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**Appendix S1** Nitrogen cycle model and allocation scheme in the LM3-PPA model

The nitrogen (N) cycle model added to the LM3-PPA model for this study is simplified from Luo & Reynolds (1999), Gerber *et al*.(2010), and Manzoni *et al*. (2010). It has a similar structure to the carbon (C) model (Fig. 2 in the main text). We add a microbial pool (C and N) for simulating the interactions between C and N in decomposition processes. We also add a mineral N pool to store mineralized N. Thus, the N model consists of ten pools, including six plant N pools and four soil N pools (Fig. 2 in the main text). The plant N pools include foliage, fine roots, sapwood, heartwood, seeds, and non-structural N (NSN) pools. The soil N pools include fast soil organic matter (SOM), slow SOM, microbial, and mineralized N pools. The N absorbed by roots enters into the NSN pool, and then is allocated to the remaining plant pools with plant growth. Dead plant tissues are divided between fast and slow SOM pools using the tissue-type-specific fractionation in Weng *et al*. (2015). When dead tissue enters a C pool, the N in the tissue is added to a corresponding N pool. As SOM decomposes, mineralized N is released to the mineral N pool.

1. Plant nitrogen uptake and allocation

The rate of plant N uptake (*U*, gN m-2 hour-1) from soil mineral N pool is an asymptotically increasing function of fine root biomass density (*Root*total, kgC m-2), following McMurtrie *et al*. (2012)

|  |  |
| --- | --- |
| , | (S1) |

where, *N*mineral is the mineralized N in soil (gN m-2), *f*U,max is the maximum rate of N absorption per hour when *Root*total approaches infinity, *Root*0 is a constant of root biomass (kgC m-2) at which the N-uptake rate is half of the parameter *f*U,max. The N uptake rate of an individual tree (*U*tree, gN hour-1 tree-1) is calculated as follows:

|  |  |
| --- | --- |
| , | (S2) |

where, *Root*tree is the fine root biomass of a tree (kgC tree2). The N taken up by the roots of a tree enters into the NSN pool.

For limiting N uptake in an N-rich soil, we define a target NSN (NSN\*), which is a function of leaf’s target biomass, C:N ratio, and lifespan and root’s target biomass and C:N ratio:

|  |  |
| --- | --- |
| , | (S3) |

where, *q*N is a constant; *λ* is leaf lifespan; *L*\*(*D*) and *FR*\*(*D*) are the target leaf and fine root biomass at diameter *D*, respectively; *CN*leaf and *CN*FR are the C:N ratios of leaves and fine roots, respectively. *L*\*(*D*) and *FR*\*(*D*) are defined in Weng *et al*. (2015). If NSN exceeds the target, then the excess NSN is returned to the mineralized N pool in the soil (i.e. as if it was never taken up to begin with because the plant did not need it).

Flows from NSN to new tissues simply piggyback on the carbon allocation described in Weng *et al*. (2015). There is an LAI target in LM3-PPA that helps plants to manage non-structural carbon (NSC) allocation. For example, as long as there is sufficient NSC, plants allocate to new leaves to close the gap between their current and target LAI. With the possibility of N limitation, we replaced the target LAI in Weng *et al*. (2015) with the minimum of two targets: a light-limited target and an N-limited target. The light-limited target LAI is the value that causes a tree’s most shaded (least productive) leaves to have lifetime GPP approximately equal to the sum of leaves’ and supportive tissues’ lifetime construction and respiration costs. It can only be reached when N is saturating. Light-limited target LAI was pre-computed for canopy trees of each PFT.

The N-limited target LAI (*L*N,target) is PFT-specific and is updated once per modeled year. The N-limited target LAI at year *i* is calculated by leaf mass per unit area (*σ*), leaf lifespan (*λ*), leaf C:N ratio (*CN*leaf), and the annual N mineralization index () at year *i* is:

|  |  |
| --- | --- |
| , | (S4) |

where, the N mineralization index is weighted mean of previous years rates of N-mineralization:

|  |  |
| --- | --- |
| , | (S5) |

where, *w* is a weighting factor, taking value 0.8 in this study; *N*m(*i*) is the N mineralization rate at year *i*; . The N mineralization index is used to smooth the inter-annual variation of N mineralization rate.

