

Drivers of terrestrial plant production across broad geographical gradients

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Abstract

Terrestrial net primary production (NPP) varies across global climate gradients, but the mechanisms through which climate drives this variation remain subject to debate. Specifically, it is debatable whether NPP is primarily influenced by 'direct' effects of climate on the kinetics of plant metabolism or 'indirect' effects of climate on plant size, stand biomass, stand age structure and growing season length. We clarify several issues in this debate by presenting multiple lines of evidence that support a primarily indirect influence of climate on global variation in NPP across broad geographical gradients. First, we highlight > 60 years of research that suggests leaf area, growing season length, plant biomass and/or plant age are better predictors of NPP than climate or latitude. Second, we refute recent claims that using biomass and age as predictors of NPP represents circular reasoning. Third, we illustrate why effects of climate on the kinetics of plant production must be evaluated using instantaneous (not annualized) rates of productivity. Fourth, we review recent analyses showing that the effects of biomass and age on NPP are much stronger than the effects of climate. Fifth, we present new analyses of a high-quality NPP dataset that demonstrate further that biomass, age and growing season length are better predictors of global variation in NPP than climate variables. Our results are consistent with the hypothesis that variation in NPP across global climate gradients primarily reflects the influence of climate on growing season length and stand biomass, as well as stand age, rather than the effects of temperature and precipitation on the kinetics of metabolism. However, this hypothesis should be evaluated further using larger, high-quality observational and experimental datasets spanning multiple geographical scales.

KEYWORDS

forests, growing season length, metabolic scaling theory, net primary production, plant age, precipitation, stand biomass, structural equation modelling, temperature

1 | INTRODUCTION

Identifying the relative importance of abiotic and biotic influences on ecosystem processes across broad geographical gradients remains a central challenge in global ecology (Chapin et al., 1997; Schimel et al., 1996). For example, comparative studies of terrestrial net primary production (NPP) across global climate gradients are essential for a more quantitative understanding of how biology responds to climate change and of the role of the biosphere within the integrated Earth system (Gillman et al., 2015; Huston & Wolverton, 2009; Xia et al., 2015). However, to understand the drivers of NPP across broad gradients, we must establish how best to compare and model ecosystem fluxes that vary by orders of magnitude (from leaf-level physiology to stand

dynamics and regional disturbance) and between sites that differ in crucial variables (such as the length of the growing season and standing biomass).

It is well established that NPP varies across gradients in mean annual temperature and precipitation (Huxman et al., 2004; Lieth, 1975; Ponce Campos et al., 2013; Schuur, 2003). However, a current debate questions whether this variation reflects a 'direct' effect of climate on the kinetics of plant metabolism or an 'indirect' effect of climate via constraints on plant size, stand biomass, stand age structure and growing season length (I_{gs}) (Chu et al., 2016; Enquist, 2011; Michaletz, Cheng, Kerkhoff, & Enquist, 2014; Piao et al., 2010). The question is not whether climate influences NPP, but how it influences NPP; whether through direct effects on the rates of physiological processes

or through indirect effects on the time and biomass available to perform those physiological processes. Recently, we showed that on both annual and seasonal time-scales, global variation in NPP is better explained by stand biomass, plant age and growing season length than by air temperature or precipitation (Michaletz, Cheng, Kerkhoff, & Enquist, 2016; Michaletz et al., 2014). We interpreted these results as support for the hypothesis that an indirect influence of climate best explains variation in NPP across broad geographical gradients.

A subsequent paper (Chu et al., 2016) criticized these findings, arguing that they are out of step with the scientific consensus and originated from flawed statistical analyses and circular reasoning. In this paper, we revisit this debate and examine the arguments of Chu et al. (2016). In doing so, we take issue with several details of their analysis and identify both procedural errors and disagreements in interpretation. We show that their analyses only provide further support for our original conclusions. Indeed, multiple lines of evidence all support the conclusion that climate influences NPP primarily through the indirect effects of the time available for physiological processes (growing season length) and the peak physiological capacity of local environments (determined by plant biomass and leaf area; Xia et al., 2015), rather than through the direct effects of precipitation and air temperature on the rate of physiological processes per unit leaf area.

