ECOLOGY LETTERS

Ecology Letters, (2015) **18**: 1163–1173 doi: 10.1111/ele.12495

LETTER

Emergence of nutrient co-limitation through movement in stoichiometric meta-ecosystems

Justin N. Marleau,[1]* Frédéric Guichard[1] and Michel Loreau[2]

[1]Department of Biology, McGill University, Montreal, Quebec, Canada
[2]Centre for Biodiversity Theory and Modelling, Experimental Ecology, Centre National de la Recherche Scientifique, 09200 Moulis, France

**Correspondence: E-mail: justin.marleau@mail.mcgill.ca*

Abstract

Evidence that ecosystems and primary producers are limited in their productivity by multiple nutrients has caused the traditional nutrient limitation framework to include multiple limiting nutrients. The models built to mimic these responses have invoked local mechanisms at the level of the primary producers. In this paper, we explore an alternative explanation for the emergence of co-limitation by developing a simple, stoichiometrically explicit meta-ecosystem model with two limiting nutrients, autotrophs and herbivores. Our results show that differences in movement rates for the nutrients, autotrophs and herbivores can allow for nutrient co-limitation in biomass response to emerge despite no local mechanisms of nutrient co-limitation. Furthermore, our results provide an explanation to why autotrophs show positive growth responses to nutrients despite 'nominal' top-down control by herbivores. These results suggest that spatial processes can be mechanisms for nutrient co-limitation at local and regional scales, and can help explain anomalous results in the co-limitation literature.

Keywords

Meta-ecosystem, modelling, nutrient co-limitation, spatial ecology, stoichiometry, top-down control.

Ecology Letters (2015) **18**: 1163–1173

INTRODUCTION

Knowing the identity of the nutrient (or other resource) that limits the productivity of an ecosystem is an important and complicated issue. The enrichment of a local ecosystem with its limiting nutrient can cause massive shifts in community structure, ecosystem functioning and complete disruption of vital ecosystem services such as potable water. For example, agricultural run-off contributed to high dissolved reactive phosphorus in Lake Erie, which stimulated massive cyanobacteria blooms in 2011 that released substantial amounts of microcystic toxin into the water (Michalak *et al.* 2013). However, it is not always clear which nutrients are limiting productivity. Within the scientific community, there is disagreement about whether phosphorus, nitrogen or both are limiting the productivity of algae in lakes, estuaries and coastal environments (Howarth & Marino 2006; Schindler *et al.* 2008; Sterner 2008; Conley *et al.* 2009; Schindler & Hecky 2009; Schindler 2012). The co-limitation of productivity by nitrogen and phosphorus in aquatic and marine ecosystems would require management of both nutrients, which is substantially more costly than controlling just one (Schindler & Hecky 2009).

The evidence for multiple limiting nutrients in ecosystems has been increasing and incorporates examples from aquatic, terrestrial and marine ecosystems (Elser *et al.* 2007; Harpole *et al.* 2011). The evidence includes stoichiometric ratios (Güsewell *et al.* 2003), short-term biochemical assays (Saito *et al.* 2008) and factorial nutrient addition experiments (Elser *et al.* 2007; Craine 2009; Harpole *et al.* 2011), though they do not necessarily measure similar ecological processes (Low-Decarie *et al.* 2014). Most of the experiments measure short-term (days to months) metabolic activity or biomass responses of primary producers to nutrients (Elser *et al.* 2007; Harpole *et al.* 2011), which measure the proximate nutrient (co)limitation of primary consumers (Vitousek *et al.* 2010). When the experiments measure long-term (years to decades) biomass responses or community composition of primary producers to nutrients, we can view those responses as being ultimately (co) limited by the nutrient(s) involved (Vitousek *et al.* 2010). For example, in the case of Lake Erie, there is evidence of proximal co-limitation by nitrogen and phosphorus within the primary producer community during blooms, but the long-term production of such blooms is ultimately controlled by phosphorus (Michalak *et al.* 2013).

Because of the differences in time scales and measures between proximate and ultimate limitation, the mechanisms invoked to account for co-limitation include short-term biochemical and physiological processes (O'Neill *et al.* 1989; Saito *et al.* 2008), and long-term community interactions between primary producers and abiotic processes (Howarth 1988; Arrigo 2005). Furthermore, additional studies have noted that interactions with other trophic levels (herbivores, microbial decomposers) can alter the proximate limitation status of the primary producer community (Daufresne & Loreau 2001; Cherif & Loreau 2007, 2009, 2013). In addition, the presence of herbivores could also interact with the nutrients to result in unexpected responses in primary producer biomass, including increases despite significant top-down herbivory (e.g. Gruner *et al.* 2008). However, the above-mentioned mechanisms focus solely on the local processes within the ecosystem, despite growing awareness of nutrient inputs and trophic interactions occurring across ecosystem boundaries (O'Neill 2001; Loreau *et al.* 2003; Polis *et al.* 2004; Leroux & Loreau 2008; Massol *et al.* 2011; Bartels *et al.* 2012).

The lack of spatial processes could lead to erroneous conclusions about the underlying mechanisms controlling primary producer biomass responses and community composition. For example, Hagerthey & Kerfoot (2005) showed that spatial variation in N : P groundwater fluxes affected algal species assemblages and biovolume across a single lake, and each local assemblage varied in their nutrient limitation status according to stoichiometric ratios. The whole lake could be characterised as being a co-limited ecosystem, but each section of the lake would generally be limited by only one nutrient. The co-limitation status of the ecosystem therefore emerges due to its spatial heterogeneity, rather than through local processes. One way of integrating these spatial processes in order to capture such effects is to look at ecosystems as meta-ecosystems, where fluxes of materials and organisms between 'local' ecosystems can interact with local processes to create emergent ecosystem functions and properties (Loreau *et al.* 2003; Massol *et al.* 2011).

