

Supporting Information. Detto, M., J. M. Levine, and S. W. Pacala. Maintenance of high diversity in mechanistic forest dynamics models of competition for light. *Ecological Monographs*.

Appendix S1: A mathematically tractable light competition hierarchical model

Table of contents

S1. The physiological model

- S1.1 Tree with access to light*
- S1.2 Growth out vs. growth up*
- S1.3 Reproduction vs. growth*
- S1.4 Reproductive threshold*
- S1.5 Survival in the shade vs. growth in the light*
- S1.6 Annual Plants*
- S1.7 Breaking the Size Hierarchy*

S2. Community model

- S2.1 Hierarchical structure*
- S2.2 Forest Mosaic*
- S2.3 Community of annual plants*

S3. Strict hierarchy

- S3.1 Forest mosaic*
- S3.2 Annual plants*
- S3.3 Conditions for establishment, continuous species-density curve and species richness*
- S3.4 Stability analysis for the annual plant system*
- S3.5 A family of analytically tractable patch-age distributions*
- S3.6 Growth in the understory*
- S3.7 An Explicit solution*

S4. The schmear model

- S4.1 A solution*
- S4.2 Pair-wise invasibility plot and Evolutionary Stable Strategy*

S5. Other tradeoffs

- S5.1 A special case of multispecies system with species-specific reproductive thresholds*
- S5.2 Continuous case for reproductive threshold*
- S5.3 Pair-wise invasibility plot*
- S5.4 A system with species-specific allocation to reproduction*
- S5.5 A system with the growth-survival*

References

Nomenclature

Table S1

Figure S1, Figure S2, Figure S3, Figure S4, Figure S5, Figure S6, Figure S7, Figure S8, Figure S9, Figure S10, Figure S11, Figure S12, Figure S13, Figure S14

Nomenclature

<i>variables</i>	<i>description</i>	<i>variables</i>	<i>description</i>
H	height	ϕ_i	species-specific allometric parameter for height
C	crown area	ν, β	allometric exponents
M	structural biomass (or total biomass for annuals)	a, b	allometric parameter for structural biomass
D	diameter at breast height	γ	$1 / (\beta - 1)$
$A(L)$	photosynthesis per unit of crown area function of light L at the top of the crown	δ	$\nu / (\beta - 1)$
A_{\max}	maximum rate of photosynthesis per unit of crown area for a fully exposed crown	ψ	leaf area index (LAI)
ω	stochastic growth factor	r_L, r_R	leaf and root respiration rates
$P(\omega)$	distribution of ω	τ_L, τ_R	leaves and fine roots turnover time
θ	parameter of the ω distribution	φ	carbon allocated to reproduction per unit of crown area
k_i, r_i	species-specific growth strategy	η	cost of carbon allocation
x_{ij}	$(r_i / r_j)^{1/\delta}$	Γ	leaf to fine root carbon ratio
n_i	number of individuals of species i per area	σ_L, σ_R	carbon per unit of leaf area and root area
$q_i(t)$	fraction of individuals of species i in the canopy at time t	λ	carbon allocated to defense or storage per unit of crown area
S	number of species	n_s	number of seeds per unit of carbon
t	patch age or time into the growing season	u	fraction of photosynthesis in the understory
T	year	z	time to reach the reproductive threshold
$p(t)$	patch-age distribution	F	expected number recruits generated by an individual per unit of crown area
t_0	time to disturbance or growing season length	w	ratio between leaf respiration+turnover and A_{\max}
t_i	closing time: time species i fills the canopy	μ	seedling mortality in the understory

S1. The physiological model

S1.1. Tree with access to light

We assume that height H and structural carbon mass M are allometric functions of crown area

$$H = \phi C^\nu \quad (\text{S1.1a})$$

$$M = (a + b\phi)C^\beta \quad (\text{S1.1b})$$

where a , b , ν , β , and ϕ are constant. These equations are most easily understood by converting them to diameter allometries. For forest trees, crown area often scales as the ≈ 1.5 power of diameter, while height is often approximately proportional to the square root of diameter, making $\nu \approx 1/3$ ($H \sim D^{1/2}$ and $C \sim D^{3/2}$, so $H \sim C^{1/3}$, e.g., Niklas & Spatz, 2004; Bohlman & O'Brien, 2006; Goodman *et al.*, 2014; Cano *et al.*, 2019). Similarly, a reasonable value of β is $\approx 5/3$ because branch wood, structural root and stem mass all typically scale as the ≈ 2.5 power of diameter. This exponent is easily understood for stem mass if $H \sim D^{1/2}$, because stem mass is proportional to diameter squared times height. The first term (S1.1b) may be thought of as the mass of branches and structural roots, while the second as the mass of the trunk.

We assume the rate of carbon fixation per unit crown area, $A(L)$, is a function of the light level at the top of a plant's crown and can be computed by integrating a model of photosynthesis, like the Farquhar model (Farquhar *et al.* 1980), through the crown's leaf area index (LAI) ψ . $A(L)$ reaches a maximum rate equal to A_{\max} , when the plant is in full sun, but becomes independent of A_{\max} for low L . With the perfect plasticity approximation, light striking the top tops of understory crowns is determined by the LAI of the closed canopy, and a model of light extinction such as Beer's Law. We further assume that plant respiration is dominated by leaf and fine root respiration, r_L and r_R , respectively, and that leaves and fine roots have turnover times τ_L and τ_R . Leaf respiration is proportional to A_{\max} because it is more costly to maintain a photosynthetic machinery with higher capacity. Typically, leaf respiration is proportional to maximum carboxylation velocity (Farquhar *et al.* 1980; Haxeltine & Prentice 1996; Atkin *et al.* 2015). Leaf respiration is generally down-regulated in the understory, but to a level still proportional to respiration in full sun (Atkin *et al.* 1997). Although we do not explicitly include down-regulation of leaf respiration, the treatment below and in the main text is robust to its inclusion. Finally, let Γ be the fixed ratio of leaf to fine root carbon (Thornley 1972), σ_L and σ_R the carbon per unit leaf area and root area, respectively, η be the carbon required by a plant to grow one gram of carbon, φ be the rate at which carbon is allocated to reproduction per unit of crown area, and λ the carbon investment in survival per unit crown area, such as defenses against lethal pathogens and herbivores or carbon storage that would help a plant to survive periods of resource deprivation such as periods of low light in the stochastic sun-flecked light environment in the understory. The physiology of investments in survival is not well understood, but the classic

interspecific tradeoff between growth in high-light and survival in the understory (e.g., Kitajima 1994; Wright *et al.* 2010; Russo *et al.* 2020) can be used to infer the relationship between these investments and mortality rate (see below).

Then, and canopy plant's carbon balance is:

$$\underbrace{\eta \frac{dM}{dt}}_{\text{structural mass change}} + \underbrace{\psi \eta (\sigma_L + \Gamma \sigma_R) \frac{dC}{dt}}_{\text{non-structural mass change}} = \underbrace{A(L)C}_{\text{photosynthesis}} - \underbrace{\psi \left(r_L + \sigma_L \frac{\eta}{\tau_L} \right) C}_{\text{leaf respiration and turnover}} - \underbrace{\psi \Gamma \left(r_R + \sigma_R \frac{\eta}{\tau_R} \right) C}_{\text{root respiration and turnover}} - \underbrace{\varphi C}_{\text{reproduction}} - \underbrace{\lambda C}_{\text{defense}} \quad (\text{S1.2})$$

carbon available for growth, reproduction and survival

Thus, the net amount of carbon flux per unit of crown area that the plant has left over after deducting respiration and the costs of replacing senescent leaves and fine roots is:

$$A(L) - \psi \left(r_L + \sigma_L \frac{\eta}{\tau_L} \right) - \psi \Gamma \left(r_R + \sigma_R \frac{\eta}{\tau_R} \right)$$

Gross photosynthesis and available carbon flux, for species with different A_{\max} , will look like the curves in Fig. S1. Note that available carbon at low light levels (L) decreases as high-light photosynthesis A_{\max} increases.

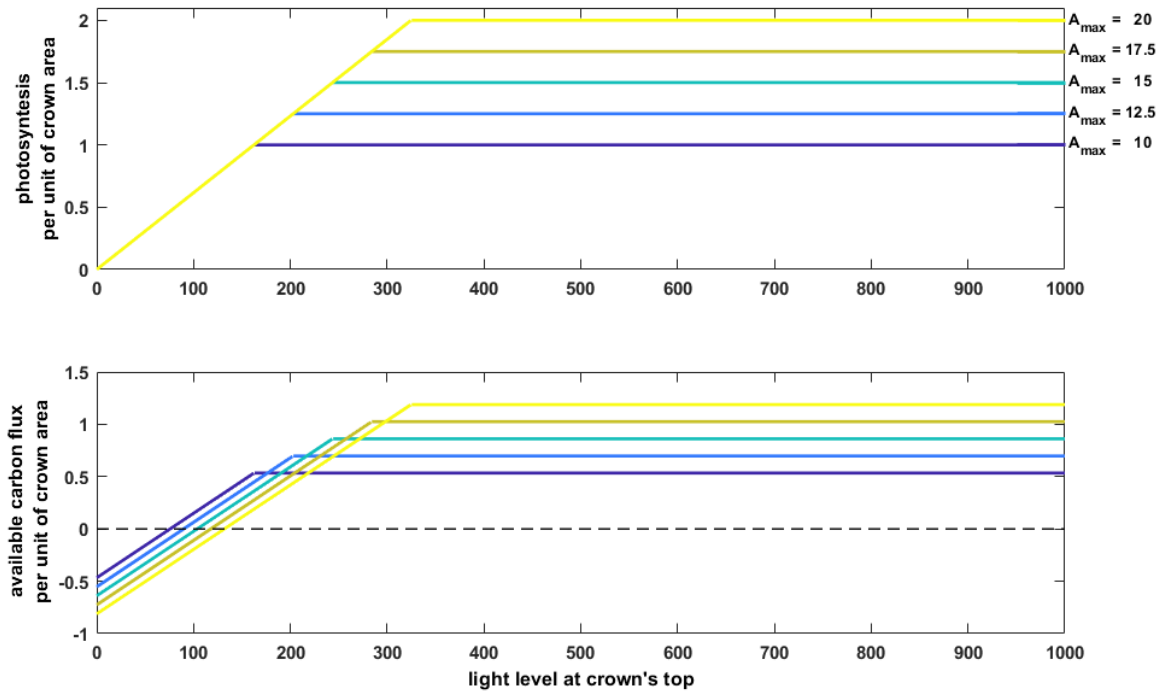


Figure S1. Photosynthesis and available carbon input as function of light level at plant crown's top for species with different photosynthetic capacity (A_{\max}). Note that a low-light photosynthesis becomes

independent on A_{\max} . Because leaf respiration is proportional to A_{\max} , at low-light species with lower A_{\max} have more available carbon.

Available carbon may be spent on growth, fecundity, or investments that increase survival, such as pathogen defense. Because suppressed understory saplings typically have negligible growth (Walters & Reich 1996) and do not set seeds, but may survive for decades, we assume that suppressed plants prioritize investments in survival over growth and reproduction. If available carbon is negative, we assume that death is instantaneous (infinite mortality rate). If available carbon is greater than zero, but less than $\lambda_{\max} C$, where λ_{\max} is the maximum that a plant will invest in survival, we assume that all available carbon is spent on survival

$$\lambda = A(L) - \psi \left(r_L + \sigma_L \frac{\eta}{\tau_L} \right) - \psi \Gamma \left(r_R + \sigma_R \frac{\eta}{\tau_R} \right)$$

and so both the left hand side of (1.2) and the investment in reproduction (φ) are zero. Finally if available carbon is greater than $\lambda_{\max} C$, then $\lambda = \lambda_{\max}$ and (1.2) gives the investments in reproduction and growth (the left hand side of the equation) and mortality is assumed to be at the background level for plants in full sun, representing death caused by unavoidable factors. The relationship between the mortality rate and the investment in survival when $\lambda < \lambda_{\max}$ is discussed below in section (1.5).

By taking the time-derivative of the mass allometry (1.1b) we have:

$$\frac{dM}{dt} = (a + b\phi_i)\beta C^{\beta-1} \frac{dC}{dt} \quad (\text{S1.3})$$

Combining (S1.2) and (S1.3) we have a differential equation for crown area:

$$\frac{dC}{dt} = \frac{A(L) - \psi \left(r_L + \sigma_L \frac{\eta}{\tau_L} \right) - \psi \Gamma \left(r_R + \sigma_R \frac{\eta}{\tau_R} \right) - \varphi - \lambda}{\psi \eta (\sigma_L + \Gamma \sigma_R) + \eta (\alpha + \beta \phi_i) a C^{\beta-1}} C \quad (\text{S1.4a})$$

which can be approximated as

$$\frac{dC}{dt} \simeq \frac{A(L) - \psi \left(r_L + \sigma_L \frac{\eta}{\tau_L} \right) - \psi \Gamma \left(r_R + \sigma_R \frac{\eta}{\tau_R} \right) - \varphi - \lambda}{\eta (a + b\phi_i) \beta} C^{2-\beta} \quad (\text{S1.4b})$$

because carbon allocated to build new non-structural biomass (i.e. new leaf and fine roots, not including the turnover of existing tissues) is much smaller than carbon allocated to structural biomass, i.e. $\psi (\sigma_L + \Gamma \sigma_R) \ll (a + b\phi_i) \beta C^{\beta-1}$, for all but the tiniest trees (Farrior et al., 2016).

Differential equation (S1.4b) has time-dependent solution:

$$C(t) = \left(C_0^{\beta-1} + \frac{G}{a+b\phi} t \right)^{\frac{1}{\beta-1}} \quad (\text{S1.5})$$

where t is age, C_0 is crown area just after germination, and:

$$G = \frac{\beta-1}{\beta\eta} \left(A - \psi \left(r_L + \sigma_L \frac{\eta}{\tau_L} \right) - \psi \Gamma \left(r_R + \sigma_R \frac{\eta}{\tau_R} \right) - \varphi - \lambda \right) \quad (\text{S1.6})$$

If initial size is negligible, we have:

$$C(t) = k t^\gamma \quad (\text{S1.7a})$$

$$H(t) = r t^\delta \quad (\text{S1.7b})$$

$$M(t) = G k t^{\gamma+1} \quad (\text{S1.7c})$$

where $k = \left(\frac{G}{a+b\phi} \right)^\gamma$, $r = \phi \left(\frac{G}{a+b\phi} \right)^{\frac{\nu}{\beta-1}}$, $\gamma = \frac{1}{\beta-1}$ and $\delta = \frac{\nu}{\beta-1}$.

