

## Notes and Comments

### Spatial Flows and the Regulation of Ecosystems

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**ABSTRACT:** Spatial flows of materials and organisms across ecosystem boundaries are ubiquitous. Understanding the consequences of these flows should be a basic goal of ecosystem science, and yet it has received scant theoretical treatment to date. Here, using a simple, open, nutrient-limited ecosystem model with trophic interactions, we explore theoretically how spatial flows affect the functioning of local ecosystems, how physical mass-balance constraints interact with biological demographic constraints in the regulation of this functioning, and how failure to consider these constraints explicitly can lead to models that are ecologically inconsistent. In particular, we show that standard prey-dependent models for trophic interactions may lead to implausible outcomes when embedded in an ecosystem context with appropriate mass flows and mass-balance constraints. Our analysis emphasizes the need for integration of population, community, and ecosystem perspectives in ecology and the critical consequences of assuming closed versus open systems.

**Keywords:** spatial flows, ecosystems, nutrient cycling, trophic interactions, model.

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Historically, there have been two main perspectives in ecology (Lotka [1925] 1956): the biologically oriented demographic perspective developed within population and community ecology, which takes the individual organism as its basic unit and focuses on the dynamics of population size and species diversity, and the physically oriented func-

tional perspective developed within ecosystem ecology that measures flows of matter and energy and focuses on the functioning of the overall system composed of biological organisms and their abiotic environment. These two perspectives have been largely separated in the history of modern ecology, although there is currently a push toward a new ecological synthesis that spans population, community, and ecosystem perspectives (DeAngelis 1992; Jones and Lawton 1995; Loreau 2000; Kinzig et al. 2001; Loreau et al. 2002).

One reason that integration of these two perspectives is necessary is that demographic and mass-balance, or energy-balance, constraints in ecosystems interact and cannot be understood in isolation. The implications of the interaction between demographic and ecosystem constraints can be profound, and they seldom have been addressed theoretically. Early theoretical attempts to understand mass- and energy-balance constraints in closed ecosystems (defined as ecosystems that do not exchange matter with the external world) suggested counterintuitive patterns and constraints in food webs (Ulanowicz 1972; May 1973; Hirata and Fukao 1977), but these were later shown to be due to physically and biologically inconsistent model formulations (Hirata and Fukao 1977; Loreau 1994). Articulating these constraints in a consistent way is a feasible but by no means trivial task (Loreau 1994). Another type of model system that has often been studied, both experimentally and theoretically, is the chemostat (Grover 1997), that is, a system that experiences homogeneous dilution across compartments due to water flow-through. We shall see, however, that closed ecosystems and chemostats represent a very special class of systems and that systems that are differentially open to spatial flows in different compartments can have vastly different properties.

Ecological stoichiometry is another area in which mass-balance constraints for different chemical elements and their interactions with demographic constraints play an important role (Lotka [1925] 1956). Despite the growing interest in this area (Sturner and Elser 2002), theory has been relatively limited, in particular at the whole-

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ecosystem level (Andersen 1997; Daufresne and Loreau 2001a, 2001b; Grover 2003), and has not specifically addressed the role of spatial flows in ecosystem functioning.

Spatial flows of materials and organisms across system boundaries have been studied theoretically in population and community ecology within the context of metapopulations (Levins 1969, 1970), source-sink dynamics (Pulliam 1988), and metacommunities (Wilson 1992; Mouquet and Loreau 2002). These studies have mainly focused on the persistence of populations and the maintenance of species diversity in sets of populations or communities connected by dispersal. Similar theoretical treatments are largely lacking in ecosystem ecology (but see Holt and Loreau 2001; Loreau et al. 2003; Holt 2004). Yet all ecosystems up to the biosphere are open in various degrees to exchanges of materials or organisms (Polis et al. 1997). Perhaps the only closed natural system is the total Earth system including the biosphere, the atmosphere, the hydrosphere, and the lithosphere, and even this system is likely to be nonequilibrium and open to some spatial fluxes (e.g., inputs of trace elements via meteorites) at the very long timescales typical for major geological processes. Local ecosystems receive and lose materials and organisms through such processes as atmospheric deposition, fixation, and volatilization of mineral elements, rock weathering, leaching and sedimentation of organic and inorganic substances, fire, water flows, plant seed dispersal, and animal movements across ecosystem boundaries. Understanding the consequences of such fluxes should be a basic goal of ecosystem science, and such understanding should be embedded in the fusion of ecosystem approaches with community and population ecology (Loreau et al. 2003).

Here we explore theoretically, using a simple open ecosystem model, how spatial flows across system boundaries affect the functioning of local ecosystems, how physical mass-balance constraints interact with biological demographic constraints in the regulation of this functioning, and how failure to consider these constraints explicitly can lead to models that are ecologically inconsistent. In particular, we show that standard models for trophic interactions may lead to implausible outcomes when embedded in an ecosystem context with appropriate mass flows and mass-balance constraints.