In this study, we propose a stoichiometrically explicit meta-ecosystem model to explore how nutrient co-limitation could emerge at local and regional scales because of spatial fluxes of organisms and nutrients. To do so, we looked at both proximate and ultimate responses of autotrophs to nutrients within local model ecosystems that are dominated by top-down control by herbivores with and without spatial fluxes and with identical local ecosystem parameters. In these model systems, the autotrophs lacked any local mechanisms for nutrient co-limitation. Despite these strict conditions, the movements of nutrients and organisms were capable of generating spatial heterogeneity in proximate limitation within the meta-ecosystem. Furthermore, the spatial fluxes removed the effects of local top-down control by herbivores, allowing for the ultimate co-limitation to emerge at the meta-ecosystem and ecosystem levels. Our results indicate that the empirical patterns of nutrient co-limitation could, in part, be generated by purely spatial processes and highlight the need to integrate fluxes of materials and organisms into the framework of nutrient limitation.

METHODS

General model development

Our model is based on a hierarchy of processes and scales within a meta-ecosystem (Fig. 1). At the level of individual ecosystem components, the stoichiometric compositions of local autotroph (X) and herbivore (Y) biomass are key drivers of higher ecosystem processes (Fig. 1a). The biomass of the autotroph can be expressed as the sum of the total amount of each element k in the biomass (P_k), or $X = \sum_{k=1}^{l} P_k$, where l is the total number of elements in the biomass (Fig. 1a; Daufresne & Hedin 2005). Similar expressions can be derived for herbivores, with $Y = \sum_{k=1}^{l} \Theta_k$, where Θ_k is the total amount of each element k in herbivore biomass. Assuming that both autotrophs and herbivores have fixed stoichiometry, then we can defined constant quotients for each element k in autotrophs (q_k) and herbivores (ρ_k; Fig. 1a):

$$q_k = \frac{P_k}{\sum_{k=1}^{l} P_k}, \quad \rho_k = \frac{\Theta_k}{\sum_{k=1}^{l} \Theta_k} \tag{1}$$

For this study, we restrict ourselves to two limiting elemental nutrients that are available in the local ecosystem, R and S, with the rest of the biomass being composed of other elements, $P_O = X - P_R - P_S$ (Fig. 1a, b). To simplify our model analysis, we will assume that the quotient of each other elements is the same for herbivores and autotrophs (i.e. $q_W = \rho_W$ for any element W that is not R or S), which we will denote by generic quotients q_O and ρ_O. In addition, we will be assuming for the rest of the paper that herbivores have a lower R: S ratio than autotrophs, leading to $q_R > \rho_R$ and $\rho_S > q_S$.

At the level of the local ecosystem, we model numerous processes which determine the available pools of nutrients R and S along with the autotroph and herbivore biomasses (Fig. 1b). The growth of autotroph biomass is determined by three processes: nutrient uptake, $U(R,S)$, intrinsic losses, MX, where M is constant, and herbivory, $H(X)Y$ (Fig 1b). Nutrient uptake obeys Liebig's Law of the Minimum in order to force autotrophs within a local ecosystem to be limited by one nutrient at a time and follows Michaelis-Menten kinetics, which leads to the following equation:

$$\begin{aligned} U(R,S) &= \min\left(\frac{u(R)}{q_R}, \frac{u(S)}{q_S}\right) \\ &= \min\left(\frac{V_R R}{q_R(K_R + R)}, \frac{V_S S}{q_S(K_S + S)}\right) \end{aligned} \tag{2}$$

where min is the minimum function, V_R and V_S are maximum uptake rates, and K_R and K_S are half-saturation constants.

Herbivore biomass increases with herbivory that is modified by a stoichiometric imbalance, $\gamma H(X)Y$, where $\gamma = \frac{q_S}{\rho_S}$, and decreases with intrinsic losses, LY, where L is constant (Fig. 1b). For the rest of this study, the herbivore will have a Type II functional response:

$$H(X) = \frac{\alpha X}{\beta + X}, \tag{3}$$

where α is the maximum rate of herbivory and β is the half-saturation constant.

The processes occurring at the local ecosystem that affect the levels of nutrient R are abiotic inputs (I) and outputs (ER), autotroph nutrient uptake ($q_R U(R,S)$), and nutrient recycling through intrinsic losses of autotrophs ($\epsilon_R q_R MX$, $0 \geq \epsilon_R \geq 1$), intrinsic herbivore losses ($\chi_R \rho_R LY$, $0 \geq \chi_R \geq 1$) and stoichiometric imbalances ($\bar{\gamma} H(X)Y$, $\bar{\gamma} = q_R - \rho_R \gamma$; Fig. 1b). Similarly, gains in the available nutrient S occur through abiotic inputs Φ and nutrient recycling from the intrinsic losses of autotrophs ($\epsilon_S q_S M(X)$, $0 \geq \epsilon_S \geq 1$) and of herbivores ($\chi_S \rho_S L(Y)$, $0 \geq \chi_S \geq 1$), and losses in available nutrient S occur through abiotic outputs ΔS and nutrient uptake ($q_S U(R,S)$; Fig. 1b).

At the meta-ecosystem level, two different elements link local ecosystems together. The diffusive movement of

