The Paradox of Enrichment in Metaecosystems

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ABSTRACT: The paradox of enrichment has been studied almost exclusively within communities or metacommunities, without explicit nutrient dynamics. Yet local recycling of materials from enriched ecosystems may affect the stability of connected ecosystems. Here we study the effect of nutrient, detritus, producer, and consumer spatial flows—combined with changes in regional enrichment—on the stability of a metaecosystem model. We considered both spatially homogeneous and heterogeneous enrichment. We found that nutrient and detritus spatial flows are destabilizing, whereas producer or consumer spatial flows are either neutral or stabilizing. We noticed that detritus spatial flows have only a weak impact on stability. Our study reveals that heterogeneity no longer stabilizes well-connected systems when accounting for explicit representation of nutrient dynamics. We also found that intermediate consumer diffusion could lead to multiple equilibria in strongly enriched metaecosystems. Stability can emerge from a top-down control allowing the storage of materials into inorganic form, a mechanism never documented before. In conclusion, local enrichment can be stabilized if spatial flows are strong enough to efficiently redistribute the local excess of enrichment to unfertile ecosystems. However, high regional enrichment can be dampened only by intermediate consumer diffusion rates.

Keywords: stability, dispersal, spatial heterogeneity, source-sink dynamics, fertility, alternative stable states.

Introduction

Rosenzweig (1971) defined the paradox of enrichment as the destabilization of consumer-resource dynamics observed after resource enrichment. This phenomenon has been recently understood as belonging to the principle of energy flux, a general response of consumer-resource dynamics to an increase in the input/output ratio of the consumer (Rip and McCann 2011). Among other causes, resource enrichment increases this input/output ratio (re-

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ferred to as the relative energy flux by Rip and McCann [2011]) and hence the consumer : resource biomass ratio (McAllister et al. 1972). The lag between consumer and resource growth makes these top-heavy consumer-resource interactions less stable and prone to oscillations. Then, overproduction of the resource alternates with overcompensation of the consumer (May 1974; Murdoch et al. 2003). Enrichment-driven instabilities (sensu Otto et al. 2007) have been observed in experimental microcosms (Luckinbill 1973; Fussmann et al. 2000; Becks et al. 2005; Van der Stap et al. 2009), controlled field experiments (Bjornsen et al. 1988; Lecomte et al. 2004; Meyer et al. 2012), and even nature (i.e., some herbivorous insect outbreaks have been linked to nitrogen enrichment; Myers and Post 1981; Brunsting and Heil 1985).

Though good examples exist, many experimental tests of these enrichment-driven instabilities are not consistent with the paradox of enrichment (e.g., Murdoch et al. 1998; Daugherty 2011). Moreover, field evidence for increased instability related to nutrient enrichments is scarce, despite widespread ecosystem enrichments (Krupa 2003; Duce et al. 2008; Elser et al. 2009). Several mechanisms have been invoked to explain why this destabilization might not happen in complex ecosystems (for a review, see Roy and Chattopadhyay 2007). These mechanisms include factors relative to the resource species that limit the nutrient input to the consumer, such as unpalatability, lower quality, inducible defenses, refuges, or alternative resources (Urabe and Sterner 1996; Genkai-Kato and Yamamura 1999; Van Baalen et al. 2001; Verschoor et al. 2004; Vos et al. 2004). Stability also emerges from factors that increase nutrient output from the consumer, such as cannibalism (Chakraborty and Chattopadhyay 2011), parasitism (Hilker and Schmitz 2008), interference (Auger et al. 2006; Cabrera 2011), or trophic complexity (Trzcinski 2005).

Spatial structure has also been shown to be an important stabilizing factor of consumer-resource interactions (Mur-

doch et al. 2003; Briggs and Hoopes 2004; Amarasekare 2008). Indeed, spatial structure increases consumer-resource persistence by creating permanent or temporary refuges for the resource (Huffaker 1958; Ellner et al. 2001; Neubert et al. 2002; Brockhust et al 2006; Hauzy et al. 2010b). Local extinctions can also be prevented by dispersal from other patches (Holyoak and Lawler 1996), and populations in unfavorable ecosystems (sinks) can be maintained by immigration from more favorable source ecosystems (Amezcua and Holyoak 2000; Casini et al. 2012). Briggs and Hoopes (2004) identified three mechanisms by which random dispersal stabilizes consumer-resource interactions in metacommunity models. (1) Oscillations of regional abundances can be dampened by intermediate dispersal that leads to spatial asynchrony in local abundances (de Roos et al. 1991; Jansen 1995, 2001; Maser et al. 2007). (2) In heterogeneous landscapes, limited dispersal can also be stabilizing if immigration is weaker when local densities peak. Dispersal is then driving an indirect negative density dependence, which dampens local oscillations (Klepac et al. 2007; Sugie and Saito 2012). (3) Dispersal can also stabilize dynamics of spatial predator-prey systems with nonlinear functional responses. If dispersal promotes a spatially heterogeneous distribution of the resource, the predator will be, on average, across the landscape less efficient at exploiting its resource compared with one with a homogeneous distribution (e.g., de Roos et al. 1998). Such a reduction of the input to the predator—relative to the output—is stabilizing (Rip and McCann 2011). In this case, dispersal in metacommunities can lead to multiple equilibria that have either symmetric or asymmetric spatial distributions of population densities, depending on initial conditions, with the latter being more stable (Jansen 1995, 2001; Hauzy et al. 2010a).