2 | A LONG HISTORY SUPPORTS THE INDIRECT CLIMATE HYPOTHESIS

Previous literature on the climatic determinants of NPP provides the context for this debate, and Chu et al. (2016) claim that our findings 'challenged the consensus' of this literature. This is not correct. For > 60 years, many studies have shown that biogeographical patterns of NPP are better explained by variation in leaf area, growing season length, plant biomass and/or plant age than by climate variables or latitude (Billings & Mooney, 1968; Bliss, 1962; Bonan, 1993; Chapin, 1983, 2003; Gillman et al., 2015; Huston & Wolverton, 2009; Kerkhoff, Enquist, Elser, & Fagan, 2005; Kikuzawa & Lechowicz, 2006; Kira, Ogawa, Yoda, & Ogino, 1967; Knapp, Carroll, & Fahey, 2014; Körner, 2002, 2006; Tadaki, Hattaya, & Tochiaki, 1969; Watson, 1952; Xia et al., 2015). In fact, these relationships are so well established that they have been discussed at length in prominent ecology textbooks since at least the 1950s (e.g., pages 69, 74 and 76–77 of Odum, 1959; page 640 of Ricklefs, 1973; pages 251, 256 and table 15.5 of Körner, 2003; pages 499–511 of Begon, Townsend, & Harper, 2006; and pages 124, 169–172, 178, table 6.7 and fig. 5.2 of Chapin, Matson, & Vitousek, 2011). These examples demonstrate that our conclusions are not out of step with the literature.

3 | BIOMASS AND AGE ARE APPROPRIATE PREDICTORS OF NET PRIMARY PRODUCTIVITY

One source of confusion in this debate is that stand biomass and age are both products and determinants of NPP. Chu et al. (2016) argue that the correlation between NPP and biomass and age is 'spurious'

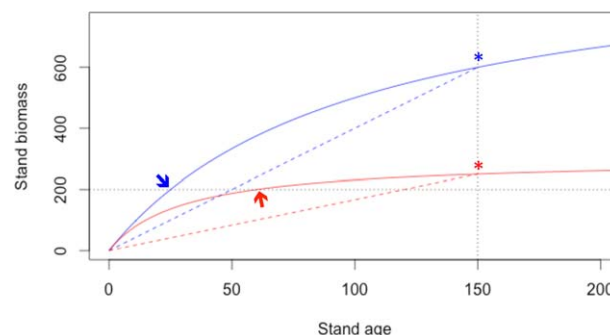


FIGURE 1 Biomass trajectory for two stands with different capacities for supporting plant biomass (blue and red lines indicate high and low biomass capacities, respectively). From this depiction, the net biomass change (NBC; the tangent to the biomass trajectory) at any given stand biomass (arrows) or age (asterisks), depends importantly on the capacity of the environment to support plant biomass, which is strongly constrained by climate and other factors. Average biomass change (ABC; slope of the dashed lines) is correlated with NBC (and thus net primary productivity) precisely because NBC depends on stand age and biomass, as determined by the climatically determined biomass capacity of the environment

owing to a 'hidden circularity.' This is false. They claim that this circularity originates from two sources.

First, Chu et al. (2016) claim that the average biomass change ($ABC = M_{tot}/a$) is 'mechanistically downstream' of NPP, so that regression of NPP on biomass (M_{tot}) and age (a) is circular. They correctly point out that M_{tot}/a represents the past ABC over the lifetime of a stand and that this is correlated with NPP. However, correlation does not define circularity. Furthermore, their perspective does not acknowledge the direct effects of biomass and age on current NPP. NPP depends strongly on the leaf area available for photosynthesis (Chapin et al., 2011; Körner, 2003), and leaf area varies allometrically (not isometrically) with plant biomass (Kerkhoff et al., 2005; Niklas & Enquist, 2001). Likewise, as stands approach their biomass capacity (Figure 1), which is constrained by climate (Kempes, West, Crowell, & Girvan, 2011; Klein, Randin, & Körner, 2015; Larjavaara, 2014; Stegen et al., 2011), they face a myriad of age-related limitations on productivity (Binkley, Stape, Ryan, Barnard, & Fownes, 2002; Drake, Davis, Raetz, & DeLucia, 2011; Gower, McMurtrie, & Murty, 1996; Ryan, Binkley, & Fownes, 1997). But as a time average, ABC is not itself part of the mechanics of current primary production and biomass change. Instead, the net biomass change of a stand (NBC, of which ABC is the long-term average) depends mechanistically on stand age and biomass. The quantitative nature of this dependence is determined by the biomass capacity of the environment (Figure 1).

