

Local diversity in heterogeneous landscapes: quantitative assessment with a height-structured forest metacommunity model

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Abstract “Mass effects,” in which “sink populations” of locally inferior competitors are maintained by dispersal from “source populations” elsewhere in the landscape, are thought to play an important role in maintaining plant diversity. However, due to the complexity of most quasi-realistic forest models, there is little theoretical understanding of the strength of mass effects in forests. Here, we develop a metacommunity version of a mathematically and computationally tractable height-structured forest model, the Perfect Plasticity Approximation, to quantify the strength of mass effects (i.e., the degree of mixing of locally dominant and subordinate species) in heterogeneous landscapes comprising different patch types (e.g., soil types). For realistic levels of inter-patch dispersal, mass effects are weak at equilibrium (i.e., in the absence of disturbance), even in some cases where differences in growth, mortality, and fecundity rates between locally dominant and subordinate species are too small to be reliably detected from field data. However, patch-scale transient dynamics are slow following catastrophic disturbance (in which post-disturbance initial abundances are determined exclusively by immigration) so that at any given time, subordinate species are present in appreciable numbers in most patches. Less severe disturbance regimes, in which

some seeds or individuals survive the disturbance, should result in faster transient dynamics (i.e., faster approach to the low-diversity equilibrium). Our results suggest that in order for mass effects to play an important role in tree coexistence, niche differences must be strong enough to prevent neutral drift, yet too weak to be reliably detected from field data.

Keywords Tree coexistence · Forest diversity · Metacommunity · Height-structured competition · Mass effects · Source–sink dynamics

Introduction

Spatial heterogeneity is thought to play a key role in maintaining the diversity of biological communities (Holt 1993; Tilman and Pacala 1993; Amarasekare and Nisbet 2001; Mouquet and Loreau 2002), and much of our current understanding of this problem builds on Simon Levin’s pioneering work (Levin 1974, 1976; Levin and Paine 1974). Environmental heterogeneity due to abiotic factors (e.g., soil or topography) and/or biotic factors (e.g., random colonization of different patches by different species that can competitively exclude each other once established) can increase diversity at both landscape and local scales (Levin 1974, p. 220): “If the environment is heterogeneous, different combinations of species are likely to be favored in the various local regions and maintained elsewhere principally by dispersal from more favored regions, and this will act to increase the overall species richness.” The notion that landscape heterogeneity could promote local mixing of species that could not stably coexist in an isolated patch was later summarized by the term “mass effect,” in which “sink populations” of locally inferior competitors are maintained by dispersal from “source populations” else-

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where in the landscape (Shmida and Ellner 1984; Holt 1993; Mouquet and Loreau 2002, 2003; Leibold et al. 2004).

Disturbance augments the underlying spatial heterogeneity of landscapes, and its potential role in maintaining diversity is well known (Levin and Paine 1974; Whittaker and Levin 1977; Huston 1979; Hastings 1980). For example, it is widely believed that disturbances such as fire and windthrow allow tree species with different successional niches to coexist (Connell 1978; Molino and Sabatier 2001). Disturbance may also facilitate coexistence among species belonging to the same successional guild if the timescale of competitive exclusion of sink species is slow (Shmida and Ellner 1984).

Despite the large body of theoretical work on the roles of spatial heterogeneity and disturbance in maintaining diversity, quantitative understanding of how these factors affect forest diversity is limited for at least two reasons. Firstly, in communities of long-lived organisms, such as trees, it is impractical to use field experiments to directly quantify the impact of different factors (e.g., mass effects) on diversity at the relevant temporal scales (e.g., >100 years). Secondly, most theoretical work relies on models that (1) are too simplistic to make quantitative predictions about real communities and/or (2) do not represent key individual-level processes needed to mechanistically “scale up” from properties of individuals that can be quantified in the field (Pacala et al. 1993, 1996). In the case of tree coexistence in closed-canopy forests, we are particularly concerned with height-structured competition for light (Horn 1971; Kohyama 1993; Canham et al. 1994) and how this mechanism may alter quantitatively (or perhaps qualitatively) the insights gained from non-height structured models.

The Perfect Plasticity Approximation (PPA; Strigul et al. 2008), a recently developed height-structured model of forest dynamics that scales from individuals to communities, provides a potentially useful framework for quantifying the degree to which different mechanisms contribute to tree diversity. The PPA captures observed inter- and intraspecific patterns in the canopy status of individual trees (i.e., the proportion of individuals that are in the canopy vs. the understory; Purves et al. 2007) and predicts successional changes in biomass and species composition in the US Lake States region (Purves et al. 2008). Unlike other quasi-realistic forest dynamics models (e.g., SORTIE; Pacala et al. 1996), the PPA is mathematically and computationally tractable so that the model can be studied in a theoretical context to gain fundamental insights (Adams et al. 2007; Strigul et al. 2008).

In this paper, we develop a metacommunity (Leibold et al. 2004) version of the PPA model to quantify the strength of mass effects in landscapes where patches are subject to catastrophic disturbance (e.g., stand-replacing fire). In particular, we quantify how the degree of mixing of habitat specialists in local communities (or “patches” sensu

Leibold et al. 2004) depends on (1) the inter-patch dispersal rate; (2) the difference between locally dominant and subordinate species in their individual performance rates (understory and canopy growth and mortality, and fecundity); and (3) the time since the last patch-scale disturbance event. Our work complements previous studies of coexistence in source–sink metacommunities (e.g., Amarasekare and Nisbet 2001; Mouquet and Loreau 2002, 2003) in two important respects. Firstly, to our knowledge, our work is the first metacommunity study to build up from a height-structured forest dynamics model whose individual-level parameters can be directly connected to field observations of individual tree growth and mortality rates. Secondly, we explore how the degree of local mixing changes over time within a patch following disturbance. Relative to the patch-scale equilibrium, mass effects may be enhanced during the transient post-disturbance phase (Shmida and Ellner 1984), but these transient dynamics have not, to our knowledge, been examined in detail in previous metacommunity studies. We first summarize key features and equilibrium results of the PPA model as previously developed for a single patch (Adams et al. 2007; Strigul et al. 2008) before turning to the metacommunity model where we introduce landscape heterogeneity and patch-scale catastrophic disturbance.

The perfect plasticity approximation

The PPA assumes that trees are infinitely plastic in their horizontal arrangement of crown area such that individual crowns may be disaggregated into infinitesimal parcels that can be positioned anywhere in horizontal space so as to maximize access to light (Strigul et al. 2008). This assumption is motivated by the observation that trees are phototropic: individual crowns tend to expand into unoccupied space and avoid interdigitating with adjacent crowns. The assumption of horizontal plasticity applies to crown area, not leaf area. Thus, the PPA allows for optimal horizontal placement of crown area (in the sense of maximizing an individual’s access to light) while maintaining self-shading within individual crowns. According to the PPA, gaps created by canopy tree deaths are immediately filled by the tallest understory individuals in a forest stand. Thus, the PPA ignores the chance opportunities provided by gaps in real forests to seedlings and small saplings (Brokaw and Busing 2000). This unrealistic level of determinism may limit the utility of the PPA in some contexts (e.g., modeling gap phase dynamics of old-growth forests).

