Predicting vegetation type through physiological and environmental interactions with leaf traits: evergreen and deciduous forests in an earth system modeling framework

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Abstract

Earth system models are incorporating plant trait diversity into their land components to better predict vegetation dynamics in a changing climate. However, extant plant trait distributions will not allow extrapolations to novel community assemblages in future climates, which will require a mechanistic understanding of the trade-offs that determine trait diversity. In this study, we show how physiological trade-offs involving leaf mass per unit area (LMA), leaf lifespan, leaf nitrogen, and leaf respiration may explain the distribution patterns of evergreen and deciduous trees in the temperate and boreal zones based on (1) an evolutionary analysis of a simple mathematical model and (2) simulation experiments of an individual-based dynamic vegetation model (i.e., LM3-PPA). The evolutionary analysis shows that these leaf traits set up a trade-off between carbon- and nitrogen-use efficiency at the scale of individual trees and therefore determine competitively dominant leaf strategies. As soil nitrogen availability increases, the dominant leaf strategy switches from one that is high in nitrogen-use efficiency to one that is high in carbon-use efficiency or, equivalently, from high-LMA/long-lived leaves (i.e., evergreen) to low-LMA/short-lived leaves (i.e., deciduous). In a region of intermediate soil nitrogen availability, the dominant leaf strategy may be either deciduous or evergreen depending on the initial conditions of plant trait abundance (i.e., founder controlled) due to feedbacks of leaf traits on soil nitrogen mineralization through litter quality. Simulated successional patterns by LM3-PPA from the leaf physiological trade-offs are consistent with observed successional dynamics of evergreen and deciduous forests at three sites spanning the temperate to boreal zones.

Keywords: dynamic global vegetation model, evolutionarily stable strategy, forest succession, game theory, leaf traits, LM3-PPA, nitrogen cycle

Received 3 April 2016; revised version received 17 October 2016 and accepted 18 October 2016

Introduction

Dynamic global vegetation models (DGVMs) are widely used in Earth system models as the land components for simulating interactions between climate and vegetation. The biodiversity of global vegetation is represented by a set of plant functional types (PFTs) in DGVMs: usually a small collection of trees, shrubs, and grasses based on the canonical biomes of the world (Prentice \(\text{et al.}, 1992\)). The parameters of each PFT are assigned according to the biome-wide averages of plant traits and the \(\text{extent}\) temperature and precipitation relationships (e.g., LPJ, Sitch \(\text{et al.}, 2003\)). This approach made it possible to predict global vegetation dynamically and to simulate the interactions between climate and vegetation when data and computational power were limited (Foley \(\text{et al.}, 1998, 2000\)). However, the use of PFTs underrepresents the variation in plant traits and artificially constrains vegetation processes, which may increase the uncertainty of model predictions (Scheiter \(\text{et al.}, 2013\); Wullschleger \(\text{et al.}, 2014\)).

Significant advances have been made recently in uncovering the most ubiquitous between-species correlations among traits and between traits and environmental conditions (Wright \(\text{et al.}, 2004, 2005\); Osnas \(\text{et al.}, 2013\); Reich \(\text{et al.}, 2014\)) and in documenting how trait distributions change during community assembly (Shipley \(\text{et al.}, 2006\); Weiher \(\text{et al.}, 2011\); Laughlin & Laughlin, 2013). These studies make it possible to improve plant functional diversity in DGVMs for realistically simulating vegetation dynamics. A straightforward approach is to directly add the empirical relationships between climate and plant traits into the models. Simulation results have shown that this approach improves model realism and predictions (e.g., Wang \(\text{et al.}, 2012\); Verheijen \(\text{et al.}, 2013, 2015\); Reich \(\text{et al.}, 2014\)). Moreover, plant traits, together with
theories of community assembly, can be used to predict vegetation dynamics and distribution based on environmental constraints (Kleidon & Mooney, 2000) and plant competition (van Bodegom et al., 2014; Violle et al., 2014).

Individual and trait-based DGVMs that link plant traits and individual physiological and demographic processes together to predict vegetation dynamics have been developed, for example, aDGVM2 (Scheiter et al., 2013), JeDi-DGVM (Kleidon & Mooney, 2000; Reu et al., 2011; Pavlick et al., 2013), ED (Moorcroft et al., 2001; Medvigy et al., 2009), and LPjML-FIT (Sakschewski et al., 2015). These models simulate competition for limited resources among individuals and can compete a large number of PFTs – now defined by combinations of plant traits – against one another to determine the most competitive trait mix. In doing so, they predict the correlations between plant traits and climate that emerge from numerical simulations (e.g., Pavlick et al., 2013; Scheiter et al., 2013; Sakschewski et al., 2015).

However, including extant relationships between climate and plant traits will not necessarily reduce model uncertainties (e.g., Pappas et al., 2016) because novel community assemblages may emerge in the future as they did with past climate change (Davis, 1986). By definition, novel community assemblages have no current observations from which to draw parameter values (Ackerly, 2003). In addition, numerical simulations of the individual- and trait-based models are unlikely by themselves to produce a mechanistic understanding of the way in which traits determine the outcome of competition for different resources, in part because of the limited number of strategies that can be competed against one another in practice and in part because of the complexity of the problem (Farrior et al., 2013b; Pappas et al., 2016).

The simulation results and behavior of individual-based models can be explained by game theoretic analyses (Maynard Smith, 1974). Game theoretic approaches have been employed to solve mathematically for the most competitive trait combination(s) in a continuous multivariate trait distribution, such as the competitively optimal biomass allocation among leaves, stems, and fine roots (Dybzinski et al., 2011, 2013, 2015; Farrior et al., 2013a,b), crown depth (Vermeulen, 2014), tree height (King, 1990; Falster & Westoby, 2003), leaf angles (Hikosaka & Hirose, 1997), and leaf area index (LAI; Anten, 2002). Although game theoretic mathematical analyses have been useful in explaining field observations and experimental results (e.g., Dybzinski et al., 2013; Farrior et al., 2013b) and improving our understanding of simulation results from complex models (e.g., Weng et al., 2015), their obvious disadvantage is the model simplicity they require.

In this study, we base our model on observed trade-offs among leaf traits and use both approaches – game theoretic analysis of a simplified mathematical model and simulation experiments using the land component of an earth system model (LM3-PPA, Weng et al., 2015) – to investigate how leaf traits affect the outcome of competition among evergreen and deciduous vegetation types in mesic environments across the temperate and boreal zones. Throughout, we use the terms ‘mathematical model’ and ‘simulation experiments’ to differentiate these approaches (even though the simulations require mathematics as well).

