Chapter 7

Implications of System Openness for Local Community Structure and Ecosystem Function

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There is growing evidence from a wide range of ecological systems that local population, community, and ecosystem dynamics can be dramatically influenced by fluxes of organisms and materials among spatially separated habitats (Holt 1993; Polis, Anderson, and Holt 1997; Power and Rainey 2000). An appreciation of the effect of such spatial coupling has led to a recent reevaluation of many traditional issues in ecology. For instance, weak coupling of different habitats may be an important source of stability in complex communities (Huxel and McCann 1998). This phenomenon has potentially important implications for the diversity-stability relationship (Polis 1998). Moreover, the spatial scale and behavioral details of consumer movement can alter the "bottom-up" effects of enrichment in food chains (Oksanen et al. 1995; Nisbet et al. 1997), and predator "spillover" can greatly depress local prey populations, in effect magnifying "top-down" effects in some habitats (e.g., Estes et al. 1998; Ekerholm et al. 2001).

The quantitative effect of spatial linkages on local dynamics, however, should vary greatly among habitats, for several reasons. First, the world is heterogeneous at almost all spatial scales for factors that affect population growth and interspecific interactions (Williamson 1981). Some habitats with high productivity can exert substantial effects on other habitats without a correspondingly large reciprocal effect. Spatial fluxes can also exhibit

strong directionality due to the action of prevailing winds, currents, or gravity (e.g., on passive dispersal down a montane slope). Because of such asymmetries, in open systems one can often pragmatically identify "source" and "recipient" habitats. The recipient habitat may have a species composition generated by spatial fluxes that is dramatically different from that expected based on local conditions alone. Second, systems may be closed with respect to one set of components, yet operationally open for others. For instance, an endemic consumer species on an oceanic island may have demographically self-contained population dynamics, so that changes in its numbers are driven solely by in situ births and deaths. Yet its birth rate may be heightened by allochthonous resource inputs, and its death rate by migratory predators (Polis, Anderson, and Holt 1997). Habitats can vary greatly in which particular components are strongly coupled by spatial fluxes to the external environment.

In this chapter, I consider two general conceptual issues that should be considered whenever one considers the dynamics of open habitats, yet which have been almost entirely ignored in the ecological literature. The first has to do with the traditional focus in community theory on mechanisms of local coexistence (e.g., Kotler and Brown 1988; Chesson and Huntly 1997). In open systems, species tending toward exclusion in a local community (e.g., due to interactions with resident competitors or predators) can persist, and even be abundant, due to recurrent immigration. A consideration of the factors controlling abundance in such species leads to a focus on *rates* of competitive exclusion, and on temporal variability in such rates, rather than just the qualitative phenomenon of exclusion versus coexistence. The second general issue I examine is the relationship between rules of community structure and ecosystem function. I will show that the exact way in which a local system is open to external subsidies and exports can profoundly influence how community interactions map onto ecosystem properties such as productivity and total biomass. I illustrate both issues with simple models that capture the flavor of more complex models.

THE CENTRAL PARADIGM OF CLASSIC COMMUNITY ECOLOGY

A key organizing theme in community ecology is that local communities are restricted subsets of a regional species pool (e.g., Weiher and Keddy 1995). Over a sufficiently long time scale, all local communities arise from a suite of successful invasions from larger spatial arenas (Ricklefs and Schluter 1993; Holt 1993; Zobel 1997; Huston 1999; Loreau and Mouquet 1999). One

general organizing factor that can generate local community structure is the exclusion of species by interactions with resident species such as predators and competitors. This insight defines a basic protocol or paradigm in community ecology, which is to articulate how local community structure arises from patterns in the success and failure of invasions, as species are "tested" against the template of local environmental conditions and interactions with resident species. If an invading species increases when rare, it is potentially a permanent community member. By contrast, if an invading species declines when rare, it is excluded. A vast body of community ecology can be boiled down to elaborations of this conceptual protocol.

More formally, let us assume that the population dynamics of species i is described by a continuous-time differential equation model. Let N_i be the density of invading species i, when it is sufficiently rare that any direct density dependence can be ignored, and let $\mathbf{N}_r$ be a vector describing the densities of resident species and resource pools in the community. The instantaneous per capita growth rate of species i is f_i (in general, a function of the abundances of resident species). The equation

$$\frac{dN_i}{dt} = N_i f_i(\mathbf{N}_r), \quad i \neq j \tag{7.1}$$

can represent a wide variety of assumptions about interactions between the invader and resident species, including resource competition, interference, and attacks by resident natural enemies. If f_i is a linear function of densities of resident species with constant coefficients, the model is the familiar Lotka-Volterra model. More generally, the growth rate of the invader will be a nonlinear function of the resident species' abundances (e.g., Abrams and Roth 1994), and the model coefficients may vary through time as well (e.g., Dunson and Travis 1991; Chesson and Huntly 1997). If the environment is constant and the resident community has settled into a stable set of abundances, the invader will have a constant per capita growth rate. If $f_i < 0$, the invader declines toward zero abundance in the focal habitat. Otherwise, the invader increases and eventually is likely to influence the preexisting community.

