# Leaf Economics of Early- and Late-Successional Plants

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abstract: The leaf economics spectrum ranges from cheap, short-lived leaves to expensive, long-lived leaves. Species with low leaf mass per area (LMA) and short leaf life span tend to be fast growing and shade intolerant (early successional), whereas species with high LMA and long leaf life span tend to be slow growing and shade tolerant (late successional). However, we have limited understanding of how different leaf mass components (e.g., metabolically active photosynthetic components vs. structural toughness components) contribute to variation in LMA and other leaf economics spectrum traits. Here, we develop a model of plant community dynamics in which species differ in just two traits, photosynthetic and structural LMA components, and we identify optimal values of these traits for early- and late-successional species. Most of the predicted increase in LMA from early- to late-successional species was due to structural LMA. Photosynthetic LMA did not differ consistently between early- and late-successional species, but the photosynthetic LMA to structural LMA ratio declined from early- to late-successional species. Early-successional species had high rates of instantaneous return on leaf mass investment, whereas late-successional species had high lifetime return. Our results provide theoretical support for the primary role of structural (rather than photosynthetic) LMA variation in driving relationships among leaf economics spectrum traits.

*Keywords:* coexistence, leaf economics, leaf traits, niche, succession.

## Introduction

Across the global flora, leaf mass per area (LMA; the mass invested in a unit of photosynthetic surface area) and leaf life span (LL; the lifetime over which photosynthetic dividends are returned) vary by more than two orders of magnitude, and much of this variation is present among co-occurring species (Westoby et al. 2000; Wright et al. 2004; Falster et al. 2012). The leaf economics spectrum (LES) describes coordinated variation in these and other leaf traits (including photosynthesis and respiration rates as well as nutrient concentrations), ranging from short-lived, low-cost leaves with a fast rate of photosynthetic return per unit leaf mass to long-lived, high-cost leaves with a slow rate of return (Wright et al. 2004; Reich 2014). Several studies have concluded that the lifetime return on investment (lifetime net carbon gain per unit leaf mass) increases from the fast (low LMA and short LL) to the slow (high LMA and long LL) ends of the LES (Westoby et al. 2000; Wright et al. 2004; Falster et al. 2012), suggesting the presence of one or more trade-offs that allow fast and slow species to coexist.

One trade-off that could contribute to coexistence along the LES is the growth versus shade tolerance trade-off that allows fast-growing, shade-intolerant, early-successional species to coexist with slow-growing, shade-tolerant, late-successional species (Connell 1978; Bazzaz 1979; Shugart 1984; Pacala et al. 1994). When light and other resources are abundant, seedling growth rates are maximized by rapid deployment of leaf area, which requires low LMA (Cornelissen et al. 1996; Wright and Westoby 2000; Falster et al. 2018). In contrast, under shaded or otherwise low-resource conditions, the return on investment is slow, and long LL (which requires high LMA) is required for a leaf to pay back its construction costs (Coley et al. 1985; Falster et al. 2018). Many empirical studies have reported correlations between leaf traits and demographic rates that are consistent with the hypothesis that the fast versus slow ends of the LES are favorable for early- versus late-successional performance, respectively. In particular, as LMA and LL increase across species, seedling and sapling growth rates often decrease, and shade tolerance often increases (Reich et al. 1992, 1995; Kitajima 1994; Cornelissen et al. 1996; Wright and Westoby 2000; Selaya and Anten 2010). These relationships are not universally strong, being weak across global species (Paine et al. 2015) and within some communities (Wright et al. 2010). Nevertheless, the strong relationships that emerge under controlled experimental conditions (Cornelissen et al. 1996; Wright and Westoby 2000) and the

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mechanistic understanding of these relationships (Falster et al. 2018) suggest a potential role for successional demographic niches in maintaining diversity along the LES.

Studies with trait-based demographic models support the hypothesis that successional processes can allow for coexistence of species with fast versus slow leaf traits. For example, process-based ecosystem models (e.g., Moorcroft et al. 2001; Smith et al. 2001) simulate successional sequences of plant types defined by multiple traits, including LMA and LL (which are assumed in these models to increase from early- to late-successional functional types). In a more detailed investigation of successional diversity, Falster et al. (2017) used a metacommunity framework to explore the role of multiple trait dimensions in tree species coexistence. Falster et al. (2017) showed that variation along a single leaf trait axis (from low to high values of LMA and LL) permitted coexistence of two to three successional types, with low and high LMA values corresponding to early- and late-successional species, respectively. Falster et al. (2017) further showed that when this leaf trait axis was combined with a second trait axis (height at maturation), a larger number of species (mostly late successional) could coexist.

The studies given above demonstrate the potential role of leaf economics in succession but provide limited insight into the sources of LMA variation and the causes of relationships among LES traits. For example, the models of Moorcroft et al. (2001) and Falster et al. (2017) assume that rates of photosynthesis and respiration per unit leaf area are constant across species. In this case, LMA variation is tied to a single function (LL), and the models provide no insights into observed relationships between LMA and other traits. In particular, net photosynthetic capacity ($A_{max}$) per unit leaf area is often observed to be roughly independent of LMA (Wright et al. 2004; Osnas et al. 2018), which implies an inverse relationship between $A_{max}$ per unit mass and LMA (Lloyd et al. 2013; Osnas et al. 2013). Because these models take the relationships among LMA, LL, and $A_{max}$ as given, they provide no insight into the causes of these relationships.

LMA is a composite trait that can be decomposed into different anatomical, chemical, and functional components (Shipley et al. 2006; Poorter et al. 2009; John et al. 2017). Recently, Osnas et al. (2018) suggested that a variety of patterns of leaf trait variation within and among species could be understood by conceptualizing LMA as the sum of photosynthetic and structural LMA components ($LMA_P$ and $LMA_S$, respectively). While this conceptual model is an obvious simplification (Osnas et al. 2018), it provides a convenient starting point to explore how variation in different LMA components may contribute to coexistence along the LES and relationships among LES traits.

In this article, we seek to gain insight into the functional significance of the LES and how diversity is maintained along it by incorporating the $LMA_P$-$LMA_S$ framework of Osnas et al. (2018) into a simple model of community dynamics that is a reformulation of classic resource competition models (Tilman 1982, 1985). We assume that species differences in LMA, LL, and $A_{max}$ arise from differences in $LMA_P$ and $LMA_S$, and we use the model to better understand the optimal (fitness-maximizing) traits of early- and late-successional species. We predict that, as in the model of Falster et al. (2017), competition for a single resource (light) will lead to early- and late-successional traits that resemble the fast and slow ends, respectively, of the LES. Furthermore, we use the optimal values of $LMA_P$ and $LMA_S$ predicted by our model for early- and late-successional species to explore the components of LMA variation along the LES and the causes of relationships among three key LES traits: LMA, LL, and $A_{max}$. In our analysis, relationships among these LES traits are not prescribed but rather emerge from differences in lower-level traits ($LMA_P$ and $LMA_S$) between early- and late-successional species.

