SUPPORTING INFORMATION FOR:

"MULTITRAIT SUCCESSIONAL FOREST DYNAMICS ENABLE DIVERSE COMPETITIVE COEXISTENCE"

Daniel S. Falster,[1,*] Åke Brännström,[2,3] Mark Westoby,[1] Ulf Dieckmann[2]

[1]Department of Biological Sciences, Macquarie University, Sydney NSW 2109, Australia
[2]Evolution and Ecology Program, International Institute for Applied Systems Analysis,
Schlossplatz 1, A-2361 Laxenburg, Austria
[3]Department of Mathematics and Mathematical Statistics, Umeå University, 901 87 Umeå, Sweden
[*]To whom correspondence should be addressed; E-mail: adaptive.plant@gmail.com

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CONTENTS

1 PHYSIOLOGICAL MODEL

Here we provide a full description of our physiological sub-model generating rates of growth, survival, and fecundity in the size-structured metacommunity model described in the main text. As noted in the Materials and Methods, we require functions $g(x', H, E_{x,y,a})$, $d(x', H, E_{x,y,a})$, and $f(x', H, E_{x,y,a})$, quantifying, respectively, the rates of height growth, death, and fecundity of plants with traits x' and height H in the environment $E_{x,y,a}$. These functions enter into Eqs. 2-3 to determine the dynamics of the density distribution N, and into Eqs. 1 and 7 to determine seed rain and invasion fitness. The vital rates g, d, and f are all derived from the rate at which living biomass is produced by a plant, which in turn is calculated based on well-understood physiology (Fig. S1a). The physiological sub-model used in our current analysis is identical to that presented in Falster *et al.* 2011 [1], who provide citations for its empirical basis. Fig. S1a overviews processes represented in the model, while Tables S1 and S2, respectively, summarize all model variables and parameters, as defined in the main text and below.

1.1 *Photosynthesis and mass production*

The vertical density distribution $q(z, H)$ of leaf area across heights z within crowns of plants with height H is described by the following equation [2],

$$q(z,H) = 2\frac{\eta}{H}\left(1-\left(\frac{z}{H}\right)^{\eta}\right)\left(\frac{z}{H}\right)^{\eta-1}, \tag{S1}$$

which has a single parameter η. Setting $\eta = 12$, as in the present study, gives a top-heavy canopy profile similar to those seen among angiosperms. The fraction $Q(z, H)$ of leaf area above height z is then

$$Q(z,H) = \left(1-\left(\frac{z}{H}\right)^{\eta}\right)^{2}. \tag{S2}$$

We denote by $p(x', E_{x,y,a}(z))$ the gross rate of leaf photosynthesis per unit leaf area within the canopy of a plant with traits x' experiencing a canopy openness $E_{x,y,a}(z)$. Here, $E_{x,y,a}(z)$ is the function describing the canopy openness (ranging from 0 to 1) at height z in a patch, which in turn depends on the traits x and the seed rains y of the resident types, as well as on the patch age a (Eq. 5). Even though p can vary with leaf photosynthetic traits, these are held constant in the present study, so p is constant with respect to changes in x'. We therefore only need to consider changes in p with respect to changes in E. Previously [1], we showed that the annual average of $p(x', E_{x,y,a}(z))$, calculated from a detailed solar model, was well approximated by a relationship to $E_{x,y,a}(z)$ of the form

$$p(x', E_{x,y,a}(z)) = \frac{c_{\mathrm{p1}}}{E_{x,y,a}(z) + c_{\mathrm{p2}}}. \tag{S3}$$

The parameters c_{p1} and c_{p2} in Eq. S3 are fitted to data generated from the detailed model; respectively, they correspond to the maximum annual photosynthesis and to the value of $E_{x,y,a}(z)$ at 50% of this maximum.

The average rate of leaf photosynthesis across the plant is then

$$\bar{p}(x', H, E_{x,y,a}) = \int_0^H p(x', E_{x,y,a}(z))\, q(z,H)\, \mathrm{d}z, \tag{S4}$$

where $q(z, H)$ is the density of leaf area at height z (Eq. S1). Note that in calculating $\bar{p}$, for simplicity we consider only the shading from surrounding plants and not self-shading generated within the canopy.

We account for five different tissues i within each plant, denoted by the subscripts l = leaves, b = bark, s = sapwood, h = heartwood, and r = fine roots. The amount of biomass available for growth, $\mathrm{d}B/\mathrm{d}t$, is given by the difference between income (total photosynthetic rate) and losses (respiration and turnover) within the plant:

$$\underbrace{\frac{\mathrm{d}B}{\mathrm{d}t}}_{\text{net biomass production}} = \underbrace{c_{\text{bio}}\, Y}_{\text{yield}} \Big(\underbrace{\omega\, \bar{p}}_{\text{photosynthesis}} - \underbrace{\sum_{i=\text{l,b,s,r}} M_i\, r_i}_{\text{respiration}} \Big) - \underbrace{\sum_{i=\text{l,b,s,r}} M_i\, k_i}_{\text{turnover}} . \tag{S5}$$

Here, M_i, r_i, and k_i refer to the mass, maintenance respiration rate, and turnover rate of the different tissues. The parameter c_{bio} measures the amount of biomass per mol of carbon and Y is yield, i.e., the fraction of assimilated carbon fixed in biomass, with the remaining fraction being lost as growth respiration. The growth respiration component comes in addition to the costs of maintenance respiration. Gross photosynthetic production is proportional to leaf area ω, with $\omega = M_{\text{l}}/\phi$ and where ϕ is the leaf mass per unit leaf area. The total mass of tissues is $M_{\text{t}} = M_{\text{l}} + M_{\text{b}} + M_{\text{s}} + M_{\text{h}} + M_{\text{r}}$.

1.2 *Allocation*

To model allocation, we use a functional-balance allometric model linking the mass of the aforementioned five plant tissues to a plant's height. This approach allows us to track only the plant's height, while also accounting for the costs of growing.

Based on empirically observed allometry [1], we assume an allometric relationship between a plant's leaf area ω and its height,

$$H = \alpha_1 \left(\omega/\mathrm{m}^2\right)^{\beta_1}, \tag{S6}$$

with parameters α_1 and β_1.

We also assume that each unit of sapwood area supports a fixed area of leaf, as in the pipe model [2], so that the cross-section area of sapwood is ω/θ, where θ is the leaf area per sapwood area. Under this assumption, and combined with Eq. S1, the total mass of sapwood in a plant is given by

$$M_{\text{s}} = \rho\, \eta_{\text{c}}\, \theta^{-1}\, \omega\, H, \tag{S7}$$

where $\eta_{\text{c}} = 1 - \frac{2}{1+\eta} + \frac{1}{1+2\eta}$ adjusts for the vertical distribution of leaf [1, 2] and ρ is the wood density.

Bark tissue (including phloem) is modelled using an analogue of the pipe model [1], leading to a similar equation as for sapwood mass (Eq. S7). The cross-section area of bark per unit leaf area is assumed to be a constant fraction b of sapwood area per unit leaf area, so that

$$M_{\text{b}} = bM_{\text{s}}. \tag{S8}$$

Also consistent with the pipe model, we assume a fixed ratio of root mass to leaf area,

$$M_{\text{r}} = \alpha_3\, \omega. \tag{S9}$$

Even though nitrogen and water uptake are not modelled explicitly, imposing a fixed ratio of root mass to leaf area ensures that approximate costs of root production are included in the carbon budget.

Finally, the amount of heartwood is assumed to increase with total leaf area based on an empirically observed allometric relationship [1],

$$M_{\mathrm{h}} = \rho\, \eta_{\mathrm{c}}\, \alpha_2 \left(\omega/\mathrm{m}^2\right)^{\beta_2}, \tag{S10}$$

with parameters α_2 and β_2.

1.3 *Height growth*

The key measure of growth required to model size-structured population dynamics is the rate of height growth, $g(x', H, E_{x,y,a})$. For quantifying height growth, we translate mass production into height increment while accounting for the costs of building new tissues, allocation to reproduction, and architectural layout. Using the chain rule, height growth can be decomposed into a product of physiologically relevant terms:

$$g(x', H, E_{x,y,a}) = \frac{\mathrm{d}H}{\mathrm{d}\omega}\frac{\mathrm{d}\omega}{\mathrm{d}M_{\mathrm{t}}}\frac{\mathrm{d}M_{\mathrm{t}}}{\mathrm{d}B}\frac{\mathrm{d}B}{\mathrm{d}t}. \tag{S11}$$

The first factor, $\mathrm{d}H/\mathrm{d}\omega$, is the growth in plant height per unit growth in total leaf area – accounting for the architectural strategy of the plant (here the same for all types). The second factor, $\mathrm{d}\omega/\mathrm{d}M_{\mathrm{t}}$, accounts for the marginal cost of deploying an additional unit of leaf area, including construction of the leaf itself and various support structures. As such, $\mathrm{d}\omega/\mathrm{d}M_{\mathrm{t}}$ can itself be expressed as a sum of construction costs across plant tissues per unit leaf area,

$$\frac{\mathrm{d}\omega}{\mathrm{d}M_{\mathrm{t}}} = \left(\frac{\mathrm{d}M_{\mathrm{l}}}{\mathrm{d}\omega} + \frac{\mathrm{d}M_{\mathrm{b}}}{\mathrm{d}\omega} + \frac{\mathrm{d}M_{\mathrm{s}}}{\mathrm{d}\omega} + \frac{\mathrm{d}M_{\mathrm{h}}}{\mathrm{d}\omega} + \frac{\mathrm{d}M_{\mathrm{r}}}{\mathrm{d}\omega}\right)^{-1}. \tag{S12}$$

The third factor, $\mathrm{d}M_{\mathrm{t}}/\mathrm{d}B = 1 - r(H, H_{\mathrm{m}})$, is the fraction of net biomass production that is allocated to growth rather than to reproduction or storage (Eq. 8), while the final factor is the rate of net biomass production (Eq. S5).

The factors $\mathrm{d}H/\mathrm{d}\omega$ and $\mathrm{d}\omega/\mathrm{d}M_{\mathrm{t}}$ are thus readily calculated from Eqs. S6-S10.

1.4 *Seed production*

The rate of seed production, $f(x', H, E_{x,y,a})$, is a direct function of mass allocated to reproduction (Eq. 8),

$$f(x', H, E_{x,y,a}) = \frac{r(H, H_{\mathrm{m}})\,\frac{\mathrm{d}B}{\mathrm{d}t}}{s\, c_{\mathrm{acc}}}, \tag{S13}$$

where s is the mass of the seed and c_{acc} is a multiplier that accounts for the cost of accessories, such as fruits, flowers, and dispersal structures (thus, $c_{\mathrm{acc}} > 1$).

1.5 *Mortality*

Instantaneous rates of plant mortality are the sum of a growth-independent and a growth-dependent rate,

$$d(x', H, E_{x,y,a}) = d_{\mathrm{I}} + d_{\mathrm{D}}(x', H, E_{x,y,a}). \tag{S14}$$

The growth-independent rate d_{I} is taken to be constant, independent of plant performance. The growth-dependent rate is assumed to decline exponentially with the rate of mass production per unit leaf area,

$$d_{\mathrm{D}}(x', H, E_{x,y,a}) = c_{\mathrm{d2}} \exp(-c_{\mathrm{d3}} X), \tag{S15}$$

where $X = \mathrm{d}B/\mathrm{d}t/\omega$. This relationship allows for plants to increase in mortality as their growth rate approaches zero.

Survival of plants during establishment is assumed to depend on the rate of biomass production per unit leaf area,

$$S_{\mathrm{G}}(x', E_{x,y,a}) = \frac{1}{(c_{\mathrm{s0}}/X)^2 + 1}, \tag{S16}$$

where c_{s0} is a constant and $X = \mathrm{d}B/\mathrm{d}t/\omega$ is the rate of mass production per unit leaf area for a seedling. Eq. (S16) is consistent with Eq. (S15), as both cause survival to decline with mass production.