Iterating over repeated invasions by species drawn from the regional species pool generates a local community of cohabiting species, defined in part by their autecological requirements and in part by mechanisms of coexistence (e.g., niche partitioning, keystone predation). The rules that determine which species persist in the local community and which are excluded can be thought of as "sorting" or assembly rules. For instance, in simple pairwise exploitative competition for a single limiting resource, the consumer that can persist at the lower resource level tends to displace the less efficient consumer (Tilman 1990). Over repeated invasions, this rule leads to a sorting of species, such that the consumer species in the regional pool that depresses local resources the most eventually dominates.

MODIFYING THE CENTRAL PARADIGM IN OPEN COMMUNITIES

This familiar conceptual protocol rests on a qualitative assumption: potential community members are assumed to be excluded, and thus absent from the community, whenever their per capita growth rates when rare are negative. This assumption can be reasonable, for instance on distant oceanic islands where colonization is a rare, sporadic event. In effect, the usual protocol assumes that communities are closed except for occasional bouts of colonization by nonresident species. But for many local communities in continental settings, spatial couplings among habitats lead to recurrent or chronic invasions (one of the mechanisms implicit in island biogeographic theory; MacArthur and Wilson 1967; Holt 1992; Rosenzweig 1995). A species excluded by the resident community could nonetheless be regularly present, and even be locally abundant, because of dispersal.

A simple extension of model (7.1) reveals that the magnitude of this effect depends on the interplay of the rate of input from external sources and the rate of local exclusion (Holt 1993). We add a term I representing allochthonous inputs of a given invading species (for simplicity, we drop the index i):

$$\frac{dN}{dt} = f(t)N + I. \tag{7.2}$$

If this species has a constant, negative growth rate—that is, $f(t) = f < 0$—the excluded species equilibrates at a standing density of

$$\bar{N} = \frac{I}{|f|}. \tag{7.3}$$

The denominator is the absolute value of the rate of exclusion of the invading species. Equation (7.3) implies that an excluded species can be locally abundant if it enjoys a low rate of exclusion or high allochthonous input.

Conversely, an excluded species will be rare (and typically missed in standard field sampling) if it is both strongly excluded and has a low rate of input from external sources. The rate of input, I, is governed by local properties of the source habitat (e.g., productivity), landscape attributes (e.g., movement rates from source into recipient habitat), and properties of the recipient habitat (e.g., edge permeability) (Polis, Anderson, and Holt 1997). The rate of exclusion, $|f|$, depends on properties of both the invader and the recipient habitat and on resident community structure. In open systems, for any model of interacting species that does not predict coexistence, one needs to know not just the mere fact of exclusion, but the *rate* of exclusion. The use of community models to quantify rates of exclusion (rather than simply exclusion vs. coexistence, as in closed communities) has largely been ignored in theoretical community ecology.

One assumption leading to equation (7.3) is that the excluded species has a constant, negative growth rate. More generally, growth rates will vary, driven by temporal variation in the external environment or in the densities or activities of resident community members. In a closed community, exclusion will still occur if the long-term average growth rate is negative. However, in an open community, further analysis reveals that temporal variation tends to enhance (sometimes quite substantially) the average abundance of species persisting because of immigration, particularly if direct intraspecific density dependence is weak (Gonzalez and Holt 2002; Holt et al., in press). Qualitatively, immigration sustains local populations through bad times, permitting populations to capitalize on runs of good times and potentially increase to high numbers, even if such times are insufficient to permit sustained persistence without immigration.

Equation (7.3) does not directly express feedbacks that arise through the effects of the invader on resident species' abundances. To assess such feedbacks, it is necessary to examine models with explicit mechanisms of potential exclusion. One can take any standard model of a community module (sensu Holt 1997a), incorporate an input term, and then evaluate how spatial subsidies modify local community structure and dynamics. Here I present two examples.