### Spatial Flows in a Simple Nutrient-Plant Model Ecosystem

We start with the simplest possible model of a nutrient-limited ecosystem (fig. 1). The model comprises only two explicit compartments, plants ( $P$ ) and a limiting inorganic nutrient ( $N$ ), each of which is measured in units of amount of nutrient. Plants consume the nutrient, which is recycled in inorganic form. For the sake of simplicity, we delib-

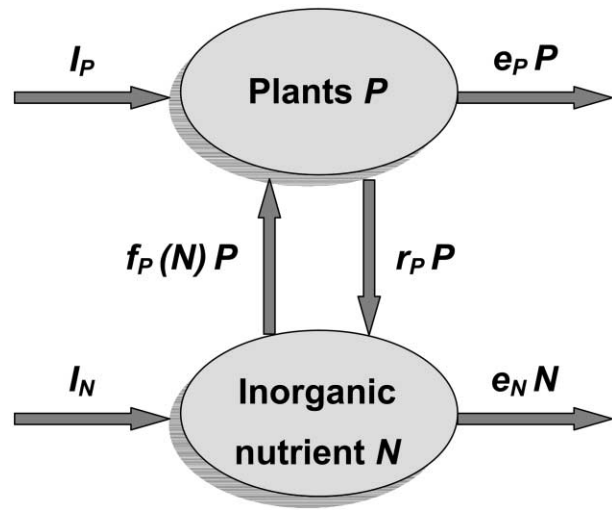


Figure 1: Flow diagram of the nutrient-plant model ecosystem with spatial flows across ecosystem boundaries.

erately ignore the detailed dynamics of organic matter decomposition and nutrient recycling, which we encapsulate in a single rate parameter. This is justified by the fact that we will focus on equilibrium behavior and only the respective proportions of nutrient recycled or lost to the system matter at equilibrium (de Mazancourt et al. 1998) unless strong stoichiometric constraints operate (Daufresne and Loreau 2001a). This very simple model shows most of the typical features of more complex models. The model reads

$$\frac{dN}{dt} = I_N - e_N N - f_p(N)P + r_p P \quad (1a)$$

$$\frac{dP}{dt} = I_p - e_p P + f_p(N)P - r_p P \quad (1b)$$

where  $I_N$  and  $I_p$  are the inputs of inorganic nutrient and plants, respectively, into the system;  $e_N$  and  $e_p$  are the loss rates of inorganic nutrient and plants, respectively, from the system;  $r_p$  is the rate of nutrient recycling within the system; and  $f_p(N)$  is the per capita functional response of plants to nutrient availability ( $f_p[0] = 0$ ,  $df_p/dN \geq 0$ ).

### Closed Ecosystems and Chemostats as a Special Class of Systems

Consider first, as a baseline, a classical chemostat subject to a homogeneous dilution rate  $e$ . This case corresponds, in our model, to setting  $e_N = e_p = e$ ,  $I_N = eN_0$  (where  $N_0$  is the inflowing amount of nutrient), and  $I_p = 0$ . At equilibrium, the time derivatives in equations (1) vanish;

in other words, inflows balance outflows for each compartment. Solving these mass-balance equations provides the equilibrium nutrient stocks, denoted by an asterisk:

$$N^* = f_p^{-1}(r_p + e), \quad (2a)$$

$$P^* = N_0 - f_p^{-1}(r_p + e), \quad (2b)$$

where  $f_p^{-1}$  is the inverse of function  $f_p$ . The total stock of nutrient is  $N^* + P^* = N_0$ . Hence, in a classical chemostat the total concentration of nutrient in the system at equilibrium just matches the input concentration. Trophic interactions and plant death rates only affect the apportionment of this total concentration between living and nonliving compartments.

In this configuration, the equilibrium inorganic nutrient stock is independent of mass-balance constraints and depends only on plant demographic parameters, a classical feature of systems in which there is no interference at the consumer level, known as recipient control or top-down control (DeAngelis 1992). The equilibrium plant nutrient stock is determined by a combination of mass-balance and demographic constraints. This equilibrium is qualitatively stable (app. A, which is available in the online edition of the *American Naturalist*).

It is straightforward to check that a closed ecosystem is only a limiting case of a chemostat in which the dilution rate tends to 0. Therefore it would seem at first sight that the popular chemostat can be used as a valid theoretical and experimental model for systems in which openness can be varied arbitrarily. This is not so. As we show next, deviations from the restrictive assumptions of the chemostat model, that is, equality of loss rates and inputs only in inorganic form, lead to ecosystems with qualitatively different functional and dynamical properties.

#### *Unequal Openness among Ecosystem Compartments*

Consider now the full model with unequal inputs and outputs in the two compartments. Unlike the classical chemostat, the total stock of nutrient no longer equilibrates at the same concentration as in the input but depends on trophic interactions. Equations (1) cannot be solved for the equilibrium nutrient stocks, but an isocline analysis easily reveals the dynamics of the system. The null isoclines of  $N$  and  $P$ , respectively, are from equations (1):

$$P = \frac{I_N - e_N N}{f_p(N) - r_p}, \quad (3a)$$

$$P = \frac{I_p}{r_p + e_p - f_p(N)}. \quad (3b)$$

Two cases must be distinguished based on equation (3a), depending on whether  $I_N/e_N$  is greater or smaller than  $f_p^{-1}(r_p)$ . The ratio  $I_N/e_N$  is the equilibrium inorganic nutrient stock to which the system tends in the absence of plants, while  $f_p^{-1}(r_p)$  is the level at which a closed plant population (without any external subsidy or loss) tends to control it. Thus the first case ( $I_N/e_N > f_p^{-1}(r_p)$ ) corresponds to a system in which the inorganic nutrient supply is sufficient to support a closed plant population (fig. 2a), while the second case ( $I_N/e_N < f_p^{-1}(r_p)$ ) corresponds to a system in which the inorganic nutrient supply is insufficient to support a closed plant population (fig. 3a). The equilibrium point may be either a focus (fig. 2a) or a node (fig. 3a), but in both cases there is a single feasible equilibrium point, and it is stable (app. A).