S1.2 Growth out vs. growth up

In this model, species differ only by the allometric parameter ϕ . Species with larger ϕ grow faster in height, species with lower ϕ grow faster in crown area. Since $C(t)$ depends on $(a+b\phi)^{1/(1-\beta)}$, crown area decreases as ϕ increases if $\beta > 1$. For β to be equal to one, stem and branch wood mass would need to be proportional to crown area, which would cause structural failure. Recall that 5/3 is a typical value for β . In contrast, if we differentiate $H(t)$ with respect to ϕ , we find that a sufficient condition for $H(t)$ to be a decreasing function of ϕ is that $\nu < \beta - 1$. Thus, $\nu < \beta - 1$ is sufficient for k and r to be inversely related, meaning that at a species with relatively rapid height will have relatively slow crown area growth and vice versa.

S1.3 Reproduction vs. growth

In this model, species differ only by the allocation to reproduction φ . Species with higher allocation invest less in growth and *vice versa* because

$G = \frac{\beta-1}{\beta\eta} \left(A(L) - \psi \left(r_L + \sigma_L \frac{\eta}{\tau_L} \right) - \psi \Gamma \left(r_R + \sigma_R \frac{\eta}{\tau_R} \right) - \varphi - \lambda \right)$. To simplify notation, let's call

$c = A(L) - \psi \left(r_L + \sigma_L \frac{\eta}{\tau_L} \right) - \psi \Gamma \left(r_R + \sigma_R \frac{\eta}{\tau_R} \right) - \lambda$ and $m = \left(\frac{\beta-1}{\beta\eta} \frac{1}{a+b\phi} \right)^\gamma$. The tradeoff produces a negative relationship between k and φ :

$$k = m(c - \varphi)^\gamma$$

The investment in reproduction is subjected to the condition $\varphi < c$ (fecundity cannot be larger than the available carbon).

S1.4 Reproductive threshold

In the previous models, plants are assumed to be always reproductive if they have access to light. In order to explore the role of species-specific reproductive threshold, here we will also introduce a model where each species starts reproducing when it reaches a minimum crown size. All of the above section applies, except that with interspecific variation in reproductive size, φ is zero for plants of species that have a crown area less than the species-specific threshold C_R . The threshold is reached at time z , which is the time when $kz^\gamma = C_R$. After reaching its size threshold, a plant increases φ so that it equals:

$$\varphi = A(L) - \psi \left(r_L + \sigma_L \frac{\eta}{\tau_L} \right) - \psi \Gamma \left(r_R + \sigma_R \frac{\eta}{\tau_R} \right) - \lambda \quad (\text{S1.8})$$

which subsequently makes $\frac{dC}{dt} = 0$.

S1.5 Survival in the shade vs. growth in the light

In this model, species differ only by maximum photosynthesis capacity, A_{\max} , which gives a growth advantage to species with higher A_{\max} when growing in full light. Typically, a lower photosynthetic capacity implies lower leaf maintenance and turnover cost (Bouma *et al.* 1995; Noguchi & Yoshida 2008). Thus, at low-light, the lower cost allows species to spare resources to

$$r_L + \psi \sigma \frac{\eta}{\tau_L} = w A_{\max}. \text{ Let's call}$$

$$b = \psi \Gamma \left(r_R + \sigma \frac{\eta}{\tau_R} \right) + \varphi + \lambda \text{ and } m = \left(\frac{\beta - 1}{\beta \eta} \frac{1}{a + b \phi} \right)^\gamma.$$

In full light a species with $A_{\max,i}$ has a k_i equal to

$$k_i = m \left(A_{\max,i} (1 - w) - b \right)^\gamma \quad (\text{S1.9})$$

In shade, photosynthesis is independent on $A_{\max,i}$ and it can supply enough carbon only for tissues respiration and turnover and some defense λ . In shade, λ can be expressed as:

$$\lambda = A_u - w A_{\max,i} - b \quad (\text{S1.10})$$

where A_u is the photosynthesis in the understory. We assume a phenomenological function between investment in defense and mortality in the form of a simple power-law:

$$\mu_i = a \lambda^{-c} \quad (\text{S1.11})$$

Substituting (S1.10) into (S1.11) we obtain an explicit expression of mortality in the shade as function of growth in the light:

$$\mu_i = a \left[A_u - \frac{1}{1-w} b - \frac{w}{1-w} \left(\frac{k_i}{m} \right)^{1/\gamma} \right]^{-c} \quad (\text{S1.12a})$$

which can be expressed in a more compact form as

$$\mu_i = \mu_0 \left(1 - (k_i / k_+)^{1/\gamma} \right)^{-c} \quad (\text{S1.12b})$$

(S1.12b) can also be used with the other three tradeoffs, in which all plants have the same A_{\max} , although this is moot because it is equivalent to assume an understory mortality rate common to all species and assume that investments in understory survival are folded into leaf and fine root respiration costs.

Incidentally, investment in survival may provide the solution to the modeling puzzle of understory plant survival. If canopy trees increase LAI until leaf construction and respiration costs are exactly balanced by carbon gain, then why are leaves at the top of the understory productive? An answer may be that leaves at the bottom of the canopy also cover investments in survival, which means

that leaves at the top of the understory have sufficient carbon to cover leaf and fine construction respiration costs. They simply have less carbon available for survival, and so suffer the observed higher mortality.

S1.6. Annual Plants

We can use a simpler carbon balance than the one in the forest model, because annual plants reproduce once, and their structural tissues, leaves and fine roots all typically live until the whole plant reproduces and dies, whereas trees reproduce continuously and their leaves and fine roots are regularly replaced. We assume the same allometries used in the forest model, but now interpret the carbon mass, M , as total plant carbon mass (Hutchings 1975). Then, the carbon balance is simply:

$$A_{net}(L) = A(L) - \psi r_L - \psi \Gamma r_R = \eta \frac{dM}{dC} \frac{1}{C} \frac{dC}{dt} = (a + b\phi_i)\eta\beta C^{\beta-2} \frac{dC}{dt} \quad (S1.13)$$

which rearranges to the differential equation:

$$\frac{dC}{dt} = \frac{A_{net}(L)C^{2-\beta}}{(a + b\phi_i)\eta\beta} \quad (S1.14)$$

with solution as (S1.5), where $G(L) = \frac{\beta-1}{\eta\beta} A_{net}(L)$, and so $C(t)$, $H(t)$ and $M(t)$ can still be expressed by (S1.7).

The light intensity should be set to a value for full sun for annuals in the canopy, and to the understory level (i.e., Beer's Law evaluated at the canopy LAI) for the case in which understory plants are still able to grow. Note that this system is nitrogen-limited (Going *et al.* 2009), and so canopy plants should have insufficient nitrogen to deploy the optimal LAI, which should allow positive net carbon gain in the understory. A plant's end of life fecundity can be any allometric function of its final size (Niklas & Enquist 2003). We present results in which plant fecundity is proportional to final mass and final crown area.

S1.7. Breaking the Size Hierarchy

Here we introduce a random variable that multiplies time instead of k_i and r_i in equations (S1.7) and that disrupts the size hierarchy. Why is that? We think of the random variable (an environmental factor or phenotypic variability) as a multiplicative factor that reduces a plant's net carbon gain, so that in the annuals model, a plant's actual net carbon gain is $A_{net}(L)\omega$ instead of simply $A_{net}(L)$. After substituting $A_{net}(L)\omega$ for $A_{net}(L)$ into (S1.14) the solutions for $C(t)$, $h(t)$ and $M(t)$ above, we obtain:

$$C(\omega, t) = k_i(\omega t)^\gamma \quad (S1.15a)$$

$$H(\omega, t) = r_i(\omega t)^\delta \quad (\text{S1.15b})$$

$$M(\omega, t) = Gk_i(\omega t)^{\gamma+1} \quad (\text{S1.15c})$$

ω does not change during the life of an individual. The same argument also holds for the forest model. We treat ω as a positive random variable, species-independent, bounded between ω_{\min} and ω_{\max} with probability $P(\omega)$.

S2. Community dynamic model

S2.1 Hierarchical structure

The Perfect Plasticity Approximation (PPA) specifies which plants remain in the canopy as they grow and overtop one another, if crown growth is sufficiently plastic and if crowns have relatively flat tops (Strigul *et al.* 2008). According to the PPA, the threshold height that separates overstory from understory is determined by the following equations:

$$\begin{cases} \sum_{i=1}^S \int_{H^*(t)}^{\infty} N_i(H, t) C(H) dH = 1 & \text{if } \sum_{i=1}^S \int_0^{\infty} N_i(H, t) C(H) dH \geq 1 \\ H^*(t) = 0 & \text{otherwise} \end{cases} \quad (\text{S2.1})$$

Because of Ecosystem Demography, ED, and the PPA, the size-structured population densities in our model can be thought of as *ensemble means* from a stochastic and spatial individual-based model with the same individual growth and death rates and an appropriate initial condition like a random scattering of seeds (Moorcroft *et al.* 2001, Strigul *et al.* 2007). The population density, $N_i(H, t)$, of species- i individuals of height H at time t in our model approximates the following ensemble mean. Imagine randomly placing a quadrat at time t in a stochastic simulation with a spatial domain of size L^2 . If the quadrat is sufficiently small, then it will contain at a Bernoulli random variable whose value is one if it contains at least one individual of species- i and height between H and $H+\Delta$, and zero otherwise. The density $N_i(H, t)$ approximates the mean of this Bernoulli random variable divided by the product of Δ and the quadrat's area, and in the limit Δ become small (Moorcroft *et al.* 2001, Strigul *et al.* 2007):

$$N_i(H, t) = \lim_{\Delta \rightarrow 0} \frac{n_i(t)}{L^2} \frac{\Pr(H \leq h < H + \Delta)}{\Delta} \quad (\text{S2.2})$$

where $n_i(t)$ is the total number of individuals of species i at time t , and $\Pr(H \leq h < H + \Delta)$ is the probability that an individual has a height between H and $H+\Delta$. Because the monotonic allometry, $N_i(H, t)$ can be expressed as a function of any other plant dimension.

We consider a system of S species distributed along a continuum of growth life strategies ranked $i = 1, 2, \dots, S$. Height defines the rank of the individuals and it is determined by the species parameter r_i , a random factor ω and an allometric exponent δ . Across species, individuals with higher r overtop individuals of species with lower r , ω being equal. Within each species, the bigger an individual's ω , the taller it is. Thus, two individuals of different species, i and j , can have the same rank if

$$\omega_j = x_{ij}\omega_i \quad \omega_{\min} \leq x_{ij}\omega_i \leq \omega_{\max} \quad (\text{S2.3})$$

where $x_{ij} = \left(\frac{r_i}{r_j}\right)^{1/\delta} = \left(\frac{\phi_i}{\phi_j}\right)^{1/\delta} \frac{G_i}{G_j} \frac{a+b\phi_j}{a+b\phi_i}$. If $x_{ij}\omega > \omega_{\max}$, species- i individuals with ω overtop all the species- j individuals.

Initially, in a newly formed gap or at the beginning of the growing season, the density of individuals of each species is n_i ($i = 1, 2, \dots, S$). The canopy will close first when the sum of all crowns equals one (the time t_2 in the illustration in Fig. S2). Immediately after, individuals of all species are continually overtopped and fall into the understory, where they become frozen in size. At any given time, the smallest (lowest rank) individuals in the canopy are the ones about to fall into the understory because of the continued growth of their taller competitors. The individuals of species i with ω falls in the understory at the time $t_i(\omega)$, which corresponds to the time when the sum of the crown area of all the individuals with higher rank equal one:

$$t_i(\omega) = \left(\sum_{j \in x_{ji}\omega_{\max} \geq \omega} n_j k_j E[\omega'^\gamma \mid \omega' \geq x_{ji}\omega] \right)^{-1/\gamma} \quad (\text{S2.4})$$

where $E[\omega'^\gamma \mid \omega' \geq x_{ji}\omega]$ is the conditional expectation of ω^γ , i.e. $\int_{\max(\omega_{\min}, x_{ji}\omega)}^{\omega_{\max}} \omega'^\gamma P(\omega') d\omega'$. In

(S2.4), the summation is carried out only for species that have a maximum rank equal or higher than the focal individual, i.e. $r_j^{1/\delta} \omega_{\max} \geq r_i^{1/\delta} \omega$, which means they are still in the canopy while species i is folding into the understory. The species i will be completely folded in the understory at time $t_i(\omega_{\max})$.

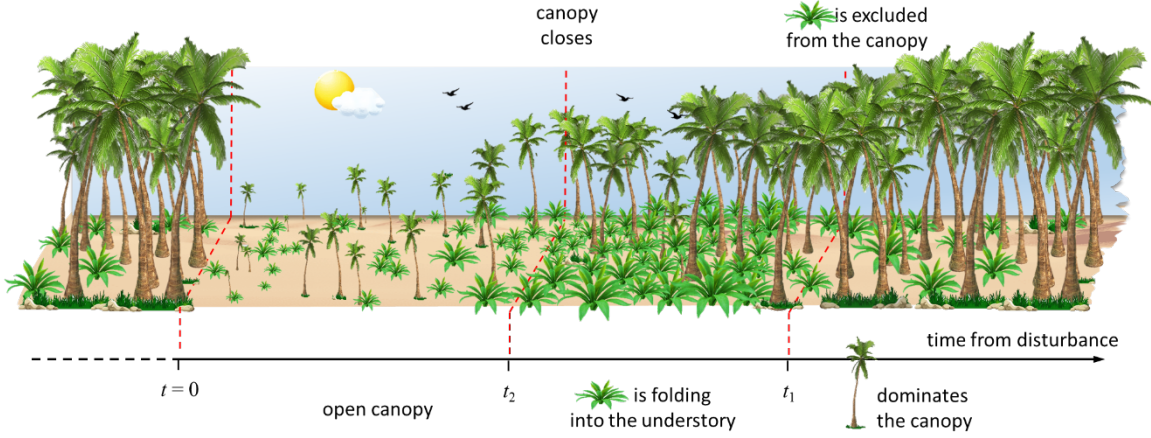


Figure S2. Illustration of light competition between two species with different allocations to primary and secondary growth. At early succession, the rosette species expands rapidly. At time t_2 , the canopy closes, and the rosettes start folding into the understory. At time t_1 , the palms occupy the whole canopy and the rosettes are entirely in the understory.

