

Interspecific vs intraspecific patterns in leaf nitrogen of forest trees across nitrogen availability gradients

Ray Dybzinski¹, Caroline E. Farrior¹, Scott Ollinger² and Stephen W. Pacala¹

¹Department of Ecology and Evolutionary Biology, Princeton University, Princeton, NJ 08544, USA; ²Institute for the Study of Earth, Oceans and Space, University of New Hampshire, Durham, NH 03824, USA

Author for correspondence:

Ray Dybzinski

Tel: +1 773 760 4092

Email: rdybzins@princeton.edu

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Summary

- Leaf nitrogen content (δ) coordinates with total canopy N and leaf area index (LAI) to maximize whole-crown carbon (C) gain, but the constraints and contributions of within-species plasticity to this phenomenon are poorly understood.
- Here, we introduce a game theoretic, physiologically based community model of height-structured competition between late-successional tree species. Species are constrained by an increasing, but saturating, relationship between photosynthesis and leaf N per unit leaf area. Higher saturating rates carry higher fixed costs.
- For a given whole-crown N content, a C gain-maximizing compromise exists between δ and LAI. With greater whole-crown N, both δ and LAI increase within species. However, a shift in community composition caused by reduced understory light at high soil N availability (which competitively favors species with low leaf costs and consequent low optimal δ) counteracts the within-species response, such that community-level δ changes little with soil N availability. These model predictions provide a new explanation for the changes in leaf N per mass observed in data from three dominant broadleaf species in temperate deciduous forests of New England.
- Attempts to understand large-scale patterns in vegetation often omit competitive interactions and intraspecific plasticity, but here both are essential to an understanding of ecosystem-level patterns.

Introduction

Because nitrogen (N) is commonly a limiting resource (Aerts & Chapin, 2000; Finzi, 2009) and because a plant's photosynthetic machinery requires N in relatively high concentrations (Field & Mooney, 1986; Evans, 1989), evolution has produced a diversity of adaptations for its efficient use. For example, it is broadly true that plants allocate N to a leaf in relation to the light available to the leaf (Field, 1983). The allocation of more N than can be used by photosynthesis would seem to be wasteful and would probably incur respiratory costs. The allocation of less would make inefficient use of light, which is another important limiting resource.

Across and, to a lesser degree, within species, changes in leaf thickness, leaf N, leaf longevity and other attributes (Wright *et al.*, 2004) interact with the leaf area index (total leaf area per ground area, LAI) and total crown N to make different species or different individuals competitive under different ecological circumstances. For a given amount of total crown N, individuals can build few N-rich leaves or many N-poor leaves. By increasing leaf longevity, more leaves can be built for a given N uptake rate. However, because of the web of constraints and trade-offs that exist between these different strategies – most notably the ways in which these traits impact on leaf-level photosynthetic capacity

and self-shading – the distribution of N within a crown of diminishing light availability will be optimized in different ways under different circumstances (Horn, 1971; Field, 1983; Givnish, 1986; Niinemets & Tenhunen, 1997; McMurtrie *et al.*, 2008; Sterck & Schieving, 2011).

Within individuals, trees often exhibit a sun-leaf to shade-leaf continuum, whereby changes in leaf thickness and leaf area distribute N and other elements throughout a tree's crown so that, within bounds (see Kull, 2002), all the subprocesses of photosynthesis operate with maximum efficiency (i.e. none is more rate limiting than any other). Studies show that such within-individual sun-leaf and shade-leaf coordination is achieved by holding leaf N per mass approximately constant and reducing the leaf mass per area (LMA) with the depth of the leaf within the crown, such that leaf N per area (leaf N per mass multiplied by LMA) also decreases with the depth of the leaf within the crown (Ellsworth & Reich, 1993; Niinemets, 1997; Niinemets & Tenhunen, 1997; Aranda *et al.*, 2004).

In addition, ecologists have demonstrated that deciduous broadleaf species with lower leaf N per area have greater shade tolerance (Hallik *et al.*, 2009). The idea is that, in deep shade, saplings must minimize losses to avoid starving to death, and that leaf N, and the highly respiring photosynthetic machinery it is

used to construct, is a liability at low light (Walters & Reich, 1999). Because understory light availability usually decreases with increasing soil N availability (Tilman, 1988; Coomes & Grubb, 2000), ever lower leaf N species are expected to dominate late-successional communities across gradients of increasing soil N availability, all other things being equal.

However, the effects of competition for light and soil N on leaf N content are not yet well understood (Chapin *et al.*, 2002), hampering our ability to scale up our understanding of leaf-level physiology to the landscape and global levels. The correct characterization of this scale transition is essential if we are to predict biosphere–atmosphere feedbacks affecting climate change (Purves & Pacala, 2008), because the carbon (C) and N economies of ecosystems are so intertwined (Hungate *et al.*, 2003). Moreover, it is unclear by what mechanisms individual plasticity is constrained by species identity. On a common soil in a temperate mixed forest, Bassow & Bazzaz (1997) found that 67% and 76% of the variance in sun leaf N per mass and per area, respectively, were explained by species differences, whereas 17% and 12% were explained by differences among individuals within species.

If these individuals were able to plastically optimize their whole-crown C gain, why were the differences between species so great?

In order to better understand the effects of competition for light and soil N on leaf N, we first build a new and relatively simple forest model (Fig. 1, Table 1) that includes relevant mechanisms: a light-limited understory stage, an N- and light-limited canopy stage, plastic within-species allocation to leaf N throughout a crown (with concomitant effects on LAI for canopy individuals) and explicit dependence of the maximum gross photosynthetic rate on leaf N per area (a relationship which we assume is not plastic within a species). We use a game theoretic analysis (McGill & Brown, 2007) to find the most competitive suite of fixed and plastic traits across a gradient of soil N availability.