## Model Overview

We conceptualize the model ecosystem as being aseasonal (e.g., evergreen tropical forest), so that seasonality in temperature and rainfall do not impose any constraints on LL. To focus our analysis on two key aspects of leaf economics, we assume that species differ only with respect to two fundamental leaf traits (from which other leaf traits are derived): $LMA_P$, which determines the potential (high-light) rate of return on investment per unit leaf area, and $LMA_S$, which determines LL and thus (along with the whole-plant mortality rate) the lifetime over which revenue is returned. We assume that these two LMA components are additive, so that total LMA is equal to the sum of $LMA_P$ and $LMA_S$. For simplicity, we ignore intraspecific trait variation across light gradients (Bazzaz and Carlson 1982; Sack et al. 2006; Niinemets et al. 2015); thus, we assume that within a given species, all leaves are identical.

$LMA_P$ and $LMA_S$ are conceptual traits that have not been directly measured, but they loosely correspond to the liquid phase (protoplasm) and cell wall components, respectively, in the model of Shipley et al. (2006). Specifically, we conceptualize $LMA_P$ as the mass per area of leaf components that contribute directly to photosynthesis (e.g., chloroplasts and other metabolically active cellular components) and $LMA_S$ as the mass per area of cell wall and other structural material constructed for the purpose of toughness and durability (Kitajima et al. 2012, 2016; Onoda et al. 2017), beyond the structural mass needed for biomechanical support, water transport, and gas exchange in the short term. See Osnas et al. (2018) for further discussion of $LMA_P$ and $LMA_S$.

We now describe the dynamic model. Consider a forest community composed of multiple tree species. For simplicity, we assume a single limiting resource (light), so that the dynamics are governed by the shade tolerance trade-off, whereby performance under high-light conditions trades off against performance in the shade (Bazzaz 1979; Pacala et al. 1994). We do not attempt to capture the complexities of height-structured competition for light (Shugart 1984; Pacala et al. 1994; Strigul et al. 2008). Rather, our model is designed to yield qualitative insights regarding optimal (fitness-maximizing) leaf traits under high-light (early-successional) versus shaded (late-successional) conditions. Thus, following Tilman (1985), we develop a minimally complex ordinary differential equation model for the leaf biomass dynamics of different plant species $i$ competing for light. The dynamics can be represented in simplified form as

$$\frac{dB_i(t)}{dt} = fG_i(t) - (\mathrm{LL}_i^{-1} + \mu_i)B_i(t), \tag{1}$$

where $f$ is the fraction of net photosynthesis available for leaf biomass production; $G_i(t)$, the net photosynthesis of species $i$ at time $t$, is the difference between gross photosynthesis (which increases with leaf area, $\mathrm{LMA_P}$, and light availability) and leaf maintenance respiration (which depends on photosynthetic and structural leaf mass and their respective per-mass respiration rates); LL increases with $\mathrm{LMA_S}$; $\mu_i$ is species $i$'s whole-plant mortality rate; and $B_i(t)$ is leaf biomass (per unit ground area) of species $i$ at time $t$. We consider cases with constant $\mu_i$ (either a single value or different values for early- and late-successional species) and cases where $\mu_i$ depends on species $i$'s investment in structural leaf mass ($\mathrm{LMA}_{Si}$). See appendixes A and B for additional model details (apps. B–D are available online). Equation (1) falls within the general framework of Armstrong and McGehee (1980) and has a form similar to the models of Tilman (1982, 1985). The key differences between our model and those of Tilman (1982, 1985) are that we formulate our model in terms of physiological processes relevant to the LES, and we assume a single limiting resource (light).

For simplicity, we assume that all leaves in the plant community experience the same light level; that is, we use a mean-field approximation, as in Tilman (1985). Early in succession, there is little shading, and this mean-field approximation is roughly valid. In contrast, late in succession, the mean-field approximation does not accurately represent height-structured competition for light (Pacala and Deutschman 1995) but does provide a useful approximation for the dynamics of understory vegetation (Tilman 1985), which to a large extent determines successional dynamics (Pacala et al. 1996). Thus, we expect the model to yield qualitatively useful insights for both early- and late-successional plants.

## Analysis Methods

An important goal of our analysis is to determine the competitively optimal values of $\mathrm{LMA_P}$ and $\mathrm{LMA_S}$ (and derived traits; see below and app. C) for early- and late-successional species. We define the competitively optimal early-successional traits as those that maximize the leaf biomass growth rate ($dB/dt$) under high-light conditions (i.e., near $B = 0$), because this growth-maximizing strategy under high light can initially overtop other species and reproduce before being excluded by longer-lived, shade-tolerant species. We define the competitively optimal late-successional traits as those that maximize shade tolerance; that is, the traits that lead to the lowest equilibrium light level and thus the competitive exclusion of all other species in the absence of disturbance (Armstrong and McGehee 1980; Tilman 1982). Despite the relatively simple form of our model, solving for the optimal early- and late-successional traits is nontrivial and requires a combination of analytical and numerical methods, which are presented in detail in appendix D.

Given the optimal values of $\mathrm{LMA_P}$ and $\mathrm{LMA_S}$ (table 1), it is straightforward to calculate the corresponding values of two LES traits that are central to our article, $A_{\max}$ (per unit leaf mass or area) and LL (see app. C). We also calculated from $\mathrm{LMA_P}$ and $\mathrm{LMA_S}$ an additional trait related to late-successional performance: $A_{\mathrm{eq}}$, the net photosynthetic rate

**Table 1:** Key symbols in the main text

| Symbol | Description | Unit |
|---|---|---|
| $A_{\mathrm{eq}}$ | Leaf net assimilation rate under the late-successional equilibrium understory light level; normalized by leaf mass ($A_{\mathrm{eq}}$/mass) or area ($A_{\mathrm{eq}}$/area) | g C g$^{-1}$ yr$^{-1}$ or g C m$^{-2}$ yr$^{-1}$ |
| $A_{\max}$ | Leaf net photosynthetic capacity (light-saturated assimilation rate); normalized by leaf mass ($A_{\max}$/mass) or area ($A_{\max}$/area) | g C g$^{-1}$ yr$^{-1}$ or g C m$^{-2}$ yr$^{-1}$ |
| LL | Leaf life span | yr |
| $\mathrm{LMA_P}$ | Photosynthetic leaf mass per unit leaf area | g C m$^{-2}$ |
| $\mathrm{LMA_S}$ | Structural leaf mass per unit leaf area | g C m$^{-2}$ |
| LMA | Total leaf mass per unit leaf area: $\mathrm{LMA} = \mathrm{LMA_P} + \mathrm{LMA_S}$ | g C m$^{-2}$ |