S2.2. Forest Mosaic

In this representation, space is divided into cells (patches), shading within but not between cells, and density-independent canopy mortality is replaced by per-cell disturbance that kills all trees except seeds and seedlings (Moorcroft *et al.* 2001). The cells interact only through seeds dispersal as the seeds produced in each cell are equally distributed among the cells. Reproductive individuals continuously produce seeds proportionally to their crown area and disperse them uniformly across the mosaic. The seeds can either stay in the soil and wait for a disturbance to germinate, or germinate and remain in the seedling stage in the understory, where they can survive and eventually start growing when the patch opens. A general expression for the number of species- i recruits in the newly formed patches, $N_i(C_0, 0, T)$ with initial size C_0 at any time T , can be given by

$$N_i(C_0, 0, T) = p_{g,i} \int_{z_i}^{\infty} p(t) \int_{C_{R,i}}^{C_i(\omega_{\max} t)} n_{s,i} \varphi_i C \int_0^T N_i(C, t, T') p_{s,i}(T - T') dT' dC dt \quad (S2.5)$$

where $p_{g,i}$ is the germination probability, $p(t)$ is the patch-age distribution, $n_{s,i}$ is the number of seeds per unit of carbon, $N_i(C, t, T')$ is the density of reproductive individuals with crown C in the patch of age t at time T' , φ_i is the per capita fecundity rate of an individual with crown C and $p_{s,i}(T - T')$ is the seed or seedling survival probability between T' and T .

Recall that the crown area of an individual at time t with ω has the form $C_i(\omega, t) = k_i(\omega t)^\gamma$

$C_i(\omega_{\max}, z_i) = C_{R,i}$ and $C_i(\omega_{\max} t)$ is the maximum size reached in a patch of age t by species i . The first nested integral is carried out for all the reproductive individuals in a given age patch. The second nested integral is carried out across the past time before T that contributed to seed accumulation in the soil or seedling pool in the understory.

At equilibrium, we can remove the dependence on T from n_i and N_i and simplify (2.3) as

$$N_i(C_0, 0) = \int_{z_i}^{\infty} p(t) \int_{S_{R,i}}^{C_i(\omega_{\max} t)} F_i C_i(t) N_i(C, t) dC dt \quad (S2.6)$$

where $F_i = \lim_{T \rightarrow \infty} p_{g,i} n_{s,i} \varphi_i \int_0^T p_{s,i}(T - T') dT'$ is the expected number recruits generated by an individual of per unit of crown area. In a patch of a given age t , a fraction of species- i individuals will be alive in the canopy, while others will be folded in the understory and do not contribute to reproduction. The value of ω for the species- i individuals at the time they fall into the understory is $\omega_i(t)$, the inverse of (S2.4). $\omega_i(t)$ determines which individuals are still in the canopy and which are in the understory. By a change of the integration variable $C \rightarrow \omega$, we can express:

$$N_i(C, t) dC = n_i u(\omega - \omega_i(t)) P(\omega) d\omega \quad (S2.7)$$

where u is the step function, and (S2.6) becomes:

$$N_i(C_0, 0) = \int_{z_i}^{t_i(\omega_{\max})} p(t) \int_{\omega_i(t)}^{\omega_{\max}} n_i F_i C_i(\omega t) P(\omega) d\omega dt \quad (S2.8)$$

The first integral in (S2.8) is carried out for patches where species i is still present in the canopy, i.e. for patches with age less than $t_i(\omega_{\max})$. The nested integral is carried out for a fraction of individuals of species i that are still in the canopy in the patch of age t , i.e., individuals with $\omega > \omega_i(t)$.

In order to integrate (S2.8), the integral needs to be split into intervals over which $t_i(\omega)$ depends on a fixed number of species:

$$N_i(C_0, 0) = \sum_{k=i}^s \int_{t_{k+1}(\omega_{\max})}^{t_k(\omega_{\max})} p(t) \int_{\omega_i(t)}^{\omega_{\max}} n_i F_i C_i(\omega t) P(\omega) d\omega dt \quad (S2.9)$$

and $t_{s+1} = 0$.

S2.3. Community of annual plants

In the system of annual plants, seeds produced in the previous year germinate at the beginning of the new growing season (as before we neglect initial age difference among individuals). Each plant grows until it remains in the canopy. After that time, the plant stops growing and turns its biomass into seeds. the ED approximation is not needed here, because there are no disturbances that reset a portion of the system back to the beginning of succession. In the annual system, the end of the growing season resets the entire system back to the beginning of succession every year. The number of individuals of species i in the next season, $T+1$, follows an annual plant dynamic:

$$n_{i,T+1} = \int_{t_i(\omega_{\min})}^{t_i(\omega_{\max})} F_i s(\omega_i(t)t) n_{i,T} \frac{dq_{i,T}}{dt} dt \quad (S2.10)$$

where F_i is the number of germinating seeds produced by an individual function of its size $s(\omega_i(t)t)$ (mass or crown) at the time it falls into the understory, i.e. when ω equals to $\omega_i(t)$. $dq_{i,T} / dt$ is the proportion of individuals that fall into the understory per unit of time.

If $t_i(\omega_{\max}) > t_f$ some species- i individuals survive in the canopy until the end of the season, t_f , while others continue to fall into the understory. For these species, the dynamic equation is modified to take into account the reproductive contribution of the individuals in the canopy at the end of the season:

$$n_{i,T+1} = \int_{t_i(\omega_{\min})}^{t_f} F_i s(\omega_i(t)t) n_{i,T} \frac{dq_{i,T}}{dt} dt + n_{i,T} \int_{\omega_i(t_f)}^{\omega_{\max}} P(\omega) F_i s(\omega t_f) d\omega \quad (S2.11)$$

The individuals of species i that fall into the understory per unit of time is given by:

$$\frac{dq_{i,T}}{dt} = -P(\omega_i(t)) \frac{d\omega_i(t)}{dt} \quad (S2.12)$$

Plugging (S2.12) into (S2.10) and changing integration variables $t \rightarrow \omega$, we obtain:

$$n_{i,T+1} = \int_{\omega_{\min}}^{\omega_{\max}} n_{i,T} F_i[\omega, t_i(\omega)] P(\omega) d\omega \quad (S2.13)$$

As before, in order to integrate (S2.13), the integral needs to be split into intervals over which $t_i(\omega)$ depends on a fixed number of species:

$$n_{i,T+1} = \int_{\omega_{\min}}^{X_{m+1} \omega_{\max}} n_{i,T} F_i[\omega, t_i(\omega)] P(\omega) d\omega + \sum_{k=m+1}^i \int_{X_{k-1} \omega_{\max}}^{X_k \omega_{\max}} n_{i,T} F_i[\omega, t_i(\omega)] P(\omega) d\omega \quad (S2.14)$$

where m is the number of species that is still present in the canopy at the time species i starts folding into the understory. For the species that are still present in the canopy at t_f , the

S2.11). At equilibrium, we can drop the dependence on T ($n_{i,T+1} = n_{i,T}$). The model can be easily modified to incorporate seed dormancy, i.e. seeds that stay in the soil for multiple seasons before germinate, as:

$$n_{i,T+1} = \sum_{j=1}^m p_{d,j} \int_{\omega_{\min}}^{\omega_{\max}} n_{i,T+1-j} F_i s[\omega, t_i(\omega)] P(\omega) d\omega \quad (\text{S2.15})$$

where $p_{d,j}$ is the probability that a seed stays dormant until the j^{th} season. At equilibrium $n_{i,T+1} = n_{i,T} = n_{i,T-1} = \dots = n_{i,T-m}$, and the model reduces to the case without dormancy because by definition $\sum_{j=1}^m p_{d,j} = 1$.

S3. Strict hierarchy

S3.1. Forest mosaic

We consider here the case of the light competition model in the absence of random environmental factors, so the species hierarchy is entirely determined by species strategy (either r or k).

The species i starts folding in the understory when $\sum_{j=1}^i n_j C_j(t) = 1$ and goes entirely in the understory when $\sum_{j=1}^{i-1} n_j C_j(t) = 1$, i.e. when the sum of the crown area of the species with higher rank equal one. The time species i closes the canopy is given by:

$$t_i = \left(\sum_{j=1}^i n_j k_j \right)^{-1/\gamma} \quad (\text{S3.1})$$

Thus, the fraction of individuals of species i still in the canopy is:

$$q_i(t) = \begin{cases} 1 & t \leq t_i \\ \frac{1 - \sum_{j=1}^{i-1} n_j C_j(t)}{n_i C_i(t)} & t_i < t \leq t_{i-1} \\ 0 & t > t_{i-1} \end{cases} \quad (\text{S3.2})$$

Assuming fecundity proportional to the crown area, no reproductive threshold, and a patch-age distribution $p(t)$, the number of individuals in the forest mosaic is:

$$n_i = F \int_0^{t_{i-1}} p(t) n_i q_i(t) C_i(t) dt \quad (\text{S3.3})$$

the above integral can be split into two parts, from 0 to t_i , when all individuals are in the canopy, and from t_i to t_{i-1} , when individuals keep folding in the understory

$$n_i = n_i F \int_0^{t_i} p(t) C_i(t) dt + F \int_{t_i}^{t_{i-1}} p(t) \left(1 - \sum_{j=1}^{i-1} n_j C_j(t)\right) dt \quad (\text{S3.4})$$

by substituting $C_j(t) = k_j t^\gamma$, $\sum_{j=1}^i n_j k_j = t_i^{-\gamma}$ and $\sum_{j=1}^{i-1} n_j k_j = t_{i-1}^{-\gamma}$ we have:

$$n_i = (t_i^{-\gamma} - t_{i-1}^{-\gamma}) F \int_0^{t_i} p(t) t^\gamma dt + F \int_{t_i}^{t_{i-1}} p(t) (1 - t_{i-1}^{-\gamma} t^\gamma) dt \quad (\text{S3.5})$$

after some algebraic manipulations we obtain

$$n_i = F \int_0^{t_{i-1}} p(t) (1 - t_{i-1}^{-\gamma} t^\gamma) dt - F \int_0^{t_i} p(t) (1 - t_i^{-\gamma} t^\gamma) dt \quad (\text{S3.6})$$

Finally, we can write (S3.6) in a more compact way as

$$n_i = F (W(t_{i-1}) - W(t_i)) \quad (\text{S3.7a})$$

where

$$W(t_i) = \int_0^{t_i} p(t) (1 - (t/t_i)^\gamma) dt \quad (\text{S3.8})$$

Species 1 never goes entirely in the understory and the budget equation is modified as follow

$$n_i = F \int_0^{t_i} p(t) n_i C_1(t) dt + F \int_{t_i}^{\infty} p(t) dt \quad (\text{S3.9})$$

Using the same simplifications above we obtain

$$n_1 = F (1 - W(t_1)) \quad (\text{S3.7b})$$

As an example, we consider the case of a asynchronous periodic disturbance that leads to a uniform patch age distribution with a fixed interval across disturbances equal to t_0 :

$$n_i = F \int_0^{t_i} \frac{1}{t_0} n_i q_i(t) C_i(t) dt \quad (\text{S3.10})$$

By solving the integrals in (S3.7a) and (S3.7b), we obtain:

$$n_i = F \frac{\gamma}{\gamma+1} \frac{t_{i-1} - t_i}{t_0} \quad (\text{S3.11a})$$

$$n_1 = F \frac{\gamma}{\gamma+1} \frac{t_0 - t_1}{t_0} + F \frac{1}{\gamma+1} \quad (\text{S3.11b})$$

S3.2. Annual plants

For the annual plants, we need to compute the density of individuals per unit of time at which species i falls into the understory by differentiating $\sum_{j=1}^i n_j q_j(t) C_j(t) = 1$ with respect of time

$$n_i \frac{dq_i}{dt} = \frac{1}{C_i} \sum_{j=1}^i n_j q_j(t) \frac{dC_j}{dt} \quad t_i < t < t_{i-1} \quad (\text{S3.12})$$

The number of offspring produced by species i in the next season is then:

$$n_{i,T+1} = F \int_{t_i}^{t_{i-1}} M_i(t) n_{i,T} \frac{dq_i}{dt} dt \quad (\text{S3.13})$$

by inserting (S3.12) into (S3.13) and noticing that $\sum_{j=1}^i n_j q_j(t) dC_j / dt = \gamma t^{-1}$ and from (S1.7a) and (S1.7c) that $M_i / C_i = Gt$, we solve the integral as:

$$n_i = \gamma F G (t_{i-1} - t_i) \quad i > 1 \quad (\text{S3.14a})$$

(we remove the sub index T assuming steady state, i.e. $n_{i,T+1} = n_{i,T}$). At equilibrium, only species-1 remains in the canopy at the end of the season:

$$n_1 = \gamma F G (t_0 - t_1) + F G t_0 \quad (\text{SS3.14b})$$

Note that (S3.14) are identical to (S3.11), except for a constant. We also consider the case of fecundity proportional to crown area. Following the same procedure we find

$$n_i = F \gamma (\ln t_{i-1} - \ln t_i) \quad i > 1 \quad (\text{S3.15a})$$

$$n_1 = F \gamma (\ln t_1 - \ln t_0) + F \quad (\text{S3.15b})$$

It is possible to show that the solutions (S3.15) can be derived from (S4.3), in the limit $\theta \rightarrow \infty$ by noticing that

$$\lim_{\theta \rightarrow \infty} x_{ij}^{\theta+\gamma} = \begin{cases} 0 & i < j \\ 1 & i = j \\ \infty & i > j \end{cases}$$

S3.3. Conditions for establishment, continuous species-density curve and species richness

In an equilibrium community of coexisting species, k are random variables defined as

$$k_i = k_{i-1}^* + \xi_i \quad k_{\min} \leq k_i \leq k_{\max} \quad (\text{S3.16})$$

where k_{i-1}^* sets the limit for the establishment of the i^{th} species. The condition for the establishment is the minimum value of k that allows invasion into a resident community of $(i-1)$ taller species, and must ensure that that invading species has a lifetime reproductive success of

one when rare. This condition is found from $-F \frac{dW(t_i)}{dn_i} \Big|_{n_i=0} = 1$ for forest or $\frac{dn_{i,T+1}}{dn_{i,T}} \Big|_{n_{i,T}=0} = 1$ for

annual plants. In the case of periodic disturbance, the condition for the establishment of species i , can be expressed as:

$$k_{i-1}^* = k_0 \left(\frac{t_0}{t_{i-1}} \right)^{\gamma+1} \quad (\text{S3.17})$$

where k_0 is the minimum value of k that allows a species to successfully colonize an empty patch given the temporal horizon t_0 , and must insure that each individual has a lifetime reproductive success equal to one. For the forest mosaic with periodic disturbance and for the annual plants, this is equivalent to say that the canopy will close exactly at final time. Inserting $t_1 = t_0$ in (S3.11b) gives $n_0 = F / (\gamma + 1)$. Consequently $k_0 = (\gamma + 1) / (F t_0^\gamma)$ (see table 3.1 for other cases). Generally, a longer season and higher fecundity promote smaller k_0 , i.e. late-succession strategies that favor height growth. An important property of the system is that the condition for establishment of the i^{th} species, Eq. (S3.17), is uniquely determined by the closing time of the $(i-1)^{\text{th}}$ species.

