partial correlation analysis does not permit the inference of direct vs. indirect drivers of NPP. Independent-effects analysis is an appropriate approach and leads to the opposite conclusion, that is, of strong direct influence of climate on

NPP (see section "Rigorous approaches to testing the direct and indirect influences of climate on NPP").

Finally, Michaletz *et al.* developed a similar model to predict NPP/l_{gs} (their eqn 4, here referred to as Eqn M4)

$$\ln\left(NPP/l_{gs}\right) = \alpha\ln(M_{tot}) + \alpha_a \ln(a) - \frac{E}{kT_{gs}} + \alpha_P \ln\left(P_{gs}\right) + \beta_{0,2}$$

$$(M4)$$

and applied this model in the same way as for Eqn (M3), finding an R^2 of 0.44, and that in a partial correlation analysis, M_{tot} and a were the best predictors, with a small additional influence of T_{gs} or P_{gs}. This analysis combined the errors described above: removing the influence of climate by dividing NPP by l_{gs}, an important climate variable that is correlated with the others; including the circular term ABC, arising from including both M_{tot} and a; and inappropriate use of partial correlation analysis to partition variance among correlated factors.

Michaletz *et al.* concluded from their analyses that climate had a negligible direct influence on NPP. They proposed that climate might perhaps *indirectly* influence NPP through M_{tot} and a (Fig. 1) although they did not test that hypothesis. In fact, our analyses showed that in their database, M_{tot} correlated very weakly with T_{ann}, T_{gs}, P_{ann}, or P_{gs} ($R^2 = 0.014$, 0.020, 0.10, 0.048, respectively; $P < 0.001$) as did a ($R^2 = -0.10$, 0.12, 0.00017, 0.012; $P < 0.001$ for all but P_{ann}, $P = 0.66$). The inability of Michaletz *et al.* to resolve the direct influence of climate on NPP arose from the flaws of their analyses.

## Rigorous approaches to testing the direct and indirect influences of climate on NPP

Michaletz *et al.* made a useful contribution by compiling a valuable database and explicitly attempting to resolve the variables that influence NPP. However, the Michaletz *et al.* analyses were subject to the flaws described above (summarized in Table 1), and their multiple regression and partial correlation analyses were not appropriate to test the relative importance of direct and indirect effects of climate on NPP. Three powerful approaches applicable to such a question – although not previously used, to our knowledge, to analyze the drivers of NPP – are maximum-likelihood model selection (MLMS; Hilborn & Mangel, 1997; Burnham & Anderson, 2002), independent-effects analysis (IEA; Murray & Conner, 2009), and structural equation modeling (SEM; Grace, 2006; Grace *et al.*, 2012). When we applied these approaches to the compiled dataset of Michaletz *et al.*, each provided special insights and they all converged in supporting climate as a direct driver of NPP across ecosystems globally (Table 2).

We applied MLMS to the Michaletz *et al.* dataset comparing Eqns (M3) and (M4) with more parsimonious models based on removing climate variables (see Appendix Table S1). In the analysis of Eqn (M3), six of seven tested models that included climate variables were selected over the model based on M_{tot} and a without climate variables ($\Delta AIC_c = 3.6–79$; note that a ΔAIC_c of ≥ 2 is a basis for rejecting models). This finding was supported whether annual or seasonal means were used for temperature or precipitation (Appendix Table S1). According to these models, global variation in l_{gs}, T_{ann}, and P_{ann} drove variation in NPP by 60%, 51%, and 30%, respectively (Appendix Table S1). The models with a removed, to eliminate the hidden circularity of including ABC as an input, also showed far greater support when including climate variables ($\Delta AIC_c = 65–414$; Table S1). According to these models, global variation in l_{gs}, T_{ann}, and P_{ann} drove NPP to vary by 4.2-fold, 3.6-fold, and 2.1-fold, respectively (Fig. 5a–c). When testing models for NPP normalized by l_{gs}, thus already removing much of the influence of climate, models with climate variables included were still selected with greater likelihood than models with M_{tot} and a alone (Table S1). This analysis demonstrates that climate variables l_{gs}, temperature, and precipitation have strong, quantitatively important influences on NPP independently of M_{tot} and a.