To explore unequal openness among ecosystem compartments, we focus on limiting cases in which effectively only a single compartment is open to inputs and outputs. First, consider a system that is open only at the top, which might be thought of as an approximation of a nutrient-poor ecosystem in which the limiting nutrient experiences little deposition and leaching, but plants immigrate and emigrate by intense seed dispersal. In this limiting case, both  $I_N$  and  $e_N$  tend to 0, but we assume that their ratio,  $I_N/e_N = N_0$ , stays constant. This has the effect of increasing the curvature of the isocline of  $N$ , which eventually merges with the vertical asymptote  $N = f_p^{-1}(r_p)$  and the  $X$ -axis  $P = 0$  (fig. 2b). The equilibrium nutrient stocks then become

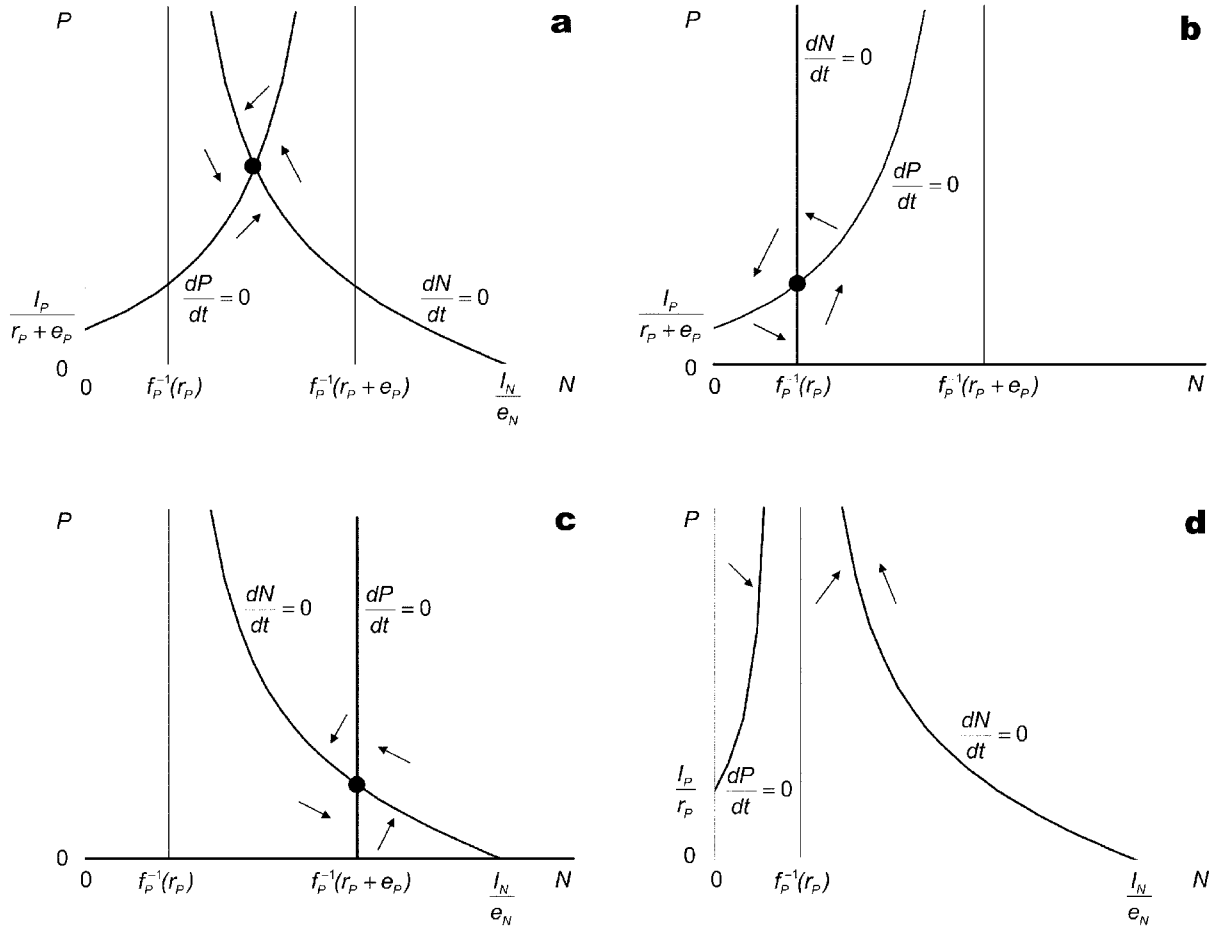
$$N^* \rightarrow f_p^{-1}(r_p), \quad (4a)$$

$$P^* \rightarrow \frac{I_p}{e_p}. \quad (4b)$$

Thus the two compartments appear to be controlled by different constraints at equilibrium: the inorganic nutrient is top-down controlled as in the classical chemostat, whereas plants are controlled by the mass-balance constraint that inputs must balance outputs for the system as a whole.

