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Nutrient flows between ecosystems can destabilize simple food chains

Justin N. Marleau [a],*, Frédéric Guichard [a], François Mallard [b], Michel Loreau [a]

[a] *Department of Biology, McGill University, 1205 ave Docteur Penfield, Montréal, Québec, Canada H3A 1B1*
[b] *École Normale Supérieure, 45 rue d'Ulm, Paris 75005, France*

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ABSTRACT

Dispersal of organisms has large effects on the dynamics and stability of populations and communities. However, current metacommunity theory largely ignores how the flows of limiting nutrients across ecosystems can influence communities. We studied a meta-ecosystem model where two autotroph–consumer communities are spatially coupled through the diffusion of the limiting nutrient. We analyzed regional and local stability, as well as spatial and temporal synchrony to elucidate the impacts of nutrient recycling and diffusion on trophic dynamics. We show that nutrient diffusion is capable of inducing asynchronous local destabilization of biotic compartments through a diffusion-induced spatiotemporal bifurcation. Nutrient recycling interacts with nutrient diffusion and influences the susceptibility of the meta-ecosystem to diffusion-induced instabilities. This interaction between nutrient recycling and transport is further shown to depend on ecosystem enrichment. It more generally emphasizes the importance of meta-ecosystem theory for predicting species persistence and distribution in managed ecosystems.

1. Introduction

Our mechanistic understanding of communities has benefited from the integration of species interactions with the study of dynamical coupling between nutrients and species (Lotka, 1956; Tilman, 1980; Andersen et al., 2004; Sterner and Elser, 2002) and with spatially structured local communities (Levin, 1992; Wilson, 1992; Tilman and Kareiva, 1997; Leibold et al., 2004; Van de Koppel et al., 2005). Surprisingly, there is a paucity of theoretical studies on how the spatial structure of ecosystems interacts with nutrient fluxes and recycling to influence community dynamics. Here, we address the current lack of integration across scales between spatial fluxes of nutrient and local trophic dynamics controlled by species interactions and recycling processes. By using the framework outlined by Loreau et al. (2003), we investigate the stability and synchrony of two coupled ecosystems (a meta-ecosystem) to elucidate the importance of interactions between nutrient recycling and diffusion on community stability and spatiotemporal heterogeneity.

The study of spatial subdivisions among communities and of limited dispersal by organisms has led to a diversity of theoretical results. For example, it has been emphasized that dispersal can stabilize the dynamics of regional communities by rescue effects, non-linear spatial averaging and statistical stabilization (Briggs and Hoopes, 2004). However, dispersal can destabilize local steady states and spatially homogeneous solutions, though the resulting dynamics may be more stable regionally through asynchronous regional dynamics (Segel and Jackson, 1972; Okubo, 1980; Jansen, 1995; Ermentrout and Lewis, 1997; Rohani and Ruxton, 1999; Jansen, 2001). The synchronization or lack thereof due to dispersal is dependent on which biotic compartment is dispersing (Vandermeer, 2004; Koelle and Vandermeer, 2005).

The application of this body of non-equilibrium theory ranges from the creation of marine and terrestrial reserves (Carr et al., 2003; Guichard et al., 2004; Hughes et al., 2005) to the community assembly and habitat selection of beetles (Resetarits et al., 2004). Equilibrium theories of metapopulations and metacommunities have already motivated managers to create wildlife corridors to link disparate communities and may help reduce local extinctions (Chetkiewicz et al., 2006). However, these theories are limited by their implicit considerations of ecosystem processes, which are vitally important to the structure and dynamics of communities (e.g. Tilman, 1980). One such ecosystem process is the cycling of nutrients within ecosystems (Vitousek, 2004).

The importance of nutrient cycling for community dynamics has been studied in both theoretical and empirical studies (DeAngelis, 1992). In well-mixed and closed model food chains, recycling of a single limiting nutrient has no distinct role and dynamics is equivalent to the simpler open consumer–resource model (Gurney and Nisbet, 1998). In contrast, spatial flows of nutrients have large impacts on primary productivity and a variety of community measures, though most of the results have been derived from empirical studies (Romme and Knight, 1982; Peterjohn and Correll, 1984; Polis et al., 1997; Pace et al., 1998, 2004;

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* Corresponding author. Tel.: +1 514 398 6697; fax: +1 514 398 5069.
E-mail addresses: justin.marleau@mail.mcgill.ca (J.N. Marleau), fred.guichard@mcgill.ca (F. Guichard), francois.mallard@ens.fr (F. Mallard), michel.loreau@mcgill.ca (M. Loreau).

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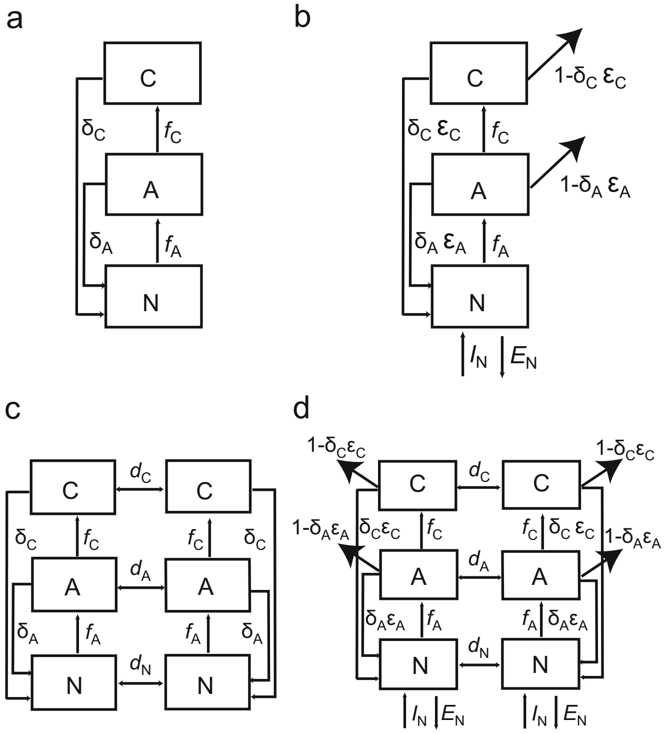

Fig. 1. A diagram describing the various sub-models of the nutrient-explicit meta-ecosystem model. Symbols are those used in the equations: consumer and autotroph abundance (C,A), nutrient concentration (N), consumer and autotroph consumption (f_C, f_A), autotroph and consumer mortality rate (δ_A, δ_C), recycling coefficients (ε_A, ε_C), coefficients of diffusion (d_N, d_A, d_C) and inputs and outputs of nutrients (I_N, E_N): (a) Well-mixed, closed, (b) Well-mixed, open, (c) meta-ecosystem, closed and (d) meta-ecosystem, open.

but see Leroux and Loreau, 2008). The few theoretical studies that have dealt with explicit spatial flows of nutrients have reported both stabilizing and destabilizing effects of nutrient diffusion (Sjoberg, 1977; Okubo, 1978) and emphasized the lack of a general understanding of recycling in spatially structured ecosystems. Here we explore the importance of recycling for trophic dynamics with spatial structure through the existence of feedbacks between local nutrient recycling and diffusive transport among communities.

We first present a simple model based upon the meta-ecosystem framework proposed by Loreau et al. (2003) in order to investigate the importance of nutrient recycling and nutrient diffusion on community dynamics. The general model is two coupled nutrient–autotroph–consumer ecosystems with explicit recycling. We then explore four general scenarios of spatial structure and nutrient fluxes: (1) well-mixed, closed ecosystem, (2) well-mixed, open ecosystem, (3) closed meta-ecosystem, and (4) open meta-ecosystem (Fig. 1). Each scenario is then subjected to analytical and numerical stability analysis to understand the impacts of nutrient flows on ecosystem dynamics and stability. Our results reveal the relative importance of nutrient recycling for the onset of diffusion-driven instability and asynchrony of population fluctuations. The results can be extended to coupled tritrophic food chains and provide a starting point for the integration of ecosystem processes into dynamical theories of metacommunities.

2. Materials and methods

2.1. Presentation and assumptions of model

Table 1
Parameters and variables of the model.

Parameters and variables	Definitions and units
Parameters	
α	Maximum uptake rate (1/time)
β	Half-saturation constant (mol nutrient)
δ	Mortality rate constant (1/time)
ε	Portion of nutrients from mortality recycled
d	Diffusion rate constant (1/time)
I_N	Inputs of nutrients into the ecosystem (mol nutrient/time)
E_N	Outputs of nutrients from the ecosystem (1/time)
Variables	
N	Diffuse limiting nutrients (mol nutrient)
A	Nutrient stock of autotrophs (mol nutrient)
C	Nutrient stock of consumers (mol nutrient)

In our study, we focus on a simple ecological model of two coupled ecosystems. In this model, we concern ourselves with the levels of a limiting nutrient (N) in the medium and the amount of this nutrient bound in the two trophic levels explicitly modeled here, autotrophs (A) and consumers (C) (Fig. 1). Nutrient in the biota can be returned to the available pool of nutrient by means of recycling. The general equations describing dynamics in ecosystem i connected to ecosystem j are

$$\begin{aligned}
\frac{dN_i}{dt} &= I_N - E_N N_i + \varepsilon_A\delta_A A_i + \varepsilon_C\delta_C C_i - f_A(N_i)A_i + d_N(N_j - N_i)\\
\frac{dA_i}{dt} &= f_A(N_i)A_i - \delta_A A_i - f_C(A_i)C_i + d_A(A_j - A_i)\\
\frac{dC_i}{dt} &= f_C(A_i)C_i - \delta_C C_i + d_C(C_j - C_i)\\
f_A(N_i) &= \frac{\alpha_A N_i}{\beta_A + N_i}\\
f_C(A_i) &= \frac{\alpha_C A_i}{\beta_C + A_i}\\
i,j &\in [1,2], i \neq j
\end{aligned} \tag{1}$$

where ε_C, ε_A are the proportions of nutrients recycled upon mortality, d_N, d_A, d_C are coefficients of diffusion between ecosystems, δ_A, δ_C are the mortality rates, I_N, E_N are external inputs and loss rates of nutrient, respectively, and f_A, f_C are the functional responses of each trophic level (A and C) to its resource (Table 1). Our meta-ecosystem model is similar to the one proposed by Loreau and Holt (2004), but allows for partial recycling and can be extended to multiple local ecosystems. Our model also prevents external inputs and outputs to and from the biotic compartments.