Second, we used independent-effects analysis based on Eqn (M3) to analyze the dataset. We found that climate variables had strong effects on NPP independently of M_{tot} and a, with climate variables amounting to 25–28% of all the variables' influence on NPP, whether climate variables were considered as annual or growing season means (Fig. 6a; Appendix Table S1). Further, when testing the model based on Eqn (M3) but removing the a term, to avoid the hidden circular term ABC, the climate variables accounted for 45–50% of all of the variables' influence on NPP, similar to the 50–55% explained by M_{tot} (Fig. 6b). The lack of importance of a was confirmed by a test of the model based on Eqn (M3) but without the M_{tot} term, which showed that a alone had only a small effect on NPP, that is, 7–8% of all the variables' influence (Fig. 6c). When testing Eqn (M4), in which NPP was controlled by l_{gs}, the influence of temperature and precipitation was much reduced, consistent with the fact that l_{gs} represents a major component of T_{ann} and P_{ann} and its being an intrinsic geophysical correlate of T_{gs} and P_{gs} (Eqns 1a and 2a) – yet the remaining climate variables explained 7–18% of all the variables' influence, or, testing the model based on Eqn (M4) but not including a, 6–16% of all the variables' influence. All these analyses indicate a strong, direct influence of climate on NPP, independently of M_{tot} and a.

Table 2 Three novel analyses applied to the database of Michaletz et al. (2014) to disentangle the effects of climate variables (mean annual and growing season temperature and precipitation, and the length of the growing season; T_{ann}, T_{gs}, P_{ann}, P_{gs}, and l_{gs}, respectively) and stand variables (stand biomass and age, M_{tot} and a, respectively) on net primary productivity (NPP) across ecosystems globally. All three analyses converged in the same result, opposite to that of Michaletz et al. (2014), that is, strong, direct climatic effects that are independent of M_{tot} and a, equal to or far stronger than any indirect effects of climate on NPP via M_{tot} or a

| Analysis	Outcome	Specific advantage of analysis	Finding	Conclusion
Maximum-likelihood model selection (MLMS)	MLMS estimates parameters for a set of candidate models, by maximizing the log-likelihood of observing the data given parameter values, and using the Akaike information criterion (AIC), one may select the model with the optimal balance between maximizing the log-likelihood of the fitted parameters and maximizing parsimony in the number of parameters (Burnham & Anderson, 2002).	Enables the comparison of models with and without climate variables to select the most likely, and the fitted models may be used to determine the direct influence on NPP of shifts in given variables.	Models for predicting NPP that included climate variables were selected over models based only on stand variables. According to models predicting NPP without circularity, the global variation in l_{gs}, T_{ann}, and P_{ann} resulted in global NPP variation of 4.2-fold, 3.6-fold, and 2.1-fold, respectively.	Climate variables l_{gs}, temperature, and precipitation have strong influences on NPP independently of M_{tot} and a, accounting for many-fold variation in NPP globally.
Independent-effects analysis (IEA)	IEA averages the contribution to variance in y of each predictor variable across all models that include a subset of the predictors, robustly partitioning the contribution of correlated predictor variables.	Enables robust partitioning of the independent contributions to NPP of correlated predictors, including the stand and climate variables.	Analyzing Eqn (M3), we found that climate variables had independent effects on NPP from M_{tot} and a, amounting to 25–28% of all the variables' influence on NPP. Testing the model based on Eqn (M3) but removing the a term, to avoid the hidden circularity, the climate variables accounted for 45–50% of all of the variables' influence on NPP, similar to the 50–55% explained by M_{tot}.	As above. Further, the influence of climate variables independently of M_{tot} and a accounted for approximately as much of the variation in NPP globally as did M_{tot}.
Structural equation modeling (SEM)	SEM analyses interrelated variables as networks of causal processes (Grace, 2006; Grace et al., 2012).	Enables disentangling the direct effects of climate on NPP, from the hypothesized indirect effects of climate on NPP via stand age and biomass.	Models showed the total effect of climate was equal to or stronger than that of M_{tot} and the direct effects of climate on NPP were approximately equal to or stronger than indirect effects (47–94% of the total effect of climate on NPP was direct).	As above. Further, climate variables have approximately equal or greater direct effects on NPP than indirect effects (i.e., via M_{tot} and a).
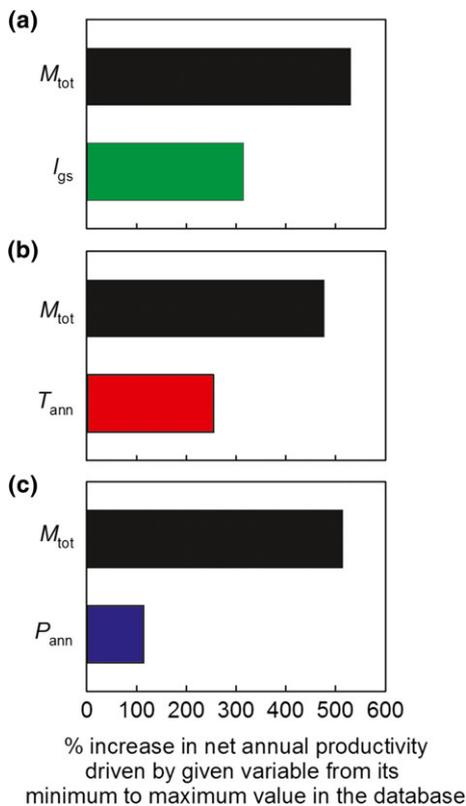
Fig. 5 Sensitivity analysis showing the strong influence of climate variables on net annual productivity (NPP) based on models including individual climate variables and stand biomass (M_{tot}), parameterized by maximum likelihood for the global database compiled by Michaletz *et al.* (2014). For each model, the effects on NPP are shown of increasing individual variables from the minimum value in the database to the maximum, with the other variable at its mean value in the database. (a) model predicting NPP from the length of the growing season and M_{tot} ($\ln(\text{NPP}) = \alpha \ln(M_{tot}) + \alpha_{l_{gs}} \ln(l_{gs}) + \beta_{0,1}$; $R^2 = 0.50$; $P < 0.001$); (b) from mean annual temperature (T_{ann}) and M_{tot} ($\ln(\text{NPP}) = \alpha \ln(M_{tot}) - (E/kT_{ann}) + \beta_{0,1}$; $R^2 = 0.50$; $P < 0.001$); and (c) from mean annual precipitation (P_{ann}) and M_{tot} ($\ln(\text{NPP}) = \alpha \ln(M_{tot}) + \alpha_P \ln(P) + \beta_{0,1}$; $R^2 = 0.35$; $P < 0.001$).

