

## Source and sink dynamics in meta-ecosystems

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**Abstract.** We present a theory extending the source–sink concept with an ecosystem perspective. We analyze a model for meta-ecosystem dynamics in a heterogeneous environment to study how the spatial flows of materials such as inorganic nutrients and nutrients sequestered into producers, herbivores, and detritus affect the community dynamics. We show that spatial flows of an inorganic nutrient (direct nutrient flow) and organic matter (indirect nutrient flow) through detritus, producer, or herbivore compartments can reverse the source–sink dynamics of a local ecosystem. More precisely, the balance between such direct and indirect nutrient flows determines the net direction of nutrient flows between two ecosystems of contrasted productivities. It allows a sink to turn into a source and vice versa. This effect of nutrient flows on source and sink dynamics is robust to the ecosystem structure (with and without herbivores) and to specific ecosystem compartments contributing to nutrient flows (primary producers, herbivores, or detritus). Ecosystems in distinct localities thus interact together with the structure at one place influencing that of the other. In meta-ecosystems, the source–sink dynamics of an organism is not only constrained by its dispersal from the source to the sink, but also by the fertility and community composition in the neighborhood responsible for spatial flows of nutrients and energy. The meta-ecosystem perspective provides a powerful theoretical framework to address novel questions in spatial ecosystem ecology.

**Key words:** *ecosystem ecology; food chain length; food web; landscape ecology; meta-ecosystem; resource recycling; source–sink; spatial ecology.*

### INTRODUCTION

Local ecosystems are never totally isolated in space because they receive and lose considerable amounts of matter and organisms in many forms and from various processes (Polis et al. 1997, 2004). Some flows are independent of the neighboring ecological context. For instance, a producer ecosystem receives nutrients through atmospheric depositions, nitrogen fixation, and rock weathering and loses them through nutrient leaching and disturbances such as fires. These flows are usually included in local ecosystem models (e.g., DeAngelis 1992) and are the basis for mass balance studies of nutrient cycling (Likens and Bormann 1995). There are also many of the spatial flows that are dependent on the characteristics of the neighboring ecosystems and on reciprocal transfers of energy and matter. These flows could be either direct, when the nutrient is moved between locations in its inorganic form, or indirect, when the nutrient is moved between locations sequestered in the biomass (live or dead) of an organism.

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There are numerous examples demonstrating how small islands and their local food web structures are heavily subsidized by marine ecosystems (e.g., Oliver and Legovic 1988, Polis and Hurd 1995, 1996, Rose and Polis 1998, Anderson and Polis 1999, Farina et al. 2003). Removing the agent of dispersal, for instance, when introduced predators reduce bird populations on islands, has considerable impact on local ecosystem structure and functioning (Fukami et al. 2006, Maron et al. 2006). Transfers from terrestrial to aquatic ecosystems (Kitchell et al. 1999, Nakano and Murakami 2001, Canham et al. 2004, Graham et al. 2006) and in the opposite direction (Nakano and Murakami 2001, Gratton et al. 2008) are also common. Transfers also occur within similar ecosystems (e.g., Vannote et al. 1980). These transfers influence both ecosystem productivity and structure (e.g., Helfield and Naiman 2001, Christie and Reimchen 2008). Moreover, energy and nutrient flows are not limited to neighboring ecosystems, as some animals migrate over considerable distances and across contrasted ecosystems. Snow geese provide a striking example, linking highly productive coastal marshes of the southern United States to low-productivity coastal ecosystems in the Canadian Arctic (Jefferies et al. 2004). This important body of studies on allochthonous subsidies is however restricted to the understanding of unidirectional flows between ecosystems and their consequences for recipient ecosystems.

Although the study of allochthonous inputs is a necessary step toward the understanding of spatial ecosystem dynamics, it is necessary to consider the metacommunity as a whole. Regional constraints might emerge from feedbacks among local communities characterized by reciprocal exchanges. In competitive metacommunities, elevated dispersal homogenizes the metacommunity, reducing regional diversity and thus limiting the mass effect (Mouquet and Loreau 2002). Reciprocal flows are occurring in nature between contrasted ecosystems, for instance at the forest-stream transition (Nakano and Murakami 2001). Reciprocal flows are also expected to occur between ecosystems of the same type but with underlying environmental variation. The productivity of the benthos often reflects that of overlying waters, while mixing and upwelling are strong determinants of the productivity of surface waters (Angel 1984, Schindler and Scheuerell 2002, Kaiser et al. 2005, Renaud et al. 2008). There are also important biological transports in oceans, varying in strength and direction on a diurnal (with tides) or seasonal (with thermal inversions) basis (e.g., Varpe et al. 2005). On the land, the forest litter dispersal will link patches with contrasted soil fertility (e.g., Gomez-Aparicio and Canham 2008). Movements of animals will also contribute to reciprocal flows between ecosystems in terrestrial and aquatic ecosystems (e.g., Durbin et al. 1979, Kitchell et al. 1979, McNaughton et al. 1988, Pastor et al. 1988, Levey and Stiles 1992, Schindler et al. 1996, Vanni 1996, Seagle 2003, Kaiser et al. 2005). Contingencies on community composition, such as a disturbance initiating succession, could also create a coupling of ecosystems with contrasted productivities (e.g., Pastor et al. 1999, Seagle 2003, Mathews et al. 2008). Loreau et al. (2003) proposed a natural extension of the metacommunity concept, the meta-ecosystem, to describe ecosystems linked together by spatial flows of materials and formulated a very general model of regional mass balance constraints. Because inflows and outflows are the drivers of primary production and food web organization, this framework should provide novel insights into the dynamics and functioning of ecosystems from local to global scales.

Spatial flows of organisms have been extensively studied within the context of metapopulation, source-sink, and metacommunity theories (Hanski and Gaggiotti 2004, Holyoak et al. 2005). The source-sink perspective (Holt 1985, Pulliam 1988) is a dominant framework in ecology, perhaps because it relates so intuitively to niche theory (Pulliam 2000). A sink is typically viewed as a locality with inappropriate environmental conditions, preventing the establishment of a species. More precisely, the mathematical definition of a sink (Pulliam 1988) is a locality in which the intrinsic rate of increase is negative. The core idea behind this concept is that sink populations may be sustained if they are open to spatial flows of propagules from an independent regional pool. For instance, the

mass effect specifies that elevated flows of immigrants to a local community could sustain elevated species diversity despite strong competitive inequalities (Shmida and Wilson 1985, Loreau and Mouquet 1999). Similarly, allochthonous inputs to local ecosystems could sustain complex food web structures (Holt 2004, Loreau and Holt 2004) and affect their dynamical stability (Huxel and McCann 1998, Huxel et al. 2002).