Briefly, we formulate a ‘universe of possible plant types’ based on the trade-offs between leaf mass per unit area (LMA) and other leaf traits (including leaf lifespan, leaf nitrogen, leaf respiration, and litter decomposition rate) and compete combinations against one another under conditions of limiting nitrogen and light. Using the mathematical model, we predict both the conceptually useful ‘optimal’ LMA that maximizes carbon (C) gain given an extrinsic nitrogen (N) mineralization rate as well as the more ecologically relevant ‘competitively dominant’ (evolutionarily stable strategy, ESS) LMA that cannot be invaded by any other strategy when explicitly including feedbacks of leaf traits on N mineralization. We show that the results qualitatively explain the mix of evergreen and deciduous forest types observed across the varying N availability in soils in temperate and boreal regions. Finally, we use the corresponding version of LM3-PPA to predict forest structure and dynamics at three sites in the temperate and boreal regions.

Materials and methods

Physiological trade-offs in leaf traits

Studies of interspecific variation in leaf traits show the critical role played by LMA (Wright et al., 2004; Lloyd et al., 2013; Osnas et al., 2013). LMA is positively correlated with leaf lifespan, area-based leaf N content, and leaf respiration rate (Osnas et al., 2013) and negatively correlated with mass-based leaf N content (Wright et al., 2004). We hypothesize that these correlations are trade-offs created by physical constraints and evolution. An increase in the potential lifespan of a leaf likely requires additional functional and structural tissues and thus increases LMA. The additional tissues in high-LMA leaves then must contain some N and respire because more mesophyll cells are in high-LMA leaves (Evans & Poorter, 2001; Osnas et al., 2013; Villar et al., 2013). However, the N content of the added structural material is low, meaning the ratio of C : N increases with LMA (Wright et al., 2004; Osnas et al., 2013), which decreases the rate of biomass decomposition (Mcclougherty et al., 1985; Garnier et al., 2004; Cornwell et al., 2008). These hypotheses form the basis of the model.
We assume that annual C fixation (photosynthesis) is an exponentially saturating function of LAI, a well-established approach used in light-use efficiency models (Monteith, 1977; Landsberg & Waring, 1997; Duursma & Makela, 2007):

\[ C_{\text{gain}} = \frac{V}{k} (1 - e^{-\frac{G}{k}}), \tag{6} \]

where \( C_{\text{gain}} \) is annual C fixation (kgC m\(^{-2}\) yr\(^{-1}\)), \( V \) is the per unit leaf area productivity of a leaf in full sun (kgC m\(^{-2}\) yr\(^{-1}\)), and the constant \( k \) captures the effect of self-shading of leaves within a plant’s crown on \( C_{\text{gain}} \). Because we are testing the effects of variation in LAI on leaf dominant strategy, we set a constant photosynthetic capacity for all the leaves (constant parameter \( V \)), regardless of their LAI. This assumption is consistent with the observation that the maximum rate of photosynthesis per unit leaf area and LMA are independent (Osnas et al., 2013). Note \( C_{\text{gain}} \) does depend indirectly on LAI here, however, as LAI is a function of LMA (Eqn 5).

Annual C cost per unit crown area of a tree’s canopy (\( C_{\text{cost}} \)) kgC m\(^{-2}\) yr\(^{-1}\)) is the sum of maintenance and building costs of the leaves:

\[ C_{\text{cost}} = (R + G \sigma) L = N_m r c \sigma + G \frac{\sigma N_m}{A + B \sigma}, \tag{7} \]

where \( G \) is building cost per unit leaf mass (kgC kgC\(^{-1}\)), including both the carbon used for constructing the leaves and the respiration of growth itself. Taken together, the net C gain of a canopy (\( C_{\text{net}} \), kgC m\(^{-2}\) yr\(^{-1}\)) is the difference between the canopy C fixation (i.e., \( C_{\text{gain}} \)) and the C cost of leaves:

\[ C_{\text{net}} = \frac{V}{k} \left( 1 - e^{-\frac{G c}{k}} \right) - N_m r c \sigma - G \frac{\sigma N_m}{A + B \sigma}. \tag{8} \]

To illustrate the plant-level trade-offs of the model’s leaf-level physiology, we plot the dependence of LAI, \( C_{\text{gain}} \), \( C_{\text{cost}} \), and \( C_{\text{net}} \) on LMA in Fig. 1 using parameters in Table 1.

For simplicity of the N cycle in the mathematical model, we assume that all plant N uptake is used in leaves (instead of half), and eliminate N retranslocation before leaf drop (instead of the half in retranslocation). Conveniently, these effects cancel and all equations derived above remain unchanged with this simplification. At equilibrium, the N mineralization rate (\( N_m \), gN m\(^{-2}\) yr\(^{-1}\)) can then be expressed as a function of total ecosystem N (\( N_{\text{total}} \), gN m\(^{-2}\)) and the residence times of N in the leaves (\( \lambda \)) and soil (\( \tau_s \)):

\[ N_m = \frac{N_{\text{total}}}{\lambda + \tau_s} = \frac{N_{\text{total}}}{\lambda + \frac{N_{\text{total}}}{|s|} \sigma_R} = \frac{N_{\text{total}}}{|c + s| \sigma_R}, \tag{9} \]

where \( s = \xi(T, M) \), and \( \sigma_R \) is the average leaf LAI of the stand’s leaf litter or the LMA of the monodominant ‘resident’ trees. (See Eqs. S31–S33 in Appendix S2 for the mathematical derivation.)

We analyze this framework mathematically to predict dominant leaf traits of plants across soil nitrogen gradients due to both total ecosystem N and climate. First, we find the optimal strategy as a function of an extrinsic environmental N mineralization rate. Second, we find the...
competitive dominant or ESS given feedbacks between dominant species LMA and the $N_m$, which includes the feedback between leaf nitrogen and the litter decomposition rate. For both of these analyses, and like many previous studies (Field, 1983; Pearcy et al., 1987; Goetz & Prince, 1999), we assume that net C gain (Eqn 8) is proportional to fitness. Note, to compute the ESS LMA ($\sigma_{ESS}$), we assume that successive invasions are sufficiently far apart enough in time for the N mineralization rate to equilibrate to the resident strategy with LMA $\sigma_R$ (Eqn 9).

We assume potential invaders are rare (i.e., they have a negligible effect on $N_m$). Thus, the net C gain of an invader with LMA, $\sigma_I$, is as follows:

$$C_{\text{net}}(\sigma_I|\sigma_R) = \frac{V}{V - 1} (1 - e^{-k(N_m(\sigma_R)|\sigma_I)/A + B}) - N_m(\sigma_R)rc.$$

where $N_m(\sigma_R)$ is the annual N mineralization rate determined by the resident. To find the $\sigma_{ESS}$, we differentiate the right-hand side of Eqn (10) with respect to $\sigma_I$, replace both $\sigma_I$ and $\sigma_R$ in the resulting expression by $\sigma_{ESS}$, and solve for $\sigma_{ESS}$.

The solution here is not sufficient to prove that $\sigma_{ESS}$ is a true ESS because the solution could be the least competitive strategy (a minimum) or invadable by strategies not nearby in strategy space (i.e., not a global maximum) (Geritz et al., 1998).