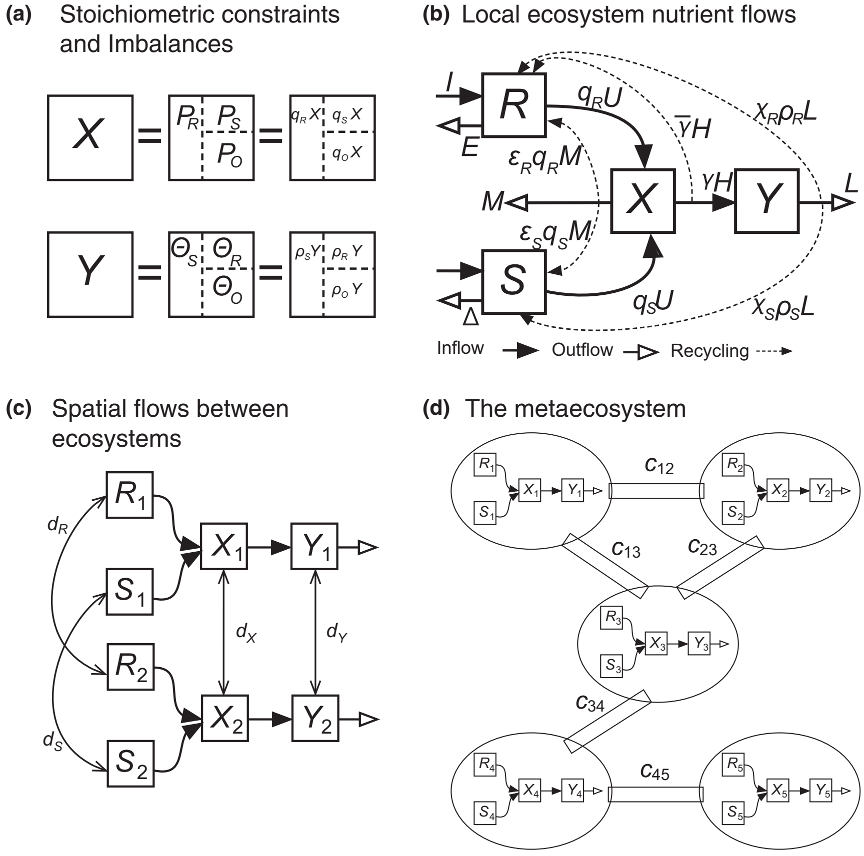

Figure 1 Hierarchy of processes and scales within the meta-ecosystem model. (a) Autotroph and herbivore biomass (X and Y) are the sum of the individual contributions (P and Θ, respectively) of each element (R, S, and all other elements, O). For a given P_k (or Θ_k), it is equal to $q_k X$ (or $\rho_k Y$), where q_k (or ρ_k) is the portion of element k in a unit of biomass. (b) Abiotic nutrient element inflows (I and Φ) and outflows (E and Δ) provide available nutrients for autotroph growth ($q_R U$ and $q_S U$), which provide nutrients for herbivore growth (γH). Biomass lost by autotrophs (M) and herbivores (L) is partially recycled ($\epsilon_R q_R M$, $\epsilon_S q_S M$, $\chi_R \rho_R L$ and $\chi_S \rho_S L$), as are nutrients not utilised due to stoichiometric imbalance ($\bar{\gamma} H$). (c) Nutrients and organisms move diffusively between the ecosystems at their own rates (d_R, d_S, d_X and d_Y). (d) The connections between ecosystems are determined by the off-diagonal elements of the connectivity matrix (c_{ij}).

nutrients (d_R and d_S), of autotrophs (d_X) and of herbivores (d_Y) connect the local ecosystems, if such connections exist (Fig. 1c). However, the structure of connections between the ecosystems is determined by connectivity matrix, whose positive off-diagonal elements, c_{ij} where $i \neq j$, indicate a connection between a pair of ecosystems (Fig. 1 d). The size of the connectivity matrix is $n \times n$, where n is the total number of local ecosystems in the meta-ecosystem. For the connectivity matrices used in this paper, we assume that the value of a positive c_{ij} is equal to $1/(n-1)$, $c_{ij} = c_{ji}$ if $i \neq j$ and $c_{ii} = -\sum_{j \neq i}^{n} c_{ij}$ in order to utilise some theorems regarding the stability of spatially homogeneous solutions (Jansen & Lloyd 2000).

Combining all these processes together gives us the following system of ordinary differential equations that describe the dynamics of the meta-ecosystem:

$$\frac{dR_i}{dt} = I - ER_i - q_R U(R_i, S_i)X_i + \epsilon_R q_R M X_i + \chi_R \rho_R L Y_i + \bar{\gamma} H(X_i) Y_i + d_R \sum_{j=1}^{n} c_{ij} R_j \tag{4a}$$

$$\frac{dS_i}{dt} = \Phi - \Delta S_i - q_S U(R_i, S_i)X_i + \epsilon_S q_S M X_i + \chi_S \rho_S L Y_i + d_S \sum_{j=1}^{n} c_{ij} S_j \tag{4b}$$

$$\frac{dX_i}{dt} = U(R_i, S_i)X_i - MX_i - H(X_i)Y_i + d_X \sum_{j=1}^{n} c_{ij} X_j \tag{4c}$$

$$\frac{dY_i}{dt} = \gamma H(X_i)Y_i - LY_i + d_Y \sum_{j=1}^{n} c_{ij} Y_j. \tag{4d}$$

Note that the model parameters are the same across the meta-ecosystem, such that in the lack of spatial processes there would be no differences in the dynamics of the local ecosystems. Furthermore, we restrict our focus on parameter values that allow for a stable coexistence equilibrium for autotrophs and herbivores, as they can also coexist through stable limit cycles after a Hopf bifurcation (Appendix S1).

Measures for proximate and ultimate nutrient (co)limitation

In order to investigate how the movement of nutrients and organisms can be a mechanism of nutrient co-limitation, we have to be precise in how we measure nutrient co-limitation. In this study, we will use two main measures: the potential uptake ratios of autotrophs in local ecosystems and the long-term growth responses of autotrophs at local and meta-ecosystem scales. The first measure serves as our indicator for proximate limitation for the autotrophs, while the second indicates ultimate limitation (Vitousek *et al.* 2010).

As mentioned previously, autotrophs within a local ecosystem can only be proximally limited by one nutrient at a time because of the presence of the minimum function, the mathematical expression of Liebig's Law of the Minimum, in eqn 2. The implication for this minimum function is if the ecosystem is at a stable equilibrium, a short-term pulse of one nutrient would lead to an instantaneous growth response in the autotrophs, while a pulse of the other nutrient would not (Appendix S2). Therefore, without any spatial processes, each local ecosystem will see the same instantaneous growth response to one nutrient, which is determined by the following ratio:

$$\begin{aligned}&\left(\frac{q_S}{q_R}\right)\left(\frac{u(R_i)}{u(S_i)}\right) > 1\\ &\qquad \Rightarrow \frac{u(R_i)}{u(S_i)} > \frac{q_R}{q_S}.\end{aligned} \tag{5}$$

In words, the above condition implies that if relative ratio of potential $R : S$ uptake is greater than the stoichiometric $R : S$ ratio in the autotrophs, then autotroph growth is proximally S-limited in ecosystem i. If the ratio of potential $R : S$ uptake is less than the autotroph $R : S$ ratio, then autotroph growth is proximally R-limited in ecosystem i.