In this study we investigate whether regional properties emerge from spatial flows between contrasted local ecosystems. The main question of our analysis is: Could direct and indirect spatial flows of a limiting nutrient influence source-sink dynamics in a spatially structured ecosystem? In other words, could it affect whether a locality is a source or a sink? Source-sink theory has thus far focused on the flows of the population of interest (Mouquet et al. 2005). Here we control for movement of populations and study source-sink dynamics in relation to other flows at the ecosystem level (nutrient and organic matter). We analyze a model of meta-ecosystem dynamics in a heterogeneous landscape and proceed by analyzing a hierarchy of ecosystems with increasing structural complexity and manipulating which compartment experiences spatial flows. The environment is spatially varying, so that the fertility and the ability of primary producers to grow differ between patches. The nutrient availability is limited and thus constrains the ability of primary producers to persist in a location. We show that spatial flows of this limiting nutrient through its abiotic (inorganic) and biotic (biomass) forms can turn a sink into a source or a source into a sink. In meta-ecosystems, the source-sink dynamics of an organism is not only constrained by its dispersal from the source to the sink, but also by the fertility and community composition in the neighborhood responsible for spatial flows of nutrients and energy.

#### THE MODEL

We present an ecosystem model (DeAngelis 1992) with nutrient recycling in a heterogeneous landscape. Fig. 1 illustrates the different structures of the regional ecosystem we analyze, with a single inorganic nutrient ( $N$ ), a primary producer ( $P$ ), an herbivore ( $H$ ), and the detritus ( $D$ ). Ecosystems from different localities, called patches, are coupled by the spatial flows of these compartments. We analyze four different ecosystem configurations: nutrient-producer (Fig. 1A), nutrient-producer-detritus with (Fig. 1C) and without (Fig. 1B) producer dispersal and nutrient-producer-herbivore-detritus (Fig. 1D). The producers deplete the limiting nutrient in the patch in which it is found. The nutrient sequestered in the biomass of producers is either consumed by the herbivore or returned to the detritus compartment following natural death. The dead biomass of the herbivore is also converted to the detritus compartment. The model accounts for regional dynam-

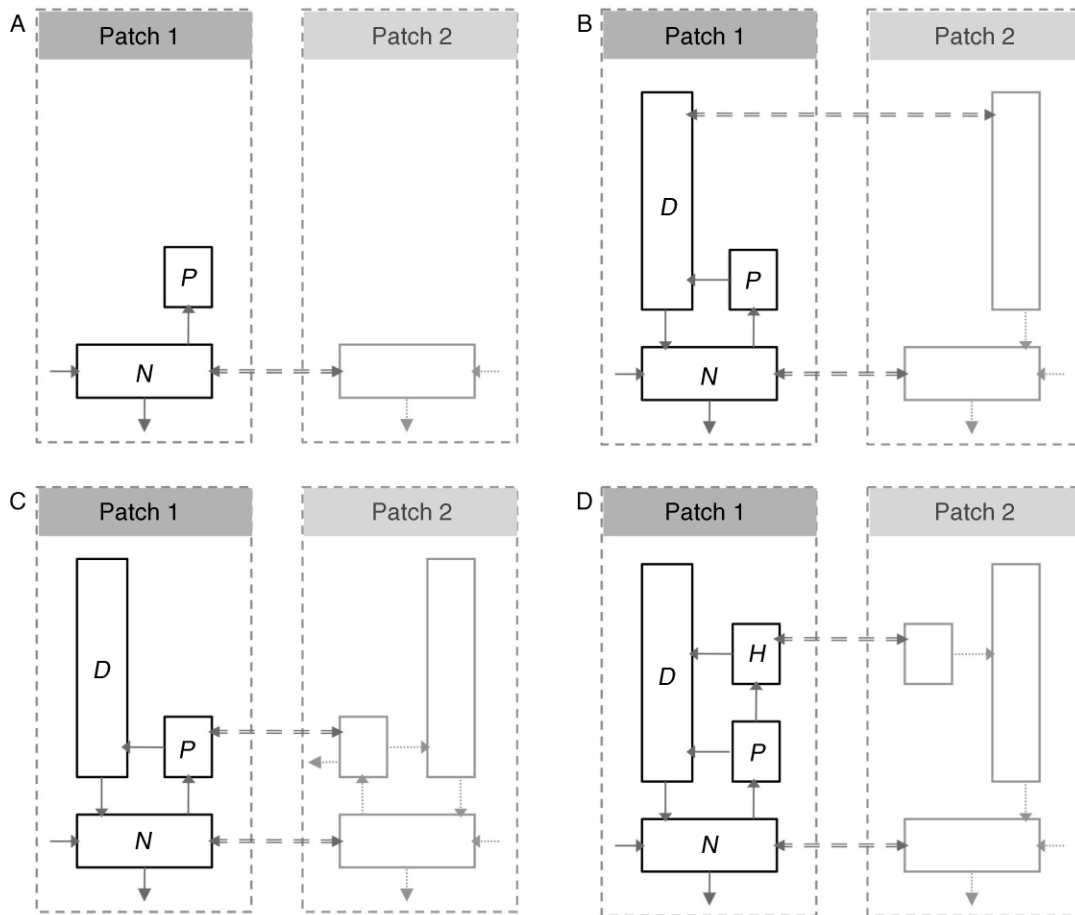


FIG. 1. The local ecosystem structure and the flows among compartments. The different panels correspond to the different scenarios described throughout the text: (A) nutrient–producer system with no recycling; (B) nutrient–producer–detritus system with detrital flows; (C) nutrient–producer–detritus system with producer flows; and (D) nutrient–producer–herbivore–detritus system with herbivore flows.

ics through flows of the inorganic nutrient, producers, herbivores, and detritus among patches.

All compartments are treated as nutrient stocks and flows. The biomasses of producers, herbivores, and detritus are proportional to their nutrient stocks (in quantity of nutrient per unit of surface or volume). The local inorganic nutrient compartment is open to external input at rate  $I_x$  (e.g., atmospheric depositions or rock alteration) and to output (e.g., nutrient leaching) at rate  $e_N$ . The subscript  $x$  refers to a patch (see Table 1 for a summary of the abbreviations). The consumption of the nutrient by the producers is given by the function  $f_{P_x}$  and the consumption of the producers by herbivores is  $f_{H_x}$ . Producers and herbivores die at the density-independent rates  $m_P$  and  $m_H$ , respectively, and their biomass is completely incorporated into the detritus compartments (results are qualitatively the same with inefficient nutrient transfer; see Appendix E). The nutrient is recycled from the detritus compartment at rate  $r$  (mineralization rate) and a fraction  $e_D$  is lost during this process. The connection to other patches for

each compartment is modeled using general dispersal functions  $\Delta_{N_x}$ ,  $\Delta_{P_x}$ ,  $\Delta_{H_x}$ , and  $\Delta_{D_x}$ , for the nutrient, producers, herbivore, and detritus, respectively. Meta-ecosystem dynamics are represented by the following equations:

$$\begin{aligned} \frac{dN_x}{dt} &= I_x - eN_x - f_{P_x}(N_x, P_x) + r(1 - e_D)D_x + \Delta_{N_x} \\ \frac{dP_x}{dt} &= f_{P_x}(N_x, P_x) - m_P P_x - f_{H_x}(P_x, H_x) + \Delta_{P_x} \\ \frac{dH_x}{dt} &= f_{H_x}(P_x, H_x) - m_H H_x + \Delta_{H_x} \\ \frac{dD_x}{dt} &= m_P P_x + m_H H_x - rD_x + \Delta_{D_x}. \end{aligned} \quad (1)$$

At equilibrium, the inflows balance the outflows to respect global mass balance.