We evaluate $C_{\text{net}}(\sigma_I|\sigma_R)$ and $C_{\text{net}}(\sigma_R|\sigma_I)$ for all possible combinations of 1000 values of $\sigma_I$ and $\sigma_R$ ranging from 0.00005 to 0.5 at intervals of 0.00005, to determine which invaders successfully invade each resident LMA (invasion succeeds if $C_{\text{net}}(\sigma_I|\sigma_R) > C_{\text{net}}(\sigma_R|\sigma_I)$ (Fig. S1). The resulting pairwise invasion plot can be interpreted to determine whether $\sigma_{ESS}$ is a global, convergence-stable maximum. Parameter values for these calculations are in Table 1. The leaf parameters in this table are adapted from the data of leaf traits studies (e.g., Reich et al., 1998a, 1999; Wright et al., 2004). Other parameters, such as photosynthetic capacity and soil C residence time, are based on relevant studies in North American temperate forests (e.g., Curtis et al., 2002; Lichter et al., 2008). These parameters are for numerically illustrating the quantitative patterns of the model and thus can be varied within reasonable ranges without changing the results.

In one of the cases considered below, any resident LMA below a critical value can always be invaded by a smaller LMA (Fig. S1d). This is unrealistic at the limit of low LMA, where clearly zero LMA is not a feasible plant strategy. This result comes from the simplified assumption that photosynthetic capacity $V$ and functional N per unit area $A$ (Eqn 2) are both constant. In the limit of low LMA, this may not be true because the low LMA may reduce the functional N and therefore reduce photosynthetic capacity. This necessitates the introduction of a boundary ESS. An ESS on a boundary constraint cannot be invaded by any trait value near to, but not on the boundary. Because any possible leaf must contain essential

Table 1 Parameter values used by the mathematical model to illustrate the quantitative patterns of N-limited leaf area index, canopy carbon gain, carbon cost, net carbon gain, optimal leaf mass per area (LMA), and competitively dominant LMA (i.e., evolutionarily stable strategy, ESS)

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Value</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>$c$</td>
<td>Leaf lifespan parameter (Eqn 1)</td>
<td>28.57</td>
<td>yr kgC$^{-1}$ m$^{-2}$</td>
</tr>
<tr>
<td>$A$</td>
<td>Functional leaf N (Eqn 2)</td>
<td>1.5</td>
<td>gN m$^{-2}$</td>
</tr>
<tr>
<td>$B$</td>
<td>Structural leaf N (Eqn 2)</td>
<td>8</td>
<td>gN kgC$^{-1}$</td>
</tr>
<tr>
<td>$r$</td>
<td>Leaf respiration parameter (Eqn 3)</td>
<td>0.015</td>
<td>kgC gN$^{-1}$ yr$^{-1}$</td>
</tr>
<tr>
<td>$V$</td>
<td>Photosynthesis parameter (Eqn 6)</td>
<td>1.2</td>
<td>kgC m$^{-2}$ yr$^{-1}$</td>
</tr>
<tr>
<td>$k$</td>
<td>Saturate rate of GPP with LAI (Eqn 6)</td>
<td>0.5</td>
<td></td>
</tr>
<tr>
<td>$G$</td>
<td>Growth carbon cost (Eqn 7)</td>
<td>1.3333</td>
<td>kgC kgC$^{-1}$</td>
</tr>
<tr>
<td>$s$</td>
<td>Soil N residence time parameter (Eqn 9)</td>
<td>500</td>
<td>yr kgC m$^{-2}$</td>
</tr>
<tr>
<td>$\sigma_{min}$</td>
<td>Minimum leaf mass per unit area (Eqn 13)</td>
<td>0.02</td>
<td>kgC m$^{-2}$</td>
</tr>
</tbody>
</table>
structures such as an epidermis, palisade layer, and transport system, we introduce a minimum possible LMA, $a_{\text{min}}$, to constrain the boundary ESS at a plausible value (0.02 kgC m$^{-2}$, Table 1). It is close to the lower limit of maple tree’s LMA as shown in GLOPNET data (Wright et al., 2004).

**LM3-PPA and nitrogen cycle model**

In order to study the potential for the leaf trait trade-offs (Eqns 1–3) to predict the emergent property of forest succession and distribution, we use the newly developed LM3-PPA (Weng et al., 2015) for simulation experiments. LM3-PPA is based on an explicit scaling of individual plants to ecosystems. Its energy, CO$_2$, and water dynamics are fully coupled to an atmospheric model, but it can also be run offline with climate forcing data. LM3-PPA includes height-structured competition for light and root allocation-dependent competition for both water and nitrogen. The representation of individual trees allows LM3-PPA to predict forest structure and succession mechanistically.

We incorporate a simple N cycle model (Fig. 2) into LM3-PPA to simulate ecosystem N dynamics based on those developed by Gerber et al. (2010) and Manzoni et al. (2010). In LM3-PPA, an individual tree has six C pools: leaves, fine roots, sapwood, heartwood, fecundity (seeds), and nonstructural carbohydrates (NSC). We add an N pool corresponding to each of these (Fig. 2). The N absorbed by roots enters the nonstructural N (NSN) pool first and then is allocated to the remaining plant pools during plant growth. The details and parameters can be found in Appendix S1 and Table S1.

In LM3-PPA, there is a target LAI that helps plants to manage NSC allocation (Weng et al., 2015). Given the possibilities of N-limitation and N-saturation in this study, we replaced the target LAI with the minimum of two targets: an N-limited target and a light-limited target. The N-limited target is calculated following the rationale of Eqn (5) by LMA, leaf lifespan, leaf N, and an annual N mineralization index (see Eqs. S4 and S5 in Appendix S1). It is updated once per modeled year. The light-limited target is the value that causes a tree’s most shaded leaves to have lifetime gross primary production (GPP) approximately equal to the total lifetime construction and respiratory costs of a leaf and its supportive tissues (i.e., sapwood and roots). It is precomputed for canopy trees of each PFT. The light-limited target can only be reached when N is saturating. Flows from NSN to new tissues simply piggyback on the carbon allocation as described in Weng et al. (2015), but using the new target LAI formulation (details are in Appendix S1).

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**Fig. 2** Schematic diagram of the coupling of carbon and N cycles in LM3-PPA. The green, brown, and black lines are the flows of carbon, nitrogen, and coupled carbon and nitrogen, respectively. The green box is for carbon only. The brown boxes are N pools. The black boxes are for both carbon and nitrogen pools, where $X$ can be C (carbon) and N (nitrogen). The C : N ratios of leaves, fine roots, and microbes are fixed. Only one tree’s C and N pools are shown in this figure. The model can have multiple cohorts of trees, which share the same pool structure. The dashed line separates the plant and soil processes.
Because soil microbes may be limited by either C or N, soil N mineralization does not simply piggyback on the decomposition processes of SOM. The SOM decomposition model in Weng et al. (2015) is replaced with one that includes interacting N and C dynamics belowground (see detail in Appendix S1). It is coupled to the soil physics and hydrology models to allow it to capture the dependence of decomposition on soil temperature and moisture and the leaching losses of mineralized N dependent on runoff.