Leaves and fine roots have fixed C:N ratios, and so the N removed from NSN to construct new leaves is simply the carbon allocated from NSC to leaves, as calculated in Weng *et al*. (2015), divided by leaf C:N. In addition, dead leaves and fine roots retranslocate half their N back to the NSN pool before they die. In cases where there is insufficient NSN to meet the carbon demand for new leaves and roots, the excess carbon is allocated to produce new sapwood. Allocation of N to sapwood follows the target sapwood N:C as in other tissues. However, if there is insufficient NSN left over after allocation to new leaves and fine roots to meet this demand for sapwood N, then all the carbon is allocated to the sapwood anyway, together with all the available NSN. Thus, sapwood has a variable C:N ratio.

2. Soil nitrogen mineralization

As SOM decomposes, N in it is mineralized and enters into the mineral N pool when the N requirement of microbes is met. N mineralization does not simply piggyback on the SOM decomposition because soil microbes may be limited by either C or N. The dynamics of the mineral N pool is represented by the following equation:

|  |  |
| --- | --- |
| , | (S6) |

where, *N*deposition is N deposition rate, assumed to be constant over the period of simulation; *N*m is the N mineralization rate of the litter pools (fast and slow SOM and microbes); *U* is the N uptake rate (gN m-2 hour-1) of plant roots (Eq. S1); and *N*loss includes the loss of mineralized N by denitrification and runoff. The N deposition (*N*deposition) is the only N input to the ecosystem.

Total N mineralization rate (*N*m) is computed from the decomposition from fast and slow SOMs and turnover of microbes. The decomposition processes of SOMs are represented by a model modified from (Manzoni *et al.*, 2010) (Fig. 2 in the main text). In this model, the out-flux of C from the *i*th pool (*Ci,*out) is calculated by:

|  |  |
| --- | --- |
| , | (S7) |

where, *ξ* is the response function of decomposition to soil temperature (T) and moisture (M), taken as the average of the values in the top 0.2 meters of the soil in the soil hydrology and energy model in Weng *et al*. (2105), *ρi* is the basal turnover rate of the *ith* litter pool at reference temperature and moisture, *QCi* is the C content in *ith* pool.

Then, the out-flux of N from the *i*th pool (*Ni,*out) is:

|  |  |
| --- | --- |
| , | (S8) |

where, *QNi* is the N content in the *ith* pool.

The mineralized N (*Ni,*mineralizedN) at this step is the difference between the out-flux of N from the *i*th pool and the N used to build microbes:

|  |  |
| --- | --- |
| , | (S9) |

where, *ε*0 is default carbon-use efficiency of litter decomposition, *Λ*microbe is microbe’s C:N ratio. And, the N flux from the *ith* litter pool to the microbial pool (*Ni,*microbe) is:

|  |  |
| --- | --- |
| . | (S10) |

Thus, the actual carbon use efficiency of the *ith* litter pool (*εi*) is:

|  |  |
| --- | --- |
| . | (S11) |

The carbon change in microbial pool (*ΔC*microbe) is then calculated as:

|  |  |
| --- | --- |
| , | (S12) |

where, *ki* is the mixing ratio of the microbes with the *ith* litter pool, *ρ*microbe is the basal turnover rate of the microbe pool at reference temperature and moisture, *QC*microbe is the C content in the microbe pool. The N change in microbial pool (*ΔN*microbe) is:

|  |  |
| --- | --- |
| , | (S13) |

where, *QN*microbe is the N content in the microbe pool.

The C changes in the *ith* litter pool (*ΔCi*) is:

|  |  |
| --- | --- |
| , | (S14) |

where, *LitterCi* is litter C input from litterfall to the *ith* litter pool. And, the N changes in the *ith* litter pool (*ΔNi*) is:

|  |  |
| --- | --- |
| , | (S15) |

where, *LitterNi* is litter N input from litterfall to the *ith* litter pool. Then, the total N mineralization (*N*mineralized) rate is calculated as follows:

|  |  |
| --- | --- |
| . | (S16) |

And, the heterotrophic respiration (*R*h) is:

|  |  |
| --- | --- |
|  | (S17) |

The N loss (*N*loss) from the mineral N pool is calculated by:

|  |  |
| --- | --- |
|  | (S18) |

where *W*runoff is the rate of water runoff (kg H2O m-2 hour-1) predicted by the hydrologic model of LM3-PPA as described in Weng et al. (2015), *η* is a parameter for mineral N taken out by runoff, *kN,25* is the denitrification rate at 25 °C, *E*a,den is active energy of denitrification (49860 J mol-1), *R* is gas constant (8.31 J mol-1 K-1). (The parameter values are in Table S1.)