Second, Chu et al. (2016) imply that $ABC = M_{tot}/a = \langle NPP \rangle_a \approx NPP$ (e.g. their appendix S4), suggesting that the analyses by Michaletz et al. (2014) involve regression of NPP on $\langle NPP \rangle_a$. They claim this is analogous to regression of velocity on distance/time, where velocity = distance/time. However, contrary to the definition provided by Chu et al. (2016), ABC is not equivalent to $\langle NPP \rangle_a$, because ABC includes only those components of NPP that accumulate as standing biomass (mostly wood);

notably missing is turnover of leaves, reproductive structures and fine roots, which can account for > 60–80% of NPP (da Costa et al., 2014; Doughty et al., 2014; Elkinington & Jones, 1974; Kira, Ogawa, Yoda, & Ogino, 1964; Malhi, Doughty, & Galbraith, 2011; Singh, 1975). Indeed, as acknowledged by Chu et al. (2016), mature forest stands often exhibit large NPP values with minimal NBC. Finally, if ABC is equivalent to NPP and $\langle \text{NPP} \rangle_a$ as Chu et al. (2016) imply, then we would expect an isometric scaling relationship such that $\text{ABC} = M_{\text{tot}}/a = c \cdot \text{NPP}^1$, where c is a normalization constant. Indeed, ordinary least squares (OLS) regression of data shown in fig. 4 of Chu et al. (2016) yields $\text{ABC} = M_{\text{tot}}/a = c \cdot \text{NPP}^{0.96}$, where the fitted exponent is not statistically different from 1 (95% confidence interval = 0.93–1.00), indicating a linear isometry between ABC and NPP. However, their isometry originates from the use of NPP data that were calculated from M_{tot} and a as described by Michaletz, Cheng et al. (2016). OLS regression of NPP data not affected by this issue shows that $\text{ABC} = M_{\text{tot}}/a = c \cdot \text{NPP}^{0.65}$, where the fitted exponent is significantly different from 1.0 (95% confidence interval = 0.47–0.84). Thus, ABC is not equivalent nor proportional to NPP. In short, the relationships between NPP, biomass and age shown by Michaletz et al. (2014) are not spurious and do not originate from a hidden circularity.

In summary, the correlation between ABC and NPP does not render the relationship between NPP, biomass and age spurious; it arises from the relationship between NPP, biomass and age. To assert that the correlation between NPP, biomass and age is spurious is to claim that NPP is not causally related in any way to standing plant biomass and stand age structure, even though these demonstrably affect the leaf area available for photosynthesis. Biomass is not an inert output of NPP; it feeds back to influence NPP. Thus, it is not 'circular reasoning' to use stand biomass and age to predict NPP; it is physiologically and ecologically sensible.

4 | NET PRIMARY PRODUCTIVITY KINETICS MUST BE EVALUATED ACROSS RELEVANT TIME PERIODS

In order to assess the direct and indirect influences of climate, it is important to consider NPP for physiologically relevant time periods. Chu et al. (2016) contend that the weak relationships between air temperature, precipitation and monthly net primary production (NPP/l_{gs}) shown by Michaletz et al. (2014) originate from a 'novel interpretation' of growing season length that inappropriately removes climate influences on production. Indeed, growing season length is determined by climate, and was calculated from temperature and precipitation in our original paper (Michaletz et al. 2014). However, our approach builds on a long history of studies that have used monthly or even daily NPP for such analyses (Billings & Mooney, 1968; Bliss, 1962; Chapin, 1983, 2003; Chapin, Miller, Billings, & Coyne, 1980; Gillman et al., 2015; Huston, 2012; Huston & Wolverton, 2009; Kerkhoff et al., 2005; Körner, 2002, 2006, 2013; Odum, 1959; Ricklefs, 1973; Watson, 1952). These studies show that annual rates of NPP can vary substantially depending on the growing season length.

Indeed, these findings underscore our approach. As illustrated in Figure 2, two sites with identical rates of monthly NPP but different growing season lengths can have dramatically different rates of annual NPP (Chapin, 2003; Huston & Wolverton, 2009; Körner, 2002; Xia et al., 2015). Thus, growing season length has a strong influence on NPP. This reflects an indirect effect of climate, however, because it does not influence rates of physiological processes, but rather the time available for those physiological processes to proceed. In order to test properly for direct climate effects on the kinetics of plant physiology and metabolism, production rates must be calculated and compared over the period of time when plants are metabolically active (i.e., NPP/l_{gs}).