The inorganic nutrient concentration in the absence of consumption by primary producers and spatial flows between patches is  $I_x/e_N$ , a quantity we refer to as patch fertility. We restrict the analysis to linear functional

TABLE 1. Summary of the abbreviations used in the text.

Symbol	Definition
<b>Variables</b>	
$N$	inorganic nutrient
$P$	primary producer
$H$	herbivore
$D$	detritus
$\lambda$	density-independent per capita population growth rate
$\Phi$	net effect of spatial flows on $\lambda$
<b>Parameters</b>	
$I_x$	inorganic nutrient input rate
$e_N, e_D$	output rates for the different compartments
$m_P, m_H$	mortality rates for the primary producer and the herbivore compartments
$\alpha_x$	primary producer consumption rate of the inorganic nutrient at locality $x$
$\beta$	herbivore consumption rate of the primary producer at locality $x$
$r$	recycling rate
$d_N, d_P, d_H, d_D$	diffusion rate of the different compartments
<b>Functions</b>	
$f$	functional responses for the primary producer and the herbivore compartments
$\Delta$	dispersal functions for the different compartments

responses, i.e., there is no satiation at elevated resource concentration (we also analyzed a type II functional response in Appendix D and show, for this particular model configuration, that it does not affect the results we derived in this study). Inorganic nutrient uptake by producers is described by the functional response  $f_{P_x} = \alpha_x N_x P_x$ , where  $\alpha_x$  is the producer consumption rate. The producer tolerance to low inorganic nutrient concentration is  $N_x^* = m_P / \alpha_x$  (Tilman 1982) and is patch-specific because the environment is heterogeneous. For the herbivore, we consider both donor control ( $f_{H_x} = \beta_x P_x$ , where  $\beta$  is the herbivore consumption rate) and recipient control ( $f_{H_x} = \beta_x P_x H_x$ ) linear functional responses. We assume that dispersal is passive, with no preferential movement to any patch (DeAngelis 1992, Okubo and Levin 2001). For a given compartment  $C$  in a meta-ecosystem of two patches (patch 1 and patch 2), spatial flow is defined as  $\Delta_{C1} = d_C(C_2 - C_1)$  for patch 1 and the opposite for patch 2. This function describes the net balance between the outflows and the inflows in a patch. It models passive spatial flows such as water circulation in soils, leaf litter dispersal, and drifting algae and carcasses and passive animal dispersal such as excretions by large herbivores (we derived results with asymmetric connection and found similar results; see Appendices B and C). The model simplifies considerably the reality for the tractability, but the result appears robust against strong modifications of the model structure (e.g., a stoichiometrically explicit model; Sterner and Elser 2002; D. Gravel, N. Mouquet, M. Loreau, and F.

Guichard, *unpublished manuscript*; see *Discussion* and *Appendices A–E* for more details).

*Effect of spatial nutrient flows on source-sink dynamics*

Consider a meta-ecosystem consisting of two patches (Fig. 2). For this specific example consider the two patches have the same fertility, but the environment varies so that the primary producer could not maintain a population in patch 2. At equilibrium and with no spatial flows of any kind, the nutrient concentration will be lower in patch 1 than in patch 2 because the primary producer depletes nutrients in the only patch (patch 1) where it can persist. Now if we allow spatial flows of the inorganic nutrient and biomass between the patches, the inorganic nutrient will flow from patch 2 to patch 1, while the nutrient sequestered in the biomass will flow in the opposite direction. If the direct and indirect flows are not equal, one patch will be a net importer of the nutrient and the other a net exporter, creating a strong asymmetric coupling between the patches. We now integrate such ecosystem-level feedback between patches to source-sink theory and show how this could determine whether patches 1 and 2 are sources or sinks.

The definition of a sink is based on the inability of the primary producer (as for other trophic levels) to maintain a population in a patch in absence of spatial flows (Pulliam 1988). The density-independent per capita growth rate is typically used to define whether a patch is a source or a sink. We derive it for patch 2 by calculating the growth rate of the primary producer when it is in a very small density (an invader) and the meta-ecosystem is at equilibrium. The fundamental density-independent per capita population growth rate of the producer accounts only for the environment in the

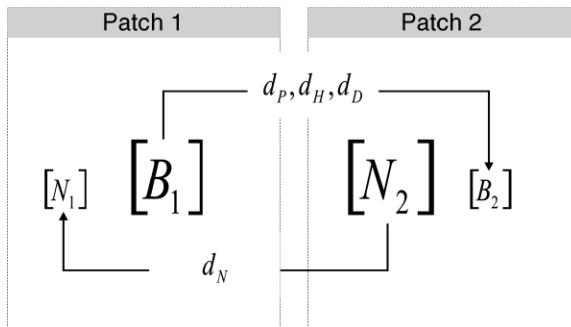


FIG. 2. Schematic representation of the dynamics of direct and indirect nutrient flows in a source-sink landscape. We consider a landscape in which patch 1 is a source because it sustains a viable ecosystem in the absence of spatial flows, while patch 2 is a sink as it does not maintain a viable ecosystem in the absence of spatial flows.  $N$  is the amount of nutrients in the inorganic compartment at equilibrium,  $B$  is the amount of nutrients sequestered in live and dead biomass at equilibrium ( $P + H + D$ ). The size of the characters is proportional to the nutrient concentration.  $N$  flows from patch 2 to patch 1 because there is no local production at patch 2 to depress  $N$ .  $B$  flows from patch 1 to patch 2 because there is no local production in patch 2. See Table 1 for explanations of parameter abbreviations.

patch and is independent from the spatial ecosystem context. It is given in our model by

$$\lambda_{2-} = \frac{I_2}{e} - N_2^* \quad (2)$$

The fundamental density-independent growth rate depends on the species tolerance to low nutrient concentration and the fertility of the patch. In our example (Fig. 2), patch 1 is a fundamental source because  $\lambda_{1-}$  is positive and patch 2 is a fundamental sink because  $\lambda_{2-}$  is negative.

Spatial flows of the nutrient and detritus between the patches will affect the inorganic nutrient concentration in patch 2 (the sink). This means the intrinsic per capita population growth rate of the primary producer in patch 2 depends on the structure, composition, and productivity of its neighboring ecosystem and on the intensity of spatial flows. The realized density-independent per capita population growth rate of the producer in patch 2 when coupled to patch 1 is defined by the local environment and by the neighboring ecological context. It is given by

$$\lambda_{21} = \hat{N}_2 - N_2^* \quad (3)$$

where  $\hat{N}_2$  is the equilibrium inorganic nutrient concentration in patch 2 when coupled to patch 1 in absence of the primary producer in patch 2. The realized growth rate in patch 2 will be affected by spatial flows of the nutrient and the ecosystem structure, composition, and productivity in patch 1. In our example in Fig. 2, patch 2 could turn into a source if the flow of biomass is much larger than the flow of the inorganic nutrient.