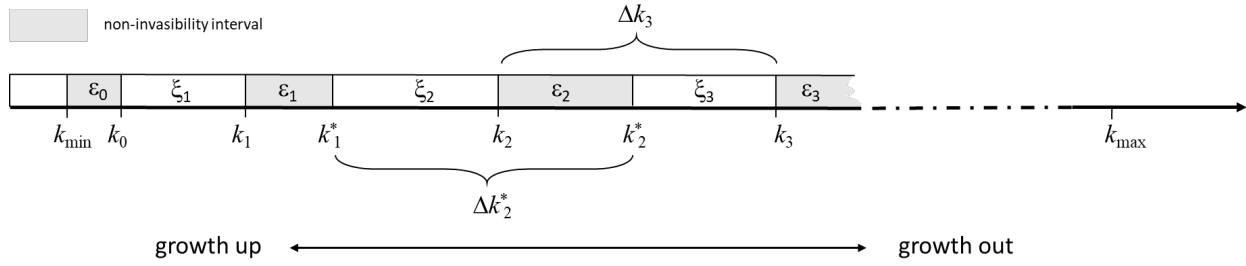


Figure S3. The strategy axis illustrates the strict hierarchy of light competition. The axis stretches from k_0 , the minimum value of k that can persist, to k_{\max} , the maximum value that is allowed by biological constraints on primary and vegetative allocation. Strategies on the left invest more in height, strategies on the right invest more in crown area. Under strict hierarchy, species with lower k overcast species with higher k . The non-invasibility intervals (ε) define the strategies that cannot invade given a resident community of species with lower k . ξ are independent exponential random variables with rate $(k_{\max} - k_{\min})/(S-1)$, where S is number of available strategies. As S increases both, ε and ξ decrease, allowing coexistence of an infinite number of species.

We assume that the possible strategies are random variables uniformly distributed in the interval $k_{\min} - k_{\max}$, the minimum and maximum values that are allowed by allometric constraints on primary and vegetative allocation. With this assumption, in (S3.16) ξ is an exponential random variable with expectation $\lambda = (k_{\max} - k_{\min}) / (S+1)$ with S is the total number of available strategies.

The difference $\varepsilon_i = k_i^* - k_i$ is another random variable that defines a non-invasibility interval, where any invasive strategy has pro capita recruitment less than one (Fig. S3). The interval between strategies is then:

$$\Delta k_i = k_i - k_{i-1} = \varepsilon_{i-1} + \xi_i \quad (\text{S3.18})$$

by noticing that $\varepsilon_i = k_i^* - k_{i-1}^* + \xi_i$, it follows that the expected value of ε and ξ are identical and equal to λ , so the expected value of Δk is 2λ , except for Δk_1 , because the first species has a different equilibrium solution. With these considerations, we can now predict the expected number of coexisting species S_c given the total number of species in the initial pool S :

$$S_c = 2(S+1) \frac{k_{\max} - \bar{k}_1^*}{k_{\max} - k_{\min}} + 1 \quad (\text{S3.19})$$

where \bar{k}_1^* is the expected value of k_1^* when $k_1 = k_0 + \lambda$ obtained from (S3.17) and (S3.11b). Fig S4 shows the analytical solution against simulations.

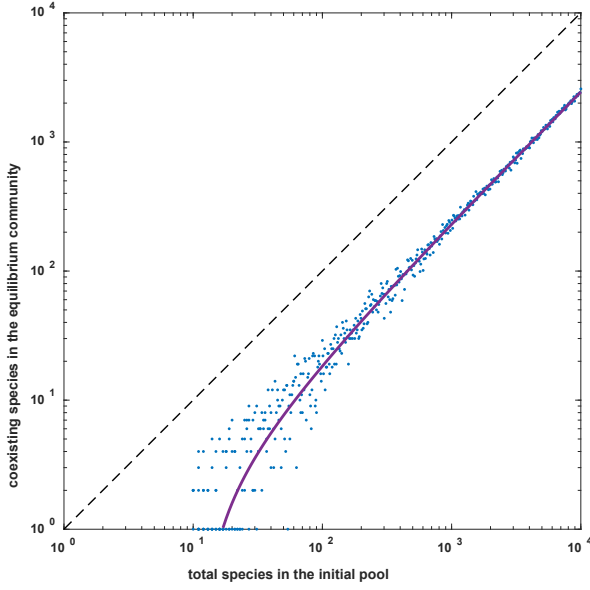


Figure S4. Simulated and predicted number of coexisting species as function of the total number of species in the initial pool using a forest mosaic model with periodic disturbance. The strategies k of initial pool are assumed to be uniformly distributed in the interval $0-k_{\max}$. Analytical solution is given in (S3.19).

As S increases, Δk decreases, allowing packing a large number of species. In the limit $S \rightarrow \infty$, $\Delta k \rightarrow 0$. This suggests that we can pass to a continuous function along k , by taking small intervals Δk , e.g. from (S3.7a)

$$\frac{n_i(k_i)}{\Delta k} = F \frac{W[t(k_i - \Delta k)] - W[t(k_i)]}{\Delta k} \quad (\text{S3.20})$$

By taking the limit of (S3.20) for $\Delta k \rightarrow 0$ we obtain:

$$n(k) = -F \frac{dW(t)}{dt} \frac{dt}{dk} \quad (\text{S3.21})$$

where $\frac{dW(t)}{dt} = \gamma t^{-(\gamma+1)} \int_0^t p(t') t'^{\gamma} dt'$. Also, in the limit $\Delta k \rightarrow 0$, we can write the summation in (S3.1) as an integral

$$t(k) = \left(\int_{k_0}^k n(k') k' dk' + n_0 k_0 \right)^{-1/\gamma} \quad (\text{S3.22})$$

Differentiating (S3.22) in respect to k and rearranging

$$n(k) = -\frac{\gamma}{k} \frac{1}{t^{\gamma+1}} \frac{dt}{dk} \quad (\text{S3.23})$$

and combining this result with (S3.21), we obtain:

$$Fk \int_0^{t(k)} p(t') t'^{\gamma} dt' = 1 \quad (\text{S3.24})$$

Note that the LHS of (S3.24) is the lifetime reproductive success of the k -strategy. Finally $n(k)$ can be obtained by expressing t and dt/dk as function of k from (S3.24), and combining with (S3.23). For example, in the case of periodic disturbance we obtain:

$$n(k) = \frac{\gamma}{\gamma+1} \left(\frac{n_0}{t_0} \right)^{\frac{\gamma}{\gamma+1}} k^{-\frac{\gamma+2}{\gamma+1}} \quad (\text{S3.25})$$

Similarly, for the annual plant with fecundity proportional to crown we obtain

$$n(k) = n_0 k^{-1} \quad (\text{S3.26})$$

The continuous limit also suggests that, by normalizing the species abundance by a proper Δk , the discrete abundances might collapse to the continuous solution. The proper Δk interval can be deduced from Fig. S3. Fig. S3 shows that k_2 is bounded by two limits, k_1^* , which is the minimum k for species 2 to establish, and k_2^* , which is the minimum k for species 3 to establish. If k_2 was exactly at k_1^* , its abundance would be zero because as an invader, it would have LRS of 1. As k_2 increases, the equilibrium abundance increases and, consequently, the non-invasibility interval k_2^* , i.e. it will be more difficult for a species 3 to invade given the condition (3.17). It can be shown that $k_i^* - k_{i-1}^*$ is the exact normalization using the case of annual plants with fecundity proportional to crown area, because from Table 3.1

$$k_i^* - k_{i-1}^* = \frac{t_{i-1}^{-\gamma} - t_i^{-\gamma}}{F} = \frac{\sum_{j=1}^i n_j k_j - \sum_{j=1}^{i-1} n_j k_j}{F} = \frac{n_i k_i}{F}$$

thus, by normalizing n_i by $k_i^* - k_{i-1}^*$ we obtain the continuous solution (S3.26). For the case of forest with fecundity proportional to crown area, we can Taylor expand for $k_i^* - k_{i-1}^*$ around $n_i = 0$, which gives:

$$k_i^* - k_{i-1}^* \simeq \frac{\gamma+1}{\gamma} k_0 \frac{t_0^{\gamma+1}}{t_i} k_i n_i$$

by using the relationship $Fk_i \frac{t_i^{\gamma+1}}{t_0} = 1$, which is valid for $n_i = 0$ we obtain

$$k_i^* - k_{i-1}^* \simeq \frac{\gamma+1}{\gamma} k_0 t_0^{\gamma+1} \left(\frac{t_0}{F} \right)^{\frac{1}{\gamma+1}} k_i^{-\frac{\gamma+2}{\gamma+1}} n_i$$

thus, by normalizing n_i by $k_i^* - k_{i-1}^*$ we obtain the continuous solution (S3.25). Although this is exact only around $n_i = 0$, it proves to be a highly accurate approximation.

S3.4 Stability analysis for the annual plant system

The annuals model can be expressed as a discrete-time amensalistic dynamical system

$$n_{i,T+1} = F_i(n_{1,T}, n_{2,T}, \dots, n_{i,T}) \quad (\text{S3.27})$$

The amensalism implies the Jacobian is a lower triangular matrix

$$J = \begin{vmatrix} \frac{dF_1}{dn_1} & 0 & \dots & 0 \\ \frac{dF_2}{dn_1} & \frac{dF_2}{dn_2} & \dots & 0 \\ \dots & \dots & \dots & \dots \\ \frac{dF_S}{dn_1} & \frac{dF_S}{dn_2} & \dots & \frac{dF_S}{dn_S} \end{vmatrix} \quad (\text{S3.28})$$

Local stability equilibrium requires that the eigenvalues, λ_i , of J at the equilibrium point $|\lambda_i| < 1$ (recall that for a triangular matrix the eigenvalues are the diagonal entries).

The eigenvalues around the equilibrium points can be computed from (S3.14)

$$\lambda_i = \frac{dF_i}{dn_i} = -\gamma FG \frac{dt_i}{dn_i} = FG k_i t_i^{\gamma+1} \quad (\text{S3.29})$$

The condition for establishment we derived earlier says that

$$k_i > k_0 \left(\frac{t_0}{t_{i-1}} \right)^{\gamma+1} \quad (\text{S3.30})$$

where $k_0 = \frac{1}{FG t_0^{\gamma+1}}$. Plugging (S3.30) into the expression for λ_i , we obtain

$$\lambda_i = \left(\frac{t_i}{t_{i-1}} \right)^{\gamma+1} < 1 \quad (\text{S3.31})$$

because $t_{i-1} > t_i$. For any $k_i > k_0 \left(\frac{t_0}{t_{i-1}} \right)^{\gamma+1}$, we notice that $FGk_i t_i^{\gamma+1}$ is the LRS of the first individuals of species- i that falls into the understory ($Gk_i t_i^{\gamma+1}$ is the mass at the time is overtopped and F is the fecundity per unit of mass). Because the average LRS at equilibrium must be one, it means that some individuals (these who fall in the understory first), must have $\text{LRS} < 1$, while others (these who fall later) must have $\text{LRS} > 1$. This argument ensures that

$$0 < \lambda_i < 1 \quad (\text{S3.32})$$

The local equilibrium is then stable and the convergence to the steady-state equilibrium is monotonic.

