

Recycling-Mediated Facilitation and Coexistence Based on Plant Size

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ABSTRACT: We introduce nutrient recycling into a model where competitors differ in the scale at which they perceive their environment. In a two-resource system with both external nutrient inputs and recycling, larger consumers (“integrators”) often generate resource distributions that favor their smaller (“nonintegrator”) competitors, and vice versa. This occurs because recycling of integrator biomass reduces between-patch resource heterogeneity, whereas recycling of nonintegrator biomass does not. Combined, recycling and throughput can allow coexistence when it is not possible with either alone. With recycling, the presence of an integrator also may facilitate higher biomass of a co-occurring nonintegrator. Our model provides a context where recycling can generate negative feedback between competitors that differ in size and so promote coexistence. This is opposite to the positive recycling-mediated feedback commonly expected on the basis of litter chemistry differences between competitors. Effects of recycling and homogenization on nonintegrators may also be negative in our model, depending on the conformation of the system’s resource supply points and the species’ relative resource requirements. Our model suggests that the effects of plant size on competitive outcomes may depend critically on the degree of resource recycling found in the system and, reciprocally, that the effects of recycling may depend on plant size.

Keywords: recycling, facilitation, resource competition, heterogeneity, spatial scale, clonal integration.

Introduction

Species differences in foraging scale can theoretically allow coexistence, because competitors that forage at different scales are expected to differ in their response to resource heterogeneity and in the effect that their consumption of resources has on that heterogeneity (Ritchie and Olff 1999; Abrams and Wilson 2004; Namba and Hashimoto 2004;

Szabó and Meszéna 2007; Golubski et al. 2008). For plants, foraging scale is expected to be closely tied to plant size, because larger plants have more expansive root systems and canopies. However, plants affect soil resource availability not only through uptake but also through the recycling of nutrients released from decomposing plant litter; this recycling of nutrients may be an important factor determining species’ effects on competitors (e.g., Hobbie 1992; Berendse 1994; Suding et al. 2004).

Plant communities with clonal species constitute a system where size differences between competitors have received considerable attention. Clonal individuals that consist of many physiologically integrated ramets are predicted to have a larger foraging footprint and effectively experience less spatial heterogeneity than their nonclonal competitors. Although much attention has been focused on resource transport due to translocation among ramets within a clonal plant (e.g., Hutchings and Wijesinghe 1997; Stuefer et al. 1998; Herben and Suzuki 2002; Magyar et al. 2007), comparatively little consideration has been given to the effects of resource transport between soil patches (due to litter deposition and decomposition). Magyar et al. (2004) modeled the implications of resource translocation among clonal ramets for soil resource heterogeneity, but their model assumed that there were only three discrete resource states (poor, rich, or full), with changes between these states (and thus the number of suitable gaps open to potential competitors) determined by ramet birth-death processes. How transport of resources between soil patches by a larger competitor will affect exploitative competition when there is continuous feedback between biomasses and resource concentrations remains unclear.

Theoretical models have repeatedly found nutrient recycling from litter, either within patches or among several patches linked by a common global pool, to be important for plant competition and coexistence (e.g., Miki and Kondoh 2002; Clark et al. 2005; Daufresne and Hedin 2005). It is therefore reasonable to expect that spatial patterns in

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litter recycling caused by size differences between competitors might be important for understanding the effects of both litter recycling and size differences on plant competition. Here, we introduce nutrient recycling from litter into a model of exploitative competition between larger and smaller plant species (based on clonal vs. nonclonal competitors). This allows us to explore how recycling alters the effects of size differences between competitors and, reciprocally, how size differences alter the effects of litter recycling. We show that the combination of recycling and size differences can facilitate coexistence and that larger species may facilitate smaller competitors via their effect on resource heterogeneity.

Model

We introduce recycling into a recently developed model of competition between plants that differ in size (Golubski et al. 2008); the model is based on resource-ratio competition (MacArthur 1972, pp. 33–58; Léon and Tumpson 1975; Tilman 1980, 1982). In the model, consumer species (with total biomasses denoted by C) compete for two essential resources (R_1 and R_2) across two patches (A and B). Larger species (“integrators”) respond to average resource levels across both patches as though the environment consisted of one larger patch. Integrators allocate their growth equally across patches, and their relative uptake of resources from each patch is proportional to the concentration of resources in each patch. Smaller species (“nonintegrators”) experience each patch separately. Here, we use a version of the model where consumer growth saturates with resource concentration (a type II functional response). This allows us to examine effects of recycling that occur via nonlinear averaging, a mechanism not possible with a linear functional response. Assuming a linear functional response does not qualitatively alter our main results.

We consider competition between one integrator (i) and one nonintegrator (j) species. Integrators are assumed to have equal starting biomass in each patch. Because integrators allocate growth equally among patches, this means that an integrator’s biomass in patch A will always be equal to its biomass in patch B (i.e., $C_{iA} = C_{iB} = C_i$). Growth rates in patch A are given by

$$\frac{dC_{jA}}{dt} = \min\left(\mu \frac{R_{1A}}{h_{j1} + R_{1A}} C_{jA}, \mu \frac{R_{2A}}{h_{j2} + R_{2A}} C_{jA}\right) - mC_{jA} \quad (1)$$

for the nonintegrator and

$$\frac{dC_i}{dt} = \min\left(\mu \frac{(1/2)(R_{1A} + R_{1B})}{h_{i1} + (1/2)(R_{1A} + R_{1B})} C_i, \mu \frac{(1/2)(R_{2A} + R_{2B})}{h_{i2} + (1/2)(R_{2A} + R_{2B})} C_i\right) - mC_i \quad (2)$$

for the integrator, where m is a loss (mortality) rate, μ a maximum per capita growth rate, and h_{nx} a half-saturation constant for consumer n ’s response to resource x . Consumer dynamics in patch B can be obtained by switching the patch subscripts in the two equations above. We incorporate recycling by assuming that a fraction $(1 - \rho)$ of the resources contained in each unit of consumer biomass is lost from the environment when that biomass dies. The remaining fraction, ρ , is instantly recycled, and the resources within it are returned to the pool of resources available in the appropriate patch. The dynamics of R_i in patch A are given by