To formalize the PPA, we define “ground area” as a region within a horizontal plane corresponding to an area of forest, and we define “crown area” as the area of the ground surface that is shaded from above. The crown area of tree i at height z is $A_i(z)$. If the total (maximum) height of tree i is z_i ,

then $A_i(z)=0$ for $z>z_i$. The PPA allows for arbitrarily defined crown shapes (Purves et al. 2007; Strigul et al. 2008), but for simplicity, we assume in this paper that individual crowns have flat tops (as in Purves et al. 2008). Thus, tree i has crown area $A_i(z)=A_i$ for $0\leq z\leq z_i$ and $A_i(z)=0$ otherwise. The height of canopy closure (i.e., the height above which the total crown area equals the ground area), z^* , is implicitly defined by

$$\text{ground area} = \sum_{\{z>z^*\}} n(z)A(z) \quad (1)$$

where $n(z)$ is the number of trees of height z ; $A(z)$ is the crown area of a tree of height z [Eq. 1 may easily be modified to allow for intra- or interspecific variation in $A(z)$]; and the summation is over all trees taller than z^* . Additional canopy closure heights may be similarly defined for forests in which the total crown area is greater than twice the ground area, as in some tropical forests (Bohlman and Pacala, in review). In this paper, we assume that the total crown area is less than twice the ground area, as in most temperate and boreal forests. We assume that individuals compete for a single resource, light, whose availability is uniform within each canopy layer. At any given time, trees taller than z^* are assumed to receive full sunlight, whereas trees shorter than z^* are assumed to experience a reduced understory light level that is independent of the size or species identity of the individuals in the upper canopy (i.e., we assume that all crowns cast the same amount of shade on a per area basis). Thus, we only consider two resource levels in this paper: full sunlight and a single understory light level. Height-structured competition for light (the only form of competition considered in this paper) occurs implicitly in the model according to the z^* criterion (Eq. 1): once the tallest individuals have filled the canopy, the remaining individuals are assumed to be in the understory where light availability is reduced. Height-structured competition for light, as represented by the z^* criterion, is the only form of competition represented in our model; thus, spatially explicit interactions between neighboring individuals are ignored. Dividing Eq. 1 by ground area, we have

$$1 = \sum_{\{z>z^*\}} N(z)A(z) \quad (2)$$

where $N(z)$ is the density of trees of height z . We assume that the number of trees is large enough so that a continuous approximation is reasonable:

$$1 = \int_{z^*}^{\infty} N(z)A(z)dz. \quad (3)$$

Strigul et al. (2008) found that the continuous approximation closely mimicked an individual-based spatially explicit simulator on a single hectare.

We assume that individual growth, mortality, and reproductive rates depend on species identity and light, but not explicitly on size: canopy and understory trees, respectively, of species j have constant trunk diameter (D) growth rates G_{jc} and G_{ju} (cm year^{-1}), mortality rates μ_{jc} and μ_{ju} (year^{-1}), and fecundity rates F_j and 0 (production of size D_0 individuals per unit crown area: individuals $\text{ha}^{-1} \text{ year}^{-1}$). Note that the mortality rates, μ , represent individual-level processes that are assumed to be uncorrelated in time and space, and which are distinct from patch-scale disturbance events that we introduce below. For simplicity, we assume that all individuals of all species share the same height and crown area allometries: $z = h_1 D^{h_2}$ and $A = a_1 D^{a_2}$. The assumption of a common height allometry implies a species-independent D^* , the minimum diameter of canopy trees, corresponding to a given z^* . Thus, we can rewrite Eq. 3 as:

$$1 = \int_{D^*}^{\infty} N(D)A(D)dD. \quad (4)$$

The above performance rates, allometries, and D^* definition lead to a simple demographic model based on the von Foerster equation (von Foerster 1959) for the dynamics of size-structured populations. We now summarize the analysis of Strigul et al. (2008) for a single species in a well-mixed uniform environment to provide context for the metacommunity model developed below. The von Foerster system for the flat-top PPA model is

$$\frac{\partial N(D,t)}{\partial t} = -G_u \frac{\partial N(D,t)}{\partial D} - \mu_u N(D,t) \text{ if } D < D^*, \text{ and} \quad (5a)$$

$$\frac{\partial N(D,t)}{\partial t} = -G_c \frac{\partial N(D,t)}{\partial D} - \mu_c N(D,t) \text{ if } D \geq D^* \quad (5b)$$

with boundary conditions

$$N(D_0,t) = \frac{1}{G_u} \int_{D_0}^{\infty} N(D,t)A(D)F(D)dD \quad (6a)$$

where $F(D)=F$ for $D>D^*$ and 0 otherwise, and

$$\lim_{D \rightarrow D^*-} G_u N(D) = \lim_{D \rightarrow D^*+} G_c N(D). \quad (6b)$$

Equation 6b conserves mass across the discontinuity at D^* . We now solve for the equilibrium size distribution, $\hat{N}(D)$, and the associated \hat{D}^* that would occur in the absence of disturbance. Population persistence implies a closed canopy (i.e., $\hat{D}^* > D_0$) (Strigul et al. 2008) so that at equilibrium, Eq. 6a becomes

$$\hat{N}(D_0) = \frac{F}{G_u} \int_{\hat{D}^*}^{\infty} \hat{N}(D)A(D)dD = \frac{F}{G_u}. \quad (7)$$

From Eqs. 5a–7, the equilibrium size distribution is

$$\hat{N}(D) = \frac{F}{G_u} e^{-\frac{\mu_u}{G_u}(D-D_0)} \text{ if } D < \hat{D}^* \quad (8a)$$

and

$$\hat{N}(D) = \frac{F}{G_c} e^{-\frac{\mu_u}{G_u}(\hat{D}^*-D_0)} e^{-\frac{\mu_c}{G_c}(D-\hat{D}^*)} \text{ if } D \geq \hat{D}^*. \quad (8b)$$

At equilibrium, and assuming $D_0=0$, Eq. 4 becomes

$$1 = \int_{\hat{D}^*}^{\infty} \frac{F}{G_c} e^{-\frac{\mu_u}{G_u}\hat{D}^*} e^{-\frac{\mu_c}{G_c}(D-\hat{D}^*)} a_1 D^{a_2} dD$$

$$= \frac{Fa_1}{G_c} e^{(\frac{\mu_c}{G_c}-\frac{\mu_u}{G_u})\hat{D}^*} \int_{\hat{D}^*}^{\infty} e^{-\frac{\mu_c}{G_c}D} D^{a_2} dD.$$

An approximate solution for \hat{D}^* is (Electronic supplementary materials [ESM] Appendix 1):

$$\hat{D}^* \approx \left(\frac{\mu_u}{G_u} - \frac{\mu_c}{G_c} \right)^{-1} \ln(R_0) \approx \frac{G_u}{\mu_u} \ln(R_0) \quad (9a)$$

where $[(\mu_u/G_u) - (\mu_c/G_c)] \approx \mu_u/G_u$ given that mortality is substantially higher and growth substantially lower in the understory than the canopy (Purves et al. 2008), and R_0 is the expected number of size D_0 offspring produced by a size D_0 individual in an empty habitat:

$$R_0 \approx \frac{Fa_1 G_c^{a_2} \Gamma(a_2 + 1)}{\mu_c^{a_2+1}} \quad (9b)$$

where $\Gamma(\cdot)$ is the gamma function. Equation 9b is exact if $D_0=0$ (ESM Appendix 1). Given the assumptions of a single understory light level (so that G_u and μ_u do not depend on the size or species identity of the canopy trees), a uniform well-mixed environment, and the absence of disturbance, the PPA predicts that the species with the largest value of \hat{D}^* (when grown in monoculture) competitively excludes all other species (Adams et al. 2007; Strigul et al. 2008).