Now, if the movement of nutrients and organisms can cause the limiting nutrient to change in some, but not all, local ecosystems, experiments would be able to detect instantaneous growth responses for the autotrophs for both nutrients within the meta-ecosystem. This result can be caused by simple diffusive movement that generates spatial heterogeneity, even when the local supply of nutrients is the same in each local ecosystem (Marleau *et al.* 2010, 2014). As long as this heterogeneity has different impacts on the availability of each nutrient in the local ecosystems, the autotrophs can then be limited by different nutrients in the local ecosystems.

Therefore, if ecologists performed a short-term nutrient addition experiment that looked at the nearly instantaneous response of autotrophs as is commonly done (e.g. Harpole *et al.* 2011), they would detect nutrient co-limitation at the meta-ecosystem scale, but not at the local ecosystem scale when the local autotrophs differed in their potential $R : S$ uptake ratios at equilibrium. Because of the metric used, we will call this form of nutrient co-limitation in a meta-ecosystem 'spatial proximate co-limitation' and we detect it by determining if at least one local ecosystem differs in its proximate nutrient limitation status from the others. In addition, the presence of spatial proximate co-limitation within a meta-ecosystem could suggest changes in the autotroph community composition, though not in this model (Wolfe *et al.* 2001; Hagerthey & Kerfoot 2005; Elser *et al.* 2009).

Another metric that can be used to detect nutrient co-limitation is to perform long-term factorial nutrient addition experiments and measure the increase in autotroph biomass after a set period of time (Harpole *et al.* 2011). If the movement of organisms and nutrients can be a mechanism for nutrient co-limitation, then according to this metric we should see co-limited growth responses of autotrophs at the local ecosystem and/or meta-ecosystem scale after the set time period. A co-limited response includes autotroph biomass increasing to the addition of R and S by themselves (independent co-limitation) and autotroph biomass increasing only with the addition of both nutrients together (simultaneous co-limitation; Harpole *et al.* 2011). Therefore, when we do detect such an increase, we will say that 'ultimate colimitation' has occurred.

The relationship between proximate and ultimate co-limitation is not simple. In this model, it is not possible for a local ecosystem to demonstrate proximate nutrient co-limitation in autotroph growth, but a local ecosystem could display ultimate co-limitation due to the movements of nutrients and organisms. In addition, a meta-ecosystem that displays spatial proximate co-limitation may or may not demonstrate ultimate co-limitation at the meta-ecosystem scale, as processes beyond autotroph responses to nutrients regulate autotroph biomass. These metrics of nutrient co-limitation are distinct and need to be considered separately.

Model analysis

Our investigation into how movement can generate co-limitation at local ecosystem and meta-ecosystem scales utilises both analytical and numerical techniques. Analytically, we perform a local stability analysis for spatially homogeneous solutions that lead to stable equilibria. In addition, we use the properties of the connectivity matrix, the Jacobian matrix associated with eqn 4 and the movement rates to determine parameter ranges that allow for spatial heterogeneity. For all Figures presented here, we use the parameter set presented in Table 1 for local ecosystem properties.

Within those ranges, we investigate whether spatial proximate and ultimate co-limitation may emerge due to the spatial processes through the use of numerical simulations. To test for ultimate co-limitation, we perform a simulation of a factorial nutrient addition experiment through permanently increasing nutrient input levels by 50% from a control level. Within these same experiments, we also examine if spatial proximate co-limitation is occurring after nutrient additions by measuring the number of proximately S-limited ecosystems within the meta-ecosystem. In addition, we evaluate the importance of the movement of both nutrients, as in the cases, we explore here only the movement of one nutrient can initially affect the spatially homogeneous solution. Furthermore, we investigate whether the spatial structure of the meta-ecosystem will affect both ultimate and spatial proximate co-limitation. All numerical simulations are performed using Matlab and the ode package.

RESULTS

Expectations from a meta-ecosystem with no spatial flows between ecosystems

At a local ecosystem equilibrium with no movement, there will be no change in autotroph equilibrium biomass with an

Table 1 The definitions and values of the ecosystem parameters used in the Figures

Parameter (unit)	Definition	Value used
I (gram R day^{-1})	Influx of available R into ecosystem	1 and 1.5
Φ (gram S day^{-1})	Influx of available S into ecosystem	0.1 and 0.15
E (day^{-1})	Efflux of available R from ecosystem	0.4
Δ (day^{-1})	Efflux of available S from ecosystem	0.3
M (day^{-1})	Mass-specific loss rate of autotrophs	1
q_R (gram R per gram of autotroph biomass)	Proportion of R that makes up 1 g of autotroph biomass	0.4
q_S (gram S per gram of autotroph biomass)	Proportion of S that makes up 1 g of autotroph biomass	0.04
V_R (gram R per gram of autotroph biomass day^{-1})	Maximum R uptake rate	2
V_S (gram S per gram of autotroph biomass day^{-1})	Maximum S uptake rate	0.2
K_R (gram R)	Half-saturation constant for R uptake	0.5
K_S (gram S)	Half-saturation constant for S uptake	0.05
ϵ_R (−)	Proportion of R lost by autotrophs that is recycled	0
ϵ_S (−)	Proportion of S lost by autotrophs that is recycled	0
ρ_R (gram R per gram of herbivore biomass)	Proportion of R that makes up 1 g of herbivore biomass	0.38
ρ_S (gram S per gram of herbivore biomass)	Proportion of S that makes up 1 g of herbivore biomass	0.06
α (gram of autotroph biomass per gram of herbivore biomass day^{-1})	Maximum herbivory rate	6
β (gram of autotroph biomass)	Half-saturation constant for herbivory	6
L (day^{-1})	Mass-specfic loss rate of herbivores	0.5
χ_R (−)	Proportion of R lost by herbivores that is recycled	0
χ_S (−)	Proportion of S lost by herbivores that is recycled	0

increase in nutrient inputs if the equilibrium remains stable (Appendix S1). This result is seen from the expression for equilibrium autotroph biomass:

$$X^* = \frac{\beta L}{\frac{q_S}{\rho_S}\alpha - L} \tag{6}$$

Note the lack of any parameter involving the nutrient inputs. The lack of response of the autotrophs to the long-term addition of nutrients is because of the top-down control exerted by the herbivore, which does respond positively in biomass to the addition of nutrients (Appendix S1). Therefore, as long as the equilibrium remains stable to the changes in nutrient input levels, the autotrophs will exhibit no long-term response to nutrient levels and cannot exhibit ultimate co-limitation at any scale.