The difference between Eqs. 2 and 3 gives the net effect of the spatial flows of the nutrient on the density-independent population growth rate:

$$\Phi_{21} = \hat{N}_2 - \frac{I_2}{e_N} \quad (4)$$

We name the quantity  $\Phi_{21}$  the meta-ecosystem effect on the density-independent growth rate. It determines whether the spatial nutrient flows increase or decrease inorganic nutrient concentration in patch 2. It also describes, more generally, whether patch 1 is a net exporter (negative) or a net importer (positive) of nutrients across all compartments when patch 2 is unoccupied. A positive value for  $\Phi_{21}$  means that the inorganic nutrient concentration in patch 2 is larger than what is expected in the absence of flows and consumption. Therefore  $\Phi_{21}$  synthesizes the net direction of the spatial nutrient flows conceptualized in Fig. 2. In terms of source-sink dynamics, the spatial flows have the potential to transform a sink into a source when  $\Phi_{21}$  is positive because it receives more nutrients than it exports and to transform a source into a sink when it is negative, because it exports more than it receives. At  $\Phi_{21} = 0$  we find the transition point between the two situations.

We now analyze the manner in which different ecosystem configurations affect the net direction and strength of nutrient flows between ecosystems. We proceed with the analysis by adding one compartment at a time. We look for the critical rate of indirect flows of the nutrient because it is a crucial quantity defining the local balance of nutrient imports and exports. Figs. 3–5 illustrate the impacts of the different parameters on the magnitude and direction of nutrient flows.

#### Nutrient–producer system

We start with an inorganic nutrient–producer system (Fig. 1A) as a baseline for our analysis. This model configuration allows us to analyze the effect of one patch on the other in the absence of nutrient recycling. The system is made of an inorganic nutrient and a producer, and we only allow for direct nutrient flows ( $\Delta_{Nc}$ ). The equilibrium inorganic nutrient concentration in patch 2 is then

$$\hat{N}_2 = \frac{I_2 + d_N N_1^*}{e + d_N} \quad (5)$$

and the meta-ecosystem effect is

$$\Phi_{21} = d_N \frac{N_1^* - \frac{I_2}{e}}{e + d_N} \quad (6)$$

There are two possible consequences of spatial flow of the inorganic nutrient between patches. First, the inorganic nutrient could flow from patch 2 to patch 1 if the producer in patch 1 depletes the nutrient to lower concentration than the fertility of patch 2 ( $N_1^* < I_2/e_N$ ). This negative effect of spatial nutrient flows on inorganic nutrient availability in patch 2 could be sufficient to transform it into a sink if it makes the realized growth rate negative ( $\lambda_{21} < 0$ ). Alternatively, if the producer in patch 1 depletes the inorganic nutrient to higher concentration than the fertility of patch 2 ( $N_1^* > I_2/e_N$ ), the inorganic nutrient flows from patch 1 to patch 2 and enriches the latter. The magnitude of this effect scales asymptotically with  $d_N$  and could turn a sink into a source (when  $\lambda_{21} > 0$ ).

A net flow of the nutrient from patch 1 (the source) to patch 2 is, however, detrimental to population size in patch 1 (see Fig. 3 for an illustration with the nutrient–producer–detritus system). The population in the source then decreases with spatial flows of the inorganic nutrient (as illustrated in Fig. 3). This effect can prevent the persistence of the primary producer even if patch 1 is a source according to its fundamental growth rate.

#### Nutrient–producer–detritus system

Next, we investigate a system with a detritus compartment (Fig. 1B) in which both nutrient and detritus can flow between patches. The effect of the spatial flows on the inorganic nutrient concentration in the patch 2 could be positive or negative, depending on the difference of fertility between patches (Fig. 4) and

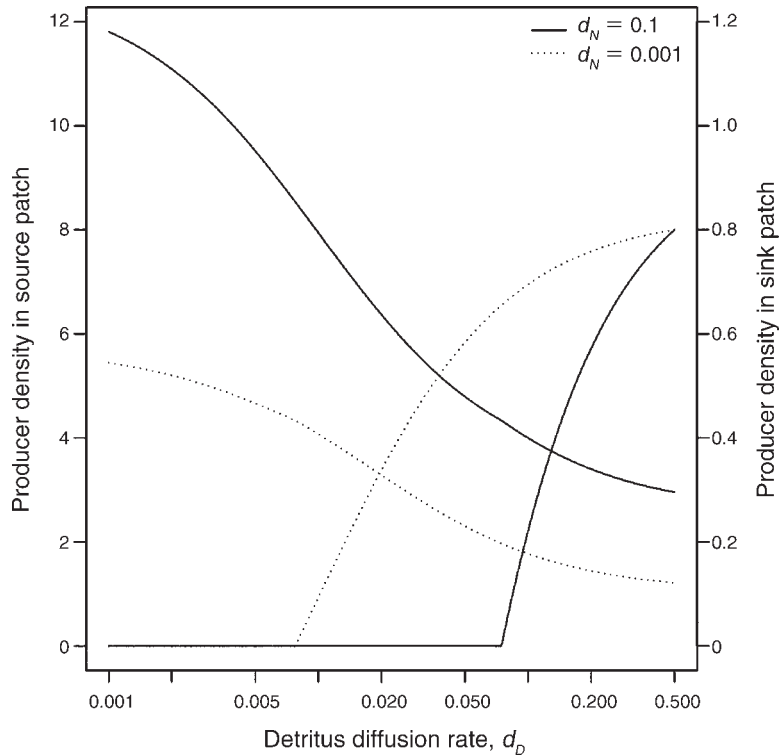


FIG. 3. Effect of the inorganic nutrient and the detritus flows on the biomass of the source and the sink patches for a nutrient–producer–detritus meta-ecosystem (see Fig. 1B). Because the model has general applicability, no units are specified. The different nutrient diffusion levels are set to illustrate extreme situations with low (dotted line) and high (solid line) nutrient flows between patches. The decreasing density with detritus diffusion rate corresponds to the producer density in the source patch (right axis) and the increasing density corresponds to the sink patch (left axis). Parameters:  $I_1 = 0.1$ ,  $I_2 = 0.1$ ,  $e_N = 0.1$ ,  $e_D = 0.1$ ,  $r = 0.2$ ,  $m_P = 0.15$ ,  $\alpha_1 = 1$ ,  $\alpha_2 = 0.125$ . See Table 1 for explanations of parameter abbreviations.

the importance of direct and indirect spatial flows of the nutrient (Fig. 5). To better understand the transition from a positive to a negative effect, we calculate the meta-ecosystem effect  $\Phi_{21}$ , and we solve  $\Phi_{21} = 0$  for  $d_D$  to find the critical detritus spatial flow  $d_D^{\text{crit}}$  distinguishing a positive from a negative effect:

$$d_D^{\text{crit}} = \frac{re_D d_N \left( \frac{I_2}{e_N} - N_1^* \right)}{e_N(1 - e_D) \left( \frac{I_1}{e_N} - N_1^* \right) - 2e_D d_N \left( \frac{I_2}{e_N} - N_1^* \right)}. \quad (7)$$