Simulated experiments with LM3-PPA

In simulation experiments, we defined two PFTs using the leaf trait relationships (Eqns 1–3). We used red maple (*Acer rubrum* L.) as the source for parameter values unrelated to LMA and its effects because red maple was used for test runs in LM3-PPA (Weng et al., 2015). One PFT had LMA = 0.035 kgC m$^{-2}$, giving it a leaf lifespan that qualifies as deciduous; the other had LMA = 0.175 kgC m$^{-2}$, giving it a leaf lifespan that qualifies ‘evergreen’ (quotation marks acknowledging the back-variation in these sites range from 35 to 55°C and the yearly mean temperatures are 13.9 °C, 8.5 °C, and ~3.2 °C, respectively (Table 3). We used the Sheffield climate data set (Sheffield et al., 2006) from the grid cells covering the three sites.

The three closed N cycle simulation experiments used climate drivers for Harvard Forest (HFR) and had total N levels of 170, 310, and 710 gN m$^{-2}$, respectively, without N deposition and loss. The sites for the open N cycle simulation experiments covered different biomes in North America: deciduous forest at Oak Ridge (OKR) (Norby et al., 2001), mixed conifer-deciduous forest at Harvard Forest (HFR) (Savage & Davidson, 2001), and evergreen conifer forest at the Northern Old Boreal forest site in Manitoba, Canada (NOBS) (Bergeron et al., 2007; Dunn et al., 2007). The latitudes of these sites range from 35°N to 55°N and the yearly mean temperatures are 13.9 °C, 8.5 °C, and ~3.2 °C, respectively (Table 3). We used the Sheffield climate data set (Sheffield et al., 2006) from the grid cells covering the three sites

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Description</th>
<th>Value</th>
<th>Unit</th>
</tr>
</thead>
<tbody>
<tr>
<td>LMA_d</td>
<td>Deciduous LMA</td>
<td>0.035</td>
<td>kgC m$^{-2}$</td>
</tr>
<tr>
<td>LMA_e</td>
<td>Evergreen LMA</td>
<td>0.175</td>
<td>kgC m$^{-2}$</td>
</tr>
<tr>
<td>A</td>
<td>Functional N</td>
<td>1.5</td>
<td>gN m$^{-2}$</td>
</tr>
<tr>
<td>B</td>
<td>Structural N</td>
<td>8</td>
<td>gN kgC$^{-1}$</td>
</tr>
<tr>
<td>c</td>
<td>Leaf lifespan parameter</td>
<td>28,57</td>
<td>yr kgC$^{-1}$ m$^2$</td>
</tr>
<tr>
<td>a</td>
<td>Photosynthesis parameter (Eqn 11)</td>
<td>3.125 × 10$^{-4}$</td>
<td>μmolC s$^{-1}$ gN$^{-1}$</td>
</tr>
<tr>
<td>r_0</td>
<td>Respiration parameter</td>
<td>3.5 × 10$^{-7}$</td>
<td>kgC gN$^{-1}$ s$^{-1}$</td>
</tr>
<tr>
<td>N_input</td>
<td>Annual N input</td>
<td>0.8</td>
<td>gN m$^{-2}$ yr$^{-1}$</td>
</tr>
<tr>
<td>L_light_D</td>
<td>Light-limited LAI of deciduous trees</td>
<td>4.0</td>
<td>m$^2$ m$^{-2}$</td>
</tr>
<tr>
<td>L_light_E</td>
<td>Light-limited LAI of evergreen trees</td>
<td>3.0</td>
<td>m$^2$ m$^{-2}$</td>
</tr>
</tbody>
</table>

Table 2 Parameter values used by the LM3-PPA model to simulate competition between deciduous and evergreen trees and forest succession

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to drive the LM3-PPA model. In the open N cycle runs, the atmospheric deposition rate was set as 0.8 gN m\(^{-2}\) yr\(^{-1}\), added to the mineral N pool in daily increments. Initial conditions for all runs are in Tables S2 and S3.

### Results

‘Optimal’ and evolutionarily stable strategy LMA in the mathematical model

In the mathematical model, the net C gain is a decreasing function of LMA because respiration per unit leaf area increases with LMA (Eqn 3), whereas photosynthesis per unit area is independent of LMA. Also, the annualized carbon construction cost of a unit of leaf area is independent of LMA. Also, the annualized carbon construction cost of a unit of leaf area is also independent of LMA ((LMA/Leaf life span) = 1/c, Eqn 1). Putting these together, the net C return per unit C invested in leaves increases as LMA decreases. In contrast, a unit of low-LMA leaf area requires more N to produce than a unit of high-LMA leaf area, because the annualized N cost of a unit of leaf area is as follows: (Leaf N/Leaf life span) = (A/c) + (B/c) (see Eqs 1 and 2). Thus, low-LMA plants should be best in N-rich environments, where the N does not significantly constrain LAI (Eqn 5) because low-LMA leaves have the highest C return per unit C invested. High-LMA plants should be best in N-poor environments, where their significantly higher LAI overwhelms their disadvantage in carbon return per unit carbon invested in each leaf layer.

The optimal LMA, \(\sigma^*\), which assumes a fixed extrinsic N mineralization rate (i.e., no feedback between LMA and mineralization rates), is found by setting the derivative of Eqn (8) with respect to \(\sigma\) equal to zero. The resulting expression contains an implicit solution for \(\sigma^*\):

\[
N_m = \frac{A + B\sigma^*}{k\sigma^*} \ln \left( \frac{V}{(A + B\sigma^*)^2r/A + G/c} \right). \tag{12}
\]

This equation is not analytically solvable for \(\sigma^*\) as a function of \(N_m\), but it is straightforward to prove that \(dN_m/d\sigma^* < 0\). That is, optimal LMA (\(\sigma^*\)) decreases as the N mineralization rate increases, thus favoring deciduous species in N-rich soils (Fig. 3a).

The most competitive LMA (\(\sigma_{ESS}\)), which allows for feedbacks between LMA and N mineralization rates, is found by substituting the right-hand side of Eqn (9) into the left-hand side of Eqn (12) and setting the resident LMA equal to the optimal LMA (\(\sigma_R = \sigma^*\)) according to the definition of ESS. The resulting expression contains an implicit solution for \(\sigma_{ESS}\) as a function of \(N_{total}\) (see Eq. S35 in Appendix S2). Because the required \(N_{total}\) for a \(\sigma_{ESS}\) varies with environmental factors (e.g., temperature and soil moisture), we define a ‘reference’ N mineralization rate \((N_{ref})\) where the resident LMA is normalized to \(\sigma_{min}\) (0.02 kgC m\(^{-2}\)) and the total N meets the N requirement of a \(\sigma_{ESS}\) at given temperature and soil moisture:

\[
N_{ref} = \frac{N_{total}}{(c + s) \cdot \sigma_{min}} = \frac{(A + B\sigma_{ESS})}{kc_{min}} \ln \left( \frac{V}{(A + B\sigma_{ESS})^2r/A + G/c} \right). \tag{13}
\]