2 VISUALIZATION OF PROCESS AND PATTERN IN THE EVOLVED METACOMMUNITIES

Figs. 1A and 5C-H illustrate successional dynamics in the evolved metacommunities for particular environmental conditions. The panels depict populations of finite size and are generated by sampling from the continuous density distribution $N(H|x_i, E_{x,y,a})$ of plant heights H. Specifically, to illustrate temporal dynamics in a patch, we take an area of ground for a given patch age a' and fill it by sampling an appropriate number of plants for each species from their size distributions $N(H|x_i, E_{x,y,a'})$, in two steps. First, the required number of plants for each species at each age is calculated by averaging $N(H|x_i, E_{x,y,a'})$ with respect to H and multiplying by patch area. Second, plants of different heights are sampled with probabilities proportional to $N(H|x_i, E_{x,y,a'})$. Similarly, the ages of patches shown in Fig. 1B are obtained by sampling a finite number of ages from the distribution $P(a)$ of patch ages (Fig. 1A). The horizontal locations of plants within each patch are sampled from a uniform distribution.

3 SUPPLEMENTARY TABLES

Table S1: Model variables.

Symbol	Unit	Description
Patch state variables		
K		Number of species in the metacommunity
a or a'	y	Patch age (time since disturbance)
$E_{x,y,a}(z)$		Canopy openness at height z within the light environment $E_{x,y,a}$
$E_{x,y,a}$		Profile of canopy openness within a patch of age a with residents of traits x and seed rain y
Abundance measures		
$P(a)$	y^{-1}	Frequency-density of patches of age a
y	$\mathrm{m}^{-2}\ \mathrm{y}^{-1}$	Vector of global seed rain for resident metacommunity
$N(H\|x', E_{x,y,a})$	$\mathrm{m}^{-1}\ \mathrm{m}^{-2}$	Density of plants at height H per unit ground area for given traits x' in a patch with light environment $E_{x,y,a}$
Plant traits		
x		Vector of traits for resident metacommunity
x_i or x'		Vector of traits for focal plant
ϕ	$\mathrm{kg\ m}^{-2}$	Leaf mass per unit leaf area
H_m	m	Height at maturation
Plant state variables		
H	m	Height of a plant
$H_0(x')$	m	Height of a seedling with traits x' after germination
z	m	Height in canopy
ω	m^2	Leaf area of a plant
$q(z, H)$	m^{-1}	Distribution of leaf area across heights z for a plant of height H
$Q(z, H)$		Fraction of leaf area above height z for a plant of height H
B	kg	Biomass produced by a plant
M_i	kg	Mass of tissue type i retained on plant
Physiological rates		
$p(x', E_{x,y,a}(z))$	$\mathrm{mol\ y}^{-1}\ \mathrm{m}^{-2}$	Photosynthetic rate per unit leaf area at height z within a plant with traits x' in the light environment $E_{x,y,a}$
$\bar{p}(x', H, E_{x,y,a}(z))$	$\mathrm{mol\ y}^{-1}\ \mathrm{m}^{-2}$	Average of p for a plant of height H in the light environment $E_{x,y,a}$
r_i	$\mathrm{mol\ y}^{-1}\ \mathrm{kg}^{-1}$	Respiration rate per unit mass of tissue type i
k_i	y^{-1}	Turnover rate for tissue type i
$r(H, H_\mathrm{m})$		Fraction of net biomass production allocated to reproduction for a plant of height H with height at maturation H_m.
Demographic rates and outcomes		
$g(x', H, E_{x,y,a})$	$\mathrm{m\ y}^{-1}$	Height-growth rate of a plant with traits x' and height H in the light environment $E_{x,y,a}$
$f(x', H, E_{x,y,a})$	y^{-1}	Seed-production rate of a plant with traits x' and height H in the light environment $E_{x,y,a}$
$d(x', H, E_{x,y,a})$	y^{-1}	Instantaneous mortality rate of a plant with traits x' and height H in the light environment $E_{x,y,a}$
$d_\mathrm{P}(a)$	y^{-1}	Instantaneous disturbance rate of a patch of age a
$H(x', E_{x,y,a}, a')$	m	Height of a plant with traits x' in a patch of age a' having germinated in light environment $E_{x,y,a}$
$S_\mathrm{G}(x', E_{x,y,a})$		Probability of a seed of a plant with traits x' to germinate in the light environment $E_{x,y,a}$
$S_\mathrm{I}(x', E_{x,y,a}, a')$		Probability of a plant with traits x' surviving to patch age a' having germinated in light environment $E_{x,y,a}$
$S_\mathrm{P}(a, a')$		Probability of a patch to remain undisturbed from patch age a to patch age a'
$\tilde{R}(x', E_{x,y,a})$		Cumulative seed output of a plant with traits x' having germinated in light environment $E_{x,y,a}$
$R(x', x, y)$		Basic reproduction ratio of a rare plant with traits x' growing in a metapopulation of resident plants with traits x and seed rains y
$F(x', x, y)$		Invasion fitness of a rare plant with traits x' growing in a metapopulation of resident plants with traits x and seed rains y

TABLE S2: Model parameters.

Description	Symbol	Unit	In C++ code[1]	Value
Construction				
Crown-shape parameter	η		`Eta`	12
Wood density	ρ	$\mathrm{kg\,m^{-3}}$	`wood_dens`	608
Leaf area per sapwood area	θ		`theta`	4669
Height of plant with leaf area of 1 $\mathrm{m^2}$	α_1	m	`a1`	5.44
Allometric exponent for height scaling	β_1		`B1`	0.306
Heartwood volume of plant with leaf area of 1 $\mathrm{m^2}$	α_2	$\mathrm{m^3}$	`a2`	6.67×10^{-5}
Allometric exponent for heartwood scaling	β_2		`B2`	1.75
Root mass per leaf area	α_3	$\mathrm{kg\,m^{-2}}$	`a3`	0.07
Ratio of bark area to sapwood area	b		`b`	0.17
Production				
Leaf photosynthesis rate per unit leaf area	c_{p1}	$\mathrm{mol\,y^{-1}\,m^{-2}}$	`c_p1`	150.36
Half-saturation constant for leaf photosynthesis rate per unit leaf area	c_{p2}		`c_p2`	0.19
Biomass per mol carbon	c_{bio}	$\mathrm{kg\,mol^{-1}}$	`c_bio`	2.45×10^{-2}
Yield	Y		`Y`	0.7
Leaf respiration rate per unit leaf area	r_{rl0}	$\mathrm{mol\,y^{-1}\,m^{-2}}$		39.27
Fine-root respiration rate per mass	r_{r}	$\mathrm{mol\,y^{-1}\,kg^{-1}}$	`r_r`	217
Sapwood respiration rate per mass	r_{s}	$\mathrm{mol\,y^{-1}\,kg^{-1}}$	`r_s`	6.59
Baseline rate of leaf turnover	α_4	$\mathrm{y^{-1}}$	`a4`	2.86×10^{-2}
Allometric exponent for leaf-turnover scaling	β_4		`B4`	1.71
Turnover rate of bark	k_{b}	$\mathrm{y^{-1}}$	`k_b`	0.2
Turnover rate of fine roots	k_{r}	$\mathrm{y^{-1}}$	`k_r`	1
Fecundity				
Seed mass	s	kg	`seed_mass`	3.8×10^{-5}
Maximum allocation to reproduction	c_{r1}		`c_r1`	1
Parameter determining steepness of $r(H, H_{\mathrm{m}})$ around H_{m}	c_{r2}		`c_r2`	50
Multiplier accounting for accessory costs of seed production	c_{acc}		`c_acc`	4
Mortality				
Probability of a seed to survive dispersal	S_{D}		`Pi_0`	0.25
Half-saturation constant for germination probability	c_{s0}	$\mathrm{kg\,m^{-2}\,y^{-1}}$	`c_s0`	0.1
Growth-independent mortality	d_{I}	$\mathrm{y^{-1}}$	`c_d0`	0.01
Maximum growth-dependent mortality	c_{d2}	$\mathrm{y^{-1}}$	`c_d2`	5.5
Scaling coefficient for growth-dependent mortality	c_{d3}	$\mathrm{y\,m^{-2}\,kg^{-1}}$	`c_d3`	20
Other				
Average interval between disturbances	$\hat{a}$	y	`disturbanceInterval`	60
Light-extinction coefficient	c_{ext}		`c_ext`	0.5

[1] Name of corresponding variables in the code accompanying this paper. See main text for link.

4 SUPPLEMENTARY FIGURES

Fig. S1: **Overview of processes represented in the model, including physiological dynamics, population dynamics, and evolutionary dynamics.** Grey arrows indicate connection between components. **A,** A plant's vital rates are jointly determined by its light environment, height, and traits according to the physiological sub-model detailed in Section S1. **B,** A metacommunity consists of a distribution of patches linked by seed dispersal. Seeds arrive from a global disperser pool, while seeds produced within a patch contribute to that pool (dashed lines). Disturbances occasionally remove all vegetation within a patch. Competitive hierarchies within developing patches are modelled by tracking the height distribution of plants across multiple species (distinguished by colors) as patches age after a disturbance. The intensity of shading indicates the density of plants at a given height. Rates of change at any given height and age are calculated from the physiological sub-model in **A**. **C,** The traits of the resident species determine the shading environment across the metacommunity via the demographic sub-model (**B**), which in turn determines fitness landscapes. Resident traits adjust through directional selection up the fitness landscape and through the introduction of new species with traits for which fitness is positive.