Third, we conducted structural equation modeling (SEM) to explicitly test for the direct and indirect dependence of NPP on climatic variables. Model A represents the hypothesis of Michaletz *et al.*, in which climate variables could have direct influence on NPP or could influence NPP indirectly via M_{tot} and a (Fig. 7a; Table S2). In model B, we removed the a term to avoid the hidden circularity (Fig. 7b). Model C was the same as model B, but with additional causal relationships representing the influence of l_{gs} on T_{ann} and P_{ann}, consistent with Eqns (1a) and (2a) (Fig. 7c). We found that model A was not supported (Table S2), probably due to its hidden circularity. Models B and C were highly supported and model B using growth season climate variables had the lowest
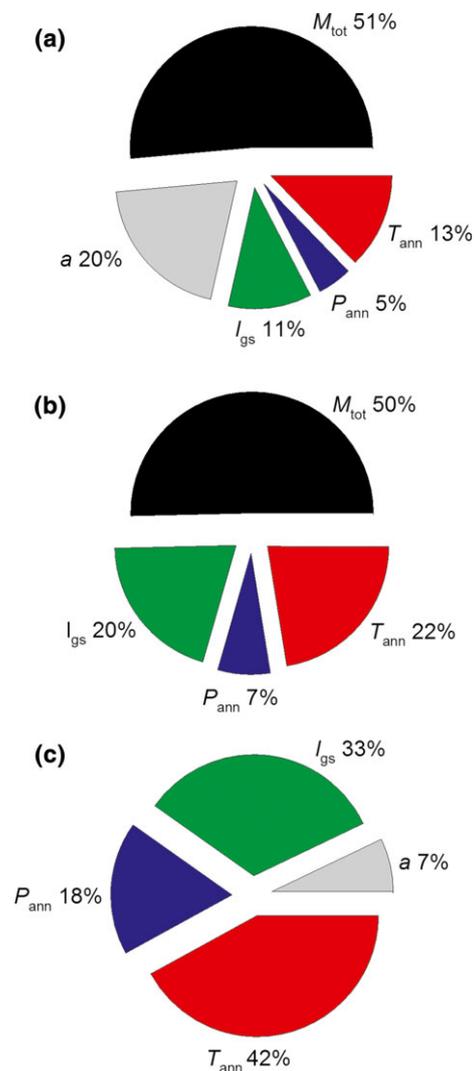
Fig. 6 Results of independent-effects analysis applied to the models for net annual productivity with climate variables, stand biomass (M_{tot}), and stand age (a) from the global database compiled by Michaletz *et al.* (2014): (a) full Eqn (M3) model, including M_{tot}, a, the length of growing season (l_{gs}), mean annual temperature (T_{ann}), and mean annual precipitation (P_{ann}) ($\ln(\text{NPP}) = \alpha \ln(M_{tot}) + \alpha_a \ln(a) - (E/kT) + \alpha_P \ln(P) + \alpha_{l_{gs}} \ln(l_{gs}) + \beta_{0,1}$; $R^2 = 0.74$; $P < 0.001$); (b) model including M_{tot}, l_{gs}, T_{ann}, and P_{ann} ($\ln(\text{NPP}) = \alpha \ln(M_{tot}) - (E/kT) + \alpha_P \ln(P) + \alpha_{l_{gs}} \ln(l_{gs}) + \beta_{0,1}$; $R^2 = 0.51$; $P < 0.001$); and (c) model including a, l_{gs}, T_{ann}, and P_{ann} ($\ln(\text{NPP}) = \alpha_a \ln(a) - (E/kT) + \alpha_P \ln(P) + \alpha_{l_{gs}} \ln(l_{gs}) + \beta_{0,1}$; $R^2 = 0.26$; $P < 0.001$). Similar results were found using growing season mean temperature and precipitation (Table S1).

