

Models Suggesting Field Experiments to Test Two Hypotheses Explaining Successional Diversity

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ABSTRACT: A simple mathematical model of competition is developed that includes two alternative mechanisms promoting successional diversity. The first underpins the competition-colonization hypothesis in which early successional species are able to persist because they colonize disturbed habitats before the arrival of late successional dominant competitors. The second underpins the niche hypothesis, in which early successional species are able to persist, even with unlimited colonization by late successional dominants, because they specialize on the resource-rich conditions typical of recently disturbed sites. We modify the widely studied competition-colonization model so that it also includes the mechanism behind the niche hypothesis. Analysis of this model suggests simple experiments that determine whether the successional diversity of a field system is maintained primarily by the competition-colonization mechanism, primarily by the niche mechanism, by neither, or by both. We develop quantitative metrics of the relative importance of the two mechanisms. We also discuss the implications for the management of biodiversity in communities structured by the two mechanisms.

Keywords: successional diversity, competition colonization, successional niche.

Early successional plant species typically have a series of correlated traits, including high fecundity, large dispersal, rapid growth when resources are abundant, and slow growth and low survivorship when resources are scarce. Late successional species usually have the opposite traits, including relatively low fecundity, short dispersal, slow growth, and an ability to grow and to survive under resource-poor conditions (Grime 1979; Tilman 1988; Garnier 1992; Rees 1993, 1996). These attributes define

MacArthur's *r*- and *K*-selection continuum (MacArthur and Wilson 1967) and underpin most explanations of secondary successional diversity (e.g., Connell and Slatyer 1977; Tilman 1988). Late successional species eventually exclude early successional species in the absence of disturbance because they reduce resources beneath the levels required by the early successional species. The early successional species persist for two reasons. High fecundity and large dispersal allows them to colonize recently disturbed sites before the dominant competitors arrive. In addition, rapid growth under resource-rich conditions allows them temporarily to outperform late successional species even if both are present in a recently disturbed site. We refer to the first mechanism as the "colonizing advantage" and the second as the "successional niche." These mechanisms often operate together but do not necessarily do so.

For example, after ploughing at Cedar Creek (Minnesota), old fields are initially dominated by annuals with high fecundity and rapid growth such as *Ambrosia artemisiifolia*. These species are subsequently displaced by perennials, such as *Schizachyrium scoparium*, that have slow growth and low fecundity and are capable of creating and tolerating low levels of soil nitrogen (species with low R^* ; Tilman 1982). *Ambrosia* tends to arrive before *Schizachyrium* and initially outgrows it (Tilman 1994), but *Ambrosia* is displaced because it cannot survive the low nitrogen availability created by *Schizachyrium* (Wedin and Tilman 1993). Similarly, in forests in northeastern North America, the most important early successional dominant Red Oak (*Quercus rubra*) easily overtops the late successional dominant Eastern Hemlock (*Tsuga canadensis*) in high light, but not in the understory where oak saplings die and hemlock saplings survive (see Pacala et al. 1996). Individual hemlocks cast more shade than individual oaks, but oak seeds disperse longer distances on average than hemlock seeds (Ribbens et al. 1994). In both the Minnesota grasslands and temperate forest, we see evidence of both an early successional colonizing advantage and an early successional niche.

Currently, the competition-colonization trade-off is

perhaps the most visible explanation of successional diversity (Tilman 1994). The simple mathematical model of the competition-colonization trade-off was formulated originally by Levins and Culver (1971) and studied later in a large number of papers including Horn and MacArthur (1972), Armstrong (1976), Hastings (1980), Shmida and Ellner (1984), Crawley and May (1987), Nee and May (1992), and Tilman (1994). For communities where diversity is maintained by the competition-colonization trade-off, extinction following habitat destruction occurs first in the competitive dominants and has a substantial time lag, the "extinction debt" (Nee and May 1992; Tilman et al. 1994; Kareiva and Wennergren 1995; Stone 1995; Banks 1997). Because the competitive dominants have a substantial impact on resource use, changes in their abundance could seriously affect ecosystem function. These conclusions depend critically on the assumption that diversity is maintained solely, or in large part, by a competition-colonization trade-off. The validity of the assumed competition-colonization trade-off is discussed in Tilman (1994), Rees (1995), and Rees et al. (1996), but see also the counterexamples reviewed in Banks (1997).