The fact that most real forests contain multiple tree species implies that the above assumptions are overly restrictive. Two conspicuous aspects of real landscapes, which we have ignored thus far, are spatial heterogeneity (e.g., edaphic or topographic variation) and disturbances that kill multiple individuals. In the sections that follow, we develop a metacommunity version of the PPA model to explore the roles of between-patch heterogeneity in the abiotic environment (e.g., soil type) and patch-scale disturbance in maintaining local (within-patch) tree diversity.

PPA metacommunity framework

We use the terms “metacommunity” and “landscape” to refer to the same scale, i.e., the metacommunity is the collection of patches on the landscape that are connected by dispersal (Leibold et al. 2004). We consider a system with n patch types (e.g., soil types) and n species. Each species is the dominant competitor in one patch type and subordinate in all other patch types. We assume a single understory light level so that in the absence of disturbance and inter-patch dispersal, the PPA predicts dominance of a single species in each patch (Adams et al. 2007; Strigul et al. 2008). We assume that all patches are the same size and that each is large enough to ignore demographic stochasticity. We assume that the landscape is large enough so that the dynamics are also deterministic at the landscape scale (i.e., there are many patches of each type). We assume a completely symmetric system: (1) each patch type and each species is equally abundant at the landscape scale; (2) in each patch, the locally dominant competitor has the highest density and the other $n-1$ subordinate species share an equal reduced density; (3) densities in all patches are identical except with respect to the identities of the dominant and subordinate species; and (4) for each of the five performance rates (G_u , μ_u , G_c , μ_c , and F), there are exactly two values in the metacommunity: one each for the dominant and subordinate species in each patch. Patches interact with each other only via dispersal, which is spatially implicit (Leibold et al. 2004). Specifically, we assume that a proportion m of seeds are dispersed uniformly and deterministically over the entire landscape (with no mortality occurring during dispersal) and a proportion $1-m$ remain in their patch of origin. We assume a single, constant germination rate for all species in all patch types so that variation in seedling recruitment solely reflects variation in seed rain. We assume zero initial size for seedlings, i.e., $D_0=0$.

Our symmetry assumptions (see above) simplify mathematical analysis of the model. We have not yet studied less restrictive systems in detail, but preliminary simulations (not shown) suggest that our results do not depend qualitatively on our symmetry assumptions. Note that despite our simplifying assumptions, a metacommunity representing many patches of each type is required to study patch-scale disturbance because each patch type may have many different states (depending on the time since disturbance) that must be considered simultaneously to quantify the global seed rain that is shared among patches. It would be possible to externally impose the global seed rain, but in this case, there would be no feedback from the local to the metacommunity scale (Leibold et al. 2004) and the system would not be internally consistent.

Given our assumptions (no demographic stochasticity; deterministic, uniform inter-patch dispersal; all species

equally abundant in the landscape), $m > 0$ should guarantee that all species are present in all patches. Thus, we do not study coexistence per se. Rather, we focus on the degree of local mixing, or “diversity,” i.e., the degree to which mass effects equalize the within-patch densities of locally dominant and subordinate competitors. Specifically, we quantify how local mixing depends on (1) the inter-patch dispersal rate, m ; (2) the degree of habitat specialization (i.e., the difference in performance rates between locally dominant and subordinate species); and (3) patch age (time since disturbance).

In the following two sections, we derive an analytical approximation for the equilibrium state of a patch in the metacommunity and then use simulations to test the approximation and to study the post-disturbance transient dynamics.

Equilibrium approximation

Here, we derive an approximation for the equilibrium proportion of canopy area in each patch occupied by the dominant species, \hat{p} , and each of the $n-1$ subordinate species, $(1-\hat{p})/(n-1)$. Other aspects of the equilibrium (e.g., \hat{D}^*) follow from \hat{p} . Given our symmetry assumptions, characterization of a single patch is sufficient to characterize the entire system. Strigul et al. (2008) showed that \hat{D}^* in the single-patch flat-top model with $a_2=2$ is locally stable if $(\mu_u/G_u)\hat{D}^* \geq 2$ and oscillates if this quantity is between 1 and 2; extinction occurs otherwise. Simulations suggest similar criteria for the metacommunity studied here, but we have not studied this problem in detail. Simulations using the parameter values in ESM Appendix 2 appear to have a globally stable internal equilibrium, and we assume this is the case in our analysis here.

In the one-patch single-species case, the rate of seedling recruitment (hereafter, “recruitment”) is simply the fecundity rate per crown area (F) if, as at equilibrium, the canopy is closed (i.e., canopy area=ground area). In each patch in the metacommunity, the equilibrium recruitment rate for the dominant species is

$$\begin{aligned}\hat{b}_d &= (1-m)\hat{p}F_d + \frac{m\hat{p}}{n}F_d + \left(\frac{n-1}{n}\right)\frac{m(1-\hat{p})}{n-1}F_s \quad (10a) \\ &= (1-m)\hat{p}F_d + \frac{m\hat{p}}{n}F_d + \frac{m(1-\hat{p})}{n}F_s\end{aligned}$$

where F_d and F_s are, respectively, fecundity rates for the dominant and subordinate species. The first term is due to seeds produced within the same patch, the second term is due to globally dispersed seeds originating from the fraction $1/n$ of the landscape where the locally dominant

species is dominant and occupies a proportion \hat{p} of the canopy area, and the third term is due to globally dispersed seeds originating from the fraction $(n-1)/n$ of the landscape where the locally dominant species is subordinate and occupies a proportion $(1-\hat{p})/(n-1)$ of the canopy area. The equilibrium recruitment rate for the subordinate species is

$$\hat{b}_s = \frac{(1-m)(1-\hat{p})}{n-1}F_s + \frac{m\hat{p}}{n}F_d + \frac{m(1-\hat{p})}{n}F_s. \quad (10b)$$

The first term is due to seeds produced within the same patch where the subordinate species occupies a proportion $(1-\hat{p})/(n-1)$ of the canopy area, and the second two terms are identical to those in Eq. 10a because locally dominant and subordinate species are assumed to be equally abundant in the landscape.

The equilibrium size distributions for the dominant and subordinate species, $\hat{N}_d(D)$ and $\hat{N}_s(D)$, respectively, are identical to Eqs. 8a and 8b, except that F in Eqs. 8a and 8b is replaced by \hat{b}_d and \hat{b}_s (Eqs. 10a and 10b) and each G and μ parameter has an additional subscript (“d” or “s”). These size distributions lead to two independent expressions for \hat{D}^* , which comprise a system of two equations with two unknowns (\hat{D}^* and \hat{p}):

$$\hat{p} = \int_{\hat{D}_d^*}^{\infty} \hat{N}_d(D)A(D)dD \quad (11a)$$

and

$$\frac{1-\hat{p}}{n-1} = \int_{\hat{D}_s^*}^{\infty} \hat{N}_s(D)A(D)dD \quad (11b)$$

where, by definition, $\hat{D}^* = \hat{D}_d^* = \hat{D}_s^*$. Equations 11a and 11b simply state that the dominant and subordinate species occupy \hat{p} and $(1-\hat{p})/(n-1)$ of the total canopy area, respectively. To obtain an approximate solution to Eqs. 11a and 11b, we first combine it with Eqs. 9a and 9b to yield the following two approximations for \hat{D}^* :