Exploitative Competition with External Inputs

The most familiar community module may be two consumers competing exploitatively for a single shared limiting resource (Tilman 1982, 1990). As is well known both theoretically and empirically (Grover 1997), given such pairwise competition, if the system is closed to immigration and settles down to an equilibrium, the equilibrium will be dominated by the consumer species that persists at the lower resource level; the other species declines to extinction.

Incorporating immigration by the superior consumer just hastens the fate of the inferior one. By contrast, incorporating regular immigration by the inferior consumer from another habitat where it persists (possibly because it is a superior exploiter of resources there) permits it to persist in the recipient habitat as well. The following model shows that the abundance of the excluded species in the focal community depends on the interplay of input rates and local rates of exclusion. Moreover, sufficiently high input rates can force the exclusion of the superior local competitor.

For simplicity, we measure abundances on scales such that each unit of consumed resource is converted into an equivalent number of consumers. Let $g_i(R)$ be the birth rate of consumer i on the single limiting resource (of abundance R), and m_i a density-independent rate of local mortality and emigration of consumer i. In general, one expects $g_i(R)$ to increase monotonically with R, approaching an asymptote at high resource levels. The net growth rate of species i is $f_i(R)$. Without resources, there should be no births (i.e., $g_i(0) = 0$). The renewal dynamics of the resource are denoted by G (which may be a function of R). With these assumptions, the model is

$$\begin{aligned}
\frac{dN_1}{dt} &= N_1[g_1(R) - m_1] = N_1 f_1(R) \\
\frac{dN_2}{dt} &= N_2[g_2(R) - m_2] + I = N_2 f_2(R) + I \\
\frac{dR}{dt} &= G - N_1 g_1(R) - N_2 f_2(R).
\end{aligned} \tag{7.4}$$

We assume that the superior local competitor, species 1, does not have external inputs. The value of R at which species i has a zero local growth rate (viz., the R such that $g_i(R) = m_i$) is $R_i = g_i^{-1}(m_i)$. If $R_1 < R_2$, then species 2 should be competitively excluded by species 1 when they co-occur in a closed community (Tilman 1990; Holt et al. 1994; Grover 1997).

If both species persist at equilibrium in an open community, we have

$$\begin{aligned}
R^* &= R_1, \\
N_2^* &= \frac{I}{|f_2(R_1^*)|}, \text{ and} \\
N_1^* &= \frac{1}{m_1}[G - N_2^* g_2(R_1^*)].
\end{aligned} \tag{7.5}$$

The ambient level of the resource is set by the superior competitor. The abundance of the inferior competitor is its input rate divided by its rate of exclusion at the ambient level of resources-exactly as in the simpler single-species model of equation (7.2) above.

A locally inferior competitor can thus be abundant in an open community if it is weakly excluded and enjoys high rates of input from external sources. Although the system potentially includes strong nonlinearities (e.g., in resource uptake rates, or in G), the relationship between the equilibrial abundances of the competitors and the rate of spatial subsidy of the inferior competitor turns out to be very simple: the abundance of the inferior competitor increases linearly with its rate of input, I, whereas the abundance of the locally superior competitor declines linearly with inputs of the inferior competitor.

A sufficiently high rate of input implies exclusion of the locally superior competitor. The rate of input needed to exclude the superior competitor is

$$I > G\frac{|f_2(R_1^*)|}{g_2(R_1^*)} = G\left[\frac{m_2}{g_2(R_1^*)} - 1\right] \qquad (7.6)$$

Inspection of this simple expression reveals that reversal of local competitive dominance arising from allochthonous inputs of a locally inferior competitor is facilitated by three circumstances: (1) factors associated with a low rate of exclusion (e.g., low m_2); (2) a habitat with a low rate of in situ renewal of the shared limiting resource; or (3) a high rate of immigration of the inferior competitor. A very effective resident competitor depletes resources to a low level, which makes it harder for it to be displaced by a subsidized inferior competitor. Conversely, if the two competing species have similar competitive abilities, low input rates can tip the balance toward an inferior resident competitor.

The quantitative effect of spatial subsidies on the competitive exclusion of species that are locally competitive dominants can be modulated by local factors. For example, assume that an invading prey species is inferior at consuming the shared resource, but enjoys a lower rate of mortality due to resident generalist predators (acting as density-independent mortality agents) than does a resident competitor. In this case, competitive exclusion should be weakened because ambient resource levels should be higher, increasing the birth rate for the invader. Along with the invader's assumed lower death rate, this implies that the intrinsically superior competitor for

resources will be more vulnerable to exclusion at lower rates of subsidized inputs of the inferior competitor. At a fixed rate of spatial subsidy (I), species specialized for habitats with lower productivity (G) are more likely to be vulnerable to competitive exclusion by spatially subsidized species. As a special case, assume that the basal resource grows logistically (so that $G = rR(1 - R/K)$) and that consumption rates (and consumer birth rates) are linear functions of resource abundance (i.e., $g_i(R) = b_iR$). If resource levels are depressed by consumption well below K, the condition for exclusion of the superior competitor due to spatial subsidy of the inferior competitor is

$$I > r\left(\frac{m_2}{b_2} - \frac{m_1}{b_1}\right).$$

Spatial subsidies are particularly likely to reverse competitive dominance if the consumers are roughly equivalent (as measured by a small magnitude for the term in parentheses) or the resource has low recruitment rates.