The implications of this decoupling of the two constraints are apparent in the second limiting case in which the system is open only at the bottom. This scenario might be realistic for isolated ecosystems such as remote islands in which nutrient deposition and leaching occur but plant dispersal is absent. Because the effects of letting  $I_p \rightarrow 0$  and  $e_p \rightarrow 0$  are very different, we consider these two cases in turn before discussing their combined effect.

Decreasing  $I_p$  to 0 has the effect of increasing the curvature of the isocline of  $P$ , which eventually merges with the vertical asymptote  $N = f_p^{-1}(r_p + e_p)$  and the  $X$ -axis



**Figure 2:** Isocline analysis of the nutrient-plant model ecosystem in the case when inorganic nutrient supply is sufficient to support a closed plant population ( $I_N/e_N > f_p^{-1}(r_p)$ ). *a*, General case: all compartments have inputs and outputs ( $I_N, e_N, I_p$ , and  $e_p > 0$ ). *b*, System open only at the top ( $I_N$  and  $e_N \rightarrow 0$ ,  $I_p$ , and  $e_p > 0$ ). *c*, System with negligible plant immigration ( $I_p \rightarrow 0$ ,  $I_N, e_N$ , and  $e_p > 0$ ). *d*, System with negligible plant loss ( $e_p \rightarrow 0$ ,  $I_N, e_N$ , and  $I_p > 0$ ).

$P = 0$  (figs. 2c, 3b). If  $I_N/e_N > f_p^{-1}(r_p + e_p)$ , there is still a stable, feasible equilibrium (fig. 2c) at

$$N^* \rightarrow f_p^{-1}(r_p + e_p), \quad (5a)$$

$$P^* \rightarrow \frac{I_N - e_N f_p^{-1}(r_p + e_p)}{e_p}. \quad (5b)$$

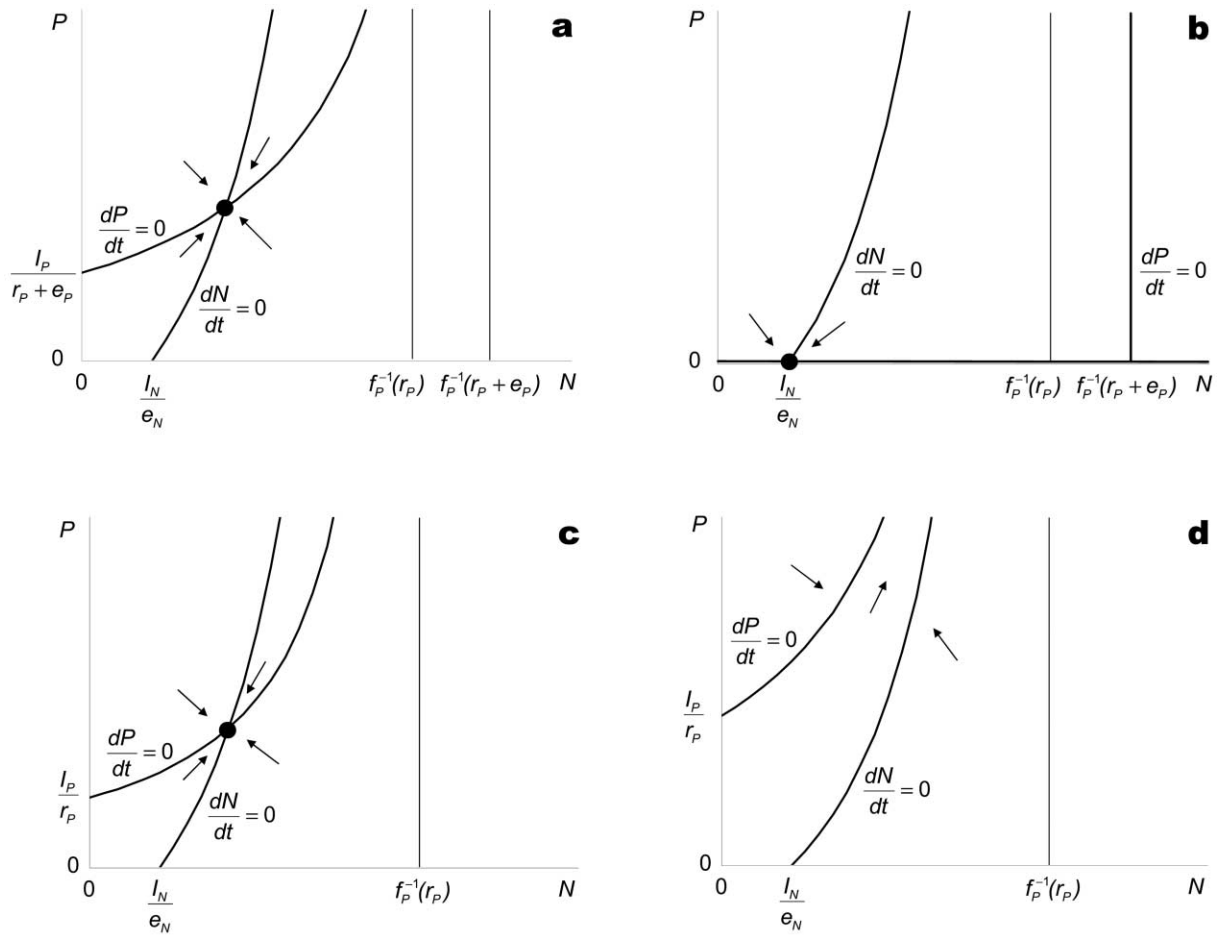
However, if  $I_N/e_N \leq f_p^{-1}(r_p + e_p)$ , the plant population is unable to persist for lack of nutrient and disappears from the system (fig. 3b).