$$\begin{aligned}\hat{D}_d^* \approx \tilde{D}_d^* &\equiv \frac{G_{ud}}{\mu_{ud}} \ln \left(\frac{\hat{b}_d a_1 G_{cd}^{a_2} \Gamma(a_2+1)}{\hat{p} \mu_{cd}^{a_2+1}} \right) \\ \text{and} \\ \hat{D}_s^* \approx \tilde{D}_s^* &\equiv \frac{G_{us}}{\mu_{us}} \ln \left(\frac{\hat{b}_s (n-1) a_1 G_{cs}^{a_2} \Gamma(a_2+1)}{(1-\hat{p}) \mu_{cs}^{a_2+1}} \right)\end{aligned}$$

where $\tilde{D}_d^* \approx \tilde{D}_s^*$ (strict equality would occur if the errors in the two approximations were the same, which they are not in general). Now, consider a small perturbation from the neutral case (where all species have equal performance in

all patches and $\hat{p} = 1/n$ such that the dominant species has a small advantage (ε) in each performance rate $\theta = (G_u, \mu_u, G_c, \mu_c, F)$:

$$\theta_d = (1 + \varepsilon/2)\theta_0,$$

$$\theta_s = (1 - \varepsilon/2)\theta_0$$

and

$$\hat{p} = (1 + \delta)/n$$

where θ_d and θ_s are, respectively, performance rates for the dominant and subordinate species; ε is a vector of performance perturbations; θ_0 are the baseline performance rates; and δ is the perturbation to \hat{p} . To simplify the presentation, we define $\tau_u \equiv \mu_u^{-1}$ and $\tau_c \equiv \mu_c^{-1}$ as expected lifetimes in the understory and canopy, respectively. Thus, $\theta = (G_u, \tau_u, G_c, \tau_c, F)$ and all elements of ε are positive. We now write \tilde{D}_d^* and \tilde{D}_s^* as functions of \hat{p} and θ , and we Taylor expand around the neutral case:

$$\tilde{D}_d^*(\hat{p}, \theta_d) \approx \tilde{D}_d^*\left(\frac{1}{n}, \theta_0\right) + \left(\frac{\delta}{n}\right) \frac{\partial \tilde{D}_d^*}{\partial \hat{p}} + \sum_i \frac{\varepsilon_i}{2} \theta_{0i} \frac{\partial \tilde{D}_d^*}{\partial \theta_{di}} \quad (12a)$$

and

$$\tilde{D}_s^*(\hat{p}, \theta_s) \approx \tilde{D}_s^*\left(\frac{1}{n}, \theta_0\right) + \left(\frac{\delta}{n}\right) \frac{\partial \tilde{D}_s^*}{\partial \hat{p}} - \sum_i \frac{\varepsilon_i}{2} \theta_{0i} \frac{\partial \tilde{D}_s^*}{\partial \theta_{si}} \quad (12b)$$

where all derivatives are evaluated at $(\hat{p} = 1/n, \theta = \theta_0)$ and i indexes the elements of θ . Noting that $\tilde{D}_d^* \approx \tilde{D}_s^*$ and that at $(\hat{p} = 1/n, \theta = \theta_0)$, $\frac{\partial \tilde{D}_d^*}{\partial \theta_{di}} = \frac{\partial \tilde{D}_s^*}{\partial \theta_{si}}$ for all i , we have

$$\begin{aligned} \delta \approx \tilde{\delta} &\equiv n \left(\frac{\partial \tilde{D}_s^*}{\partial \hat{p}} - \frac{\partial \tilde{D}_d^*}{\partial \hat{p}} \right)^{-1} \sum_i \varepsilon_i \theta_{0i} \frac{\partial \tilde{D}_d^*}{\partial \theta_i} \\ &= \frac{n-1}{mn} [(\varepsilon_{G_u} + \varepsilon_{\tau_u}) \ln(R_0) + \varepsilon_{G_c} a_2 + \varepsilon_{\tau_c} (a_2 + 1) + \varepsilon_F] \end{aligned} \quad (13)$$

where all derivatives are evaluated at $(\hat{p} = 1/n, \theta = \theta_0)$ and R_0 (Eq. 9b) is evaluated at $\theta = \theta_0$. Equation 13 yields an approximation for the canopy area of the local dominant at equilibrium: $\hat{p} \approx (1 + \tilde{\delta})/n$. Because the approximation is linear, it is accurate only for sufficiently small ε . If ε is sufficiently large, the approximation yields predictions outside of the meaningful range ($\hat{p} > 1$), which we interpret qualitatively as predictions of little local mixing (weak mass effects).

Implications of equilibrium results

Equation 13 suggests that the canopy area of the locally subordinate competitor increases with inter-patch dispersal,

m , which in turn should depend on patch size (i.e., the scale of heterogeneity) and the dispersal kernels of the species in the community. Given observed dispersal kernels (e.g., Ribbens et al. 1994; Clark et al. 1999) and our assumption that patch size is large enough to ignore demographic stochasticity, we consider $m=0.1$ (10% of seeds globally dispersed) a realistic upper bound. Combining $m=0.1$ with realistic performance rates of late-successional trees (ESM Appendix 2) leads to the prediction of weak mass effects (little local mixing) if the dominant species has a 1% or greater advantage in all performance rates (i.e., $\varepsilon > 0.01$; Fig. 1b). To put this result in concrete terms, consider the problem of using field data to distinguish the mean growth rates of two co-occurring species, with typical coefficients of variation of 50% for individual growth rates within canopy classes (e.g., canopy vs. understory) in a given environment (ESM Appendix 3; note that empirical estimates of individual-level variance reflect both sampling error and individual-level process variation, which our model ignores; see “Discussion”). Using a two-sample, one-tailed t test with a type I error rate of 0.05 and a coefficient of variation of 50%, detecting a 1% difference in mean growth rate with 80% probability (type II error rate=0.2) requires sample sizes of about 31,000 per species (differences in mortality and fecundity should require even larger sample sizes as both are more difficult to measure than growth). With realistic sample sizes of 100 per species, an 80% detection rate requires $\varepsilon > 0.17$ (17% difference in mean growth rate). Even with $m=1$, $\varepsilon > 0.17$ leads to the prediction of weak mass effects (Fig. 1c). For $m=0.01$ (which we do not view as unrealistically small), local mixing is predicted to occur only for extremely small values of ε (< 0.001 ; Fig. 1a).

The key insight from our equilibrium analysis is that habitat specialization (i.e., differences in performance between locally dominant and subordinate species) that is too small to be reliably detected from field data (small ε) can nevertheless lead to nearly complete numerical dominance by the locally dominant competitor. Additional insights may be gleaned by examining the terms in Eq. 13. For example, assuming $R_0 \gg 1$ and $a_2 = 1.5$ (ESM Appendix 2), equilibrium diversity is predicted to be more sensitive to specialization in understory performance (ε_{G_u} and ε_{τ_u}) than canopy performance (ε_{G_c} , ε_{τ_c} and ε_F). Using the parameter values for late-successional species in ESM Appendix 2, the “sensitivity” of $\tilde{\delta}$ to ε_{G_u} and ε_{τ_u} is $\ln(R_0) = 6.8$ compared to 1.5, 2.5, and 1 for ε_{G_c} , ε_{τ_c} and ε_F , respectively. Another prediction of Eq. 13 is that local diversity should decrease with R_0 (which should increase with habitat productivity) if $\varepsilon_{G_u} + \varepsilon_{\tau_u} > 0$. However, the strength of this effect is modest, even for large changes in R_0 (Fig. 1).