AIC. In all the models, the total effect of climate was approximately equal to or stronger than that of M_{tot} (each contributing about 50% of the determination of NPP), and the direct effects of climate on NPP were approximately equal to or stronger than indirect effects (47–94% of the total effect of climate was direct; Table S2).

(a) Model A

(b) Model B

(c) Model C
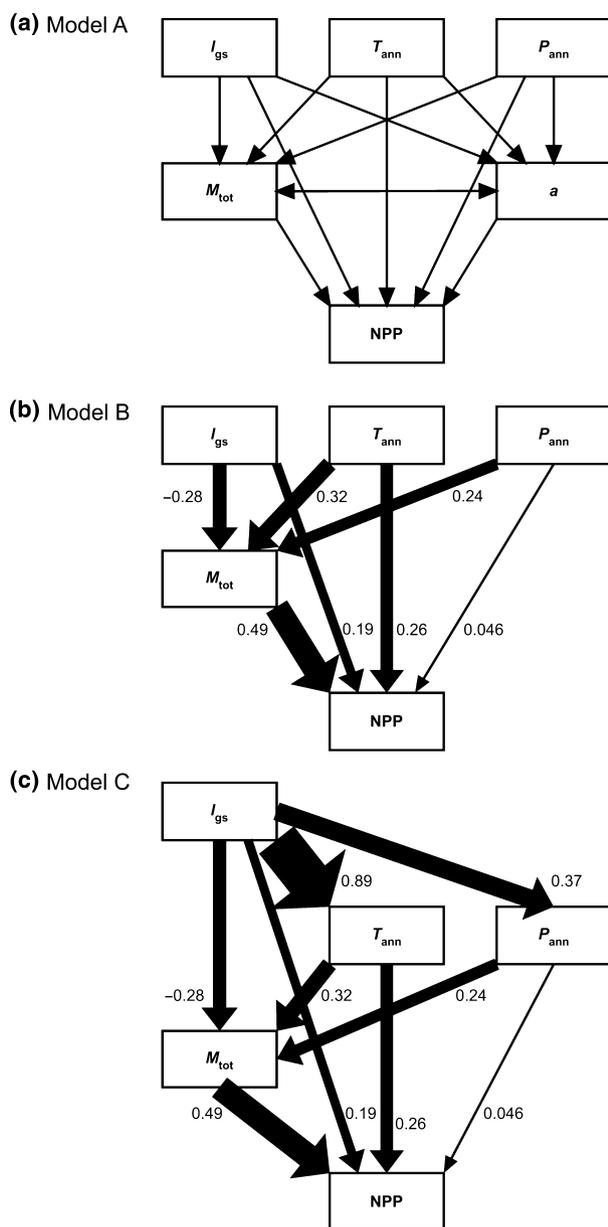
Fig. 7 Structural equation models (SEM) for net annual productivity (NPP) as determined by climate variables, stand biomass (M_{tot}), and stand age (a) applied to the 1247 ecosystems worldwide in the dataset of Michaletz *et al.*, 2014; climate variables include length of growing season (l_{gs}), and mean annual or mean growing season temperature and precipitation (T_{ann}, T_{gs}, P_{ann}, and P_{gs}, respectively). Model A was based on the hypothesis of Michaletz *et al.* that climate variables would have direct effects on NPP or indirect effects via M_{tot} and stand age (a) and that model was not supported, likely due to the circularity of including M_{tot} and a (and therefore ABC) as predictors of NPP. Model B was the same model without including the a term, and model C had additional influence of l_{gs} on T and P (as explained in the text). Each model was tested using annual or mean temperature and precipitation (shown here), or growing season means (T_{gs} and P_{gs} rather than T_{ann} and P_{ann}). The best supported model by AIC was model B using growing season mean climate variables (Table S2 for direct and indirect effects of each factor). To obtain the standardized path coefficients, z-transformation was used to adjust the means of variables to zero and their variances to 1.0. Directional arrows linking two variables depict direct effects (all significant at $P < 0.05$). The thickness of the solid arrows reflects the magnitude of the standardized SEM coefficients, which are listed beside each path.