5 | GLOBAL VARIATION IN NET PRIMARY PRODUCTIVITY IS BETTER EXPLAINED BY BIOMASS AND AGE THAN BY CLIMATE

The complexity of comparative studies of NPP across broad climatic gradients presents several statistical hurdles. Chu et al. (2016) used maximum likelihood model selection (MLMS), independent effects analysis (IEA) and structural equation modelling (SEM) to conclude that effects of temperature and precipitation on NPP were similar in magnitude to those for biomass and age. They argued that their MLMS favoured inclusion of climate variables, challenging the conclusions of Michaletz et al. (2014). But a careful reexamination of their models with and without climate variables (mod1 and mod8, respectively, in their supplemental information table S1 section B) reveals only a minimal difference in variation explained (R^2 of 0.77 and 0.74, respectively). This underscores our original conclusions that the increase in explanatory power for average climate conditions is minor. Likewise, in their IEA, stand biomass explained c. 10 times more variation in annual NPP than did temperature or precipitation, and age explained c. 3.5 times more variation (mod1 in their supplemental information table S1 section B); results for monthly NPP during the growing season are even more striking (their supplemental information table S1 section D). Thus, their MLMS and IEA analyses do not contradict our conclusions, but instead support our finding that biomass and age are stronger predictors of NPP than temperature or precipitation.

Based on traditional variance–covariance SEM with Akaike's information criterion (AIC) model selection (their fig. 7 and supplemental information table S2), Chu et al. (2016) argue that age should be excluded from the analysis and that climate and biomass have similar influences on NPP. However, these conclusions are incorrect because of two crucial errors. First, the apparent lack of χ^2 support for their model A that included age resulted not from 'circularity of including M_{tot} and a ... as predictors of NPP' as they claimed, but rather from an erroneous interpretation of the SEM. Specifically, a p -value could not be calculated for this SEM and thus overall model fit could not be evaluated (this was confirmed with R code sent to us by Chu et al., 2016). Second, their conclusion that biomass and climate have equivalent influences on NPP is based on an inappropriate comparison between the direct effect of biomass and the summed direct effects of growing season length, temperature and precipitation. It is more appropriate to compare total effect sizes (summed direct and indirect effects; Grace,

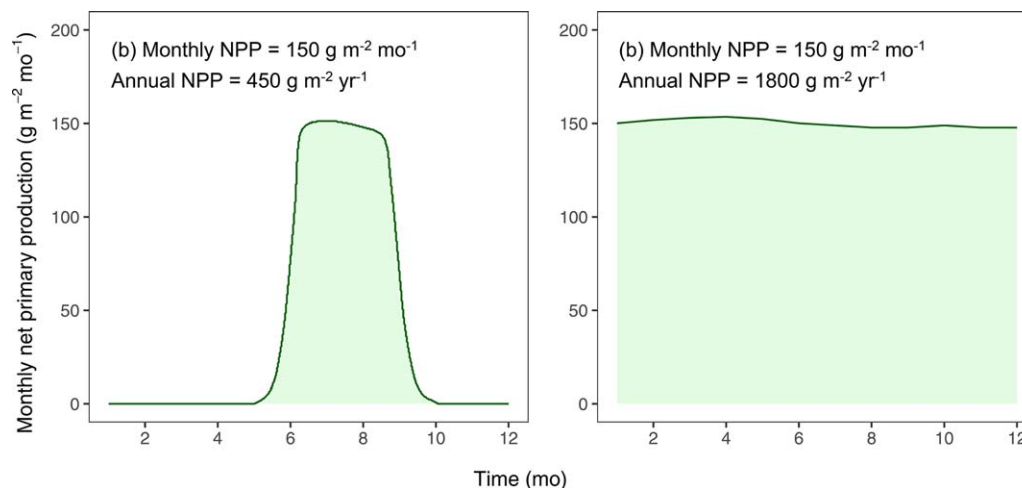


FIGURE 2 Two sites with nearly identical rates of monthly net primary productivity (NPP; in grams per square metre per month) but different growing season lengths (in months) can have substantially different rates of annual NPP (in grams per square metre per year). In this hypothetical example, both sites have an identical monthly NPP of $150 \text{ g/m}^2/\text{month}$, but their different growing season lengths of (a) 3 and (b) 12 months yield time-integrated annual NPP values of 450 and $1800 \text{ g/m}^2/\text{yr}$, respectively. Dark green lines indicate monthly NPP rates, and light green areas show time-integrated annual NPP rates. This illustrates why studies that evaluate the influence of temperature and precipitation on the kinetics of production should use monthly (not annual) rates of NPP