All these studies argue for a stabilizing effect of spatial dynamics, but none of them integrates the spatial dynamics of inorganic nutrients. However, an increasing number of studies have emphasized that nutrient enrichment occurs naturally as a result of inorganic and organic spatial flows (Polis et al. 1997; Loreau et al. 2003; Massol et al. 2011). These spatial flows have now been well documented. They include migration roads linking distant ecosystems (Jefferies et al. 2004; Varpe et al. 2005), nutrient transfers by whales linking euphotic and deep zones in oceans (Lavery et al. 2010; Roman and McCarthy 2010), detritus and organisms linking lakes and surrounding landscapes (Gratton et al. 2008; Paetzold et al. 2011; Rösel et al 2012), or sea-to-land transport of nutrients by seabirds (Fukami et al. 2006; Maron et al. 2006). In addition, local spots of enrichment due to human activities are widespread (Halpern et al. 2007). Spatial flows from these spots may affect the stability of neighboring ecosystems. Inorganic nutrient flows have been shown to potentially de-

stabilize consumer-resource interactions (Marleau et al. 2010; Suzuki and Yoshida 2012). But it is also likely that local recycling of organic matter brought by dispersal from enriched ecosystems will impact the fertility of ecosystems that receive it. Recycling plays a crucial role in the primary productivity of many ecosystems (Simon et al. 2002; Van der Heidjen et al. 2008). Therefore, the combination of spatial flows with local recycling might play an essential role in consumer-resource regional dynamics under enrichment.

Spatial exchanges of nutrients and organic material are formalized in the concept of metaecosystem, defined as a set of local ecosystems linked by spatial flows of inorganic nutrients, detritus, and/or organisms (Loreau et al. 2003; Massol et al. 2011). By integrating explicitly the dynamics of inorganic nutrients with recycling and spatial flows, the metaecosystem framework efficiently addresses questions related to feedbacks between species interactions and ecosystem processes. The metaecosystem study of Marleau et al. (2010), for instance, has shown how nutrient flows can affect the response of simple ecosystems to enrichment across homogeneous landscapes. Two natural extensions are required to draw up a comprehensive analysis of the consequences of dispersal on enrichment-driven instabilities. First, the effect of spatial flows of organic compartments (producer, consumer, and detritus) has to be investigated. Indeed, organisms and detritus spatial flows may affect ecosystem stability by changing local nutrient supply through mineralization (Wolf et al. 2013). Second, heterogeneity in the distribution of enrichment may also have important impacts on stability. Spatial heterogeneity generates spatial flows, with local enrichment inevitably corresponding to impoverishment elsewhere (Loreau et al. 2003; Gravel et al. 2010a, 2010b).

In this study, we revisit the paradox of enrichment within the perspective of metaecosystems. We use a simple two-ecosystem model integrating space, trophic interactions, and explicit nutrient dynamics. Our metaecosystem can represent the coupling between pelagic and benthic areas (Schindler and Scheuerell 2002) or between lakes (Griffiths et al. 2013). Aquatic systems are commonly impacted by enrichment (Halpern et al. 2007). They can be spatially heterogeneous because of physical structures—such as small bays or abrupt changes in floor depth—or because of environmental gradients (e.g., light). Moreover, recycling plays an important role in these systems (Kiørboe 2001) and often couples different ecosystems (Roman and McCarthy 2010; Ryabov and Blasius 2011). We analyze how metaecosystem stability is affected by nutrient enrichment and dispersal of the different ecosystem compartments. This study addresses two main questions. (1) How do the spatial flows of specific ecosystem compartments (nutrient, detritus, and organisms) act on the de-

stabilizing effect of enrichment? (2) What is the impact of spatial heterogeneity of ecosystem enrichment on stability? The metaecosystem framework reveals that the effects of diffusion on local dynamics depend crucially on the nature (alive vs. inert) of the spatial flows. Moreover, we show that heterogeneity is not stabilizing for well-connected ecosystems and that consumer spatial flows can lead to a specific stabilizing effect by maintaining a part of the enrichment into inorganic form.

Methods

The Metaecosystem Model

We considered two open ecosystems inhabited by a producer-consumer species pair where organic matter is locally recycled (after Gravel et al. 2010*a*). The ecosystems are connected by passive spatial flows of organisms and matter, thereby forming a metaecosystem (fig. 1). We used a compartment model in which the dynamics of the densities in ecosystem i ($i \in \{1, 2\}$) are given by the following differential equations:

$$\frac{dN_i}{dt} = I_i - e_N N_i + r D_i - P_i f_P(N_i) + d_N \Delta_{N_i},$$

$$\frac{dP_i}{dt} = P_i f_P(N_i) - (m_P + e_P) P_i - C_i f_C(P_i) + d_P \Delta_{P_i},$$

$$\frac{dC_i}{dt} = C_i f_C(P_i) - (m_C + e_C) C_i + d_C \Delta_{C_i}, \tag{1}$$

$$\frac{dD_i}{dt} = m_P P_i + m_C C_i - (r + e_D) D_i + d_D \Delta_{D_i}.$$

In each local ecosystem, the (primary) producer P consumes the single limiting inorganic nutrient N and is grazed by the consumer C. The metabolism and the mortality of the producer and consumer generate detritus D at rates m_P and m_C, respectively. Detritus is mineralized into inorganic nutrient N at a rate r. We considered Holling type II functional responses (f_P and f_C; Holling 1959) for both the producer and the consumer, following Rosenzweig's (1971) predator-prey model: $aX/(1 + bX)$, where a is the attack rate on resource X (either N or P) and b is a parameter taking into account physical limitations of the organisms (e.g., time required to metabolically transform a resource into new matter, satiety of the consumer).