$$\begin{aligned} \frac{dR_{1A}}{dt} = & D(S_{1A} - R_{1A}) + \rho \cdot \text{loss}_{jA} - \text{growth}_{jA} \\ & + \rho \cdot \text{loss}_{iA} - 2\text{growth}_{iA} \left(\frac{R_{1A}}{R_{1A} + R_{1B}} \right), \end{aligned} \quad (3)$$

where S_{1A} is the supply point for R_1 in patch A and D is the dilution rate of standard chemostat equations (e.g., see Grover 1997), which gives the rate at which resources flow into and out of the environment. For analytical tractability, equation (3) assumes that there is one unit of each resource contained within each unit biomass of any consumer (giving both species the same 45° consumption vector). Relaxing this assumption does not alter our key results, and in fact, simulations in which species were given different consumption vectors often led to more pronounced facilitative effects (simulation results not shown). The dynamics of either resource in either patch can be obtained by switching the appropriate subscripts throughout equation (3). The shorthand “growth” is used to refer to the output of the min function in a consumer’s growth equation (1) or (2), and the shorthand “loss” refers to the absolute value of the remaining term in the equation (e.g., mC_{jA} for consumer j in patch A).

The implications of integration for competitive coexistence when there is no recycling ($\rho = 0$) are discussed in detail by Golubski et al. (2008). A few aspects of an integrator’s effect on resources are relevant here. Integrators will draw the average concentration of a limiting resource down to their zero net growth isocline (ZNGI). In doing so, they will draw that resource down further (below their ZNGI) in the patch with the lower supply point for the resource (“overdepletion”) and not draw the resource

down as far (leaving it above their ZNGI) in the patch with the higher resource supply point ("underdepletion"). This can give nonintegrators an opportunity for successful invasion against an integrator in a rich patch, an opportunity that would not exist against an equivalent nonintegrator, while reducing the nonintegrators' abilities to invade poor patches. When each patch has a sufficiently higher supply of one resource than the other patch, an integrator may draw overall resources below its ZNGI in both patches, reducing the invasibility of both patches. Our model considers a single two-patch system, and we do not explicitly model reproduction or dispersal between patches. In larger systems, where reproduction and dispersal are limited, the applicability of our results may depend on the particulars of reproduction and dispersal processes.

Results

In the model with nutrient recycling, single-species equilibrium biomasses of a nonintegrator (we use the example of a nonintegrator limited by R_1 in patch A) and an integrator (limited by R_1) in the absence of interspecific competition are, respectively,

$$C_i^* = \frac{D}{m(1-\rho)} \left[\frac{1}{2} (S_{1A} + S_{1B}) - \frac{mh_{i1}}{(\mu - m)} \right], \quad (4)$$

$$C_{jA}^* = \frac{D}{m(1-\rho)} \left[S_{1A} - \frac{mh_{j1}}{(\mu - m)} \right]. \quad (5)$$

With only the nonintegrator present, recycling does not alter equilibrium resource concentration in either patch, and with only the integrator present, recycling does not change the average equilibrium resource concentration across patches (fig. 1). This is because both resources are present in equal concentrations within any consumer's biomass and are recycled at the same rate. Because equilibrium biomasses are undefined at $\rho = 1$, we exclude the special case where $\rho = 1$ unless otherwise noted.

Recycling of integrator biomass tends to homogenize the resource environment across patches (fig. 1). This can be seen by solving for the equilibrium ratio of either of the resources (R_1 or R_2) in patch A to that in patch B under a resident integrator. This is

$$\left(\frac{R_{1A}}{R_{1B}} \right)^* = \frac{DS_{1A} + \rho m C_i^*}{DS_{1B} + \rho m C_i^*}. \quad (6)$$

When there is no recycling ($\rho = 0$), this ratio equals the ratio of the supply points from each patch. When equation

(4) is plugged in for C_i^* , it can be seen that this ratio approaches 1 as recycling increases.

From equation (3), it can be seen that the nonintegrator (j) can have a positive effect on resource levels in a patch only when its losses exceed its growth (which can be the case only transiently). The integrator (i), however, can increase resource levels in a patch even if its growth equals or exceeds its losses, provided that the concentration of a resource in that patch is sufficiently low compared to that in the neighboring patch (e.g., R_{1A} sufficiently less than R_{1B} in eq. [3]). This causes resources to move from patches of higher concentration to patches of lower concentration, thus reducing heterogeneity in the environment.

Effects on Invasibility and Coexistence

We explore the potential for coexistence of integrators and nonintegrators by examining each species' ability to achieve positive growth as a rare invader (with low initial biomass) in a system where its competitor is at its single-species equilibrium with resources, with mutual invasibility implying coexistence. In resource-ratio models, species are able to invade whenever their competitor as a resident leaves behind equilibrium resource levels above the invader's ZNGI (in the case of integrators, average resource levels across both patches must be above their ZNGI). Because recycling does not change equilibrium resource levels under a resident nonintegrator (given our simplifying assumptions), recycling has no effect on the integrator's ability to invade and affects only invasibility by the nonintegrator. For this reason, we focus on the effects of recycling on equilibrium resource levels under a resident integrator. The consequences of recycling for invasibility and coexistence are straightforward, as shown by a graphical analysis of the feasible patterns of single-species resident equilibrium resource concentrations that may be encountered by an invading nonintegrator (fig. 2).