Note: See table A1 for a complete list of model parameters and state variables. Throughout this article, assimilation rates ($A_{\mathrm{eq}}$ and $A_{\max}$) are annualized rates that are qualitatively similar to (but quantitatively different from) instantaneous rates reported in the literature (e.g., Wright et al. 2004).

of a leaf at the late-successional equilibrium light level (i.e., the understory light level at which only the optimal late-successional species can persist; app. C). We considered LL × $A_{max}$/mass and LL × $A_{eq}$/mass as indices of lifetime return on investment for leaves in full sunlight and in the late-successional understory, respectively. The first index (LL × $A_{max}$/mass) is only an approximation for lifetime return, because even in our simple model no leaf spends its entire lifetime under full-sun ($A_{max}$) conditions. The second index (LL × $A_{eq}$/mass) is exact for leaves at the late-successional equilibrium in our model and is easily modified to include the effect of whole-plant mortality on leaf turnover (see "Results"). In reality, numerous factors complicate the estimation of lifetime return—for example, decreases in both light availability and photosynthetic capacity with leaf age (Falster et al. 2012). Thus, the indices of lifetime return considered here are intended to provide only qualitative insights and are not intended as realistic estimates.

Although an overarching goal of our study is to gain insight into how diversity can be maintained along the LES, we do not study coexistence per se in our model. Doing so would require considering disturbance in a spatially heterogeneous landscape, as in numerous prior studies (e.g., Tilman 1994; Pacala and Rees 1998; Roxbaugh et al. 2004; Gravel et al. 2010; Falster et al. 2017). Thus, we focus our analysis on identifying the values of $LMA_P$ and $LMA_S$ that maximize the competitive performance of early- versus late-successional species, and we rely on previous studies as evidence that these contrasting successional types can coexist.

To evaluate whether our results were sensitive to the choice of model parameter values (e.g., constants that translate $LMA_P$ and $LMA_S$ into LL and rates of photosynthesis and respiration; app. A), we performed an uncertainty analysis. In this analysis, values for all model constants were drawn randomly—and independently of each other—from a uniform distribution spanning 0.75 to 1.25 times the baseline values given in table A1. We performed 1,000 replicates of this uncertainty analysis.

Finally, although it is straightforward to evaluate late-successional performance in our model by focusing on equilibrium conditions, evaluating early-successional performance requires either a metacommunity framework (e.g., Lichstein and Pacala 2011; Falster et al. 2017) or making somewhat arbitrary decisions (as in this study) about the timescale of analysis (e.g., the trait values that maximize growth during the first year of succession differ from those that maximize average growth over multiple years). Therefore, in addition to solving for the trait values that maximize $dB/dt$ near $B = 0$ (the extreme short-term case), we also identified the trait values that maximize mean wood biomass growth rate over timescales ranging from 1 month to 2 years. We simulated wood biomass dynamics according to equation (A8) in appendix A, which is a simple modification of our model of leaf biomass dynamics (eq. [1]). To identify the trait values that maximized wood biomass growth over a given time period, we systematically searched the two-dimensional trait space ($LMA_P$, $LMA_S$). Because of the high computational cost of this analysis, we ignored parameter uncertainty and considered only the baseline parameter values (table A1).

## Results

Model predictions were qualitatively robust to alternative assumptions about whole-plant mortality rates (figs. B1–B6; figs. B1–B6, D1–D3 are available online) and to perturbing the baseline parameter values (table A1) by ±25% (fig. 1). Most predictions were also qualitatively robust to alternative indices of early-successional performance, as explained below.

Optimal early-successional species had lower LMA and a higher $LMA_P$ : LMA ratio than optimal late-successional species (fig. 1*a*, 1*b*). Thus, most of the difference in LMA between early- and late-successional species was due to $LMA_S$, which comprised the majority of late-successional LMA (fig. 1*a*, 1*b*). These contrasts between optimal early- and late-successional traits were qualitatively similar for a wide range of early-successional performance indices, including $dB/dt$ near $B = 0$ (fig. 1*a*, 1*b*) and wood biomass growth rates averaged over different time periods (fig. 2*a*, 2*b*). Specifically, for all early-successional indices we considered, optimal early-successional species had lower LMA, lower $LMA_S$, and higher $LMA_P$/LMA than optimal late-successional species (figs. 1*a*, 1*b*, 2*a*, 2*b*).

In contrast to these results, predictions for optimal early-successional $LMA_P$ (and thus $A_{max}$) were sensitive to the choice of early-successional performance index. When the optimal early-successional species was identified by maximizing $dB/dt$ near $B = 0$, early-successional species had lower $LMA_P$ and lower $A_{max}$/area than late-successional species (fig. 1*a*, 1*c*). Maximizing wood growth rates over very short timescales (far left of *X*-axis in fig. 2) yielded equivalent results as maximizing $dB/dt$ near $B = 0$ (fig. 1); that is, as the timescale of growth optimization approaches zero in figure 2, the results converge on the early-successional values in figure 1. However, maximizing growth rate over longer timescales (e.g., >1 year) requires values of $LMA_P$ and $A_{max}$/area (fig. 2*a*, 2*c*) that are similar to those of optimal late-successional species (triangles in fig. 1*a*, 1*c*; black symbols in fig. 1 correspond to the parameter set used in fig. 2). Although optimal $LMA_P$ and $LMA_P$/LMA increased with the timescale of growth optimization (fig. 2*a*, 2*b*), optimal $A_{max}$/mass decreased (fig. 2*d*) as a result of the diminishing marginal increase in photosynthetic returns with increasing $LMA_P$, which follows from our assumption of