Thus, \(N_{ref}\) has two meanings: As an index of N requirement of a \(\sigma_{ESS}\), it is solely determined by leaf traits and independent of environmental factors (i.e., temperature and soil moisture), and as an index of N availability that determines \(\sigma_{ESS}\), it integrates the influences of environmental factors on N availability. Like Eqn (12), this equation cannot be solved analytically for the ESS LMA on the right-hand side, but unlike

<table>
<thead>
<tr>
<th>Location</th>
<th>Oak Ridge/Walker Branch (OKR)</th>
<th>Harvard Forest (HFR)</th>
<th>Northern Old Black Spruce site (NOBS)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location</td>
<td>Tennessee, USA</td>
<td>Massachusetts, USA</td>
<td>Manitoba, Canada</td>
</tr>
<tr>
<td>Coordinates (Lat., Long.)</td>
<td>35.96°, -84.29°</td>
<td>42.54°, -72.18°</td>
<td>55.88°, -98.48°</td>
</tr>
<tr>
<td>Vegetation type</td>
<td>Deciduous broadleaf forest</td>
<td>Deciduous broadleaf/mixed forest</td>
<td>Evergreen needleleaf forest</td>
</tr>
<tr>
<td>Major species</td>
<td>Oaks (Quercus alba, Quercus prinus), hickory (Carya ovata), red maple (Acer rubrum), tulip poplar (Liriodendron tulipifera), and loblolly pine (Pinus taeda)</td>
<td>Red oak (Quercus rubra), red maple (Acer rubrum), black birch (Betula lenta), white pine (Pinus strobes), hemlock (Tsuga canadensis)</td>
<td>Black spruce (Picea mariana)</td>
</tr>
<tr>
<td>Annual precipitation (mm)</td>
<td>1371</td>
<td>1050</td>
<td>517</td>
</tr>
<tr>
<td>Yearly mean temperature (°C)</td>
<td>13.9</td>
<td>8.5</td>
<td>-3.2</td>
</tr>
</tbody>
</table>

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Case 1, ‘Evergreen’. If $N_m^{ref}$ is less than a threshold value $N_1$, then there is a single convergence-stable ESS with relatively large LMA and leaf lifespan. This threshold value is as follows:

$$N_1 = \frac{(A + B\sigma_{min})}{k c \sigma_{min}} \ln \left( \frac{V}{(A + B\sigma_{min})^2 r/A + G/c} \right). \quad (14)$$

Invasion tests confirm that this ESS is both global and convergence stable (see Fig. S1 for invasion tests). Theoretically, the maximum value of $\sigma_{ESS\text{,}\text{max}}$ given by the intercept of the vertical axis in Fig. 3b is as follows:

$$\sigma_{ESS\text{,}\text{max}} = \left( \frac{\sqrt{G/c + rA}}{k c B} - 1 \right) A/B. \quad (15)$$

Case 2, ‘Bistable’. If $N_m^{ref}$ is greater than $N_1$ and less than a value $N_2$ in Fig. 3b, then there are two stable ESSs, one at a relatively large value and one at the lower boundary value $\sigma_{min}$, (Fig. 3b). These two ESSs are separated by an uninvadable but convergence-unstable point, and so indicate founder control. If the LMA of the initial resident type is below this convergence-unstable point, then a series of successful invasions by ever smaller LMAs leads to the boundary ESS, $\sigma_{min}$, with its minimum leaf lifespan, highly decomposable litter, and a high N mineralization rate. In contrast, if the initial LMA is above this convergence-unstable point, then a series of invasions leads to the upper ESS, with relatively long-leaf lifespan, calcitrant litter, and a low N mineralization rate.

The upper threshold $N_2$ can be approximated by the following equation (see Appendix S2 for mathematical derivation):

$$N_2 \approx \frac{A}{k c \sigma_{min}} \sqrt{V} \ln \left( \frac{V}{V/e^2 + G/c} \right). \quad (16)$$

Case 3, ‘Deciduous’. If $N_m^{ref}$ is greater than $N_2$, then there is a single ESS at the minimum value $\sigma_{min}$ (the brown line in Fig. 3b).

The above three cases qualitatively predict the distributions of deciduous and evergreen trees in mesic temperate and boreal regions. Because $N_m^{ref}$ increases with both $N_{total}$ and temperature (s in the denominator decreases as temperature increases, Eqn 13), competitively dominant LMA (i.e., $\sigma_{ESS\text{,}\text{maj}}$) depends on both environmental factors and total N (Fig. S2). Trees with short-leaf lifespans (low LMA) are predicted to be the endpoint of succession in warm regions, unless soil N is low, whereas species with long-lived leaves (high LMA) dominate in cold regions unless soil N is particularly high. The prediction of both evergreen and deciduous forests under intermediate conditions is caused by founder control, driven by the litter feedback of LMA on N mineralization through changing litter quality. The high C : N of leaf litter, associated with high LMA, leads to low N mineralization (Eqn 4), which reinforces the competitive advantage of long-leaf lifespan, high-LMA leaves in N-poor habitats (Eqn 13). Similarly, low leaf C : N leads to high N mineralization, reinforcing the competitive advantage of short-leaf lifespan/low-LMA leaves in N-rich habitats (the high net C return per unit C invested in leaves).
Sensitivity of ESS LMA to alternative leaf trait trade-offs

We have assumed a linear relationship between LMA and leaf lifespan (Eqn 1). Although this relationship is strong in empirical data, there is also considerable residual variation (Wright et al., 2005). We analyze the impact of this uncertainty on the predicted ESS by assuming a power law for the LMA–leaf lifespan relationship:

\[ \lambda = ca^q. \]  

(17)

If \( q < 1 \), the increase in leaf lifespan slows down at high LMA; if \( q > 1 \), the increase in leaf lifespan accelerates at high LMA (\( d\lambda /da = qca^{q-1} \)). Based on this equation, we obtain a new equation for ESS LMA following the method used to derive Eqn (13) (ESS LMA):

\[
N_m = \frac{N_{total}}{(c + s)a^{q-1} + (A + Ba^q)k} \cdot \ln \left( \frac{Vc[qAa^{q-1} + (q - 1)Ba^q]}{(A + Ba^q)^qrc^{q-1} + GA} \right),
\]

(18)

This equation is the same as Eqn (13) when \( q = 1 \) (i.e., leaf lifespan changes with LMA isometrically). The patterns of ESS LMA are similar for different values of \( q \) (Fig. 4a). But, at a low reference \( N_m \) where ESS LMA exists, ESS LMA increases with \( q \) because the benefit gained from additional LMA increases as \( q \) increases.