We use our model to control for openness of the meta-ecosystem and for connectivity between ecosystems. Each local ecosystem can be open or closed and can be unconnected or connected. The openness of a meta-ecosystem is determined by the values of I_N, E_N, ε_C and ε_A while the connectivity is determined by the values of d_N, d_A and d_C. We therefore investigate four types of meta-ecosystems with respect to openness and connectivity: closed and well-mixed, closed meta-ecosystem, open and well-mixed, and open meta-ecosystem (Fig. 1 and Table 2). For the open and well-mixed meta-ecosystem (Fig. 1b), the equations governing the dynamics are

$$\begin{aligned}
\frac{dN}{dt} &= I_N - E_N N + \varepsilon_A\delta_A A + \varepsilon_C\delta_C C - f_A(N)A\\
\frac{dA}{dt} &= f_A(N)A - f_C(A)C - \delta_A A\\
\frac{dC}{dt} &= f_C(A)C - \delta_C C
\end{aligned} \tag{2}$$

Table 2
Parameter values that define the model studied.

System Under Consideration	Parameter Space
Well-mixed, Closed	$I_N=0$, $E_N=0$, $d_N=0$, $d_A=0$, $d_C=0$, $\varepsilon_C=1$, $\varepsilon_A=1$
Meta-ecosystem, Closed	$I_N=0$, $E_N=0$, $d_N>0$, $d_A\geq 0$, $d_C\geq 0$, $\varepsilon_C=1$, $\varepsilon_A=1$
Well-mixed, Open	$I_N>0$, $E_N\geq 0$, $d_N=0$, $d_A=0$, $d_C=0$, $\varepsilon_C\geq 0$, $\varepsilon_A\geq 0$
Meta-ecosystem, Open	$I_N>0$, $E_N\geq 0$, $d_N>0$, $d_A\geq 0$, $d_C\geq 0$, $\varepsilon_C\geq 0$, $\varepsilon_A\geq 0$

When the well-mixed ecosystem is closed to external inputs and outputs of nutrients (Fig. 1a), the system of differential equations reduces from three to two

$$\begin{aligned} \frac{dA}{dt} &= f_A(S-A-C)-f_c(A)C-\delta_A A \\ \frac{dC}{dt} &= f_c(A)C-\delta_C C \\ S &= N+A+C = \text{constant} \end{aligned} \tag{2a}$$

where S is the total amount of nutrients in the ecosystem.

In order to simplify our analysis, we assume instant recycling of nutrients lost from the biotic compartments and symmetric diffusion between discrete patches. Furthermore, we parameterize our model to achieve fixed point equilibrium under well-mixed conditions, though many of our results apply to parameter regimes that give rise to limit cycles under well-mixed conditions (Supplementary Information). These simplifications allowed us to use analytical tools that would not be available otherwise.

2.2. Focus and biological relevance of model

For the purpose of this study, we limit the scope of our general model in order to accentuate the effects of nutrient diffusion and recycling on biotic communities. To do so, we do not allow the movement of autotrophs and of consumers between ecosystems for the limited model (i.e. $d_A=d_C=0$). We justify such a focus by the fact that the effects of movement of organisms between ecosystems have been extensively studied (e.g. Briggs and Hoopes, 2004), yet the movement of nutrients between ecosystems is rarely modeled. Still, we did examine the robustness of our results to non-zero values for d_A and d_C, with preliminary results suggesting that the dispersal rate of organisms needs to be small compared to the diffusion of nutrients for nutrient-diffusion instabilities to occur (results not shown).

While our general and our limited model (i.e. $d_A=d_C=0$) are highly abstracted, both can be applied to real-world ecosystems. For example, the similarities between our general model and nutrient–phytoplankton–zooplankton (NPZ) models suggest that our model should be applicable to oceanic plankton communities (Franks, 2002). For our limited model, we suggest Lake Tanganyika as an example of a meta-ecosystem where the movement of nutrients between ecosystems occurs frequently but the movement of organisms is rare.

Lake Tanganyika is nearly closed concerning flows of nutrients and is dependent on biological nutrient recycling for high levels of primary productivity (Kilham and Kilham, 1990; Langenberg et al., 2003). The shoreline of the lake is divided into rocky and sandy areas of various lengths (e.g. Wagner and McCune, 2009). A major group of autotrophs in the rocky areas is periphyton that is dependent on the substrate for their growth (McIntyre et al., (2008)). A number of herbivorous cichlid species specialize on the periphyton and the cichlids rarely go over the sandy areas to reach other rocky areas (Wagner and McCune, 2009; P. McIntyre, pers. comm.). Therefore, both the autotrophs and their consumers suffer from barriers to their potential dispersal between ecosystems, while nutrients can easily mix. The degree of the mixing can then be described using d_N parameter of the model, with d_N approaching infinity being a perfectly well-mixed lake in terms of nutrients.

2.3. Analysis

For the well-mixed ecosystems, we determine the stability conditions of the possible equilibria using linear stability analysis. We also use the dominant eigenvalue of the Jacobian matrix (Eq. C.1) to determine the resilience of our well-mixed ecosystem, where resilience is the return speed to the original ecosystem state (Loreau et al., (2002)). We complement our analytical results with numerical simulations to illustrate our model's behavior.

For the meta-ecosystems, both ecosystems have identical parameter values and we use parameter values that guarantee a stable equilibrium in each ecosystem when there is no nutrient diffusion. The equilibrium that both ecosystems achieve is called a spatially homogeneous (flat) solution and we analyze its linear stability using the analytical techniques developed by Jansen and Lloyd (2000). To determine the linear stability of the flat solution, one must determine the eigenvalues of a series of k matrices, $\mathbf{V}(k)$, and all the eigenvalues of each matrix $\mathbf{V}(k)$ must have negative real parts for the spatially homogeneous solution to be stable. The formula for each $\mathbf{V}(k)$ matrix is

$$\mathbf{V}(k) = \mathbf{J} + \lambda_k \mathbf{M} \tag{3}$$

where $\mathbf{J}$ is the Jacobian matrix of the well-mixed ecosystem evaluated at the flat solution, $\mathbf{M}$ is the 'migration' or diffusion coefficient matrix and λ_k are the eigenvalues of the connectivity matrix $\mathbf{C}$, which describes the spatial arrangement of the ecosystems. For our study, $\mathbf{M}$, $\mathbf{C}$ and λ_k are

$$\mathbf{M} = \begin{pmatrix} d_N & 0 & 0 \\ 0 & d_A & 0 \\ 0 & 0 & d_C \end{pmatrix}, \quad \mathbf{C} = \begin{pmatrix} -1 & 1 \\ 1 & -1 \end{pmatrix}, \quad \lambda_1 = 0, \ \lambda_2 = -2 \tag{4}$$

The flat solution can also be a limit cycle or a chaotic attractor, but we only investigated the stability of limit cycles numerically (Supplementary Information).

To further understand our model beyond the stability analyses, we utilize numerical simulations and statistical methods. The dynamical regimes and the regional stability of meta-ecosystems are examined by bifurcation plots (local extrema of time series) and recording the minimum abundance of all trophic levels as we vary d_N. We use covariance to measure spatial synchrony between ecosystems (N_1–N_2, A_1–A_2 and C_1–C_2), as correlation cannot be used when the dynamical regime is a stable equilibrium (i.e. no variance). Covariance is also used to quantify net coupling between net autotroph growth and both nutrient diffusion and recycling, in relation to diffusion rate d_N.

Autotroph growth is key to the meta-ecosystem effect studied here because it directly depends on both nutrient recycling and diffusion. Its coupling can be predicted from direct feedbacks imposed within our model (Eq. (1)): local net autotroph growth increases with local nutrient load ($I_N - E_N N_1 + \varepsilon_A \delta_A A_1 + \varepsilon_C \delta_C C_1$) and in turn directly contributes to the nutrient gradient ($d_N(N_2 - N_1)$) that drives its diffusion into the local ecosystem. In contrast, recycling rate increases with both net consumer growth and net autotroph growth, but consumer growth negatively impacts net autotroph growth. The direct feedbacks mean that under oscillating dynamics, autotroph growth is predicted to co-vary positively with nutrient diffusion and could co-vary positively or negatively with recycling. Covariance is used to study the net effect of these feedbacks on meta-ecosystem dynamics.

All numerical simulations were run on Matlab (MathWorks) for 5000 time steps, and the first 2500 time steps were discarded as transient prior to analysis, except when analyzing short-term responses to perturbations.

3. Results

3.1. *Properties of well-mixed meta-ecosystems*

The behavior of the closed, well-mixed ecosystem (Eq. (2a)) is nearly identical to that proposed by Gurney and Nisbet (1998). Parameter values allow for the existence of one autotroph–consumer fixed point, one autotroph-only fixed point, one nutrients-only fixed point and a limit cycle with autotrophs and consumers coexisting (Appendix A). The model's behavior closely resembles that of the Rosenzweig–MacArthur predator–prey model and lead Gurney and Nisbet (1998) to conclude that an explicit nutrient compartment could be replaced by a carrying capacity for the autotrophs for a closed ecosystem. The validity of this conclusion is shown to not hold when space is considered, as seen below.

For the well-mixed, open ecosystem (Fig. 1b), we investigated how differing sources of ecosystem enrichment (nutrient recycling and external nutrient inputs) effect ecosystem resilience. We controlled total nutrient stock of the ecosystem at equilibrium (S^*, which is equal to $N^*+A^*+C^*$) by fixing recycling levels (ε_C, ε_N) and letting external nutrient inputs (I_N) vary such that S^* was the same across ecosystems. Any differences between the types of recycling are not due to differential allocation of nutrients between compartments (see proof in Appendix B). Therefore, any impact of recycling on resilience is due to changes of nutrient flows between compartments.