S3.5. A family of analytically tractable patch-age distributions

In order to obtain analytical solutions for the continuous species density curve, the equation $-F \frac{dW(t(k))}{dt} = 1$ needs to be invertible to express t as function of k . If we take the disturbance rate in the form:

$$m(t) = -\frac{1}{p(t)} \frac{dp}{dt} = c(\gamma+1) \frac{t^\gamma}{b+t^{\gamma+1}} \quad (\text{S3.33})$$

the patch-age distribution is

$$p(t) = p(0) \left(\frac{b}{b+t^{\gamma+1}} \right)^c \quad (\text{S3.34})$$

and the distribution of the disturbance intervals

$$\frac{1}{p(0)} \frac{dp}{dt} = (\gamma+1) \frac{c}{b} \left(\frac{b}{b+t^{\gamma+1}} \right)^{c+1} t^\gamma \quad (\text{S3.35})$$

where the constant $p(0)$ is

$$p(0) = \frac{\gamma+1}{b^{\frac{1}{\gamma+1}}} \frac{\Gamma(c)}{\Gamma\left(\frac{1}{\gamma+1}\right) \Gamma\left(c - \frac{1}{\gamma+1}\right)} \quad (\text{S3.36})$$

we can solve analytically the integral for lifetime reproductive success in (S3.24) as

$$\frac{Fkp(0)b}{(c-1)(\gamma+1)} \left[1 - \left(\frac{b}{b+t(k)^{\gamma+1}} \right)^{c-1} \right] = 1 \quad (\text{S3.37})$$

The moments of the distribution can also be computed analytically. The k^{th} -moment is given by

$$M_k = b^{\frac{k}{\gamma+1}} \frac{\Gamma\left(\frac{k+1}{\gamma+1}\right) \Gamma\left(c - \frac{k+1}{\gamma+1}\right)}{\Gamma\left(\frac{1}{\gamma+1}\right) \Gamma\left(c - \frac{1}{\gamma+1}\right)} \quad (\text{S3.38})$$

In order to obtain the continuous species density curve we need express t and dt/dk as function of k . From above we have

$$t(k)^{\gamma+1} = b \left(\frac{k}{k-k_0} \right)^{\frac{1}{c-1}} - b \quad (\text{S3.39a})$$

$$\frac{dt}{dk} = -\frac{1}{k^2} \frac{k_0 b^{\frac{1}{\gamma+1}}}{(\gamma+1)(c-1)} \left[\left(\frac{k}{k-k_0} \right)^{\frac{1}{c-1}} - 1 \right]^{\frac{\gamma}{\gamma+1}} \left(\frac{k}{k-k_0} \right)^{\frac{c}{c-1}} \quad (\text{S3.39b})$$

where $k_0 = \frac{(c-1)(\gamma+1)}{Fp(0)b}$. By combining (S3.39) with the derivative of the closure time expression in (S3.23), after some algebraic manipulations, we found

$$n(k) = \frac{\gamma}{k^2} \frac{k_0}{k} \frac{b^{\frac{\gamma}{\gamma+1}}}{(\gamma+1)(c-1)} \left[\left(\frac{k}{k-k_0} \right)^{\frac{1}{c-1}} - 1 \right]^{\frac{2\gamma+1}{\gamma+1}} \left(\frac{k}{k-k_0} \right)^{\frac{c}{c-1}} \quad (\text{S3.40})$$

Using this distribution, we can study how the properties of the forest community change as function of the spatial variability of patch ages, by holding the mean patch age constant (e.g. expressing b from (S3.38) as function of M_1 and c).

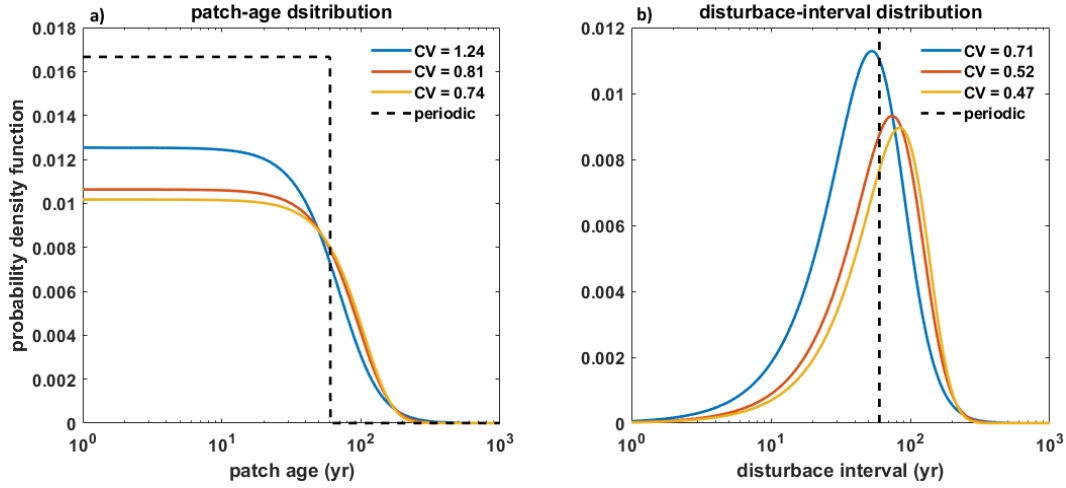


Figure S5. Patch-age distributions (a) and disturbance-interval distributions (b), for different values of b and c , corresponding to different coefficients of variation (CV in the legend). For all cases, the mean patch-age was set to 60 yr. The distributions of asynchronous periodic disturbance are shown as dashed-lines.

S3.6. Growth in the understory

In this variant of the annual plant model, when a species falls in the understory it keeps growing but at lower rate, so (S1.14) can be expressed as

$$\frac{dC}{dt} = \frac{A_{net}(L)C^{2-\beta}}{(a + b\phi_i)\eta\beta} \quad t \leq t' \quad (\text{S3.41a})$$

$$\frac{dC}{dt} = \frac{A_{net}(Le^{-\Omega LAI})C^{2-\beta}}{(a + b\phi_i)\eta\beta} \quad t > t' \quad (\text{S3.41b})$$

where t' is the time the individual falls in the understory and Ω is a light extinction coefficient and LAI is the leaf area index in the overstory. If we call u is the reduction of photosynthesis per unit of crown area in the understory, i.e. $u = A(Le^{-\Omega LAI}) / A(L)$, the crown area evolves as:

$$C_i(t', t) = k_i \left((1-u)t' + ut \right)^\gamma \quad t > t' \quad (\text{S3.42})$$

Considering the annual plant dynamic with fecundity proportional to crown, the number of seeds at the end of the growing season can be computed as:

$$n_i = F \int_{t_i}^{t_{i-1}} C_i(t', t_0) \frac{dq_i}{dt} n_i dt' \quad (\text{S3.43})$$

Using (S3.12) to express dq_i / dt , we obtain:

$$n_i = F\gamma \int_{t_i}^{t_{i-1}} \frac{\left((1-u)t' + ut_f\right)^\gamma}{t'^{\gamma+1}} dt' = F \left(H(t_i) - H(t_{i-1}) \right) \quad (\text{S3.44})$$

where the function $H(t_i) = -\left(u \frac{t_0}{t_i}\right)^\gamma {}_2F_1\left(-\gamma, -\gamma, 1-\gamma, \frac{u-1}{u} \frac{t_i}{t_0}\right)$ with ${}_2F_1$ being the hypergeometric function. For the highest rank species we have

$$n_1 = F \left(H(t_0) - H(t_1) \right) + F \quad (\text{S3.45})$$

The non-invasibility region is obtained by taking the derivative of (S3.44) respect of n_i in the limit $n_i = 0$ and equaling to 1, which gives

$$k_i \geq \frac{\left(t_{i-1} + u(t_0 - t_{i-1})\right)^{-\gamma}}{F} \quad (\text{S3.46})$$

The limiting continuous distribution is obtained as before

$$n(k) = -F \frac{dH(t)}{dt} \frac{dt}{dk} \quad (\text{S3.47})$$

Combining (S3.47) and (S3.23) we obtain (after some algebraic manipulations):

$$n(k) = \frac{(1-u)^\gamma}{\left(1 - ut_0(Fk)^{1/\gamma}\right)^{\gamma+1}} \frac{F}{k} \quad (\text{S3.48})$$

For $u = 0$ we obtain the case of annual plant community without growth in the understory (S3.26). However, because the nonlinearity in the dominator of (S3.48), for sufficiently high values of u , $n(k)$ can be non-monotonic.

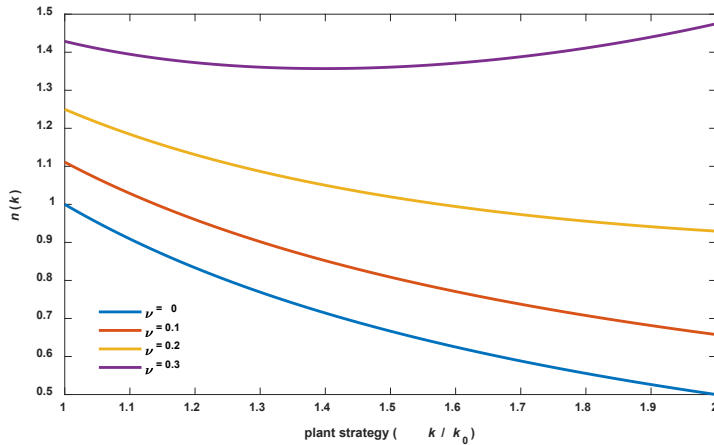


Figure S6. The continuous limit of species abundance as function of plant strategies for different value of growth in the understory.

S3.7 An Explicit solution

(S3.11a) and (S3.11b) form a closed system of equation, but n_i cannot be given in explicit form because the nonlinearity of $t_i = \left(\sum_{j=1}^i k_j n_j \right)^{-1/\gamma}$ except for the special case $\gamma = 1$ (see below). Numerically, it is straightforward and computationally inexpensive to evaluate n_i . However, it can be convenient to derive an explicit solution. To simplify notation let's normalize n_i by n_0 , k_i by k_0 and t_i by t_0 , so we can write the solutions for the equilibrium species density (S3.11a) as

$$n_i = \gamma(t_{i-1} - t_i) \quad (\text{S3.49})$$

A very good approximation can be given by

$$n_i \simeq \alpha \gamma (t_{i-1} - t_{r,i}) \quad (\text{S3.50})$$

where $t_{r,i}$ is the time required by plants of species- i to reach replacement size, i.e.

$$t_{r,i} = k_i^{-\frac{1}{\gamma+1}} \quad t_{i-1} < t_{r,i} < t_i \quad (\text{S3.51})$$

$t_{r,i}$ is bigger than t_i , because at t_i the first individual that falls into the understory has a LRS < 1. It is smaller than t_{i-1} , because t_{i-1} is the time the last individual falls in the understory and its LRS > 1. The approximation assumes that

$$\frac{t_{i-1} - t_i}{t_{i-1} - t_{r,i}} \simeq \alpha \quad (\text{S3.52})$$

because as k_i increases, both, closure time t_i and the time needed to reach LRS = 1, $t_{r,i}$ decrease (Fig. S7).

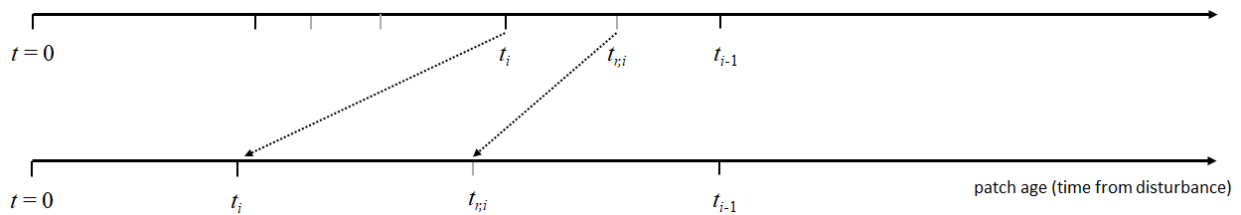


Figure S7. Schematic illustration of closure times t_i and replacement time $t_{r,i}$ for the focal species i .

$t_{r,i}$ is the time at which an individual reaches the reproductive size with LRS = 1. As k_i increases (bottom) both, t_i and $t_{r,i}$, decrease, and the ratio $\frac{t_{i-1} - t_i}{t_{i-1} - t_{r,i}}$ remains approximatively constant.

But what is α ? We can obtain α asymptotically, taking the limit

$$\alpha = \lim_{k_i \rightarrow k_{i-1}^*} \frac{t_{i-1} - t_i}{t_{i-1} - t_{r,i}} \quad (\text{S3.53})$$

where k_{i-1}^* is the limiting similarity for the establishment of species i (S3.17). To solve the limit we apply L'Hôpital's rule, because both, numerator and denominator go to zero in that limit

$$\alpha = \lim_{k_i \rightarrow k_{i-1}^*} \frac{dt_i/dk_i}{dt_{r,i}/dk_i} \quad (\text{S3.54})$$

where

$$\left. \frac{dt_{r,i}}{dk_i} \right|_{k_i=k_{i-1}^*} = \frac{1}{\gamma+1} t_{i-1}^{\gamma+2} \quad (\text{S3.55a})$$

and

$$\left. \frac{dt_i}{dk_i} \right|_{k_i=k_{i-1}^*} = -\frac{1}{\gamma} t_{i-1}^{\gamma+1} k_i \frac{dn_i}{dk_i} \quad (\text{S3.55b})$$

In order to compute $\frac{dn_i}{dk_i}$ we need an explicit expression for n_i , which we obtain with a Taylor expansion. Expanding t_i around $n_i = 0$, which correspond to $k_i = k_{i-1}^*$ we obtain

$$t_i = \left(\sum_{j=1}^{i-1} k_j n_j + k_i n_i \right)^{-\frac{1}{\gamma}} \simeq t_{i-1} - \frac{1}{\gamma} t_{i-1}^{\gamma+1} k_i n_i + \frac{1}{2} \frac{\gamma+1}{\gamma^2} t_{i-1}^{2\gamma+1} (k_i n_i)^2 \quad (\text{S3.56})$$

inserting (S3.56) this into (S3.49), we obtain an explicit solution for n_i

$$n_i \simeq 2 \frac{\gamma}{\gamma+1} \left(\frac{1}{t_{i-1}^{\gamma} k_i} - \frac{1}{t_{i-1}^{2\gamma+1} k_i^2} \right) \quad (\text{S3.57})$$

again, we point out that this expression and its derivative are correct only around $n_i = 0$ or equivalently at $k_i = k_{i-1}^*$. Taking the derivative of (S3.57) we can write

$$k_i \left. \frac{dn_i}{dk_i} \right|_{k_i=k_{i-1}^*} = 2 \frac{\gamma}{\gamma+1} t_{i-1} \quad (\text{S3.58})$$

Finally, using (S3.55a), (S3.55b) and (S3.58) into (S3.54), we obtain $\alpha = 2$, so we can write the approximate solution as

$$n_i \simeq 2\gamma \left(t_{i-1} - k_i^{-\frac{1}{\gamma+1}} \right) \quad (\text{S3.59})$$

Combining (S3.49) and (S3.49) we derive t_i iteratively as

$$t_i \simeq 2k_i^{-\frac{1}{\gamma+1}} - t_{i-1} \quad (\text{S3.60})$$

If we start from species-0, which is the species that closes exateley at t_0 with normalized density $n_0 = 1$, we can iterate the solution as

$$\begin{aligned} t_1 &= 2k_1^{-\frac{1}{\gamma+1}} - 1 \\ t_2 &= 2k_2^{-\frac{1}{\gamma+1}} - t_1 = 2k_2^{-\frac{1}{\gamma+1}} - 2k_1^{-\frac{1}{\gamma+1}} + 1 \\ t_3 &= 2k_3^{-\frac{1}{\gamma+1}} - t_2 = 2k_3^{-\frac{1}{\gamma+1}} - 2k_2^{-\frac{1}{\gamma+1}} + 2k_1^{-\frac{1}{\gamma+1}} - 1 \\ &\dots \\ t_i &= 2k_i^{-\frac{1}{\gamma+1}} - t_{i-1} = (-1)^i + 2 \sum_{j=1}^i (-1)^{i-j} k_j^{-\frac{1}{\gamma+1}} \end{aligned} \quad (\text{S3.61})$$

so we get the final formula

$$n_i \simeq 2\gamma \left((-1)^{i-1} + 2 \sum_{j=1}^{i-1} (-1)^{i-j-1} k_j^{-\frac{1}{\gamma+1}} - k_i^{-\frac{1}{\gamma+1}} \right) \quad (\text{S3.62})$$

The analytical solution works reasonably well, it oscillates but it does not diverge (Fig. S8).