The proximate limitation status of the local ecosystems will also all be the same when there is no movement, which means addition of nutrients can only change the proximate limitation status of the whole meta-ecosystem when there is no movement between ecosystems (Appendix S1). This result means that spatial proximate co-limitation is also not possible without the local ecosystem equilibrium becoming destabilised.

The local ecosystem equilibrium can be destabilised by high movement rates for the herbivores and the limiting nutrient as long as the movement rate of autotrophs remains small (Appendix S1; Marleau *et al.* 2014). This destabilisation causes the emergence of spatially heterogeneous equilibria in each local ecosystem (Marleau *et al.* 2014). The movement rate of the non-limiting nutrient at equilibrium has no impact on the stability of the local equilibrium (Appendix S1). Therefore, we chose a set of movement rate parameters ($d_Y = 10$, $d_X = 0.001$, $d_S = 10$ and $d_R = 1$) that allowed for this destabilisation, though many other parameter sets with low autotroph movement rates and sufficient herbivore and limiting nutrient movement rates would generate similar results. For the remainder of this paper, we will assume that S is proximately limiting the autotrophs at the spatially homogeneous equilibrium.

Emergence of nutrient co-limitation through movement

Adding movement to the meta-ecosystem ($d_Y = 10$, $d_X = 0.001$, $d_S = 10$, $d_R = 1$) causes the emergence of both types of co-limitation in response to nutrient additions (Fig. 2). For a meta-ecosystem where each ecosystem is connected to every other ecosystem (Fig 2d), we can observe ultimate co-limitation for autotroph growth at the meta-ecosystem scale (Fig 2a). Furthermore, the local ecosystems differ in their limitation status for autotrophs, which indicates spatial proximate co-limitation (Fig. 2b and Fig. S1).

Two local ecosystems display large increases in autotroph biomass to simultaneous additions of R and S, while autotroph biomass collapses elsewhere (Fig. 2c). Heterogeneity in local ecosystem responses is driven by the initial conditions, such that the identities (but not the number) of ecosystems with low autotroph biomass vary with initial conditions (compare Fig. 2c with Fig. 3c). The collapse and the increase of local autotroph biomass can be explained through the actions of the other ecosystem compartments (Fig. 3).

The spatial heterogeneity seen across the meta-ecosystem and within each ecosystem compartment is generated by the differences in movement rates between ecosystem compartments amplifying differences in the initial autotroph biomass (Fig. 3). High local autotroph biomass leads to a local increase in herbivores and a decrease in available nutrient S, which can still be seen at equilibrium (Fig. 3b, d). However, the high herbivore movement rate causes most of the new herbivore biomass to leave the local ecosystem while the high nutrient S movement rate causes nutrients from neighbouring ecosystems to flood in, leading to fairly even distribution of both nutrient S and herbivores across the meta-ecosystem (Fig. 3b, d).

The autotrophs in the surrounding ecosystems then suffer higher herbivory and have less limiting nutrient, which causes them to decline. The lower autotroph biomass then frees up more nutrient S, which is then quickly moved to the