In this article, we observe that the competition-colonization model includes only one of the above two mechanisms maintaining successional diversity. It includes the colonizing advantage of early successional species but does not include their successional niche. We add a successional niche to the model in a simple way, by relaxing perhaps the most restrictive assumption of the model, namely, the instantaneous exclusion of weak competitors. Analysis of this new model identifies field experiments that determine whether successional diversity is maintained by the colonizing advantage, the successional niche, a combination of the two, or neither. We also provide measures of the relative importance of the two mechanisms when both are important. Finally, we show that the two mechanisms have markedly different implications for management and harvesting. Unlike the competition-colonization trade-off, the niche mechanism does not imply lagged extinction of late successional dominants following habitat destruction.

The Competition-Colonization Model

The idea behind the competition-colonization model is that species can be ordered in a perfect linear competitive hierarchy, with competitive ability trading off against colonizing ability. By convention, species are numbered in order of their competitive abilities. The habitat is assumed to be divided into an infinite number of spatial cells, with a fraction X_i at time t occupied by species i . Although the X_i are formally functions of time (as in $X_i[t]$), we will write them simply as X_i to keep the formulas clean.

Two processes control the dynamics. Disturbance converts space occupied by species i into vacant space at rate D_i . The parameter D_i represents cell mortality and is equivalent to the parameter m_i in the models of Tilman and coworkers (e.g., Tilman 1994; Tilman et al. 1994). It summarizes all forms of density independent mortality of adults. Randomly dispersing colonists of species i are produced at rate c_i (per cell occupied by species i), and a colonist instantaneously captures the cell in which it lands if the cell is either vacant or occupied by a less competitive species. Thus, change in the abundance of species i (dX_i/dt) is equal to the space lost because of disturbance ($-D_iX_i$) or colonization by a superior competitor ($-X_iZ_i$), where Z_i is the fraction of space occupied by each superior competitor multiplied by its colonization rate ($Z_i = c_1X_1 + c_2X_2 + \dots + c_{i-1}X_{i-1}$), plus the new space captured by the species ($c_iX_iW_i$), where W_i is the fraction of space not occupied either by species i or by a stronger competitor ($W_i = 1 - X_1 - X_2 - \dots - X_i$). Like the rate of collision between randomly moving gas molecules, the rate of space capture is given by the product of the per cell abundance of the randomly dispersing species- i propagules (c_iX_i) and the abundance of cells that can be colonized by species i (W_i). To summarize, the model for N different species is

$$\frac{dX_i}{dt} = -D_iX_i - X_iZ_i + c_iX_iW_i; \quad i = 1, 2, 3, \dots, N. \quad (1)$$

For simplicity, we will focus on the two-species version of equation (1) with equal death rates ($D = D_1 = D_2$), although all of the results below can be easily generalized. Also, it is convenient to write the colonizing rate of species 1 as simply c and the colonizing rate of species 2 as a number α times c . Note that α is assumed to be >1 because species 2 produces more colonizing propagules than species 1.

If both species in the model are initially rare, like most plant species immediately after agricultural abandonment, then each grows exponentially for a time (if $c > D$ for species 1 and $\alpha c > D$ for species 2; otherwise the species is unable to persist in monoculture). Because species 2 grows at a faster exponential rate than species 1 ($\alpha c - D$ instead of $c - D$), the poor competitor initially dominates the site (fig. 1). Eventually, the species are attracted to a globally stable equilibrium (Hastings 1980). The dominant competitor invariably attains the same abundance as it would if growing by itself, $X_1^* = 1 - D/c$, whereas the subordinate competitor attains $X_2^* = D/c - 1/\alpha$, giving a relative abundance of

$$\text{Relative abundance} = \frac{X_2^*}{X_1^* + X_2^*} = \frac{D\alpha - c}{c(\alpha - 1)}. \quad (2)$$

Species 1 generally becomes the numerical dominant

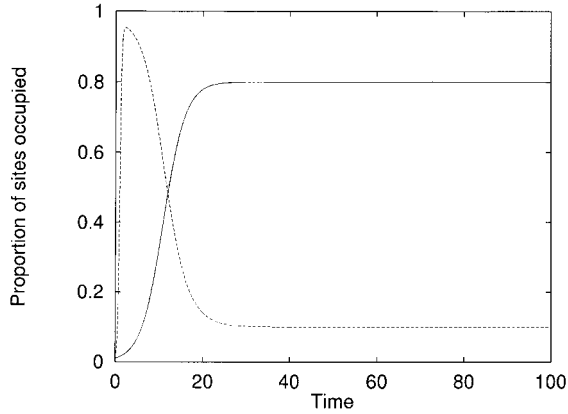


Figure 1: Successional dynamics generated by the two-species version of equation (1). The initial dominant (*dotted line*) is the weaker competitor but has a colonization advantage, which allows its population to grow rapidly in the absence of the competitive dominant (*solid line*). Parameter values: $D = 0.1$, $c = 0.5$, $\alpha = 10$.

over time, giving successional turnover, unless its colonizing ability is extremely low or the disturbance level is high. To fail to become the numerical dominant, species 1 must have such limited colonizing ability that it would be unable to occupy even 50% of available space when growing in monoculture (because its equilibrium abundance when growing with species 2 is the same as in monoculture: $1 - D/c$).