If  $d_D > d_D^{\text{crit}}$ , the primary producer in patch 2 will benefit from the presence of the primary producer in patch 1. If patch 2 is a sink, it becomes a source if spatial flows increase nutrient concentration to values above the fundamental growth rate ( $\lambda_{21} > 0$ ). Similarly, if patch 2 is a source, it becomes a sink if spatial flows decrease the inorganic nutrient concentration below the fundamental growth rate ( $\lambda_{21} < 0$ ). An essential aspect of Eq. 7 is that the critical detritus spatial flow depends on within-patch fertility values ( $I_1$  and  $I_2$ ; see Fig. 4) and on the tolerance to low resource level in patch 1 ( $N_1^*$ ; see Fig. 5). This result illustrates the importance of considering the meta-ecosystem as a whole to understand the impacts of nutrient flows: the net nutrient flow into a patch depends

on the fertility and the community composition of the patches within its neighborhood. This result also applies to situations with asymmetric spatial flows (see Appendices B and C) and is a feature that is missing in models with a non-explicit source of allochthonous inputs such as island–mainland models.

There are three possible situations that can be distinguished from Eq. 7 (Fig. 4). The first and simplest situation corresponds to the case in which the fertility is equal between patches ( $I_1 = I_2$ ). In this case, the critical detritus flow reduces to

$$d_D^{\text{crit}} = \frac{re_D d_N}{e_N(1 - e_D) - 2e_D d_N}.$$

Low recycling efficiency, expressed through low  $r$  and  $e_D$ , high  $e_N$ , and low inorganic nutrient flow ( $d_N$ ), promotes a net flow from patch 1 to patch 2. Note that neither the consumption rate in patch 1 nor the input rate is found in this criterion, which means the net direction of the spatial flows is independent from fertility when the two patches have similar fertility. These parameters do, however, affect the magnitude of the net spatial flows between patches.

The second situation corresponds to the case in which the fertility is higher in patch 1 ( $I_1 > I_2$ ). In this case,

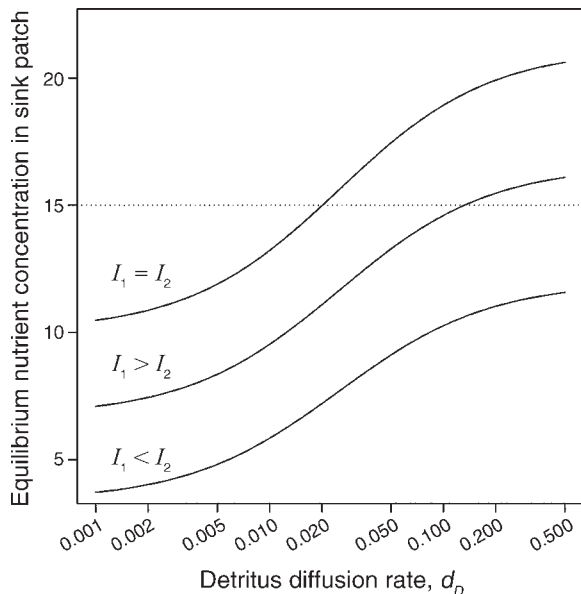


FIG. 4. Effect of the detritus flows on the inorganic nutrient concentration in the sink patch for different fertilities ( $I$  = inorganic nutrient input rate) in the source and the sink patches. Because the model has general applicability, no units are specified. Parameters:  $e_N = 0.1$ ,  $e_D = 0.1$ ,  $r = 0.2$ ,  $m_P = 0.15$ ,  $\alpha_1 = 1$ ,  $\alpha_2 = 0.125$ ,  $d_N = 0.05$ . See Table 1 for explanations of parameter abbreviations.

both the inorganic nutrient and the detritus flow will promote a net flow from patch 1 to patch 2. Elevated inorganic nutrient flow will reduce  $d_D^{crit}$  for a flow from patch 1 to patch 2 to occur. The third situation occurs if the fertility is higher in patch 2 ( $I_1 < I_2$ ). Then the nutrient is more likely to flow from patch 2 to patch 1, even for high  $d_D$  values, thus reducing the inorganic nutrient concentration in patch 2 below its fertility (Fig. 4). In all three situations, a net flow of the nutrient from patch 1 to patch 2 is again detrimental to the population in patch 1 (equation not shown, but see Fig. 3). Population size in patch 1 is reduced by the spatial flow of the inorganic nutrient and this reduction could be sufficient to prevent the persistence of the primary producer in that patch even if it is a source according to the fundamental growth rate.

The criterion described at Eq. 7 is based on the density-independent per capita growth rate (Eq. 3), but it also describes the net interaction between primary producers of two patches when both patches are sources (Fig. 6; detailed analysis is presented in Appendix A). The reason for this correspondence is simple: beyond the effect of nutrient flows on the source–sink dynamics, Eq. 3 summarizes the net direction of the nutrient between the two patches. In a situation in which primary producers inhabit the two patches, there still will be flows between them unless the fertility of the two patches and the  $N^*$  of the primary producers are absolutely identical. What is less intuitive though is that the

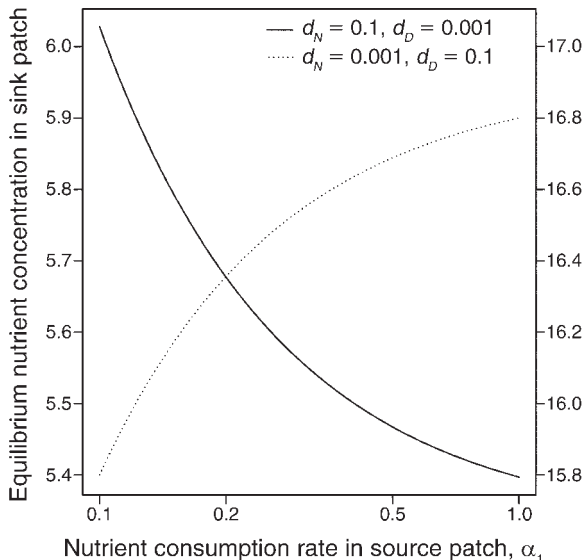


FIG. 5. Effect of the primary producer traits (here the consumption rate) in the source patch on the inorganic nutrient concentration in the sink patch. Because the model has general applicability, no units are specified. Note that the scale differs for the two combinations of parameters: the solid line corresponds to the left axis, and the dotted line corresponds to the right axis. Parameters:  $I_1 = 0.1$ ,  $I_2 = 0.1$ ,  $e_N = 0.1$ ,  $e_D = 0.1$ ,  $r = 0.2$ ,  $m_P = 0.15$ ,  $\alpha_1 = 1$ . See Table 1 for explanations of parameter abbreviations.