Apparent Competition with External Inputs

Similar phenomena arise in systems in which exclusion is driven by shared predation leading to apparent competition (Holt 1984, 1997a; Holt and Lawton 1994; Huxel and McCann 1998). Consider the following model, in which an effective generalist predator keeps all its prey at low densities and in which the predator's functional response to each prey is linear. For simplicity, the system in the absence of external subsidies is assumed to be stabilized by interference competition among predators, with no direct density dependence in the prey. The model is

$$\begin{aligned}\frac{dP}{dt} &= P\left(\sum_i a_iR_i - m - qP\right)\\ \frac{dR_1}{dt} &= R_1(r_1 - a_1P)\\ \frac{dR_2}{dt} &= R_2(r_2 - a_2P) + I.\end{aligned} \qquad (7.7)$$

Here, m is the density-independent mortality rate of the predator, and q gauges direct density dependence due to predator interference competi-

tion. The per capita attack rate by the predator on prey species i is a_i (prey densities are scaled so that prey consumption and predator births are in equivalent units). The r_i are the prey species' intrinsic growth rates, and I is the rate of spatial subsidy for prey species 2. We assume that $r_1/a_1 > r_2/a_2$, which implies that in a closed community, prey species 1 will sustain enough predators to eliminate prey species 2 via apparent competition (Holt and Lawton 1994). With immigration, species 2 persists. The equilibrium with all species present is

$$\begin{aligned} P^* &= \frac{r_1}{a_1}, \\ R_2^* &= \frac{I}{|r_2 - a_2 P^*|}, \\ R_1^* &= \frac{1}{a_1}\left[m + qP^* - \frac{a_2 I}{|r_2 - a_2 P^*|}\right]. \end{aligned} \tag{7.8}$$

As in the model of exploitative competition, the abundance of the inferior prey species is governed by the interplay of the immigration rate and a rate of local exclusion (the denominator in the expression for R_2^*). The abundance of the superior prey species is depressed by the inferior prey, and the superior prey species is eliminated at high inputs of the allochthonous inferior prey. Given that the two prey coexist, there is a linear relationship between their abundances and the rate of spatial subsidy for the inferior prey. Elimination of the non-subsidized prey occurs if

$$I \geq \frac{1}{a_2}(m + qP^*)|r_2 - a_2 P^*| = \left(m + \frac{qr_1}{a_1}\right)\left(\frac{r_1}{a_1} - \frac{r_2}{a_2}\right). \tag{7.9}$$

A subsidized prey species that is only weakly excluded by the resident prey-predator community via apparent competition (as measured by relative r/a ratios) can readily exclude a non-subsidized prey. Such exclusion is more likely if the predator is very effective at catching each prey type (high a's) or if the habitat is low in productivity (low r's). Conversely, changes in parameters that depress the predator's growth rate (increased m) or dampen its numerical response (increased q) make it harder for a subsidized prey to exclude a non-subsidized prey.

The above model assumes that the system is spatially closed for the predator and open for one (but not both) prey species. If instead the system is closed for both prey species, but open for the predator (with an input term I added to the expression for dP/dt and $I = 0$ in model [7.7]), prey coexistence is impossible: the prey species with the higher r/a dominates, excluding the alternative prey. Moreover, if the predator input rate is sufficiently great, then both prey species will be excluded (Holt 1984; see also Holt 1996b; Polis, Anderson, and Holt 1997; Huxel and McCann 1998).

The two models suggest that spatial subsidies can substantially influence community structure, and they give guidelines as to where such effects might be sought. In particular, both models suggest that spatial subsidies should have a particularly marked effect in low-productivity habitats and when considering species that are roughly equivalent. Species that are specialized for low-productivity habitats are particularly vulnerable to exclusion by "spillover" of species from other habitats.