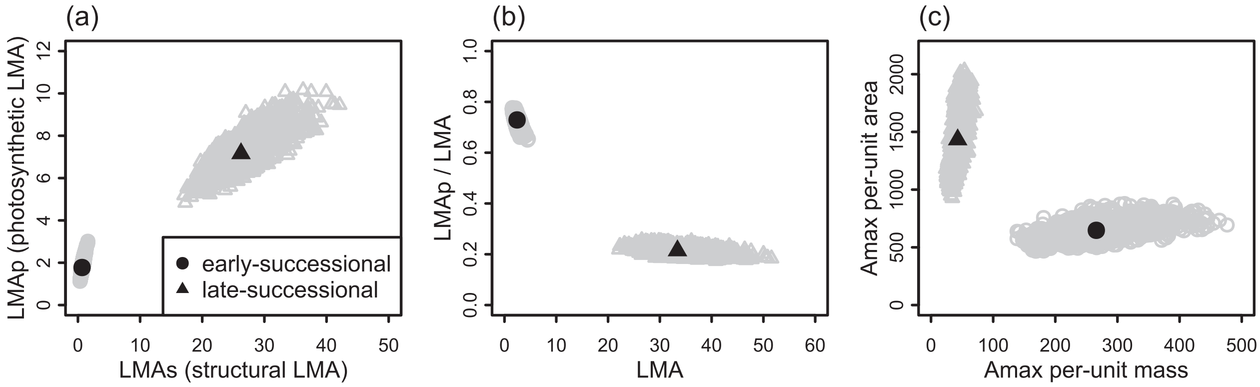


**Figure 1:** *a*, Competitively optimal photosynthetic and structural leaf mass per area components ($LMA_P$ and $LMA_S$, respectively) for early- and late-successional species. Black symbols show results for the baseline parameter values in table A1, and gray symbols show results from an uncertainty analysis in which 1,000 parameter vectors were generated by randomly perturbing the baseline parameter values by up to ±25%. *b*, Optimal early-successional species have a high ratio of $LMA_P$ to total LMA and low total LMA, whereas optimal late-successional species have low $LMA_P$/LMA and high LMA. *c*, Annualized rate of net photosynthetic capacity per unit leaf mass ($A_{max}$/mass; g C $g^{-1}$ $yr^{-1}$) and area ($A_{max}$/area; g C $m^{-2}$ $yr^{-1}$) corresponding to a given combination of $LMA_P$ and $LMA_S$. Net photosynthetic capacity is the rate of gross photosynthesis under full sunlight minus the rate of leaf maintenance respiration.

self-shading of chloroplasts within leaves (eq. [A6]; Terashima et al. 2011). Nevertheless, across the range of timescales considered, optimal early-successional $A_{max}$/mass values (fig. 2*d*) were larger than optimal late-successional values (fig. 1*c*, black triangle).

The optimal early-successional traits were relatively close to the $A_{max}$/mass maximum (fig. 3*a*), whereas the optimal late-successional traits were relatively close to the LL × $A_{max}$/mass maximum (fig. 3*b*). The optimal late-successional traits were very close to the LL × $A_{eq}$/mass maximum (fig. 3*c*), where $A_{eq}$ is the net photosynthetic rate of a leaf at the late-successional equilibrium light level (at which only the optimal late-successional species can persist). The slight difference between the late-successional LL × $A_{eq}$/mass and the peak of the surface in figure 3*c* is due to whole-plant mortality ($\mu$), as follows: The leaf turnover rate, including $\mu$, is $LL^{-1} + \mu$. Substituting the $\mu$-adjusted LL, $(LL^{-1} + \mu)^{-1}$, for LL in figure 3*c* results in a perfect match between the late-successional value and the peak of the surface (fig. 3*d*; see proof in app. D, proposition 3).

## Discussion

Our trait-based model of plant community dynamics predicts that competitively optimal early-successional plants have a fast rate of return per unit investment in leaf mass (high $A_{max}$/mass) but a short LL and low lifetime return on investment, whereas competitively optimal late-successional plants have the opposite properties (low rate of return but long LL and high lifetime return). These predictions suggest that the fast and slow end points of the LES (Wright et al. 2004) correspond to competitively optimal traits for early- and late-successional species, consistent with a previous theoretical study of trait variation and successional diversity (Falster et al. 2017). The association between LES traits and successional niches that emerges from models of community dynamics (our study and Falster et al. 2017) are consistent with a mechanistic model of individual growth and shade tolerance (Falster et al. 2018) and with many empirical studies relating leaf traits to individual vital rates (e.g., Reich et al. 1992; Kitajima 1994; Cornelissen et al. 1996; Wright and Westoby 2000; Poorter and Bongers 2006) and successional changes in species composition (e.g., Reich et al. 1995; Garnier et al. 2004).

Our analysis provides new insights about the leaf economics of plant succession. Consistent with the association between low LMA and the rapid growth rates needed to dominate early in succession (Falster et al. 2017), our model predicts higher $A_{max}$/mass for early- than for late-successional species. In our model, $A_{max}$/mass is maximized when structural leaf mass ($LMA_S$, assumed to affect LL but not photosynthesis) is zero and when photosynthetic leaf mass ($LMA_P$) approaches zero (fig. 3*a*), due to the assumed within-leaf shading of chloroplasts (eq. [A6]; Terashima et al. 2011). Despite maximizing $A_{max}$/mass, the extreme low-LMA strategy is not ecologically viable because it results in values of $A_{max}$/area that are too low to replace leaf area losses due to leaf and whole-plant turnover. Although the quantitative predictions of our model are undoubtedly affected by our simplifying assumptions, we expect the following qualitative prediction to be robust:

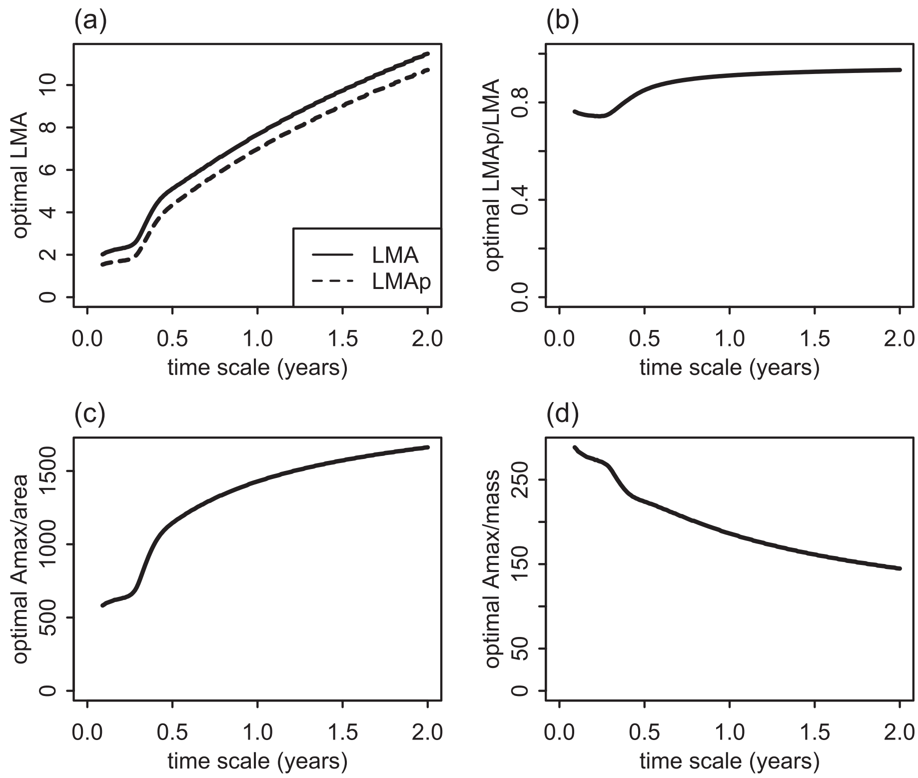


**Figure 2:** Leaf traits that are optimal for early-successional growth depend on the timescale over which growth is evaluated. Here, the two-dimensional trait space ($LMA_P$, $LMA_S$) was systematically searched to identify the trait combination that maximized mean wood biomass growth rate over timescales ranging from 1 month to 2 years. *a*, The *Y*-axis shows the total LMA and $LMA_P$ values that maximized mean growth rate over the timescale given by the *X*-axis; $LMA_S$ is the difference between the two curves. *b*, Ratio of $LMA_P$ to total LMA. *c*, *d*, Values of $A_{max}$/area and $A_{max}$/mass that result from the optimal values of $LMA_P$ and $LMA_S$. For very short timescales (far left of *X*-axis), this analysis predicts early-successional traits similar to those in our other analyses (e.g., fig. 1), where the most competitive ("optimal") early-successional traits are defined as those that maximize growth rate under full sunlight (zero biomass).

optimal $A_{max}$/mass is greater for early- than for late-successional species (because of the benefits of fast economic returns early in succession) but less than the theoretical maximum $A_{max}$/mass (because of constraints imposed by leaf turnover).