Each ecosystem i is open to external inputs and outputs. Inorganic nutrients are supplied locally with a fixed input flow I_i. Matter can be lost from each local compartment N_i, P_i, C_i, and D_i at rates e_N, e_P, e_C, and e_D, respectively (e.g., consumption by other species [which is not considered here], sedimentation, or volatilization). Ecosystems are connected by spatial flows between homologous com-
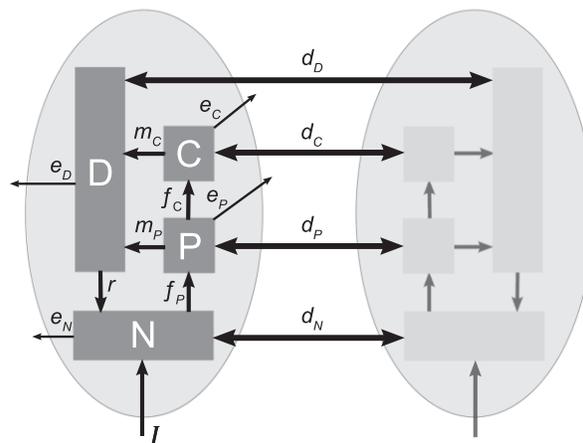
Figure 1: Metaecosystem model (adapted from Gravel et al. 2010*a*). In each of the two ecosystems, the primary producer P consumes the inorganic nutrient N and is consumed by the primary consumer C. P and C produce detritus D at respective rates m_P and m_C, mineralized into N at a rate r. The functional responses of the organisms, f_P and f_C, take a Holling type II form. N receives constant input I from the outside. Each compartment loses material at constant output rates e_N, e_P, e_C, e_D. The ecosystems are connected by spatial flows between their homologous compartments N, P, C, D, according to constant diffusion rates d_N, d_P, d_C, and d_D, respectively.

partments (fig. 1). We assume passive spatial flows, with a net movement of matter from high- to low-concentration compartments occurring at constant diffusion rates d_X for a given compartment X, with $\Delta_{X_1} = X_2 - X_1$ in ecosystem 1 and the opposite for ecosystem 2. We use input of inorganic nutrients I as a proxy for fertility (keeping e_N constant) and the diffusion rates as indicators of metaecosystem connectivity. Units are expressed in standard dimensions (mass, length, time; see table 1).

Analysis

We focused on the local stability of the metaecosystem. We analyzed the effect of fertility and diffusion rates on the real part of the dominant eigenvalue, λ_{max}, obtained numerically from equations (1) linearized at each equilibrium. We first determined the possible equilibria of the system, that is, the set of positive densities that are reached when the growth rates of all the compartments are simultaneously set to 0. We then computed the Jacobian matrix and its eigenvalues. The absolute value of the real part of the dominant eigenvalue ($|\lambda_{max}|$) is a measure of resilience (May 1974), and the equilibrium is stable when λ_{max} is negative. The analytical solutions of this system of eight equations were intractable, and we consequently used numerical analysis with a solver from R 2.10.1 (package rootSolve; Soetaert and Herman 2009) to find the equi-

Table 1: Summary of abbreviations

Symbol	Definition	Unit	Value
N, P, C, D	Densities of inorganic nutrient, producer, consumer, and detritus compartments	mass length^{-2}	...
I_i	Inorganic nutrient flow in ecosystem i	mass length^{-2} time^{-1}	...
e_N, e_P, e_C, e_D	Output rates of the different compartments	time^{-1}	.1
r	Mineralization rate	time^{-1}	.5
a_P, a_C	Producer and consumer consumption rates	time^{-1}	.5
b_P, b_C	Producer and consumer saturation rates	time^{-1}	.5
m_P, m_C	Producer and consumer mortality rates	time^{-1}	.5
d_N, d_P, d_C, d_D	Diffusion rates of the different compartments	time^{-1}	0
f_P, f_C	Functional responses of the producer and the consumer	time^{-1}	...
ΔI	Environmental heterogeneity ($\Delta I = I_1 - I_2$)	...	...
λ_{max}	Real part of dominant eigenvalue of Jacobian matrix	...	...

libria. To get an overview of the system behavior, we plotted the stability isocline ($\lambda_{max} = 0$) for a given parameter space (for more details, see app. A; apps. A–D available online).