Recycling alters the range of enrichment in which the fixed point can be stable and the resilience of the ecosystem (Fig. 2a). Consumer recycling decreases stability for low values of enrichment while increases stability and the range of stability for higher enrichment values compared to an open ecosystem with no recycling (Fig. 2a). Nutrients recycled by the autotrophs, on the other hand, strictly decrease stability compared to the open ecosystem with no recycling (Fig. 2a). Recycling by both biotic compartments results in effects similar to that of consumer recycling with greater resilience (Fig. 2a).

To understand these changes in resilience, we perturb the system and see how flows of nutrients alter the return time

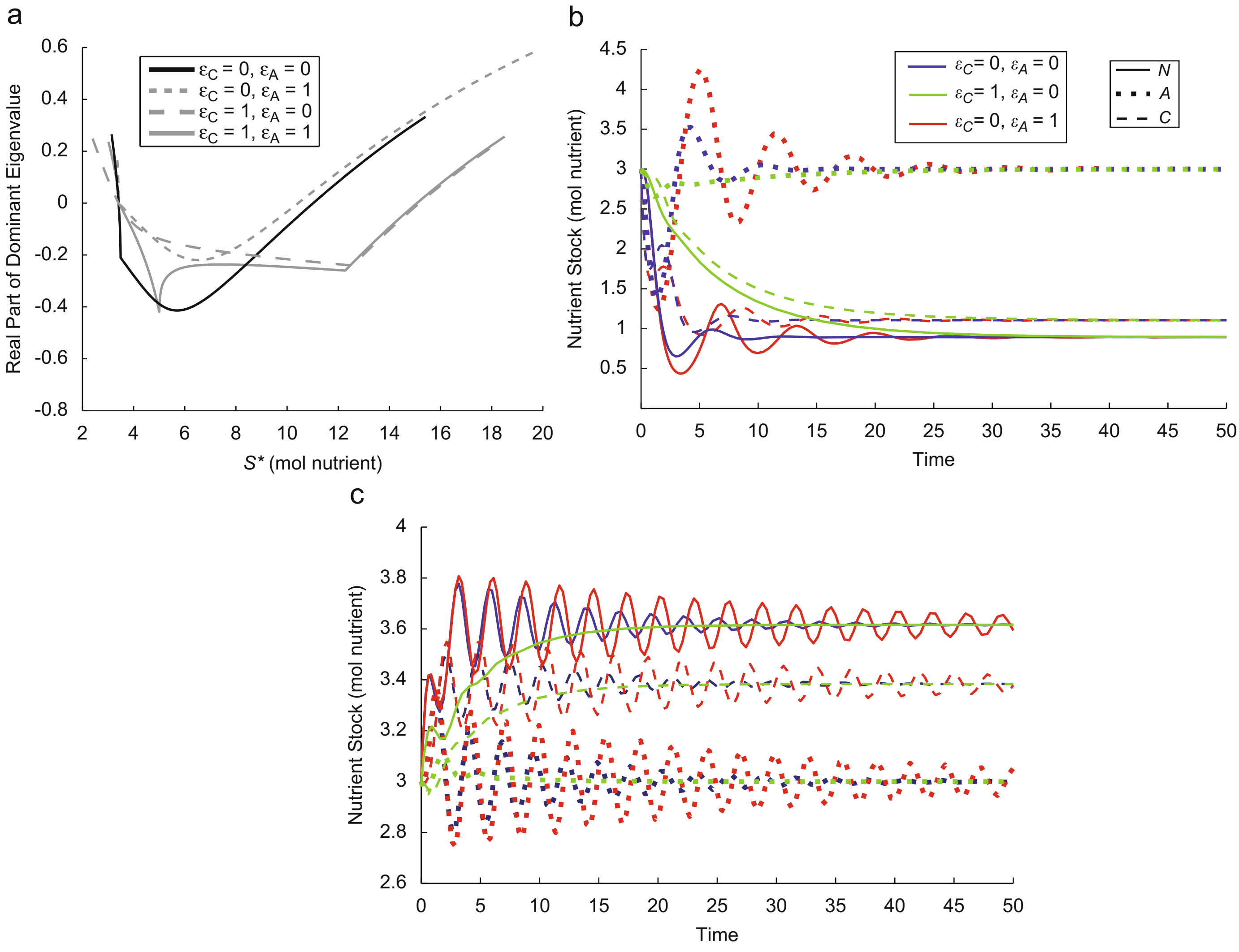

Fig. 2. Analysis of the effects of differing sources of enrichment on ecosystem resilience. (a) Examination of dominant eigenvalues for a well-mixed, open ecosystem with inputs only (solid black), autotroph recycling and inputs (dashed black), consumer recycling and inputs (dashed grey), total recycling and inputs (solid grey). (b) and (c) Dynamics of recovery from perturbation with $S^*=5$ (for (b)) and $S^*=10$ (for (c)). Lines indicate compartments (N, A, C) and colors indicate recycling regime (no recycling, autotroph recycling and consumer recycling). Parameters values for the generation of the figure are $\delta_C=2$, $\delta_A=0.4$, $\alpha_A=\beta_A=10$, $\alpha_C=\beta_C=6$, $E_N=0.4$.

(Fig. 2b–c). Without any recycling, the open ecosystem exhibits dampened oscillations when perturbed from the fixed point due to overcompensation by the consumer under high autotroph biomass (Fig. 2b–c). With only autotroph recycling, overcompensation by the consumer increases since the autotroph population can grow even larger (Fig. 2b–c). Consumer recycling, on the other hand, reduces overcompensation by providing a source of nutrients during periods of high mortality from consumers (Fig. 2b–c). This reduction of overcompensation leads to greater resilience only for high levels of enrichment (Fig. 2c).

3.2. *Diffusion-induced instabilities: effects and feedbacks*

Using Eq. (3) and the Routh–Hurwitz conditions to determine the stability of the flat solution (an equilibrium), we discovered that there exists a positive value of d_N, denoted as $d_{N,crit}$, at which the flat solution is no longer stable (Appendix C). This result is not sensitive to the values of model parameters and occurs for both the closed and open meta-ecosystem, though the value of $d_{N,crit}$ is sensitive to parameter values (Appendix C). Numerical examination of the eigenvalues of $\mathbf{V}(i)$ matrices indicates that at $d_{N,crit}$, the

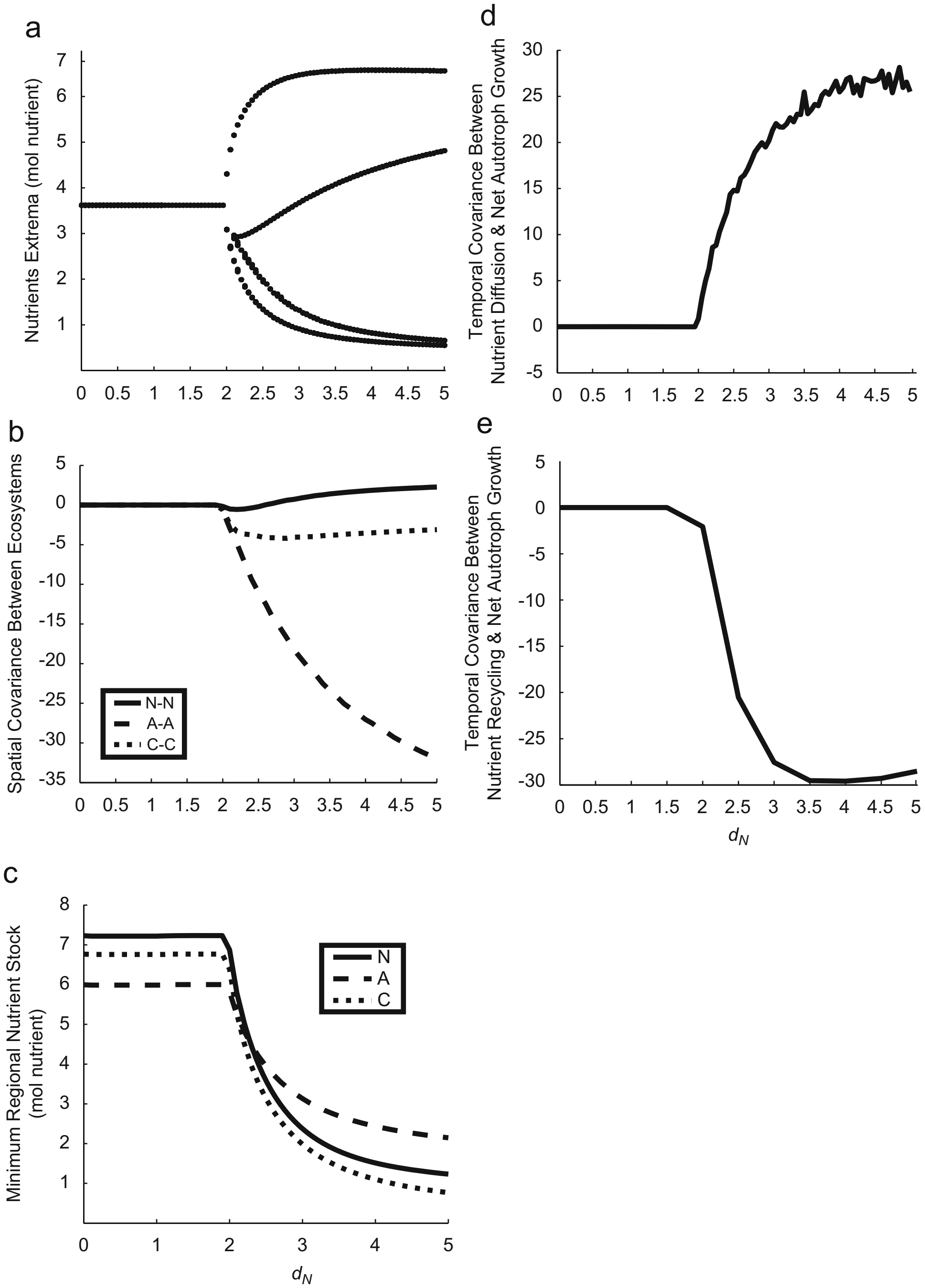

Fig. 3. Analysis of the effect of increasing the diffusion coefficient (d_N) on: (a) local stability, (b) spatial synchrony between ecosystems, (c) minimum regional nutrient stocks, (d) the covariance between nutrient diffusion and autotroph growth and (e) the covariance between nutrient recycling and autotroph growth. For (b) and (c), solid, dashed and dotted lines denote nutrients, autotrophs and consumers, respectively. Autotroph growth in one ecosystem is defined as $f_A(N_1)A_1-f_c(A_1)C_1-\delta A_1$, nutrient diffusion as $d_N(N_2-N_1)$ and nutrient recycling as $\varepsilon_A\delta_A A_1+\varepsilon_C\delta_C C_1$. Parameter values for the generation of the figure are $\delta_C=2$, $\delta_A=0.4$, $\alpha_A=\beta_A=10$, $\alpha_C=\beta_C=6$, $S_1=S_2=10$.

system undergoes a Hopf bifurcation, which is a called a spatial Hopf bifurcation as it is caused by diffusion (Appendix C).