While a high rate of return ($A_{max}$/mass) is advantageous early in succession, high LL (and thus high LMA and low $A_{max}$/mass) enhances shade tolerance and late-successional performance (Falster et al. 2017, 2018). Specifically, the whole-plant light compensation point (WPLCP), the light level where carbon gains (photosynthesis) and losses (turnover and respiration) are balanced, is minimized (i.e., shade tolerance is maximized) for LL values that are higher than those that maximize high-light growth (Falster et al. 2018). Given the uniform understory light level in our model, as in Tilman (1985), there is a single late-successional dominant species whose traits minimize the WPLCP. At this light level, the traits of the late-successional dominant roughly maximize an index of lifetime return on investment, LL × $A_{eq}$/mass (fig. 3*c*), and exactly maximize the mortality-adjusted form of this index, $(\mathrm{LL}^{-1} + \mu)^{-1} \times A_{eq}/\mathrm{mass}$ (fig. 3*d*). Thus, while early-successional species have high rates of instantaneous return, shade-tolerant species (which are the late-successional dominants in our model) maximize the lifetime return on investment.

In addition to providing insights into how LES traits relate to successional niches, our study also provides a theoretical perspective on the causes of relationships among LES traits. In our model, LES relationships are not prescribed; rather, they emerge from the assumed functions of photosynthetic and structural leaf mass ($LMA_P$ and $LMA_S$) and the optimal values of $LMA_P$ and $LMA_S$ predicted for early- and late-successional species. For example, our model predicts that LL increases with LMA across species because the long LL that leads to shade tolerance (Falster et al. 2018) requires high concentrations of structural leaf mass (e.g., cellulose; Kitajima et al. 2012, 2016), which is represented in our model by $LMA_S$. The assumed

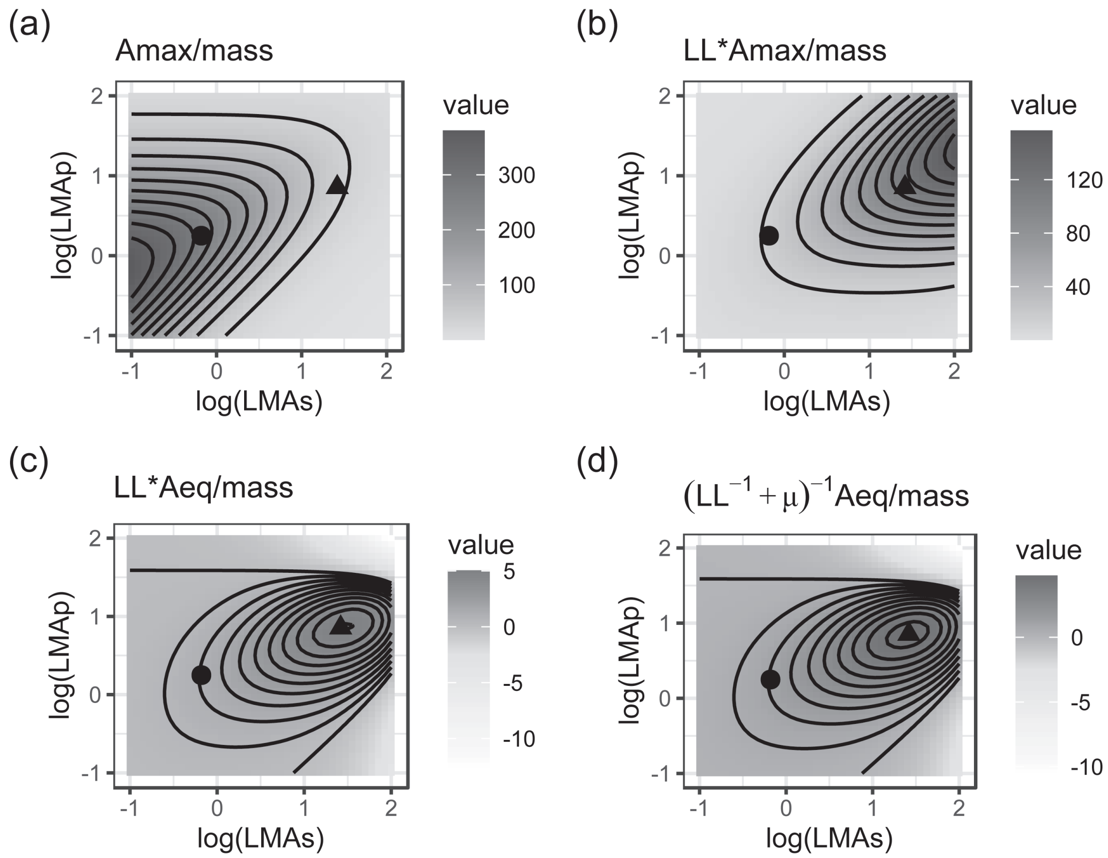


**Figure 3:** Values of four leaf economics indices as a function of photosynthetic and structural leaf mass per area ($LMA_P$ and $LMA_S$, respectively). The black circle and black triangle show the competitively optimal values of $LMA_P$ and $LMA_S$ for early- and late-successional species, respectively. *a*, Net photosynthetic capacity per unit leaf mass ($A_{max}$/mass); that is, the rate of return per unit investment under full sunlight. *b*, $A_{max}$/mass times leaf life span (LL); that is, the lifetime return per unit investment under full sunlight. *c*, $A_{eq}$/mass times LL, where $A_{eq}$ is net photosynthesis under the late-successional equilibrium light level; that is, the lifetime return per unit investment in the late-successional understory light environment. *d*, $A_{eq}$/mass times the mortality-adjusted leaf turnover rate, $(LL^{-1} + \mu)^{-1}$, which is maximized by the late-successional species (see proof in app. D, proposition 3). $A_{max}$/mass and $A_{eq}$/mass are expressed on an annual timescale (g C $g^{-1}$ $yr^{-1}$).

increase in LL with $LMA_S$ (eq. [A2]) does not, by itself, ensure that LL increases with total LMA, which also depends on $LMA_P$. However, our model predicts that $LMA_S$ accounts for most of the LMA variation across species (e.g., fig. 1*a*, 1*b*), consistent with the observation that cell wall mass per unit leaf area is strongly correlated with LMA across global species (and within some plant groups, such as woody evergreens), with cell wall comprising up to 70% of total leaf mass in species with high LMA (Onoda et al. 2017).