2006) among variables; their supplemental information table S2 data shows that total effect size is substantially larger for biomass (0.55) than for temperature (0.11) or precipitation (0.12). These results support the original conclusions of Michaletz et al. (2014), especially given that growing season length does not influence physiological rates and thus represents an indirect climate effect.

6 | CONFIRMING THE IMPORTANCE OF BIOMASS, AGE AND GROWING SEASON LENGTH FOR NET PRIMARY PRODUCTIVITY

A final challenge for broad-scale comparisons of NPP is variability in data quality, an especially difficult problem for studies based on global data compilations (Šimová & Storch, 2017). Since the publication of Michaletz et al. (2014) and Chu et al. (2016), we learned that the China NPP data analysed in both studies were calculated from stand biomass and plant age. These data are thus inappropriate for analyses that use stand biomass and plant age as predictors of NPP. This is further explained in a corrigendum to our original study (Michaletz, Cheng et al., 2016), which was published to raise awareness of the issue in the studies by Michaletz et al. (2014) and Chu et al. (2016) and several other past studies, so that it does not proliferate in the future.

In light of this, here we present new analyses using data ($n = 138$) for which NPP was not calculated from stand biomass and plant age. These analyses use piecewise SEM (Grace et al., 2012) with AIC model selection (Shipley, 2013) using the R package piecewiseSEM (Lefcheck, 2015). Piecewise SEM is more appropriate than traditional SEM for small datasets that contain non-independent observations of multivariate non-normally distributed variables, as in this dataset (Supporting Information Figure S1).

Our new analyses support the hypothesis that global variation in NPP primarily reflects the influence of climate on biomass, age and

growing season length, rather than the effects of temperature and precipitation on the kinetics of metabolism. We began with the preferred model B from Chu et al. (2016), which was fitted to data including growing season climate (Figure 3a; analyses using mean annual climate data are included in Supporting Information Appendix S1). Given that their model excluded age, we tested for independence of age using d-separation (Lefcheck, 2015; Shipley, 2013). For the fitted model [corrected Akaike's information criterion (AICc) = 138], significant paths were found from age to biomass ($p = 0$) and age to NPP ($p = 0$; Figure 3 and Table 1). Next, these missing paths were incorporated into the model (Figure 3b), which vastly improved model fit (AICc = 29; Table 1). We then removed growing season length as a predictor and used it to calculate monthly net primary production as the response (Figure 3c). This model (AICc = 24; Table 1) was strongly favoured over the preferred model B from Chu et al. (2016) ($\Delta\text{AICc} = 114$), and showed that the total effect size for biomass (0.76) was three times larger than for temperature (-0.22) or precipitation (-0.23). Furthermore, comparison with traditional SEM showed that this piecewise SEM provided a better fit ($p = 0.00$ and $p = 1.00$, respectively). This model (Figure 3c and Table 1) shows that although age has strong direct and indirect effects on monthly NPP, the effects are approximately equal in magnitude and opposite in direction, yielding a total effect of approximately zero (Table 1). Thus, although age-related declines in NPP appear to be counterbalanced by age-related increases in biomass, age plays a crucial role in regulating stand biomass effects. The partial correlations for direct effects in this model (Table 1) are shown in Figure 4a; these agree with a separate IEA (Murray & Conner, 2009), which shows that biomass explains c. 12 times more variation in monthly NPP than temperature and about six times more variation in monthly NPP than precipitation (Figure 4b). To summarize, all analyses are consistent in supporting biomass and age as the strongest statistical predictors of