Avoiding pitfalls and improving resolution in future studies of the drivers of NPP

We agree with Michaletz *et al.* that novel analyses are needed to clarify NPP and its drivers and to improve predictive power. However, we disagree with the overall conclusion of Michaletz *et al.* that climate has a negligible direct impact on NPP. We found that strong direct effects of climate on NPP can be resolved at the global scale using rigorous approaches such as MLMS, IEA, and SEM. Our analyses are especially novel in demonstrating that combining stand structure and climate data enables a prediction of NPP across ecosystems (R^2 of approximately 0.50), with climate variables and M_{tot} contributing strongly to this predictive power.

Michaletz *et al.* proposed several explanations for why climate should not directly influence NPP at the global scale. First, they suggested that the influence of climate may be indirect via stand variables, because NPP would increase with M_{tot} and decline with a, and these stand variables might in turn be constrained by climate, although our analyses showed that direct effects were equal to or outweighed such indirect effects. Second, they posited that plants should be selected globally for rapid growth and that biochemical adaptation and/or acclimatization to cold temperatures may offset temperature effects, resulting in a dampened relationship of NPP to temperature. We argue that local adaptation and plasticity cannot completely overcome the effects of global climate variation on growth, and

Thus, rather than finding negligible direct effects of climate variables on NPP, all three of our analyses converged in the same result, opposite to that of Michaletz *et al.* (2014). We found strong, direct climatic effects, equal to or stronger than indirect effects of climate on NPP via M_{tot} or a. We found that l_{gs} is the strongest climatic driver of NPP with additional, important, and independent explanatory power of temperature and precipitation, whether averaged annually or for the growing season. All these analyses highlighted the crucial and direct role of climate in determining NPP, consistent with mechanistic principles, and underlining the need to address the influence of climate change impacts on global vegetation.

sometimes they can reinforce the effects of climate, as shown by studies of field and common garden plants in which growth-related traits are equally or more strongly related to climate of origin in the field than when grown in a common garden, and studies showing that cold temperatures limit growth in many terrestrial ecosystems (Clausen *et al.*, 1940; Cordell *et al.*, 1998; Reich & Oleksyn, 2008). Because they did not see an effect of temperature, Michaletz *et al.* also argued that 'future studies move away from using mean annual temperature and instead use air and plant body temperatures measured during the growing season and/or key periods of development'. This is bad advice; it is well known that leaf temperatures correlate closely with air temperature over hourly and daily timescales (Jones, 2014). Finally, Michaletz *et al.* questioned the appropriateness of their own climate data, interpolated from climate models using 29-year means. We agree that such data are imprecise. Yet, our analyses were able to identify strong direct influences of climate on NPP and ABC.