Under a resident integrator, high recycling draws (R_1^* , R_2^*) in each separate patch toward the across-patch average (fig. 1). When that average (R_1^* , R_2^*) is above the nonintegrator's ZNGI, this means that both patches will be invisable when ρ is sufficiently high, and therefore the effect of recycling is to increase invasibility (fig. 2A–2D). Relative resource abundance in each patch under a resident integrator reflects the two patches' relative supply points. If one patch has higher S_1 and S_2 than the other, that patch must be invisable under a resident integrator that draws the average (R_1^* , R_2^*) to a point above the nonintegrator's ZNGI regardless of recycling (fig. 2A, 2B). In these cases, the invasibility of the other patch under the resident integrator may be less relevant than its invasibility at the two-species equilibrium where both species are already coexisting in the richer patch. When the average (R_1^* ,

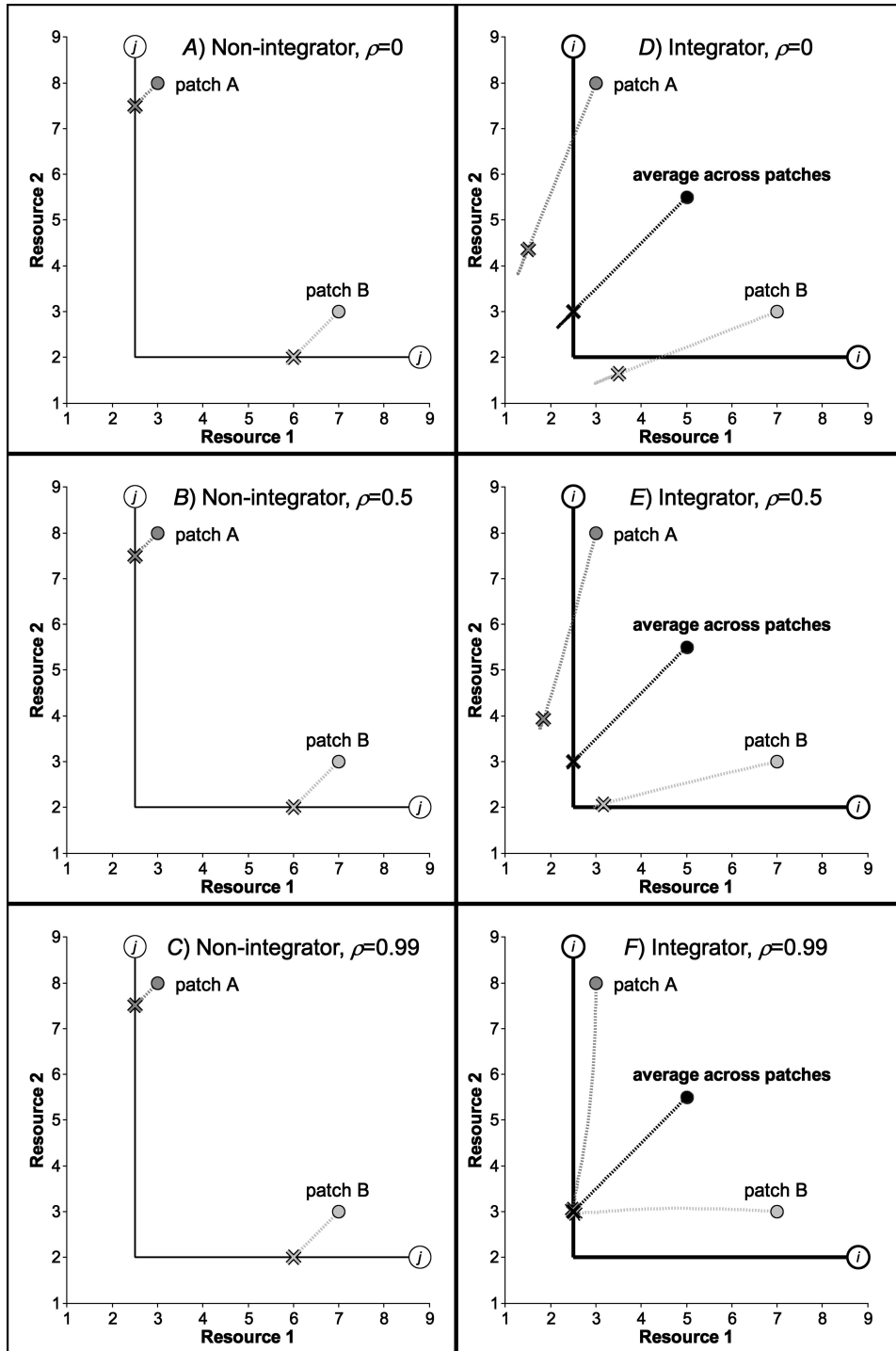


Figure 1: Single-species resource dynamics, under a resident nonintegrator (A–C) versus a resident integrator (D–F). Increasing recycling (ρ) has no effect on equilibrium resource levels under nonintegrators but causes levels of each resource to become more similar across patches under integrators. Thick and thin solid lines give zero net growth isoclines for the integrator (i) and nonintegrator (j), respectively. Gray circles indicate resource supply points for each patch, which are also used as starting conditions; gray dashed lines track resource trajectories within each patch; and gray crosses show equilibrium resource levels in each patch. Black circles, dashed lines, and crosses show the respective averages across patches.