Our numerical results revealed similar dynamical behavior, spatial covariance and regional stability to increasing d_N for the meta-ecosystems whether they were closed (Fig. 3) or open with no recycling (i.e. $\varepsilon_A=\varepsilon_C=0$; Fig. 4). Our bifurcation diagrams indicate that increasing d_N above its critical level destabilizes the stable equilibrium in the local ecosystems and leads to stable oscillatory dynamics with 2 local extrema (for consumers and autotrophs) or 4 local extrema (nutrients) to emerge (Figs. 3a and 4a). These local oscillations in the meta-ecosystem followed a pulse-relaxation pattern with much larger amplitudes and longer periods between high extrema than in oscillations within a well-mixed ecosystem (Fig. C.1).

At the same critical d_N required for destabilization of local dynamics, we witness negative spatial (between ecosystem) covariance across all trophic levels in the coupled-ecosystems (Figs. 3b and 4b). As the coupling is further increased, the spatial covariance of nutrients becomes positive and phase synchronous while the spatial covariance of the autotrophs and the spatial covariance of the consumers remain negative, indicating a nutrient-induced anti-phase synchrony of biotic levels (Figs. 3b and 4b).

The diffusion-induced instability at local ecosystems results in the biotic compartments being negatively impacted across the

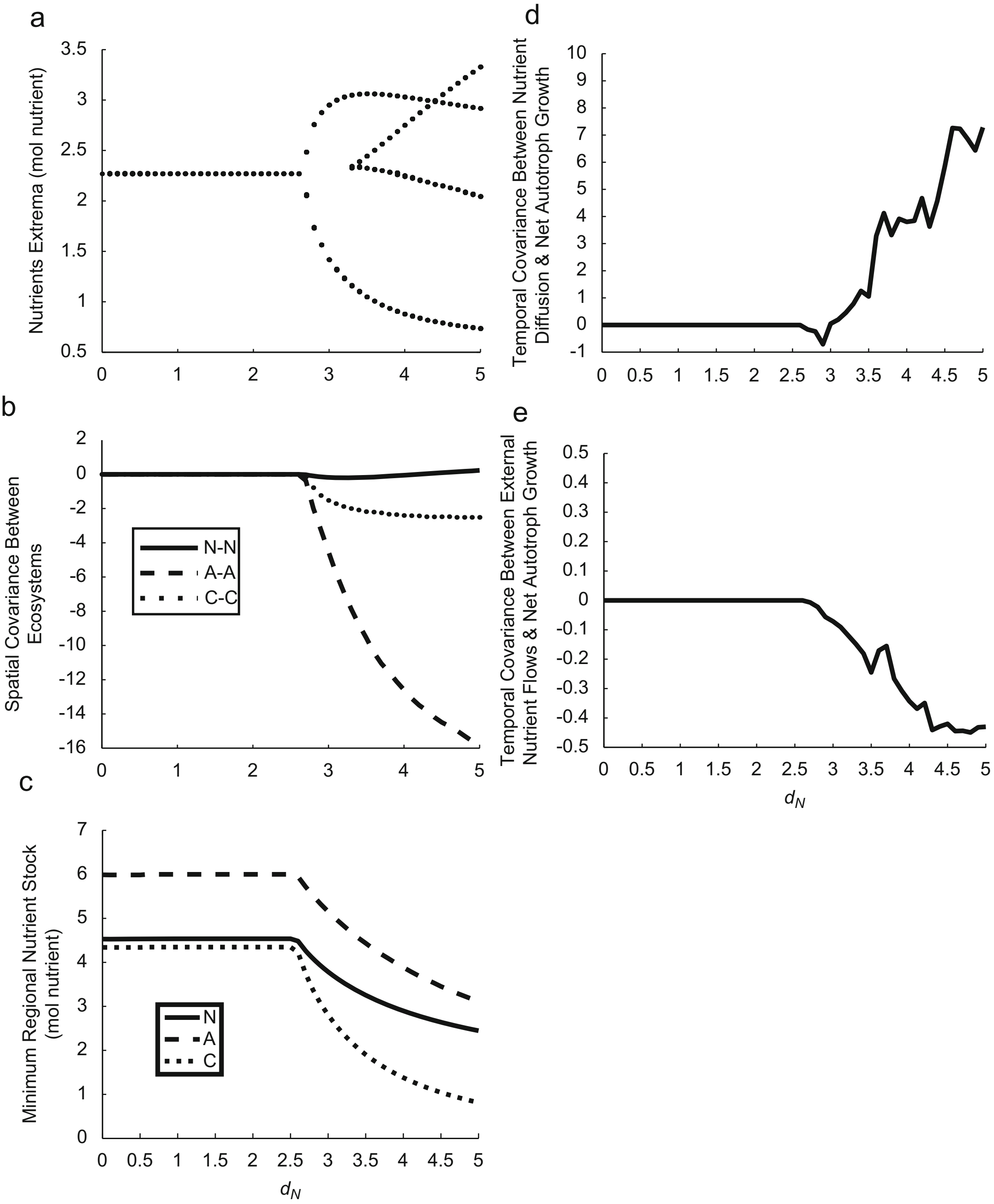

Fig. 4. Analysis of the effect of increasing the diffusion coefficient (d_N) on: (a) local stability, (b) spatial synchrony between ecosystems, (c) minimum regional nutrient stocks, (d) the covariance between nutrient diffusion and autotroph growth and (e) the covariance between external nutrient flows and autotroph growth. External nutrient flows in one ecosystem are defined as $I_N-E_NN_1$. Parameters are the same as Fig. 3 except $\varepsilon_A=\varepsilon_C=0$, $I_N=6$, $E_N=0.2$.

meta-ecosystem (Figs. 3c and 4c). The transition from equilibrium to a pulse-relaxation cycle is accompanied by a sharp decrease in the minimum regional (summed across ecosystems) nutrient stock of consumers and autotrophs, making stochastic extinction more likely (Figs. 3c and 4c). This result suggests that the meta-ecosystem is less stable regionally after the diffusion-induced instability.

Greater understanding of spatiotemporal instabilities above the critical d_N value can be gained from the analysis of feedbacks between nutrient flow and population growth across trophic levels as measured by their covariance (see *Analysis*). In both the closed and open meta-ecosystems, there is a positive covariance between net autotroph growth and nutrient diffusion when spatiotemporal instabilities occur (Figs. 3d and 4d). In contrast, nutrient recycling (in the closed meta-ecosystem) and nutrient inputs (in the open meta-ecosystem with no recycling) co-vary negatively with autotroph growth, though the effect is much less for nutrient inputs (Figs. 3e and 4e). It should be noted that the negative covariance associated with recycling is due to consumer recycling for autotroph recycling must co-vary positively with autotroph growth (result not shown).

The above results indicate a positive feedback (positive covariance) induced by the spatial process of nutrient diffusion, while recycling (or nutrient input) is linked to a negative feedback