The competition-colonization model accords well with some of the most obvious features of natural secondary successions. Perhaps the most undesirable feature of this model is the instantaneous exclusion of the inferior competitor whenever a superior competitor colonizes a site. In the next section, we develop a simple model that incorporates the biologically reasonable assumption that the successional dynamics of competitive exclusion take time, in part because early successional species typically grow quickly in the resource-rich conditions immediately following disturbance.

Finite Rates of Succession

Unfortunately, we now require a model with a minimum of four state variables. We must divide the fraction of space in which species 1 is present alone into two pieces. Let S be the fraction of space in which species 1 has recently invaded an empty cell and is susceptible to invasion by species 2. These sites are susceptible because resources are not yet reduced below the levels required by the early successional species (species 2). Also, let R be the fraction in which species 1 is alone and resistant to invasion because resources concentrations are too low for

species 2. Similarly, we must divide the fraction of space in which species 2 is present into two pieces: the fraction E , in which it is alone, and the fraction M , in which it is present with species 1 (M for mixed). By definition, the fraction of free space (F), is $1 - S - R - E - M$.

To specify the dynamics, we must formalize three processes: colonization, succession, and disturbance. Although each of the types of space containing species 1 (S , R , and M) could in principle produce species-1 colonists at a different rate (i.e., greater fecundity in R than in S or M), we assume, for simplicity, that each produces colonists at rate c . Similarly, we shall assume that the two types of space containing the early successional species both produce species-2 colonists at rate αc . Although succession could proceed at different rates in cells of type S and M (i.e., at a faster rate in S than in M if species 2 temporarily slows the growth of species 1), we assume that both types are converted into resistant species 1 cells (type R) at the same rate γ . The assumptions of equal fecundities in cells of different types and of equal rates of succession in cells of types S and M are easily relaxed. The conclusions of this study do not depend qualitatively on these assumptions. Finally, we again assume that each type of cell is disturbed at the same rate D . With these assumptions, the model is

$$\begin{aligned}\frac{dS}{dt} &= [c(S + R + M)]F - [\alpha c(M + E)]S - \gamma S - DS, \\ \frac{dR}{dt} &= \gamma S + \gamma M - DR, \\ \frac{dM}{dt} &= [\alpha c(M + E)]S + [c(S + R + M)]E - \gamma M - DM, \quad (3) \\ \frac{dE}{dt} &= [\alpha c(M + E)]F - [c(S + R + M)]E - DE,\end{aligned}$$

and

$$F = 1 - S - R - M - E.$$

The expressions in square brackets are the rates at which colonists of the two species are produced. In the first equation, the first term is *colonization of free space by species 1*, the second is *colonization of susceptible species-1 space by species 2* (thereby turning S into M), the third term is *successional conversion of susceptible species-1 space into resistant species-1 space*, and the final term is *disturbance loss*. These descriptions can be used as a guide to understand the terms in the remaining equations.

These equations can describe many of the standard models of succession (e.g., tolerance, facilitation, and inhibition; Connell and Slatyer 1977). In its current form, the model corresponds to a type of tolerance model, where succession proceeds by the replacement of early,

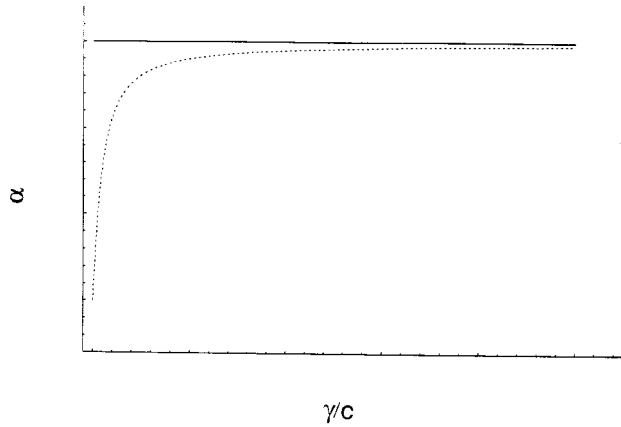


Figure 2: Coexistence criterion (5) for the model (3). The two species coexist if α is above the dotted line and if the height of the solid line (c/D) is >1 .

fast-growing species by plants capable of regenerating in conditions of depleted light and nutrient resources that these early species create. By making the rate of succession in mixed sites slower than in monocultures, we would have the inhibition model. Facilitation can be modeled by assuming that the late successional species can only colonize sites already occupied by the early successional species. The relationship between the different models of succession is discussed in Miles (1987). In what follows, keep in mind that both facilitation and inhibition would strengthen the importance of the successional niche relative to the competition-colonization trade-off. If added to model (3), inhibition would weaken species 1's ability to colonize patches of type E , while facilitation would weaken its ability to colonize free space.