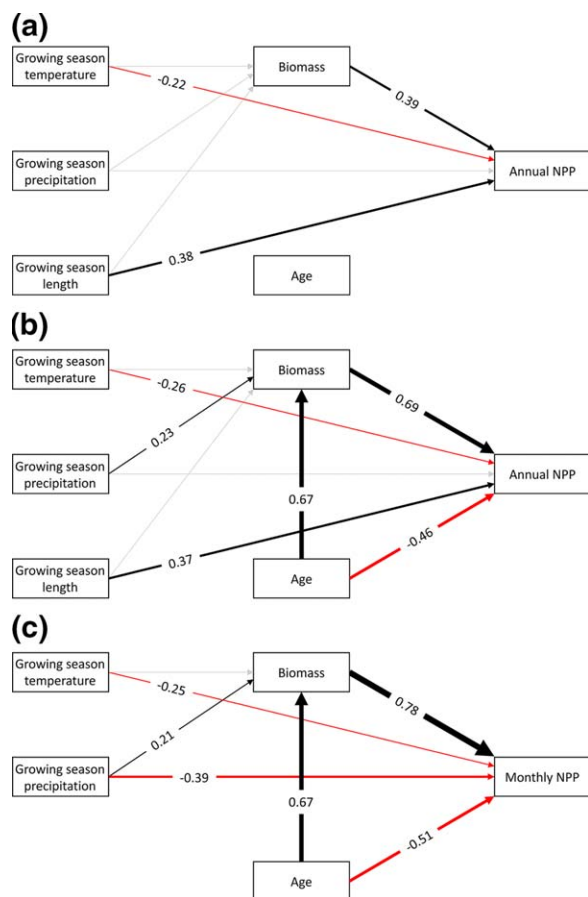


FIGURE 3 Piecewise structural equation models exploring drivers of global net primary production (NPP) for 138 woody plant communities. (a) Shipley's test of d-separation (Shipley, 2013) revealed significant missing paths from age to biomass and age to NPP in model B from fig. 7 of Chu et al. (2016) [corrected Akaike's information criterion (AICc) = 138]. (b) Inclusion of these pathways vastly improved model fit (AICc = 29). (c) Model fit was further improved when growing season length was removed as a predictor variable and used to calculate the monthly net primary production response variable (AICc = 24). To conform with theory in the paper by Michaletz et al. (2014), all variables were \log_e -transformed except for the average growing season temperature $\langle 1/kT \rangle_{gs}$, where k is the Boltzmann constant (8.617×10^{-5} eV/K) and T is temperature (in kelvin). Boxes represent measured variables and arrows represent unidirectional relationships between variables. Black arrows represent positive relationships, red arrows represent negative relationships, and grey arrows represent non-significant paths at $\alpha = 0.05$. Arrow thickness has been scaled according to standardized effect sizes, which are also reported as path coefficients

terrestrial plant production, whereas the kinetic effects of temperature and precipitation are relatively weak predictors.

7 | DISCUSSION AND CONCLUSIONS

This debate is in part semantic, reflecting different interpretations of 'direct' climate effects. To be clear, we use the term only to mean climate effects on instantaneous physiological rates, that is, the kinetics

of photosynthesis and respiration (Körner, 2006). Furthermore, we do not (and have not) claim(ed) that climate is unimportant to understanding terrestrial productivity. Instead, based on the relatively weak direct effects of temperature and precipitation, we argue that variation in NPP across broad geographical gradients is consistent with an indirect influence of climate on growing season length and stand biomass (leaf area), rather than a direct influence on the kinetics of instantaneous leaf-level physiology.

Our conclusions are based on analysis of only five variables that may potentially influence NPP. However, many other variables may also influence variation in NPP, including soil structure, nutrient content and toxicity, as well as episodic events, such as flooding and seasonal drought. It is unclear how inclusion of additional variables would influence our conclusions given that global NPP analyses are limited by a lack of suitable data (Šímová & Storch, 2017). Woody plant production is exceptionally difficult to measure, and available data are based on inconsistent combinations of methods, including diameter growth and allometry, litterfall traps, root excavation and coring, herbivory, frugivory, etc. (see source data file). Additionally, available data are heavily biased towards temperate regions, whereas tropical regions are strongly underrepresented relative to their importance for the global carbon cycle (Clark et al., 2001; Malhi et al., 2011; Taylor et al., 2017). Consequently, our conclusions should be re-evaluated in future studies that use large, high-quality observational and experimental datasets.