We compare the model's qualitative predictions with data from a soil N availability gradient in New Hampshire, USA (originally published in Ollinger *et al.*, 2002). This is the only dataset we are aware of that includes plot-level measures of species-specific leaf N per mass, relative species abundance and net N mineralization rate (a measure of soil N availability). We focus on the three co-dominant broadleaf species in old growth forests

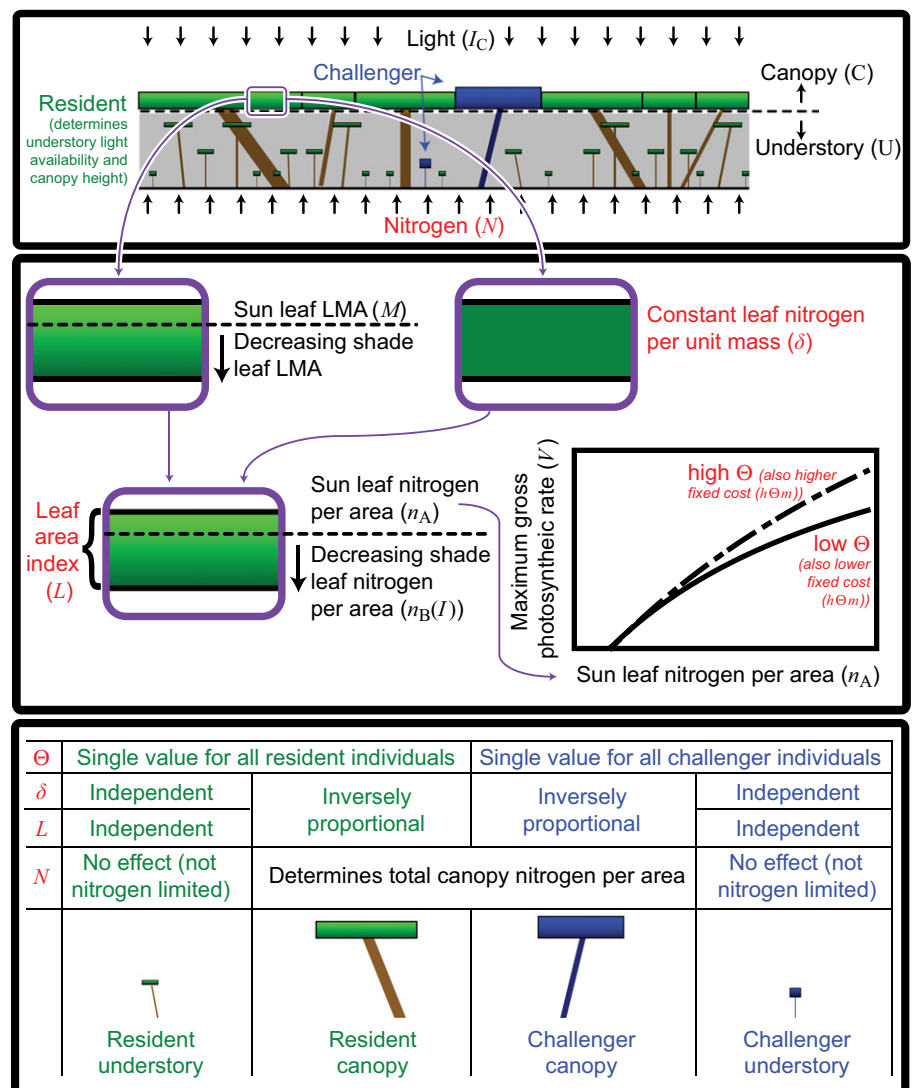


Fig. 1 Model overview. Red denotes state variables, and the bottom box shows how the state variables affect resident individuals vs challenger individuals, as well as canopy individuals vs understory individuals. Table 1 provides a description of all parameters and equations.

Table 1 Model summary

Variable	Value	Determination	Eqn
V	Gross photosynthetic rate — g C m ⁻² s ⁻¹	$V = \frac{\Theta n_A(\delta)}{f(\Theta) + n_A(\delta)} - u$	1
n_A	Sun leaf nitrogen per area — g N m ⁻²	$n_A = Mv\delta$	2
Θ	Maximum potential gross photosynthetic rate — g C m ⁻² s ⁻¹	State variable	
f	Half-saturation constant — g N m ⁻²	$f = 4850 \Theta - 0.675$, (i)	
u	Negative of intercept of gross photosynthesis on leaf nitrogen 10 ⁻⁴ g C m ⁻² s ⁻¹	(i)	
M	Sun leaf carbon mass per area 45 g C m ⁻²	(i)	3
v	Leaf biomass to carbon mass 2 g g C ⁻¹	Assumed	
δ	Fraction leaf nitrogen — g N g C ⁻¹	State variable	4
K	Crown depth (in leaf layers) at which leaves become light limited — m ⁻² m ⁻²	$\phi l_0 e^{-kK} = V(\Theta, \delta) \Rightarrow K = \frac{1}{k} \log_e \left(\frac{\phi l_0}{V(\Theta, \delta)} \right)$	5
ϕ	Quantum yield 0.498 g C (mol quanta) ⁻¹	(ii)	
l_0	Mean photosynthetically active radiation at the top of the crown — mol quanta m ⁻² s ⁻¹	$l_0 = \begin{pmatrix} l_C & \text{for individuals in the canopy} \\ l_U & \text{for individuals in the understory} \end{pmatrix}$	6
l_C	Mean photosynthetically active radiation at the top of the canopy 932 × 10 ⁻⁶ mol quanta m ⁻² s ⁻¹	(ii)	
l_U	Mean photosynthetically active radiation at the top of the understory as a function of resident (i.e. <i>not</i> challenger, see W) canopy LAI, L_C — mol quanta m ⁻² s ⁻¹	$l_U = l_C e^{-k\gamma L_C}$	7
k	Light extinction coefficient 0.5 m ² m ⁻²	(iii)	
χ	Canopy disturbance adjustment 0.5 —	(iii), assumed	
N_B	Total canopy nitrogen in light-limited leaves — g N m ⁻²	$N_B = \rho N - N_A$	8
N	Net nitrogen mineralization rate — g N m ⁻² yr ⁻¹	State variable	
ρ	Fraction of N available for foliage, accounting for 50% yearly retranslocation reinvested in foliage (understory, canopy) (0.29, 0.58) —	(iii), assumed	
N_A	Total canopy nitrogen in light-saturated leaves — g N m ⁻²	$N_A = n(\delta)K(\Theta, \delta)$	9
n_B	Shade leaf nitrogen per area as a function of leaf layer (x) and thus light, assuming perfect plasticity of LMA such that the photosynthetic capacity of shade leaves per unit light matches the quantum yield — g N m ⁻²	$\phi l_0 e^{-kx} = \frac{\Theta n_B(x)}{f(\Theta) + n_B(x)} - u \Rightarrow n_B(x) = \frac{(\phi l_0 e^{-kx} + u)f(\Theta)}{\Theta - (\phi l_0 e^{-kx} + u)}$	10
L	One-sided leaf area per ground area (LAI), which is defined implicitly and solved numerically for canopy individuals and optimized for understory individuals — m ⁻² m ⁻²	$L = \begin{pmatrix} N_B = \int_K^{L_C} n_B(x) dx & \text{for individuals in the canopy} \\ L_U & \text{for individuals in the understory} \end{pmatrix}$	11
P	Annual net carbon gain as the sum of the gross photosynthesis of sun leaves and shade leaves minus respiration — g C m ⁻² yr ⁻¹	$P = s \int_0^K (zV(\Theta, \delta) - m_A) dx + s \int_K^L (z\phi l_0 e^{-kx} - m_B(\Theta, \delta, x)) dx$	12
s	Scale conversion between measured (per second) and annual rates 5.876 × 10 ⁶ s yr ⁻¹	(iii), assumed	
z	Fraction of the day that is light 0.5 —	Assumed	
r	Foliage respiration rate 6.27 × 10 ⁻⁶ g C g N ⁻¹ s ⁻¹	(i)	
Q	Annual cost of leaf construction — g C m ⁻² yr ⁻¹	$Q = \left(\int_0^K n_A(\delta) dx + \int_K^L n_B(\Theta, \delta, x) dx \right) (\gamma + h\Theta) m$	13
γ	Leaf carbon and build respiration, assuming annual leaf turnover 1.25 g C g C ⁻¹ yr ⁻¹	(iii)	
h	Associated cost of higher maximum potential gross photosynthetic rate 5000 m ² s g C ⁻¹ yr ⁻¹	Assumed	14
m	Scale conversion between leaf nitrogen and leaf carbon budget 12.5 g C g N ⁻¹	Assumed	
G	Stem diameter growth rate (subscripted U or C when embedded parameter values take on understory or canopy values, respectively) — cm yr ⁻¹	$G = g(P - Q - \omega)$	15
g	Scale conversion between per ground area carbon and stem diameter growth rate 1.74 × 10 ⁻³ cm m ² g C ⁻¹	(iii)	