At equilibrium, the total abundance of patches containing species 1 is simply

$$X_1^* = S^* + R^* + M^* = 1 - \frac{D}{c}, \quad (4)$$

which is the same as in the competition-colonization model. It is easy to show that equation (4) is globally stable if it is positive (if $c > D$). The corresponding equilibrium abundance for species 2 (the expression for X_2^*) is given in the appendix. The conditions for the coexistence of the two species (conditions ensuring the instability of the boundary equilibria and the positivity and local stability of the internal equilibrium) are

$$c > D,$$

and

$$\alpha > \frac{c(\gamma + D)^2}{(D\gamma + cD)(\gamma + D) + (c - D)Dc}.$$

The coexistence criterion is illustrated in figure 2. The

species coexist if α is above the threshold given by the dotted line. Note that in the limit of rapid succession, as γ/c increases to infinity, the threshold approaches the coexistence threshold from the simple competition-colonization model: c/D .

To understand the implications of this model, it is useful to define new parameters and to set a new time-scale. If $L = \gamma/(\gamma + D)$, $N = 1 - D/c$, and $d\tau = dtD$, then

$$\frac{dS}{d\tau} = \frac{(S + R + M)F - \alpha(M + E)S}{1 - N} - \frac{S}{1 - L},$$

$$\frac{dR}{d\tau} = \frac{L}{1 - L}(S + M) - R,$$

$$\frac{dM}{d\tau} = \frac{\alpha(M + E)S + (S + R + M)E}{1 - N} - \frac{M}{1 - L}, \quad (6)$$

and

$$\frac{dE}{d\tau} = \frac{\alpha(M + E)F - (S + R + M)E}{1 - N} - E.$$

It is important to understand that equations (3) and (6) are mathematically equivalent. The advantage of (6) is that the new parameters L and N control the strengths of alternative mechanisms maintaining successional diversity and are measurable through simple experiments. Parameter L , which stands for "Levins and Culver," controls how similar the system is to the simple competition-colonization model (1). Parameter L ranges from 0 to 1, and as $L \rightarrow 1$, the system (6) converges exactly to the system (1). As L approaches 1, the average time between disturbances becomes infinitely long relative to the average time required for local succession ($\gamma \gg D$). Parameter N also ranges from 0 to 1 if the first condition in (5) is true ($c > D$), and as $N \rightarrow 1$, the system (6) converges to a new model that we label the "niche model" (N stands for "niche"). As N approaches 1, the average time between disturbances becomes infinitely long relative to the average time required for colonization ($c \gg D$). Thus, the niche model assumes unlimited availability of colonists of both species. Using the original parameters, the niche model is

$$\frac{dM}{dt} = DR - \gamma M,$$

$$R = 1 - M, \quad (7)$$

and

$$S = E = 0.$$

This model is linear, with a single, globally stable equilibrium at $X_2^* = M^* = D/(D + \gamma)$. If both species are in-

roduced into abandoned agricultural land, then after initially occupying all sites, species 2 will decline as species 1 locally excludes it until the relative abundance of sites in which species 2 is present is

$$\text{Relative abundance} = \frac{D}{2D + \gamma}. \quad (8)$$

In equation (8), the faster local succession occurs (large γ) the rarer species 2 becomes.

Diversity in model (7) is maintained by a successional niche. Species 2 is able to invade and to reproduce within all recently disturbed sites no matter what the abundance of species-1 colonists. The niche model, thus, provides a different explanation of successional diversity than the competition-colonization model. Species 2 persists in model (7) because it is adapted to grow under early successional conditions—by exploiting the resource-rich window that occurs before the ever-present but slower-growing species-1 colonists are able to drive resources down to critically low levels. In contrast, species 2 persists in the competition-colonization model only because propagules of the dominant fail to reach some sites after local disturbance. The biological justification for the niche model is that early successional species typically have faster growth rates than late successional species under the resource-rich conditions immediately following disturbance. Because of their faster growth rates, early successional species may temporarily dominate after disturbance even in the presence of propagules of the late successional dominants.