As a preliminary analysis, we first studied the stability of a local ecosystem without spatial flows ($d_N = d_P = d_C = d_D = 0$). The effects of the 12 parameters on stability were consistent with the principle of energy flux (app. A). To address our questions, we then restricted our analysis of the metaecosystem stability to changes of fertility and diffusion rates, keeping the same set of values for other parameters (see table 1). We characterized the effect of each spatial flow independently (either N, P, C, or D) and in combination on the critical fertility level inducing destabilization. These scenarios of connectivity represent extreme cases where spatial flows can be either strongly unbalanced or equivalent. The spatial flows may be unbalanced if the factors involved in diffusion rates act differently on the different compartments. For instance, the intensity of mixing between pelagic and benthic areas may differ according to the specific density of the compartment components (Herbert 1999). Moreover, the one-flow scenarios enabled us to characterize the particular effects resulting from the diffusion of each ecosystem compartment. We explored a range of diffusion rates from low to high compared with the rate of local dynamics. We started with the simplest case of a homogeneous enrichment and then introduced spatial heterogeneity of the enrichment, ΔI, defined as the difference between local fertilities ($\Delta I = I_1 - I_2$). We present here the case for $\Delta I = 0$ (e.g., atmospheric deposition over all ecosystems; Carpenter et al. 1998; Krupa 2003; Greaver et al. 2012) and for $\Delta I = 0.5$ (e.g., localized enrichment of a lake in a watershed; Fisher et al. 2000; Carpenter 2005). We kept ΔI constant while varying the regional fertility of the metaecosystem (($I_1 + I_2$)/2) to separate the effects of heterogeneity from those of enrichment. We expected environ-

mental heterogeneity to influence metaecosystem stability through source-sink dynamics (Gravel et al. 2010a).

Results

We first analyzed the effect of a single spatial flow (d_N, d_P, d_C, or d_D) while setting the others to 0 (fig. 2). In a homogeneous environment (i.e., ecosystems with similar local fertilities; $I_1 = I_2$), we found that ecosystems are less robust to enrichment when they are connected by spatial flows of detritus or nutrient, than isolated ecosystems (fig. 2A, 2B, dashed lines). In contrast, spatial flows of producers and consumers do not impact ecosystem stability (fig. 2C, 2D, dashed lines).

Spatial heterogeneity of fertility ($I_1 \neq I_2$) destabilizes at low diffusion rates and stabilizes at high diffusion rates (fig. 2, solid and dashed lines), except with detritus spatial flows (fig. 2B). Under high diffusion rates, we observed the same destabilizing effect of nutrient spatial flows and no effect of producer spatial flows, as found for homogeneous metaecosystems. Interestingly, high consumer spatial flows seem to produce an additional stabilizing effect in heterogeneous metaecosystems.

The metaecosystem is overall more stable at low diffusion rates when all compartments are diffusing compared with single spatial flows (figs. 2, 3, solid lines). However, in contrast to single spatial flows, heterogeneity does not have a stabilizing effect at high diffusion rates. Isoclines of homogeneous and heterogeneous metaecosystems converge to the same fertility threshold observed in isolated ecosystems (fig. 3).

We found that consumer diffusion can generate multiple equilibria when intermediate diffusion rates are combined with high values of regional fertility (fig. 4). In a homogeneous metaecosystem, we found up to three nontrivial equilibria, corresponding to two very different biomass distributions. The first one is the most intuitive: the two
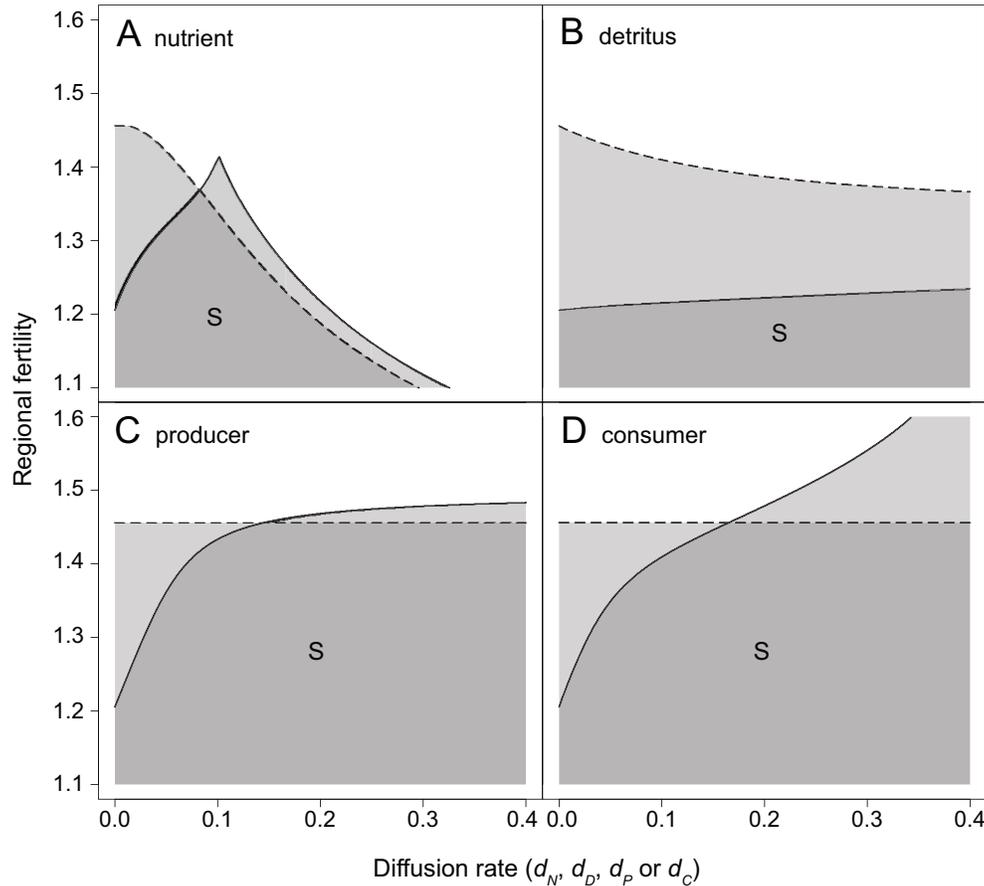
Figure 2: Stability with a single spatial flow. Each panel represents the stability isoclines under changes of one diffusion rate (the others set to 0)—either d_N, d_D, d_P, or d_C for *A–D*, respectively—versus regional fertility of the metaecosystem $((I_1 + I_2)/2)$. The stability isoclines are the pairs of parameter values for which λ_{max} equals 0 either in a homogeneous metaecosystem with $\Delta I = 0$ (dashed lines) or in a heterogeneous metaecosystem with $\Delta I = 0.5$ (solid lines). Stability isoclines delimit the gray parameter space (*S*) where λ_{max} is negative, and thereby the equilibrium is stable. For symbols and other parameter values, see table 1. For details regarding *B*, see figure B3, available online.