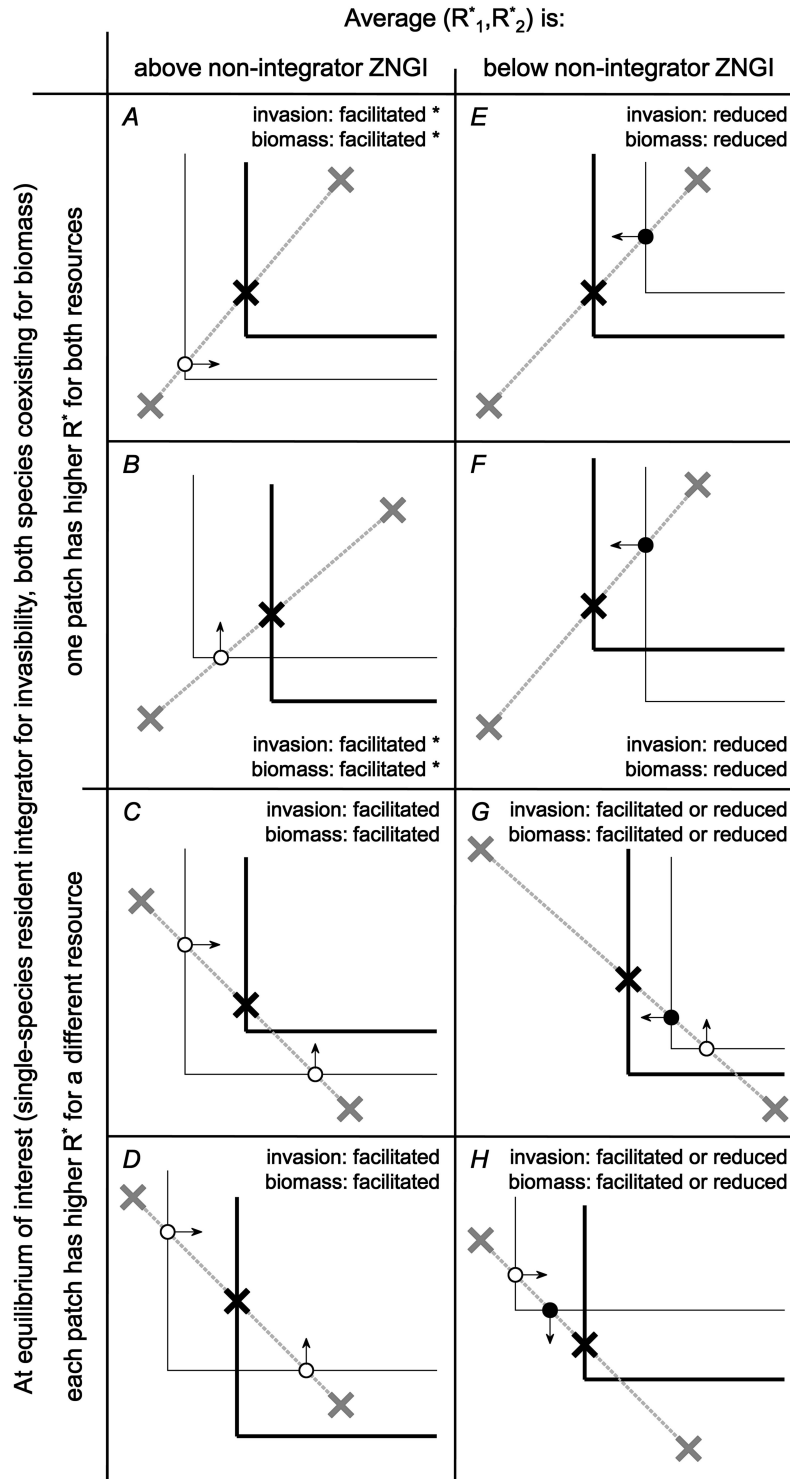


Figure 2: Effects of recycling on each potential configuration of equilibrium resource levels (in R_1, R_2 space) under a resident integrator. Supply points are not shown. Dashed lines show the qualitative change in equilibrium resource levels as the system goes from no recycling ($\rho = 0$; gray crosses) to very high recycling (ρ approaching 1), where resource levels in each patch approach their across-patch average (black crosses), which is independent of recycling. Circles indicate potential coexistence equilibria. Recycling increases nonintegrator biomass at white circles and (when systems with equal total resource supply are compared, as discussed in the text) decreases nonintegrator biomass at black circles. Arrows indicate

R_2^*) to which a resident integrator draws resources is below the nonintegrator's ZNGI, sufficiently high ρ decreases invasibility (fig. 2E–2H). However, when each patch has a higher supply point for a different resource (fig. 2G, 2H), the concentration of one of the two resources is increased by recycling in each patch. Because of this, intermediate recycling may facilitate invasion of a patch whose resource concentrations would be below the nonintegrator's ZNGI when $\rho = 0$.

The effects illustrated in figure 2 can be seen when invasibility is plotted across a range of resource supply point pairs (fig. 3). The abrupt white versus dark regions in figure 3D and the upper portion of figure 3H show that with very high recycling, the nonintegrator is able to invade both patches whenever the resident integrator draws the average (R_1^* , R_2^*) to a point above the nonintegrator's ZNGI and is able to invade neither patch when the average (R_1^* , R_2^*) is drawn to a point below its ZNGI. Regions that are white in figure 3B and 3D but gray in figure 3C, or those that are white in figure 3F and 3H but gray in figure 3G, show the potential for intermediate recycling to facilitate invasion even when the average (R_1^* , R_2^*) is drawn to a point below the nonintegrator's ZNGI.

Because we focus on the effects of recycling and recycling does not affect invasibility by integrators in our model, figure 2 focuses solely on invasibility by nonintegrators. Invasibility by integrators is straightforward to determine graphically; it requires that a resident nonintegrator leave average resource concentrations above the integrator's ZNGI. Integrator invasibility when ZNGIs cross is discussed by Golubski et al. (2008), and figures 3A and 3E illustrate regions of supply points that allow integrator invasion in such a case. When the integrator is able to invade, facilitation of nonintegrator invasion by recycling can cause the predicted outcome of competition to change from exclusion of the nonintegrator to coexistence, and inhibition of invasion by recycling can cause the reverse change (although there may be no effect at the scale of the entire system if only one patch's invasibility is changed). If the integrator cannot invade, increased invasibility by the nonintegrator due to recycling may change the predicted outcome from founder control to exclusion of the integrator, and reduced invasibility may cause the opposite change. However, because our model considers competitive interactions that would presumably be embedded in a community much larger than our two-patch

system, facilitative or inhibitive effects of integrators on nonintegrators may be of interest even in cases where integrators are predicted to ultimately be excluded from the two-patch system.

Effects on Equilibrium Biomass

Recycling may have significant effects on the relative growth and biomass of integrators and nonintegrators when they coexist. In models of this type, equilibrium biomasses will generally increase with an increase in the level of recycling ρ independently of spatial effects (e.g., see single-species equilibria given by eqq. [5] and [6]), because recycling effectively increases the total supply of resources to the system (Daufresne and Hedin 2005). To account for this and to better highlight the effects that recycling has specifically via resource heterogeneity, we preclude this possibility by setting D equal to $m(1 - \rho)$ for the following analyses and figures. Doing so couples external resource inputs and recycling, so that total resource supply to the system is independent of ρ . Thus, when we compare systems with increasing ρ values, we are comparing systems where recycling is becoming increasingly important relative to throughput (from systems without recycling, at $\rho = 0$, to the unrealistic extreme of completely closed systems, at $\rho = 1$) but in which the total supply rate of resources is equal. We use this approach to show more clearly that the facilitative effects of integrators do not depend on an increase in total resource supply from the recycling of litter but rather are due to homogenization of the environment. Our assumption that $D = m(1 - \rho)$ does not qualitatively alter the invasibility results previously discussed. Analytical results analogous to those that follow but without this assumption are presented in appendix B in the online edition of the *American Naturalist*; the main effect of relaxing the assumption is to introduce cases where recycling benefits both species because of the associated increase in total resource supply.