Results presented in this section should be qualified for at least two reasons. Firstly, they apply to a community at

equilibrium, which may rarely if ever be reached in reality (Whittaker and Levin 1977; Connell 1978). Secondly, they rely on a linear approximation that yields unrealistic values ($\hat{p} > 1$) for modest values of ε (Fig. 1). To assess the robustness of the above results, we now turn to simulations.

Transient dynamics following catastrophic disturbance

We used simulations to study the within-patch transient dynamics in metacommunities with two patch types. We studied two-species systems (each species dominant in one patch type) using the late-successional parameter values in ESM Appendix 2. To determine whether interactions between late-successional species are qualitatively altered by the presence of early-successional species, we also studied systems that included early-successional species (each successional guild with one dominant and one subordinate competitor per patch type; see ESM Appendix 2 for parameter values). Early- and late-successional species were assumed to differ only in their growth and mortality rates (G_u , μ_u , G_c , and μ_c), i.e., they had the same values for allometry (a_1 , a_2 , h_1 , and h_2), fecundity (F), and the proportion of seeds that are globally dispersed (m).

We assumed a catastrophic disturbance regime in which all trees and seeds in a patch are killed so that the initial seed rain in disturbed patches is solely from the fraction m of seeds that are globally dispersed. This assumption facilitates a numerical solution for the landscape-scale equilibrium (see details below), which obviates the need for lengthy simulations that would otherwise be necessary. As with the mathematical analysis above, simulations were deterministic at the within-patch scale (where we assumed there were many individuals) and the landscape scale (where we assumed many patches), and each patch type

was equally abundant in the landscape. We simulated a multispecies version of the von Foerster system (Eqs. 5a and 5b) by simulating the dynamics of cohorts as described in Purves et al. (2008). We used a 0.2 yearly time step (i.e., every 0.2 years, 20% of the annual growth, mortality, reproduction, and recruitment occurred), which nearly eliminated high-frequency fluctuations observed with longer time steps [we have not studied this problem in detail, but we believe these fluctuations occur in discrete time simulations of the PPA model because the negative density dependence imposed by the z^* criterion (Eq. 1) is applied at the patch scale (i.e., the PPA model is a mean-field approximation), as opposed to more localized neighborhood interactions in spatially explicit forest models (e.g., Pacala et al. 1996). Such erratic behaviors are well known in discrete time mean-field models (May 1976)].

We assumed that disturbances occur randomly in space and time at rate d (year^{-1}) so that the patch age distribution is negative exponential: $f(y) = de^{-dy}$, where y is the number of years since a patch was last disturbed. We also studied the case where each patch is disturbed when it is $2d^{-1}$ years old so that the age distribution is uniform: $f(y) = 2d^{-1}$. In both the exponential and uniform cases, the mean age is d^{-1} . We studied cases with $d=0.005$ and $d=0.01$. Results were qualitatively similar for either distributional form and either disturbance rate. We only report results for the exponential case with $d=0.005$.

Given that the system is deterministic and that disturbance is catastrophic (i.e., all seeds and trees in a patch are killed), the dynamics are uniquely determined once the recruitment rate from global seed rain (hereafter “global recruitment”) reaches its equilibrium, \hat{B}_j , for all species j (in our symmetric system, there is only value of \hat{B}_j per successional guild. The algorithm described below is not restricted to the symmetric case, so we retain the subscript j

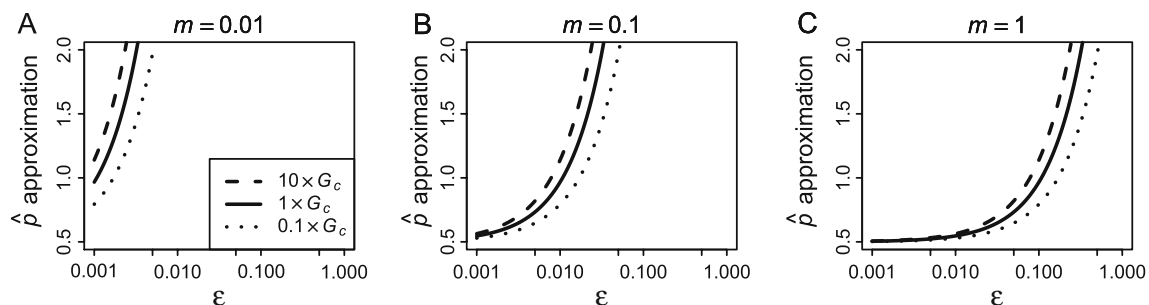


Fig. 1 Equilibrium approximation for the proportion of canopy area occupied by the dominant species as a function of ε (proportional difference between dominant and subordinate species in all five individual performance rates: growth and mortality in the understory and canopy, and fecundity). The approximation is $\hat{p} \approx (1 + \tilde{\delta})/n$, where $\tilde{\delta}$ is given by Eq. 13 and $n=2$ (two species). Local diversity increases (\hat{p} decreases) as inter-patch dispersal (m) increases and as R_0 (Eq. 9b) decreases. The effects of R_0 (which should increase with

habitat productivity) are illustrated by multiplying the baseline canopy growth rate (G_c) for both dominant and subordinate species by 10, 1, or 0.1, yielding $\ln(R_0)=10.3$, 6.8, and 3.4, respectively. If ε is sufficiently large, the linear approximation yields predictions outside the meaningful range ($\hat{p} > 1$), which we interpret as predictions of little mixing ($\hat{p} \approx 1$). Note the logarithmic x -axis scale. Baseline parameter values (i.e., $\varepsilon=0$) are for the late-successional species in ESM Appendix 2

for generality). In other words, each patch can be characterized by the transient dynamics that would occur when the landscape, or metacommunity, is at equilibrium (i.e., when the statistical mean across many patches is at steady state). In contrast, if at least some seeds or trees survive disturbance, then the transient dynamics depend on the pre-disturbance state of the patch. We do not address this situation in this paper. Assuming that there is a single internal equilibrium $\hat{\mathbf{B}}$ (the vector of \hat{B}_j values), it can eventually be attained, in principle, from any reasonable initial condition by simulating a large number of patches with a stochastic disturbance process. However, the assumption of catastrophic disturbance allows for a more robust and efficient numerical solution for $\hat{\mathbf{B}}$. Note that equilibrium global recruitment for species j is:

$$\hat{B}_j = m \int_0^{\infty} f(y) \hat{b}_j(y) dy \quad (14)$$

where m is the proportion of seeds that are globally dispersed; $f(y)$ is the patch age distribution; $\hat{b}_j(y) = \sum_k \pi_k \hat{C}_{jk}(y) F_{jk}$ is species j 's seedling production, averaged across patch types k , in patches of age y ; π_k is the proportion of the landscape comprising type k patches ($\pi_k = 1/n$ for all k in our symmetric system); $\hat{C}_{jk}(y)$ is species j 's equilibrium proportion of canopy area in patches of type k and age y ; and F_{jk} is species j 's seedling production rate (per unit canopy area) in type k patches. "Equilibrium" here refers to the landscape, or metacommunity, rather than a patch, i.e., the function $\hat{C}_{jk}(y)$ gives the within-patch transient (non-equilibrium) dynamics of species j 's canopy area in patch type k when the landscape is at steady state. Let $\hat{\mathbf{C}}(y)$ be the matrix of values $\hat{C}_{jk}(y)$ at each age y describing the expected patch-scale transient dynamics of canopy area for each species in each patch type at the landscape-scale equilibrium. The following algorithm can be used to iteratively solve for $\hat{\mathbf{B}}$ and $\hat{\mathbf{C}}(y)$:

1. Choose an initial guess \mathbf{B}' for $\hat{\mathbf{B}}$.
2. Simulate the post-disturbance dynamics of a single patch of each type from time $t=0$ (with 0 initial biomass) to time $t=T$, with T sufficiently large such that $f(T) \approx 0$. Recruitment in the simulator is calculated at time t for each species j in each patch k as $r_{jk}(t) = (1 - m)C_{jk}(t)F_{jk} + B'_j$, where $C_{jk}(t)$ is simulated canopy area; the first term is recruitment due to within-patch seed production and the second term is the current estimate for global recruitment, which is externally imposed on the simulator.
3. Substitute $C_{jk}(t)$ for the unknown values $\hat{C}_{jk}(y)$ in Eq. 14 to calculate, for each species j , a current estimate \hat{B}'_j for the unknown \hat{B}_j .

4. If $\hat{B}'_j \approx B'_j$ for all j , then the algorithm terminates with $\hat{B}_j \approx \hat{B}'_j$ and $\hat{C}_{jk}(y) \approx C_{jk}(y)$. Otherwise, if $\hat{B}'_j < B'_j$, decrease B'_j by a small amount and return to step 2. Otherwise, increase B'_j by a small amount and return to step 2.

Intuitively, the above algorithm combines the known patch age distribution, $f(y)$, with the temporal dynamics observed in a single simulated patch of each type to calculate $\hat{\mathbf{B}}'$, the global recruitment that would occur in a landscape comprising many patches whose age-dependent states match those of the simulated patches and whose global recruitment is the externally imposed vector \mathbf{B}' . The algorithm converges if the global recruitment implied by the simulator ($\hat{\mathbf{B}}'$) matches the global recruitment imposed on the simulator (\mathbf{B}'). Our convergence criterion was that the implied and imposed values must be within 1% of each other for all species. Upon convergence, we introduced random perturbations to ensure that the system returned to the neighborhood of the putative equilibrium, i.e., to ensure that the algorithm had identified a stable equilibrium.

Simulation results

Not surprisingly, disturbance allowed for stable coexistence of early- and late-successional species (ESM Appendix 4). Except where noted below, the presence of early-successional species did not qualitatively alter the competitive dynamics between late-successional species. Therefore, our presentation here focuses on the two-species system (no early-successional species). For consistency with the equilibrium analysis above, we use canopy area as an abundance index. Basal area and biomass patterns are qualitatively similar to canopy area patterns because only a small proportion of tree biomass is in the understory.

Figure 2 shows the patch-scale transient dynamics in metacommunities with different values of m and ε (same ε for all performance rates: G_u , μ_u , G_c , μ_c , and F). Canopy area of both species (two solid curves in Fig. 2) increases until the canopy closes (total canopy area=1), at which point the subordinate species' area declines. The equilibrium approximation (dotted lines in Fig. 2) appeared accurate in most cases, but the transient dynamics were slow for realistic values of m (0.01 or 0.1; two top rows in Fig. 2) and small values of ε (0.01 or 0.05; two left columns in Fig. 2) such that the subordinate species occupied >10% of the canopy area for >1,000 years (which spans >99% of the cumulative patch age distribution). In contrast, for $\varepsilon=0.25$ (which is large enough to be reliably detected from field data; see power analysis in the preceding section), the subordinate species' canopy area approached zero shortly after the time of canopy closure (Fig. 2, right column).

When all seeds were globally dispersed ($m=1$), the dominant species' canopy area in some cases reached an

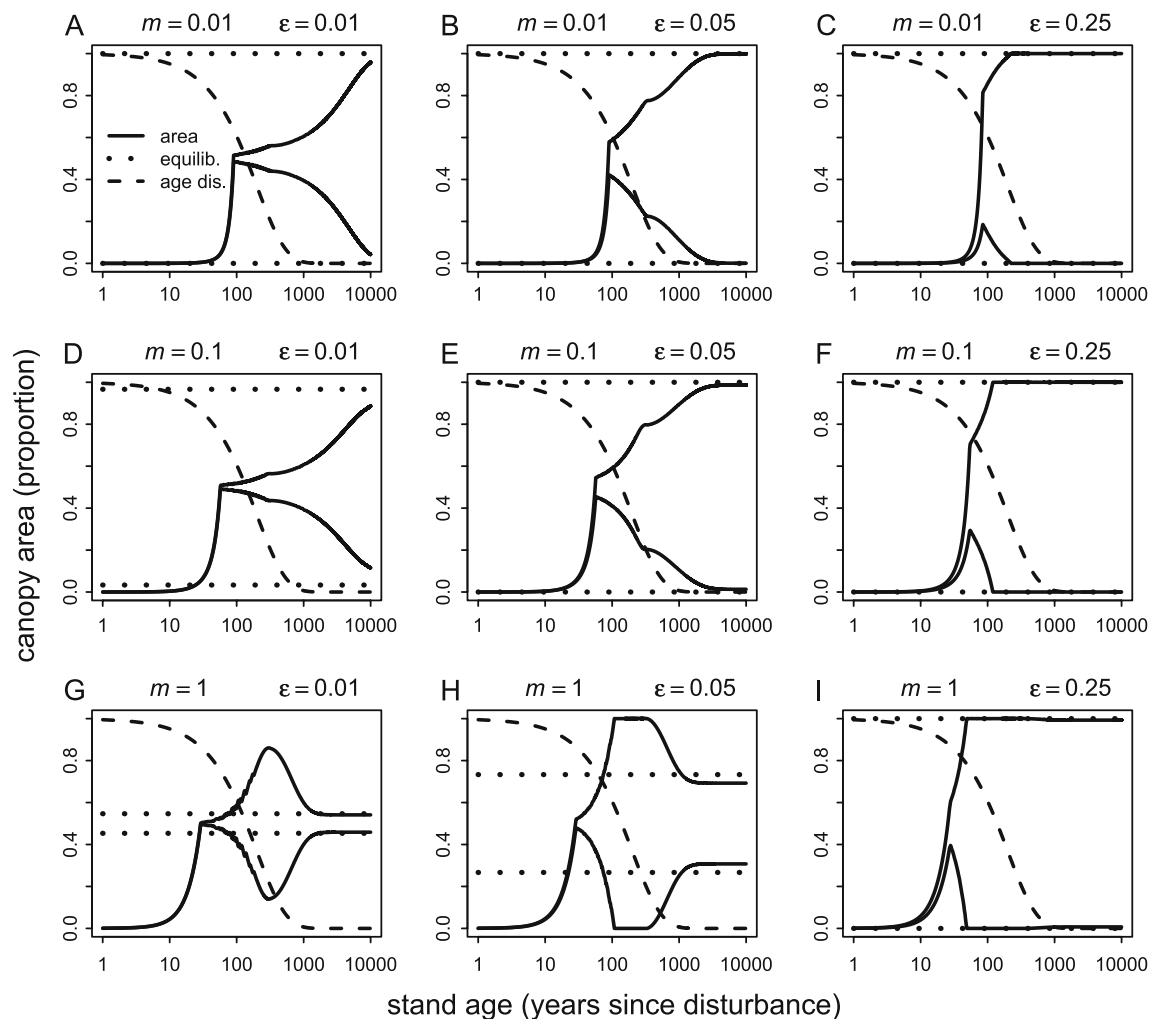


Fig. 2 Transient dynamics of canopy area in a single patch in two-species systems. The canopy areas (proportion of ground area) of the dominant and subordinate species are shown by the *upper* and *lower solid curves*, respectively. The dominant species has a proportional advantage ε in each of the five performance rates: growth and mortality in the canopy and understory, and fecundity. *Columns 1–3* have $\varepsilon=0.01$, 0.05 , and 0.25 , respectively. *Rows 1–3* have m (inter-patch dispersal rate) $=0.01$, 0.1 , and 1 , respectively. The probability density function (pdf) for the negative exponential patch age distribution (with mean age $=200$ years) is shown by the *dashed line*