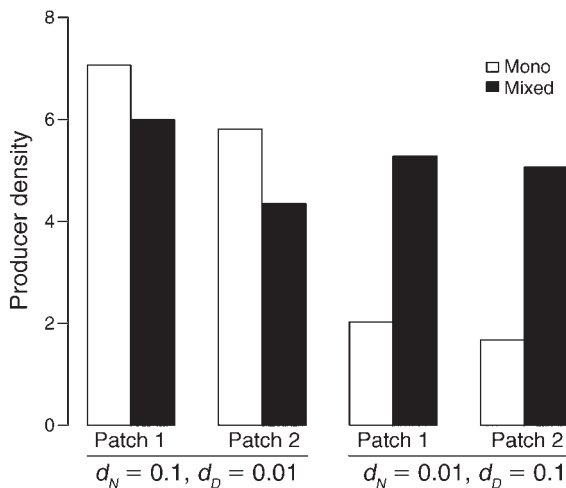


FIG. 6. The indirect interaction between populations of producers in two patches connected by flows of the inorganic nutrient and the detritus. Patch 1 is inhabited by a highly productive producer ( $\alpha_1 = 1$ ), and patch 2 is inhabited by a weakly productive producer ( $\alpha_2 = 0.5$ ). This difference creates asymmetry in the patches and flows of detritus from patch 1 to patch 2 and flows of the inorganic nutrients from patch 2 to patch 1. “Mono” corresponds to the producer density in one patch when the other patch is empty, and “Mixed” corresponds to the producer density in one patch when the other patch is occupied. Parameters:  $I = 1$ ,  $e_N = 0.1$ ,  $e_D = 0.1$ ,  $r = 0.2$ ,  $m_P = 0.15$ . See Table 1 for explanations of parameter abbreviations.

presence of the primary producer in the patch that is the recipient of the nutrient is also beneficial to the primary producer in the patch from which it originates. In the absence of the latter, the detritus flowing to the recipient patch is eventually lost by leaching. By its presence, even if that species is less productive, it contributes by consuming the nutrients recycled from the imported detritus, and eventually a fraction of that extra production is exported to the other patch. In other words, the recipient patch also returns detritus to the exporting patch, and the latter then sees a reduction in the net flow of detritus exported. The productivity at the local and the regional scales is thus maximized when both patches are occupied. This result shows that the populations located in the two patches are interacting together, even if they are never in direct contact.

*Generality of the result: other types of indirect nutrient spatial flows*

Is the effect of indirect nutrient flows dependent on the compartment from which indirect spatial flows occur? Our results so far have focused on detritus-mediated indirect flows. Can other trophic compartments also drive a net flow of nutrient from sources to sinks?

To answer this question, we allow for dispersal of producers ( $\Delta_{P_x}$ ) in the nutrient-producer-detritus system and neglect detritus flow (Fig. 1C). We restrict our analysis to the special case of equal patch fertility ( $I_1 = I_2$ ) to provide tractable results. (Conclusions are the same as in other situations, while the solution is much more complex algebraically.) We assume that nutrient consumption by the immigrants in patch 2 is negligible to emphasize the role of spatial flows of the nutrient sequestered in the biomass; in other words, patch 2 is an extreme sink with  $N_2^*$  approaching infinity (numerical analyses demonstrated the results are robust to this assumption). Following the same approach as above to calculate the meta-ecosystem effect and the  $d_D^{crit}$  we find

$$d_P^{crit} = d_N \frac{e_D m_P}{e_D(1 - e_D) - 2e_D d_N}. \tag{8}$$

Eq. 8 confirms the net flow of the nutrient could go in either direction between patches. Indirect nutrient flows mediated by primary producer dispersal between patches can thus contribute to the enrichment of the sink patch. Note that this criterion is influenced by the mortality rate of the producer since it determines the rate at which immigrants to patch 2 are converted to detritus. Numerical simulations confirm that these results are robust when both  $d_P > 0$  and  $d_D > 0$ .

We further assessed the generality of our findings by analyzing a nutrient-producer-herbivore-detritus system (Fig. 1D). In this analysis, we allow only direct flow ( $\Delta_{N_x}$ ) and indirect flow mediated by the movement of the herbivore ( $\Delta_{H_x}$ ). Patch 2 is a sink for the primary producer. The herbivores migrating to patch 2 die from starvation and contribute to the local detritus compart-

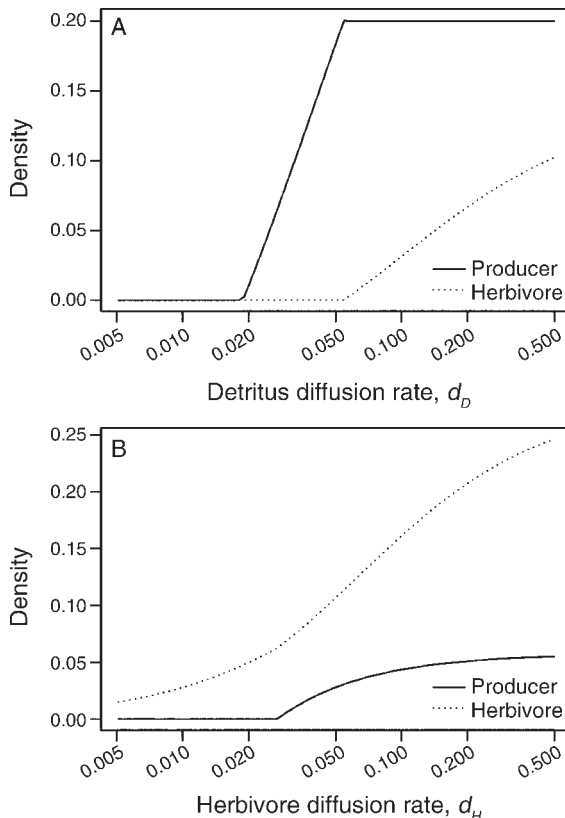


FIG. 7. Effect of (A) detritus and (B) herbivore dispersal rates on the food chain assemblage in a sink patch. One patch has a high supply rate and is, therefore, a fundamental source, supporting the producer and the herbivore, and the other patch has a low supply rate and is, therefore, a sink, supporting no producer. Parameters:  $I_1 = 0.1$ ;  $I_2 = 0.015$ ;  $e_N = e_D = 0.1$ ;  $\alpha_1 = \alpha_2 = 1$ ;  $\beta = 1$ ;  $m_P = 0.2$ ;  $m_H = 0.2$ ;  $r = 0.5$ ;  $d_N = 0$ ;  $d_P = 0$ ;  $d_H = 0$  for panel (A) and  $d_D = 0$  for panel (B). See Table 1 for explanations of parameter abbreviations.

ment. Following the same approach as above, we find for the special case of the donor control functional response:

$$d_H^{crit} = d_N \frac{(m_P + \beta)e_D m_H}{e_N \beta(1 - e_D) - 2e_D d_N(m_P + \beta)}. \tag{9}$$

This solution also shows that the indirect spatial flow of the nutrient through an herbivore allows a net flow of nutrients in both directions. The same conclusion applies for a recipient control functional response (not shown because the solution is algebraically too complex to be informative, but see Fig. 7). Eqs. 8–9 lead us to the suggestion that a net spatial flow of the nutrient can occur in both directions between a source and a sink and that the effect of spatial nutrient flows on source-sink dynamics can be mediated by indirect spatial flows at any trophic compartment.