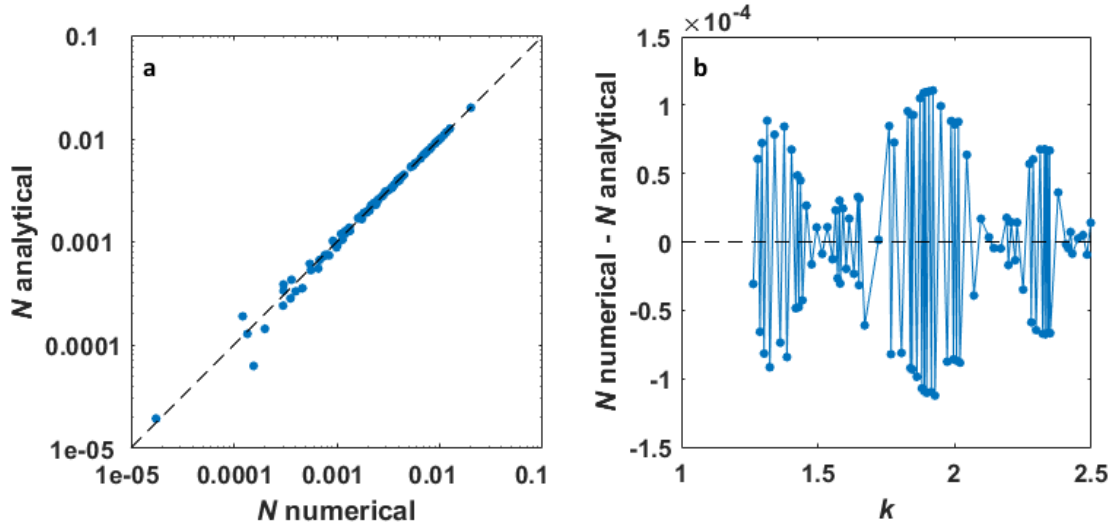


Figure S8. Comparison between the numerical solution of (S3.49) and the analytical approximation (S3.62) in log space (a) and the difference in natural space (b).

Special case $\gamma = 1$ (again all variables are normalized as above), the system simplifies as

$$n_i = t_{i-1} - t_i \quad (\text{S3.63a})$$

$$t_i = \left(\sum_{j=0}^i k_j n_j \right)^{-1} \quad (\text{S3.63b})$$

which can be easily solved into the iterative solution

$$n_i = t_{i-1} - \frac{1}{k_i t_{i-1}} \quad (\text{S3.64a})$$

$$t_i = \frac{1}{k_i t_{i-1}} \quad (\text{S3.64b})$$

Again, if we start from species-0, we can iterate the solution as

$$t_i = \frac{1}{k_1}, t_2 = \frac{k_1}{k_2}, t_3 = \frac{k_2}{k_1 k_3}, t_4 = \frac{k_1 k_3}{k_2 k_4}, \dots, t_i = \prod_{j=1}^i k_j^{(-1)^{i-j+1}} \quad (\text{S3.65})$$

so we get the final exact solution as

$$n_i = \prod_{j=1}^{i-1} k_j^{(-1)^{i-j}} - \prod_{j=1}^i k_j^{(-1)^{i-j+1}} \quad (\text{S3.66})$$

Table S1. Summary of the analytical results derived under the strict hierarchy for different models at equilibrium.

Description	Model formulation	minimum k	invasibility condition	limit $\Delta k \rightarrow 0$
<i>forest mosaic with uniform patch-age distribution</i>	$F \int_0^{t_{i-1}} t_0^{-1} q(t) C_i(t) dt = 1$ $n_1 = F \frac{\gamma}{\gamma+1} \frac{t_0 - t_1}{t_0} + F \frac{1}{\gamma+1}$ $n_i = F \frac{\gamma}{\gamma+1} \frac{t_{i-1} - t_i}{t_0}$	$n_0 = \frac{F}{\gamma+1}$ $k_0 = \frac{\gamma+1}{F t_0^\gamma}$	$k_i > k_0 \left(\frac{t_0}{t_{i-1}} \right)^{\gamma+1}$	$n(k) = \frac{\gamma}{\gamma+1} \left(\frac{n_0}{t_0} \right)^{\frac{\gamma}{\gamma+1}} k^{-\frac{\gamma+2}{\gamma+1}}$
<i>annual plants with fecundity proportional to mass</i>	$F \int_{t_i}^{t_{i-1}} M_i(t) \frac{dq_i}{dt} dt = 1$ $n_1 = \gamma FG(t_0 - t_1) + FG t_0$ $n_i = \gamma FG(t_{i-1} - t_i)$	$n_0 = FG t_0$ $k_0 = (FG t_0^{\gamma+1})^{-1}$	$k_i > k_0 \left(\frac{t_0}{t_{i-1}} \right)^{\gamma+1}$	$n(k) = \frac{\gamma}{\gamma+1} (FG)^{\frac{\gamma}{\gamma+1}} k^{-\frac{\gamma+2}{\gamma+1}}$
<i>annual plants with fecundity proportional to crown area</i>	$F \int_{t_i}^{t_{i-1}} C_i(t) \frac{dq_i}{dt} dt = 1$ $n_1 = F \gamma (\ln t_1 - \ln t_0) + F$ $n_i = F \gamma (\ln t_{i-1} - \ln t_i)$	$n_0 = F$ $k_0 = F^{-1} t_0^{-\gamma}$	$k_i \geq \frac{t_{i-1}^{-\gamma}}{F}$	$n(k) = \frac{n_0}{k}$
<i>forest mosaic with exponential patch-age distribution</i>	$F \int_0^{t_{i-1}} m e^{-mt} q(t) C_i(t) dt = 1$ $n_1 = FM(\gamma, \gamma+1, -mt_1)^{\dagger}$ $n_i = FM(\gamma, \gamma+1, -mt_i) - FM(\gamma, \gamma+1, -mt_{i-1})$	$n_0 = 0$ $k_0 = \frac{m^\gamma}{\Gamma(\gamma+1)F}$	$k_i \geq \frac{m^\gamma}{F \Gamma(\gamma+1, mt_{i-1})}$	-
<i>annual plants with growth in the understory</i>	$F \int_{t_i}^{t_{i-1}} C_i(t', t_0) \frac{dq}{dt'} dt' = 1$ $n_1 = F (H(t_0) - H(t_1)) + F^{\S}$ $n_i = F (H(t_{i-1}) - H(t_i))$	$n_0 = F$ $k_0 = F^{-1} t_0^{-\gamma}$	$k_i \geq \frac{[(1-\nu)t_{i-1} + \nu t_0]^{-\gamma}}{F}$	$n(k) = \frac{(1-\nu)^\gamma}{[1 - \nu(k/k_0)^{1/\gamma}]^{\gamma+1}} \frac{n_0}{k}$

$\dagger M$ is the Kummer's (confluent hypergeometric) function

$$\S H(t_i) = - \left(\nu \frac{t_f}{t_i} \right)^\gamma {}_2F_1 \left(-\gamma, -\gamma, 1-\gamma, \frac{\nu-1}{\nu} \frac{t_i}{t_f} \right) \text{ with } {}_2F_1 \text{ being the hypergeometric function.}$$

S4. The schmear model

S4.1. A solution

In order to provide an analytical expression for the species densities, we need to define a distribution for the random factor ω . We take $P(\omega) = \theta\omega^{\theta-1}$ ($0 \leq \omega \leq 1$) and multiply k by $\frac{\theta+\gamma}{\theta}$ to account for the fact that growth rates go to zero as $\theta \rightarrow 0$. This random variable is governed by a parameter θ , such that intraspecific variability increases as $\theta \rightarrow 0$, and the system resembles the strict hierarchy as $\theta \rightarrow \infty$. To see this more clearly, we define the effective height growth rate of an individual of species- i as: $r_i\omega^\delta$, which comes from (S1.7b). **Error! Reference source not found.** S9 shows the distribution of these effective height growth rates for ten hypothetical species and for different values of θ . Note that the height growth rate hierarchy becomes better defined as θ increases.

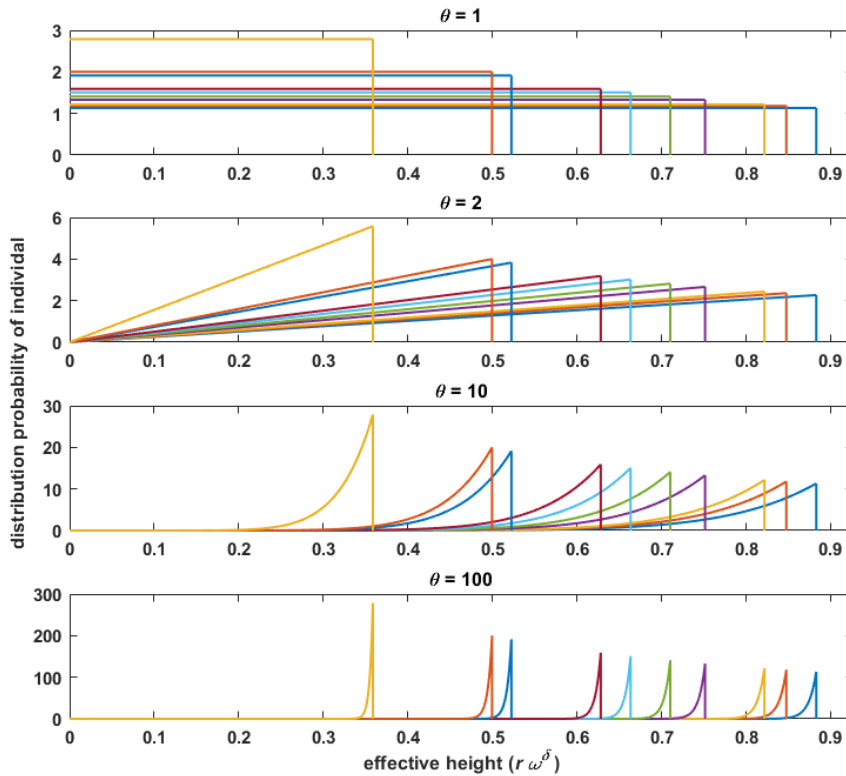


Figure S9. Distribution of the effective height growth rates of individuals ($r_i\omega^\delta$) for ten species and for different values of θ . The probability density of ω is $\theta\omega^{\theta-1}$. As θ increases, the distributions resemble a Dirac's delta and the species' height growth rates become almost perfectly segregated by species.

We also consider the annual plant system with per capita fecundity proportional to crown area, i.e. $F_i(\omega, t) = f k_i(\omega t)^\gamma$. With these assumptions, we can provide an analytical expression for (S2.14) as:

$$n_{i,T+1} = F k_i n_{i,T} \frac{\theta + \gamma}{\theta} \int_0^1 \frac{\theta \omega^{\theta + \gamma - 1}}{\sum_{j \in x_{ji} \geq \omega} n_j k_j [1 - (x_{ij} \omega)^{\theta + \gamma}]} d\omega \quad (\text{S4.1})$$

the above integral can be split as

$$n_{i,T+1} = F k_i n_{i,T} \frac{\theta + \gamma}{\theta} \sum_{k=i}^S \int_{x_{k+1i}}^{x_{ki}} \frac{\theta \omega^{\theta + \gamma - 1}}{\sum_{j=1}^k n_j k_j [1 - (x_{ij} \omega)^{\theta + \gamma}]} d\omega \quad (\text{S4.2})$$

and analytically integrated to give

$$n_{i,T+1} = F^\gamma n_{i,T} k_i \sum_{k=i}^S \frac{\ln t_{k-1} - \ln t_k}{\sum_{j=1}^k n_{j,T} k_j x_{ij}^{\theta + \gamma}} \quad \forall i \mid t_{i-1} < t_0 \quad (\text{S4.3a})$$

where $t_k = \left(\sum_{j=1}^k n_j k_j (1 - x_{kj}^{\theta + \gamma}) \right)^{-1/\gamma}$ is the time at which species $k+1$ goes entirely in the understory and $t_S = \left(\sum_{j=1}^S n_j k_j \right)^{-1/\gamma}$ is the first time canopy closes. For species that remain in the canopy at the end of the season, we have:

$$n_{i,T+1} = F^\gamma n_{i,T} k_i \left[\sum_{k=m}^S \frac{\ln t_{k-1} - \log t_k}{\sum_{j=1}^k n_{j,T} k_j x_{ij}^{\theta + \gamma}} + \frac{1 - t_0^\gamma \sum_{j=1}^m n_j k_j (1 - x_{ij}^{\theta + \gamma})}{\gamma \sum_{j=1}^m n_j k_j x_{ij}^{\theta + \gamma}} \right] \quad \forall i \mid t_{i-1} \geq t_0 \quad (\text{S4.3b})$$

where m is the lowest rank that is still present in the canopy at the end of the season and $t_{m-1} = t_0$.