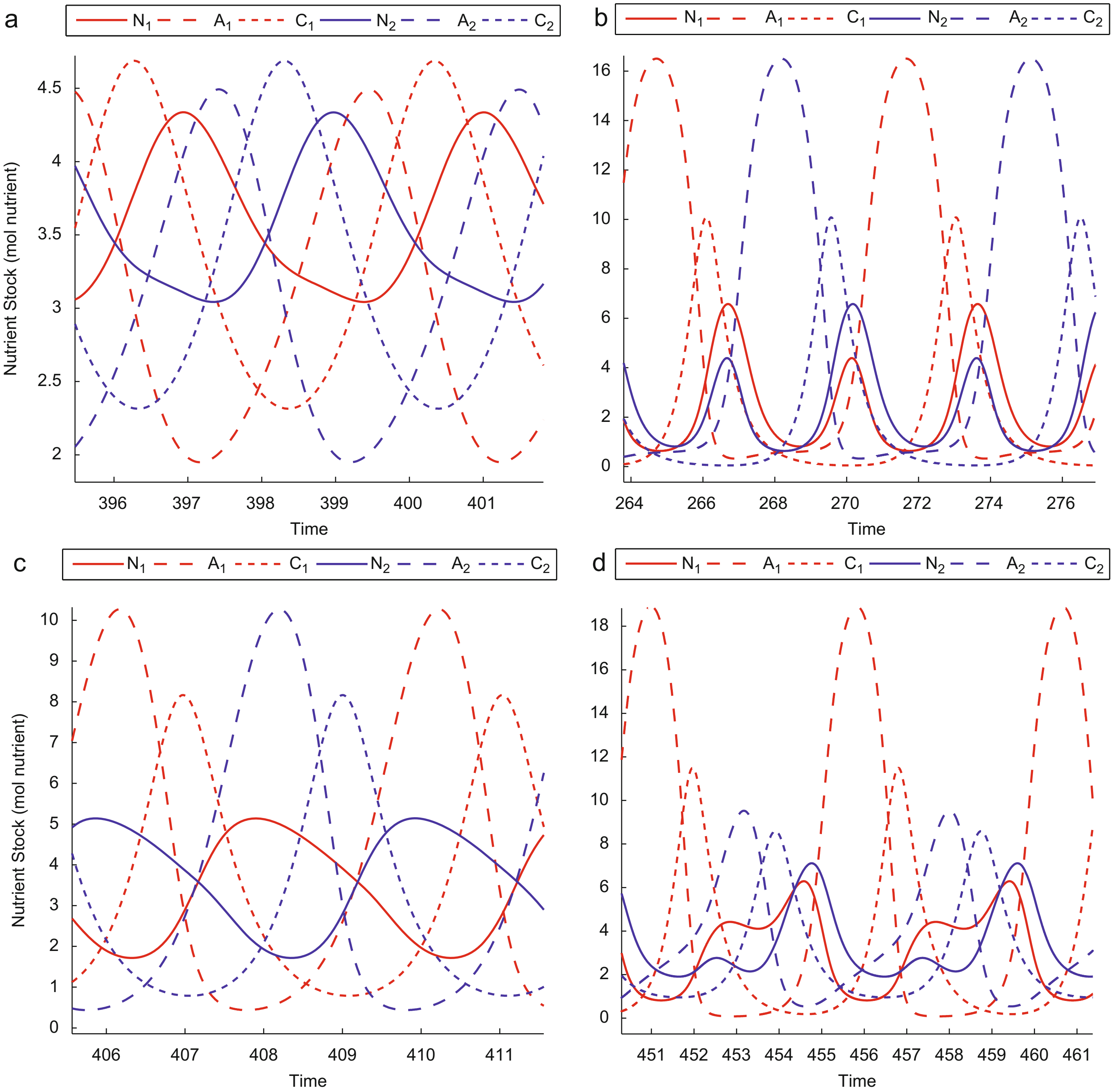

Fig. 5. The dynamics of a closed meta-ecosystem ((a) and (b)) and an open meta-ecosystem with no recycling ((c) and (d)) after they are perturbed from an unstable flat solution. The colors of the lines indicate the ecosystem, while the solid lines, the thick dashed lines and thin dashed lines denote nutrients, autotrophs and consumers, respectively. The parameters are the same as Fig. 2, except $E_N=0.2$ for the open meta-ecosystem. I_N and S values were chosen to have $S^*=10$ at the fixed point. For the figures with low diffusion rates ((a) and (c)), $d_N=2$ and for figures with higher diffusion ((b) and (c)), $d_N=4$.

(negative covariance; Fig. 3d – e and 4d – e). An increase in autotroph growth in one ecosystem depletes nutrients in that ecosystem, allowing nutrient input from the second ecosystem through diffusion, which positively feeds back on autotroph growth (e.g. Fig. 5b). The negative feedback between autotroph growth and nutrient recycling occurs through a top-down effect: recycling of dead autotroph and consumer biomass is not able to sustain autotroph growth because of increased consumer consumption.

The feedbacks are somewhat weak at lower levels of nutrient diffusion and results in complete asynchronous dynamics between ecosystems and small amplitude oscillations in closed (Fig. 5a) and open (Fig. 5c) meta-ecosystems. Increasing diffusion results in a strengthening of the feedbacks, which gives rise to large amplitude cycles, and nearly complete spatial phase synchronization of nutrients in closed (Fig. 5b) and open (Fig. 5d) meta-ecosystems.

Overall, the movement of nutrients between ecosystems can destabilize the local dynamics of each ecosystem and results in asynchronous dynamics between ecosystems (Figs. 3 and 4). This asynchrony does not allow greater stability at the regional scale because we also observe greater variation and lower minimum values in consumer and autotroph populations (Figs. 3 and 4). The emergence of the spatiotemporal instability is due to the positive feedback between nutrient diffusion and autotroph growth, but recycling can play a role in determining the critical d_N value, as seen below.

3.3. The relative importance of recycling

The results from Section 3.2 suggest that the bifurcation to spatiotemporal complexity is solely diffusion driven. However, recycling strongly affects the strength of feedbacks – positive and negative – between nutrient availability and growth that in turn drive the critical diffusion rate leading to the spatial Hopf bifurcation (Fig. 6). The specific effect of recycling on the diffusive instability depends on enrichment. We created four regimes: a closed meta-ecosystem, an open meta-ecosystem with perfect recycling, with imperfect recycling and with no recycling (Fig. 6). To assess the impact of recycling on the diffusion-induced instabilities while controlling for enrichment, we modified the parameter S in the closed meta-ecosystem and the parameter I_N in the open meta-ecosystems such that S^*, the total amount of nutrient stock in one ecosystem at equilibrium, was the same across recycling regimes.

The results show that meta-ecosystems with no recycling are more resistant to diffusion-induced instabilities when exposed to weak enrichment ($4 < S^* < 7$) compared to strong enrichment ($S^* > 8$; Fig. 6a). The open meta-ecosystem with perfect recycling is always less stable than the closed meta-ecosystem due to the loss of nutrients (Fig. 6a). In all cases, greater enrichment results in lower $d_{N,Crit}$ values, so the gains instability are relative (Fig. 6a).

However, the above trend holds only when there is an equal amount of recycling occurring for autotrophs and consumers. When only consumers recycle nutrients, the meta-ecosystem is more stable than a meta-ecosystem with no recycling for all enrichment levels (Fig. 6b). In contrast, when only autotrophs recycle nutrients, the meta-ecosystem is less stable than a meta-ecosystem with no recycling for all enrichment levels (Fig. 6b). These results hold for all parameter values that lead to a stable flat solution when nutrient diffusion is not present (Appendix C). The destabilizing effect of autotroph recycling predominates at low enrichment while the stabilizing effect of consumer recycling predominates at high enrichment in a meta-ecosystem with perfect recycling (Fig. 6b). Recycling can thus facilitate or interfere with diffusion-driven destabilization depending on enrichment and source (Fig. 6).

Overall, the above results indicate that nutrient diffusion rather than nutrient recycling is necessary to the development of instabilities. However, recycling interacts with diffusion to control the strength of its positive feedback with local autotroph growth and hence the critical diffusion rate that marks the onset of diffusion-driven instabilities. Furthermore, the outcome of the recycling-diffusion reaction is dependent on the level of enrichment and source of recycling.

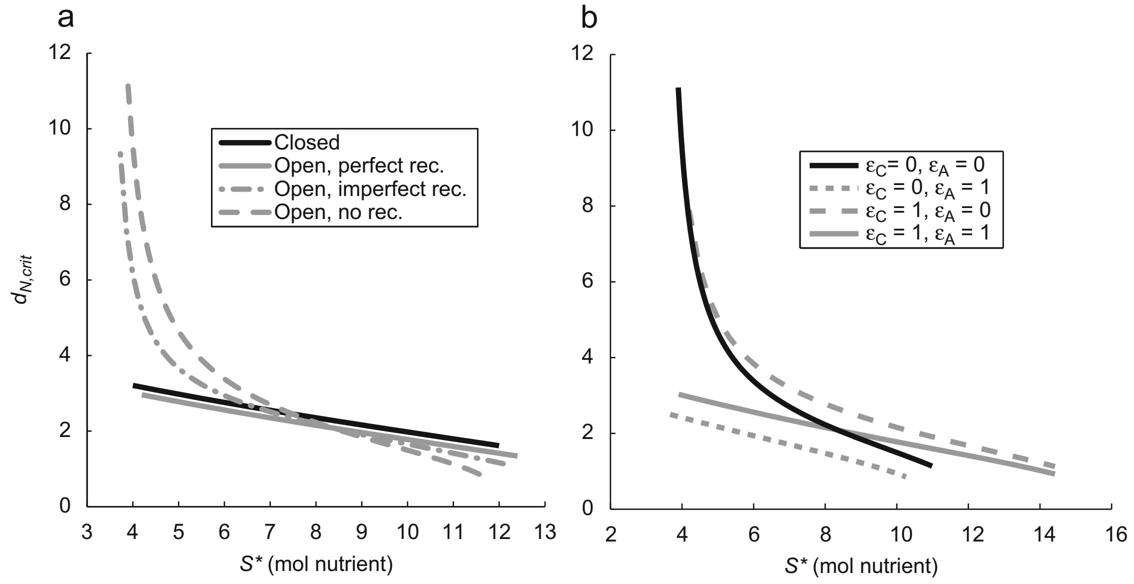

Fig. 6. Comparing $d_{N,crit}$ for (a) a closed (black line), open with perfect recycling (grey line), open with imperfect recycling (dashed dotted grey line) and open with no recycling (dashed grey line) meta-ecosystems or (b) open with no recycling (black line), open with only consumer recycling (large dashes grey line), open with only autotroph recycling (small dashes grey line) and open with perfect recycling (grey line) meta-ecosystems across various levels of enrichment. Parameters are the same as Fig. 3 for closed but $S_1 = S_2$ is allowed to vary. For open with perfect recycling, parameters are the same as closed but E_N=0.4 and I_N is allowed to vary. For open with imperfect recycling and open with no recycling, parameters are the same as open and perfect recycling except $\varepsilon_A = \varepsilon_C$=0.5 and $\varepsilon_A = \varepsilon_C$=0, respectively.

4. Discussion

We have shown that nutrient flows within (recycling) and between (diffusion) ecosystems can interact to cause large shifts in the dynamics and local stability of autotroph–consumer communities, contradicting previous conclusions derived from well-mixed models (Gurney and Nisbet, 1998). We show how spatiotemporal stability is lost through the positive feedback between nutrient diffusion and autotroph growth. Nutrient recycling controls the strength of this nutrient-growth feedback and determines the critical diffusion rates at which diffusion-driven instabilities occur. We finally show how the sign of the interaction between nutrient diffusion and recycling is controlled by ecosystem enrichment. Our results emphasize the importance of nutrient flows and of meta-ecosystem theory in predicting species persistence and distribution.