*Impacts on community organization*

We now illustrate the consequence of these results with a more applied situation, mimicking the study of



Polis and Hurd (1995, 1996) on spider densities on islands subject to elevated marine allochthonous inputs in the Gulf of California. Polis and Hurd (1995) noted that some islands in that region support very high numbers of arthropod predators despite very low intrinsic primary productivity. However, all islands receive considerable amounts of marine detritus via the deposition of drifting algae and carcasses. They observed that allochthonous inputs enhanced productivity by several orders of magnitude and that the amount of energy coming from external inputs relative to the intrinsic productivity was closely related to island size. Within our modeling framework, this example can be represented as the coupling of a patch with a high nutrient supply rate (the source) to a patch with a very limited supply rate (the sink). The among-patch flow rate of detritus is then conceptually analogous to island area studied by Polis and Hurd (1995). Once translated into our framework with reciprocal flows, their question becomes: How does indirect nutrient transport affect food web assemblage in a sink patch?

Results from numerical simulations of this system (nutrient–producer–herbivore–detritus) are presented in Fig. 7A for increasing rates of detritus flows (as in Polis and Hurd 1995, 1996). In order to match their system,  $d_H$  was set to 0. The results are very similar to the classical studies on the relationship between food chain length and ecosystem productivity (Oksanen et al. 1981, Pimm 1982, DeAngelis 1992) and match the results of Polis and Hurd (1995, 1996). As  $d_D$  increases, productivity in the sink patch increases until the primary producer can establish a viable population, i.e., until the sink patch becomes a source for the producer. As  $d_D$  is further increased, primary productivity increases until the herbivore is in turn able to establish a viable population (i.e., the sink patch becomes a source for the herbivore). This sequence of food chain assembly could easily be extended to higher trophic levels. The opposite situation occurs in the source patch. As  $d_D$  increases, the herbivore and the producer biomass decrease but only the herbivore goes extinct because of elevated  $d_D$  (not shown). This last result emerges because we consider the meta-ecosystem, which is not limited to an island–mainland situation such as in Polis and Hurd (1995, 1996).

An interesting case arises when the herbivore disperses instead of the detritus (Fig. 7B). At low  $d_H$ , the herbivore dies from starvation in the sink patch because the producer is absent, but the constant inflow of herbivore immigrants maintains the population. Herbivore biomass is recycled locally, thereby increasing the inorganic nutrient availability. Consequently, as  $d_H$  increases, the herbivore eventually facilitates the establishment of a viable population of the producer (Fig. 7B). Eventually, the latter would reach a population of a sufficient size to allow the herbivore population in the sink patch to become a source, which confirms the results in Loreau and Holt (2004). However, if the

primary producer is eliminated from the sink patch, elevated dispersal could lead to the regional extinction of the herbivore (not shown). This demonstrates a positive feedback loop between the producer and the herbivore: the presence of the producer species in the sink patch is necessary for the maintenance of the herbivore meta-population, and the flow of the herbivore from the source to the sink patch is, in turn, necessary for regional persistence of the producer. With the producer present at high  $d_H$ , the herbivore is regionally maintained because losses by emigration from the source are recycled in the sink patch and incorporated back through local production. Such feedbacks naturally lead to more complicated situations in which the elimination of a single species could lead to catastrophic trophic cascades at both local and regional scales.

#### DISCUSSION

The importance of external subsidies on local community dynamics and structure has been studied empirically over the last decades (see reviews in Polis et al. 1997, 2004), but theoretical advances have been limited to island–mainland models (Huxel and McCann 1998, Huxel et al. 2002, Takimoto et al. 2002, Holt 2004, Loreau and Holt 2004, Leroux and Loreau 2008). Here we show that the direct (inorganic compartment) and indirect (organic compartment) flows of a limiting nutrient substantially affect source–sink dynamics. In our model, inorganic nutrients flow directly from the localities with elevated nutrient concentration to the localities with low nutrient concentration, while they flow indirectly from localities with elevated biomass to localities with low biomass. As a consequence, the net balance between direct and indirect nutrient flows determines whether a species in a locality will suffer or benefit from the occupancy of its coupled locality. Ecosystems in different localities thus interact together; the structure at one place will influence that of others.

We have shown that nutrients will flow between patches and affect source–sink dynamics under the different model configurations we considered. This suggests a general mechanism that should be robust to the different empirical situations occurring in nature: the connection between asymmetric ecosystems, in which more nutrient consumption and biomass production is expected in one location than in the other, generates flows of inorganic and organic nutrients likely to affect community organization. This asymmetry could result from different environmental conditions, such as different soils and lake physico-chemical properties, from benthic–pelagic coupling in aquatic systems (Angel 1984, Kaiser et al. 2005, Renaud et al. 2008) or from heterogeneous community structure owing to historical contingencies or disturbances (D. Gravel, N. Mouquet, M. Loreau, and F. Guichard, *unpublished manuscript*). We should expect the amount of material exchanged between ecosystems to be proportional to the difference between them. For instance, the magnitude of flows

between a stream and a forest are expected to be higher than between two patches with contrasted soil types within this forest.

Another result emerging from our analysis, extending previous work on meta-ecosystems (Polis et al. 1997, Huxel and McCann 1998, Huxel et al. 2002, Holt 2004, Loreau and Holt 2004, Leroux and Loreau 2008), is the control of spatial flows and of their ecological effects by community composition in both source and sink patches. Altering the community structure in one location will affect the structure of the coupled location. For instance, the replacement of a productive primary producer in a source location by a less productive one will be harmful to the sink location when the detritus flows are important. Similarly, the introduction of an herbivore in the source patch can result in a spatial trophic cascade (Schmitz 2008), as it will reduce nutrient consumption in that patch and thus considerably modify the amount of nutrients exchanged between patches. The introduced herbivore might not affect the net direction of the flow, but can instead drive primary productivity in neighboring patches. The mechanism we report on here also has consequences extending beyond source-sink dynamics. The spatial nutrient flow influences both the exporting and the recipient patches. Our analysis revealed how this flow will impact the ability of a species to grow in the sink patch, but it will more generally affect the productivity and structure of both patches.

The spatial flows of nutrients will affect source and sink dynamics as long as there are asymmetric flows benefiting one location to the detriment of the other. This principle will hold under different ecological contexts, but the more specific knowledge of direct flow properties, of organisms responsible for indirect flows, and of community structure is important to predict the direction of nutrient flows. We analyzed a meta-ecosystem model that involved a number of assumptions to keep results tractable, restricting the realm of inference of the model. When we relaxed some of these assumptions, we found that the spatial flows of the nutrient still affect the source-sink dynamics but it could change the net direction of the nutrient flow or the magnitude of the flow. For instance, we emphasized bidirectional flows because we were interested in the emerging feedbacks between patches. The size asymmetry between patches indeed affects the magnitude of the spatial flows of nutrients, as obviously a larger source patch has a stronger impact, but it does not change the critical transition between a positive and a negative effect. Ultimately, the net direction of nutrient flows depends on the relative importance of the direct (inorganic) and the indirect (organic) contributions to these flows. Flows can be passive, as was assumed in this study, while others can be active and associated with habitat selection. In the field, what one needs to know is the relative importance of spatial nutrient flows to local productivity (e.g., Dolson et al. 2009, Gratton and

Zanden 2009) and how these are influenced by community structure.