The effects of recycling on integrator and nonintegrator equilibrium biomasses mirror the effects of recycling on invasibility and can also be determined graphically. Circles in figure 2 show each potential configuration of equilibria at which integrators and nonintegrators coexist. At these equilibria, recycling again causes resources to move out of the patch where they are at a higher concentration and into the patch where they are at a lower concentration.

recycling's effect on the resource limiting the nonintegrator at each equilibrium point. Asterisks following invasibility or biomass results highlight cases where, regardless of recycling, one patch is invulnerable (above the nonintegrator's zero net growth isocline [ZNGI]) but not currently occupied by a resident nonintegrator, which is not a stable situation. If that patch were successfully invaded, the configuration of the system would change to that depicted in one of the other panels. Figure A1 in the online edition of the *American Naturalist* shows additional scenarios for some panels (omitted here for clarity because of their similarity to those already shown).

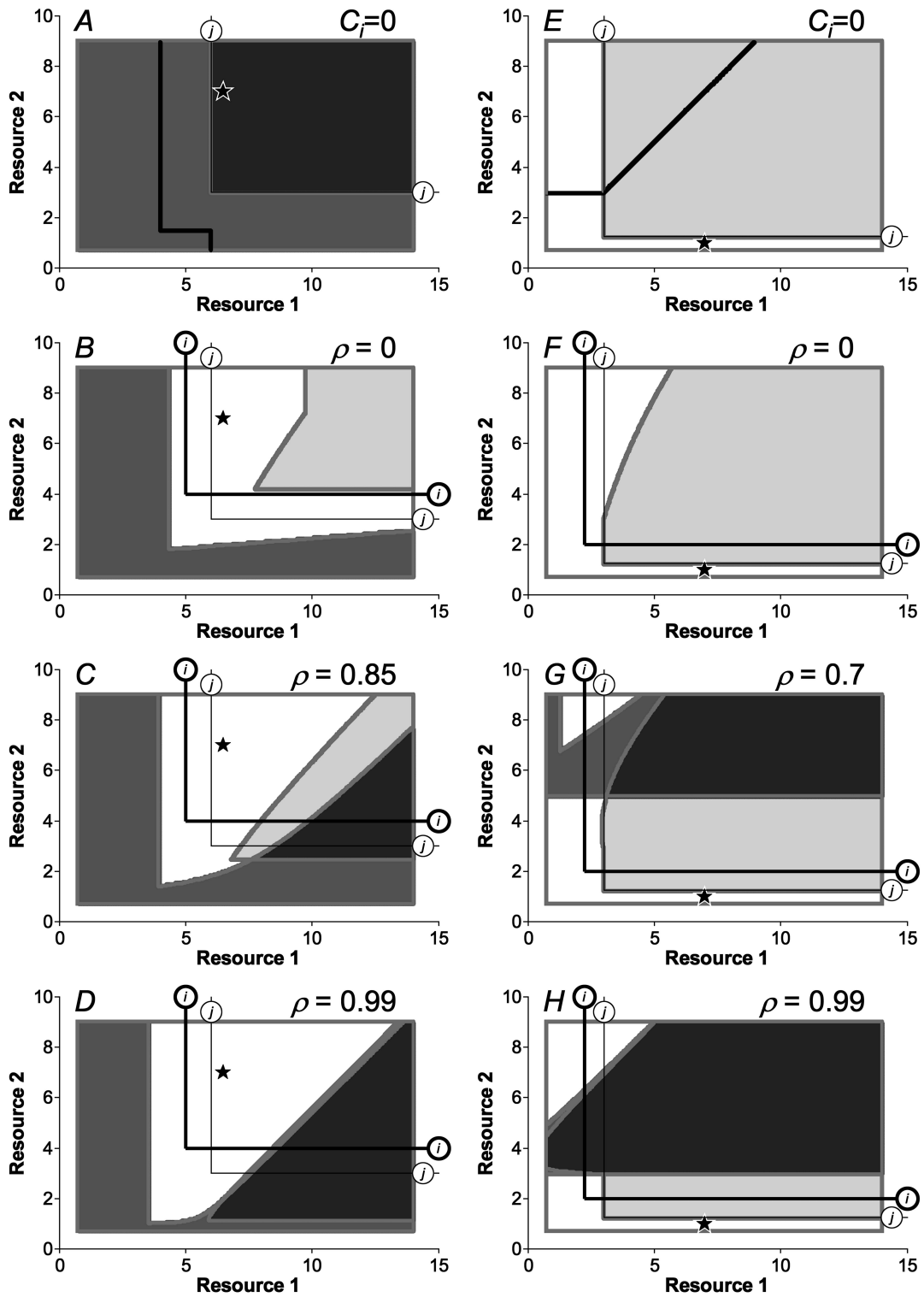


Figure 3: Invasibility of patches under a resident integrator (i) by a nonintegrator (j), plotted by location of patch B's supply point (stars indicate patch A's supply point). Shading indicates which patches are invulnerable: white for neither, light gray for patch B only, medium gray for patch A only, and dark gray for both (gray lines are drawn between regions and to surround the total range of supply points explored). Only immediate invasibilities

Nonintegrators are limited by R_1 at any equilibria located on the vertical portion of their ZNGIs and by R_2 at any equilibria located on the horizontal portion. Recycling of integrator biomass causes a net flux of resources from patches where they are at a higher concentration to patches where they are at a lower concentration. Therefore, recycling will increase the supply of the resource limiting a nonintegrator and increase nonintegrator biomass whenever the nonintegrator occurs in the patch with a lower concentration of that limiting resource (fig. 2, *white circles*). Conversely, if the nonintegrator occurs in the patch with a higher concentration of its limiting resource, recycling will reduce the nonintegrator's biomass (fig. 2, *black circles*). Because recycling (under our assumptions) does not affect either the total supply of resources or the average levels to which each resource is drawn across patches, it can only benefit one species at the expense of another. This can be seen most clearly by the fact that in any of the following sets of equations, the sum of all equilibrium biomasses, $C_{jA}^* + C_{jB}^* + 2C_i^*$ (e.g., eq. [7] plus 2 times eq. [8]), reduces to $S_{1A} + S_{1B} - 2mh_{i1}/(\mu - m)$, which is independent of ρ . Wherever recycling causes an increase in nonintegrator biomass, it does so at the expense of integrator biomass, and whenever it leads to lower nonintegrator biomass, integrator biomass is increased. It is worth highlighting that when both species coexist, it is possible for each patch to be richer in a separate resource at equilibrium even if one patch has higher supply points than the other for both resources. Thus, coexistence equilibria shown in figure 2C, 2D, 2G, and 2H may occur even though supply points for the two resources covary positively across patches.