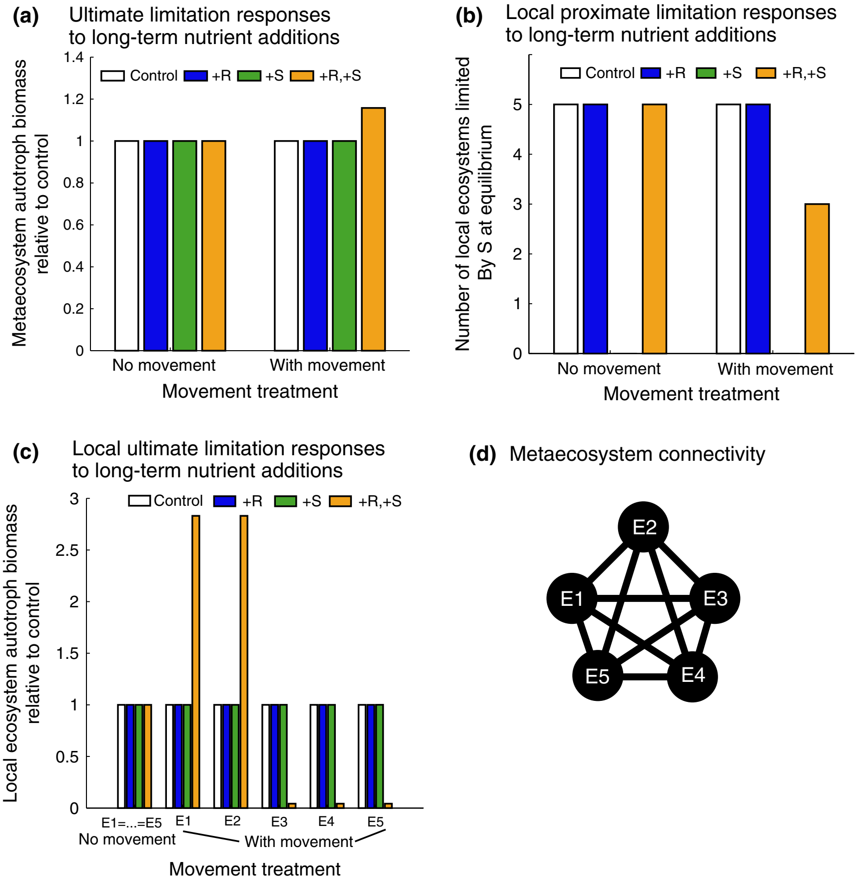

Figure 2 The emergence of co-limitation due to the movement of nutrients and organisms. The movement rates in the movement 'treatment' are $d_R = 1$, $d_S = 10$, $d_X = 0.001$ and $d_Y = 10$. (a) At the meta-ecosystem scale, there is ultimate (and simultaneous) co-limitation of the autotrophs to the addition of nutrients when movement is present, while no response is observed without movement due to top-down control of herbivores. (b) The meta-ecosystem also exhibits spatial proximate co-limitation with the addition of both nutrients when movement is present, while no such co-limitation is observed when movement is absent. (c) At the local ecosystems, there is both ultimate co-limitation and collapses for autotroph biomass when movement is present, but no such responses without movement. (d) Diagram indicating the meta-ecosystem connectivity used in the simulations.

ecosystem with high autotroph biomass and leads to even greater disparity in autotroph biomass, which is maintained as very little autotroph biomass is transferred between ecosystems due to the low autotroph movement rate (Fig. 3c). The very high levels of autotroph biomass cause large declines in local available nutrient R level, which cannot be replaced as nutrient R does not diffuse as fast as nutrient S, and causes the autotrophs to become proximately limited by R (Fig. 3a). This leads to the spatial proximate co-limitation because the ratios of R to S differ between local ecosystems and leads to the patterns seen in Fig. 2b.

The key ingredients to the generation of this proximate co-limitation is the differences in movement rates and the loss of top-down control at a local level, which then allows autotrophs to respond to nutrient additions. These general mechanisms are also involved in the generation of the ultimate co-limitation (Fig. 2a).

Nutrient co-limitation is dependent on movement rates and meta-ecosystem connectivity

To explain the ultimate co-limitation seen at the meta-ecosystem level, it is necessary to alter the movement rate of nutrient R (d_R), though we leave the other movement rates unchanged ($d_Y = 10$, $d_X = 0.001$, $d_S = 10$; Fig. 4). When there is no movement of nutrient R, we see only a weak co-limitated response at the meta-ecosystem level (Fig. 4a). This result occurs despite spatial proximate co-limitation and the presence of ultimate co-limitation within local ecosystems (Fig. 4b, c).

Increasing the movement rate of nutrient R results in stronger co-limited response at the meta-ecosystem level and the eventual elimination of spatial proximate co-limitation (Fig. 4a, b). Furthermore, at high d_R values, one ecosystem demonstrates a very large increase in autotroph biomass to nutrient additions, while all the others show a large decline in autotroph biomass (Fig. 4d). However, the increased movement in nutrient R allows for more nutrients R to reach the autotrophs whose biomass is no longer strictly controlled by herbivores as indicated by eqn 6 in the spatially homogeneous case, leading to a greater meta-ecosystem autotroph biomass than when d_R is lower (Fig. 4a). Increasing d_R further allows for serial limitation, where the autotrophs demonstrate limitation by nutrient S, but demonstrate a greater biomass response to the addition of both nutrients (Fig. S2).

We also controlled for the topology of meta-ecosystem connectivity to see how much of this behaviour is driven by the

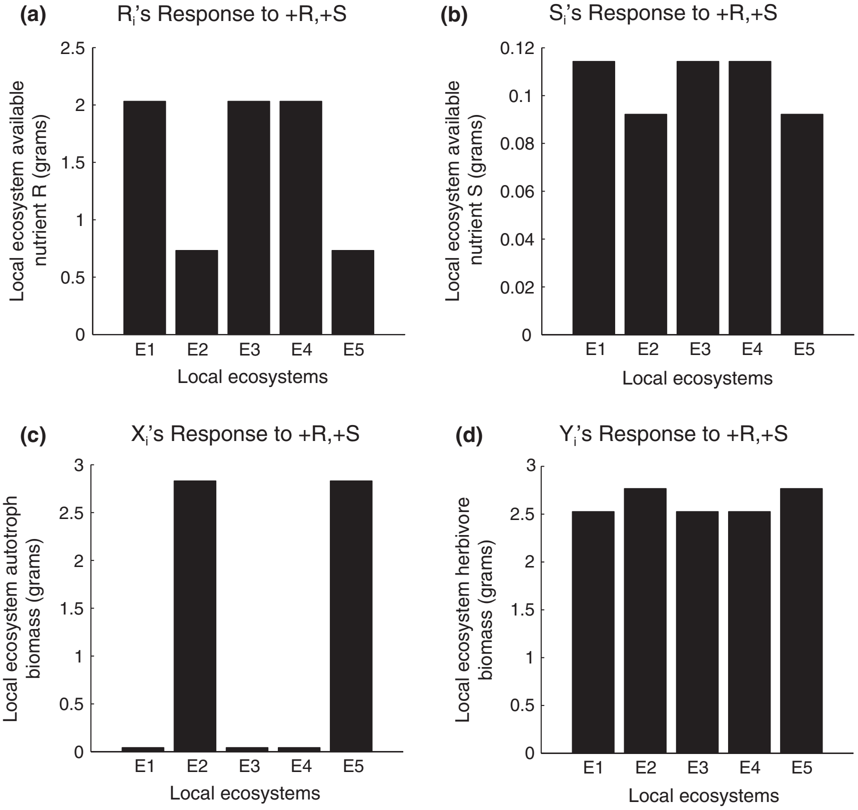

Figure 3 The local ecosystem levels of available nutrients R (a) and S (b) and of biomasses of autotrophs (c) and (d) herbivores after increases in I and Φ destabilise the spatially homogeneous solution (parameters are the same as in Fig. 2). Large movement rates for nutrient S and herbivores allow for an even distribution across the meta-ecosystem, but small movement rates for nutrient R and autotrophs make them more isolated from the rest of the meta-ecosystem. These differences in movement rates allows for spatial heterogeneity in autotroph biomass to emerge because herbivore biomass is now dictated by regional, not local, autotroph biomass. Local differences in autotroph biomass then leads to differential pressures on nutrients in local ecosystems, with S availability being maintained by influxes from other ecosystems, while R availability declines due to lack of movement between ecosystems. These effects together give rise to the co-limitations seen in this study.