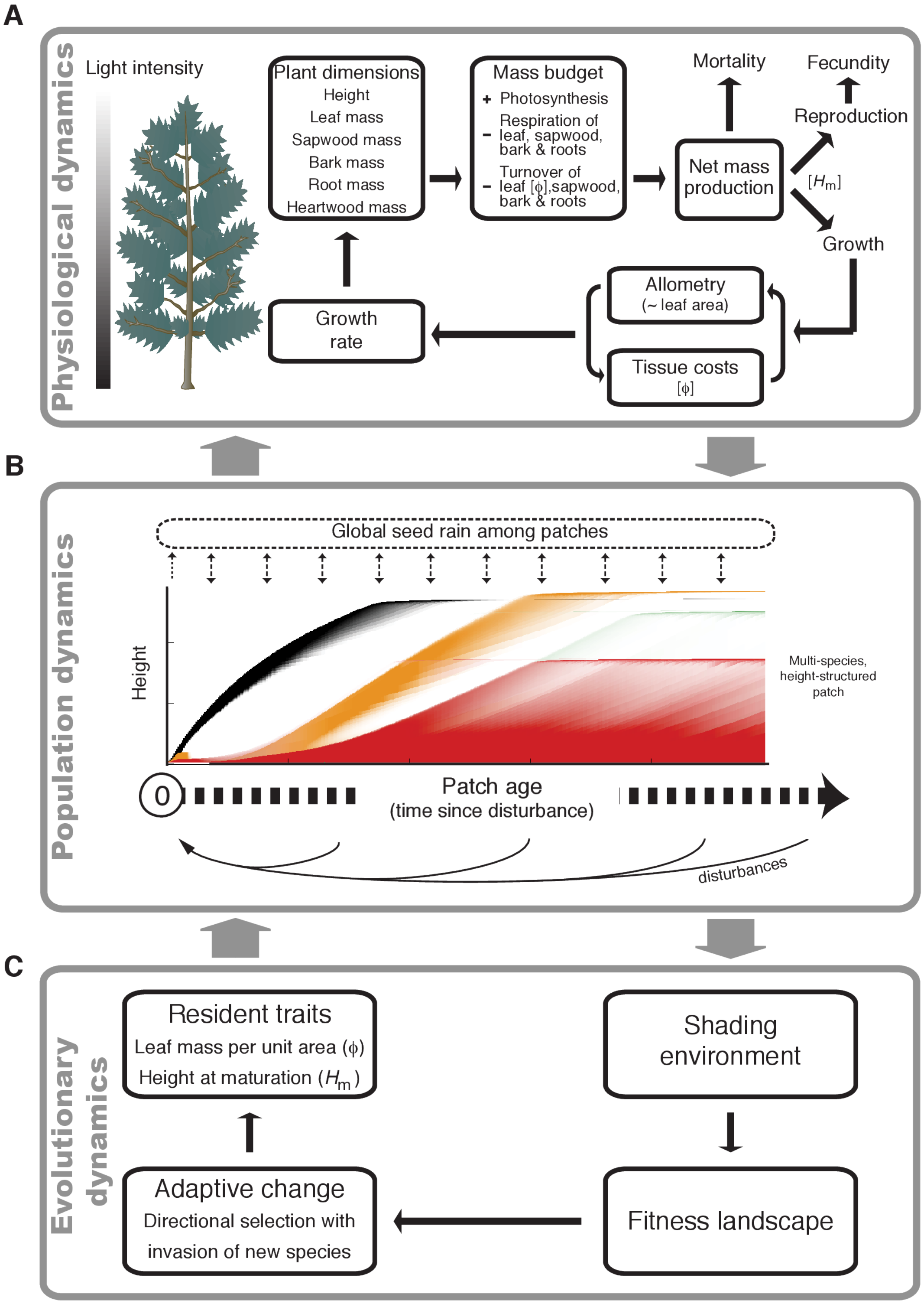

A
Physiological dynamics
Light intensity
Plant dimensions
Height
Leaf mass
Sapwood mass
Bark mass
Root mass
Heartwood mass
Mass budget
+ Photosynthesis
- Respiration of leaf, sapwood, bark & roots
- Turnover of leaf [ϕ], sapwood, bark & roots
Mortality
Fecundity
Reproduction
Net mass production
[Hm]
Growth
Allometry (~ leaf area)
Tissue costs [ϕ]
Growth rate
B
Population dynamics
Global seed rain among patches
Height
Multi-species, height-structured patch
0
Patch age (time since disturbance)
disturbances
C
Evolutionary dynamics
Resident traits
Leaf mass per unit area (ϕ)
Height at maturation (Hm)
Shading environment
Fitness landscape
Adaptive change
Directional selection with invasion of new species

Fig. S1

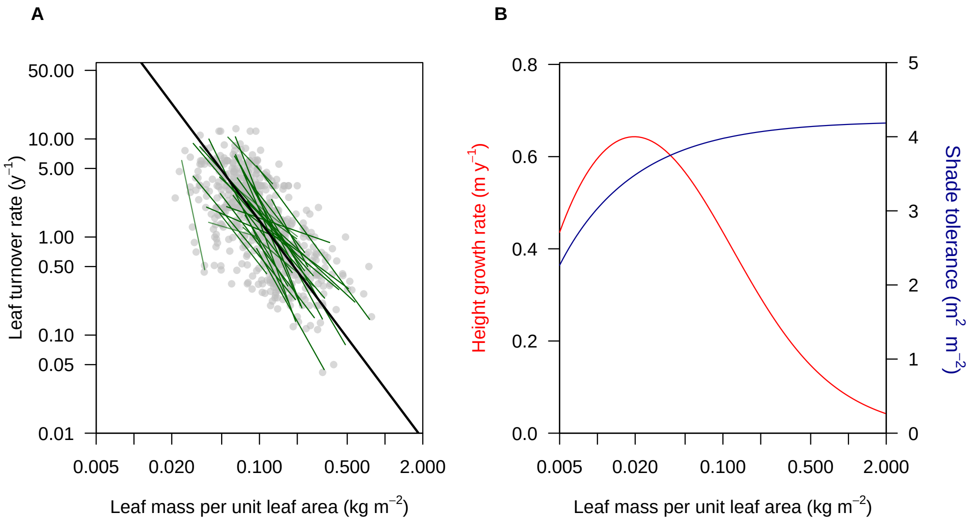


FIG. S2: **Tradeoff between leaf mass per unit leaf area and leaf-turnover rate, and its demographic consequences. A,** Across species, leaf mass per unit leaf area (LMA) is inversely related to leaf-turnover rate. Data are for 678 species from 51 sites [3]. Green lines show standardized major axes fitted to the data from each site, with the intensity of shading adjusted according to the strength of the relationship. The black line indicates the allometric relation used in the present study, as described by the equation for k_l in the main text. **B,** Modelled height-growth rate and shade tolerance for 25 cm tall seedlings differing in leaf mass per unit leaf area. Shade tolerance is quantified as the amount of leaf area above a plant that can be endured before its carbon budget becomes negative.

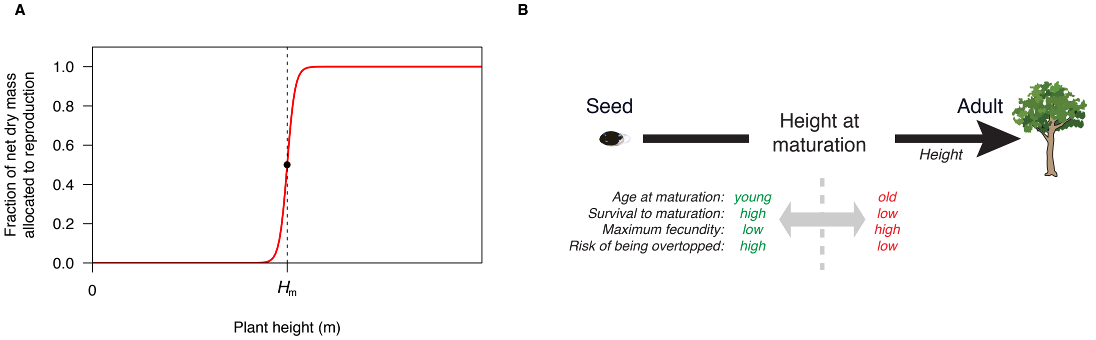
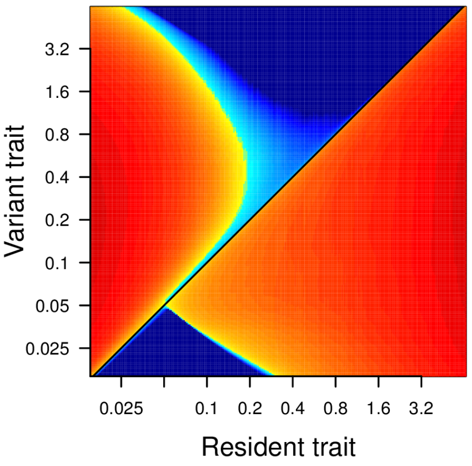


Fig. S3: **Tradeoff between growth and reproduction, and its demographic consequences. A,** The fraction of net dry mass allocated to reproduction varies throughout ontogeny, with a sharp increase from nearly 0% to nearly 100% when a plant reaches its height at maturation, as described by Eq. 8 in the main text. **B,** Height at maturation influences four key demographic factors, giving rise to several emergent life-history tradeoffs. Grey arrows the direction of change for various life-history outcomes arising from changes in height at maturation.

Figs. S4 and S5: **Examples of community assembly when only leaf mass per unit leaf area is evolving, for different values of height at maturation**. In Fig. S4, height at maturation is set to 6.57 m. In Fig. S5, height at maturation is set to 23.58 m. Each figure comprises three parts and shows the process of community assembly in a metacommunity with a mean interval between disturbances of 60 y, as in Figs. 1-4. Fig. S5 corresponds to the metacommunity shown in Fig. 2A. See Fig. 4A for trait mixtures with other values of height at maturation. **A,** A pairwise invasibility plot [4, 5] summarizes the potential outcomes of singles-species evolution. Coloring indicates the invasion fitness $F(x', x, y)$ of a rare variant type (vertical axis) competing with an established resident type (horizontal axis), with values as in Fig. 3. Yellow and red regions represent combinations (x', x) for which the variant type with trait value x' can invade a resident population consisting of plants with trait value x. These plots show that in all cases, metacommunities comprising a single type at its evolutionary attractor can be invaded by variant types with larger trait values. **B-C,** Properties of the metacommunity during a stochastic assembly process. Assembly starts with a type randomly selected across the trait space (Step 1). At each step, the abundance of residents is updated according to their fitness, and new types are added around existing residents ("mutants") and across the trait space ("immigrants"). Mutation and immigration are only successful in regions with positive fitness, delineating the available niche space. Types that successfully invade, but then find themselves in regions of negative fitness, are ultimately driven extinct. In these examples, the metacommunity is fully differentiated after 1,000 steps, as indicated by a stable mean and covariance of trait values, and a fitness landscape with no regions of positive fitness. **B,** Panels show trait values present in the metacommunity at each step during the assembly process: (top) raw values with shading indicating abundance; (middle) abundance-weighted mean trait value; (bottom) coefficient of variation. **C,** Panels show the resultant one-dimensional fitness landscapes at different moments of the assembly process.

A Pairwise invasibility plot



B Stochastic assembly

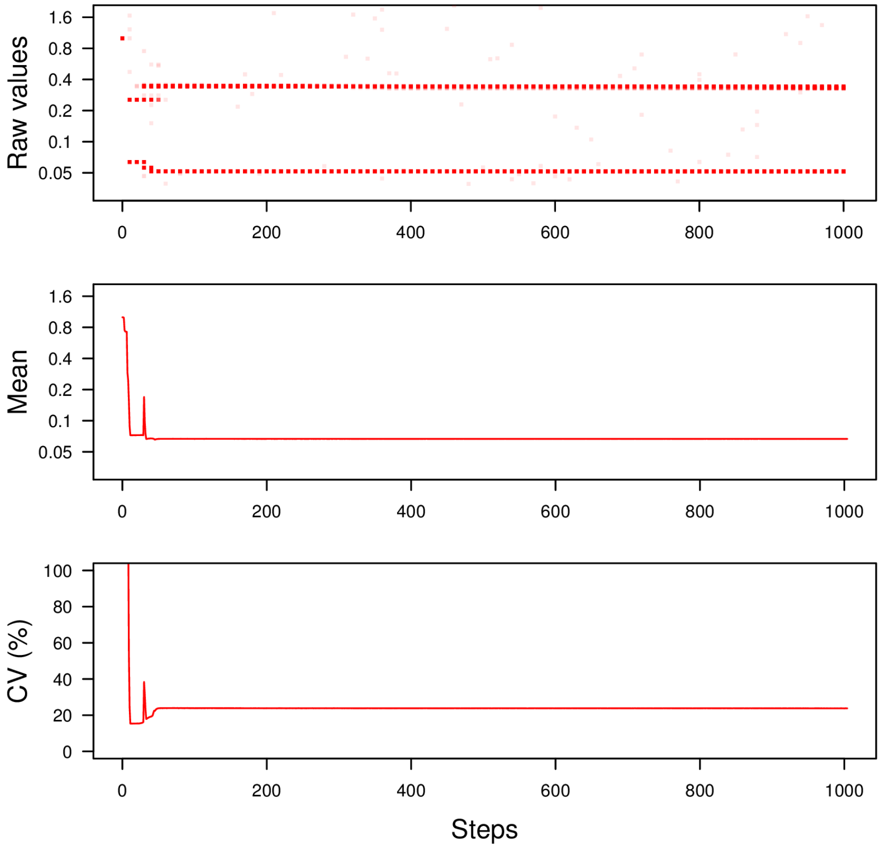
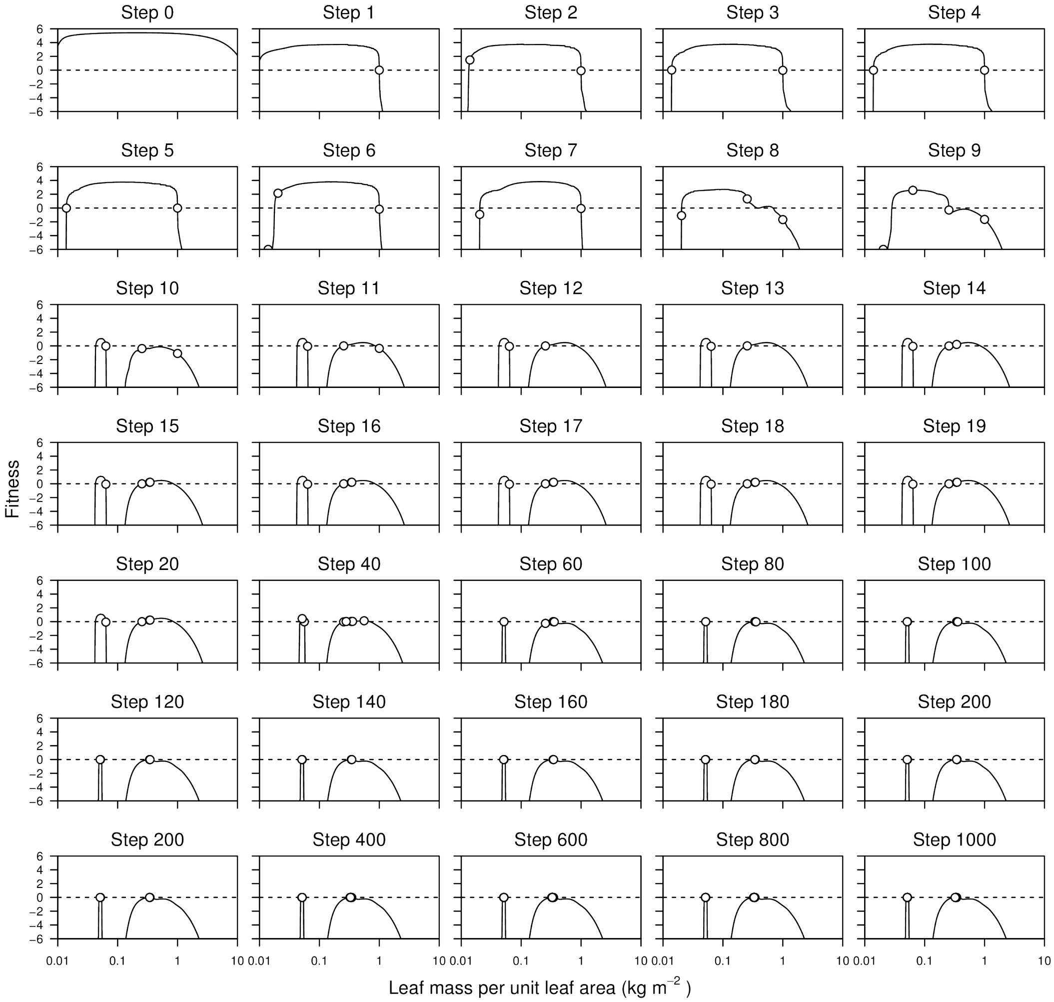
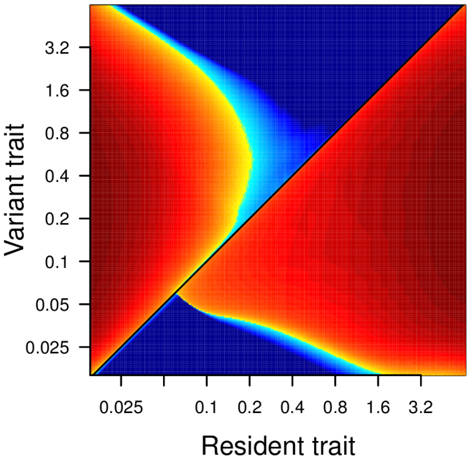