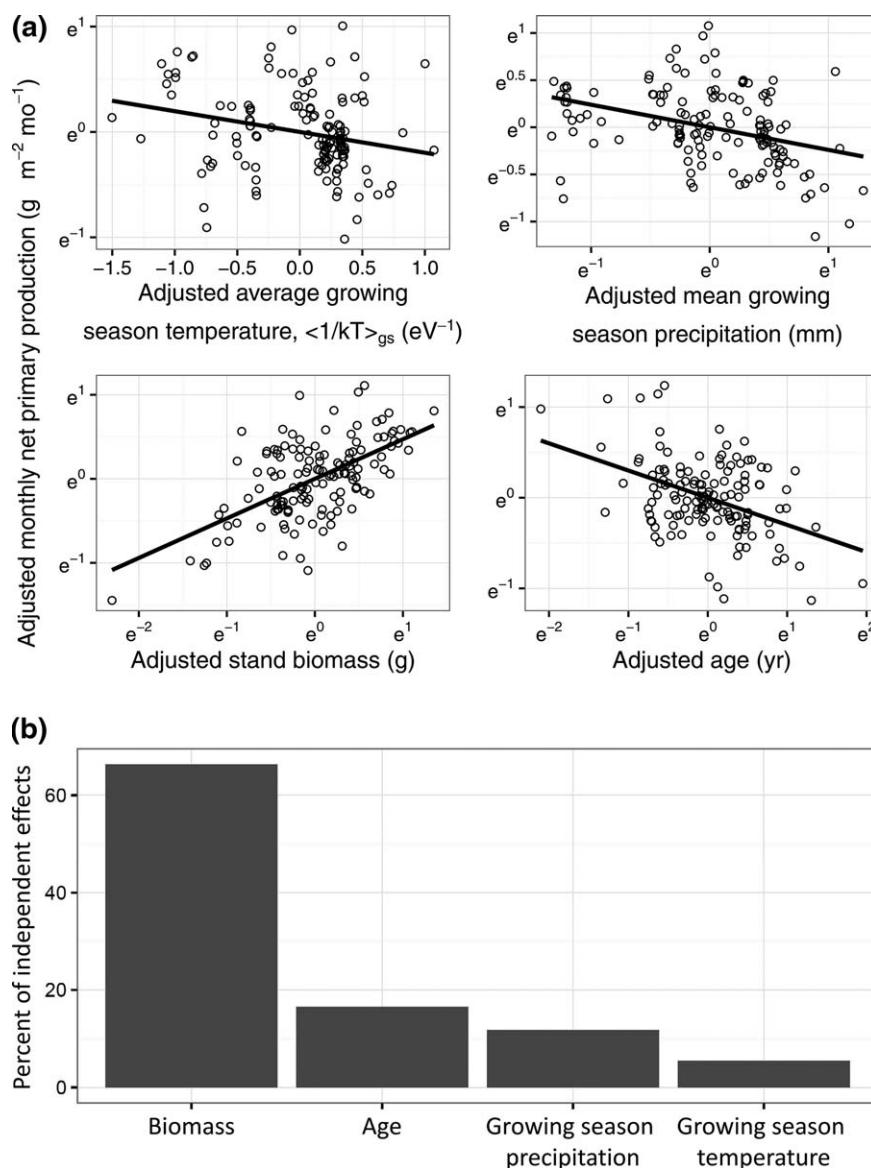
Our conclusions should also be evaluated in systems dominated by non-woody plants, such as grasslands. Although our theory predicts the same general scaling relationship for grasslands and forests, we expect grasses to be more productive than woody plants for a given biomass (i.e., a larger growth normalization constant) because of differences in biomass allocation (grasses have a higher leaf mass fraction than woody plants; Poorter et al., 2012). In other words, grasses should have more 'bang for the biomass buck'. This prediction appears to be borne out in available data (fig. 17.6 of Begon et al., 2006; Oliveras et al., 2014), although we are unaware of any studies that examine biomass, age and climate effects on grassland NPP.

Perhaps another source of confusion in this debate is the relative influence of climate on variation in NPP within and across sites. The conclusions of our analyses may seem counterintuitive because temperature and water availability do directly influence plant physiology and growth within sites (Way & Oren, 2010). Indeed, the direct effects of temperature on the kinetics of photosynthesis and respiration at local scales are well established (Atkin & Tjoelker, 2003; Berry & Bjorkman, 1980; Yamori, Hikosaka, & Way, 2014). Furthermore, temporal variation in gross primary productivity and NPP within a site can be predicted by temporal variation in temperature and precipitation (Doughty et al., 2015; Enquist et al., 2003; Knapp & Smith, 2001; Taylor et al., 2017). For example, within a given site or region, heat and drought can decrease primary production (Brookshire & Weaver, 2015; Ciais et al., 2005). Our results are fundamentally different from these local-scale studies. It is important to emphasize that our findings (a) do not negate or question earlier studies showing a strong role for direct climate effects on temporal variation NPP within sites; and (b) apply to comparison of NPP across sites spanning broad climate gradients.