4.1. *The importance of the diffusion of nutrients on stability*

Our results help reveal the nature of the interaction between spatial structure and ecosystem processes. In well-mixed closed ecosystems, the dynamics are not qualitatively different from that of a simple predator–prey system, which led previous authors to conclude that "strong similarities between this result and the paradox of enrichment [*sensu* Rosenzweig (1971)] [...] suggest that nutrient conservation within a closed system has little effect on the unstable interaction between a consumer with a saturating functional response and a producer with limited total population" (Gurney and Nisbet, 1998).

By introducing a simple spatial division and allowing only nutrients to diffuse between the two ecosystems, we were able destabilize the local dynamics of the biota in each ecosystem at levels of total nutrients (e.g. $S_{\text{tot}}=S_1+S_2=10$) that could not induce such destabilization in a well-mixed ecosystem (Fig. 2; Fig. 6). Such destabilization would never arise if one simply subsumed the nutrient compartment into a carrying capacity, which would be implemented as a natural corollary to the conclusions of the well-mixed model. We suggest that explicit modeling of nutrients in a meta-ecosystem framework is necessary to explain population stability in spatially structured ecosystems.

Furthermore, our results add to previous studies on the potential stabilizing (or destabilizing) effects of dispersal in spatial predator–prey systems (Sjoberg, 1977; De Roos et al., 1991; Jansen, 1995; Gurney et al., 1998; Rohani and Ruxton, 1999; Jansen, 2001; Gurney and Veitch, 2000; Holt, 2002; McCann et al., 2005; Maser et al., 2007). In spatial predator–prey systems, if the destabilization of local dynamics led to asynchronous dynamics between communities, then one would obtain higher regional densities of both predator and prey (Rohani and Ruxton, 1999; Jansen 2001). In our model, however, though the destabilization of local dynamics due to nutrient diffusion did lead to asynchronous dynamics between ecosystems, this lead to lower regional densities of the biotic compartments (Figs. 3 and 4). Therefore, asynchronous dynamics between ecosystems do not guarantee greater regional densities of organisms.

Overall, our results show that nutrient diffusion can destabilize local and regional community dynamics and therefore a more holistic view of ecosystems must be considered by linking the mechanistic understanding of species within communities with flows of matter within and across ecosystems (Polis et al., 1997; Loreau et al., 2003; Loreau and Holt, 2004).

4.2. *Nutrient recycling, stability and enrichment*

Nutrient recycling has been evoked as a mechanism of either stabilization or destabilization of ecosystem dynamics (DeAngelis, 1980, 1992; DeAngelis et al., 1986; Loreau, 1994; Loeuille et al., 2002; Scheffer and Carpenter, 2003). Some theorists have argued that adding recycling to an ecosystem will add a positive feedback, causing the ecosystem to be less stable (DeAngelis, 1980, 1992; DeAngelis et al., 1986). Others have noted that recycling can increase stability if one considers resistance to perturbation (Loreau, 1994). Even when recycling does not affect stability, it can still alter results, such as the leading to an evolutionary arms race in a model with recycling versus evolutionary cycles in one without recycling (Loeuille et al., 2002).

Our results indicate that recycling has an ambiguous relationship with ecosystem stability. This relationship is highly dependent on the amount of enrichment within the ecosystem and the source of the nutrients (Figs. 2 and 6). In well-mixed ecosystems at low nutrient enrichment, ecosystem resilience is highest for ecosystems with no recycling, but ecosystems with perfect recycling have the highest resilience at high nutrient enrichment. However, most of the benefits of recycling for ecosystem resilience comes from consumer recycling. In meta-ecosystems, increasing the relative contribution of consumer recycling vis-à-vis other nutrient sources will increase $d_{N,crit}$ at all enrichment levels, while increasing the relative contribution of autotroph recycling will decrease $d_{N,crit}$ at all enrichment levels. This pattern can be explained by the fact that consumer recycling is temporally asynchronous with autotroph growth, leading to attenuation of consumer–autotroph cycles, while autotroph recycling is temporally synchronous with autotroph growth, leading to amplifications of consumer–autotroph cycles (e.g. Fig. 2c).

In meta-ecosystems with perfect recycling we see relatively low $d_{N,Crit}$ values at low enrichment and relatively high $d_{N,Crit}$ values at high enrichment compared to meta-ecosystems with no recycling. This effect can be explained by the fact that the amount of nutrient in autotrophs at the fixed point remains constant independent of enrichment, while the amount of nutrient in consumers increases. Therefore, the relative contribution of nutrients from the biota moves from the autotrophs towards consumers with increasing enrichment, which would then render the meta-ecosystem relatively more stable.

Overall, our results predict that stability properties of ecosystems depend on recycling and indicates need to integrate meta-ecosystem dynamics with nutrient diffusion. Our results provide a spatial mechanism to the contention that closed ecosystems are not necessarily less stable than open ecosystems (Loreau, 1994).

4.3. *Potential for empirical testing of model results*

Our model predicts that nutrient diffusion can cause destabilization of simple food chains and that nutrient recycling and enrichment can influence this effect. These predictions could be tested experimentally using connected chemostats, i.e. a gradostat, which can allow the movement of nutrients, but not of organisms, between chemostats. One of the main benefits of these experiments is that physiological parameters of plankton species (e.g. diatoms, *Daphia*) are well understood (e.g. Grover 2003). With these parameters and control of nutrient flows, it should be possible test the level of nutrient diffusion predicted to lead to non-equilibrium population dynamics. There is also potential to apply the model and the predicted patterns of phase synchrony to meso-cosms and natural experiments, which has been recently done for consumer–resource theory (Benincà et al., 2009). Using time series analysis (e.g. wavelet, Benincà et al. ,2009), it is possible to detect whether observed patterns of spatial phase synchrony are compatible with predicted changes in phase synchrony (full vs. phase locked) across trophic compartments.

5. Conclusion

We have shown how nutrient flows can alter the dynamics and the stability of a meta-ecosystem. Our study predicts that high rates of nutrient diffusion between ecosystems destabilize equilibrium and spatially homogeneous dynamics. We also show how nutrient recycling and enrichment influence the critical diffusion rates needed to induce such spatiotemporal instability. This model reinforces the importance of spatial structure for the understanding of ecosystem processes. The model presented here should be extended to larger scales and to natural systems to give better ecosystem-level understanding of food webs in landscapes (Polis et al., 1997). Our predictions can be tested experimentally in aquatic micro- and meso-cosms where nutrients can be controlled independently from population densities. Applied to managed systems, our results suggest that greater emphasis should be put on exploring the connectivity of ecosystems due to the interaction between nutrient flows and recycling. Such understanding would, for example, impact the management of watersheds that can result in greater community instability due to increased nutrient diffusion and enrichment.

Acknowledgements

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Appendix A. Analysis of the closed, well-mixed ecosystem

In this section, we present our analysis of the closed, well-mixed ecosystem (Eq. (2a)) in regards to the stability of the fixed points. The overall conclusion from the analysis is that a closed nutrient-autotroph–consumer ecosystem has similar properties of a predatory–prey or consumer–resource model, which has been noted by others (Gurney and Nisbet, 1998).

The model defined by Eq. (2a) has three possible fixed points. The first fixed point, the nutrients-only fixed point ($N^N = S$, $A^N = 0$, $C^N = 0$), always exists and is stable if and only if the following inequality holds:

$$\delta_A > \frac{\alpha_A S}{\beta_A + S} \tag{A.1}$$

This condition implies that the autotroph cannot maintain positive growth at the level of nutrients present in the ecosystem. If it can maintain positive growth, than the nutrients-only fixed point is unstable. The second fixed point of interest is the autotroph-only fixed point ($N^A = f_A^{-1}(\delta_A)$, $A^A = S - f_A^{-1}(\delta_A)$, $C^A = 0$), which exists when the autotroph can maintain positive growth at the level of nutrients present in the ecosystem (i.e. flip the inequality of (A.1)). For the autotroph only fixed point to be stable, the following inequality must hold:

$$\delta_C > \frac{\alpha_C A^A}{\beta_C + A^A} \tag{A.2}$$

The biological interpretation of this condition is that the consumer cannot maintain positive growth at the level of autotrophs present in the ecosystem at autotroph only fixed point. Therefore, if the consumer can maintain positive growth, then the autotroph only fixed point is unstable. The last fixed point of interest is the autotroph-consumer fixed point, which is quite complicated mathematically

$$\begin{aligned}
N^* &= S + A^* + C^* \\
A^* &= \frac{\beta_C \delta_C}{\alpha_C - \delta_C} \\
C^* &= \frac{-\mathrm{B} - \sqrt{\mathrm{B}^2 - 4\alpha_C \mathrm{X}}}{2\alpha_C} \\
\mathrm{B} &= -\alpha_A(A^* + \beta_C) - \alpha_C(S + \beta_A - A^*) + \delta_A(A^* + \beta_C) \\
\mathrm{X} &= \alpha_A(SA^* + S\beta_C - (A^*)^2 - \beta_C A^*) + \delta_A(A^*\beta_C + (A^*)^2 \\
&\quad - \beta_A A^* - SA^* - \beta_C \beta_A - S\beta_C)
\end{aligned} \tag{A.3}$$

The condition for existence of this fixed point is the maintenance of positive growth of the consumer, which means the inequality in Eq. (A.2) is reversed when met. The stability conditions for the autotroph–consumer fixed point are not easily presented and do not have simple biological interpretations, though it becomes unstable with increasing ecosystem enrichment (Fig. A.1). Other than fixed points, the dynamics of the model can enter into limit cycles at high levels of enrichment, as indicated by numerical simulations (Fig. A.1).

Therefore, the closed nutrient–autotroph–consumer ecosystem model demonstrates the same dynamical regimes as a predator–prey model (fixed points or limit cycles) and exhibits similar responses to enrichment (Rosenzweig, 1971). Such results suggest that little is gained by considering the dynamics of the nutrients and it would be simpler to use a carrying capacity and a predator–prey (or consumer–resource) formulation for closed ecosystems with two trophic levels (Gurney and Nisbet, 1998).