Fig. S4

C Fitness landscapes



A Pairwise invasibility plot



B Stochastic assembly

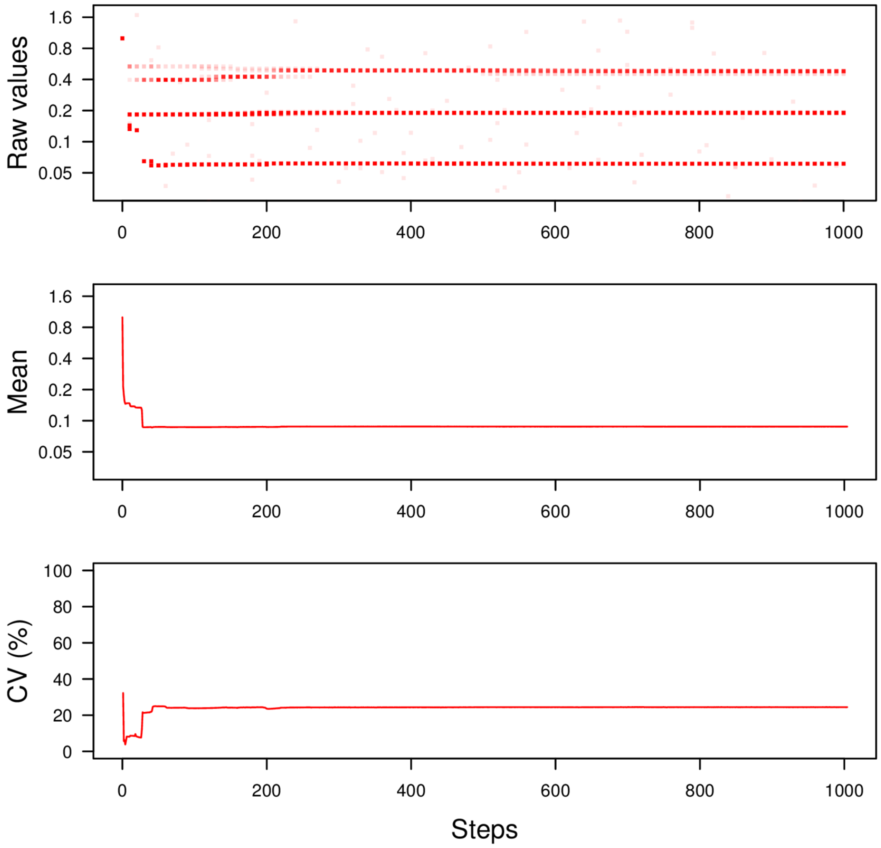
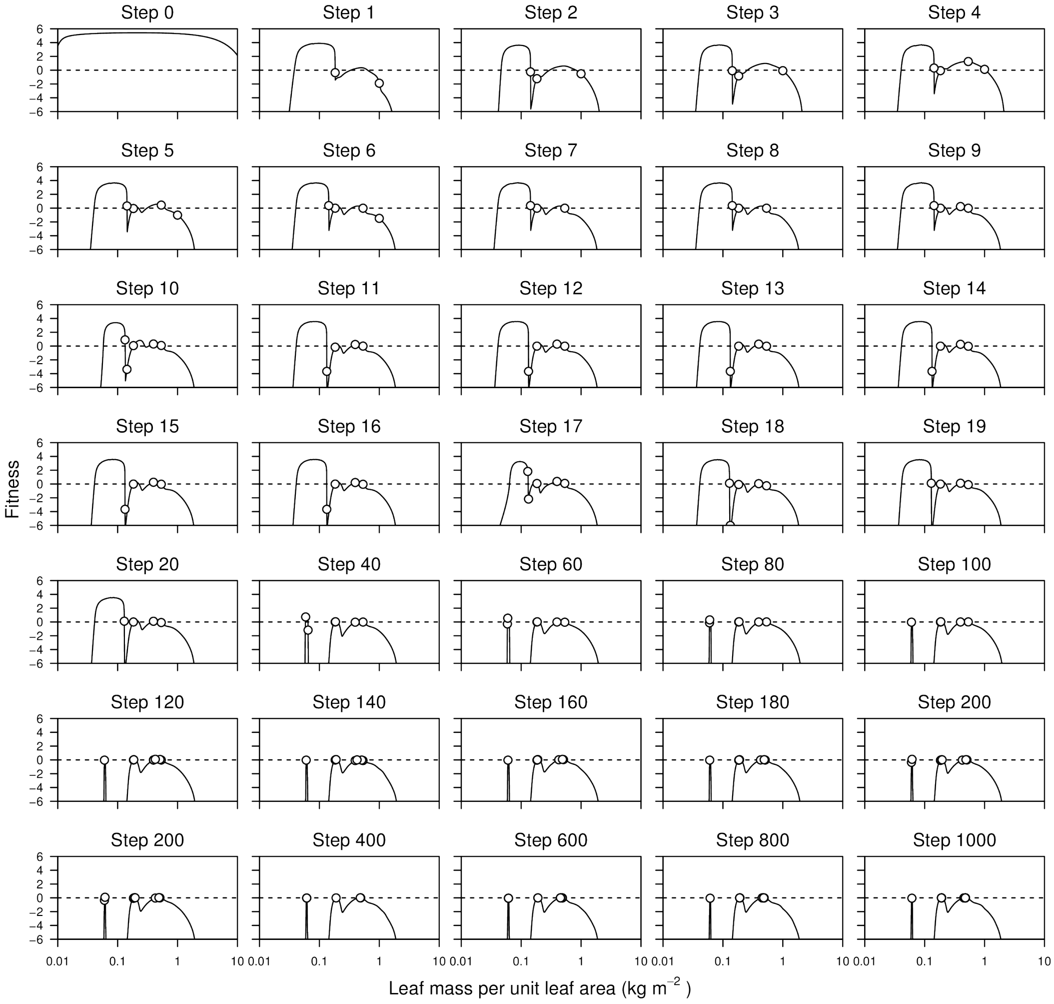


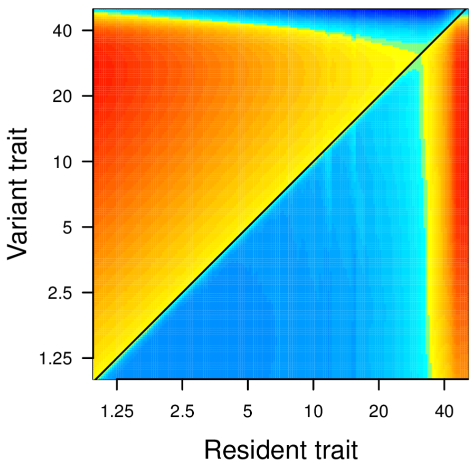
FIG. S5

C Fitness landscapes



Figs. S6 and S7: **Examples of community assembly when only height at maturation is evolving, for different values of leaf mass per unit leaf area**. In Fig. S6, leaf mass per unit leaf area is set to 0.63 kg m^{-2}. In Fig. S7, leaf mass per unit leaf area is set to 4.22 kg m^{-2}. Each figure comprises three parts and shows the process of community assembly in a metacommunity with a mean interval between disturbances of 60 y, as in Figs 1-4. Fig. S7 corresponds to the metacommunity shown in Fig. 2B. See Fig. 4B for trait mixtures with other values of leaf mass per unit leaf area. **A,** A pairwise invasibility plot [4, 5] summarizes the potential outcomes of singles-species evolution. Coloring indicates the invasion fitness $F(x', x, y_x)$ of a rare variant type (vertical axis) competing with an established resident type (horizontal axis), with values as in Fig. 3. Yellow and red regions represent combinations (x', x) for which the variant type with trait value x' can invade a resident population consisting of plants with trait value x. These plots show that in the first case, a single type at its evolutionary attractor cannot be invaded, i.e., is an evolutionarily stable strategy; whereas in the following case a single type at its evolutionary attractor can be invaded by variant types with lower trait values. **B-C,** Properties of the metacommunity during a stochastic assembly process. Assembly starts with a type randomly selected across the trait space (Step 1). At each step, the abundance of residents is updated according to their fitness, and new types are added around existing residents (″mutants″) and across the trait space (″immigrants″). Mutation and immigration are only successful in regions with positive fitness, delineating the available niche space. Types that successfully invade but then find themselves in regions of negative fitness are ultimately driven extinct. In these examples, the metacommunity is fully differentiated after 1,000 and 3,500 steps, respectively, as indicated by a stable mean and covariance of trait values, and a fitness landscape with no regions of positive fitness. **B,** Panels show trait values present in the metacommunity at each step during the assembly process: (top) raw values with shading indicating abundance; (middle) abundance-weighted mean trait value; (bottom) coefficient of variation. **C,** Panels show the resultant one-dimensional fitness landscapes at different moments of the assembly process.