THE INFLUENCE OF COMMUNITY SORTING ON ECOSYSTEM PROCESSES: PROFOUND CONSEQUENCES OF SYSTEM OPENNESS

A basic challenge in ecology today is linking community dynamics with ecosystem processes (Jones and Lawton 1995; Loreau 1998; Kinzig et al. 2002). In the previous section, I examined how system openness within a given trophic level influences species coexistence via spatial subsidies that modify the outcome of "sorting" by local interactions such as exploitative and apparent competition. In this section, I use very simple models with detrital feedbacks to demonstrate that allowing system compartments to be open also controls how species sorting rules affect local ecosystem function. Holt and Loreau (2002) analyze much more complex, realistic ecosystem models and arrive at essentially the same conclusions derived below for simple models.

My basic approach is to splice compartment models of local ecosystem processes (DeAngelis 1992) to species sorting rules. The ecosystem models describe how nutrients flow among various compartments in a community defined by food chain interactions. Figure 7.1 shows three systems, differing only in whether or not there is spatial coupling between the local system and an external environment, and if so, the compartment that is involved in the coupling. The abiotic compartments of the local system include a pool of a limiting resource, of abundance R, and detrital pools generated by each trophic level (D denotes detritus produced by producer mortality; D_1, that produced by the herbivore). For each detrital pool, a constant

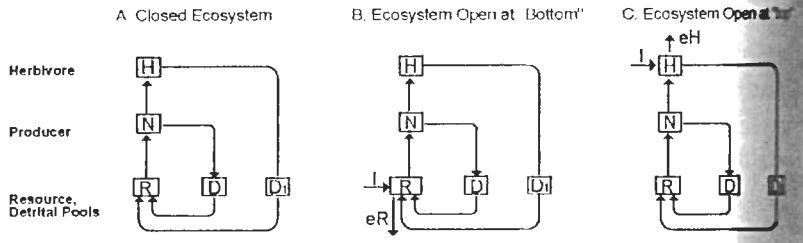

Figure 7.1 Ecosystems with a defined trophic structure can be coupled spatially to the external world in various ways. (A) Closed ecosystem (no spatial coupling). (B) Ecosystem with fluxes only at the basal resource level. (C) Ecosystem with fluxes (immigration and emigration) only at the top consumer level.

rate of decomposition frees resources. The biotic compartments include a producer population, of abundance N, fed upon by a herbivore, of abundance H. Figure 7.1A depicts a closed ecosystem; figure 7.1B, a system in which the basal resource compartment is spatially open, importing and exporting nutrients; and figure 7.1C, a system in which the top consumer alone is linked to the external world.

We imagine that at the producer trophic level, there are a large number of species potentially available in the regional species pool, but that the local community has just a single top consumer species. The attributes of the producers, as expressed in the local environment, imply that just a single species competitively dominates in pairwise competition. With occasional colonization at very low densities, one expects to observe species sorting, as species superior at persisting in the local environment invade and supplant other species. At the producer trophic level, the factors that determine local superiority include both exploitative and apparent competition (Holt et al. 1994; Liebold 1996; Grover 1997). With respect to ecosystem processes such as local nutrient cycling and spatial fluxes in nutrient pools, biotic colonization can be trivial. Except during transient phases of invasion and exclusion, the local system is thus a simple unbranched food chain. The question we address is how species sorting driven by species replacement at the producer trophic level maps onto changes in the ecosystem attributes of primary productivity and total biomass.

Closed Ecosystem

We start with the closed ecosystem in figure 7.1A. The ecosystem model is defined by linear functional responses between the producer and the lim-

iting resource and between the herbivore and the producer (scaled by attack rates a and a_1, respectively); by constant density-independent death rates for both the producer and the herbivore (m and m_1, respectively); and by constant rates of detrital regeneration of the nutrient (at decomposition rates of d and d_1, corresponding to the detrital pools generated by the producer and the consumer, respectively). The abundances of all compartments are measured in terms of nutrient content. In the closed system, we assume that the total pool of nutrients is Q. These assumptions lead to the following model:

$$\begin{aligned}
\frac{dR}{dt} &= dD + d_1 D_1 - aRN \\
\frac{dN}{dt} &= aRN - mN - a_1 NH \\
\frac{dH}{dt} &= a_1 NH - m_1 H \\
\frac{dD}{dt} &= mN - dD \\
\frac{dD_1}{dt} &= m_1 H - d_1 D_1.
\end{aligned} \tag{7.10}$$

Model (7.10) implies the following equilibrial abundances:

$$\begin{aligned}
\hat{N} &= \frac{m_1}{a_1} \\
\hat{D} &= \frac{m}{d}\hat{N} \\
\hat{H} &= \frac{Q - \frac{m}{a} - \frac{m_1}{a_1}\left(1 + \frac{m}{d}\right)}{1 + \frac{a_1}{a} + \frac{m_1}{d}} \\
\hat{D}_1 &= \frac{m_1}{d_1}\hat{H} \\
\hat{R} &= \frac{m}{a} + \frac{a_1}{a}\hat{H}.
\end{aligned}$$

Note that biomasses (living and dead) and free nutrients sum to Q, the total nutrient pool present in the closed system. Gross primary production, W, defined as the rate of production of new tissue by the producer, is $a\hat{R}\hat{N}$ at equilibrium.