Equation (3) implicitly assumes that the \( N \) which is proportional to LMA in Eqn (2) results in the same respiration rate as the \( N \) which is not. However, because leaf lifespan is proportional to LMA, whereas photosynthetic rate per unit leaf area is independent of LMA, a reasonable hypothesis is that some of the \( N \) which is proportional to LMA may not contribute to respiration because it is \( N \) in structural tissues like cell walls. We analyze the sensitivity of ESS LMA to alternative relationships between leaf respiration and leaf \( N \) by adding a parameter \( f \) to Eqn (3):

\[
R = (A + fB\sigma)\tau,
\]

(19)

where \( f \) ranges from 0 to 1. With Eqn (19), we obtain a new equation for ESS LMA:

\[
N_m = \frac{N_{total}}{(c + s)a^{q-1} + (A + Ba^q)k} \cdot \ln \left( \frac{VAc}{cr(A^2 + 2fAB\sigma + fB^2\sigma^2) + AG} \right).
\]

(20)

This equation is the same as Eqn (13) if \( f = 1.0 \) (i.e., all leaf \( N \) has the same effect on respiration) (Fig. 4b). As \( f \) decreases, the ESS LMA increases at a given \( N \) availability because of decreases in maintenance cost.

When \( f \) approaches zero (i.e., the \( N \) which is proportional to LMA does not contribute to respiration), ESS LMA goes to infinity (i.e., no ESS LMA) at the \( N \) availabilities lower than \( N_s \) (Eqn 14) or goes to a bistable state (infinitely large or at minimum possible LMA) at the \( N \) availabilities higher than \( N_s \).

Simulated forest succession patterns and final forest types by LM3-PPA

In the first set of simulation experiments, we assume a closed \( N \) cycle and vary total system nitrogen, holding all other parameters constant at the values of Harvard Forest (HFR). These simulation experiments simulate secondary succession at sites with different total nitrogen level. Using basal area of a PFT as the index of abundance, deciduous trees have a higher basal area than ‘evergreen trees’ at the beginning, but are soon exceeded by ‘evergreen’ trees at low ecosystem total \( N \) (170 gN m\(^{-2}\)) (Fig. 5a). At the medium total \( N \) (310 gN m\(^{-2}\)), ‘evergreen’ trees take more than 400 years to surpass deciduous trees’ basal area (Fig. 5b). At high total \( N \) (710 gN m\(^{-2}\)), the basal area of deciduous trees is always higher than that of ‘evergreen’ trees (Fig. 5c).

Fig. 4 Sensitivity of ESS LMA to physiological trade-offs between leaf lifespan and LMA (a) and between maintenance cost and leaf \( N \) in protective tissues (b). In panel (a), \( q \) is the exponent of LMA in the equation of leaf lifespan–LMA relationship (\( \lambda = ca^q \)). In panel (b), \( f \) is the ratio of respiration induced by a unit of \( N \) which is proportional to LMA to that induced by a unit of \( N \) independent of LMA (\( R = (A + fB\sigma)\tau \)).
The N mineralization rate peaks in the early stage of ecosystem development, leading to higher LAI of deciduous than 'evergreen' canopy individuals initially (Fig. 5d–f). The very large spike in N mineralization in each run is the result of the initial condition that almost all ecosystem N is in undecomposed organic matter (Table S3 and Fig. S3). After the large initial spike in mineralized N, the N mineralization rate decreases as the stand develops, locking N in the fresh and high C:N ratio litter (Fig. S3). Eventually, in the low and medium N_{total} runs (170 and 310 gN m\(^{-2}\), respectively), the LAI of deciduous trees becomes lower than that of 'evergreen' trees (Fig. 5d and e). At high total N (710 gN m\(^{-2}\)), the deciduous LAI is always higher than the 'evergreen' LAI because of the high N mineralization rate throughout the simulation (Fig. 5f).

In the second set of simulation experiments, we assume an open N cycle with a constant input rate and a temperature-dependent loss rate and vary site latitude, holding all other parameters constant (Fig. 6a–c). These simulation experiments simulate primary succession across a latitudinal gradient. The basal area of 'evergreen' trees is higher than that of deciduous trees in the early stages of forest succession at the three sites. The 'evergreen' trees are replaced by deciduous trees after a few decades of succession in the Oak Ridge simulations (OKR), the southern-most site (Fig. 6a). In the Harvard Forest simulations (HFR), deciduous trees take approximately 400 years to surpass the basal area of 'evergreen' trees (Fig. 6b). Finally, in the Northern Old Black Spruce site (NOBS) simulations, the northern-most site, the 'evergreen' trees dominate the site during the entire simulation and deciduous trees present at initialization are quickly driven extinct (Fig. 6c).

The dynamics of the N mineralization rate (Figs 5 and 6, blue lines in right panels) combined with our insights from the mathematical model provide the necessary insights to explain the patterns of 'evergreen' and deciduous abundance in the open N cycle simulations. The N mineralization rate at the end of a run is highest at OKR and lowest at NOBS (blue lines in Fig. 6d–f), consistent with the sites' differences in yearly mean temperatures. Individual LAIs of deciduous and 'evergreen' trees increase with time, consistent

![Fig. 5 Basal area, leaf area index (LAI), and N mineralization rate of canopy individuals from the simulation experiments with fixed ecosystem N at Harvard Forest. The panels of the left column (a, b, and c) show the simulated basal areas of 'evergreen' and deciduous PFTs at the total N of 170, 310, and 710 gN m\(^{-2}\), respectively. The brown and green lines are the basal areas of deciduous and 'evergreen' trees, respectively. The panels of the right column (d, e, and f) show the annual N mineralization rate and LAIs of deciduous and 'evergreen' PFTs. The blue lines in the panels d, e, and f are the annual N mineralization rate (N_{min}). The brown and green lines are the LAIs of deciduous and 'evergreen' trees, respectively. The simulated N_{min} peaks in the early stages of ecosystem development, leading to greater LAI of deciduous trees than that of 'evergreen' trees. In later stages however, N_{min} decreases, making the LAI of deciduous trees lower than that of 'evergreen' trees in panels d and e. In panel f, where the N_{total} is the highest, the LAI of deciduous trees is always higher than that of 'evergreen' trees.](image-url)
with the primary successional increase in the N mineralization rate at the three sites (blue lines Fig. 6d–f).

At OKR, the LAI of ‘evergreen’ trees is initially larger than that of deciduous trees because ‘evergreen’ trees require less N per leaf layer per year than deciduous trees (Fig. 6d). However, increasing N availability allows ‘evergreens’ to reach their light-limited maximum LAI within 100 years. The LAI of deciduous trees also starts low, but increases to its larger maximum value in about 300 years (Fig. 6d). The dynamics of N mineralization and LAI at HFR are qualitatively similar to OKR, but delayed in time due to the site’s lower temperatures. At HFR, ‘evergreen’ trees require more than 100 years to reach maximum LAI and the deciduous nearly 600 (Fig. 6e). At NOBS, the coldest site, the N mineralization rate never reaches the level at which the deciduous is competitively dominant, and the ‘evergreen’ trees need about 200 years to reach their maximum LAI (Fig. 6f).