ecosystems are symmetric (i.e., with identical densities), and dynamics oscillate in complete phase synchrony (fig. 4*C*, 4*E*). The second is an asymmetric source-sink structure (fig. 4*D*, 4*F*), which can be a stable point for intermediate consumer diffusion rates (fig. 4*A* [orange area, Mix.], 4*B* [orange line]). An initial perturbation allows the producer of one of the two ecosystems to exploit its abundant resource. This ecosystem produces numerous consumers and therefore becomes a realized source (sensu Gravel et al. 2010*a*), which means here a net exporter. The consumers are exported to the second ecosystem, where they prevent the growth of the producer despite abundant inorganic resources. Subsequently, the organic matter brought by the consumers is mainly stored in the nutrient compartment of the second ecosystem, which becomes a realized sink (a net importer). This results in a stabilizing spatial asymmetry in ecosystem control (top-down vs. bottom-up controlled ecosystems). Hence, consumer spatial flows allow a regional stabilization for a set of intermediate diffusion rates, even when enrichment reaches high levels. This area of possible stabilization expands with the heterogeneity of enrichment distribution, because asymmetry in fertility induces source-sink dynamics that facilitates the set up of asymmetry in ecosystem control (fig. B1).

Discussion

The metaecosystem framework makes three new predictions regarding the stability of ecosystems under enrichment. First, the nature of the compartment diffusing between ecosystems determines whether diffusion enhances enrichment-induced instabilities. Spatial flows of nonliv-
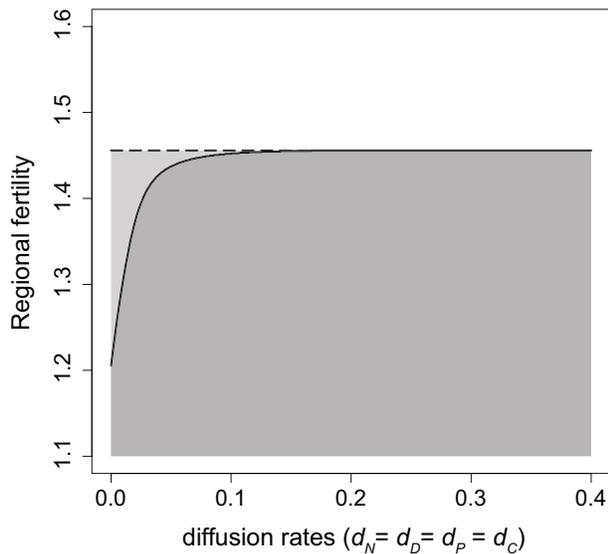
Figure 3: Multiple spatial flows. Stability isoclines (for definition, see fig. 2) under increasing diffusion rates for all compartments versus metaecosystem regional fertility (($I_1 + I_2$)/2). Stability isoclines delimit the gray area where the equilibrium is stable for homogeneous (dashed lines; $\Delta I = 0$) and heterogeneous (solid lines; $\Delta I = 0.5$) metaecosystems. For other parameter values, see table 1.

ing compartments (nutrients or detritus) are destabilizing, whereas spatial flows of living compartments (producer or consumer) are either neutral or stabilizing. Second, spatial heterogeneity in supply rates is no longer stabilizing in well-connected ecosystems and can even be destabilizing when diffusion is restricted to detritus. Third, intermediate spatial flows of consumers can switch dynamics from oscillating to stable even under high enrichment. We discuss the underlying mechanisms driving these three predictions, the robustness of our results, and future directions.

Living versus Nonliving Spatial Flows

We found neutral versus negative effects on stability of living versus nonliving spatial flows, respectively. We attribute this difference to their opposite effect on spatial synchrony (covariation between time series; Liebhold et al. 2004). Indeed, spatial flows of living organisms lead to in-phase synchrony (positive covariation), whereas spatial flows of nonliving matter lead to asynchrony (for examples, see fig. B2). Spatial synchrony usually has negative effects on ecosystem stability by increasing the global extinction risk or reducing the effect of dispersal (Earn et al. 2000). In homogeneous metaecosystems, we observe perfect in-phase synchrony even for very low diffusion rates of living compartments (phase locking; Jansen 1999; Goldwyn and Hastings 2008), which cancels any potential

stabilization via source-sink dynamics (Vogwill et al. 2009). However, if heterogeneity prevents perfect synchrony, diffusion can synchronize the dynamics while they are stabilized by other mechanisms (e.g., Abbott 2011). In contrast, spatial flows of nonliving compartments (inorganic nutrients and detritus) promote asynchrony and thereby sustain enrichment-induced instabilities in each ecosystem alternatively. Spatial asynchrony makes regional densities less variable (de Roos et al. 1991; Wilson et al. 1993; Briggs and Hoopes 2004) but accentuates parallel local instabilities (Maser et al. 2007). We also observed this destabilization, as have other recent metaecosystem studies (Marleau et al. 2010; Suzuki and Yoshida 2012) and tritrophic connected systems (Koelle and Vandermeer 2005). This asynchrony stems from the restriction of diffusion to basal resources, which boiled the system down to oscillators coupled by resource competition (Vandermeer 2004).