How is primary production influenced by producer sorting? Consider the producer isocline in a space defined by herbivore and resource abundances (Holt et al. 1994; Liebold 1996; Grover 1997). In the above model, this isocline is a straight line with positive slope, intersecting the R-axis at the R^* value required to sustain the producer in the absence of herbivory (fig. 7.2A). Different producer species in the regional species pool can vary in any one (or more) of three parameters defining producer dynamics: m, a

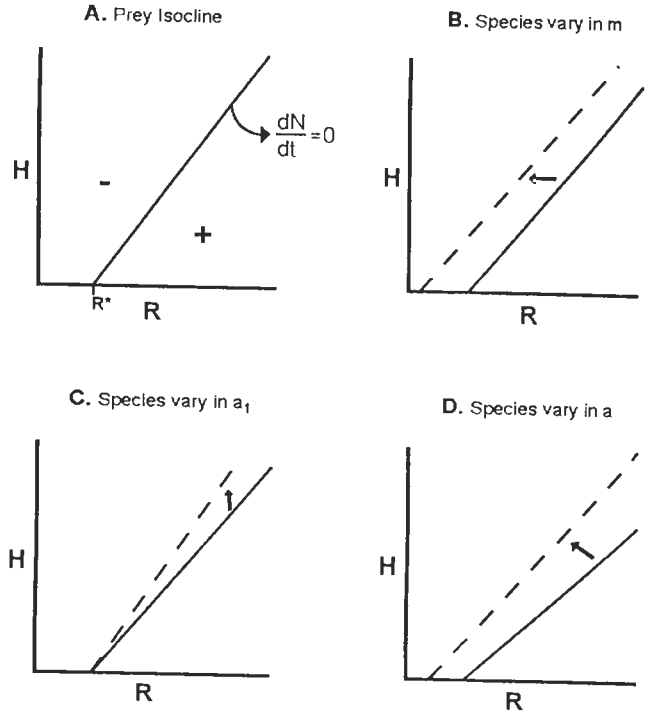

Figure 7.2 A graphic depiction of sorting rules among producers competing for a single limiting resource and sharing a common herbivore. (A) Each producer species has a zero growth isocline in a phase plane with axes of resource density (R) and herbivore abundance (H). The positive slope reflects how increasing resource abundance is required to offset losses to the herbivore. For producer coexistence, the isoclines must cross (due to trade-offs; see Holt et al. 1994). The examples considered in the text do not have crossing isoclines, so single species should dominate in pairwise competition. (B) Producers differ only in resistance to density-independent mortality, m. At any given herbivore abundance, a species with lower m can persist at lower resource abundances. (C) Producers differ only in resistance to herbivory, a_1. All species have the same R^* (intercept on R-slope); species that are more vulnerable to herbivory have shallower isoclines. (D) Producers differ only in assimilation rate, a. More efficient consumers can persist at lower resource abundances and withstand more consumption; the isocline shifts to the left and tilts upward. (Adapted from Holt et al. 1994; Liebold 1996; Grover 1997.)

basic mortality rate (fig. 7.2B); a, a resource assimilation rate (fig. 7.2D); and a_1, vulnerability to herbivory (fig. 7.2C). We assume that the species pool varies with respect to just one parameter at a time; thus, the isoclines of alternative producers do not intersect. This implies that in pairwise competition in the local environment, just one producer species persists, due to the combined effects of exploitative competition for the shared limiting resource and apparent competition via the shared resident top consumer (Holt et al. 1994; Liebold 1996; Grover 1997).

If species colonize at random (relative to their local abilities), the first species present is not likely to be the one that ultimately dominates. With continued colonization, the community should evolve by species replacement, with sorting toward producer species with lower intrinsic death rates (m), higher assimilation rates (a), or lower vulnerabilities to herbivory (a_1). Substitution of equilibrial values for N^* and R^* into the expression for primary production, W, permits one to examine how the dynamics of species sorting at the producer level influences primary production (Holt and Loreau 2002). Rather than presenting algebraic details, here I simply sketch the results.