Appendix B. Proof of invariance of N^*, A^* and C^* for given S^*

In this section, we show that the allocation of nutrients to the three compartments (N, A and C) for a given total nutrient stock in the ecosystem (S) at equilibrium must be the same independent of the proportions of nutrients recycled (ε_A, ε_C) or the external nutrient input (I_N). This result is proved by postulating that the

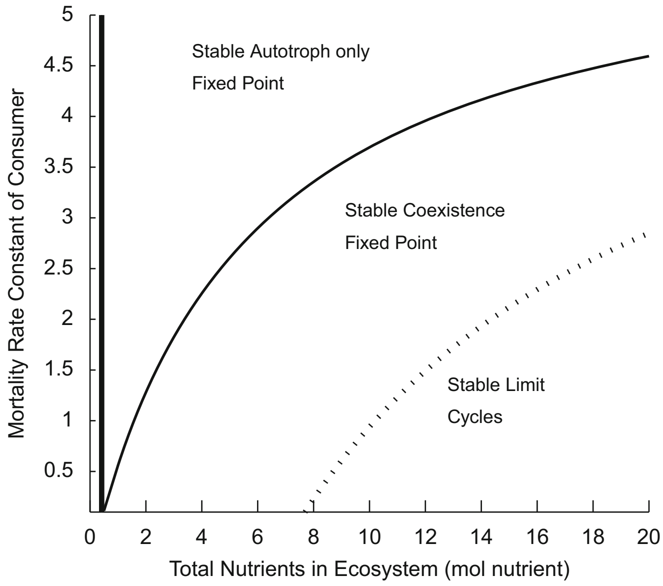

Fig. A1. Dynamical regimes of the well-mixed closed model. The area left of the heavy black line indicates the level of total nutrients at which autotrophs cannot persist in the ecosystem. Parameter values are the same as Fig. 3a.

existence of two solutions to a particular equation, but then showing that the solutions must be identical, resulting in a proof by contradiction. The consequence of the result is that the origin of the nutrients and the temporal patterns of these flows are what explain the stability of the ecosystems, not the allocation of the nutrients to different compartments.

The first step in the proof is to write out the formula for the total amount of nutrients in the ecosystem at equilibrium (S^*)

$$S^* = N^* + A^* + C^* \tag{B.1}$$

Here, N^*, A^* and C^* are the amount of nutrients in the medium, in the autotrophs and in the consumers at equilibrium, respectively. The value of A^* is not dependent on the parameters controlling nutrient recycling (ε_A, ε_C) or nutrient input (I_N ; see Eq. A.3 for expression). Therefore, A^* can be treated as a constant, meaning $S^* - A^*$ will also be a constant, which we will call S^{**}, N^* and C^*, on the other hand, are dependent on those parameters and can be expressed as having a functional dependence on the nutrient recycling and input parameters. The above facts lead to the following equation:

$$S^* - A^* = S^{**} = N^*(I_N, \varepsilon_A, \varepsilon_C) + C^*(I_N, \varepsilon_A, \varepsilon_C) = \text{constant} \tag{B.2}$$

We can also remove C^* from Eq. (B.2) by noting it can be expressed as a function N^*, which is clearly seen by solving for C^* by setting dA/dt from Eq.(2) to zero

$$\frac{dA}{dt} = 0 = f_A(N^*)A^* - \delta_A A^* - f_C(A^*)C^*$$

$$\Leftrightarrow C^* = \frac{f_A(N^*)A^* - \delta_A A^*}{f_C(A^*)} = h(N^*(I_N, \varepsilon_A, \varepsilon_C)) \tag{B.3}$$

We can now express S^{**} solely as a function of N^*, which is itself dependent on I_N, ε_A and ε_C:

$$S^{**} = N^*(I_N, \varepsilon_A, \varepsilon_C) + h(N^*(I_N, \varepsilon_A, \varepsilon_C)) \tag{B.4}$$

Now for a particular value of S^* and of A^*, there can be only one value of S^{**}, but it may be possible to have multiple values of N^* (and therefore C^*) that could result in having the same value of S^{**}. We postulate that there exists one value of $N^*$and N_1^*, that satisfies a particular value of S^{**}. We now wish to know if there can be a second value of N^* and N_2^*, that can satisfy a particular value of S^{**}. An important fact that will aid us in this task is noting that since $f_A(N^*)$ is a strictly increasing function of N^*, then $h(N^*)$ is also a strictly increasing function of N^*.

If N_2^* is less than N_1^*, then $h(N_2^*(I_N, \varepsilon_A, \varepsilon_C))$ is less than $h(N_1^*(I_N, \varepsilon_A, \varepsilon_C))$, so S^{**} is greater than $h(N_2^*(I_N, \varepsilon_A, \varepsilon_C)) + N_2^*(I_N, \varepsilon_A, \varepsilon_C)$ and N_2^* fails to satisfy the equality of Eq. B.4. If N_2^* is greater than N_1^*, then $h(N_2^*(I_N, \varepsilon_A, \varepsilon_C))$ is greater than $h(N_1^*(I_N, \varepsilon_A, \varepsilon_C))$, so S^{**} is less than $h(N_2^*(I_N, \varepsilon_A, \varepsilon_C)) + N_2^*(I_N, \varepsilon_A, \varepsilon_C)$ and N_2^* fails to the equality of Eq. B.4. Therefore, N_2^* must be equal to N_1^*. Therefore, for all values of the recycling parameters, N^*, C^* and A^* remain fixed for fixed S^*.

Appendix C. Derivation of $d_{N,crit}$

The derivation of the critical value for d_N in the case of a spatially homogeneous fixed point solution was made possible by a theorem proved by Jansen and Lloyd (2000). The theorem states that for suitably defined connectivity and diffusion matrices, one can determine the stability of the spatially homogeneous solution by checking the eigenvalues of $\mathbf{V}(i)$ matrices as defined in the text above (Jansen and Lloyd, 2000). If any of $\mathbf{V}(i)$ matrices have a positive eigenvalue, then the spatially homogeneous solution is unstable. A simple way of finding the signs of eigenvalues of a matrix is using the Routh–Hurwitz conditions (Edelstein-Keshet 1988). Using Jansen & Lloyd's theorem with the Routh–Hurwitz conditions, we can derive value at which there will be a bifurcation of some sort.

We start with the Jacobian of Eq. (2):

$$\mathbf{J} = \begin{pmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{pmatrix}$$

$$= \begin{pmatrix} -E_N - \dfrac{\alpha_A \beta_A A^*}{(N^* + \beta_A)^2} & -\dfrac{\alpha_A N^*}{\beta_A + N^*} + \varepsilon_A \delta_A & \varepsilon_C \delta_C \\ \dfrac{\alpha_A \beta_A A^*}{(N^* + \beta_A)^2} & \dfrac{\alpha_A N^*}{\beta_A + N^*} - \delta_A - \dfrac{\alpha_C \beta_C C^*}{(A^* + \beta_C)^2} & -\dfrac{\alpha_C A^*}{\beta_C + A^*} \\ 0 & \dfrac{\alpha_C \beta_C C^*}{(\beta_C + A^*)^2} & 0 \end{pmatrix} \tag{C.1}$$

The Routh–Hurwitz conditions without diffusion are

$$1. -\mathbf{tr}(\mathbf{J}) > \mathbf{0}$$

$$2. -\mathbf{det}(\mathbf{J}) > \mathbf{0}$$

$$3. -\mathbf{tr}(\mathbf{J})^*(\mathbf{J}_{11} + \mathbf{J}_{22} + \mathbf{J}_{33}) + \mathbf{det}(\mathbf{J}) > 0 \tag{C.2}$$

The Routh–Hurwitz conditons with diffusion are

$$1. -\mathbf{tr}(\mathbf{V}(k)) > \mathbf{0}$$

$$2. -\mathbf{det}(\mathbf{V}(k)) > \mathbf{0}$$

$$3. -\mathbf{tr}(\mathbf{V}(k))^*(\mathbf{V}(k)_{11} + \mathbf{V}(k)_{22} + \mathbf{V}(k)_{33}) + \mathbf{det}(\mathbf{V}(k)) > 0 \tag{C.3}$$

If the spatially homogeneous solution is stable without diffusion, then conditions 1 and 2 with diffusion still hold. The proof is as follows:

$$1. -\mathbf{tr}(\mathbf{V}(k)) = -(\underbrace{\mathbf{tr}}_{<0}(\mathbf{J}) + \underbrace{\lambda_k}_{<0} d_N)$$

$$\therefore -\mathbf{tr}(\mathbf{V}(k)) > 0$$

$$\begin{aligned} 2.\mathbf{det}(\mathbf{J}) &= a_{11}(a_{22}a_{33} - a_{23}a_{32}) - a_{12}(a_{21}a_{33} - a_{23}a_{31}) \\ &\quad + a_{13}(a_{21}a_{32} - a_{22}a_{31}) \\ &= \underbrace{-a_{11}a_{23}a_{32}}_{<0} + \underbrace{a_{13}a_{21}a_{32}}_{>0} \end{aligned}$$

$$\therefore \text{ if } \mathbf{det}(\mathbf{J}) < \mathbf{0}, \text{ then } a_{11}a_{23}a_{32} > a_{13}a_{21}a_{32},\ a_{11} < 0$$

$$\begin{aligned} \text{for } \mathbf{det}(\mathbf{V}(k)) &= (a_{11} + \lambda_k d_N)(a_{22}a_{33} - a_{23}a_{32}) \\ &\quad - a_{12}(a_{21}a_{33} - a_{23}a_{31}) + a_{13}(a_{21}a_{32} - a_{22}a_{31}) \\ &= \underbrace{-a_{11}a_{23}a_{32}}_{<0} + \underbrace{a_{13}a_{21}a_{32}}_{>0} \underbrace{-\lambda_k d_N a_{23}a_{32}}_{<0} \end{aligned}$$

$$\therefore \text{ if } \mathbf{det}(\mathbf{J}) < \mathbf{0}, \text{ then } \mathbf{det}(\mathbf{V}(k)) < 0$$

$$\therefore -\mathbf{det}(\mathbf{V}(k)) > 0 \tag{C.4}$$

If change in stability occurs, then it must be condition 3 that is not satisfied. The critical diffusion coefficient value necessary for it to occur in the system here studied can be calculated in the following manner. First, we set the left-hand side of the condition to be equal to zero:

$$-\mathbf{tr}(\mathbf{V}(k))(\mathbf{V}(k)_{11} + \mathbf{V}(k)_{22} + \mathbf{V}(k)_{33}) + \mathbf{det}(\mathbf{V}(k)) = 0$$

$$\begin{aligned} &\rightarrow -(a_{11} + a_{22} + \lambda_k d_N)(-a_{23}a_{32} + a_{22}\lambda_k d_N + a_{22}a_{11} - a_{12}a_{21}) \\ &\quad - a_{11}a_{23}a_{32} + a_{13}a_{21}a_{32} - \lambda_k d_N a_{23}a_{32} = 0 \end{aligned} \tag{C.5}$$