In contrast to the simple relationship between LL and LMA that emerges from our model, predicted relationships involving net photosynthetic capacity ($A_{max}$) were more complex. Depending on the timescale of our early-successional analysis, our model predicts a range of early-successional $LMA_P$ and thus $A_{max}$/area (fig. 2*a*, 2*c*), including values that are both lower than and higher than late-successional values (triangles in fig. 1*a*, 1*c*). The predicted increase in $LMA_P$ with the timescale of growth optimization (fig. 2*a*) likely reflects the diminishing benefits of additional leaf area relative to the benefits of increased carbon gain per unit leaf area, as self-shading increases early in succession. Although we did not study coexistence among different early-successional species, the range of predicted growth-maximizing traits (fig. 2) might help explain why relationships between $A_{max}$/area and other traits are often weak (e.g., Reich et al. 1997; Wright et al. 2004; Poorter and Bongers 2006; Falster et al. 2012). Specifically, our model suggests potential LMA variation across early-successional species due to variation in $LMA_P$ (fig. 2*a*), which determines $A_{max}$/area (fig. 2*c*). However, this LMA variation is modest relative to the difference in LMA between early- and late-successional species, which is primarily due to $LMA_S$ (fig. 1*a*, 1*b*). Thus, the dominant role of $LMA_S$ in determining community-wide LMA variation leads not only to a decline in $A_{max}$/mass with LMA (Osnas et al. 2018) but also a weak relationship between $A_{max}$/area and LMA (because $LMA_P$ and thus $A_{max}$/area may be highly variable yet contribute little to community-wide LMA variance).

### *Limitations and Future Directions*

Our model assumed a constant environment and a single limiting resource, light. In reality, high $LMA_P$ and/or low $LMA_S$ (and thus short LL and low nutrient-use efficiency) would be possible only if nutrients can be acquired at a sufficient rate to build and replace nutrient-rich photosynthetic tissue (Reich 2014). Thus, nutrient limitation could impose an upper bound on $LMA_P$ and/or a lower bound on $LMA_S$ because of limited nutrient supply (e.g., low mineralization rates) and/or the allocational trade-off between fine root production (nutrient acquisition) and stem growth (light competition; Dybzinski et al. 2011). In addition to nutrient constraints, temperature and moisture regimes may impose additional environmental and competitive filters (van Bodegom et al. 2012; Reich 2014). For example, even if nutrients are not limiting, water limitation could reduce the benefits of high $LMA_P$ (high potential carbon gain) relative to building and maintenance costs (Farrior et al. 2013). In general, we expect limitation by nutrients or other factors to constrain trait differences between early- and late-successional species.

Accounting for multiple limiting factors may reveal constraints on successional trait differentiation but would also allow for a more complete exploration of trait diversity. Weak relationships between LES traits and successional demographic indices are sometimes observed (e.g., Wright et al. 2010), which may reflect the presence of additional niche axes beyond the one-dimensional growth/shade tolerance trade-off (Clark et al. 2010). Herbivores, climate variability, and edaphic heterogeneity have all likely contributed to the origin and maintenance of diversity along the LES and other trait dimensions (Tilman 1988; Coley and Barone 1996; Cavender-Bares et al. 2004; Engelbrecht et al. 2007; Baraloto et al. 2010). Future work with trait-based models of community dynamics could explore coexistence in a multidimensional environmental space to better understand diversity maintenance of leaf and other traits. Process-based demographic models that link individual vital rates to multiple environmental drivers (e.g., Moorcroft et al. 2001; Smith et al. 2001; Scheiter et al. 2013; Fisher et al. 2015; Sakschewski et al. 2015) are well equipped for this task, but their mathematical complexity and computational cost make them unwieldy for studying coexistence. Simplified analogs of these process models have been developed (Dybzinski et al. 2011; Farrior et al. 2013), but their analytical solutions are available only for equilibrium (late-successional) conditions. Patch-scale transient dynamics (e.g., succession) in heterogeneous landscapes could be studied by embedding these simplified process models within a computational metacommunity framework (e.g., Lichstein and Pacala 2011; Falster et al. 2017).

The simplistic framework adopted here, in which LMA is assumed to be the sum of $LMA_P$ and $LMA_S$, needs further development to account for factors beyond light limitation (e.g., the implications of leaf venation for drought tolerance and LMA; Sack and Scoffoni 2013) and to forge stronger links to empirical studies. A critical step is to identify measurable traits that allow empirical tests of hypotheses related to LMA variation. LMA can be decomposed into different chemical and anatomical components (Poorter et al. 2009; John et al. 2017), but attributing LMA variation to different functions is less straightforward. For example, some $LMA_S$ can be viewed as contributing to both toughness and photosynthesis, as the latter requires a minimum amount of structural mass for biomechanical support and water transport (Niinemets and Sack 2006; Niinemets et al. 2007; Sack and Scoffoni 2013). On the other hand, the high concentrations of structural mass needed for long LL can impair photosynthesis due to the decrease in mesophyll conductance with cell wall thickness (Terashima et al. 2011; Onoda et al. 2017). Thus, the simple framework adopted here for partitioning LMA variation, in which photosynthetic and structural components are assumed independent, has limitations. Expanding this framework by linking measurable chemical and anatomical LMA components to multiple functions would facilitate empirical tests of model predictions and allow for improved understanding of leaf trait relationships and diversity.

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## Statement of Authorship

J. W. Lichstein conceptualized the study and drafted the main text; S. A. McKinley, B. T. Peterson, and J. Langebrake formulated the mathematical proofs; J. W. Lichstein, B. T.

Peterson, and J. Langebrake produced the simulations, numerical analyses, and figures; and all authors contributed to developing ideas for the study, interpreting results, and editing the article.