In addition to being consistent with previous synchrony-stability studies, our analysis highlights the link between spatial synchrony and the diffusion of the different compartments of ecosystems. What matters is whether the compartment is donor or recipient controlled. If the compartment actively consumes a resource, diffusion of this compartment will be fundamentally homogenizing. The consumption activity buffers the spatial differences of resource densities, while diffusion buffers spatial differences of consuming species densities. This crucial role of consumption for the process of homogenization and spatial synchrony has also been reported in an experimental algal-rotifer metacommunity (Vasseur and Fox 2009). In contrast, spatial flows of inert matter (detritus or inorganic nutrients) will increase spatial differences in densities of all compartments by fueling both resource and growth of organisms in one ecosystem at the expense of the other. Hence, it desynchronizes the dynamics and produces punctual overproduction in each ecosystem.

We noticed also a much weaker destabilization with detritus than with nutrient diffusion. The delay of mineralization that transforms detritus into available resource lessens the impact of detritus diffusion on regional stability. Detritus act as a storage compartment whose inertia temporarily removes matter from the enrichment destabilization process. Parameters favoring the accumulation of detritus (e.g., low recycling, high mortality rates) are therefore stabilizing (fig. B3). The effect of detritus diffusion on stability saturates quickly because recycling constitutes a bottleneck for the energy flux into the system. This suggests that even if detritus spatial flows constitute substantial subsidies to some webs (Shen et al. 2011), their increased transfer between ecosystems (e.g., with storms) should not have a strong impact on stability. Note that this result probably does not hold for detritivorous-based metaecosystems, where organisms feeding on detritus by-
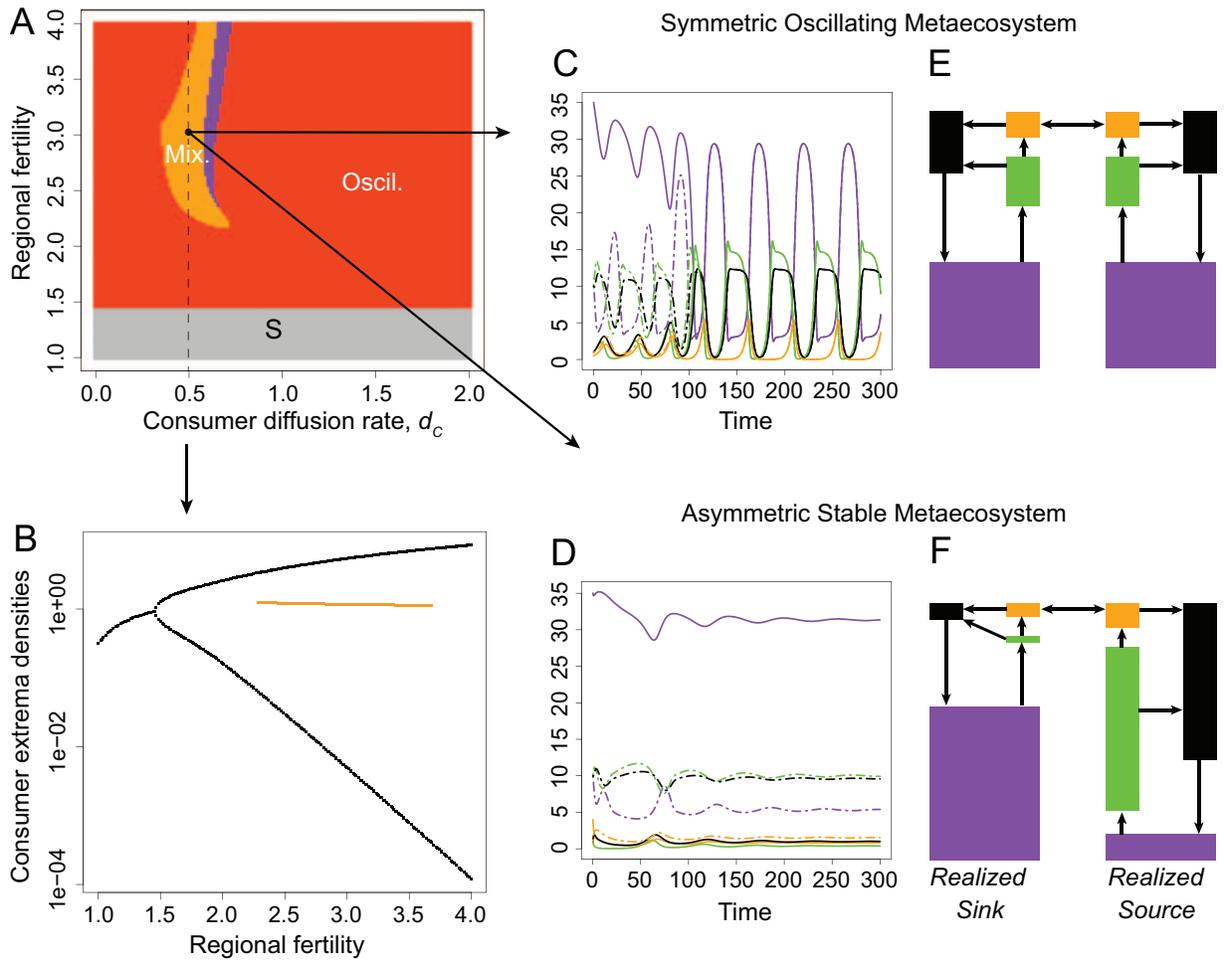
Figure 4: Multiple equilibria with intermediate consumer diffusion rates and high enrichment levels in homogeneous metaecosystems. *A*, Areas of stability for an extended parameter space with regard to figure 2*D* (d_C ranges from 0 to 2 and regional fertility from 1 to 4) for the homogeneous case, with $\Delta I = 0$ (for the heterogeneous case, see app. C, available online). Gray area (*S*), stable equilibria ($\lambda_{max} < 0$). Red area (Oscil.), unstable equilibria ($\lambda_{max} > 0$). Orange and purple areas have multiple equilibria, either all unstable (purple area) or one unstable and two stable (Mix.; orange area). *B*, Bifurcation diagram of consumer extreme densities (spatial average) according to regional fertility for the consumer diffusion rate $d_C = 0.5$ (dashed line in *A*). The orange equilibria are stable (maximum = minimum), the black unstable. *C–F* illustrate the two equilibria types for the pair of parameters ($d_C = 0.5$, regional fertility = 3). *C* and *D* show the dynamics of all the compartments. *E* and *F* show the relative densities of the different compartments (heights are proportional to the temporal mean density at equilibrium). Between the two cases, initial densities vary only for the consumer of ecosystem 2: $C_2 = 0.5$ (*C*, *E*); $C_2 = 4$ (*D*, *F*). For symbols and other parameter values, see table 1.