Table 1 (Continued)

Variable	Value	Determination	Eqn	
ω	Total costs of roots and fecundity (understory, canopy)	(100, 434.6) g C m ⁻² yr ⁻¹	(iii)	
\bar{D}	Stem diameter implicitly linked to height allometry at which individuals transition from the understory to the canopy in an equilibrium, closed-canopy monoculture (calculated using resident type only, never a challenger type)	— cm	$\bar{D} \approx \frac{G_U}{\mu_U} \log_e \left(F\alpha\Gamma(\theta + 1) \frac{G_C^\theta}{\mu_C^{\theta+1}} \right)$	16
μ	Mortality rate (understory, canopy)	(0.038, 0.013) yr ⁻¹	(iii)	
F	Fecundity rate	0.01 individuals m ⁻² yr ⁻¹	(iii)	
α	Power law coefficient relating stem diameter to crown area	0.422 m ² /θ cm ⁻¹	(iii), refit to consolidate parameters	17
θ	Power law exponent relating stem diameter to crown area	1.4 —	(iii)	18
W	Lifetime reproductive success (i.e. fitness) of a challenger strategy at infinitesimally low population density in a monoculture of a resident type	Individuals	$W \approx F\Gamma(\theta + 1)\alpha\mu_C^{-(\theta+1)}G_{C,\text{challenger}}^\theta \exp\left(-\bar{D}\mu_U G_{U,\text{challenger}}^{-1}\right)$	19

(i) Assumption within range of reasonable values based on temperate, non-nitrogen-fixing trees in the GLOPNET dataset (Wright *et al.*, 2004); (ii) Ellsworth & Reich (1992), tables 1 & 2; (iii) Dybzinski *et al.* (2011).

of northern New England: yellow birch (*Betula alleghaniensis* Britt., intermediate shade tolerance), American beech (*Fagus grandifolia* Ehrh., very shade tolerant) and sugar maple (*Acer saccharum* L., very shade tolerant) (shade tolerance from Burns & Honkala, 1990). Supporting Information Methods S1 contains the details of our analysis of the data of Ollinger *et al.* (2002).

Description

Model overview

Our model, as summarized conceptually in Fig. 1 and mathematically in Table 1, borrows most of its structure from Dybzinski *et al.* (2011), which contains a detailed description of its assumptions and development. Here, our significant departures from Dybzinski *et al.* (2011) are the explicit dependence of photosynthesis and respiration on leaf N per area (Eqn 1), the optimization of leaf mass per unit area (LMA) between sun and shade leaves so as to optimize whole-crown N use (Eqn 10), and the simplifying assumption that fine root investment, and hence N uptake per unit crown area, is equivalent among species at any given soil N availability. Figure 1 depicts the main components of the model. First, we describe the demographic and physiological mechanisms of a resident monoculture. The challenger strategy, depicted in blue, is discussed in the Model solution section later.

We begin with a physiologically based population model of height-structured competition for light, with distinct understory and reproductive canopy stages (Fig. 1), based on the Perfect Plasticity Approximation (PPA; Strigul *et al.*, 2008; Dybzinski *et al.*, 2011; Farrior *et al.*, 2013). The PPA takes advantage of the fact that trees are phototropic and capable of bending trunks and proliferating crowns in areas of higher light. The better plants are at this horizontal foraging for light, the more similar are the crown joint heights of canopy trees. The PPA makes the approximation

that plants are perfect in this process and, as a result, there is a single height that separates canopy individuals from understory individuals (depicted as a dashed line in the top panel of Fig. 1). This strict approximation is analytically tractable, allowing for the exact understanding of model predictions. The approximation is remarkably close to a fully spatially explicit model of trees with realistic estimates of horizontal foraging (Strigul *et al.*, 2008). The PPA has been shown to successfully predict basal area and changes in species abundance over 85 yr in forests of the lake states of the USA (Purves *et al.*, 2008). In our model, individuals hold light-intercepting territories (tree crowns, Strigul *et al.*, 2008) and, unlike game theoretic models developed for herbaceous vegetation (Schieving & Poorter, 1999; Anten, 2002), do not shade other members of their own crown class. This is a simplification that improves model tractability; studies suggest that relaxing this assumption would increase competitive LAI (Anten, 2002). However, canopy individuals *do* shade understory individuals, and the traits of the individuals comprising a stand combine to set the canopy height as a dynamic equilibrium between the growth of living trees and mortality (Eqn 16). All seeds produced by canopy individuals are assumed to stay within the stand and to give rise to new understory individuals. Because fecundity scales with crown area, larger canopy individuals produce more seeds than smaller canopy individuals.

In order to maintain model tractability, we make the simplifying assumption that each canopy individual takes a fraction of a given soil N proportional to its crown area (i.e. there are no different strategies of belowground competition, either among individuals or species), and we assume that there are no feedbacks between litter and soil N availability. Given the known importance of both of these processes (Coomes & Grubb, 2000; Decker & Boerner, 2006), it would be worthwhile to relax these assumptions in future investigations. As described later, our model relates C capture to N and light availability, and a full C

budget (including respiration) determines the amount of C that can be allocated to wood (Eqn 15) for allometrically related diameter growth, height growth and crown diameter growth (Eqns 17, 18).