A Pairwise invasibility plot



B Stochastic assembly

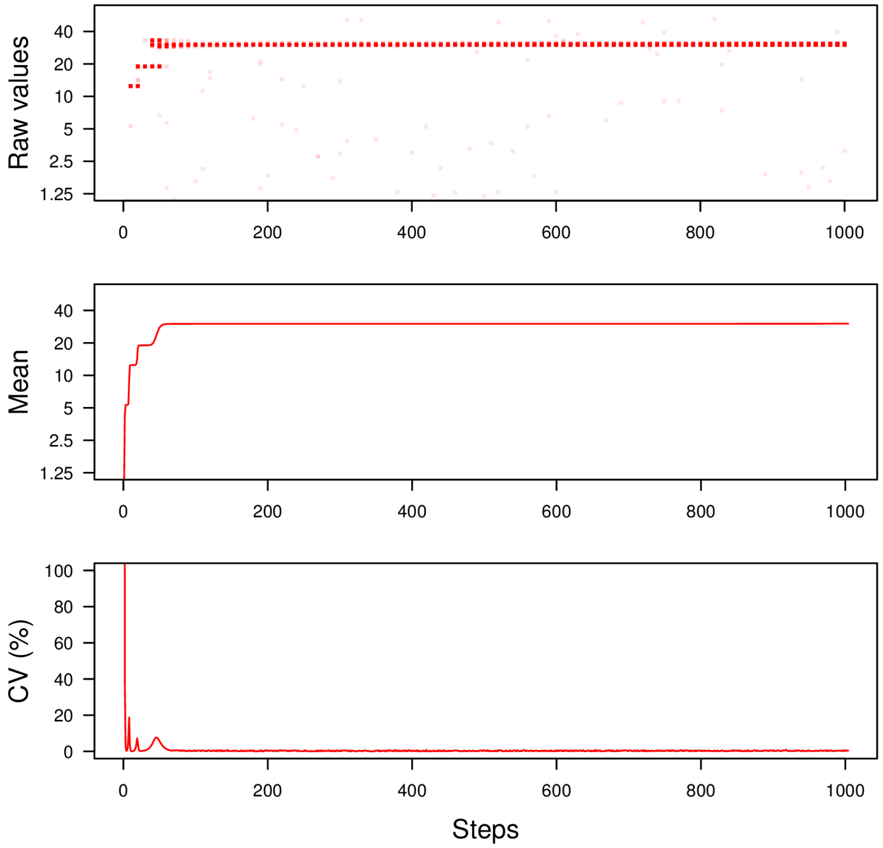
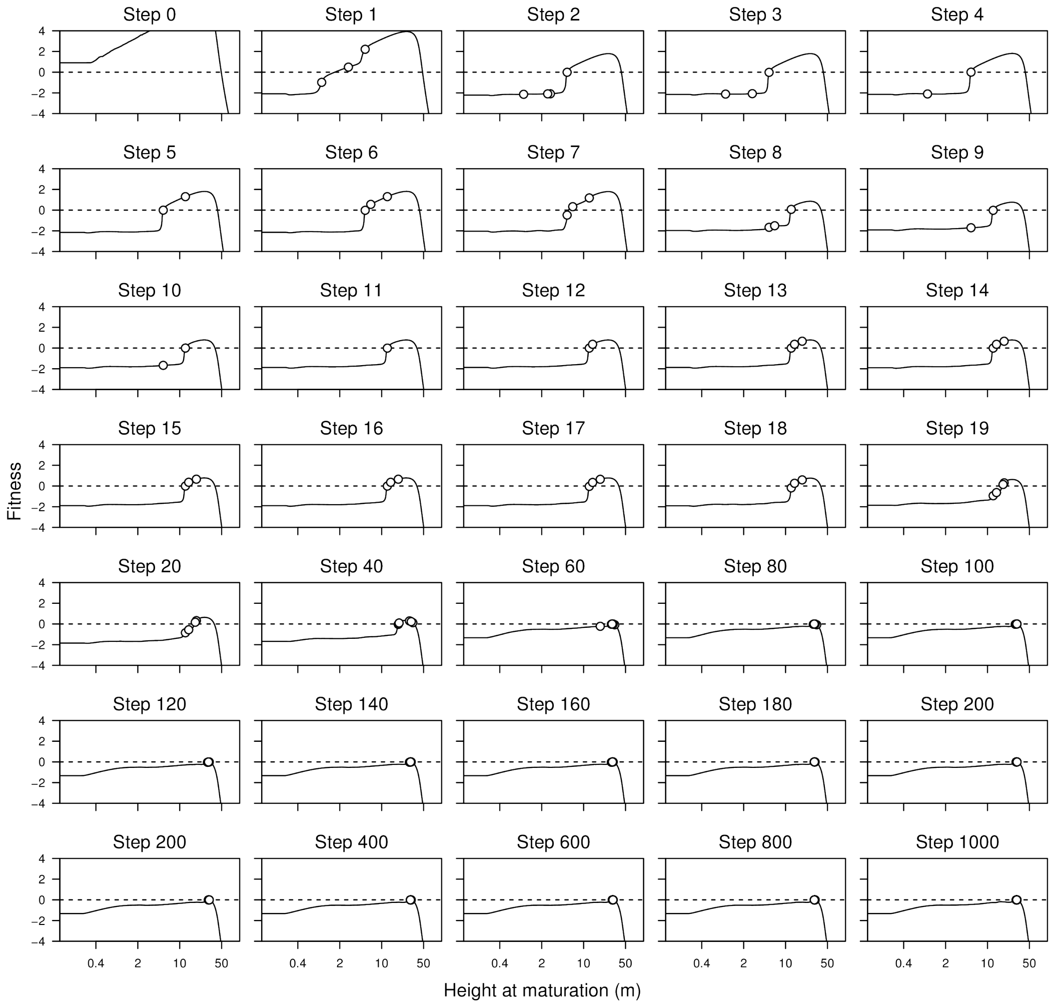
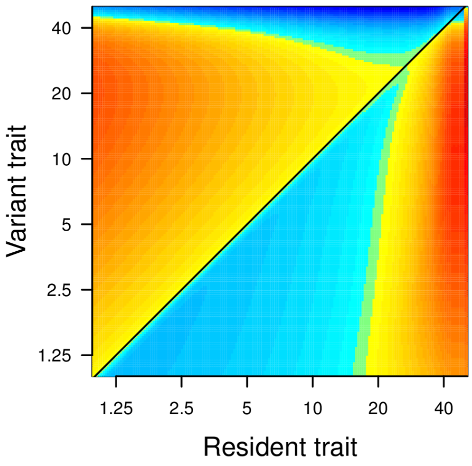


Fig. S6

C Fitness landscapes



A Pairwise invasibility plot



B Stochastic assembly

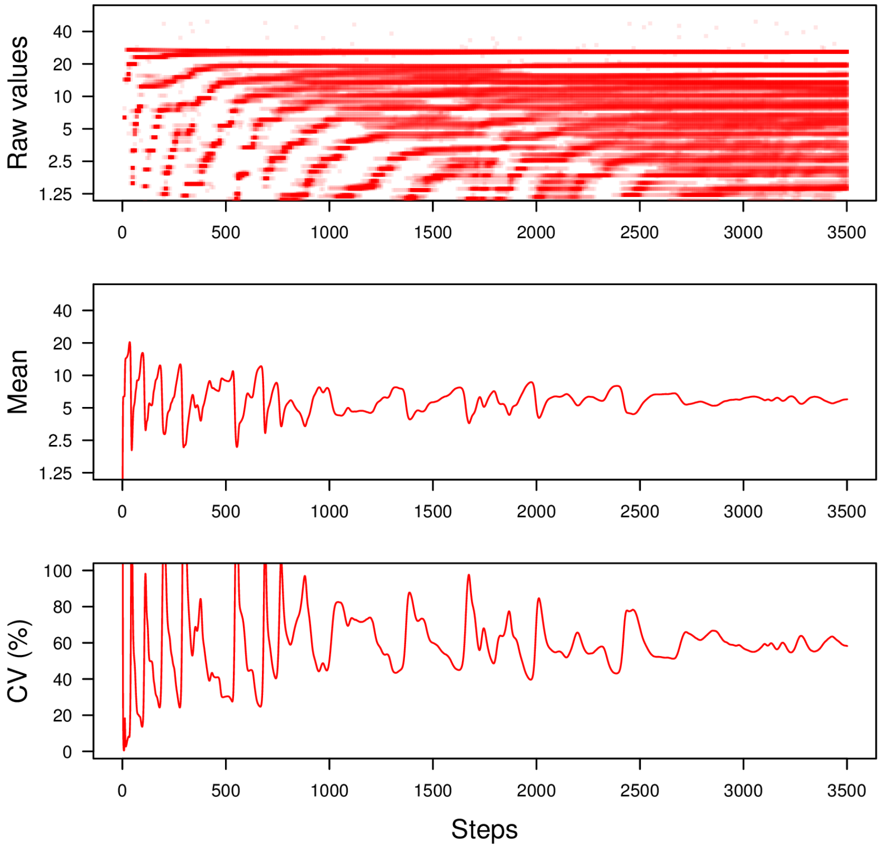
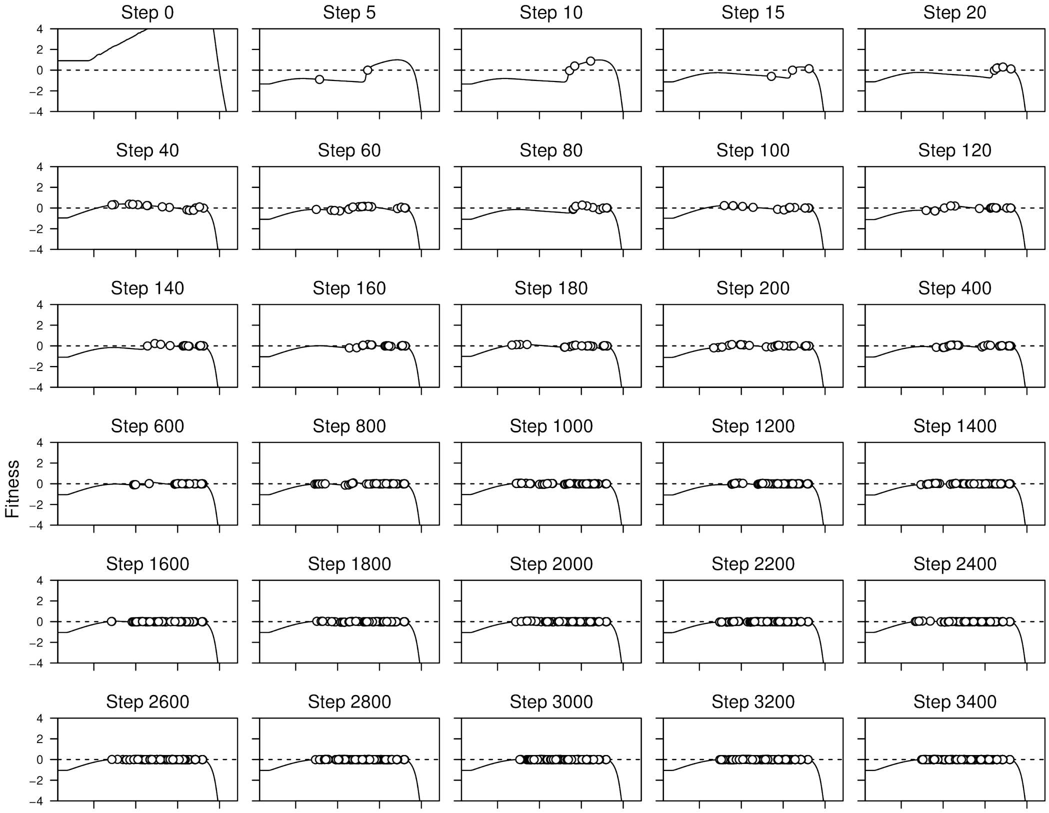


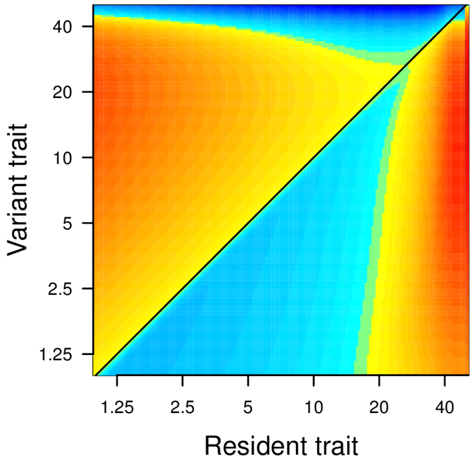
Fig. S7

C Fitness landscapes



Figs. S8 and S9: **Sensitivity of results when only height at maturation is evolving to reduced mutation and immigration rates**. In both figures leaf mass per unit leaf area is set to 4.22 kg m^{-2}, as in Fig. S7. In Fig. S8, the rates of mutation and immigration are lowered ten-fold relative to the default rates used in S7. A similar mixture of traits is assembled as without this reduction, only at a slower pace over a longer time period. Fig. S9 shows the result of taking the community from Fig. S7 after 1,100 steps of the assembly and then halting any further mutation or immigration. A wide range of strategies persist without further input of new variants. Other details as in Fig. S7.