#### *Defining and testing a meta-ecosystem effect*

The meta-ecosystem perspective involves the addition of two fundamental aspects to the metacommunity framework: nutrient recycling and a regional mass balance constraint. Nutrient recycling has the ability to create a feedback loop from the top species to the basal species of an ecosystem. In local ecosystem models, this could result in counterintuitive situations in which a consumer (e.g., a herbivore) could maximize the productivity of its prey (e.g., the grazing optimization concept; de Mazancourt et al. 1998). This phenomenon arises because factors promoting nutrient cycling efficiency will benefit the overall productivity of the system (DeAngelis 1992, Loreau 1998, Wardle 2002). In a meta-ecosystem, nutrient recycling and regional mass balance constraints scale this feedback to the region. A meta-ecosystem with unoccupied locations is inefficient at nutrient recycling because nutrients will be moved indirectly to these locations rather than being consumed locally and will eventually be exported from the system (e.g., by leaching). In short, we could define a meta-ecosystem effect (positive or negative) as the effect of the ecosystem composition, structure, and productivity in one locality on the ecosystem dynamics in another locality resulting from spatial flows and recycling of matter. The sign of this effect is determined by the relative magnitudes of the different flows and by parameters of nutrient cycling efficiency. The applicability of such meta-ecosystem effects in nature relies on the strength of nutrient and spatial coupling in a natural system.

The crucial quantity we found in our analysis is the ratio between the flow of the nutrient contained in biomass ( $d_P$ ,  $d_D$ , or  $d_H$ ) and the flow of the inorganic nutrient ( $d_N$ ). These quantities are fairly abstract and obviously difficult to measure in the field. Perhaps we could estimate them in aquatic marine environments, but it would be much harder to do so in terrestrial environments. Nonetheless, we could get a qualitative sense of their relative magnitude. For instance, in a forest, leaf litter dispersal is most likely higher than horizontal nutrient flows (high  $d_D/d_N$ ). In contrast, the  $d_D/d_N$  ratio will be much smaller in a grassland, where plants are smaller and the litter is less prone to dispersal. The  $d_H/d_N$  ratio will be very large, however, when large herbivores migrate and connect distant ecosystems. In aquatic and marine environments,  $d_N$  is likely to be much higher, especially when strong water flows limit the active foraging of zooplankton. In contrast, intense upwelling areas will increase  $d_D$ . There is thus a wide range of situations in natural systems in which our predictions could be tested. Indeed, many empirical studies of allochthonous subsidies suggest that external inputs are necessary to maintain ecosystem structure in sink locations (Oliver and Legovic 1988, Polis and Hurd

1995, 1996, Rose and Polis 1998, Anderson and Polis 1999, Christie and Reimchen 2008). Our results provide the spatial and regional integrations of such spatial flows of resources and of their effect on ecosystem function.

A fundamental prediction we make here is that the structure of an ecosystem in one locality depends on the structure of the ecosystem to which it is connected and on the relative magnitude of direct and indirect flows of the limiting nutrient. We could test this prediction by either manipulating the structure in one location and looking at the response in the coupled location or, alternatively, by manipulating the relative importance of direct and indirect flows. This could be done in a very controlled experimental setting (e.g., Howett and Leibold 2008) or one could make use of “natural” experiments following the control of population or incidental introductions and look at the response in connected localities. An example of such a case is found in Maron et al. (2006), in which an introduced predator (a fox) considerably reduced seabird populations and thus reduced nutrient subsidies to the islands. This study does not account explicitly for the meta-ecosystem, but it shows how the disruption of indirect spatial flows of nutrients affects local ecosystem structure.

The results we present here also set the stage for a new research agenda in spatial ecosystem ecology. Many of the empirical examples cited here are systems with contrasted boundaries between them. We need methodological advances to evaluate spatial flows between less contrasted ecosystems. Ecosystem ecologists are familiar with local nutrient cycling, tracing various flows of elements and molecules throughout their cycle (e.g., Likens and Bormann 1995). Local nutrient budgets allow the calculation of some important quantities such as cycling efficiency, expected turnover rate, and lifetime expectancy of a nutrient (DeAngelis 1992). It is now important to develop the tools to perform similar analyses in space. The scale at which nutrient budgets are conducted should also be revisited. Traditional studies of whole system cycles are conducted at the landscape scale, such as small watersheds. We believe the next step is to build spatially explicit nutrient budgets, such as the spatially explicit mass balance dissolved organic carbon (DOC) model in Adirondack lakes (Canham et al. 2004).

#### *Generalization of the source–sink concept*

The traditional concept of source and sink in population ecology is based on the intrinsic rate of increase and dispersal of organisms (see Mouquet et al. 2005 for a review). In ecosystem ecology, source and sink refers to the direction of flows between two localities (Loreau et al. 2003) and the combination of these historical perspectives (Loreau and Holt 2004) provides a novel approach to spatial ecosystem ecology. We have shown here that the coupling of ecosystems could enrich a sink patch to a point at which it would facilitate the establishment of a population. This means

a viable population could be maintained in a sink location in the absence of immigration, despite difficult environmental conditions. In the context of population dynamics, the implications of the negative intrinsic growth rate as a definition of a sink is clear, but this concept does not necessarily translate to spatial ecosystem ecology. Both the population and ecosystem interpretations of source and sink are not satisfying in an ecosystemic context, as they could lead to an inadequate assessment of habitat quality. For instance, a low-productivity patch benefiting from nutrient imports from surrounding productive patches would be able to sustain a population and would be interpreted as a source, while a similar patch surrounded by less productive ones would be interpreted as a sink. These two different landscape configurations, but with the same environmental characteristics of the focal patch, will have different responses to fragmentation or disruption of spatial flows that could be problematic for study by conservation ecologists. In light of our results, we believe the source–sink concept must integrate more explicitly aspects of ecosystem ecology as well as population ecology.

The meta-ecosystem perspective provides a powerful theoretical framework to address population-level to ecosystem-level questions in spatial ecology. Future studies in that direction will be at the basis of a new integrated mechanistic landscape ecology, which promises novel fundamental insight into the dynamics of ecosystems from the local to the global scales and valuable predictions of the consequences of altering the basic processes of spatial nutrient flows on community dynamics.

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#### APPENDIX A

Analysis of the net interaction between primary producers in distinct patches connected by nutrient flows (*Ecological Archives* E091-151-A1).

#### APPENDIX B

Analysis of unilateral flows between patches (*Ecological Archives* E091-151-A2).

#### APPENDIX C

Analysis of asymmetric patch size (*Ecological Archives* E091-151-A3).

#### APPENDIX D

Analysis of a type II functional response (*Ecological Archives* E091-151-A4).

#### APPENDIX E

Analysis of inefficient resource transfer (*Ecological Archives* E091-151-A5).