With the N it captures, a canopy individual builds a crown with a particular leaf N per mass and a particular LAI (Eqn 11). Given a particular soil N availability, canopy individuals with greater leaf N per mass necessarily have lower LAI. The model correctly accounts for the N allocated to a gradient of shade leaves (i.e. thicker shade leaves towards the top with greater leaf N per area to thinner shade leaves towards the bottom with less leaf N per area, but with the same leaf N per mass throughout the crown, consistent with empirical relationships; Ellsworth & Reich, 1993; Niinemets & Tenhunen, 1997; Aranda *et al.*, 2004). In contrast with canopy individuals, which are both N and light limited, understory individuals are assumed to be only light limited and are thus free to optimize leaf N per mass and LAI independently.

Although field studies often report a linear relationship between leaf N per area and photosynthesis (Reich *et al.*, 1991; Lambers *et al.*, 2008), glasshouse studies that control for leaf N per area experimentally report a saturating relationship between leaf N per area and photosynthesis (Cheng *et al.*, 2001; Grassi *et al.*, 2002). A saturating relationship is consistent with the idea that limits to plasticity in leaf physiology (e.g. metabolic rates) or morphology (e.g. vein architecture) place limits on the photosynthetic response to ever greater leaf N. Linear responses measured in the field probably represent either an apparently ‘linearized’ subset of a full saturating response and/or the effects of concomitant changes in leaf physiology or morphology. Here, we take the maximum potential rate of gross photosynthesis (Θ) as a function of leaf N per area as a fixed trait of a species. Thus, unlike leaf N per mass and LAI, the maximum potential rate of gross photosynthesis as a function of leaf N per area remains unchanged as an individual transitions from the understory to the canopy.

Area-based leaf respiration is proportional to area-based maximum potential gross photosynthetic rate, such that shade leaves (low LMA) respire less and sun leaves (high LMA) respire more for the same leaf N per unit mass (Eqn 12). In addition, species with higher maximum potential gross photosynthetic rates pay higher C costs for that potential (Eqns 13, 14), independent of leaf N.

Model solution

First, we determine the most competitive strategy across a soil N availability gradient by finding ‘Evolutionarily Stable Strategies’ (Maynard Smith, 1982; Geritz *et al.*, 1998; McGill & Brown, 2007; McNickle & Dybzinski, 2013). We used numerical methods to find, for any particular soil N availability (N): ESS maximum potential gross photosynthetic rate shared by canopy and understory individuals (Θ^*), canopy ESS leaf N per mass (δ_C^*), canopy ESS LAI (L_C^*), understory ESS leaf N per mass (δ_U^*) and understory ESS LAI (L_U^*). Although our parameter values and solutions are within biologically realistic bounds, we emphasize that our goal is to reveal the robust qualitative patterns in the model’s predictions. These ESS solutions reflect interspecific

patterns that are predicted to cause shifts in species abundance across the soil N availability gradient. Second, we determine how three example species, which are defined by different Θ values and are competitive dominants at different points along the soil N availability gradient, would shift leaf N per mass and LAI across the gradient as a result of changes in the optimal leaf N per area distribution within their crowns, thus revealing intraspecific patterns.

To calculate the ESS values, we first constructed a ‘resident’ type by selecting a value for δ_C and a value for Θ and by employing Eqns 1–16 (Table 1) to determine the conditions that it would create in monoculture: I_U , light availability in the understory; and \tilde{D} , the stem diameter at which understory individuals transition to the canopy according to the PPA (Strigul *et al.*, 2008). After ensuring that the resident was capable of sustaining a closed-canopy monoculture in dynamic equilibrium, we selected ‘challenger’ types (or in the common, but potentially confusing, parlance of theoretical ecology, ‘invader’ or ‘mutant’ types) with every permutation of slightly smaller, equal and slightly larger values of δ_C and Θ (see step sizes below). The choice of the challenger’s δ_C determined its L_C (note that, with one degree of freedom, we could have just as easily chosen a value for L_C and determined δ_C), and understory challenger individuals were allowed to optimize δ_U and L_U given the challenger’s Θ . We calculated their respective expected lifetime reproductive successes (i.e. fitnesses) in the environment created by the resident (i.e. I_U and \tilde{D}) using Eqn 19. We repeated the process of creating residents and challengers across the full range of soil N, δ_C and Θ values displayed in Fig. 2 in all permutations using a step size of $0.1 \text{ g N m}^{-2} \text{ yr}^{-1}$ for soil N, $0.0005 \text{ g N g C}^{-1}$ for δ_C and

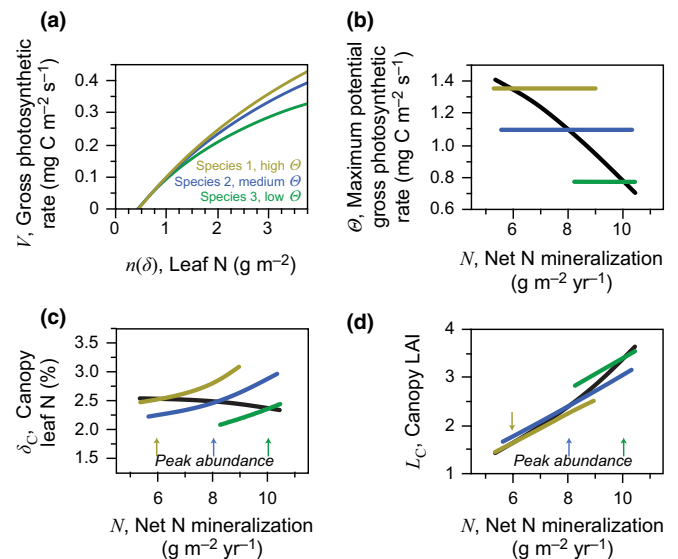


Fig. 2 Model definitions (a) and predictions (b, c, d). Three example species are defined by the saturating relationship between the maximum potential gross photosynthetic rate and leaf nitrogen (N) per area (a), with a higher maximum rate (i.e. a higher Θ) incurring a higher fixed cost (not shown). Black solid lines (b, c, d) represent the Evolutionarily Stable Strategy (ESS). On a landscape with stochastic source–sink dynamics, peak abundance is predicted to occur when the intraspecific trends intersect the ESS (c, d).

$5 \times 10^{-5} \text{ g C m}^{-2} \text{ s}^{-1}$ for Θ . Resident types were found for which no challengers could invade (i.e. $W_{\text{challenger}} < 1 = W_{\text{resident}}$), and these residents were thus deemed the ESS. For most values of soil N , this process found a single ESS that fell cleanly within the trend line suggested by the ESS values on adjacent soil N values. However, a few solutions initially fell outside of this suggested trend line because the step size interacted with the starting value, so as to straddle or otherwise miss the peak in the adaptive landscape. In these cases, we cut the step sizes in half and found that robust solutions did fall on the trend line suggested by the ESS values at surrounding soil N values. To find understory optimal δ_U^* and L_U^* , we used the FindMaximum function in Mathematica 7 (Wolfram Research, 2008) employing the default settings.