pass the bottleneck of recycling, changing the storage status of detritus (Edwards 2001; Cross et al. 2006).

Nonstabilizing Heterogeneity

With only one compartment diffusing between ecosystems (fig. 2), heterogeneity of enrichment is destabilizing at low diffusion and stabilizing at high diffusion, such as in metacommunities (Hauzy et al. 2013). At low diffusion, the oscillations of the most fertile ecosystem are spread to the stable less fertile one, such as environmental noise (Pog-

giale et al. 2008). Past a certain intensity of diffusion, heterogeneous metaecosystems are more resistant to enrichment than homogeneous ones (fig. 2*A*, 2*C*, 2*D*). The stabilizing effect of heterogeneity emerges from the nonlinearity of species dynamics. Spatial heterogeneity reduces the regional productivity because of inefficient consumption by the producer in the most fertile patch (fig. B4). This mechanism, originating from the saturating functional response, belongs to what was previously reported as nonlinear averaging (sensu Briggs and Hoopes 2004; Nisbet et al. 1998; Hauzy et al. 2013). The more saturating

the producer functional response, the larger the stabilization (app. C).

What novel insight our metaecosystem framework adds is that this positive effect of heterogeneity can be decreased or even canceled by diffusion (fig. 3). When all compartments are diffusing, source-sink dynamics can be so strong that even inorganic nutrient availability is homogenized, despite the fixed differences of external inputs between ecosystems. Subsequently, heterogeneity and its stabilizing property disappear. As a side effect, homogenization increases the regional productivity. These effects of homogenization cannot be expressed in metacommunities where heterogeneity in fertility is modeled by carrying capacities (Hauzy et al. 2013), because the stabilizing effect of heterogeneity is independent from diffusion. Similarly, stabilization can be maintained in our metaecosystem if we add spatial heterogeneity in demographic parameters independent from nutrient supply (app. C). The explicit representation of nutrient dynamics in metaecosystems reveals that heterogeneity in fertility has to be associated with restricted diffusion (single spatial flows) to produce a stabilizing effect. In addition, if only detritus diffuses, the regional redistribution of the enrichment via source-sink dynamics might be so weak that heterogeneity is destabilizing, whatever the diffusion rate (fig. 2D; fig. B3). Spatial flows of detritus have neither the homogenizing properties of organisms that actively consume their resource nor the stabilizing efficiency of nutrient flows, which directly redistribute excess enrichment (because of the time needed for mineralization). Hence, exportation of detritus is unlikely to dampen the oscillations generated by a local enrichment.

Consumer Spatial Flows and the Nutrient Storage Mechanism

Intermediate consumer spatial flows can stabilize the metaecosystem (figs. 2D, 4; fig. B1). Above a threshold rate, consumer emigration relaxes enrichment-induced instability in the most fertile ecosystem. At the same time, heterogeneity maintains asynchrony such that immigration becomes negatively correlated with consumer density in the less fertile ecosystem, which limits the overcompensation inducing oscillations (app. D). This indirect negative density dependence is one of the main mechanisms invoked to explain the stabilizing effect of dispersal (Briggs and Hoopes 2004; Goldwin and Hastings 2009; Howeth and Leibold 2013). When fixed spatial differences maintain asynchrony, immigration can be negatively correlated with local per capita growth rate, reducing the amplitude of oscillations (De Roos et al. 1998; Jansen 2001; Neubert et al. 2002).