The first rule of statistical inference that students learn is that correlation does not necessarily imply causation. It therefore follows that the strength of a correlation does not necessarily imply the strength of a causal relationship. If we can do experiments, we can disentangle causal networks with strong inferences. When we have only descriptive data, we have to make assumptions before we can make inferences about causal factors, and any conclusions we reach are highly dependent on those assumptions. Michaletz *et al.* made several assumptions about what are and are not climate variables and about causal chains, assumptions that did not withstand critical analysis. They used input variables that already include the effects of climate (i.e., ABC = M_{tot}/a) and removed climate from a predicted variable before testing (i.e., NPP/l_{gs}). Therefore, adding climatic variables in these analyses did not provide additional predictive power. Statistical approaches such as MLMS, IEA, and SEM not only help us to get the strongest inferences from data, but also force us to be clear and 'up front' about the assumptions we are making, so that these can be scrutinized and open to criticism.

There is actually a great deal of experimental evidence for the direct role of climate in determining NPP. If we irrigate a dryland, NPP increases enormously. If we warm arctic tundra, NPP increases significantly (Natali *et al.* 2012). These are obvious direct effects, and many strange assumptions would be necessary to interpret these as indirect effects.

This debate highlights the extent to which our understanding of climate impacts on ecosystems worldwide has been fragmentary. Our work focused mainly on approaches to testing the direct influence of climate on NPP given the database compiled by Michaletz *et al.* However, further improvements are needed both in the quality and the representativeness of the dataset for NPP (see Appendix S5). Local climate data are scarce for many ecosystems of the world, a situation currently being ameliorated (Anderson-Teixeira *et al.*, 2014; Schimel & Keller, 2015; Sternberg & Yakir, 2015). As data become available, analyses will require close scrutiny if we are to tease apart the direct and indirect influences of climate on NPP and other aspects of ecosystem structure and function. In the models we tested that predicted NPP from climate and M_{tot}, excluding a to avoid circularity, the R^2 values were approximately 0.50. We need to include other factors beyond climate and stand biomass for the prediction of NPP, including soil fertility (Fernandez-Martinez *et al.*, 2014), composition and diversity of communities (Dijkstra *et al.*, 2011; Gillman *et al.*, 2015), species interactions (Adler *et al.*, 2012), and disturbance (Chave *et al.*, 2001). Analyses with improved sampling, avoiding the described pitfalls, and implementing a range of high-resolution statistical approaches will result in greatly improved predictive models relating ecosystem functioning to climate (and other factors), in turn leading to more accurate projections for given ecosystems, and reliable information for next-generation dynamic global vegetation models (Prentice *et al.*, 2015), which will best inform policies to enhance the preservation of ecosystems and the mitigation of ongoing climate change.

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Supporting Information

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

Table S1. (Excel spreadsheet). Models for predicting annual net primary productivity (NPP) for ecosystems worldwide from stand biomass (M_{tot}), stand age (a), and climate variables representing temperature (T), precipitation (P) and growing season length (l_{gs}).

Table S2. Structural equations modeling of net primary productivity (NPP) across 1247 ecosystems worldwide in the dataset of Michaletz *et al.* (2014) analyzed by stand biomass and climate variables.

Table S3. Mean values ± standard error for NPP and climate variables for stands categorized by ages as conducted by Michaletz *et al.* (2014).

Figure S1. Structural equation models (SEM) for net annual productivity (NPP) as determined by climate variables, stand biomass (M_{tot}) and stand age (a) applied to the 1247 ecosystems worldwide in the dataset of Michaletz *et al.* (2014).

Figure S2. Plots to illustrate the spurious analysis of Michaletz *et al.* (2014) from which they concluded that NPP was driven by stand age in their database.

Appendix S1. Statistical methods.

Appendix S2. Supplementary results: on estimating the influence of stand age on NPP.

Appendix S3. Derivation of Eqn (M3a).

Appendix S4. Supplementary discussion: relationship of NPP and ABC.

Appendix S5 Improvements needed for datasets and analyses of drivers of NPP globally.

Appendix S6. Supplementary references.