(the pdf is scaled in the figure to have a maximum of 1). Equilibrium approximations for the dominant and subordinate species' canopy areas (from Eq. 13) are shown by the *dotted lines*. In cases where the linear approximation yields values outside the meaningful range (i.e., canopy area of dominant >1 ; Fig. 1), the approximations are plotted at 0 and 1 (no local mixing). Baseline parameters values ($\varepsilon=0$) are for the late-successional species in ESM Appendix 2. The corresponding figure for a four-species system (two early- and two late-successional species) is in ESM Appendix 4

early-successional peak before declining to an asymptote (Figs. 2g, h). This behavior was not observed among late-successional species when early-successional species were included because even in the limiting case of $m=1$, early-successional species prevented late-successional species from overshooting their equilibrium abundances (ESM Appendix 4).

In contrast to the equilibrium, where local mixing is most sensitive to differences in understory performance, differences in canopy performance dominated much of the transient phase (Fig. 3). Following catastrophic disturbance, there is initially no understory (early-arriving cohorts are in full sunlight and are classified as being in the canopy). Even after the canopy

closes (between about 10 and 100 years in our simulations; Fig. 2), there can be a considerable delay before understory differences begin to exert a strong influence on the dynamics of canopy area (after about 400 years in our simulations; Fig. 3). This delay is due to the long life span of early-arriving cohorts that were born in full sunlight.

Discussion

Our analysis of a height-structured forest metacommunity model, based on the PPA (Purves et al. 2008; Strigul et al. 2008), suggests that tree species whose rates of individual

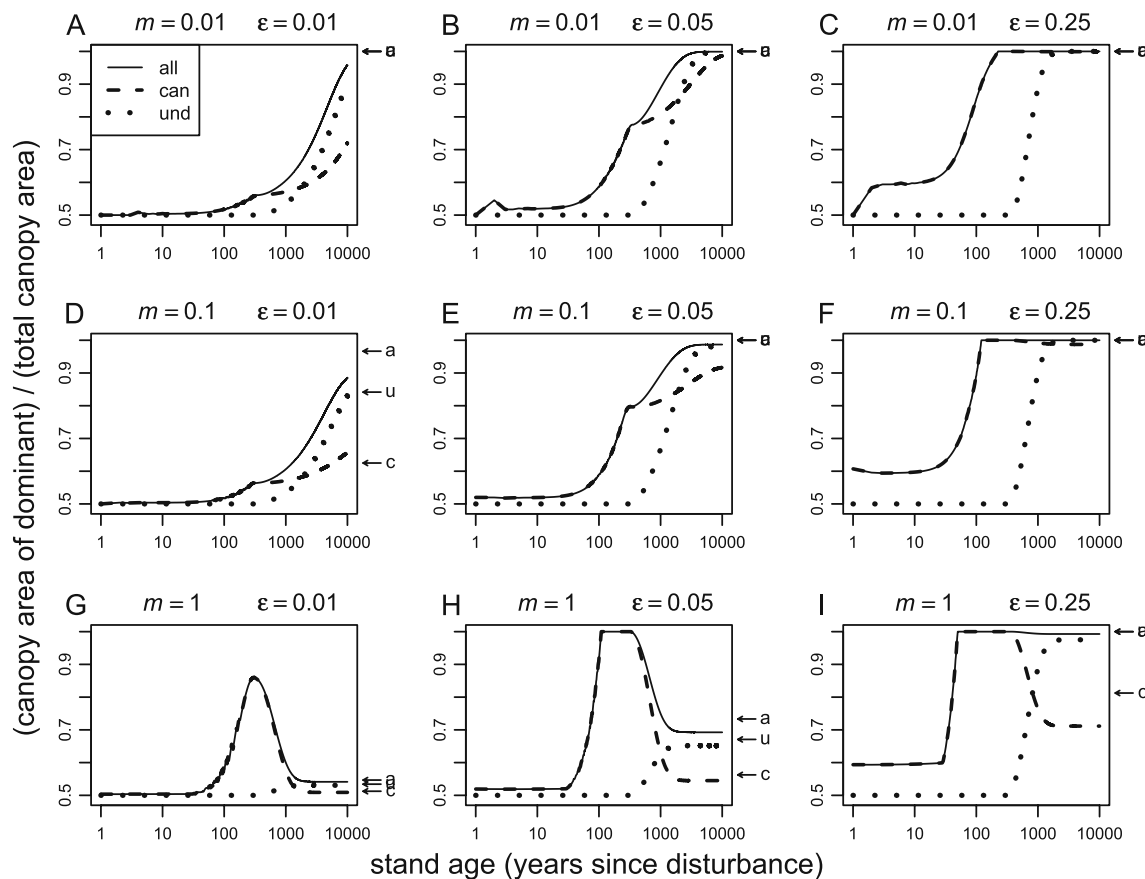


Fig. 3 Transient dynamics of local dominance in a single patch in two-species systems. The y-axis is the canopy area of the dominant species divided by the canopy areas of the dominant and subordinate species combined (0.5 indicates equal abundances). The solid, dashed, and dotted curves, respectively, show the dynamics for cases where the dominant species has a proportional advantage ε in (1) all performance rates (both canopy and understory), (2) only canopy performance (growth, mortality, and fecundity), or (3) only understory

performance (growth and mortality). Columns 1–3 have $\varepsilon=0.01$, 0.05, and 0.25, respectively. Rows 1–3 have m (inter-patch dispersal rate)=0.01, 0.1, and 1, respectively. Equilibrium approximations (from Eq. 13) are shown along the right margin of each panel for the cases where the dominant species has a performance advantage in all parameters (“a”), canopy parameters only (“c”), or understory parameters only (“u”). Baseline parameters values ($\varepsilon=0$) are for the late-successional species in ESM Appendix 2

performance (growth, mortality, and fecundity) are different enough to be reliably distinguished from field data are unlikely to locally mix in appreciable numbers (i.e., “mass effects” are predicted to be weak) even if specialization to different habitats and regional similarity (Amarasekare and Nisbet 2001; Mouquet and Loreau 2002) ensure coexistence at the landscape scale. Performance differences that are large enough to detect, given the variability of field data and realistic sample sizes, have such a strong effect on competitive dynamics so as to quickly overwhelm the initially equal post-disturbance abundances in our model. Perhaps more surprisingly, given realistic rates of inter-patch dispersal ($\leq 10\%$ of seeds globally dispersed) and in the absence of patch-scale disturbance, mass effects are weak even for performance differences as small as 1%. Differences of this magnitude are much too small to be reliably detected from field data. In this case, however, the transient dynamics following catastrophic disturbance are

slow such that locally subordinate species comprised $>10\%$ of the canopy area for $>1,000$ years in our simulations. Under many, if not most, natural and anthropogenic disturbance regimes (e.g., Canham and Loucks 1984), most of the landscape would be younger than the age required for competitive displacement of such mildly disadvantaged species. An important question, which we have not yet addressed, is whether or not species can be similar enough so that mass effects are strong (i.e., “sink” species are relatively common), yet different enough so that the metacommunity dynamics are not dominated by neutral drift (Hubbell 2001; Chave 2004).