Like competition-colonization model (1), the niche model (6) paints a picture that is broadly concordant with the natural history of secondary succession. How is one to distinguish between these two fundamentally different mechanisms? Natural or artificial gradients in the level of disturbance are not of much help because both models predict an increase in the relative abundance of the early successional species with increased disturbance (eqq. [2] and [8]). The fact that the competition-colonization model predicts the absolute loss of species 1 when D reaches c whereas the niche model does not is not particularly helpful because equation (7) counts all habitats as being occupied by species 1. If we modify the model so that species 1 is prereproductive and subordinate in the early successional sites in state M , then species 1 is driven extinct in the niche model when D is too large, just as in the competition-colonization model.

Two experiments allow one to determine the relative importance of the competition-colonization trade-off and the successional niche. Consider a field system governed by model (6) and composed of an early successional and late successional species or suppose that we

group species into an early successional guild (species 2) and a late successional guild (species 1). Adding propagules of both species at saturating levels experimentally forces N to be equal to 1 by making $c \gg D$. The dynamics of the manipulated system then follow the simple niche model (7), and the value of L is equal to 1 minus the ultimate (equilibrium) abundance of species 2 (see the value of X_2^* immediately after eq. [7]). Thus, the seed addition experiment suggested by Tilman (1994) to test the competition-colonization model actually allows one to measure the value of L in model (6) and so to determine how close the system is to the simple competition-colonization model.

The second experiment removes the successional niche. Continual removals of species 2 from any cell containing both species experimentally forces L to be equal to 1 by making $\gamma \gg D$. The dynamics then follow the simple competition-colonization model (1), and the value of N is given by the ultimate abundance of species 1 (see eq. [4]). Note that N is also the equilibrium abundance of species 1 in the unmanipulated system under the assumptions behind model (6). However, this result is not robust to the assumption of equal rates of succession and equal fecundities of species 1 in cells of different types. If the presence of species 2 temporarily slows the advance of species 1 or reduces its fecundity, then the equilibrium abundance of species 1 will be $<N$ in the unmanipulated system but will still be N in the niche removal experiment.

Together, the two experiments allow one to measure L and N . The colonizer additions remove all recruitment limitation and expose the dynamics of the successional niche, while the niche removal experiment eliminates the successional niche and lays bare the dynamics of the competition-colonization trade-off. Note that one could also measure N and L by fitting the simple niche and competition-colonization models to the transient dynamics of the manipulated plots rather than by waiting until abundances reach approximate equilibrium.

If the measured value of L is much closer to 1 than the measured value of N , then successional diversity is maintained primarily by the competition-colonization trade-off whereas, if the reverse is true, then successional diversity is maintained primarily by the successional niche. What happens if both L and N are nearly 1? The regions in figure 3 labeled "No Coexistence" give the values of L and N that violate the coexistence criterion (5) for three different values of α . Note that if L is equal to 1, then coexistence requires that N is less than a threshold value (equal to $1 - 1/\alpha$), which is itself <1 . The only region in which coexisting species could have values of L and N close to 1 is the sliver in each graph along the $N = 1$ margin in the upper right-hand corner. It is easy to