Solutions for equilibrium biomasses can be obtained to support the graphical analysis discussed above. Note that each set of equations that follows is based on assumptions that species coexist in specific patches and are limited by specific resources and that each set is applicable only for considering ranges of parameter values consistent with those scenarios. When the nonintegrator and integrator coexist in only one patch, the nonintegrator may be limited by either the same resource as the integrator (we will assume that this is R_1) or the opposite resource (R_2). Equilibrium biomasses when the nonintegrator is limited by R_1 (assuming that coexistence occurs in patch A) are

$$C_{jA}^* = \left[\frac{\rho}{(1-\rho)} - \frac{h_{j1}}{h_{i1}(1-\rho)} \right] C_i^* + S_{1A} - \frac{mh_{j1}}{(\mu - m)}, \quad (7)$$

$$C_i^* = \frac{S_{1B} + [mh_{j1}/(\mu - m)] - [2mh_{i1}/(\mu - m)]}{1 + [(h_{i1} - h_{j1})/h_{i1}(1-\rho)]}. \quad (8)$$

Equation (8) decreases with ρ and equation (7) increases with ρ whenever $h_{i1} > h_{j1}$ (i.e., the integrator has the higher ZNGI for R_1), and the reverse is true when $h_{i1} < h_{j1}$ and the integrator has the lower ZNGI for R_1 . This agrees with what is illustrated by the black and white circles on the vertical portions of j 's ZNGIs in figure 2.

When single-patch coexistence occurs with a nonintegrator limited by R_2 (let us say in patch B), equilibrium biomasses are

$$C_{jB}^* = \left(\frac{\rho}{(1-\rho)} - \frac{[2mh_{j2}/(\mu - m)]}{(1-\rho)[S_{2A} + S_{2B} - S_{1A} - S_{1B} + [2mh_{i1}/(\mu - m)]]} \right) \times C_i^* + S_{2B} - \frac{mh_{j2}}{(\mu - m)}, \quad (9)$$

$$C_i^* = \left\{ (1-\rho) \left[S_{2A} + S_{2B} - S_{1A} - S_{1B} + \frac{2mh_{i1}}{(\mu - m)} \right] \times \left[S_{1A} + S_{1B} - S_{2B} - \frac{2mh_{i1}}{(\mu - m)} + \frac{2mh_{j2}}{(\mu - m)} \right] \right\} \left/ \left\{ (1-\rho) \left[S_{2A} + S_{2B} - S_{1A} - S_{1B} + \frac{2mh_{i1}}{(\mu - m)} \right] + \left[S_{2A} + S_{2B} - S_{1A} - S_{1B} + \frac{2mh_{i1}}{(\mu - m)} - \frac{2mh_{j2}}{(\mu - m)} \right] \right\} \right. \quad (10)$$

In equation (10), the first term in brackets in the numerator equals $(R_{2A} + R_{2B})^*$, and the second equals the difference between the total consumption of R_1 and the consumption of R_2 from patch B. Both of these must be positive, as must the entire expression. Therefore, equation (10) will increase with ρ whenever the last term in the denominator is negative and will decrease with ρ whenever that term is positive. That term represents twice the difference between the average R_2^* and the nonintegrator's ZNGI for R_2 . Thus, whenever the former is greater, re-

are shown; potential effects of successful invasion in one patch on subsequent invasibility of the other patch (as discussed by Golubski et al. [2008]) are not included. In A–D, the integrator can invade a resident nonintegrator whenever patch B's supply point is to the right of the black line in A. In E–H, the integrator can invade a resident nonintegrator whenever patch B's supply point is above the black line in E (lines are shown only in A and E, to avoid clutter).