### Data and Code Availability

The only data used in this study are values extracted from the literature, as reported in table A1. Code to generate the figures is provided in a zip file (available online).[1]

## APPENDIX A

### Model Details

We derive an ordinary differential equation model for the leaf biomass dynamics of tree species competing for light. All model parameters are assumed constant across species except for two species-specific traits, photosynthetic and structural leaf mass per area ($LMA_P$ and $LMA_S$, respectively), which together determine species differences in leaf photosynthetic capacity, leaf respiration costs, and leaf life span (LL). Leaf biomass per unit ground area (i.e., per unit of land-surface area within which trees compete for light) of species $i$ is denoted $B_i$ (g C m$^{-2}$), and its change (g C m$^{-2}$ yr$^{-1}$) is modeled as

$$\frac{dB_i}{dt} = f_L(1 - f_R)G_i - (LL_i^{-1} + \mu_i)B_i, \tag{A1}$$

where $f_L$ is the fraction of leaf net primary production ($G_i$; see below) allocated to leaf growth, $f_R$ is the fraction of $G_i$ used for growth respiration, $G_i$ is the rate of net photosynthesis per unit ground area of species $i$ leaves (gross photosynthesis minus leaf maintenance respiration per unit ground area; g C m$^{-2}$ yr$^{-1}$), $LL_i^{-1}$ is the turnover rate of individual leaves (yr$^{-1}$) of species $i$ (i.e., the inverse of leaf life span, $LL_i$), and $\mu_i$ (yr$^{-1}$) is the whole-plant mortality rate. We considered alternative assumptions for $\mu_i$, including cases with constant $\mu_i$ (either a single value or different values for early- and late-successional species) and cases where $\mu_i$ decreases with $LMA_S$ (see details in app. B). These alternative assumptions had little effect on our results (figs. B1–B6).

We assume that LL increases across species with $LMA_S$, consistent with observations linking LL and leaf toughness to leaf structural properties such as cellulose concentration (Kitajima et al. 2012, 2016):

$$LL_i = c_{LL}LMA_{Si}, \tag{A2}$$

1. Code that appears in *The American Naturalist* is provided as a convenience to readers. It has not necessarily been tested as part of peer review.

where $c_{LL}$ is a constant. The linear form of equation (A2) is qualitatively consistent with the observed global scaling relationship $LL = aLMA^b$, with $b > 1$ (Wright et al. 2004). To see this, note that in our model, $LMA = LMA_P + LMA_S$, with LL depending only on $LMA_S$ (eq. [A2]). Also, note that according to our model predictions (see "Results") and arguments presented in Osnas et al. (2018), most interspecific variation in LMA is due to interspecific variation in $LMA_S$ rather than $LMA_P$, which implies that a doubling of LMA across species is associated with a greater than doubling of $LMA_S$ and LL.

We now present the details of the photosynthesis term, $G_i$, in equation (A1). See table A1 for a list of model terms, units, parameter values, and literature sources. The term $G_i$, the annualized rate of leaf net photosynthesis of species $i$ per unit ground area (g C m$^{-2}$ yr$^{-1}$), is

$$G_i = LAI_iP_i - R_i, \tag{A3}$$

where $LAI_i$ is species $i$'s leaf area index (leaf area per ground area), which is equal to $B_i/LMA_i$; $P_i$ is species $i$'s annualized rate of gross photosynthesis per unit leaf area (g C m$^{-2}$ leaf area yr$^{-1}$), which depends on $LMA_P$ and light availability (see below), and $R_i$ is species $i$'s annualized rate of leaf maintenance respiration per unit ground area (g C m$^{-2}$ yr$^{-1}$), which depends on photosynthetic and structural leaf mass per ground area ($B_P$ and $B_S$, respectively):

$$R_i = r_PB_{Pi} + r_SB_{Si}, \tag{A4}$$

where $r_P$ and $r_S$ are, respectively, annualized respiration rates per unit photosynthetic and structural leaf mass (g C respiration g$^{-1}$ C leaf mass yr$^{-1}$). Note that $B_{Pi} = B_i \times LMA_{Pi}/LMA_i$ and $B_{Si} = B_i \times LMA_{Si}/LMA_i = B_i(1 - (LMA_{Pi}/LMA_i))$. The annualized rate of gross photosynthesis per leaf area at time $t$ depends on species $i$'s photosynthetic capacity per unit leaf area, $v_i$ (g C m$^{-2}$ leaf area yr$^{-1}$) and light availability (proportion of full sunlight) at time $t$, $L(t)$:

$$P_i(t) = \frac{v_i L(t)}{k_P + L(t)}, \tag{A5}$$

where $k_P$ is a half-saturation constant and the function is concave down (Bazzaz 1979). Note that $L$ and $P_i$ (and thus $G_i$) are time dependent, but we typically omit the "($t$)" from our notation for conciseness. Also, note that in our model photosynthesis and respiration are expressed on an annual timescale, and we do not explicitly account for seasonal or diurnal variation in light or other abiotic conditions. The first simplification (lack of seasonality) makes our analysis most relevant for aseasonal ecosystems—for example, evergreen tropical forest, as noted in the main text (see "Model Overview"). The second simplification (lack of diurnal cycle) should not qualitatively affect our conclusions, and we tuned the parameter values in equations (A4)–(A6) to yield annualized rates of gross photosynthesis and respiration similar to those reported in the literature (see the table A1 note). We assume that photosynthetic capacity increases across species with $\mathrm{LMA_P}$:

$$v_i = \frac{a_v \,\mathrm{LMA}_{\mathrm{P}i}}{k_v + \mathrm{LMA}_{\mathrm{P}i}}, \tag{A6}$$

where $a_v$ and $k_v$ are constants, and the form of equation (A6) is assumed concave down because of self-shading of chloroplasts within leaves (Terashima et al. 2011). For simplicity, we ignore photosynthetic acclimation to different light environments (Bazzaz and Carlson 1982; Strauss-Debenedetti and Bazzaz 1991) and photosynthetic decline with leaf age (Field and Mooney 1983; Kitajima et al. 1997; Mediavilla and Escudero 2003).

Finally, light availability decreases with the total leaf area index of the plant community ($\mathrm{LAI_{tot}}$) according to the Beer-Lambert equation (Monsi and Saeki 2005) with a decay constant of 0.5 (White et al. 2000):

$$L = \exp(-0.5\,\mathrm{LAI_{tot}}) = \exp\left(-0.5\sum_i \frac{B_i}{\mathrm{LMA}_i}\right). \tag{A7}$$

Equation (A7) can be interpreted as the understory light level in the community, which has a strong effect on successional dynamics (Tilman 1985; Pacala et al. 1996). As explained in the main text (see "Model Overview"), we make the simplifying assumption that all leaves in the community experience this light level, and we therefore ignore the complexities of height-structured competition for light (Canham et al. 1994; Strigul et al., 2008).

The complete form of our model is obtained by substituting equations (A2)–(A7) into equation (A1). Despite our simplifying assumptions, mathematical analysis of the model is nontrivial and is explained in detail in appendix D.

To simulate aboveground wood biomass dynamics ($W_i$) for species $i$, we modified the leaf biomass model (eq. [A1]) as follows:

$$\frac{dW_i}{dt} = f_\mathrm{W}(1 - f_\mathrm{R})G_i - 4\,\mu_i W_i, \tag{A8}$$

where $f_\mathrm{W}$ (the fraction of leaf net photosynthesis allocated to aboveground wood biomass production) is $0.3 \times 0.8 = 0.24$ (assuming 30% allocation to wood and that 80% of wood is aboveground; Malhi et al. 2011) and $\mu_i$ is multiplied by four to account for branch turnover and stem respiration (Malhi et al. 2011); other terms in equation (A8) are defined as in equation (A1). To simulate equation (A8), we converted it to a difference equation with a time step of 0.01 years (this time step was short enough to remove noticeable effects of discretization).