Finally, to demonstrate intraspecific patterns in leaf N per mass, we selected ESS species (as defined by their Θ^* values) on low, intermediate and high soil N levels. We then determined the range of soil N over which these three example species could sustain closed-canopy forests. Over this range, we found the changes in δ_C (and thus canopy LAI) that would maximize the canopy growth rate given the dependence of the maximum potential gross photosynthetic rate on leaf N per area for each example species (i.e. each species' Θ).

Results

ESS Θ (maximum potential gross photosynthetic rate), which understory and canopy individuals of a species are assumed to share, decreases with increasing soil N (Fig. 2b). This is because the increasingly dark understory conditions (Eqn 7) created by increasing canopy LAI (Eqns 10, 11, Fig. 2d) on these high soil N sites favor species with the reduced C costs associated with low Θ (Eqn 13).

The ranges of leaf N per mass expressed by the three example species (Θ^* from low soil N , Θ^* from medium soil N and Θ^* from high soil N) overlap across the soil N gradient (Fig. 2c). That is, the example species are capable of building leaves of the same leaf N per mass and, under different soil N conditions, they will do so. However, on any given soil N , the high Θ species has the highest leaf N per mass and the low Θ species has the lowest leaf N per mass (Fig. 2c). The leaf N per mass of the competitive dominant species, that is, the ESS leaf N per mass, decreases only slightly with increasing soil N (black line, Fig. 2c).

Similarly, the ranges of LAI expressed by the three example species overlap across the soil N gradient (Fig. 2d). However, because leaf N per mass and LAI are inversely proportional for canopy individuals, the pattern reverses: the high Θ species has the lowest LAI and the low Θ species has the highest LAI on any given soil N (Fig. 2d). The LAI of the competitive dominant species, that is, the ESS LAI, increases with increasing soil N (black line, Fig. 2d).

Discussion

The model predicts that, as soil N availability increases, the canopy leaf N per mass of individual species should increase (Fig. 2c), but community composition should shift to species with lower canopy leaf N per mass (Fig. 2c). As a result, species

abundance-weighted mean canopy leaf N per mass, as reflected in the ESS, should change very little with soil N availability (Fig. 2c). As we describe more fully later, two mechanisms are responsible for these theoretical results. First, increasing intraspecific canopy leaf N per mass with increasing soil N availability results from an optimal redistribution of whole-canopy N with changes in the absolute amount of whole-canopy N . For a given species (where a species is defined by its relationship between the maximum potential gross photosynthetic rate and leaf N per area), it is beneficial not only to increase LAI as soil N availability increases (Fig. 2d), but also to enrich the N content of existing leaf layers (Fig. 2c). Second, the community composition shifts to species with lower canopy leaf N per mass because these species are better able to persist in the dark conditions of the understory stage in an N -rich forest. The assumed species-defined physiology that achieves a more favorable understory C balance in deep shade (i.e. low Θ , Fig. 2) causes canopy leaf N per mass to optimize at a lower level; hence, the consistent interspecific difference in canopy leaf N per mass at a *common* soil N availability despite an interspecific overlap in canopy leaf N per mass *across* the gradient of soil N availability (Fig. 2c).

Data from Ollinger *et al.* (2002) include changes in sun leaf N per mass and relative abundance of the three dominant broadleaf species of New Hampshire, USA. We discuss these data in the context of our model predictions below by comparing measured sun leaf N per mass with the model's prediction of canopy leaf N per mass (compare Figs 3b and 2c), and by comparing measured relative abundance with the model's predicted intersection between ESS (i.e. most competitive) traits and intraspecific traits (compare Figs 3c and 2c). This interpretation assumes that the co-occurrence of multiple species in any given stand is the result of source-sink dynamics, whereby the most competitive species on a given soil (i.e. the ESS) is dominant, but not *completely* dominant (Lichstein & Pacala, 2011).

Amthor *et al.* (1990) measured area-based net photosynthesis on these three species growing in a clearing and found that yellow birch had a higher maximum rate than American beech and sugar maple, which were comparable. Beaudet *et al.* (2000) measured area-based net photosynthesis on these three species growing in both clearings and shade, and found that yellow birch and American beech had comparable maximum rates growing under full sun that were greater than the maximum rate of sugar maple. When growing in shade, the maximum rates of the three species were ranked yellow birch, American beech and sugar maple, from highest to lowest (Beaudet *et al.*, 2000). Together, the findings of these two studies are consistent with the relationship between photosynthesis and leaf N that we assume in our model.

Several patterns are evident in the data (Fig. 3). Notably, the *lowest* sun leaf N per mass of yellow birch overlaps with the *highest* sun leaf N per mass of sugar maple and the range of sun leaf N per mass of American beech is well within the ranges of the other two (Fig. 3b). *Thus, what differentiates these three species is not the inability to build leaves of a particular leaf N per mass.* Why then, on any particular soil, are they so well separated (Fig. 3b)? Moreover, given the considerable plasticity in leaf N per mass exhibited by these three species, *it is not clear why a*

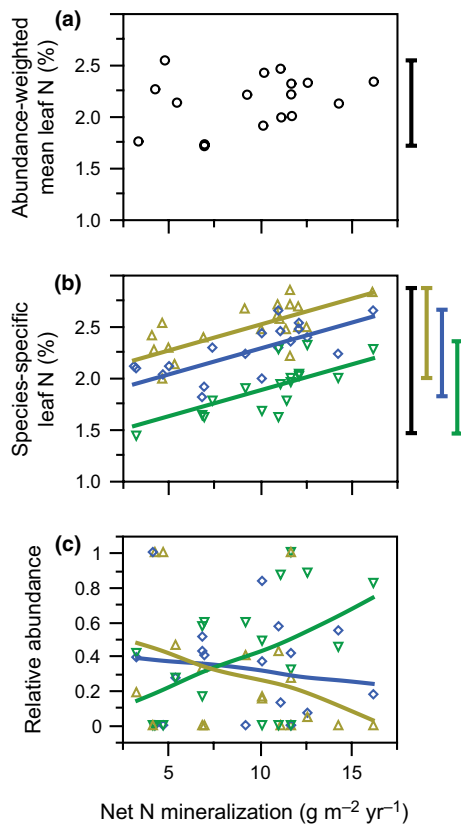


Fig. 3 Data from temperate forest stands in New Hampshire, USA as first published in Ollinger *et al.* (2002); see Supporting Information Methods S1 for methodological details. Mean leaf nitrogen (N) per mass shown in (a) calculated as the average species-specific leaf N per mass (b) weighted by relative abundance (c). We focus on the three broadleaf species, yellow birch (*Betula alleghaniensis*, yellow upward triangles), American beech (*Fagus grandifolia*, blue diamonds) and sugar maple (*Acer saccharum*, green downward triangles), that comprise > 75% of the broadleaf canopy area in the dataset. Black bars show the range of plot-level leaf N per mass, whereas colored bars show the range of species-specific leaf N per mass. Linear regression of data in (a): $P = 0.26$, $R^2 = 0.08$. Multiple linear regression of data in (b): species identity $P < 0.0001$, net N mineralization $P < 0.0001$, $R^2 = 0.79$. Multiple linear regression of data in (c): species identity by net N mineralization interaction $P = 0.03$, species identity $P = 0.59$, net N mineralization $P = 1$, $R^2 = 0.14$.