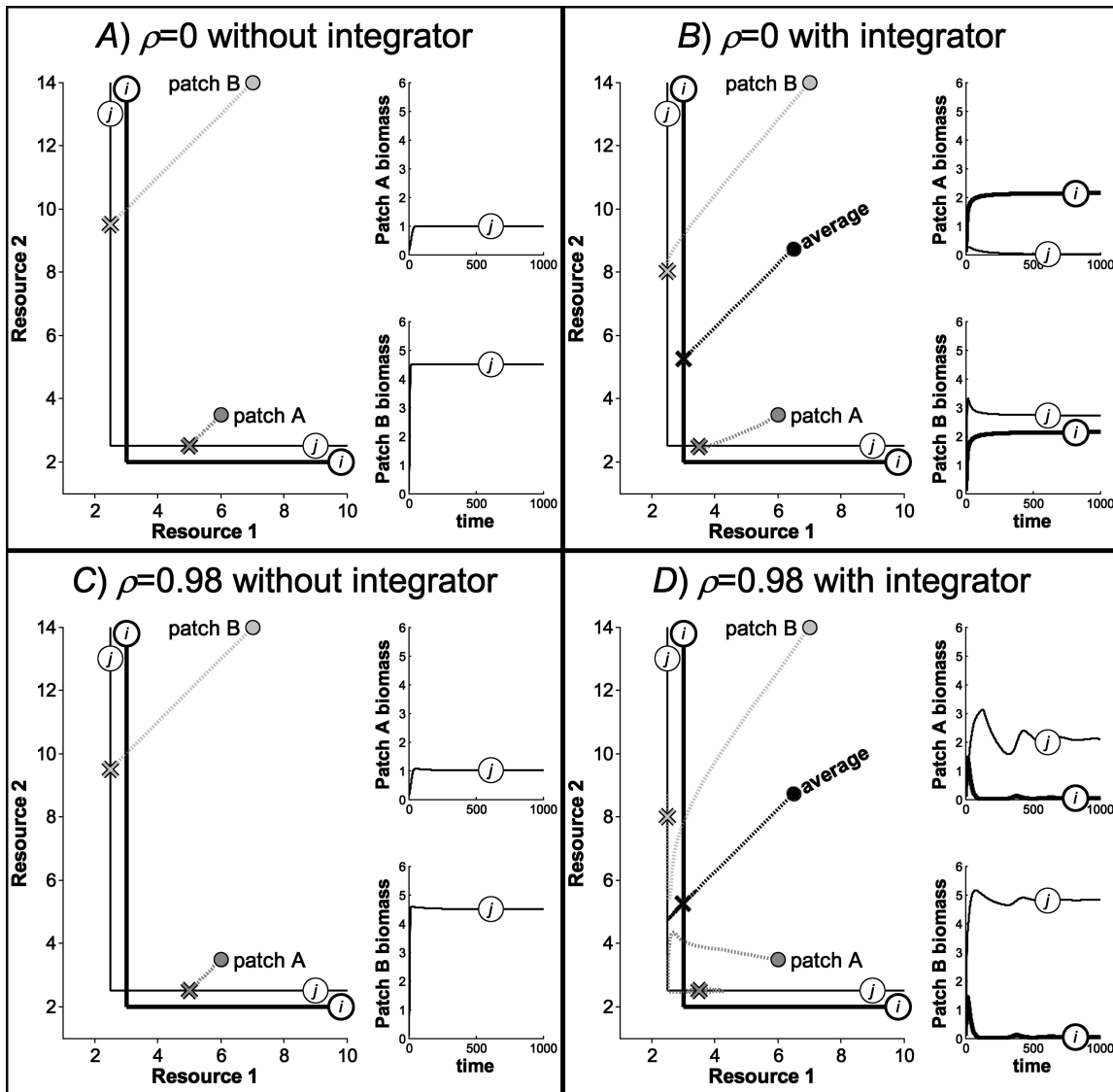


Figure 5: Simulations where an integrator (*i*) negatively affects its nonintegrating competitor (*j*) in the absence of recycling (A vs. B; biomass of *j* decreases in each patch) but facilitates the nonintegrator with recycling (C vs. D; biomass of *j* increases in each patch). Note that facilitation occurs despite one patch (B) having higher supply points for both resources. Symbols are as in figure 1; parameter values are $h_{i1} = 12$, $h_{j1} = 10$, $h_{i2} = 8$, $h_{j2} = 10$, $\mu = 2$, $m = 0.4$, and $D = m(1 - \rho)$; initial biomasses are 0.1 per patch.

has long been appreciated (e.g., see Caraco and Kelly 1991), and it provides a mechanism whereby homogenization of the environment by integrators may benefit nonintegrators even in single-resource models. Simulations that we ran using single-resource models to explore this mechanism often found its effect to be subtle (app. C in the online edition of the *American Naturalist*). This is partly because it is most pronounced when average resource levels are high relative to the nonintegrator's requirements. For this to be the case under a resident in-

tegrator requires the integrator to have a ZNGI much higher than that of the nonintegrator. However, such integrators did not grow quickly enough to have a pronounced effect when both species were introduced simultaneously at low biomass into an empty environment.

Discussion

We have shown here that with recycling, a consumer that integrates across patches can have net positive effects on

invasion by and growth of a smaller competitor that experiences more between-patch heterogeneity. Recycling of integrator biomass moves resources from the patch where they are in a higher concentration to the patch where they are in a lower concentration, and under a resident integrator it draws resource levels in each patch closer to the across-patch average (at the integrator's ZNGI). Thus, recycling is most likely to have net positive effects on non-integrators when the integrator is an inferior competitor for the resource by which it is limited, when each patch has higher supply of a different resource, and when non-integrators in each patch are limited by resources that are at a higher concentration in the opposite patch (fig. 2). These facilitative effects are common and always occur when both species coexist in both patches and/or the integrator is the inferior competitor for both resources (assuming that it is not excluded by the nonintegrator). The facilitative effects may allow the smaller nonintegrator to invade an environment where one or both patches would be unsuitable in the absence of the integrator. Thus, our model provides an example of facilitation expanding a species' realized niche (*sensu* Bruno et al. 2003), with relative sizes of competitors in this case determining which species is the facilitator and which is facilitated. There is currently great interest in clarifying the concept of facilitation and the mechanisms by which it occurs (e.g., Brooker and Callaway 2009); our model highlights that species effects on spatial distributions of resources constitute a potential factor to be considered.

It has been suggested that the creation of spatial heterogeneity by a resident can promote species coexistence (e.g., Tilman and Pacala 1993; Huston and DeAngelis 1994; Pacala and Levin 1997; Barot and Gignoux 2004). In contrast, our model presents a case where a species can promote coexistence by reducing spatial heterogeneity. This requires that a heterogeneous environment favor the competitor that does the homogenization, a plausible case for plants of different sizes. Spatial resource heterogeneity might be expected to be detrimental to plant growth if some patches have a low supply of resources that are abundant elsewhere or if plants show saturating (e.g., type II) responses to resources. In this situation, smaller plants should experience the negative consequences of heterogeneity more keenly than their larger competitors. Thus, if larger competitors reduce resource heterogeneity, smaller plants will benefit. In some cases, such as when the integrator is a superior competitor and one patch has a higher supply than the other of both resources (e.g., fig. 2E), the nonintegrator may benefit from between-patch heterogeneity (e.g., the integrator's underdepletion of the rich patch). In such cases, recycling may negatively affect the smaller (nonintegrating) competitor. While facilitation of the smaller plant in our model occurred mainly because

of complementarity in equilibrium resource concentrations between patches, it is important to note that facilitation did not require resource supply to covary negatively between patches (fig. 5). The mechanism at play in our model also somewhat resembles the way in which species with high dispersal rates in metacommunity models may reduce temporal heterogeneity in a way that favors their slower-dispersing competitors (Schreiber and Saltzman 2009).