It is important to understand that the fact that the ‘evergreen’ has a lower light-limited target LAI than the deciduous represents an advantage for the ‘evergreen’ not present in the mathematical model (where the forest is assumed to always be N-limited). The diameter growth rates during the simulations reflect the changes in fitness through time as N availability changes (Fig. 7). Note, however, that the N mineralization rate above which deciduous trees grow faster than ‘evergreens’ differs among the simulations: roughly 4 gN m\(^{-2}\) yr\(^{-1}\) at OKR (Fig. 7a), 5 gN m\(^{-2}\) yr\(^{-1}\) at HFR (Fig. 7b), and 7–8 gN m\(^{-2}\) yr\(^{-1}\) at NOBS (Fig. 7c). This was not expected from the ESS analysis of the mathematical model and implies that the ‘evergreen’ PFT has additional relative advantages in cold sites, which are included in LM3-PPA, but not in the mathematical model. As described below, this is explained by the increased carbon-use efficiency (CUE) and early- and late-season photosynthesis of the ‘evergreen’ PFT, which has a relatively greater effect in the shorter growing season of colder climates.

We define CUE as the ratio of annual net primary production (NPP) to annual GPP in this study. Consistent with the theoretical predictions, the simulated CUE of deciduous trees is greater than that of ‘evergreen’ trees at the three sites (Table 3).
trees (Fig. 8a), and the simulated N-use efficiency (NUE, the ratio of annual NPP to annual N input to the canopy, i.e., the lifetime C return per unit N) of ‘evergreen’ trees is greater than that of deciduous trees (Fig. 8b) at all three sites. The higher LAI and eventual dominance by deciduous trees at OKR and HFR are due to the greater CUE of their low-LMA leaves. However, the difference in CUE between the two PFTs unexpectedly decreases with temperature from OKR to HFR to NOBS. This is evidence of an additional advantage of the ‘evergreen’ PFT in cold sites present in our new LM3-PPA that was not included in our mathematical model.

‘Evergreen’ trees have a longer growing season than the deciduous trees (Fig. 9a–c). This advantage is most significant in cold regions, where the growing season of deciduous trees is short and the added length of the ‘evergreen’ growing seasons creates the largest relative increase in carbon gain. This reduces the cost that species with high LMA pay for their added leaf respiration per unit leaf area and so decreases the leaf respiration advantage of low-LMA leaves (Fig. 9d–f). This explains why the difference between the CUEs of the ‘evergreen’ and deciduous PFTs decreases as mean temperature decreases from OKR to HFR to NOBS (Fig. 9d–f); it is because the CUE of the ‘evergreen’ increases faster than that of the deciduous PFT (Fig. 8a).

Discussion

It has long been recognized that deciduous leaves tend to be more carbon efficient than evergreen leaves, whereas evergreen leaves tend to be more nutrient conservative, and that these differences work to determine the geographical distributions of the two types (Chabot & Hicks, 1982). Here, we show that empirical leaf trait relationships set up a trade-off between carbon- and nitrogen-use efficiency that can together explain the emergent property of observed distribution patterns of evergreen and deciduous trees in the temperate and boreal zones. Our simulation results imply that the primary and secondary succession on the relative dominance of evergreen and deciduous species may be caused by their adjustments to the NUE-CUE trade-off associated with LMA presented here.

Evolutionarily stable strategy analysis explains why short-lived leaves dominate when the rate of N mineralization is sufficiently high due to warm temperatures and/or N-rich soils, whereas long-lived leaves dominate where the rate of N mineralization is sufficiently low due to cold temperatures and/or N-poor soils. The simulation experiments show that an individual-based vegetation model with two PFTs differing only in leaf traits can generate realistic forest succession patterns in temperate and boreal regions, primarily because of the mechanisms identified in the mathematical model. These simulations suggest that the same mechanisms as revealed by the ESS analysis explain the dominance of deciduous trees early in secondary succession in the boreal zone when N availability is relatively high and the dominance of evergreens early in primary succession when N availability is low.
Leaf traits, C- and N-use efficiency, and plant competition strategy

Both our mathematical model and simulation experiments are based on the same trade-offs of leaf traits (Eqns 1–3) discovered by analyses of global plant traits data (e.g., Wright et al., 2004; Osnas et al., 2013). Leaf photosynthesis capacity is almost entirely independent of LMA (Osnas et al., 2013), making the dense conifer needles and thin broadleaf leaves approximately equivalent in photosynthetic capacity per unit leaf area (Reich et al., 1995; Kattge et al., 2009). However, the rate of net C gain per unit time of high-LMA leaves is lower than that of low-LMA leaves because of the high maintenance respiration of high-LMA leaves per unit area (Wright et al., 2004; Osnas et al., 2013). Although the carbon construction cost of a unit of leaf area is likely to be proportional to its LMA, the annualized construction cost is likely to be independent of LMA because leaf lifespan is proportional to LMA (LMA/Leaf life span = 1/c) (Wright et al., 2004).

Together, these relationships imply that the rate of carbon return on a carbon investment in leaves (i.e., CUE) decreases as LMA increases. Contrary to CUE, the NUE increases as LMA increases. The annualized N cost of a unit of leaf area decreases as LMA increases (Leaf N/Leaf life span = A/ca + B/c). Thus, the longevity of evergreen leaves allows evergreen trees to maintain higher LAI than deciduous trees in N-limited ecosystems (Gower et al., 1993) and higher lifetime return in carbon (Falster et al., 2012). Overall, high-LMA leaves have high NUE because of their long lifespan but low CUE because of their high maintenance cost.

The differences in CUE and NUE explain why deciduous trees win in N-rich soils, whereas evergreen trees win in N-poor soils. At low N availability, high-LMA trees have higher net C gain than low-LMA trees because their N retention allows them to maintain more leaf layers (i.e., higher LAI). High N availability eliminates or reverses the LAI advantage of high-LMA species and favors the CUE advantage of low-LMA species. Thus, the leaf trait relationships in our mathematical model and simulation experiments cause a trade-off between the productivity of each leaf layer and the number of leaf layers that a tree can produce when N is limiting.

Model structural sensitivity and uncertainty

Variations in the relationships between LMA and leaf lifespan and between leaf respiration and leaf N do not change the qualitative results about the ESS of LMA (Fig. 4), but they do change the relative costs and benefits of leaves with different LMAs and thus the quantitative patterns. For example, if the marginal leaf lifespan increases as LMA increases (e.g., q > 1), ESS LMA tends to be high. Similarly, if the marginal respiratory cost of LMA is low (e.g., f < 1), the ESS LMA will also be high. An ESS LMA does not exist only when the protective tissues have no maintenance cost (i.e., f = 0).

However, variation in LMA involves changes in mesophyll cells (Poorter et al., 2009; Villar et al., 2013), suggesting that the N which is proportional to LMA must come at a respiration cost, although its contribution to the total respiration rate may be lower than that of N (which is independent of LMA). These sensitivity analyses indicate that the model only requires monotonically increasing relationships between LMA and leaf lifespan and between leaf respiration and leaf N to create a trade-off between CUE and NUE. The ESS represented in Eqn (13) is the simplest case that assumes leaf lifespan is proportional to LMA and the structural N has the same respiration coefficient with functional N (Eqns 1 and 3).