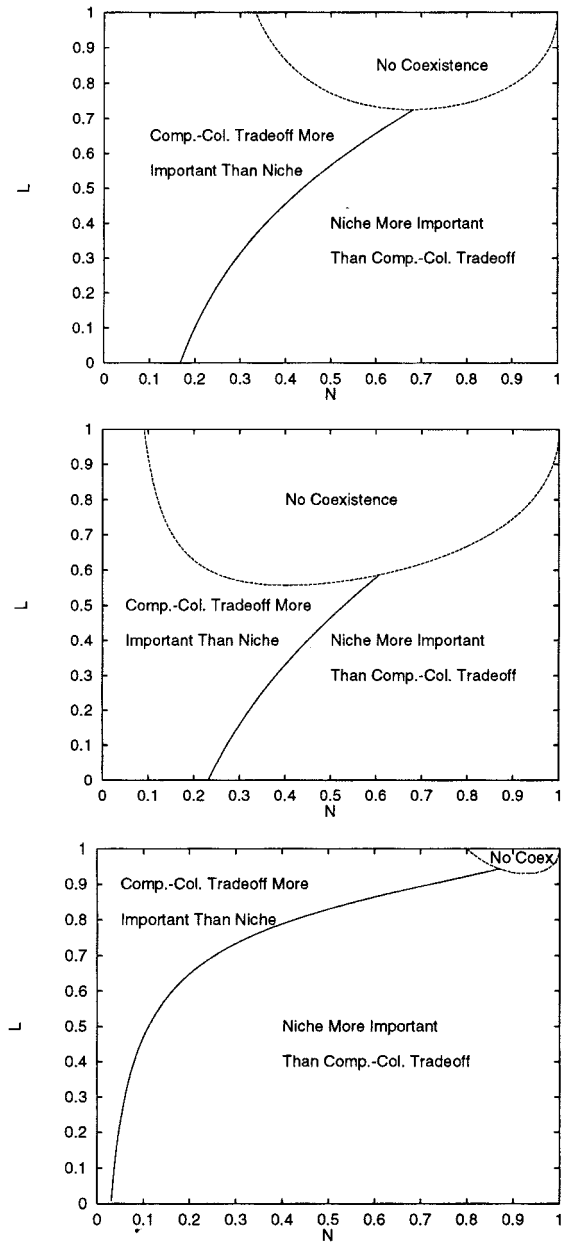


Figure 3: Relative importance of the competition-colonization trade-off and niche. Along the solid line, the sensitivity of the equilibrium abundance of the early successional species to a small change in the value of N is equal to its sensitivity to a small change in L . Below and to the right of the solid line, a change in N has a greater effect (absolute value) than a change in L , while above and to the left of the line, the reverse is true. The two species cannot coexist above the dotted line. A, $\alpha = 1.5$; B, $\alpha = 1.1$; C, $\alpha = 5.0$.

show analytically that, within this sliver, $1 - N$ is of order $(1 - L)^2$ or smaller. Thus, if L and N are both close to 1, then N must be much closer than L to 1, and so the niche primarily maintains the successional diversity.

A

In contrast, if both L and N are substantially < 1 , then both mechanisms are important, and model (6) does not reduce approximately either to (1) or (7). The competition-colonization and niche hypotheses are not mutually exclusive alternatives. We suspect that mixed results will be common because good colonizing ability is correlated with rapid growth under resource-rich conditions and poor colonizing ability is correlated with an ability to create and to tolerate low resource levels. MacArthur's theory of r - and K -selection suggests that natural selection causes these associations and implies that a system governed by the pure competition-colonization model will evolve a successional niche. This is because selection should favor specialization of the weak competitor on the resource-rich conditions typical of recently disturbed sites.

B

The solid curve in each panel in figure 3 separates, by one metric, the region of parameter space in which the competition-colonization trade-off is quantitatively more important than the successional niche from the region in which the reverse is true. Along the solid curve, the sensitivity of species 2's equilibrium abundance to a change in N equals its sensitivity to a change in L (the derivative of X_2^* with respect to N equals its derivative with respect to L). The curves of equal sensitivity verify that L and N are sensible metrics of the relative importance of the competition-colonization trade-off and niche because the curves very roughly follow the diagonal. Note, however,

C

that the position of the curve changes with the value of α (cf. the panels in fig. 3: A, $\alpha = 1.5$; B, $\alpha = 1.1$; and C, $\alpha = 5.0$). Paradoxically, as the colonization advantage of the early successional species grows, the successional niche also grows in importance relative to the competition-colonization trade-off. We suspect that this is because the early successional species is better able to colonize the recently disturbed sites to which it is adapted if α is large. In other words, a colonizing advantage improves the value of a successional niche.

The finding shown in figure 4 strengthens this view. Above the curve for each value of α , the relative abundance of species 2 will increase following saturating additions of colonists of both species. Because the competition-colonization model predicts the opposite (the extinction of species 2), this increase must be caused by the successional niche. The relative abundance of species 2 increases in the seed addition experiment whenever the early successional species is more recruitment limited than the late successional species and, thus, has greater difficulty filling its niche. Additions of colonists then dif-

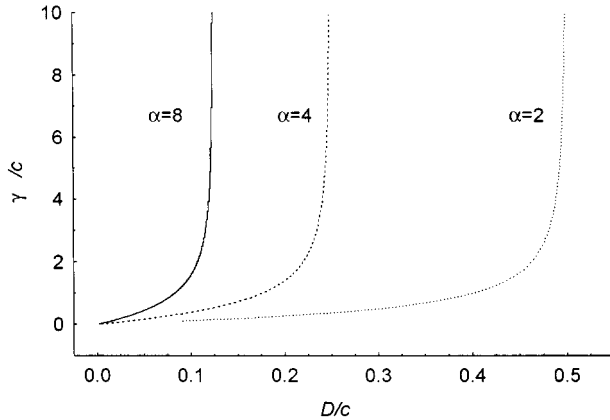


Figure 4: Effect of saturating additions of colonists of both species on the relative abundance of species 2 in model (6). The relative abundance of species 2 increases above the line for a given value of α and decreases below the line.

ferentially benefit species 2 because they differentially improve its capacity to “find” the locations in which it can survive and reproduce. Species 2 will be more recruitment limited than species 1, despite species 2’s greater colonizing ability ($\alpha > 1$), if the early successional niche is sufficiently rare. The early successional niche may be rare because of low disturbance (small D), rapid local succession (large γ), or abundant species 1 (large c relative to D). The region in figure 4 corresponding to increased relative abundance of species 2 becomes smaller as α increases because the recruitment limitation of species 2 becomes less as its per capita fecundity grows.