1. Species sorting by exploitative efficiency. If producer species differ only in resource assimilation rates, production increases as more efficient producers replace less efficient producers. The direct effect of increased assimilation by the producer is to depress the resource supply. However, assimilated nutrients are passed on to the herbivore population and recycled through the detrital pool, leading indirectly to increased production at the producer level.

2. Sorting by resistance to mortality factors other than herbivory. If producer species differ in m, the intrinsic death rate, the dominant producer should be the one with the lowest mortality rate in the local environment. If $d > d_1 m_1/(d_1 + m_1)$, then sorting lowers production, because lowering the basic mortality rate for producers delays the reentry of nutrients into the detrital pool. This inequality is satisfied if the decomposition rate of detritus from producers at least equals that of dead herbivores, or if herbivores have a sufficiently low death rate. If this inequality is reversed, species sorting enhances primary production because of more rapid nutrient recycling.

3. Sorting by resistance to herbivory. More complex patterns are possible here, with species sorting either increasing or decreasing production. Given sufficiently high Q, prey sorting increases production. With lower nutrient pools, prey sorting can depress production.

For instance, the latter situation arises if producers have low intrinsic mortality rates, or if decomposition rates for producer detritus are low.

Ecosystem with Resource Imports and Exports

We now change the assumption of a closed ecosystem. Consider an ecosystem open to nutrient flux at the "bottom," but otherwise closed (fig. 7.1B). The model is unchanged, except that the resource equation becomes

$$dR/dt = I - eR + dD + d_1D_1 - aNR.$$

Assume that the system settles into a steady state. At equilibrium, from conservation of mass, nutrient imports into the entire system must match exports. Since coupling with the external world is entirely through the resource compartment, the imports and exports of this compartment must balance; hence $I = eR^*$, or $R^* = I/e$. In effect, coupling the resource compartment to the rest of the world constrains that system variable. With R^* fixed, the other compartments have the same abundances as before, except that $H^* = (aR^* - m)/a_1$.

Once again, we imagine that a set of producer species is sorted by pairwise competitive encounters. Gross primary production is $aR^*N^* = (am_1I)/(a_1e)$. This expression leads to the following conclusions:

1. Prey species sorting by assimilation rate always increases primary production, matching the closed ecosystem pattern.

2. Prey species sorting by resistance to mortality factors other than the herbivore has *no* effect on primary production, in sharp contrast to the closed ecosystem, in which such sorting could either increase or decrease production. The basic reason for this is that system openness leads to a nutrient pool that is no longer dependent on flows through the decomposer system.

3. Prey species sorting by resistance to the herbivore always increases primary production. Again, this conclusion differs from that drawn for the closed ecosystem model, in which invasion by species able to resist the herbivore could either increase or decrease the long-term productivity of the system.

Species sorting can now also influence biomass and, in general, tends to increase the total biomass (living plus detrital pools) of the system (sorting by m increases total biomass if $1/d < 1m_1 + 1d_1$). In effect, species sorting permits the system to capture and retain more of the influx of nutrients before those nutrients are lost to the external world.

Ecosystem with Herbivore Imports and Exports

Finally, we assume that the herbivore compartment is coupled to the external world, whereas the rest of the ecosystem is closed (fig. 7.1C). The herbivore equation becomes

$$dH/dt = I - eH + a_1NH - m_1H,$$

and the rest of the model is as in equation (7.10). At equilibrium, nutrient inputs into the entire system should match outputs, so $H^* = I/e$. The equilibrial abundances of the other components are as before, except that standing abundance of the resource is now $R^* = (a_1I/e + m)/a$. Gross primary production is $m_1(I/e + m/a_1)$. Species sorting in the producer level now has the following implications:

1. Sorting by assimilation rate has *no* effect on primary production. This conclusion sharply contrasts with those from the other scenarios.

2. Sorting by resistance to mortality factors other than the herbivore now uniformly *reduces* primary production. This conclusion also differs from that for the closed system and the system open at the base. The reason for this difference is that with lower density-independent mortality, the flux of nutrients into the free nutrient pool is reduced, leading to less nutrient being available for use by the producer.

3. Sorting by resistance to the herbivore always increases primary production. This is comparable to what happens in the system that is open at the base, but differs from the closed system. Once again, modifying where the ecosystem is open versus closed has radically changed how the community process of species sorting maps onto ecosystem functioning.

With respect to total biomass (living and dead), producer sorting by assimilation rate has no effect, sorting by resistance to herbivory increases total biomass, and sorting by intrinsic mortality decreases biomass. These outcomes of species sorting differ sharply from those expected in an otherwise similar system that is open at the resource level, rather than the consumer level.