A Pairwise invasibility plot



B Stochastic assembly

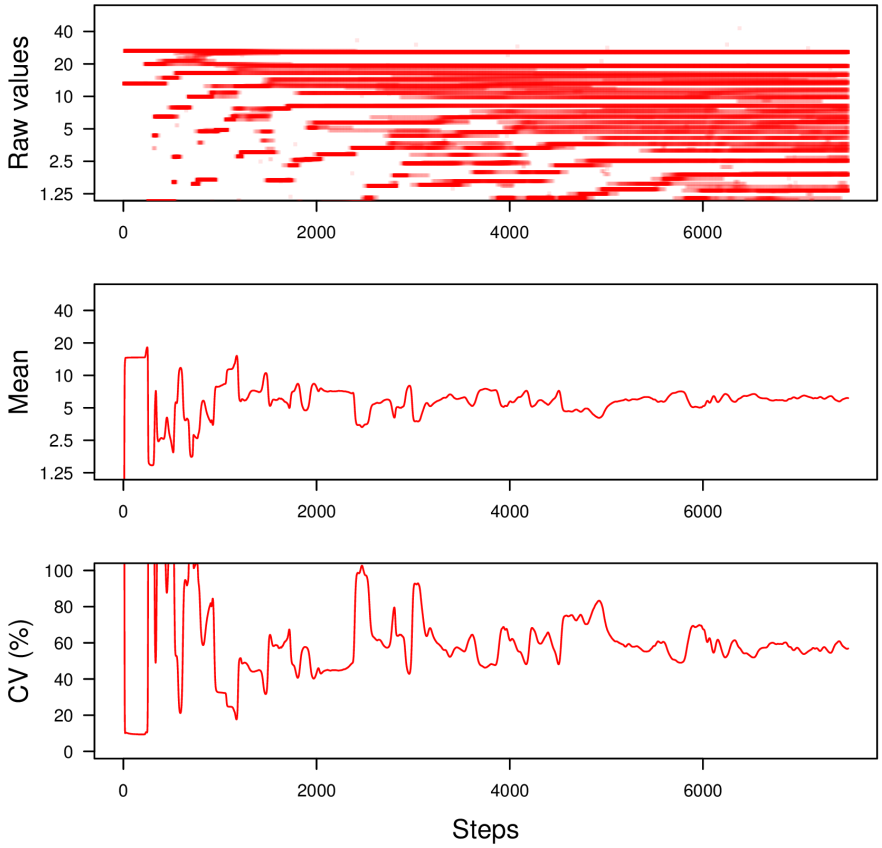
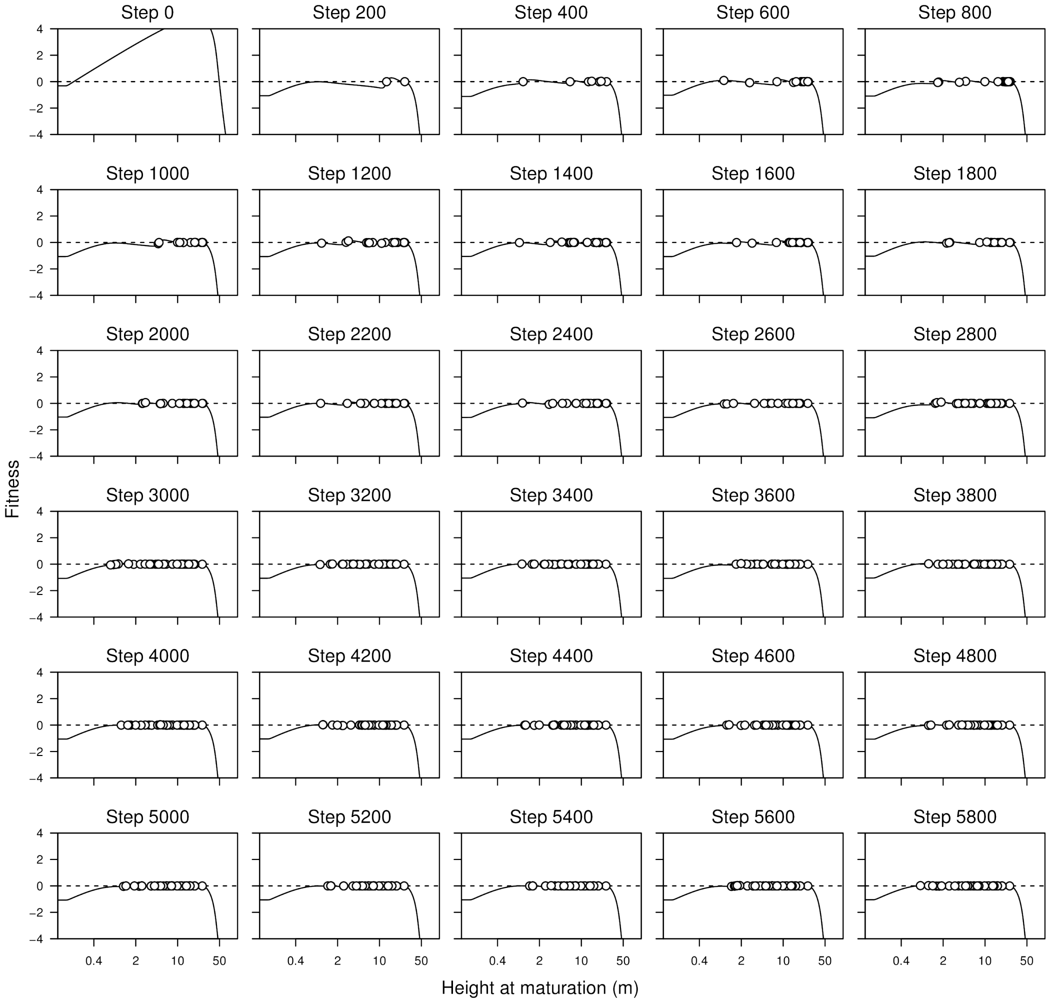
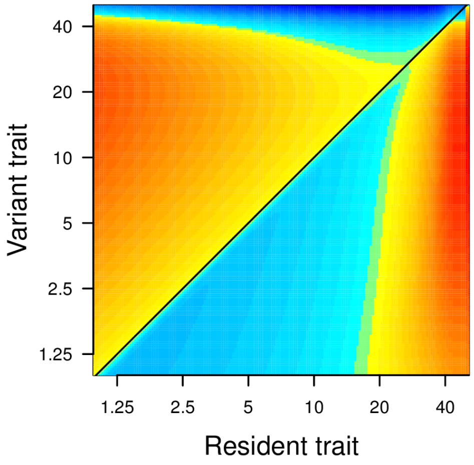


Fig. S8

C Fitness landscapes



A Pairwise invasibility plot



B Stochastic assembly

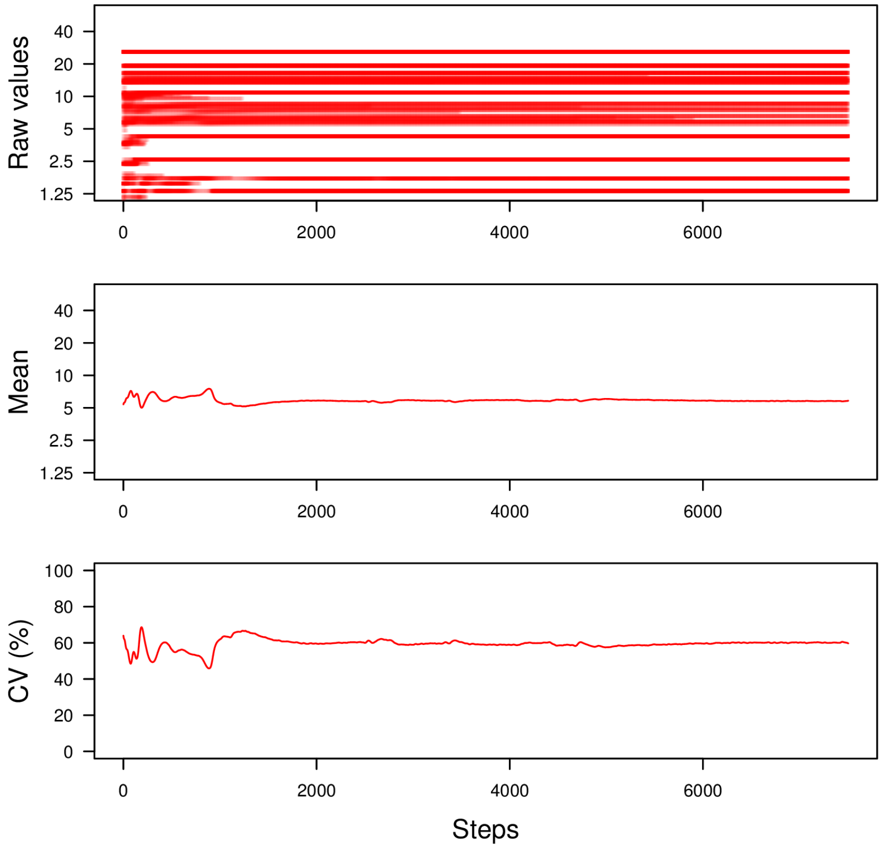
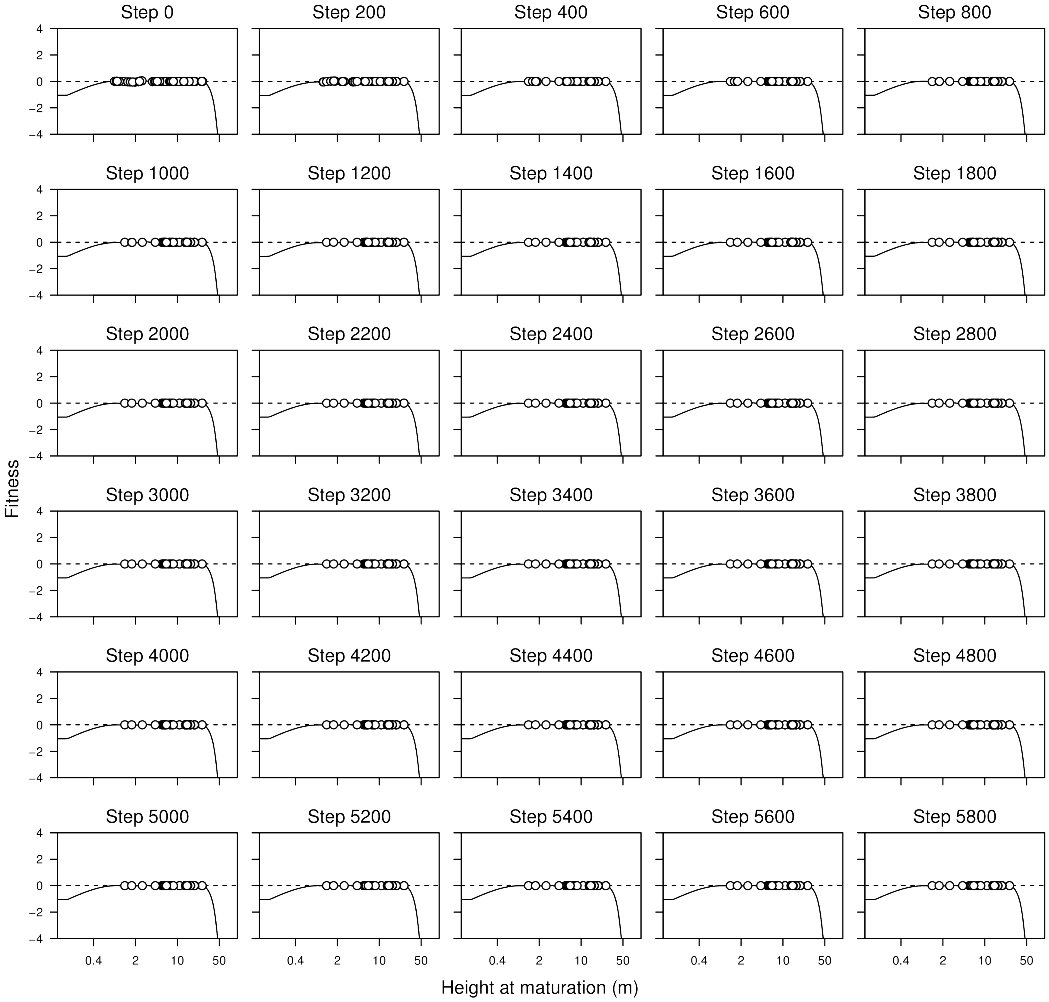