A final implication of figure 3 is that precise quantification of the relative importance of the competition-colonization trade-off and successional niche requires measuring all parameters in the model in addition to L and N . These include α in (6) as well as parameters controlling differential rates of succession and fecundities in cells of different types if these were added to the model.

Conclusions and Discussion

Colonizer addition and niche removal experiments are practical to perform in the field, at least in some systems, and have the capacity to determine if successional diversity is maintained primarily by the competition-colonization trade-off, primarily by a successional niche, or by both mechanisms. First, neither mechanism is supported if both the colonizer additions fail to increase the absolute abundance of species 1 and the niche removals fail to decrease the absolute abundance of species 2. In this case, either the experimental manipulations themselves failed (i.e., seed additions to increase colonization in a system dominated by clonal growth) or en-

tirely separate mechanisms maintain successional diversity. Three alternatives remain, given that colonizer additions increase species 1, niche removals decrease species 2, or both. If species 1 eventually occupies nearly every site in the niche removal experiment, then a successional niche primarily maintains the diversity. If this does not happen and if the early successional species nearly becomes extinct in the colonizer addition experiment, then diversity is maintained primarily by the competition-colonization trade-off. If neither of these two alternatives happens, then both mechanisms are important, and a precise quantitative separation of the relative importance of the two requires measuring additional parameters.

The distinction between the niche and competition-colonization hypotheses is important, in part because the two hypotheses have strikingly different management implications. Tilman et al. (1997) showed that a diverse system governed solely by the competition-colonization model would lose late successional species catastrophically if even a small fraction of habitat were lost (e.g., converted to agriculture). The reason is that rare late successional species in the model cling to the brink of extinction because of their poor colonizing ability. Any conversion of habitat to agriculture causes them to waste seeds that disperse to the newly agricultural sites. This small additional loss of colonizing ability pushes rare late successional species to extinction. In contrast, because species are not recruitment limited in the pure niche model, habitat loss will not cause any extinctions. This surprising result arises from the assumption of very large fecundity, which ensures that all species instantaneously colonize all sites. Relaxing this assumption, so that there is recruitment limitation in the model, can result in extinction of either early or late successional species, depending on which are more recruitment limited, or no extinctions at all providing the proportion of habitat destroyed is sufficiently small. The more recruitment limited the species, the more likely habitat destruction will result in extinction. Habitat loss is most likely to cause extinctions of the late successional species if successional diversity is maintained by the competition-colonization trade-off and least likely to cause extinctions if diversity is maintained by the successional niche.

We speculate that disturbances of small spatial extent (like single-individual gaps) will maintain successional diversity primarily by the niche mechanism rather than the competition-colonization mechanism, especially in productive habitats. This is because late successional perennial grasses or shade tolerant forest trees eventually occupy almost all sites in the absence of a large-scale disturbance, with fugitive forbs or shade intolerant trees

hopping among comparatively rare gaps. Because the value of N is no smaller than the abundance of the late successional type, N is apparently close to 1 in these systems. We also suspect that large-scale disturbance favors the competition-colonization mechanism but only if disturbance is severe enough to destroy colonizing propagules already present in a site. Note that windthrow and all but severe fire usually spare colonizing propagules of late successional dominants, thus reducing or eliminating the delay until colonization necessary for the competition-colonization mechanism. In contrast, severe and large-scale disturbance such as temporary conversion of forest to agriculture, landslide, or stand- and seed-destroying fire will favor the competition-colonization mechanism.