4.2. Pair-wise invasibility plot and Evolutionary Stable Strategy

In this section, we derive the conditions for invasibility into a monodominant culture by an invader that is initially rare using the solutions (S4.3).

Let us call n_1 is the equilibrium density of the resident, satisfying the equation

$$n_1 = F \log(k_1 n_1 t_0^\gamma) + F \quad (\text{S4.4})$$

and n_i the density of the invader, which is described by (S4.3b) or (S4.3a), depending on whether some of the invader individuals will remain in the canopy at the end of the season, or they will be completely folded into the understory. The two cases depend on whether $n_1 k_1 (1 - x_{21}^{\theta + \gamma}) t_0^\gamma < 1$ or > 1 .

As before, the condition for invasibility can be expressed as $R_2 = \left. \frac{dn_{2,T+1}}{dn_{2,T}} \right|_{n_{2,T}=0, n_1} = 1$.

The invader per capita fecundity ratios are:

$$R_2^{can} = \frac{k_2}{k_1} \frac{1 - f k_1 t_0^\gamma (1 - x_{21}^{\theta+\gamma})}{x_{21}^{\theta+\gamma}} \quad x_{21}^{\theta+\gamma} > 1 - \frac{1}{k_2 n_2 t_0^\gamma} \quad (S4.5a)$$

$$R_2^{und} = -f \frac{k_2}{k_1} \frac{\log(1 - x_{21}^{\theta+\gamma})}{n_1 x_{21}^{\theta+\gamma}} \quad x_{21}^{\theta+\gamma} < 1 - \frac{1}{k_1 n_1 t_0^\gamma} \quad (S4.5b)$$

for the canopy and understory case, respectively, derived by differentiating (S4.3b) and (S4.3a).

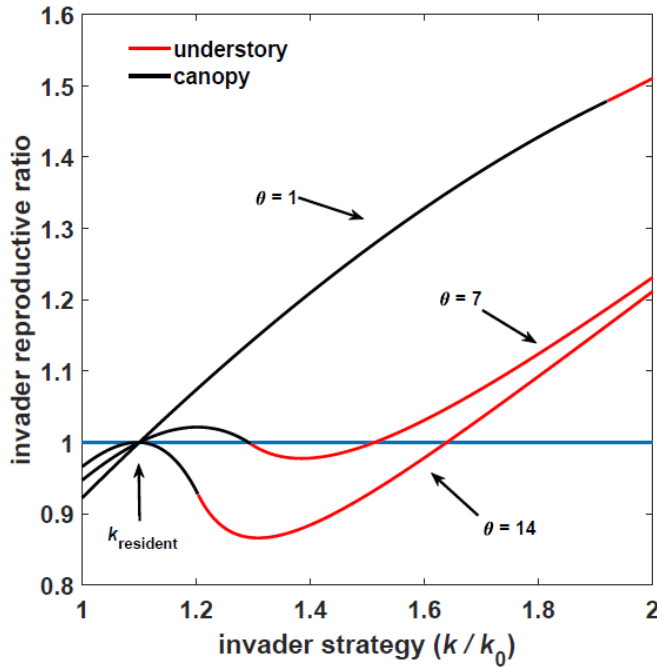


Figure S10. Invader per capita reproductive ratio in a monoculture as function of invader strategy and for different values of θ (schmeat reduces as θ increases). The resident strategy is fixed. The red lines indicate that the invader will be in the canopy at the end of the season. Note the intermediate case ($\theta = 7$), the invader can be successful when the strategy is very similar to the resident, but not able to invade when the two strategies diverge. When the two strategies are sufficiently different, the invader always establishes (and probably coexist in the long term).

Note that, by switching the subscripts, (S4.5a) and (S4.5b) also represent the long-term reproductive ratio of a resident in the case the invader takes over the community. Therefore, $R_1^{und} > 1$ and $R_2^{can} > 1$ determine the necessary conditions for long-term coexistence (and for symmetry also $R_2^{can} > 1$ and $R_1^{und} > 1$).

From the invader reproductive ratio, we can compute the ESS, i.e. the strategy that satisfies the following condition: $\left. \frac{dR_2}{dk_2} \right|_{k_1=k_2} = 0$. By noticing that the ESS can be satisfied only if the invader stays in the canopy, taking the derivative of (S4.5a), and making it equal to zero, we obtain:

$$k_{ESS} = \frac{\lambda + 1}{\lambda} \frac{1}{f t_f^\gamma} \quad (\text{S4.6})$$

where $\lambda = \frac{1 - \delta}{\delta} \frac{\theta + \gamma}{\gamma}$ and we have made the approximation that $x_{21} = (k_1 / k_2)^{1/\gamma}$, i.e., that $b\phi \gg a$.

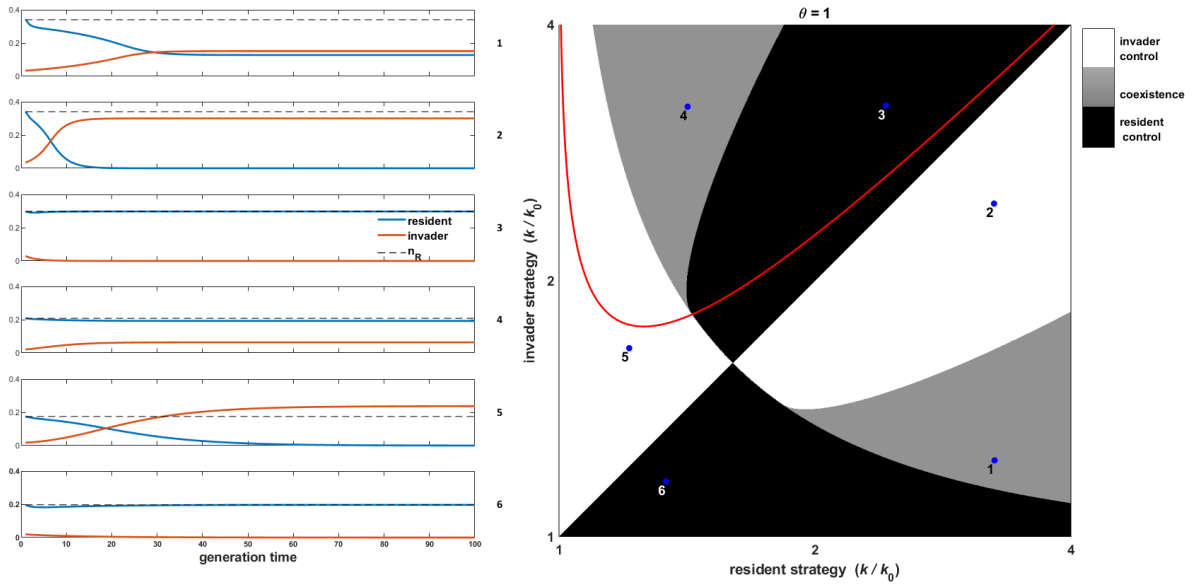


Figure S11. Simulations of an invasion into a monoculture for each of the six regions defined by the pairwise invasibility plot. Each of the plot on the left corresponds to the point with the same number on the invasibility plot. The simulations solve iteratively (S4.3a) and (S4.3b). Each simulation starts with the resident (—) at equilibrium (---), and the invader (—) at low density. The simulations are carried out for 100 generations, when the species density are at equilibrium. They agree exactly with the theoretical predictions of the pairwise invasibility plot (compare the outcome of the invasion with the corresponding color on the invasibility plot). The red line (—) in the invasibility plot divides the space in two regions: below the line, the invader will remain in the canopy at the end of the season when initially rare, so R is given by (S4.5a); above the red, the invader will be completely folded into the understory, and R is given by (S4.5b).

S5. Other tradeoffs

S5.1. A special case of multispecies system with species-specific reproductive thresholds

Here we analyze a particular case of a system of species with different reproductive thresholds where species with lower reproductive threshold invade a monoculture with the highest reproductive threshold, as illustrated in Fig S12. We call z_i the time when species i reaches the reproduction threshold, and t_{i-1} the time the species i is excluded from the canopy. Species i reproduces between z_i and t_{i-1} . While reproducing, species i does not grow, but species that have not reached the reproductive threshold keep growing, eventually filling the canopy above.

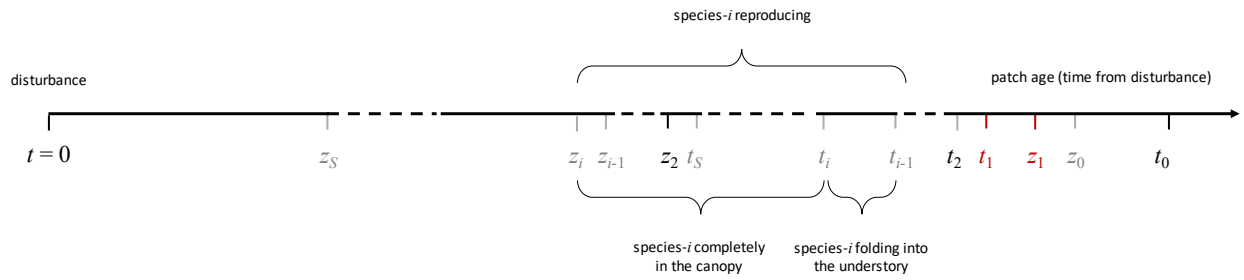


Figure S12. Schematic illustration of the hierarchical structure of a multi-species system with different reproduction threshold (z) along a successional axis. Species are ranked from late to early successional (species 1 in red is the species with the highest reproductive threshold). In this example, we assume the first species is already established in the system. We also assume that for the subsequent species, the canopy is filled after the species reaches maturity, and the last species fills the canopy after z_2 . Species i reproduces between z_i and t_{i-1} . Between z_i and t_i it is entirely in the canopy, between t_i and t_{i-1} it is folding into the understory.

The reproduction period can be split into two sub-periods depending on whether species i is entirely in the overstory or is folding into the understory (Fig. S12). The switch happens at time t_i , i.e., when the species i closes the canopy and the species with earlier reproduction goes entirely in the understory.

Furthermore, during the reproduction period, other species will reach maturity, and their crown will stop growing; however, in this special case we consider only the species that reach maturity before the canopy closes for the first species (i.e. $z_2 < t_S < z_1$, Fig. S12). With these assumptions, we can write the total amount of propagule produced by species i as

$$n_i = F \underbrace{\int_{z_i}^{t_i} p(t) n_i k z_i^\gamma dt}_{\text{reproduction while in the canopy}} + F \underbrace{\int_{t_i}^{t_{i-1}} p(t) \left(1 - n_1 k t^\gamma + \sum_{j=2}^{i-1} n_j k z_j^\gamma \right) dt}_{\text{reproduction while folding into the understory}} \quad (\text{S5.1})$$

where the closure time for species i is obtained from

$$n_1 k t_i^\gamma + \sum_{j=2}^i n_j k z_j^\gamma = 1 \quad (\text{S5.2})$$

Integration of (S5.1) for uniform patch-age distribution ($p(t) = t_0^{-1}$) gives

$$n_i = F n_i k z_i^\gamma \frac{t_i - z_i}{t_0} + F \left(1 - \sum_{j=2}^{i-1} n_j k z_j^\gamma \right) \frac{t_{i-1} - t_i}{t_0} - F n_i k \frac{t_{i-1}^{\gamma+1} - t_i^{\gamma+1}}{(\gamma+1)t_0} \quad (\text{S5.3})$$

The condition for establishment when rare is $F k z_i^\gamma \frac{t_{i-1} - z_i}{t_0} \geq 1$.

S5.2. Continuous case for reproductive threshold

The continuous case is derived taking the limit $n(z) = \lim_{\Delta z \rightarrow 0} \frac{n_i}{\Delta z}$. In this limit, (S5.1) reduces to

$$n(z) = F n(z) k z^\gamma \frac{t(z) - z}{t_0} + O(dz) \quad (\text{S5.4})$$

where $O(dz)$ is the infinitesimal contribution from $t(z)$ to $t(z+dz)$. The closing time $t(z)$ can be derived from

$$\int_z^{z_+} n(z') k z'^\gamma dz' + n_1 k t(z)^\gamma = 1 \quad (\text{S5.5})$$

where z_+ is the highest threshold behind z_1 satisfying the condition $F k z_+^\gamma (t_1 - z_+) = 1$. (S5.4) establishes a relationship between z and t

$$t(z) = z + \frac{t_0}{f k z^\gamma} \quad (\text{S5.6a})$$

$$\frac{dt}{dz} = 1 - \gamma \frac{t_0}{f k z^{\gamma+1}} \quad (\text{S5.6b})$$

Taking the derivative of (S5.5) and combining with (S5.6) we obtain the final solution

$$n(z) = \frac{n_1}{z^\gamma} \gamma \left(z + \frac{t_0}{f k z^\gamma} \right)^{\gamma-1} \left(1 - \gamma \frac{t_0}{f k z^{\gamma+1}} \right) \quad (\text{S5.7})$$

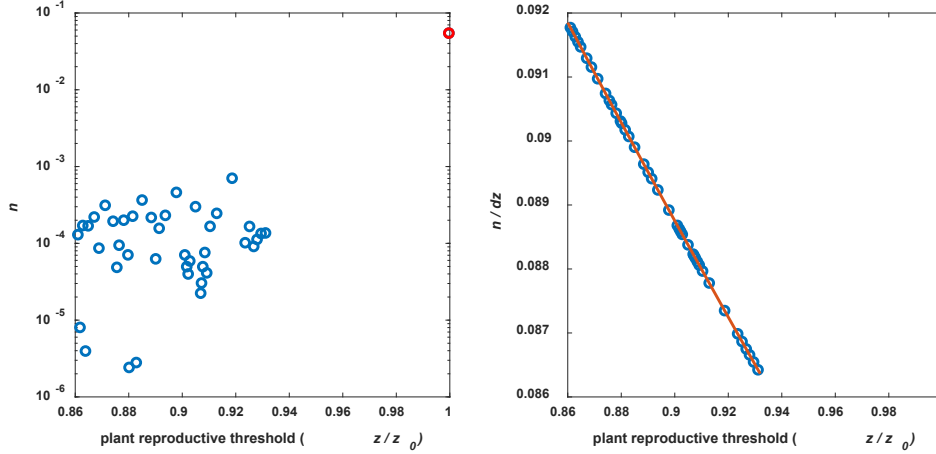


Figure S13. Abundance as function of reproductive threshold in a simulation where the threshold of each species is randomly drawn from $z_i = z_i^* - \varepsilon_i$ where ε is an exponential random variable and z_i^* is the condition for establishment $fkz_i^{\gamma}(t_i - z_i^*) = 1$. The plot on the right shows n_i normalized by $\Delta z_i = z_i^* - z_{i+1}^*$ along with the solution in the continuous case (Eq.(S5.7)).