Letting  $e_p \rightarrow 0$  has the effect of shifting the vertical asymptote of the isocline of  $P$ ,  $N = f_p^{-1}(r_p + e_p)$ , to the left until it merges with that of the isocline of  $N$ ,  $N = f_p^{-1}(r_p)$ . When  $I_N/e_N > f_p^{-1}(r_p)$ , this precludes any intersection of the two isoclines and hence any feasible equilibrium. The plant population then grows indefinitely (fig.

2d). When  $I_N/e_N < f_p^{-1}(r_p)$ , a stable, feasible equilibrium is possible, provided that  $I_p$  is small enough, thereby ensuring sufficient curvature of the isocline of  $P$  and making intersection of the two isoclines possible (fig. 3c). If  $I_p$  is too large, however, this intersection is impossible, and the plant population again grows without bounds (fig. 3d). The condition ensuring stable coexistence of the two ecosystem compartments (fig. 3c) is obtained easily by setting  $e_p \rightarrow 0$  in equations (1) and solving for the equilibrium nutrient stocks:

$$N^* \rightarrow \frac{I_N + I_p}{e_N}, \quad (6a)$$

$$P^* \rightarrow \frac{I_p}{r_p - f_p[(I_N + I_p)/e_N]}. \quad (6b)$$



**Figure 3:** Isocline analysis of the nutrient-plant model ecosystem in the case when inorganic nutrient supply is insufficient to support a closed plant population ( $I_N/e_N < f_p^{-1}(r_p)$ ). *a*, General case: all compartments have inputs and outputs ( $I_N, e_N, I_p,$  and  $e_p > 0$ ). *b*, System with negligible plant immigration ( $I_p \rightarrow 0, I_N, e_N,$  and  $e_p > 0$ ). *c*, System with negligible plant loss ( $e_p \rightarrow 0, I_N, e_N,$  and  $I_p > 0$ ) and small nutrient inputs ( $I_N + I_p < e_N f_p^{-1}(r_p)$ ). *d*, System with negligible plant loss ( $e_p \rightarrow 0, I_N, e_N,$  and  $I_p > 0$ ) and large nutrient inputs ( $I_N + I_p \geq e_N f_p^{-1}(r_p)$ ).

This equilibrium is feasible, provided that

$$\frac{I_N + I_p}{e_N} < f_p^{-1}(r_p), \tag{7}$$

which requires that both  $I_N$  and  $I_p$  be small enough, as derived graphically above.

Combining the effects of  $I_p \rightarrow 0$  and  $e_p \rightarrow 0$ , we see that closure at the top precludes any feasible equilibrium in the system: either plants go extinct when  $I_N/e_N < f_p^{-1}(r_p)$  (similar to fig. 3*b*) or they grow indefinitely when  $I_N/e_N > f_p^{-1}(r_p)$  (similar to fig. 2*d*).

Why is this the case? The system cannot persist because the two constraints of top-down control and mass balance are again decoupled, but they both apply to the same compartment. To see this, let  $I_p$  and  $e_p$  tend to 0 in equa-

tions (1) while keeping their ratio,  $I_p/e_p = P_0$ , constant. Equation (1*b*) can be rewritten as

$$\frac{dP}{dt} = e_p(P_0 - P) + f_p(N)P - r_p P. \tag{8}$$

This amounts to a separation of two timescales in the system's dynamics: the first term controlled by  $e_p$  is close to 0 and only affects plant dynamics on a very slow timescale, while the other terms determine the system's dynamics on a fast timescale. Ignoring the first term, this equation leads to an equilibrium on a fast timescale, such that

$$N^* \rightarrow f_p^{-1}(r_p). \tag{9}$$

But equation (1a) then also implies that

$$N^* \rightarrow \frac{I_N}{e_N}. \quad (10)$$

Equation (9) expresses the constraint of top-down control that plants exert on the inorganic nutrient stock, while equation (10) expresses the mass-balance constraint that is exerted on the same compartment. Since these two constraints are in general incompatible, there is no feasible equilibrium in such a system. When  $I_N/e_N > f_p^{-1}(r_p)$ , the supply of inorganic nutrient constantly exceeds its demand by the plants, and the latter grow indefinitely. In the opposite case, the supply of inorganic nutrient is too low compared with plant demand, which drives plants to extinction.