shade-tolerant habit in the understory should constrain performance in the canopy. Put simply, why can't individuals deploy a sugar maple physiology whilst in the understory and a yellow birch physiology in the canopy?

With increasing soil N availability, intraspecific leaf N per mass increases

There is a vast literature concerning the coordination of leaf N as a function of self-shading and total crown N (see reviews in Kull, 2002; Hirose, 2005; Anten & During, 2011). A simple theme that emerges from this research is that, because selection acts at the level of the individual plant, not the leaf, plants operating within constraints of plasticity (Kull, 2002) should optimize whole-crown C gain, not leaf-level C gain. The three example species all increase leaf N per mass with increasing soil N availability

(Fig. 2c). The reason why can be understood as follows. An additional unit of N in the crown of an N-limited tree can be used to enrich existing leaves, to build new leaves or some combination of the two. Enriching existing leaves and building new leaves both have diminishing returns. The allocation of an additional unit of N to existing leaves will return less additional net photosynthate than the unit of N allocated before it, because of the saturating relationship between the maximum potential gross photosynthetic rate and leaf N per area (Figs 1, 2a). Similarly, the allocation of this additional unit of N to new leaves will return less additional net photosynthate than the unit of N allocated before it, because of increased self-shading. The best return on the allocation of N will occur when the marginal returns on enriching existing leaves and building new leaves are equal. At higher soil N availability, the maximum return occurs at a lower marginal return, which is nevertheless still equalized between the enrichment of existing leaves and the building of new leaves. Thus, both leaf N per mass (Fig. 2c) and LAI (Fig. 2d) are higher at higher soil N availability.

Consistent with this, the sun leaf N per mass expressed by the three broadleaf species focused on in Ollinger *et al.* (2002) all increase with increasing soil N availability (with statistically indistinguishable slopes, Methods S1). This pattern supports the well-developed literature demonstrating that sun leaf N is often a reasonable proxy for soil N availability (Vitousek, 1982; Shaver & Melillo, 1984; Hobbie & Gough, 2002; Ordóñez *et al.*, 2009).

With increasing soil N availability, community composition shifts to species with lower leaf N per mass

With increasing soil N availability, our model predicts an interspecific shift in community composition from species with high leaf N per mass to species with low leaf N per mass. This pattern is driven by the understory stage (Methods S2). Loosely speaking, the canopy stage is wasting light for lack of photosynthetic machinery, so that the understory stage will be successful in the low-light conditions that it must endure. Such a one-sided compromise between the canopy and understory preferences is predicted by the calculation of lifetime reproductive success (i.e. fitness, Eqn 19), which is more sensitive to understory vital rates than canopy vital rates (Adams *et al.*, 2007). In an empirical study of the same compromise, Poorter (2007) measured the leaf physiology (including leaf N per mass and photosynthetic rates) and morphology of the seedlings, saplings and adults of 58 tropical moist tree species and related them to the species-specific light environments characteristic of these stages. He found that the leaf characteristics of the species (including leaf N per mass) were most strongly related to their seedling or sapling light environment, and that the adult light environment did not significantly explain any of the residual variation.

To our knowledge, ours is the first game theoretic model of leaf N that includes the distinct understory and canopy stages characteristic of forest trees. It is the explicit consideration of these two stages, together with their relative contributions to lifetime reproductive success and some limits to plasticity between the stages (Marksteijn *et al.*, 2007), that causes community composition to shift to low leaf N per mass species at high

soil N availability. Like a fast runner who fails to make it to the race, species with high maximum rates of photosynthesis may perform poorly in the dark understory of high N soils, which may prevent them from competing in the canopy on those soils (where they might do quite well). We suggest that this result does not depend on many of the particulars of our model formulation, and that future models that include these few core mechanisms will make the same qualitative prediction.

Consistent with our model predictions, sun leaf N per mass of the three dominant broadleaf species in the data of Ollinger *et al.* (2002) almost always consistently ranked by species on any particular soil, despite overlapping considerably across the N availability gradient. Mirroring the qualitative prediction of the model (Fig. 2c), they are ranked from the species that dominates low soil N availability (yellow birch) to the species that dominates high soil N availability (sugar maple) in descending order (Fig. 3). Similarly, Pastor *et al.* (1984) found that, among the broadleaf species, oaks, which tend to have higher leaf N, dominated low soil N availability sites, whereas maples, which tend to have lower leaf N, dominated high soil N availability sites.

Ecosystem-level effects

The opposing patterns of increasing leaf N per mass and increasing abundance of low leaf N per mass species with increasing soil N availability combine to cause little change in abundance-weighted mean broadleaf leaf N per mass in the data of Ollinger *et al.* (2002) (Fig. 3a). It is worth emphasizing that this pattern would be incomprehensible without simultaneously considering *both* the intraspecific and interspecific changes that occur along the gradient. Our model qualitatively predicts this pattern (Fig. 2c, dark line). Our result underscores the importance of including the community ecology of species interactions in studies of physiological traits and ecosystem responses along resource availability gradients. In the data and model presented here, we would have predicted much greater changes in leaf N at the ecosystem level than actually observed if we had left out the species-level interactions. This phenomenon – the moderation of an ecosystem-level response by within-functional type biodiversity – may be a general feature of competitive interactions. Because evolution favors individual-level fitness even at the expense of community-level attributes, successful competitors often display traits that would appear to be suboptimal in the absence of competition and that fail to maximize attributes at the community and ecosystem levels (Schieving & Poorter, 1999; Gersani *et al.*, 2001; Anten, 2002; Craine, 2006; Dybzinski *et al.*, 2011; Fariori *et al.*, 2013; McNickle & Dybzinski, 2013). Because they do not consider diversity within functional types, such moderations are not currently included in global models. If such ecosystem-level moderation turns out to be a general feature of within-functional type biodiversity, its inclusion might dramatically alter the predictions of global models.