S5.3. Pair-wise invasibility plot

For the resident, at equilibrium, the whole canopy is occupied at the time of reproduction, z_1 , and the total number of offspring is

$$n_1 = f \frac{t_0 - z_1}{t_0} \quad (\text{S5.8})$$

An individual that reaches maturity will generate $R_1 = fkz_1^{\gamma}(t_0 - z_1)/t_0$ offspring, which has an optimum at $z_1^* = \frac{\gamma}{\gamma+1}t_0$ (Fig. S14). At the minimum, R_1 must be one if all individuals are reproductive, which implies that no individuals are folded into the understory before reproduction, or equivalently, that canopy closes exactly at z_1 , that is

$$n_1 k z_1^{\gamma} = 1 \quad (\text{S5.9})$$

if we substitute n_1 with $f(t_0 - z_1)/t_0$ into (S5.9), we obtain again $fkz_1^{\gamma}(t_0 - z_1)/t_0 = 1$. This condition, which as two roots, sets the limits to the maximum, optimum and minimum reproductive threshold that can be sustained given fk and t_0 (Fig. S14).

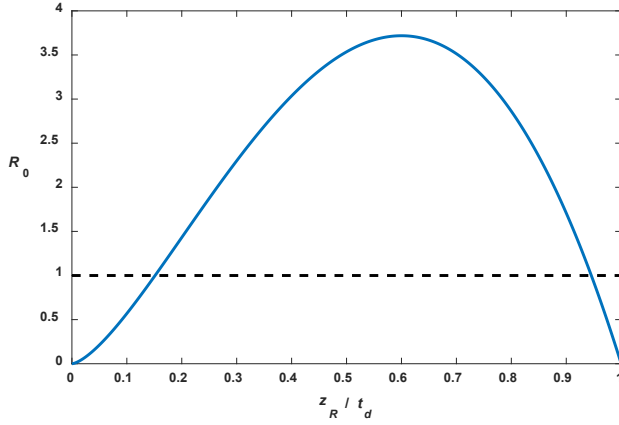


Figure S14. Reproductive ratio (R_0) of individuals that reach maturity as function of reproductive threshold divided by time to disturbance. The curve has an optimum at $z_0^* = \frac{\gamma}{\gamma+1} t_0$. Other parameters: $\gamma = 1.5, fk = 20$. Dashed line indicates the minimum reproductive threshold.

For $fkz_1^\gamma(t_0 - z_1)/t_0 \geq 1$, the canopy closes at $t_1 = [fk(t_0 - z_1)/t_0]^{-1/\gamma}$, which implies $t_1 \leq z_1$ (canopy must close before or at maximum at z_1).

Different dynamics can be derived if the resident is invaded from above or below. If invaded from above (i.e., $z_2 > z_1$), the invasion will be successful if R_2 of the invader is bigger than R_1 of the resident. This can be shown by considering that between time t_1 and z_1 , as both species are identical, they fold in the understory at the same rate. Consequently, at z_1 the invader density decreases by a factor of $(t_1 / z_1)^\gamma$.

The condition for successful invasion is thus $(t_1 / z_1)^\gamma fkz_2^\gamma \frac{t_0 - z_2}{t_0} \geq 1$, where from above

$$t_1 = \left(fk \frac{t_0 - z_1}{t_0} \right)^{-1/\gamma} \quad \text{Making the substitution, we obtain}$$

$$fkz_2^\gamma(t_0 - z_2) \geq fkz_1^\gamma(t_0 - z_1) \quad z_2 > z_1 \quad (\text{S5.10})$$

If the resident is invaded from below (i.e., $z_2 < z_1$), the invader will be completely overtopped at t_1 , so the condition for the establishment becomes

$$fkz_2^\gamma(t_1 - z_2)/t_0 \geq 1 \quad (\text{S5.11})$$

This condition states that z_2 must be sufficiently small to allow enough time to reproduce before species 1 closes the canopy, but not too small, to allow the crowns to reach a size large enough to provide the necessary carbon. Note how this condition is identical to the condition for the resident by replacing t_1 with t_0 .

S5.4. A system with species-specific allocation to reproduction

Here we analyze a case of a system of species with different allocation to reproduction φ_i . The solutions can be derived as in section 3, so here we report only the final results. Species with higher allocation invest less in growth and *vice versa*. Recall that

$$c = A - \psi \left(r_L + \sigma \frac{\eta}{\tau_L} \right) - \psi \Gamma \left(r_R + \sigma \frac{\eta}{\tau_R} \right) - \lambda \text{ and } m = \left(\frac{\beta - 1}{\beta \eta} \frac{1}{a + b\phi} \right)^\gamma \text{ so, } k_i = m(c - \varphi_i)^\gamma.$$

The general solution can be given using (S3.7a)

$$n_i = F_i (W(t_{i-1}) - W(t_i)) \quad (\text{S5.12})$$

where $F_i = g_s n_s \varphi_i \frac{1 - e^{-\mu_0}}{\mu}$, is a species-specific parameter and n_s the number of seeds per unit of carbon. The condition for establishment when rare is

$$\varphi_i (c - \varphi_i)^\gamma \geq \varphi_0 (c - \varphi_0)^\gamma \left(\frac{t_0}{t_{i-1}} \right)^{\gamma+1} \quad \varphi_i < c \quad (\text{S5.13})$$

where

$$\varphi_0 (c - \varphi_0)^\gamma = \frac{\gamma + 1}{n_s m t_0^\gamma} \quad (\text{S5.14})$$

defines a lower limit for φ . The continuous case is derived by expanding (S3.23) as

$$n(\varphi) = -\frac{\gamma}{k(\varphi)} \frac{1}{t(\varphi)^{\gamma+1}} \frac{dt}{d\varphi} \frac{d\varphi}{dk} \quad (\text{S5.15})$$

$t(\varphi)$ and $\frac{dt}{d\varphi}$ are derived by (S3.21):

$$t(\varphi) = \left(\frac{n_s \varphi m (c - \varphi)^\gamma}{(\gamma + 1) t_0} \right)^{\frac{1}{\gamma+1}} \quad (\text{S5.16a})$$

$$\frac{dt}{d\varphi} = -\frac{1}{\gamma + 1} \left(\frac{1}{(\gamma + 1) t_0} \right)^{\frac{1}{\gamma+1}} \left(n_s \varphi m (c - \varphi)^\gamma \right)^{\frac{\gamma+2}{\gamma+1}} \left(n_s \varphi - \frac{c - \varphi}{\gamma} n_s \right) \quad (\text{S5.16b})$$

after some algebraic manipulation, we obtain

$$n(\varphi) = n_s \gamma \frac{c - \varphi(\gamma + 1)}{\left((\gamma + 1)^{2\gamma+1} t_0^\gamma n_s \varphi m (c - \varphi)^{2\gamma+1} \right)^{\frac{1}{\gamma+1}}} \quad (\text{S5.17})$$

The pairwise invasibility plot can be obtained by the condition (S5.13) when invading with $\varphi_2 > \varphi_1$. Note that condition (S5.13) has two solutions, so the invader allocation must be bounded by these two limits. When invading with $\varphi_2 < \varphi_1$, the invasion is always successful until the limit (S5.14).

S5.5. A system with the growth-survival tradeoff

Here we analyze a case of a system of species with different maximum photosynthetic capacity (A_{\max}). Species with higher A_{\max} grow faster in full light, but allocate less carbon in survival when in shade. Recall that

$$k_i = m \left(A_{\max,i} (1 - w) - b \right)^\gamma$$

and

$$\mu_i = \mu_0 \left(1 - (k_i / k_+)^{1/\gamma} \right)^{-c} \quad k_i < k_+$$

where μ_0 is a background mortality and k_+ is a scaling factor. We assume that $c > 1$ to give a concaved up curve between growth and survival, consistent with observations.

The solution for equilibrium densities and the continuous distribution follows the case of the growth-reproduction tradeoff with. The fecundity parameter is (for simplicity we assume $t_0 \gg 1/\mu_i$)

$$F_i = \frac{g_s n_s \varphi}{\mu_i}$$

The condition for establishment when rare is

$$\frac{g_s n_s \varphi}{\mu_0} \left(1 - (k_i / k_+)^{1/\gamma} \right)^c k_i t_{i-1}^{\gamma+1} = \gamma + 1 \quad (\text{S5.18})$$

The continuous case is derived by expanding (S3.23) as

$$n(\mu) = -\frac{\gamma}{k(\mu)} \frac{1}{t(\mu)^{\gamma+1}} \frac{dt}{d\mu} \frac{d\mu}{dk} \quad (\text{S5.19})$$

$t(\mu)$ and $\frac{dt}{d\mu}$ are derived by (S3.21):

$$t(\mu) = \left(\frac{g_s n_s \varphi}{(\gamma + 1) \mu} k_+ \left(1 - (\mu_i / \mu_0)^{-1/c} \right)^\gamma \right)^{\frac{1}{\gamma + 1}} \quad (\text{S5.20})$$

References

- Atkin, O.K., Bloomfield, K.J., Reich, P.B., Tjoelker, M.G., Asner, G.P., Bonal, D., *et al.* (2015). Global variability in leaf respiration in relation to climate, plant functional types and leaf traits. *New Phytol.*, 206, 614–636.
- Atkin, O.K., Westbeek, M.H.M., Cambridge, M.L., Lambers, H. & Pons, H. (1997). Leaf Respiration in Light and Darkness. *Plant Physiol.*, 113, 961–965.
- Bohlman, S. & O’Brien, S. (2006). Allometry, adult stature and regeneration requirement of 65 tree species on Barro Colorado Island, Panama. *J. Trop. Ecol.*, 22, 123–136.
- Bouma, T.J., De Visser, R., Van Leeuwen, P.H., De Kock, M.J. & Lambers, H. (1995). The respiratory energy requirements involved in nocturnal carbohydrate export from starch-storing mature source leaves and their contribution to leaf dark respiration. *J. Exp. Bot.*, 46, 1185–1194.
- Cano, I.M., Muller-Landau, H.C., Joseph Wright, S., Bohlman, S.A. & Pacala, S.W. (2019). Tropical tree height and crown allometries for the Barro Colorado Nature Monument, Panama: A comparison of alternative hierarchical models incorporating interspecific variation in relation to life history traits. *Biogeosciences*, 16, 847–862.
- Farquhar, G.D., von Caemmerer, S. & Berry, J.A. (1980). A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species. *Planta*, 149, 78–90.
- Going, B.M., Hillerislambers, J. & Levine, J.M. (2009). Abiotic and biotic resistance to grass invasion in serpentine annual plant communities. *Oecologia*, 159, 839–847.
- Goodman, R.C., Phillips, O.L. & Baker, T.R. (2014). The importance of crown dimensions to improve tropical tree biomass estimates. *Ecol. Appl.*, 24, 680–698.
- Haxeltine, A. & Prentice, I.C. (1996). A General Model for the Light-Use Efficiency of Primary Production. *Funct. Ecol.*, 10, 551.
- Hutchings, M.J. (1975). Some statistical problems associated with determinations of population parameters for herbaceous plants in the field. *New Phytol.*, 74, 349–363.
- Kitajima, K. (1994). Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia*, 98, 419–428.

- Moorcroft, P., Hurtt, G. & Pacala, S. (2001). A method for scaling vegetation dynamics: the ecosystem demography model (ED). *Ecol. Monogr.*, 71, 557–586.
- Niklas, K.J. & Enquist, B.J. (2003). An allometric model for seed plant reproduction. *Evol. Ecol. Res.*, 5, 79–88.
- Niklas, K.J. & Spatz, H.C. (2004). Growth and hydraulic (not mechanical) constraints govern the scaling of tree height and mass. *Proc. Natl. Acad. Sci. U. S. A.*, 101, 15661–15663.
- Noguchi, K. & Yoshida, K. (2008). Interaction between photosynthesis and respiration in illuminated leaves. *Mitochondrion*, 8, 87–99.
- Russo, S.E., McMahon, S.M., Detto, M., Ledder, G., Wright, S.J., Condit, R.S., *et al.* (2020). The interspecific growth–mortality trade-off is not a general framework for tropical forest community structure. *Nat. Ecol. Evol.*
- Strigul, N., Pristinski, D., Purves, D., Dushoff, J. & Pacala, S. (2008). Scaling from trees to forests: Tractable macroscopic equations for forest dynamics. *Ecol. Monogr.*, 78, 523–545.
- Thornley, J.H.M. (1972). A balanced quantitative model for root: Shoot ratios in vegetative plants. *Ann. Bot.*, 36, 431–441.
- Walters, M.B. & Reich, P.B. (1996). Are shade tolerance, survival, and growth linked? Low light and nitrogen effects on hardwood seedlings. *Ecology*, 77, 841–853.
- Wright, S.J., Kitajima, K., Kraft, N.J.B., Reich, P.B., Wright, I.J., Bunker, D.E., *et al.* (2010). Functional traits and the growth–mortality trade-off in tropical trees. *Ecology*, 91, 3664–3674.