It may be argued that this outcome is ecologically unrealistic, at least for the scenario depicted in figures 2d and 3d, because at high plant density, some density dependence or loss from the system must hold the plant population in check. The above analysis does imply that losses from the plant compartment stabilize the system, and it is easy to show that density dependence has the same stabilizing effect (app. B, which is available in the online edition of the *American Naturalist*). Our simple model, however, is a simple extension of the popular food-chain models and shows dramatically the limitations of these models when explicit mass-balance constraints are taken into account. This supports the view that spatial processes, nutrient cycling and mass-balance constraints (DeAngelis 1992; Holt et al. 1994; Loreau 1995; Holt 2004), and interference (DeAngelis et al. 1975; Beddington 1975) cannot generally be ignored in the population dynamics of resource-consumer interactions.

Note that the inconsistency between top-down control and mass balance does not occur when both compartments experience roughly equal closure. If  $I_N$ ,  $I_p$ ,  $e_N$ , and  $e_p$  all tend to 0 simultaneously, then setting  $I_N/e_N = N_0$  and  $I_p/e_p = P_0$  and performing a separation of timescales as above leads to an equilibrium in which

$$N^* \rightarrow f_p^{-1}(r_p), \quad (11a)$$

$$P^* \rightarrow P_0 + \frac{e_N}{e_p}[N_0 - f_p^{-1}(r_p)]. \quad (11b)$$

This equilibrium is feasible because the two compartments experience the same openness, or closure, and thus both can be adjusted to meet the overall mass-balance constraint exerted on the system as a whole. Note, however, that this equilibrium is not identical to the one obtained in a perfectly closed system (eqq. [2] with  $e = 0$ ) because

relative differences in loss rates are preserved when closure is achieved only asymptotically.

### *The Dual Effect of Immigration at the Top*

There is another feature of the simple nutrient-plant model ecosystem above that is well worth emphasizing. Immigration at the top of the system, here through the plant input term  $I_p$ , has a dual effect on the resource under top-down control. When the inorganic nutrient supply is high enough to support a viable closed plant population ( $I_N/e_N > f_p^{-1}[r_p]$ ), increasing plant immigration  $I_p$  has the effect of raising plant biomass while depressing the inorganic nutrient stock (cf. fig. 2a, 2c). Plant immigration maintains a positive demographic balance for a level of inorganic nutrient at which plant growth would stop in the absence of immigration and hence pushes plant biomass up and inorganic nutrient down. That external subsidies to consumer populations can further depress their resources has been suggested or documented in a number of systems (Polis et al. 1997).

Plant immigration, however, can also have the opposite, counterintuitive effect of increasing the amount of inorganic nutrient and even of supporting the whole resource-consumer system. This occurs when the inorganic nutrient supply is too low to support a viable closed plant population ( $I_N/e_N < f_p^{-1}[r_p]$ ). Increasing plant immigration  $I_p$  then has the effect of raising both plant biomass and the inorganic nutrient stock (cf. fig. 3a, 3b). From a demographic perspective, the ecosystem holds a sink plant population (Pulliam 1988). External subsidy is the factor that supports the plant population, which generates a net flow of nutrient to the inorganic nutrient stock at equilibrium through nutrient recycling ( $r_p - f_p[N^*] > 0$  because  $N^* < f_p^{-1}[r_p]$ ), thereby increasing the inorganic nutrient stock. When the input of nutrient in inorganic form is absent altogether ( $I_N \rightarrow 0$ ), it is plant immigration that maintains the two ecosystem compartments, leading to a counterintuitive system in which the top supports the bottom. Polis et al. (1997) discuss a number of examples in which inputs of nutrients by consumer movement could be essential for the functioning of an ecosystem.

### **Generalizing to Multitrophic Systems**

Our main findings generalize to food chains with multiple trophic levels. The following model includes a herbivore compartment added to the previous nutrient-plant model:

$$\frac{dN}{dt} = I_N - e_N N - f_p(N)P + r_p P + r_H H, \quad (12a)$$

$$\frac{dP}{dt} = I_p - e_p P + f_p(N)P - r_p P - f_H(P)H, \quad (12b)$$

$$\frac{dH}{dt} = I_H - e_H H + f_H(P)H - r_H H. \quad (12c)$$

In this model, the parameters and functions with an H subscript apply to the herbivores but have the same meaning as the corresponding parameters and functions for the plants.

This model is more complex and analytically less tractable than the previous one. Not only is it impossible to obtain a general solution for the equilibrium nutrient stocks, the three-dimensional nature of the system also precludes an isocline analysis, and stability of equilibria is no longer guaranteed. Despite these limitations, a number of results can be obtained for systems that admit a stable equilibrium and can be comparable to the system without herbivores. In particular, it is easy to show that the closed system is again recovered as the limiting case of a chemostat with a zero dilution rate.

To facilitate comparison with the system without herbivores, we concentrate our analysis of the effects of unequal openness among ecosystem compartments in a system that is closed with respect to inorganic nutrient ( $I_N$  and  $e_N \rightarrow 0$ ). In such a configuration, herbivores replace plants as the top trophic level, plants replace the inorganic nutrient as the next lower trophic level, and closure at the top trophic level then has exactly the same effects as in the system without herbivores.