Asynchrony—and subsequent stabilizing negative den-

sity dependence—can also occur in homogeneous systems. Intermediate consumer diffusion rates can lead to two different types of equilibria (fig. 4): a symmetric unstable one and another more stable one, which displays asynchronous dynamics and spatial asymmetry between equilibrium densities. In homogeneous metacommunities, this equilibrium displays higher minimal densities than in isolated systems, and the amplitude of oscillations is insensitive to enrichment (Jansen 1995, 2001; Hauzy et al. 2010a). Stabilization can emerge from adaptive movements of the consumer (Abrams and Ruokolainen 2011; Ruokolainen et al. 2011). Here we show that asymmetric equilibrium can be stable even with random movements in metaecosystems, through the storage of the extra nutrient input in inorganic form. Diffusion makes one ecosystem become a source of consumers, while in the other, the strong top-down control of immigrate consumers prevents the producer from using its resource. This ecosystem becomes a sink (Loreau et al. 2012). For intermediate consumer diffusion rates, the sink ecosystem stores a sufficient part of the enrichment in inorganic form to stabilize the metaecosystem, without increasing the consumer density in the sink such that the spatial flow direction would reverse and the asymmetric structure be canceled. In this way, the consumer spatial flows limit in the metaecosystem the two drivers of destabilization: overproduction in a top-down controlled sink and overcompensation in a bottom-up controlled source. Hence, both stability and spatial heterogeneity in the distribution of resources can emerge from random movements of consumers when accounting explicitly for nutrient dynamics.

The spatial asymmetry in biomass distribution is analogous to the coupling of fast and slow energy channels by consumers reported for various systems (Rooney et al. 2006), such as link between pelagic and benthic areas of lakes by fishes (Schindler and Scheuerell 2002), connected lakes (Griffiths et al. 2013), or soil food webs (Moore et al. 2004). The two channels display differences in productivities due to traits of organisms (Abrams et al. 2012) or environmental variations (e.g., gradients in the water column; Morozov et al. 2011), which can produce asynchronous dynamics. The stability results from the rapid foraging of the predator shifting between two energy channels (Rooney et al. 2006) or from the preference of the consumer for the slow energy channel (Blanchard et al. 2010). We demonstrate that such asymmetric coupled channels can potentially emerge from the consumer movements themselves and induce a stabilizing spatial heterogeneity in top-down regulation. Hence, we hypothesize that if spatially structured ecosystems, like connected lakes, experience homogeneous enrichment (e.g., atmospheric deposition; Greaver et al. 2012) such that algae-grazer dynamics should be destabilized, initial differences might

make dynamics more stable through grazer movements between ecosystems. This mechanism could apply as well to other patchy aquatic habitats, such as the Everglades, where phosphorus is currently massively released through the cutting of trees on islands (Wetzel et al. 2009).

Robustness of the Results

The effects of diffusion on the stability of enriched ecosystems described here rely on fundamental mechanisms related to synchronization, nonlinear averaging, source-sink dynamics, and top-down control. The stability boundary we find varies quantitatively with parameter values, but the qualitative effects of diffusion are robust to any change that would not turn off or counteract the underlying mechanisms. As an example, heterogeneity-induced stabilization can disappear if the functional response of the producer is more linear because the effect of nonlinear averaging will be lost (app. C). In contrast, stability can be maintained despite enrichment homogenization through multiple spatial flows if heterogeneity in demographic parameters has an opposite effect on ecosystem productivity than heterogeneity in fertility, because it will induce a nonlinear averaging mechanism resistant to diffusion homogenization (app. C). Finally, the importance of the different mechanisms described depends on the metaecosystem connectivity and the spatial variation of demographic parameters. This shapes the stability of the enriched ecosystems.

Future Directions

The study of our very simple model lays foundations to understand the effects of diffusion of the main ecosystem compartments on the stability of ecosystems under enrichment. The results suggest a more moderate role of heterogeneity as a stabilizing factor than previously reported in metacommunities and stress the importance of metaecosystem configuration (defined as the number, nature, and relative intensity of the flows)—rather than the net amount of spatial flows between ecosystems—as a predictor of stability. Further research should develop the metaecosystem theory to fully integrate such topological properties to insure complex ecosystems against the consequences of the so-called paradox of enrichment.

Our model with random dispersal better fits simple aquatic webs than, for instance, terrestrial webs. Further research should investigate more complex webs and other dispersal strategies (Amarasekare 2007), which are more relevant for terrestrial ecosystems. Next important steps include the integration in metaecosystems of (1) nonrandom dispersal of organisms, since foraging behavior could modify the spatial redistribution of resources (Abbas et al. 2012; Wolf et al. 2013), and (2) more complex scenarios

of detritus pathways. Detritus is considered here only as a delayed resource in a purely autotroph-based web. However, plants or scavengers can also directly use dead organic matter (Wilson and Wolkovich 2011). In addition, generalist consumers commonly feed on both autotroph and detritivorous webs where detritus constitute the basal resource (e.g., Davic and Welsh 2004). This might increase in complex ways the effects of detritus spatial flows on productivity (Attayde and Ripa 2008) and thereby on enrichment-induced instabilities.

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