We now gather like terms and solve for d_N using the quadratic formula

$$\underbrace{-a_{22}\lambda_k^2}_{A} d_N^2 + \underbrace{(-2a_{11}a_{22} - a_{22}^2 + a_{12}a_{21})\lambda_k}_{B} d_N$$

$$+\underbrace{(a_{11}(-a_{22}a_{11}+a_{12}a_{21})+a_{22}(a_{23}a_{32}-a_{22}a_{11}+a_{12}a_{21})+a_{13}a_{21}a_{32})}_{C}=0$$

$$d_{N,crit}=\frac{-B\pm\sqrt{B^2-4AC}}{2A} \tag{C.6}$$

We can prove there will only be one positive value for $d_{N,crit}$. As all parameters are positive and N^*, C^*, $A^*>0$, then we can easily determine the signs of most of the elements of the Jacobian

$$\mathbf{J}=\begin{pmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{pmatrix}=\begin{pmatrix} - & ? & + \\ + & ? & - \\ 0 & + & 0 \end{pmatrix} \tag{C.7}$$

The sign of a_{12} can be determined by using the fact that $dA/dt=0$ at equilibrium for our model equations

$$\frac{dA}{dt}=0=\frac{\alpha_A N^* A^*}{\beta_A+N^*}-\delta_A A^*-\frac{\alpha_C A^* C^*}{\beta_C+A^*}$$

$$\frac{\alpha_C A^* C^*}{\beta_C+A^*}=\frac{\alpha_A N^* A^*}{\beta_A+N^*}-\delta_A A^* \quad \text{Now divide through by } A^* \text{ as } A^*>0$$

$$\frac{\alpha_C C^*}{\beta_C+A^*}=\frac{\alpha_A N^*}{\beta_A+N^*}-\delta_A \Rightarrow \frac{\alpha_A N^*}{\beta_A+N^*}-\delta_A>0$$

$$\frac{\alpha_A N^*}{\beta_A+N^*}-\delta_A>0 \Rightarrow -\frac{\alpha_A N^*}{\beta_A+N^*}+\delta_A<0 \Rightarrow -\frac{\alpha_A N^*}{\beta_A+N^*}+\varepsilon_A\delta_A<0 \text{ as } \varepsilon_A\delta_A\le\delta_A$$

$$\therefore \quad a_{12}<0 \tag{C.8}$$

The sign of a_{22} can be determined from the same derivation as a_{12} by seeing if $\alpha_C C^*/\beta_C+A^*>\alpha_C\beta_C C^*/(\beta_C+A^*)^2$is true for if it is, $a_{22}>0$:

$$\frac{\alpha_C C^*}{\beta_C+A^*}=\frac{\beta_C+A^*}{\beta_C+A^*}\frac{\alpha_C C^*}{\beta_C+A^*}=\frac{\alpha_C\beta_C C^*}{(\beta_C+A^*)^2}+\frac{\alpha_C C^* A^*}{(\beta_C+A^*)^2}>\frac{\alpha_C\beta_C C^*}{(\beta_C+A^*)^2}$$

$$\therefore \quad a_{22}>0 \tag{C.9}$$

We can now look at the signs of A, B and C of the $d_{N,crit}$ and notice A is negative, B is positive (some algebra involving the non-spatial Routh–Hurwitz conditions will show that $2a_{11}a_{22}$ is larger than $a_{22}a_{22}+a_{12}a_{21}$) and C is positive (also involves some algebra with non-spatial Routh–Hurwitz conditions). Therefore, $(B^2-4AC)^{0.5}$ is real, $B<(B^2-4AC)^{0.5}$ and there is one negative value and one positive value of $d_{N,crit}$. The positive value is given by the following:

$$d_{N,Crit}=\frac{-B-\sqrt{B^2-4AC}}{2A} \tag{C.10}$$

What kind of bifurcation occurs was investigated by inspecting the eigenvalues of **V(i)** matrix as d_N. There was one real negative eigenvalue and two complex eigenvalues which are complex conjugates. The complex eigenvalues have real negative parts for values less than $d_{N,crit}$, but have real positive parts for values greater than $d_{N,crit}$. Such a change in eigenvalues indicates a Hopf bifurcation (Edelstein-Keshet, 1988). This leads to the development of limit cycles when the initial spatially homogeneous solution is a fixed point for both the closed and open meta-ecosystems. These limit cycles have a pulse-relaxation profile unlike those found when the well-mixed ecosystem's fixed point loses stability (Fig. C.1).

We also investigated whether any discernible relationship existed between $d_{N,Crit}$ and the recycling parameters when ecosystem enrichment was fixed at an arbitrary value (i.e. increasing ε_A and ε_C does not increase S^*). By fixing ecosystem enrichment to some arbitrary value, we can take the partial derivative of $d_{N,Crit}$ with respect to the recycling parameters without having to worry about changes to N^*, A^* and C^* as the recycling parameters increase or decrease. Before taking the partial derivative of $d_{N,Crit}$ with respect to the recycling parameters, we examine the partial derivatives of A, B and C (as defined in Eq. (C.6)) with respect to the recycling parameters

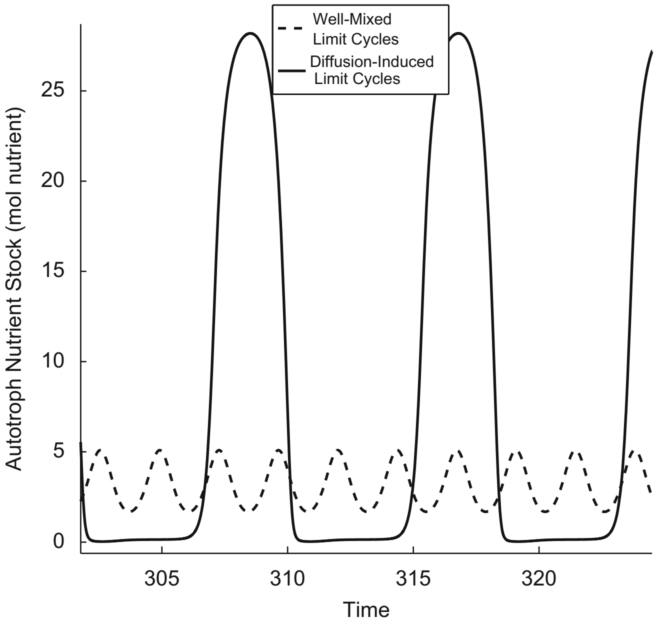

Fig. C1. Comparing the dynamics of the well-mixed limit cycles (dotted line) to the diffusion-induced limit cycles (solid line) with the same parameter values except for d_N. Note the long periods of very low autotroph biomass followed by a pulse of autotroph nutrient stock in the diffusion-induced limit cycle.

$$\frac{\partial A}{\partial\varepsilon_A}=0,\frac{\partial B}{\partial\varepsilon_A}=\lambda_i\delta_A A^* a_{21}<0,\frac{\partial C}{\partial\varepsilon_A}=\delta_A A^* a_{21}(a_{11}+a_{22})<0$$

$$\frac{\partial A}{\partial\varepsilon_C}=0,\frac{\partial B}{\partial\varepsilon_C}=0,\frac{\partial C}{\partial\varepsilon_C}=\delta_C C^* a_{21}a_{32}>0 \tag{C.11}$$

The above partial derivatives combined with the knowledge of the signs of A, B and C makes it fairly simple to determine the signs of the partial derivatives of $d_{N,Crit}$ with respect to the recycling parameters

$$\frac{\partial d_{N,Crit}}{\partial\varepsilon_A}=\frac{\partial}{\partial\varepsilon_A}\left(\frac{-B-\sqrt{B^2-4AC}}{2A}\right)=\frac{1}{2A}\frac{\partial}{\partial\varepsilon_A}\left(-B-\sqrt{B^2-4AC}\right)$$

$$=\frac{1}{2A}\left(-\frac{\partial B}{\partial\varepsilon_A}-0.5\frac{2B\frac{\partial B}{\partial\varepsilon_A}-4A\frac{\partial C}{\partial\varepsilon_A}}{\sqrt{B^2-4AC}}\right)<0$$

$$\frac{\partial d_{N,Crit}}{\partial\varepsilon_C}=\frac{\partial}{\partial\varepsilon_C}\left(\frac{-B-\sqrt{B^2-4AC}}{2A}\right)=-\frac{1}{2A}\frac{\partial}{\partial\varepsilon_C}\left(\sqrt{B^2-4AC}\right)$$

$$=-\frac{1}{4A}\left(\frac{-4A\frac{\partial C}{\partial\varepsilon_C}}{\sqrt{B^2-4AC}}\right)>0 \tag{C.12}$$

Therefore, to increase $d_{N,Crit}$ (i.e. make the meta-ecosystem more 'stable' to diffusion-induced instabilities) one has to either increase ε_C and/or decrease ε_A.

Appendix D. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jtbi.2010.06.022.

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