Fig. 8 Carbon- and N-use efficiencies from the open N cycle simulation experiments. Panel (a) shows the carbon-use efficiency (CUE), which is defined as the ratio of annual NPP to annual GPP, at Oak Ridge (OKR), Harvard Forest (HFR), and the Northern Old Black Spruce (NOBS) sites. Panel (b) shows the N-use efficiency (NUE), which is defined as the ratio of the NPP of a tree to the N allocated to new leaves from the N uptake by roots in a year at the three sites. The simulated CUE of deciduous trees is greater than that of ‘evergreen’ trees (a), whereas the simulated NUE of ‘evergreen’ trees is greater than that of deciduous trees (b) at all the three sites. The difference in CUE between these two PFTs decreases from OKR to HFR to NOBS.

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An additional factor included in the simulation experiments, but not in the mathematical model, is that the low respiration rate of low-LMA leaves means that low-LMA trees can maintain more leaf layers with positive carbon balance than high-LMA trees when the N supply is sufficient to produce the extra layers (i.e., the high LAI of deciduous trees at high N availability as shown in Fig. 6d–f). This reinforces the inverse relationship between CUE and LMA. A factor not included in either the mathematical model or simulation experiments is the decline of the gross and net photosynthetic rates as a leaf ages (Wilson et al., 2000; Kitajima et al., 2002; Warren, 2006), which would also strengthen the inverse relationship between CUE and LMA.

**Bistable state**

The positive feedback between LMA and the rate of decomposition of SOM (Cornwell et al., 2008; Zhang et al., 2008) leads to the prediction of founder control by the mathematical model at intermediate N availability (intermediate values of $N_{\text{ref}}$). High-N litter produced by a low-LMA species accelerates decomposition and thus increases N mineralization rate, which competitively favors a species with an even lower LMA. Similarly, low-N litter produced by high-LMA species reduces N mineralization rate, which competitively favors an even higher LMA. With founder control, one expects a patchy mosaic of a high-LMA PFT with long-lived leaves and a low-LMA PFT with short-lived leaves that reflects patchy initial conditions. A very similar explanation was proposed by Pastor & Post (1986) for the patchy mix of evergreen conifers and broadleaf species on Black Hawk Island (Pastor et al., 1982) and by Gower & Richards (1990) for the patchy coexistence of deciduous larches and birches with evergreen conifers throughout the boreal zone. Although we observed no evidence of founder control in the simulation model, we did not systematically search for it.

**Simulated forest succession, C- and N-use strategy, and temperature effects**

The simulated secondary (closed N cycle runs) succession (Fig. 5a–c) and primary (open N cycle runs) succession (Fig. 6a–c) by the LM3-PPA are consistent with
those reported in the literature (Gower & Richards, 1990; Givnish, 2002). In particular, secondary succession from deciduous to evergreen dominance is consistent with field observations in regions where conifers are the late-successional dominants. In boreal forests, recovery after a large disturbance event (e.g., fire) is usually pioneered by deciduous trees (e.g., Betula spp. and Larix spp.), which are subsequently replaced by evergreen conifer trees (Pinus, Abies, and Picea) (Chapin et al., 1994; Lichter, 1998; Schulze et al., 2005). The simulated pattern of N mineralization during secondary succession (Fig. 5d–f), which causes the progression from deciduous to evergreen dominance, is also consistent with field measurements. The N mineralization rate is usually high after a stand-replacing disturbance event (Deng et al., 2014) and then gradually decreases with the replacement of early species by late species (Vitousek et al., 1989; Vanclere et al., 1993). The simulation experiments predict dominance by evergreens late in secondary succession wherever the N mineralization rate falls beneath the threshold below which evergreens become competitively dominant (Fig. 5d and e) and dominance by deciduous trees if the N mineralization rate stays above this threshold (Fig. 5f).

During primary succession, the simulation experiments predict evergreen trees early in succession and a shift to deciduous dominance in the temperate zone because the buildup of total ecosystem N eventually drives the N mineralization rate above the threshold for deciduous dominance (Fig. 6). Elsewhere, the N mineralization rate stays low enough throughout primary succession so that evergreens remain dominant. These patterns are consistent with observations. For example, primary succession in the Southern Lake Michigan sand dunes is from evergreen conifers, for example, jack or white pine (Pinus banksiana, P. strobus), to broadleaf deciduous, for example, black oak (Quercus velutina) (Olson, 1958).

Temperature drives the distribution of deciduous and evergreen forests in both the mathematical model and the simulation experiments because the N mineralization rates that define the distributions of evergreen and deciduous forests are strongly dependent on temperature. Similarly, in traditional DGVMs, temperature is directly used to select leaf traits, limiting the distributions of deciduous and evergreen tree PFTs. However, in our model, temperature affects the outcome of competition primarily because it changes the N mineralization rate. In the simulation experiments with an open N cycle, temperature also affects how much N builds up in an ecosystem because it affects leaching and dissolved organic nitrogen losses by affecting evapotranspiration and thus runoff and by directly affecting the rate of denitrification (see Appendix S1).

Evolutionarily stable strategy and site productivity

Usually, the models that predict optimal trait combinations in different environments assume the strategies (i.e., combinations of plant traits) that lead to high productivity will be dominant (e.g., Haxeltine & Prentice, 1996; Kleydon & Mooney, 2000; Pavlick et al., 2013; van Bodegom et al., 2014). However, as shown in this study, the more ecologically relevant ESS of LMA does not always maximize the stand’s net C gain because ESS excludes the trait combinations that are ineffective competitively. For example, at a low $N_{\text{min}}^\text{max}$ (i.e., the total N of 100 gN m$^{-2}$, Fig. S4a), any resident LMA below the ESS can always be invaded by a slightly higher LMA, which is closer to the ESS value (Fig. S4a). In this case, the net C gain of the resident decreases as its LMA increases (Fig. S4b) and so the succession of residents on the approach to the ESS is associated with a monotonic decrease in canopy net carbon gain (Fig. S4b). Invasion succeeds despite this decrease because invaders with LMAs closer to the ESS value have higher C gain than the resident at the N mineralization rate created by the resident’s leaf litter (Fig. S4b). But once the old resident is replaced by the invader and the N mineralization rate has equilibrated to its new lower value (because of the higher C : N ratio of the higher LMA litter), the net C gain of the forest under the new resident is less than it was under the old resident. This is a partial tragedy of the commons driven by shared access to resources (Hardin, 1968; Gersani et al., 2001; Rankin et al., 2007; McNickle & Dybzinski, 2013; Farrior, 2014).

Acknowledgements

Funding was provided by USDA Forest Service Northern Research Station (Agreement 13-JV-11242315-066) and Princeton Environment Institute. We thank Dr. Sergey Malyshev for his help in preparing forcing data and Dr. Cleo Chou for her helpful comments on an earlier version of this manuscript. We thank Prof. I. Colin Prentice and other three reviewers for their insightful comments and suggestions, which greatly improved this manuscript. This work was conducted while CEF was a postdoctoral fellow at the National Institute for Mathematical and Biological Synthesis, sponsored by the National Science Foundation through NSF Award #DBI-1300426, with additional support from The University of Tennessee, Knoxville.

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