Assume first that herbivore immigration is also negligible ( $I_H \rightarrow 0$ ). From equations (12), the equilibrium that the system approaches is then found to be

$$P^* \rightarrow f_H^{-1}(r_H + e_H), \quad (13a)$$

$$H^* \rightarrow \frac{I_p - e_p f_H^{-1}(r_H + e_H)}{e_H}, \quad (13b)$$

$$N^* \rightarrow f_p^{-1}\left(r_p + \frac{r_H H^*}{P^*}\right). \quad (13c)$$

Note that the last equation for  $N^*$  holds in all the cases analyzed here (i.e., when  $I_N$  and  $e_N \rightarrow 0$ ); it implies that  $N^*$  simply follows changes in  $H^*$ . This equilibrium is feasible (i.e.,  $H^* > 0$ ), provided that  $I_p/e_p > f_H^{-1}(r_H + e_H)$ . Otherwise, herbivores become extinct and  $P^* \rightarrow I_p/e_p$ . Thus we obtain not only the same outcomes but also the same quantitative conditions determining these outcomes as in the system without herbivores, except that herbivores

now substitute for plants, and plants substitute for the inorganic nutrient.

Assume next that herbivore loss from the system is negligible ( $e_H \rightarrow 0$ ). The equilibrium that the system approaches is then

$$P^* \rightarrow \frac{I_p + I_H}{e_p}, \quad (14a)$$

$$H^* \rightarrow \frac{I_H}{r_H - f_H[(I_p + I_H)/e_p]}, \quad (14b)$$

and  $N^*$  is as above (eq. [13c]). This equilibrium is feasible ( $H^* > 0$ ) provided that  $(I_p + I_H)/e_p < f_H^{-1}(r_H)$ . Otherwise, herbivores have a positive demographic balance and grow indefinitely. Again we obtain the same outcomes and quantitative conditions as in the system without herbivores.

Finally, assume that both herbivore immigration and loss are negligible ( $I_H$  and  $e_H \rightarrow 0$ ). There is then a conflict between top-down control of plants by herbivores, which imposes

$$P^* \rightarrow f_H^{-1}(r_H), \quad (15)$$

and the mass-balance constraint, which imposes

$$P^* \rightarrow \frac{I_p}{e_p}. \quad (16)$$

If  $I_p/e_p > f_H^{-1}(r_H)$ , plant supply is greater than plant demand, and the herbivore population grows without bounds; if  $I_p/e_p < f_H^{-1}(r_H)$ , plant supply is smaller than plant demand, and herbivores become extinct. Thus, in all cases, the outcomes of system closure at the top trophic level are identical in the two- and three-trophic-level systems.

Therefore we are led to the same conclusion that a system that is open only at the trophic level below the top level does not have a feasible equilibrium unless some additional density dependence limits herbivore growth. This conclusion can be further generalized by noting that systems that receive inputs either in inorganic form alone ( $I_N > 0$ ;  $I_p$  and  $I_H \rightarrow 0$ ) or in both inorganic and plant form ( $I_N$  and  $I_p > 0$ ,  $I_H \rightarrow 0$ ) lead to the same conflict between top-down control and the mass-balance constraint as long as nutrient loss occurs only in plants ( $e_N$  and  $e_H \rightarrow 0$ ). Indeed, the source of this conflict lies in the fact that the system's output, which has to balance inputs at equilibrium, is only a function of plant biomass. This sets one potential equilibrium value for plant biomass, which conflicts with the other potential equilibrium value set by the top-down control exerted by herbivores when the latter have no stabilizing density dependence or outputs. This

also implies that other nonlinear functional forms of plant outputs cannot resolve this conflict. However, nutrient losses in inorganic form, which almost always occur in real ecosystems, do remove this conflict by providing an alternative pathway for restoring the system's mass balance.

The effects of immigration at the top of the system are more complex and difficult to analyze than in the system without herbivores, but the general trends are similar. When the nutrient-plant system is able to support an unsubsidized herbivore population ( $H^* > 0$  when  $I_H \rightarrow 0$ ), herbivore immigration acts to depress plant biomass, just as plant immigration acted to depress the inorganic nutrient stock in the system without herbivores. Indeed, as herbivore immigration approaches 0, the equilibrium plant nutrient stock approaches

$$P^* \rightarrow f_H^{-1}(r_H + e_H), \quad (17)$$

provided that herbivores are able to persist. But when herbivore immigration is nonzero, the equilibrium herbivore nutrient stock is

$$H^* = \frac{I_H}{r_H + e_H - f_H(P^*)}, \quad (18)$$

which implies

$$P^* < f_H^{-1}(r_H + e_H). \quad (19)$$

Thus plant biomass is reduced by herbivore immigration.

At the other extreme, herbivore immigration in a system that is entirely supported by the top ( $I_H > 0$ ;  $I_N$  and  $I_P \rightarrow 0$ ) clearly benefits all ecosystem compartments since these would disappear in its absence.

To sum up, although trophic complexity provides opportunities for other effects of spatial flows that we do not explore here, the main conclusions obtained using the simple nutrient-plant model are unchanged after addition of a herbivore trophic level, and they could be shown to remain valid upon further addition of carnivorous trophic levels. The main difference is that the constraints on ecosystem regulation identified in the nutrient-plant model are shifted one trophic level higher after addition of each new trophic level to the system.