The timescales of the two mechanisms described here may be critical to the prediction of changes in forest composition in response to elevated N deposition. Specifically, short-term changes may favor species that have inherently high maximum

photosynthetic rates per leaf N, which perform well in the canopy stage (Methods S2, Fig. S1), but long-term changes – at the time-scale of species turnover – may favor species that have inherently low maximum photosynthetic rates per leaf N, which perform well in the understory stage (Methods S2, Fig. S1).

Concluding remarks

Other more sophisticated models of whole-canopy photosynthesis and N biogeochemistry would probably improve the quantitative prediction of leaf N and may also provide other qualitative insights. For example, different species construct sun leaves of different LMA in a manner that is almost certainly adaptive (Poorter *et al.*, 2009); different species compete more effectively for soil N (Zak *et al.*, 2012); different species have different leaf lifespans with associated differences in leaf physiology (Wright *et al.*, 2004); and litter chemistry feeds back to affect soil N availability (Decker & Boerner, 2006). In addition, although N itself is often treated as a single resource, plants acquire N in a variety of forms (ammonium, nitrate and organic N) that differ greatly in availability and requirements for uptake and assimilation (Schimel & Bennett, 2004), and eastern US forests are subject to elevated levels of atmospheric N deposition (Aber *et al.*, 2003), which may shift contemporary patterns of species dominance relative to historical patterns. Differences across species in how belowground components of the N cycle are managed have implications for whole-plant C budgets that could influence optimal N concentrations in foliage. As a compromise to improve tractability, and because some of these mechanisms are still not well understood, our model ignores all of these potentially important factors.

Nevertheless, we believe that the two core mechanisms captured in our model, a marginal but diminishing benefit to increasing sun leaf N per area with increasing whole-canopy N and leaf physiology of the canopy stage that is constrained by the low-light requirements of the understory stage, will be necessary to predict the qualitative patterns found in the data of Ollinger *et al.* (2002). Tests of future models will be greatly improved by datasets (which are currently surprisingly scarce) that pair plot-level measures of resource availability (e.g. N mineralization rates, light availability, water regime) with the more common measures of community composition and species-specific traits.

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References

- Aber JD, Goodale CL, Ollinger SV, Smith ML, Magill AH, Martin ME, Hallett RA, Stoddard JL. 2003. Is nitrogen deposition altering the nitrogen status of northeastern forests? *BioScience* 53: 375–389.