**Appendix S2** Mathematical derivations of Evolutionarily Stable Strategy of LMA

We begin with four physiological and environmental influences of leaf mass per unit area (LMA): leaf lifespan, area-based leaf nitrogen content, leaf maintenance respiration rate (*R*), and residence time of nitrogen in soil organic matter (*τS*). The relationships between these characteristics are based on decades of effort by plant physiologists, who have compiled and analyzed large databases of global plant traits. Yet, because there is a large amount of scatter around each relationship, the following equations (B1-B4) specifically represent our model’s hypotheses. In short, this model can be viewed as a hypothesis of the important physiological connections among leaf traits and the environment that set up the tradeoffs that drive variation in LMA via natural selection.

1) Leaf lifespan (*λ*, yr) is proportional to LMA (*σ*, kgC m-2) (Osnas *et al.*, 2013, Wright *et al.*, 2004):

|  |  |
| --- | --- |
| , | (S19) |

where *c* is a constant (yr kg C-1 m2).

2) Leaf N content per unit leaf area (*n*, gN m-2) is a linear function of LMA (Osnas et al. 2013):

|  |  |
| --- | --- |
| , | (S20) |

where *A* (gN m-2) and *B* (gN kgC-1) are constants.

3) The maintenance respiration rate of leaves (*R*, kgC m-2 yr-1) is proportional to leaf N (Reich et al. 1998):

|  |  |
| --- | --- |
| , | (S21) |

where *r* is a constant (kgC gN-1 yr-1).

4) The residence time of nitrogen in soil organic matter (SOM) (*τS*, yr) is proportional to LMA of the stand’s leaf litter:

|  |  |
| --- | --- |
| , | (S22) |

where, (unitless) is a function of soil temperature (*T*) and moisture (*M*) modifying the SOM decomposition rate. The parameter, *s\**, captures the dependence of the SOM residence time on stand LMA at the reference temperature and moisture (yr kgC-1 m2). Because we do not explore the effects of temperature and moisture on decomposition in this study, for convenience we define a parameter *s* (yr kgC-1 m2):

|  |  |
| --- | --- |
| , | (S23) |

and thus simplify the above to the following:

|  |  |
| --- | --- |
| . | (S24) |

Several sources provide evidence for the dependence of nitrogen residence time on soil organic matter (Cornwell *et al.*, 2008, Zhang *et al.*, 2008). Here we assume the functional form of this dependence is linear for simplicity.

In this model, LMA (*σ*) is a fundamental parameter determining leaf lifespan (λ, Eq. S19), leaf nitrogen per unit area (*n*, Eq. S20), leaf respiration rate (*R*, Eq. S21), and soil N mineralization rate (Eq. S22, residence time is the reverse of decomposition rate).

We assume an N-limited system, where the net nitrogen mineralization rate is approximately equal to the rate of plant uptake. If the forest canopy of such an N-limited system is full of individuals with the same leaf area index (*L*, m2 m-2) and assuming (1) the uptake rate of understory individuals is negligible compared to that of the canopy, (2) approximately half of a leaf’s nitrogen is retranslocated prior to senescence, and (3) approximately half of a tree’s nitrogen is allocated to foliage (Dybzinski *et al.*, 2011, Table E1 , Dybzinski *et al.*, 2015, Eq. S18), then the leaf N per unit crown area for a canopy tree will equilibrate to the product of the net N mineralization rate (*N*m, gN m-2 yr-1) and leaf lifespan (Dybzinski *et al.*, 2011, Eq. G26):

|  |  |
| --- | --- |
| . | (S25) |

For an N-limited individual with leaf lifespan () in soil with a net-nitrogen mineralization rate of *N*m, the individual’s leaf area index can be expressed as a function of its LMA (*σ*):

|  |  |
| --- | --- |
| . | (S26) |

We express the dependence of yearly gross primary productivity or carbon gain (*C*gain, kgC m-2 yr-2) as a saturating function of the individual’s leaf area index to account for self-shading within the plant following light use efficiency models (Duursma & Makela, 2007, Landsberg & Waring, 1997, Monteith, 1977):

|  |  |
| --- | --- |
| , | (S27) |

where *V* and *k*  (kgC m-2 yr-1 and unitless, respectively) are here summary parameters capturing the shape of the yearly total photosynthetic dependence on leaf area index.