movement rates compared to the other spatial variables (Fig. 5a). Using a linear arrangement of ecosystems in the meta-ecosystem managed to alter many of the effects of increasing d_R, but both types of co-limitation still occurred (Fig. 5). There is only a limited increase in meta-ecosystem autotroph biomass with the addition of both nutrients even at large d_R values (Fig. 5b), and the range of d_R values that allow for spatial proximate co-limitation is more limited (Fig. 5c). Lastly, the local ecosystems can exhibit a range of responses to the addition of both nutrients that do not necessarily appear with other spatial configurations of meta-ecosystems (Fig. 5d).

DISCUSSION

We developed a stoichiometrically explicit meta-ecosystem model to evaluate if spatial processes can give rise to the emergent phenomena of nutrient co-limitation at local and regional scales. In addition, we distinguished types of nutrient co-limitation that could occur at regional scales, which are ultimate and spatial proximate co-limitation. Our results show that the movement of nutrients and organisms can create spatial heterogeneity in both local autotroph nutrient uptake limitation and long-term growth responses to nutrient additions, thereby leading to the detection of nutrient co-limitation at local and regional scales. Without this regional mechanism of spatial flows, no detectable nutrient co-limitation could be observed at equilibrium. The presence of these types of nutrient co-limitation is modulated by the movement rate of the non-limiting nutrient at the local ecosystem equilibrium. Furthermore, these results are robust across different meta-ecosystem topologies, though the spatial structure impacts the quantitative effects at the regional level and qualitative responses at the local ecosystem level.

Nutrient co-limitation at local scales: limitations of local processes to explain patterns

Ecologists have proposed a number of mechanisms to explain the persistent patterns of nutrient co-limitation in autotroph biomass responses observed in nutrient addition experiments (Arrigo 2005; Danger *et al.* 2008; Saito *et al.* 2008; Craine 2009; Harpole *et al.* 2011). The mechanisms include differences in nutrient uptake and chemical composition in the autotroph community (Arrigo 2005; Danger *et al.* 2008), forms of biochemical dependence (Arrigo 2005; Saito *et al.* 2008), low nutrient availabilities (Arrigo 2005) and adaptive changes in the nutrient uptake complexes of plants to achieve 'balanced growth' (Klausmeier *et al.* 2007). While the

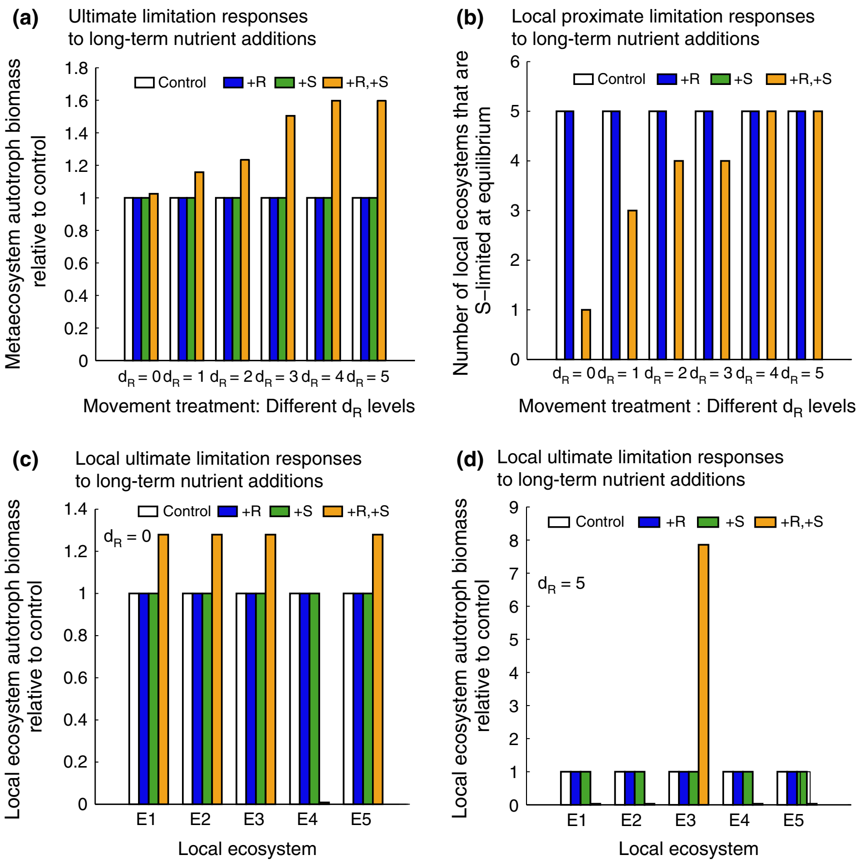

Figure 4 The effects of changing nutrient R's movement rate (d_R) on the local ecosystem and meta-ecosystem responses to nutrient additions. (a) At the meta-ecosystem level, the ultimate co-limitation becomes much stronger as d_R increases (50% increase at $d_R = 5$). (b) The number of ecosystems limited by nutrient S at equilibrium after both nutrients are added varies greatly with d_R, with only one ecosystem being S-limited at equilibrium for $d_R = 0$ to all being S-limited at $d_R = 4$ and greater. (c) The autotroph biomass shows ultimate co-limitation to the addition of both nutrients in local ecosystems at low d_R in four ecosystems, while one ecosystem had a collapse of its autotrophs. (d) The biomass responses of autotrophs to the addition of both nutrients in local ecosystems at high d_R show only one ecosystem being ultimately co-limited, while the other ecosystems see their autotroph biomass collapse.

effectiveness of these mechanisms to generate increases in autotroph biomass with the addition of multiple nutrients and our ability to distinguish the mechanisms by such responses are open questions (Marleau and Loreau, in revision), it is clear that local processes are used to explain the observed patterns.