### Discussion

Throughout ecology, there is an increasing interest in going back to first principles by embedding ecological theories in fundamental laws and constraints from the physical sciences, such as the importance of stoichiometric considerations in trophic interactions (Andersen 1997; Sterner

and Elser 2002) and the role of temperature and body size as modulators of ecological processes at all levels of ecological organization (Gillooly et al. 2001). Here too, we have shown that ecosystem processes can provide fundamental constraints on the action and consequences of trophic interactions. In particular, simple Lotka-Volterra prey-dependent models may lead to impossible outcomes in some ecosystem contexts. There has been considerable debate in recent years about the need to refine predator-prey and consumer-resource models, so as to incorporate behavioral details such as interference behavior. We suggest that an additional line of argument in support of such generalizations comes from a quite different direction, namely, the fundamental physical constraints within which trophic interactions must play out in any realistic landscape.

There is increasing interest in population and community ecology in the implications of source-sink dynamics in heterogeneous landscapes. Our results reveal a potentially important ecosystem dimension to such systems. In some cases, a species may locally maintain a demographic sink and exert top-down control on the component beneath (e.g., the herbivore may constrain plant numbers in classical top-down fashion). In short-term manipulative experiments, a reduction in (say) herbivore density by reducing or eliminating immigration will lead to an upsurge in plant abundance. Thus, from the typical perspective of population and community ecology, these two species are locked in a (+, -) interaction. Yet if the herbivore is the main conduit of nutrients into the local ecosystem, the herbivore is an indirect mutualist of the plant population over longer timescales, sustaining the plants via ecosystem feedbacks. Ecological and evolutionary plant-herbivore mutualisms have been shown to be possible when herbivores are more efficient than plants at recycling limiting nutrients locally (Loreau 1995; de Mazancourt et al. 1998, 2001). Our analysis further stresses spatial flows as a critical factor that determines the nature of species interactions within ecosystems. Ecosystem processes imply a rich array of indirect feedbacks in ecological systems, well beyond the typical density-mediated and trait-mediated indirect interactions that have been the focus of so much attention in recent community ecology.

We believe these theoretical results also bear on another issue of topical interest. As noted above, in recent years there has been a resurgence of interest in the use of microcosms to examine basic ecological theories. There has been considerable debate about the utility of microcosms to address basic ecological questions (Daehler and Strong 1996). We do feel that chemostats and closed ecosystems provide useful tools for many purposes. However, the results presented here suggest that great caution needs to be applied in extrapolating from such studies to natural sys-



tems, which are typically open and, moreover, open differentially at different trophic levels. Making ecological systems open versus closed can have qualitative effects on both the dynamics and statics to be expected. We suggest that a rich avenue for future experimental work with microcosms will be to examine impacts of different patterns of system openness in a laboratory setting. Such experiments will help us understand some of the fundamental constraints that govern the organization of natural ecosystems.

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# Appendix 1: Stability of the nutrient–plant system

The Jacobian or community matrix associated with the equilibrium of the nutrient–plant system is

$$\mathbf{A} = \begin{bmatrix} -e_N - P^* \left. \frac{df_P}{dN} \right|^* & -f_P(N^*) + r_P \\ P^* \left. \frac{df_P}{dN} \right|^* & f_P(N^*) - r_P - e_P \end{bmatrix}$$

The equilibrium is locally stable if and only if the trace of  $\mathbf{A}$  is negative and its determinant is positive. Both conditions are automatically satisfied when the equilibrium is feasible ( $N^* > 0$ ,  $P^* > 0$ ,  $r_P + e_P \geq f_P(N^*)$ ). Therefore any feasible equilibrium is qualitatively stable.

## Appendix 2: Incorporating density dependence in the nutrient–plant system

The simplest way to incorporate density dependence in the nutrient–plant system is to allow for mutual interference in the consumption process (DeAngelis et al. 1975; Beddington 1975), and hence let the functional response of plants to nutrient availability,  $f_P(N, P)$ , be a function of both  $N$  and  $P$ , with  $\frac{\partial f_P}{\partial N} \geq 0$  and  $\frac{\partial f_P}{\partial P} \leq 0$ .

No equilibrium is possible in the system without density dependence when the system is open only at the bottom ( $I_P$  and  $e_P \rightarrow 0$ ). Under the same conditions in the system with density dependence,

$$N^* \rightarrow I_N / e_N$$

$$f_P(I_N/e_N, P^*) = r_P$$

Since the latter equation generally admits a solution for  $P^*$ , a feasible equilibrium is now possible.

Feasible equilibria are also qualitatively stable. Their associated Jacobian matrix is

$$\mathbf{A} = \begin{bmatrix} -e_N - P^* \left. \frac{\partial f_P}{\partial N} \right|^* & -f_P(N^*, P^*) + r_P - P^* \left. \frac{\partial f_P}{\partial P} \right|^* \\ P^* \left. \frac{\partial f_P}{\partial N} \right|^* & -e_P + f_P(N^*, P^*) - r_P + P^* \left. \frac{\partial f_P}{\partial P} \right|^* \end{bmatrix}$$

of which the trace is always negative and the determinant is always positive for any feasible equilibrium ( $N^* > 0, P^* > 0, r_P + e_P \geq f_P(N^*, P^*)$ ).