Following Eqs. S19-S21, the total maintenance and building cost of the leaves of a canopy per unit crown area (*C*cost, kgC m-2 yr-1) is:

|  |  |
| --- | --- |
| , | (S28) |

where *G* is building cost coefficient (1.33 kgC kgC-1). Taken together, the net C gain of a canopy (*C*net, kgC m-2 yr-1) is the difference between *C*gain and Ccost:

|  |  |
| --- | --- |
| . | (S29) |

The optimal LMA (*σ\**) is that which maximizes *C*net *for a given* *N*m, i.e. the “optimal LMA” assumes no feedback between LMA and the nitrogen mineralization rate. The optimal LMA is conceptually useful, but its omission of the litter feedback makes it less ecologically-relevant. The optimal LMA can be found by differentiating Eq. S29 with respect to LMA and setting it equal to zero. Because *σ\** cannot be isolated in the result, optimal LMA (*σ\**) is defined implicitly:

|  |  |
| --- | --- |
| . | (S30) |

To keep the model of decomposition and nitrogen supply simple, 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. It is possible to complete the analysis with multiple plant and organic matter N-pools, but this complicates the formulae without changing the qualitative insights that we seek from the ESS analysis.

|  |  |
| --- | --- |
| , | (S31) |

where *N*total is the total ecosystem N (gN m-2), *N*soil is the soil N, and *N*leaves is the N in leaves.

At equilibrium () we find:

|  |  |
| --- | --- |
|  | (S32) |

The N mineralization rate (*N*m, gN m-2 yr-1) can then be expressed as a function of only *N*total, gN m-2 (assumed to be constant) and the residence times of N in the leaves (λ) and soil (τs):

|  |  |
| --- | --- |
| , | (S33) |

where *σ*R is the average leaf LMA of the stand’s leaf litter or the LMA of the monodominant “resident” trees.

We substitute Eq. S33 into Eq S30 and find:

|  |  |
| --- | --- |
| . | (S34) |

In contrast to the “optimal” LMA, the ESS LMA includes the feedback between the LMA of the monodominant resident trees and the nitrogen mineralization rate. By definition, when the ESS is the monodominant resident, the optimal LMA is equal to resident or ESS LMA (*σ*ESS=*σ*R =*σ*\* ), simplifying Eq. S34 to the following:

|  |  |
| --- | --- |
| . | (S35) |

The required ecosystem total N (*N*total) of an ESS LMA varies with environmental factors such as temperature and soil moisture because parameter *s* is a function of soil temperature and moisture. For convenience, we define a reference value of *Nm* as the N mineralization rate for an environment with given *N*total, temperature, and soil moisture at the resident species with an LMA equal to *σ*min (0.02 kgC m-2):

|  |  |
| --- | --- |
| . | (S36) |

According to this equation, the reference *N*m () is determined by leaf’s intrinsic properties and independent of ecosystem total nitrogen (*N*total), temperature, and soil moisture, and it defines the integrated environment of *N*total and soil temperature and moisture required by a *σ*ESS. Because soil’s N mineralization rate (*N*m) increases with both *N*totaland temperature (*s* in the denominator decreases as temperature increases, Eq. S33), the competitively dominant LMA (i.e., *σ*ESS) depends on both environmental factors and ecosystem total N.

There are four key values that define the property of the curve plotted with Eq. S36 as shown in Fig. 3 in the main text: 1) the threshold of at *σ*min (*N*1) that delimits the single convergence stable ESS with relatively low and the bi-stable states of ESS at intermediate , 2) the upper threshold of (*N*2) that define the minimum value of the upper boundary of *σ*ESS, 3) the upper-boundary *σ*ESS at *N*2 (i.e., the mathematically minimum *σ*ESS, *σ*ESS,min), and 4) the maximum ESS LMA when the total N approaches zero (*σ*ESS,max). If is greater than *N*1 and less than the upper threshold (*N*2 ), then there are two stable ESSes, one at a relatively large value and one at the lower boundary value *σ*min. We solve these four key values with Eqs. S35 and S36:

1) *N*1 is obtained by substituting the minimum possible LMA (*σ*min) for *σ*ESS in Eq. S36:

|  |  |
| --- | --- |
| . | (S37) |

2) We can obtain an approximation of the minimum of the upper-boundary *σ*ESS (i.e., *σ*ESS,min) by differentiating the right-hand side (RHS) of Eq. S35 with respect to *σ*ESS and setting the result equal to zero:

|  |  |
| --- | --- |
| . | (S38) |

Since *G/c* is very small, we let G/C=0 and then is:

|  |  |
| --- | --- |
| . | (S39) |

we get the minimum of the upper-boundary *σ*ESS (*σ*ESS,min) at =0:

|  |  |
| --- | --- |
| . | (S40) |

3) By replacing the *σESS* of Eq. S36 with the RHS of Eq. S40, we obtain an approximation for the upper threshold of the reference equilibrium N mineralization rate, *N*2:

|  |  |
| --- | --- |
| . | (S41) |

4) Also, the maximum value of *σ*ESS can be obtained by setting *N*total equal to 0 in Eq. S35:

|  |  |
| --- | --- |
| . | (S42) |

**Table S1** Parameters of the N model in LM3-PPA

|  |  |  |  |
| --- | --- | --- | --- |
| **Symbol** | **Definition** | **Unit** | **Default value** |
| *f*U,max | Maximum mineral N absorption rate | hour-1 | 0.5 |
| *Root*0 | Root biomass at which the N-uptake rate is half of the maximum | kgC m-2 | 0.3 |
| *CNFR* | The C:N ratio of fine roots | kgC gN-1 | 0.06 |
| *qN* | Multiple of target leaf and root nitrogen to target NSN | - | 5.0 |
| *ε*0 | Default carbon-use efficiency of litter decomposition | - | 0.4 |
| *C:N*microbe | Microbial C:N ratio | kgC gN-1 | 0.01 |
| *ρ*microbe | Turnover rate of the microbe pool at reference temperature and moisture | yr-1 | 2.5 |
| *ρ*1 | Turnover rate of slow SOM pool at reference temperature and moisture | yr-1 | 1.25 |
| *ρ*2 | Turnover rate of fast SOM pool at reference temperature and moisture | yr-1 | 0.025 |
| *k*1 | Mixing ratio of the microbes with fast SOM pool | - | 0.5 |
| *k*2 | Mixing ratio of the microbes with slow SOM pool | - | 0.5 |
| *Η* | Parameter for N taken out by runoff | hour-1 kgH2O-1 | 0.05 |
| *kN,25* | Denitrification rate at 25 °C | yr-1 | 2.0 |
| *E*a,den | Active energy of denitrification | J mol-1 | 49860 |

**Table S2** Initial conditions for the N-open runs at the three forest sites, Oak Ridge/Walker Branch (OKR), Harvard Forest (HFR), Northern Old Black Spruce site (NOBS)

|  |  |  |  |
| --- | --- | --- | --- |
| **State variable** | **Value** | **State variable** | **Value** |
| **Initial seedling density** | | | |
| Deciduous | 500 seedlings/ha | Evergreen | 500 seedlings/ha |
| **Initial sizes of plant pools for each seedling\*** | | | |
| Leaves | 0 | Fine roots | 0 |
| Sapwood C | 0.2 kgC /seedling | Sapwood N | 0.57 gN |
| Heartwood | 0 | Seeds | 0 |
| Non-structural C | 0.05 kgC/seedling | Non-structural N | 0.64 gN/seedling |
| **Initial soil pools** | | | |
| Fast soil C pool | 0.3 kgC m-2 | Fast soil N | 20 gN m-2 |
| Slow soil C pool | 0.7 kgC m-2 | Slow soil N | 20 gN m-2 |
|  |  | Mineral N | 0.5 gN m-2 |

\*Note, the initial pool sizes of deciduous and evergreen seedlings are the same.