Fig. S9

C Fitness landscapes



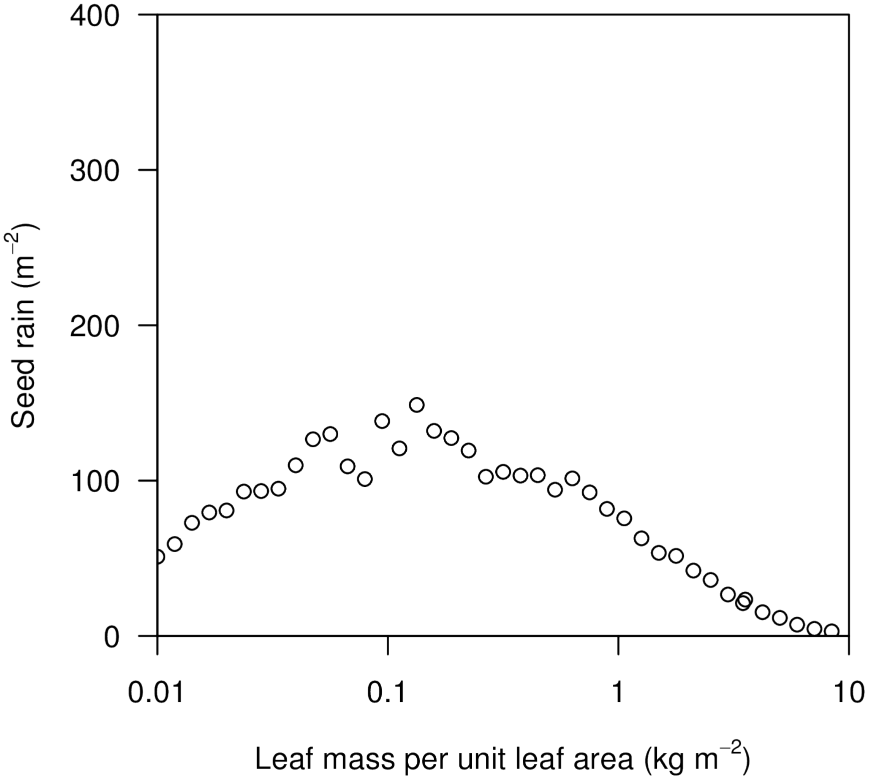


Fig. S10: **Dependence of equilibrium seed rain of tallest species on leaf mass per unit leaf area when only height at maturation is evolving.** Results are based on the metacommunities shown in Fig. 4B.

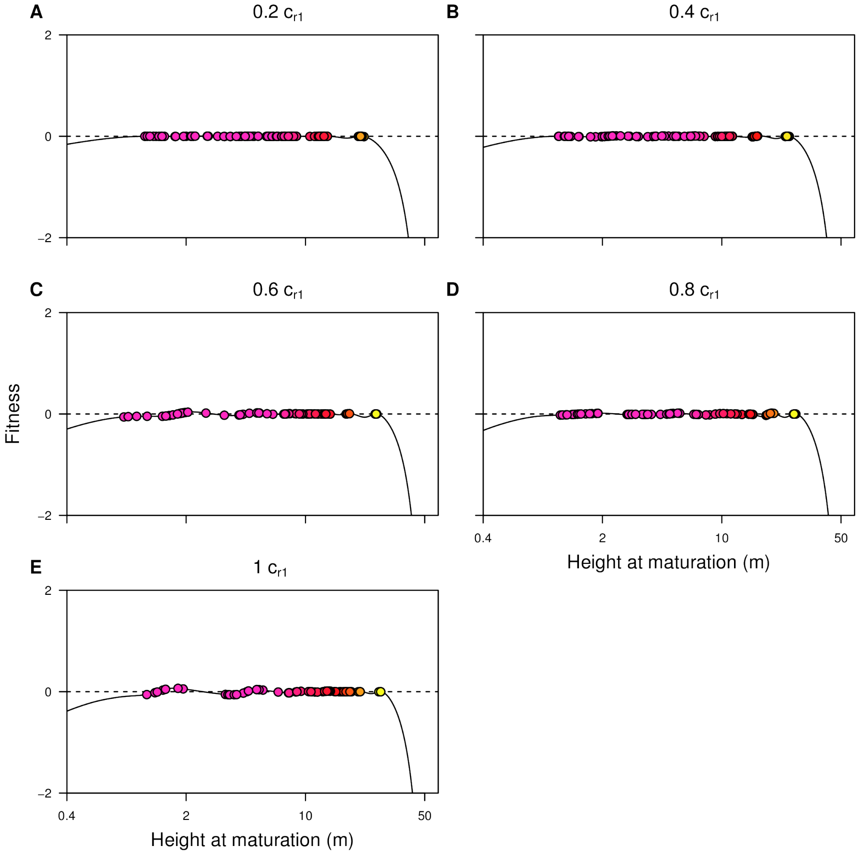


Fig. S11: **Sensitivity of results when only height at maturation is evolving to changes in the maximum allocation to reproduction.** Each panel shows the metacommunity's trait mixture resulting when the maximum allocation to reproduction, specified by the parameter c_{r1}, is set to the value indicated above the panel. For these panels, the leaf mass per unit leaf area is set to $\phi = 3.46$ kg m^{-2}, a value enabling coexistence of different heights at maturation in Fig. 4B. Colors indicate trait values as in Fig. 1. The panels show fitness landscapes after 1,000 steps of the assembly process.

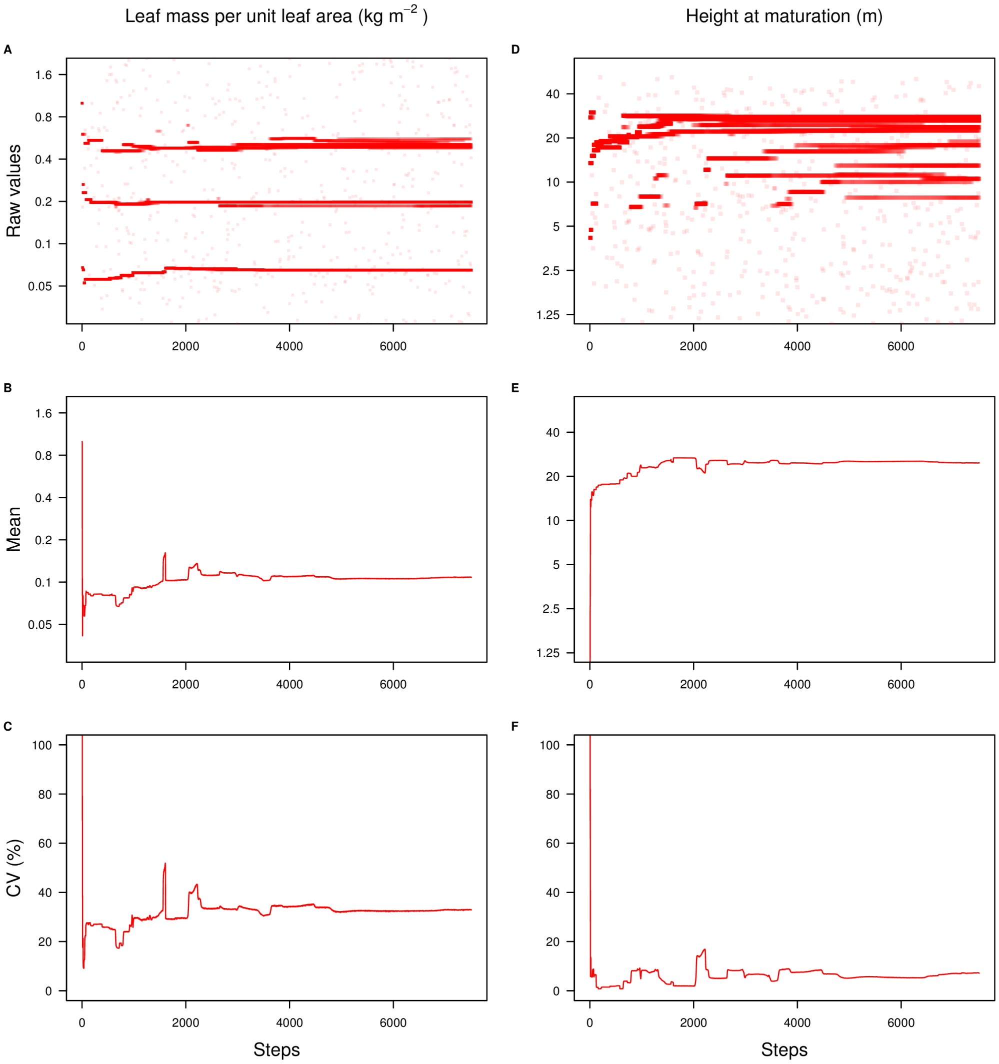


Fig. S12: **Example of community assembly when both traits are evolving.** Panels show properties of the metacommunity during a stochastic assembly process in a metacommunity with a mean interval between disturbances of 60 y, as in Figs 1-4. Panels show the resident trait values present in the metacommunity at each step of the assembly process: (A,D) raw values with shading indicating abundance; (B,E) abundance-weighted mean trait value; (C,F) coefficient of variation. Fitness landscapes corresponding to this assembly sequence are shown in Fig. 3. of the main text. Assembly starts with a type randomly selected across the trait space (Step 1). At each step, the abundance of residents is updated according to their fitness, and new types are added around existing residents ("mutants") and across the trait space ("immigrants"). Mutation and immigration are only successful in regions with positive fitness, delineating the available niche space. Types that successfully invade, but then find themselves in regions of negative fitness, are ultimately driven extinct. In this example, the metacommunity is fully differentiated after 5,000 steps, as indicated by a stable mean and covariance of trait values, and a fitness landscape with no regions of positive fitness.