- Adams TP, Purves DW, Pacala SW. 2007. Understanding height-structured competition in forests: is there an r^* for light? *Proceedings of the Royal Society B: Biological Sciences* 274: 3039–3047.
- Aerts R, Chapin FS III. 2000. The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. *Advances in Ecological Research* 30: 1–67.
- Amthor JS, Gill DS, Bormann FH. 1990. Autumnal leaf conductance and apparent photosynthesis by saplings and sprouts in a recently disturbed northern hardwood forest. *Oecologia* 84: 93–98.
- Anten NPR. 2002. Evolutionarily stable leaf area production in plant populations. *Journal of Theoretical Biology* 217: 15–32.
- Anten NPR, During HJ. 2011. Is analysing the nitrogen use at the plant canopy level a matter of choosing the right optimization criterion? *Oecologia* 167: 293–303.
- Aranda I, Pardo F, Gil L, Pardos JA. 2004. Anatomical basis of the change in leaf mass per area and nitrogen investment with relative irradiance within the canopy of eight temperate tree species. *Acta Oecologica-International Journal of Ecology* 25: 187–195.
- Bassow SL, Bazzaz FA. 1997. Intra- and inter-specific variation in canopy photosynthesis in a mixed deciduous forest. *Oecologia* 109: 507–515.
- Beaudet M, Messier C, Hilbert DW, Lo E, Wang ZM, Lechowicz MJ. 2000. Leaf- and plant-level carbon gain in yellow birch, sugar maple, and beech seedlings from contrasting forest light environments. *Canadian Journal of Forest Research-Revue Canadienne de Recherche Forestiere* 30: 390–404.
- Burns RM, Honkala HH. 1990. *Silvics of North America: hardwoods*. Agriculture handbook 654. Washington, DC, USA: US Department of Agriculture, Forest Service.
- Chapin FS III, Matson PA, Mooney HA. 2002. *Principles of terrestrial ecosystem ecology*. New York, NY, USA: Springer Verlag.
- Cheng LL, Fuchigami LH, Breen PJ. 2001. The relationship between photosystem II efficiency and quantum yield for CO₂ assimilation is not affected by nitrogen content in apple leaves. *Journal of Experimental Botany* 52: 1865–1872.
- Coomes DA, Grubb PJ. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. *Ecological Monographs* 70: 171–207.
- Craine JM. 2006. Competition for nutrients and optimal root allocation. *Plant and Soil* 285: 171–185.
- Decker KLM, Boerner REJ. 2006. Mass loss and nutrient release from decomposing evergreen and deciduous *Nothofagus* litters from the Chilean Andes. *Austral Ecology* 31: 1005–1015.
- Dybzinski R, Farris C, Wolf A, Reich PB, Pacala SW. 2011. Evolutionarily stable strategy of carbon allocation to foliage, wood, and fine roots in trees competing for light and nitrogen: an analytically tractable, individual-based model and quantitative comparisons to data. *American Naturalist* 177: 153–166.
- Ellsworth DS, Reich PB. 1992. Leaf mass per area, nitrogen-content and photosynthetic carbon gain in *Acer saccharum* seedlings in contrasting forest light environments. *Functional Ecology* 6: 423–435.
- Ellsworth DS, Reich PB. 1993. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia* 96: 169–178.
- Evans JR. 1989. Photosynthesis and nitrogen relationships in leaves of C3 plants. *Oecologia* 78: 9–19.
- Farris CE, Dybzinski R, Levin SA, Pacala SW. 2013. Competition for water and light in closed-canopy forests: a tractable model of carbon allocation with implications for carbon sinks. *American Naturalist* 181: 314–330.
- Field C, Mooney HA. 1986. The photosynthesis–nitrogen relationship of wild plants. In: Givnish T, ed. *On the economy of plant form and function*. Cambridge, UK: Cambridge University Press, 25–55.
- Field CB. 1983. Allocating leaf nitrogen for the maximization of carbon gain: leaf age as a control on the allocation program. *Oecologia* 56: 341–347.
- Finzi AC. 2009. Decades of atmospheric deposition have not resulted in widespread phosphorus limitation or saturation of tree demand for nitrogen in southern New England. *Biogeochemistry* 92: 217–229.
- Geritz SAH, Kisdi E, Meszina G, Metz JAJ. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology* 12: 35–57.
- Gersani M, Brown JS, O'Brien EE, Maina GM, Abramsky Z. 2001. Tragedy of the commons as a result of root competition. *Journal of Ecology* 89: 660–669.
- Givnish TJ. 1986. *On the economy of plant form and function*. Cambridge, UK: Cambridge University Press.
- Grassi G, Meir P, Cromer R, Tompkins D, Jarvis PG. 2002. Photosynthetic parameters in seedlings of *Eucalyptus grandis* as affected by rate of nitrogen supply. *Plant, Cell & Environment* 25: 1677–1688.
- Hallik L, Niinemets U, Wright IJ. 2009. Are species shade and drought tolerance reflected in leaf-level structural and functional differentiation in northern hemisphere temperate woody flora? *New Phytologist* 184: 257–274.
- Hirose T. 2005. Development of the Monsi–Saeki theory on canopy structure and function. *Annals of Botany* 95: 483–494.
- Hobbie SE, Gough L. 2002. Foliar and soil nutrients in tundra on glacial landscapes of contrasting ages in northern Alaska. *Oecologia* 131: 453–462.
- Horn HS. 1971. *The adaptive geometry of plants*. Princeton, NJ, USA: Princeton University Press.
- Hungate BA, Dukes JS, Shaw MR, Luo YQ, Field CB. 2003. Nitrogen and climate change. *Science* 302: 1512–1513.
- Kull O. 2002. Acclimation of photosynthesis in canopies: models and limitations. *Oecologia* 133: 267–279.
- Lambers H, Chapin FS, Pons TL. 2008. *Plant physiological ecology*. New York, NY, USA: Springer-Verlag.
- Lichstein JW, Pacala SW. 2011. Local diversity in heterogeneous landscapes: quantitative assessment with a height-structured forest metacommunity model. *Theoretical Ecology* 4: 269–281.
- Markestijn L, Poorter L, Bongers F. 2007. Light-dependent leaf trait variation in 43 tropical dry forest tree species. *American Journal of Botany* 94: 515–525.
- Maynard Smith J. 1982. *Evolution and the theory of games*. New York, NY, USA: Cambridge University Press.
- McGill BJ, Brown JS. 2007. Evolutionary game theory and adaptive dynamics of continuous traits. *Annual Review of Ecology Evolution and Systematics* 38: 403–435.
- McMurtrie RE, Norby RJ, Medlyn BE, Dewar RC, Pepper DA, Reich PB, Barton CVM. 2008. Why is plant-growth response to elevated CO₂ amplified when water is limiting, but reduced when nitrogen is limiting? A growth-optimisation hypothesis. *Functional Plant Biology* 35: 521–534.
- McNickle GG, Dybzinski R. 2013. Game theory and plant ecology. *Ecology Letters* 16: 545–555.
- Niinemets U. 1997. Role of foliar nitrogen in light harvesting and shade tolerance of four temperate deciduous woody species. *Functional Ecology* 11: 518–531.
- Niinemets U, Tenhunen JD. 1997. A model separating leaf structural and physiological effects on carbon gain along light gradients for the shade-tolerant species *Acer saccharum*. *Plant, Cell & Environment* 20: 845–866.
- Ollinger SV, Smith ML, Martin ME, Hallett RA, Goodale CL, Aber JD. 2002. Regional variation in foliar chemistry and N cycling among forests of diverse history and composition. *Ecology* 83: 339–355.
- Ordóñez JC, van Bodegom PM, Witte JPM, Wright IJ, Reich PB, Aerts R. 2009. A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Global Ecology and Biogeography* 18: 137–149.
- Pastor J, Aber JD, McClaugherty CA, Melillo JM. 1984. Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. *Ecology* 65: 256–268.
- Poorter H, Niinemets U, Poorter L, Wright IJ, Villar R. 2009. Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist* 182: 565–588.
- Poorter L. 2007. Are species adapted to their regeneration niche, adult niche, or both? *American Naturalist* 169: 433–442.
- Purves D, Pacala S. 2008. Predictive models of forest dynamics. *Science* 320: 1452–1453.
- Purves DW, Lichstein JW, Strigul N, Pacala SW. 2008. Predicting and understanding forest dynamics using a simple tractable model. *Proceedings of the National Academy of Sciences, USA* 105: 17018–17022.
- Reich PB, Walters MB, Ellsworth DS. 1991. Leaf age and season influence the relationships between leaf nitrogen, leaf mass per area and photosynthesis in maple and oak trees. *Plant, Cell & Environment* 14: 251–259.

- Schieving F, Poorter H. 1999. Carbon gain in a multispecies canopy: the role of specific leaf area and photosynthetic nitrogen-use efficiency in the tragedy of the commons. *New Phytologist* 143: 201–211.
- Schimel JP, Bennett J. 2004. Nitrogen mineralization: challenges of a changing paradigm. *Ecology* 85: 591–602.
- Shaver GR, Melillo JM. 1984. Nutrient budgets of marsh plants: efficiency concepts and relation to availability. *Ecology* 65: 1491–1510.
- Sterck F, Schieving F. 2011. Modelling functional trait acclimation for trees of different height in a forest light gradient: emergent patterns driven by carbon gain maximization. *Tree Physiology* 31: 1024–1037.
- Strigul N, Pristinski D, Purves D, Dushoff J, Pacala S. 2008. Scaling from trees to forests: tractable macroscopic equations for forest dynamics. *Ecological Monographs* 78: 523–545.
- Tilman D. 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton, NJ, USA: Princeton University Press.
- Vitousek P. 1982. Nutrient cycling and nutrient use efficiency. *American Naturalist* 119: 553–572.
- Walters MB, Reich PB. 1999. Low-light carbon balance and shade tolerance in the seedlings of woody plants: do winter deciduous and broad-leaved evergreen species differ? *New Phytologist* 143: 143–154.
- Wolfram Research. 2008. *Mathematica, version 7.0*. Champaign, IL, USA: Wolfram Research, Inc.
- Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M *et al.* 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.
- Zak DR, Kubiske ME, Pregitzer KS, Burton AJ. 2012. Atmospheric CO₂ and O₃ alter competition for soil nitrogen in developing forests. *Global Change Biology* 18: 1480–1488.

Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Depiction of the understory and canopy components of the Evolutionarily Stable Strategy (ESS) for maximum potential gross photosynthetic rate as a function of soil nitrogen availability.

Methods S1 Summary and re-analysis of empirical data originally presented in Ollinger *et al.* (2002).

Methods S2 Description of an analysis that decomposes the Evolutionarily Stable Strategy (ESS) for maximum potential gross photosynthetic rate into its understory and canopy components.

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