TABLE 1 Piecewise structural equation models exploring drivers of net primary production for 138 globally distributed woody plant communities

Model	C (d.f., p)	AICc	Δ AICc	Standardized effect size: total effect, direct effect, indirect effect				
				Total stand biomass	Age	Growing season length	Growing season temperature	Growing season precipitation
Model 1 [Chu et al. (2016) model B]	114 (4, 0)	138	114	0.39 , 0.39, n.a.	n.a., n.a., n.a.	0.35 , 0.38, -0.03	-0.24, -0.22, -0.02	-0.03, -0.09, 0.06
Model 2	0 (0, 1)	29	5	0.69 , 0.69, n.a.	0.00 , -0.46, 0.46	0.34 , 0.37, -0.03	-0.24, -0.26, 0.02	-0.03, -0.19, 0.16
Model 3	0 (0, 1)	24	0	0.78 , 0.78, n.a.	0.01 , -0.51, 0.52	n.a., n.a., n.a.	-0.22, -0.25, 0.03	-0.23, -0.39, 0.16

Note. AICc is the corrected Akaike's information criterion and Δ AICc is the difference in AICc relative to model 3 estimated from Shipley's d-separation test (Shipley, 2013). To conform with theory in the study by Michaletz et al. (2014), all variables were \log_e -transformed except for the average growing season temperature, which was expressed as $\langle 1/kT \rangle_{gs}$, where k is the Boltzmann constant (8.617×10^{-5} eV K⁻¹), T is temperature (in kelvin), and gs indicates growing season. Bold text indicates the total standardized effect size.

**FIGURE 4** Drivers of terrestrial plant production. Piecewise structural equation model selection via d-separation and Akaike's information criterion (Lefcheck, 2015; Shipley, 2013) yielded the final model shown in Figure 3c and (a) partial correlations of direct effects. (b) These results agree with a separate independent effects analysis (Murray & Conner, 2009) of direct effects of drivers on monthly net primary productivity (NPP). All analyses were consistent in supporting biomass and age as the strongest predictors of monthly NPP. To conform with theory in the paper by Michaletz et al. (2014), all variables were \log_e -transformed except for the average growing season temperature $\langle 1/kT \rangle_{gs}$, where k is the Boltzmann constant (8.617×10^{-5} eV/K) and T is temperature (in kelvin)

Our findings challenge the idea that annual NPP is higher in warm and wet environments because physiological rates 'run faster' in these conditions. This does not stand up to available evidence, as we and many others have shown (e.g., Chapin, 2003; Körner, 2006). As we originally pointed out (Michaletz et al., 2014), the direct physiological effects of climate on NPP across sites may be mediated by plant–air temperature differences (Helliker & Richter, 2008), thermal adaptation along broad-scale temperature gradients (Enquist, Kerkhoff, Huxman, & Economo, 2007), ecohydrological separation of precipitation and plant-available water (Renee Brooks, Barnard, Coulombe, & McDonnell, 2010) and/or scale mismatch of available climate and NPP data (Michaletz et al., 2014). Our results underscore the importance of understanding how water–energy balance influences maximal plant size and stand structure (Kempes et al., 2011; Klein et al., 2015; McDowell & Allen, 2015), how climate and adaptive plant traits may interact to decouple leaf temperatures and physiological rates from ambient air temperature (Michaletz et al., 2015; Michaletz, Weiser et al., 2016), and how acclimation and adaptation of plant physiology can help to maximize carbon gain across climate gradients (Atkin & Tjoelker, 2003; Atkin et al., 2015; Yamori et al., 2014). In any case, our conclusions do not depend simply on which variables are included as significant model predictors, they are not out of step with the consensus understanding of ecosystem function, and they are not the product of circular reasoning.

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DATA ACCESSIBILITY

Data used in the analyses are provided in the accompanying source data file.

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SUPPORTING INFORMATION

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