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APPENDIX

Equilibrium of Model (3)

Here we briefly outline the equilibrium solution of equation (3). First, note that the dominant competitor's equilibrium abundance is $X_1^* = 1 - D/c$, and so, if resistant sites are created at rate γ , then

$$R^* = \left(1 - \frac{D}{c}\right) \frac{\gamma}{\gamma + D}. \quad (\text{A1})$$

If the subordinate competitor's equilibrium abundance is $X_2^* = E^* + M^*$, then straightforward manipulation of equation (3) shows that, providing equation (5) is satisfied, X_2^* is given by the positive root of the quadratic equation,

$$X_2^{*2} + X_2^* \left[\frac{\gamma + D + c}{\alpha c} - (1 - R^*) \right] + \left[\frac{Dc - \gamma(\alpha D - c)}{\alpha^2 c^2} - \frac{(1 - R^*)}{\alpha} \right] = 0. \quad (\text{A2})$$

Having obtained X_2^* , we can then calculate E^* and M^* , which are given by the following expressions:

$$E^* = \frac{X_2^* \alpha D}{c(1 + \alpha X_2^*)}, \quad (\text{A3})$$

and

$$M^* = \frac{1}{\gamma} [\alpha c X_2^* (1 - X_2^* - R^*) - D X_2^*]. \quad (\text{A4})$$

The proportion of susceptible sites can then be calculated by subtraction, $S^* = X_1^* - R^* - M^*$.

Literature Cited

- Armstrong, R. A. 1976. Fugitive species: experiments with fungi and some theoretical considerations. *Ecology* 57:953–963.
- Banks, J. E. 1997. Do imperfect trade-offs affect the extinction debt phenomenon? *Ecology* 78:1597–1601.
- Connell, J. H., and R. O. Slatyer. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. *American Naturalist* 111:1119–1144.
- Crawley, M. J., and R. M. May. 1987. Population dynamics and plant community structure: competition between annuals and perennials. *Journal of Theoretical Biology* 125:475–489.
- Garnier, E. 1992. Growth analysis of congeneric and perennial grass species. *Journal of Ecology* 80:665–675.
- Grime, J. P. 1979. *Plant strategies and vegetation processes*. Wiley, Chichester.
- Hastings, A. 1980. Disturbance, coexistence, history, and competition for space. *Theoretical Population Biology* 18:363–373.
- Horn, H. S., and R. H. MacArthur. 1972. Competition among fugitive species in a harlequin environment. *Ecology* 53:749–752.
- Kareiva, P., and U. Wennergren. 1995. Connecting landscape patterns to ecosystem and population processes. *Nature (London)* 373:299–302.
- Levins, R., and D. Culver. 1971. Regional coexistence of species and competition between rare species. *Proceedings of the National Academy of Sciences of the USA* 68:1246–1248.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, N.J.
- Miles, J. 1987. Vegetation succession: past and present perceptions. Pages 129–149 in A. J. Grey, M. J. Crawley, and P. J. Edwards, eds. *Colonization, succession and stability*. Blackwell, London.
- Nee, S., and R. M. May. 1992. Dynamics of metapopulations: habitat destruction and competitive coexistence. *Journal of Animal Ecology* 61:37–40.
- Pacala, S. W., C. D. Canham, J. Saponara, J. A. Silander,

- R. K. Kobe, and E. Ribbens. 1996. Forest models defined by field measurements. II. Estimation, error analysis and dynamics. *Ecological Monographs* 66:1–44.
- Rees, M. 1993. Trade-offs among dispersal strategies in the British flora. *Nature (London)* 366:150–152.
- . 1995. Community structure in sand dune annuals: is seed weight a key quantity? *Journal of Ecology* 83:857–863.
- . 1996. Evolutionary ecology of seed dormancy and seed size. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 351:1299–1308.
- Rees, M., P. J. Grubb, and D. Kelly. 1996. Quantifying the impact of competition and spatial heterogeneity on the structure and dynamics of a four-species guild of winter annuals. *American Naturalist* 147:1–32.
- Ribbens, E., J. A. Silander, and S. W. Pacala. 1994. Seedling recruitment in forests—calibrating models to predict patterns of tree seedling dispersion. *Ecology* 75:1794–1806.
- Shmida, A., and S. Ellner. 1984. Coexistence of plant species with similar niches. *Vegetatio* 58:29–55.
- Stone, L. 1995. Biodiversity and habitat destruction: a comparative study of model forest and coral reef ecosystems. *Proceedings of the Royal Society of London B, Biological Sciences* 261:381–388.
- Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, N.J.
- . 1988. Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton, N.J.
- . 1994. Competition and biodiversity in spatially structured habitats. *Ecology* 75:2–16.
- Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. *Nature (London)* 371:65–66.
- Tilman, D., C. L. Lehman, and C. Yin. 1997. Habitat destruction, dispersal, and deterministic extinction in competitive communities. *American Naturalist* 149:407–435.
- Wedin, D., and D. Tilman. 1993. Competition among grasses along a nitrogen gradient: initial conditions and mechanisms of competition. *Ecological Monographs* 63:199–229.

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