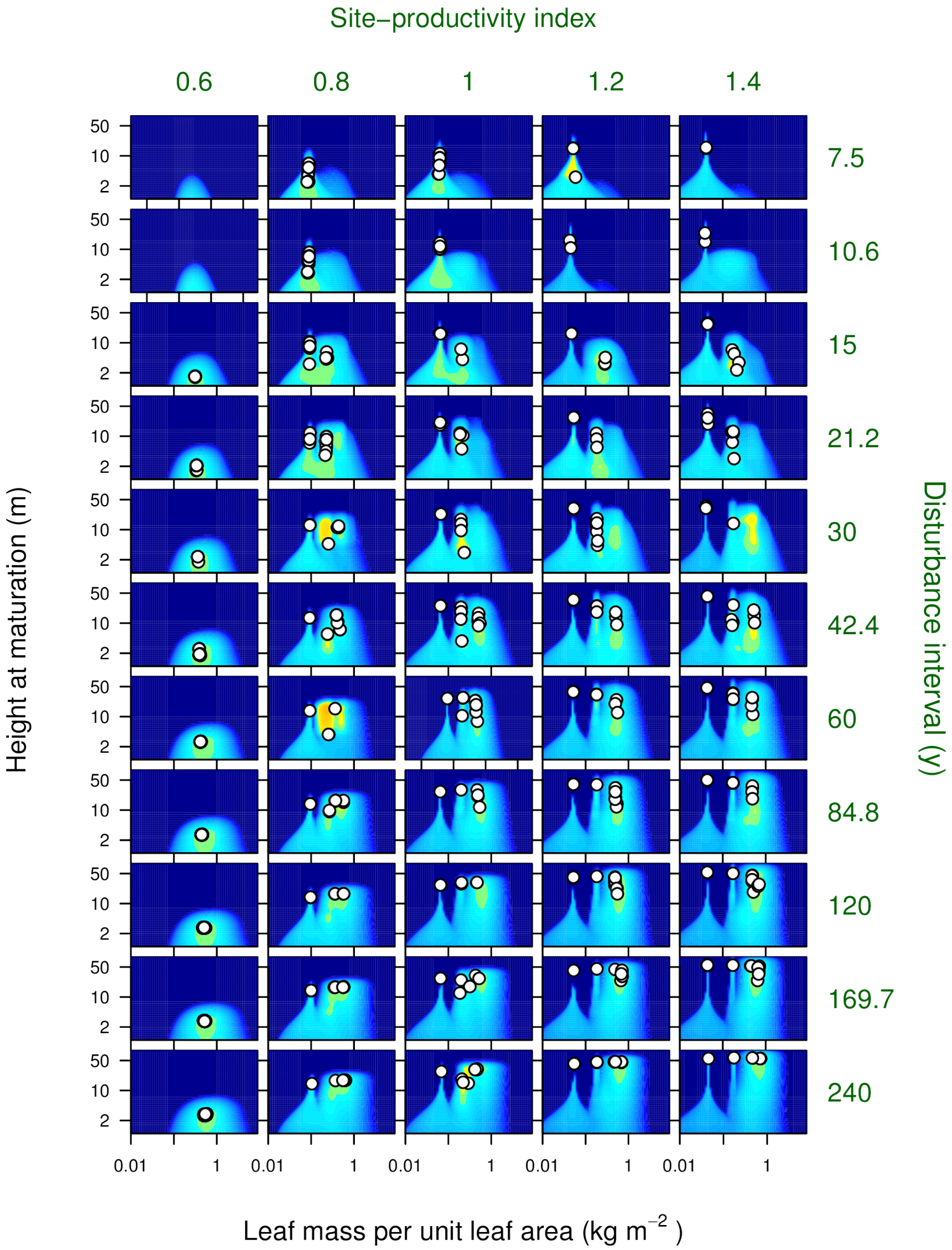


Fig. S13: **Sensitivity of results when both traits are evolving to changes in disturbance interval and site productivity.** Coloring indicates the invasion fitness across the trait space of rare species competing with the resident species (white circles), as in Fig. 3. The panels show fitness landscapes after 5,000 steps of the assembly process, after which most metacommunities have reached a stable trait mixture. In contrast, a few metacommunities exhibit oscillatory dynamics in trait mixtures: across panels, these can be discerned by large residual regions of positive invasion fitness (yellow).

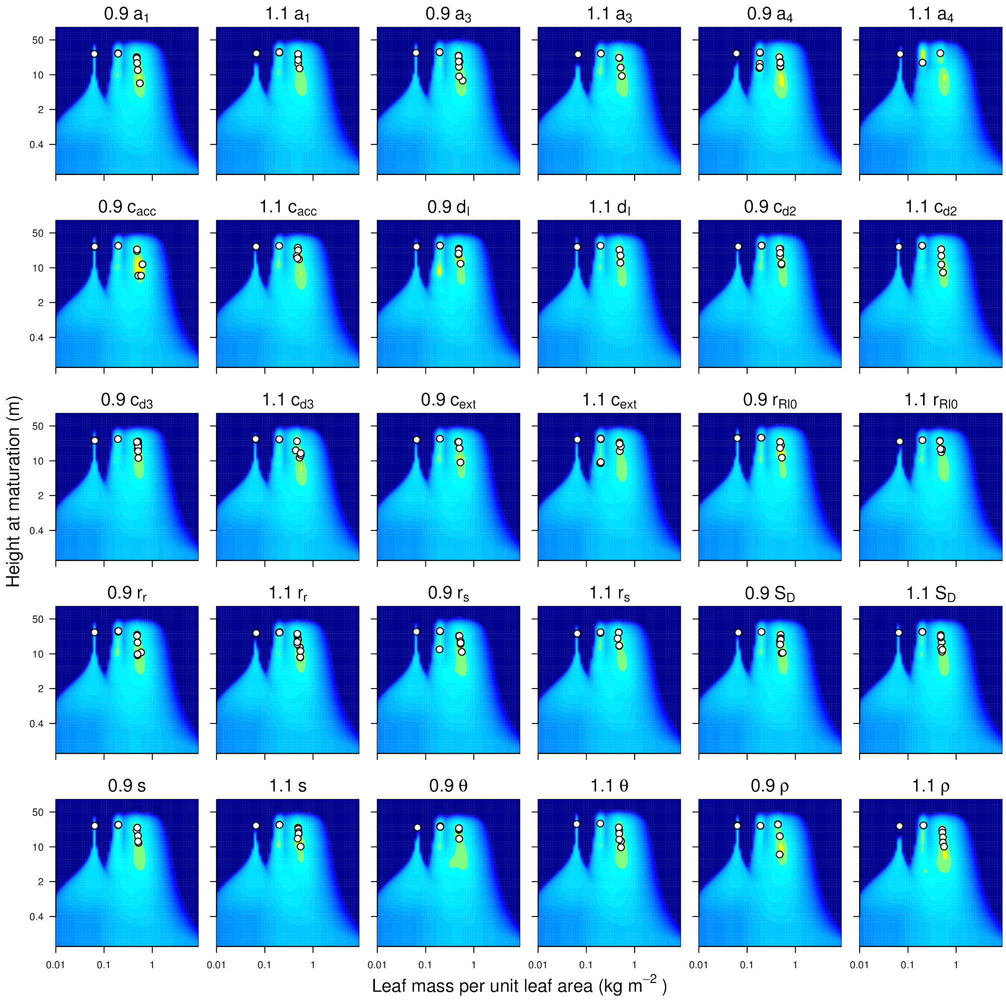


Fig. S14: **Sensitivity of results when both traits are evolving to changes in a range of model parameters.** Each panel shows the metacommunity's trait mixture resulting when a single parameter is changed to 90% or 110% of its original value. All parameter symbols are listed in Table S2. Coloring indicates the invasion fitness across the trait space of rare species competing with the resident species (white circles), as in Fig. 3. The panels show fitness landscapes after 5,000 steps of the assembly process.

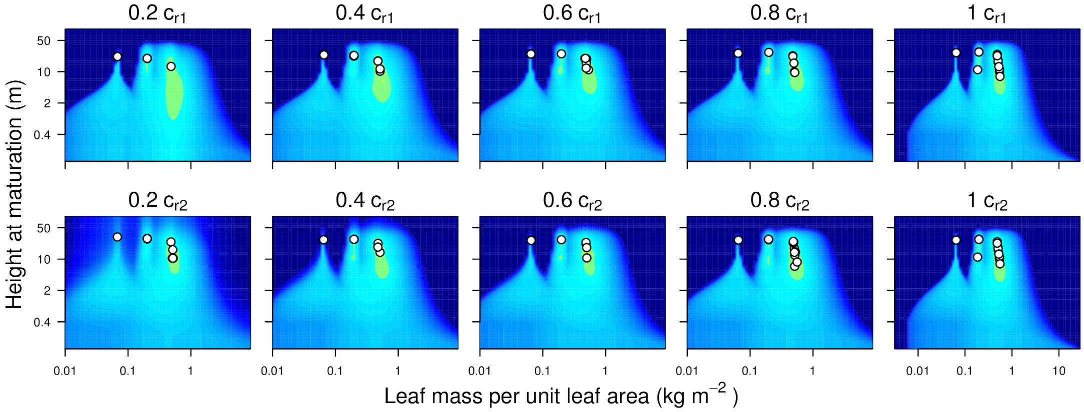


Fig. S15: **Sensitivity of results when both traits are evolving jointly to changes in the shape of the reproductive allocation function.** Each panel shows the metacommunity's trait mixture resulting when a single parameter determining the shape of the reproductive allocation function is changed to a fraction of its original value. Coloring indicates the invasion fitness across the trait space for rare species competing with the resident species (white circles), as in Fig. 3. The panels show fitness landscapes after 5,000 steps of the assembly process.

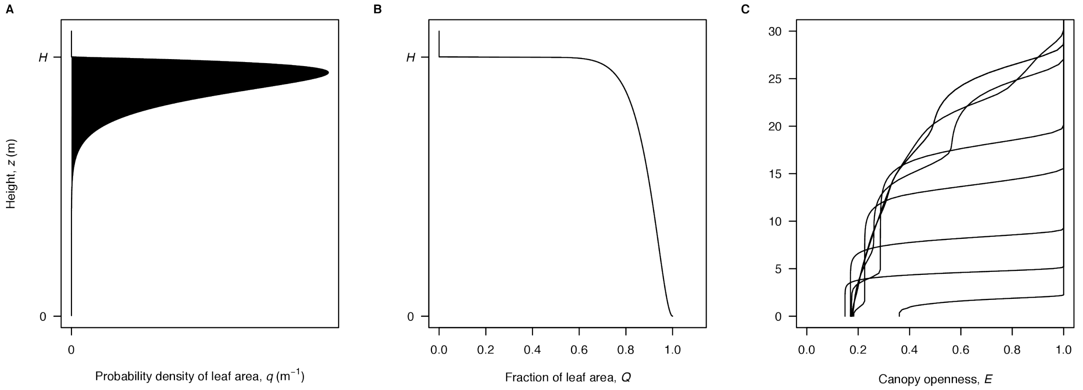


Fig. S16: **Illustration of the competitive feedback via shading.** All plants within a patch contribute to, and experience, a continuous vertical profile in shading. **A**, The leaf area of individual plants is distributed continuously over a range of heights (Eq. S1). **B**, The contribution of a plant to shading at a given height in a patch is determined by the fraction of its leaf area above that height (Eq. S2). **A**, Lines show the canopy openness E that results in patches with ages 2, 5, 10, 20, 30, 60, 100, and 180 y in a metacommunity in which both traits are evolving as shown in Fig. 2C. The light environments in **C** are obtained by integrating the product of two continuous functions (via Eq. 5): the continuous size-density distribution N of plants from different species at a given patch age (as shown in Fig. 2C) and the vertical distribution Q of leaf area within individual plants (as shown in **B**).

5 REFERENCES

[1] Falster DS, Å. Brännström, Dieckmann U, Westoby M (2011) Influence of four major plant traits on average height, leaf-area cover, net primary productivity, and biomass density in single-species forests: a theoretical investigation. *Journal of Ecology* 99: 148–164.

[2] Yokozawa M, Hara T (1995) Foliage profile, size structure and stem diameter plant height relationship in crowded plant-populations. *Annals of Botany* 76: 271–285.

[3] Wright IJ et al. (2004) The world-wide leaf economics spectrum. *Nature* 428: 821–827.

[4] Brännström Å, Johansson J, von Festenberg N (2013) The hitchhikers guide to adaptive dynamics. *Games* 4: 304–328.

[5] Metz JAJ, Nisbet R, Geritz SAH (1992) How should we define 'fitness' for general ecological scenarios? *Trends in Ecology and Evolution* 7: 198–202.