**Table A1:** Model parameters and state variables

| Symbol | Description | Unit | Value |
|---|---|---|---|
| $a_v$ | Maximum possible value of $v$ (gross photosynthetic capacity) | g C m$^{-2}$ yr$^{-1}$ | 3,000 |
| $\mu_i$ | Whole-plant mortality rate | yr$^{-1}$ | .02 |
| $\rho$ | Alternate symbol for $\mathrm{LMA}_{\mathrm{P}i}$ in app. D | g C m$^{-2}$ | ... |
| $\sigma$ | Alternate symbol for $\mathrm{LMA}_{\mathrm{S}i}$ in app. D | g C m$^{-2}$ | ... |
| $B_{\mathrm{P}i}$ | Photosynthetic leaf biomass per unit ground area | g C m$^{-2}$ | ... |
| $B_{\mathrm{S}i}$ | Structural leaf biomass per unit ground area | g C m$^{-2}$ | ... |
| $B_i$ | Total leaf biomass per unit ground area: $B_i = B_{\mathrm{P}i} + B_{\mathrm{S}i}$ | g C m$^{-2}$ | ... |
| $c_\mathrm{LL}$ | Constant that converts $\mathrm{LMA_S}$ into leaf life span as follows: $\mathrm{LL}_i = c_\mathrm{LL} \times \mathrm{LMA}_{\mathrm{S}i}$ | m$^2$ yr g$^{-1}$ C | .1 |
| $f_\mathrm{L}$ | Fraction of NPP allocated to leaf growth | unitless | .3 |
| $f_\mathrm{R}$ | Fraction of NPP used for growth respiration | unitless | .3 |
| $G_i$ | Rate of leaf net photosynthesis per unit ground area | g C m$^{-2}$ yr$^{-1}$ | |
| $k_\mathrm{P}$ | Half-saturation constant for the relationship between gross photosynthesis and light | unitless | .2 |
| $k_v$ | Half-saturation constant for the relationship between photosynthetic capacity and $\mathrm{LMA_P}$ | g C m$^{-2}$ | 5 |
| $L$ | Proportion of full sunlight that reaches the understory | unitless | ... |
| $\mathrm{LAI}_i$ | Leaf area index (leaf area per unit ground area) | m$^2$ m$^{-2}$ | ... |
| $\mathrm{LL}_i$ | Leaf life span | yr | ... |
| $\mathrm{LMA}_{\mathrm{P}i}$ | Photosynthetic leaf mass per unit leaf area | g C m$^{-2}$ | ... |
| $\mathrm{LMA}_{\mathrm{S}i}$ | Structural leaf mass per unit leaf area | g C m$^{-2}$ | ... |
| $\mathrm{LMA}_i$ | Total leaf mass per unit leaf area: $\mathrm{LMA}_i = \mathrm{LMA}_{\mathrm{P}i} + \mathrm{LMA}_{\mathrm{S}i}$ | g C m$^{-2}$ | ... |
| $P_i$ | Rate of gross photosynthesis per unit leaf area | g C m$^{-2}$ yr$^{-1}$ | ... |
| $r_\mathrm{P}$ | Rate of leaf maintenance respiration per unit photosynthetic leaf mass | g C g$^{-1}$ C yr$^{-1}$ | 4 |

**Table A1** (*Continued*)

| Symbol | Description | Unit | Value |
|---|---|---|---|
| $r_S$ | Rate of leaf maintenance respiration per unit structural leaf mass | g C $g^{-1}$ C $yr^{-1}$ | .4 |
| $R_i$ | Rate of leaf maintenance respiration per unit ground area | g C $m^{-2}$ $yr^{-1}$ | ... |
| $v_i$ | Gross photosynthetic capacity per unit leaf area | g C $m^{-2}$ $yr^{-1}$ | ... |

Note: The "Value" column gives baseline values for global (non-species-specific) constants (which were perturbed in our uncertainty analysis), and ellipses are used for species-level parameters ($LMA_P$, $LMA_S$, and derived parameters) and state variables. Subscript *i*'s refer to species *i* and indicate species-specific parameters or state variables. The value for $\mu_i$ in the table was used for both early- and late-successional species for analysis results reported in the main text and in appendix D; alternative mortality assumptions are described in appendix B. Carbon is abbreviated as "C." Global constants were taken from the literature or tuned to match stand-level values (e.g., gross primary productivity estimates reported in the literature). When available, we used values for evergreen tropical forests because our model ignores LL constraints as a result of seasonality in temperature and rainfall (see "Model Overview"). We expect our qualitative conclusions to be robust to uncertainty in model parameters, as suggested by our uncertainty analysis (fig. 1). Therefore, we did not conduct a comprehensive literature search for parameter values but rather limited our sources to a few representative articles, and we used approximate average values if more than one of these sources provided information for a given constant. The net primary productivity (NPP) fraction allocated to leaf construction ($f_L$) is from Luyssaert et al. (2007) and Malhi et al. (2011). For the NPP fraction used for growth respiration ($f_G$), we adopt a value of 0.3, similar to other models (Krinner et al. 2005; Weng et al. 2015). Other constants were chosen to yield realistic model outputs for annualized rates of gross primary productivity, total autotrophic respiration, and leaf respiration (Luyssaert et al. 2007; Malhi et al. 2011); leaf area index (Asner et al. 2003); leaf mass per area (Poorter et al. 2009); and leaf life span (Wright et al. 2004). Allocation of leaf maintenance respiration to photosynthetic versus structural leaf mass components ($r_P = 10 \times r_S$) follows from the assumption that maintenance costs for metabolically active photosynthetic leaf mass components (e.g., chloroplasts) should be much greater than those for structural components (e.g., cellulose; Osnas et al. 2018).

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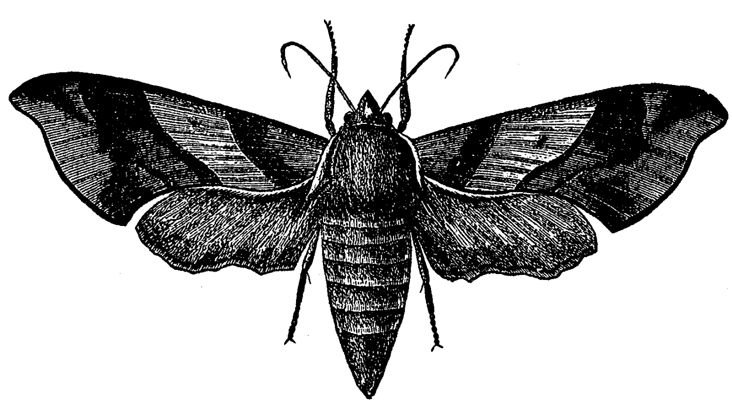

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