Our prediction of weak mass effects in the presence of easily detected species differences is based on empirical estimates of individual growth variance (coefficient of variation of 50% for a given species, locality, and crown class; ESM Appendix 3), which we would expect to be at least as large as the variance associated with mortality and

fecundity (which are more difficult than growth to measure in the field). Individual-level variance reflects sampling error as well as individual-level processes (Clark et al. 2003), which our model ignores. It would be straightforward to account for individual variation in our model by simulating the dynamics of individuals rather than cohorts, and this would be an interesting avenue for future work. In many cases, uncorrelated variation in individual performance has little impact on community dynamics (Lichstein et al. 2007), whereas correlated variation in the form of trade-offs should promote coexistence (Clark et al. 2007, 2010).

It is difficult to directly compare our results to other source–sink metacommunity studies (e.g., Mouquet and Loreau 2003) due to fundamental differences in model structure. Nevertheless, the weak mass effects predicted by our height-structured model are not obviously inconsistent with predictions from Mouquet and Loreau’s (2003) non-height-structured model (see their Fig. 1 with inter-patch dispersal rate of 0.1). In general, however, we would expect mass effects to weaken as the intensity of height structured competition increases (i.e., as the expected time for a seedling to reach the canopy increases) because the understory stage in tree life cycles acts as an additional filter on community composition that is absent in non-height-structured systems. Future work should aim to formulate height-structured and non-height-structured metacommunity models that can be directly compared so that the role of height-structured competition in community dynamics can be quantified.

In quantifying mass effects, we have focused on the abundance of sink species, as opposed to local coexistence per se (e.g., Shmida and Ellner 1984; Amarasekare and Nisbet 2001; Mouquet and Loreau 2002). It is important to note that mass effects may be too weak to allow sink species to be locally common, yet strong enough to allow them to persist at low density. Thus, the perceived strength of mass effects depends in part on whether it is evaluated in terms of species richness or species abundances.

The transient dynamics following catastrophic disturbance studied here should differ from the dynamics following less severe forms of disturbance in at least two important respects. Firstly, we would expect the rate of competitive displacement of subordinate species to be faster following less severe disturbances in which pre-disturbance abundances would at least partially carry over to the post-disturbance initial condition; that is, if the dominant species has a numerical advantage immediately following disturbance, this should hasten the approach to the patch-scale equilibrium relative to our analysis in which post-disturbance abundances are initially equal. Although it is possible that certain forms of disturbance that disproportionately affect different tree size classes could result in post-disturbance

initial conditions that favor locally subordinate species, we suspect that the transient dynamics presented here represent an upper bound to the expected level of transient mixing under most realistic disturbance scenarios. Secondly, following catastrophic disturbance, differences in understory performance are irrelevant until the canopy closes and may have relatively weak effects on mixing for some time thereafter. Less severe disturbances would increase the importance of understory differences early in succession by (1) diminishing the time to canopy closure (before which there is no understory) and (2) transferring to the post-disturbance initial condition some or all of the dominant species’ pre-disturbance numerical advantage (at least some of which is likely due to understory differences in performance). Thus, if at least some understory individuals survive the disturbance (as is often the case; Foster et al. 1998), differences in understory performance may initially have a stronger impact on mixing than canopy differences, as predicted at equilibrium (Eq. 13).

Succession following disturbance is one of most conspicuous and ubiquitous aspects of ecological systems (Levin and Paine 1974; Connell and Slatyer 1977; Whittaker and Levin 1977). Previous theoretical work with the PPA model has ignored succession. Our numerical analysis demonstrates that the PPA allows for stable coexistence (at the landscape scale) of early- and late-successional species, which suggests that the model may provide a useful framework for studying succession despite its simplistic assumption that open space created by the death of canopy trees (“gaps”) is always filled by the tallest understory individuals. We have not yet completed a thorough study of successional dynamics and diversity in the PPA framework. Although it is often assumed that disturbance allows for the coexistence of many tree species (Connell 1978; Molino and Sabatier 2001), this has, to our knowledge, never been demonstrated with a height-structured forest model (Gravel et al. 2010). Thus, the limit to successional forest diversity remains an open question.

Levin (1974, 1976) emphasized that the patchiness that can contribute to local diversity via mass effects may arise even in a homogenous abiotic environment due to random colonization and founder control by species that can competitively exclude each other. Our analysis here is limited to patchiness due to habitat (e.g., soil type) specialization, and we do not know if our results apply to biotic heterogeneity as well. We note, however, that such heterogeneity (i.e., founder control) is predicted to occur in the PPA model if the assumption of a constant understory light level is relaxed (Adams et al. 2007; Strigul et al. 2008). By embedding these richer PPA systems within the metacommunity framework developed here, we can more fully explore the research agenda that Simon Levin articulated for spatial ecology over three decades ago.

Conclusions

Mass effects in forests appear to be weak and are thus unlikely to contribute appreciably to local tree diversity if habitat specialization is strong enough so that species differences in individual performance can be reliably detected from field data. Conversely, mass effects could potentially be an important mechanism of local coexistence among species whose performance differences are too subtle to be reliably detected. Another way of stating these conclusions is that mass effects are unlikely to matter in forest systems where most species are common enough and different enough so that their autecology is well understood (e.g., many temperate and boreal forests; Burns and Honkala 1990), whereas mass effects may be important in forest systems where species are too rare or too similar for their habitat preferences to be easily characterized (e.g., diverse tropical forests; Hubbell and Foster 1986). Whether or not mass effects can play a strong role in mediating coexistence in high-diversity forests will depend on whether or not niche differences can simultaneously be strong enough to prevent neutral drift, yet too weak to be easily detected at the species level. This is an important question for future theoretical work. If the answer is “yes,” the next challenge would be to develop approaches to detecting niche differences in such systems where traditional species-level approaches would (by definition) be unlikely to succeed. Hierarchical statistical approaches to estimating community-level parameters and/or constraining parameters for rare species (e.g., Condit et al. 2006; Dietze et al. 2008; Lichstein et al. 2010) may be useful in this context.

Our conclusion that mass effects are unlikely to have a strong impact on temperate and boreal forest diversity is consistent with the traditional view that tree species in these regions have well-defined associations with local edaphic and topographic factors (Whittaker 1956; Curtis 1959; Van Cleve et al. 1983; Burns and Honkala 1990) and is not necessarily inconsistent with the view that mass effects are strong in the non-forest systems where they were first emphasized by plant ecologists (Shmida and Ellner 1984; Shmida and Wilson 1985). In closed-canopy forests, where height-structured competition has a strong impact on dynamics, the protracted understory phase in the life cycle of late-successional trees (Canham 1985, 1990; Wright et al. 2000) magnifies the advantage of locally superior competitors, thereby weakening the tendency for dispersal to homogenize community composition in heterogeneous landscapes.

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