**Table S3** Initial carbon and nitrogen pools for the N-closed runs at Harvard Forest (HFR)\*

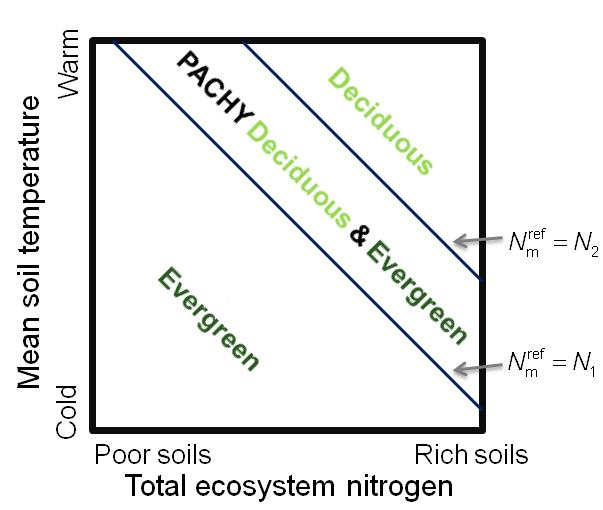
|  |  |  |  |
| --- | --- | --- | --- |
| **State variable** | **Low N** | **Medium N** | **High N** |
| Fast soil C (kgC m-2) | 1.0 | 1.0 | 1.0 |
| Slow soil C (kgC m-2) | 3.5 | 8.2 | 22.2 |
| Fast soil N (gN m-2) | 67 | 67 | 67 |
| Slow soil N (gN m-2) | 100 | 234 | 634 |
| Ecosystem total N  (gN m-2) | 173 | 307 | 707 |

\*The initial conditions of plants are the same with those of the N-open runs.



**Figure S1** Pairwise invasion plots of LMA strategies across a gradient in total N.

In the pairwise invasion tests, we compare the net carbon gains (*C*net) of invaders and residents at the *Nm* created by residents (with LMA *σR*). If invader’s *C*net is larger than the resident’s, the invader can successfully invade the residents at this resident LMA. Coordinate points marked in gray represent successful invasion of the invader in the environment of the resident. The red lines represent the optimal LMA of invaders that has the highest *C*net at the *Nm* created by the corresponding residents. A local ESS occurs where the red line crosses the 1:1 line. Panels *a* and *b* show the cases with only one convergent stable ESS at low ecosystem total N (50 and 100 gN m-2, respectively). Panel *c* shows the case with two equilibrium states (Case 2) at a total N of 150 gN m-2. Note only the high ESS and minimum LMA are convergent stable ESS’s and would likely be seen in nature. Panel d shows the case without an equilibrium state at total N 200 gN m-2 (Case 3). The ESS LMA converges to the minimum LMA (*σ*min) in this case.

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**Figure S2** Schematic diagram of predicted deciduous and evergreen forest distribution along the axes of temperature and soil nitrogen content.

The black lines represent the required relative changes in temperature with ecosystem total N to keep = *N*1and =*N*2. Because increases with both total ecosystem N and temperature (Eq. 14 in the main text), these two lines have negative slopes. Trees with short leaf lifespans (deciduous) are the endpoint of succession in warm regions, unless soils are poor, whereas species with long-lived leaves (evergreen) dominate in cold regions. The prediction of mixed forest between *N*1 and *N*2is caused by founder control, which is itself due to a litter feedback (high LMA litter decomposes slowly).



**Figure S3** Redistribution of nitrogen stocks and N mineralization rate during the process of secondary succession in N-closed runs

The parameters for these three simulation experiments are in Table C2. A detailed description of the N model is in Appendix A. This figure shows the decompositions of fast and slow SOM lead to high N mineralization rates (slashed blue lines) at the beginning of the secondary successions at the three levels of ecosystem total N (*N*total, 173, 307, and 707 gN m-2, respectively). With the buildup of soil and wood pools, a large fraction of N is locked in slow SOM and wood pools, decreasing N mineralization rates.



**Figure S4** Net carbon gain at optimal and ESS LMA

This figure shows the invasion of residents by the invaders with optimal LMA at an ecosystem total N (*N*total) of 100 gN m-2 (a) and their net carbon gains as the resident and invader change (panel b). . In panel a, red dashed line is the invaders with optimal LMA at given residents and the black line is 1:1 line (resident : invader). In panel (b), the black line represents the net C gain (*C*net) of residents; dashed red line is the *C*net of optimal invaders; and the dotted brown line represents the differences in *C*net between the residents and optimal invaders. The vertical blue dotted line marks the ESS LMA (*σ*ESS).

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