Our results may also be relevant to the debate as to whether plant competition for soil resources is size symmetric (plants acquiring resources proportionally to their size) or size asymmetric (larger plants acquiring a disproportionately large share). It has been suggested that resource heterogeneity may promote asymmetry if large plants are able to encounter and exploit rich patches more effectively (Schwinning and Weiner 1998). However, as we show here, if large plants occupy and recycle resources into poorer patches, they may reduce the heterogeneity that affords them an advantage.

The negative feedback that often results from recycling here is the opposite of what is often expected from litter quality effects (Vitousek 1982; Wedin and Tilman 1990; Hobbie 1992; Aerts 1999; Miki and Kondoh 2002; Suding et al. 2004). Species that use nutrients efficiently and have lower nutrient requirements (low R^* s) are expected to have recalcitrant litter, which will decompose slowly and further reduce nutrient availability, favoring those species. Rapidly growing species with high nutrient demand are expected to have highly decomposable litter that will quickly release nutrients and thus to favor those species. This is expected to generate positive feedback (although the predictions may change when multiple nutrient forms are considered, when species preferentially promote losses of their limiting nutrient over their competitors' limiting nutrient, or when the reverse relationship between species' R^* s and litter decomposabilities holds; see Clark et al. 2005, Daufresne and Hedin 2005, and Miki and Kondoh 2002, respectively). Our model shows that the spatial effects of recycling also may be critically important to the coexistence and dominance of species. Thus, in evaluating the effects of recycling on plant competition, we must consider not only differences in litter quality between species but also differences in how that litter is distributed in space by different species relative to where the nutrients were acquired. Our model focuses on spatial effects of recycling, but it could be extended to incorporate litter quality effects as well, for example, by allowing recycling rates to be resource and/or species specific. Preliminary explorations of some of these extensions suggest that while they add a great deal of complexity, the general result that recycling of integrator biomass tends to homogenize patches often remains valid

(A. J. Golubski, K. L. Gross, and G. G. Mittlebach, unpublished results).

In our model, we assumed that integrators were constrained to allocate equal growth to each patch. This approach is a way of modeling a trade-off between the maximum and minimum scales at which competitors can forage, and it helps ensure that integrators and nonintegrators are as equivalent as possible, since nonintegrators are not able to forage selectively at scales smaller than one patch (although, presumably, resource concentrations within a patch would in reality represent an average across some finer-scale heterogeneity). However, we have also explored the implications of relaxing this assumption and allowing integrators to preferentially allocate growth to the more profitable patch. Because resource uptake by an integrator does not depend on relative allocation to each patch in the current model, exploring the implications of allowing integrators to forage more flexibly requires a different variant of the model (the “uptake-limited” model discussed in the data supplement of Golubski et al. 2008). Simulations using that model and allowing integrators unlimited flexibility to allocate growth optimally among patches often did not qualitatively change our results (app. D in the online edition of the *American Naturalist*). Although optimal allocation eliminates under- and over-depletion when the same resource is limiting in each patch, integrators are still able to take advantage of complementarity between patches. Realistically, some intermediate case between the two extremes of completely equal growth among patches and completely flexible growth might be expected, which suggests that any effects presented here that depend on our assumption of equal growth would be reduced but not eliminated by relaxing it. Other allocation patterns that may change the implications of recycling by large plants are also possible; for example, shrubs in arid regions can create “fertility islands” by gathering resources from extensive root system and then concentrating them beneath a relatively small canopy (e.g., Schlesinger et al. 1996). Scenarios such as this are less likely with clonal plants, where most ramets will have shoots as well as roots.

In our model, resource heterogeneity is characterized by discrete patches, and the difference in size between nonintegrators and integrators is modeled as the ability to obtain resources from one versus two patches. These assumptions abstract much of the reality of natural plant communities. For example, both an integrator and a non-integrator may begin life as a small seedling occupying a single patch. In this case, our assumption that integrators occupy two patches would be violated. Moreover, invasion by integrators may not be possible if they must initially grow through a small size at which they are limited by resource availability at the single-patch scale and a non-integrator is the superior competitor (i.e., has the lower

ZNGI for both resources). Although ontogenetic changes in plant size may limit the applicability of our simple model to natural systems, there are a number of factors that may lessen this concern. For example, in many clonal species, reproduction occurs commonly (perhaps most commonly) through vegetative growth, with separation of the connections between ramets occurring over time. In this case, mother ramets may initially subsidize daughter ramets, and this could allow new ramets to escape limitation by their local environment when they are at their smallest. In addition, if patches are colonized after disturbance, during dormant periods, or during diebacks, when resource uptake is reduced, then the time it takes for established residents or other colonizing competitors to draw resources to their ZNGIs may be sufficient for an integrator to grow large enough to respond to resources at a scale larger than a single patch. Incorporating ontogenetic changes in plant size or more continuous variation in size between individuals and species into models of competition and resource recycling in patchy environments would be a valuable next step.

Although several models predict that resource uptake by consumers that forage across multiple patches (as our integrators do) may maintain or exacerbate underlying heterogeneity in resources (McLaughlin and Roughgarden 1992; de Roos et al. 1998; Abrams and Wilson 2004; Namba and Hashimoto 2004; Golubski et al. 2008), our study suggests that the implications of consumers interacting with resources across multiple patches will depend on the interplay of both heterogeneity-preserving and heterogeneity-reducing effects. This also means that transient dynamics may be particularly important if resource uptake by large competitors maintains or increases spatial heterogeneity in the short term, while over the longer term recycling of their biomass reduces it. Ongoing long-term experiments in grasslands are yielding results consistent with this dynamic, with the effects of sustained increases in nutrient supply on soil nutrient concentrations lessening over several years in the presence of clonal species (K. L. Gross, G. G. Mittelbach, and H. L. Reynolds, unpublished data). The potential significance of resource uptake and recycling acting at different timescales has been highlighted by other recent theoretical models (Menge et al. 2009), and time lags associated with litter effects have been highlighted by recent work combining field surveys and models in dune systems (Farrer et al. 2010).

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