The above models are quite simple, but can be made more complex in various ways without changing the basic message (Holt and Loreau 2002; R. D. Holt and M. Loreau, unpublished data). For instance, the import and

export terms for the system with an open resource compartment could be replaced by $I - e(R)$, where $e(R)$ is a nonlinear function increasing with R. If the basal resource is the only open compartment in the local ecosystem, then there will be some R^* at which imports equal exports; this defined resource level then constrains the remainder of the system. Species sorting could also occur at the top consumer level, or at both levels simultaneously. Preliminary study of a wide range of models suggests that the following qualitative message is robust: the relationship between community dynamics and ecosystem processes is sensitive to whether—and if so, how—a system is open to external subsidies and exports.

The above conclusions all assume that species sorting arises from rare colonization episodes, so that there is no local coexistence. If there is recurrent immigration, then we need to fuse ecosystem models with models for local interspecific interactions, comparable to equations (7.4) and (7.7) above. This strategy permits one to examine the effects of local biodiversity on ecosystem function in open systems. As discussed in more detail elsewhere (Holt and Loreau 2002; M. Loreau and R. D. Holt, unpublished data), whether or not local biodiversity enhances an ecosystem process depends in a detailed manner on which functional parameter determines local dominance, and on the pattern of spatial openness in the ecosystem. Finally, most natural systems are temporally variable as well as spatially open, and such variation can be expressed in both the magnitude of subsidies and the strength of local population and community processes. An important direction for future work is to examine subsidies in nonequilibrial, temporally varying systems (see Sears et al., chap. 23 in this volume; Holt 2002, Holt et al., in press).

CONCLUSIONS

The ideas presented above underscore several important implications of community and ecosystem openness that warrant further attention from theoretical and empirical ecologists.

The central paradigm of community ecology must be modified to accommodate spatial coupling. Equation (7.2) describes the dynamics of species that are excluded from a local community, yet maintained by recurrent subsidies from an external source. This model highlights the importance of understanding quantitative *rates* of exclusion. A general methodological conclusion is that if rules of local community structure arise from patterns of colonization and local extinction, such rules are likely to be difficult to discern when communities are open. This should be particularly true in

habitats with high rates of allochthonous inputs and within which exclusion by competition or predation occurs weakly. The effects of spatial subsidies on population size can be particularly pronounced when the local environment also varies temporally (Gonzalez and Holt 2002). It should thus be particularly difficult to detect rules of local community organization in systems that are both open and temporally variable.

Spatial subsidies can control the results of local competition. Models (7.4) and (7.7) for exploitative and apparent competition with spatial subsidies show that local competitive interactions can be readily reversed by allochthonous inputs of subordinate species.

System openness influences the mapping of community dynamics onto ecosystem processes. The ecosystem models presented above demonstrate that the influence of species sorting on ecosystem properties such as primary production or total biomass is altered by system openness. Moreover, the implications of species-level "sorting rules" (defining local community membership) for ecosystem processes can be strongly influenced by which components of a system are spatially coupled with external sources. This conclusion suggests that across ecological systems, one should not expect a one-to-one mapping of rules determining community assembly onto ecosystem effects.

System openness influences species redundancy. A topic of growing concern is the functional redundancy of species (Lawton and Brown 1993). The above models shed light on this issue. For instance, in a system with an open resource compartment, producers that differ only in their resistance to mortality factors other than the herbivore all have the same gross primary production, and so by this measure are functionally redundant. However, this redundancy is not really a function of *species* properties, but of species properties as expressed in a particular *system*. If the resource compartment is instead closed (and the herbivore compartment either closed or open), then these same producer species exhibit different productivities at equilibrium and so are no longer functionally redundant.

System openness alters the importance of local decomposition processes. In the closed ecosystem model, primary production is influenced by rates of decomposition from the detrital pools. In the two open ecosystem scenarios, however, these rates do not appear at all in the expression defining primary production at equilibrium. In open systems, local primary production may be largely dominated by coupling with the external environment.

The specific results presented above are, of course, tied to specific models. I suggest, however, that the qualitative insights drawn from these models are applicable to a much wider range of models (see also Holt and

Loreau 2002). More broadly, I suspect that as population, community, and ecosystem ecology become more tightly integrated into a holistic theory of ecological systems in the coming years, a fundamental theme that will tie different strands of ecological thought together is an abiding concern with the issues of system openness, spatial subsidies, and asymmetries in a heterogeneous world.

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