However, there is growing evidence that ecosystem processes occurring outside the focal ecosystem can drive patterns within the focal ecosystem through unidirectional and bidirectional flows of materials, nutrients and organisms (Polis *et al.* 2004; Leroux & Loreau 2008; Gravel *et al.* 2010; Massol *et al.* 2011; Loreau *et al.* 2013). For example, our study adds to this literature by further demonstrating that local nutrient proximate limitation, which can alter the autotroph community composition (e.g. Wolfe *et al.* 2001; Hagerthey & Kerfoot 2005), can be determined by herbivores and limiting nutrients moving between locally identical ecosystems. Furthermore, examining nutrient limitation at only local scales could give a false impression about the limiting nutrients at the meta-ecosystem scale, as local ecosystems showed both R and S proximate limitation such that autotroph limitation was co-limited spatially. This emergent form of co-limitation could only be examined through explicit analysis of spatial processes.

Our results also indicate that autotroph ultimate co-limitation at local scales can also be generated through spatial processes, despite the lack of local mechanisms for nutrient co-limitation. This result indicates integrating local nutrient co-limitation mechanisms into ecosystem models based on autotroph-only models and assuming the ubiquity of co-limited autotroph growth responses (Danger *et al.* 2008; Harpole *et al.* 2011), could be detrimental. As our analysis suggests, the ultimate co-limitation could be instead driven by spatial processes. Therefore, adding putative nutrient co-limitation mechanisms to models when we have difficulty identifying the mechanisms that drive ultimate co-limitation (e.g. Marleau and Loreau, in revision), may not lead to greater realism and accuracy in model predictions if spatial processes are operating, and need greater justification than currently given, such as physiological data on nutrient uptake rates (e.g. Saito *et al.* 2008).

Linking nutrient co-limitation to spatial and trophic structure

Previous studies on nutrient co-limitation have focused primarily on autotrophs and local processes to the exclusion of other trophic levels and of spatial fluxes (though see Sperfeld *et al.* 2012). Our study has demonstrated the importance of

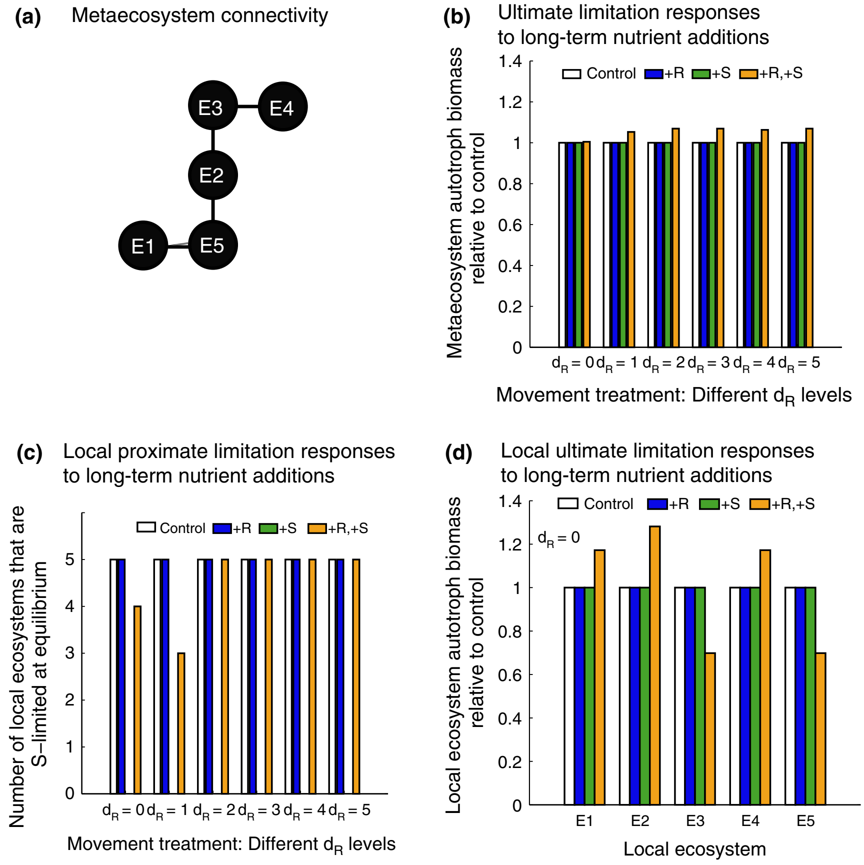

Figure 5 The effects of changing meta-ecosystem connectivity on the local ecosystem and meta-ecosystem responses to nutrient additions. (a) Diagram indicating the meta-ecosystem connectivity used in the simulation of Fig. 5. (b) At the meta-ecosystem level, the ultimate co-limitation does not become much stronger as d_R increases, unlike in Fig. 4. (c) The number of ecosystems limited by nutrient S at equilibrium after both nutrients are added varies only for low d_R, with all ecosystems being S-limited at equilibrium for d_R greater than 2. (d) The autotrophs show ultimate co-limitation in three ecosystems, while two ecosystems show a slight decline in their autotrophs.

considering the role of spatial and trophic structure in generating both proximate and ultimate co-limitation at different spatial scales.

For spatial structure, we provided a clear signal that the presence of spatially heterogeneous nutrient limitation of autotrophs and of strong co-limited growth responses in the meta-ecosystem was dependent on meta-ecosystem connectivity, which is similar to metapopulation studies on the effects of spatial structure (Hanski & Ovaskainen 2000; Fagan 2002; Ovaskainen & Hanski 2002; Keeling & Eames 2005). However, it is possible to go beyond dependence. In other work, we have shown that the eigenvalues of the connectivity matrix, which defines the connection of the meta-ecosystem, can be used in conjunction with their eigenvectors to predict relative biomass of organisms in the meta-ecosystem (Marleau *et al.* 2014). Since in our model, high autotroph biomass indicates ultimate co-limitation in the local ecosystem, we could predict which local ecosystems should display nutrient co-limitation (with certain caveats, see Marleau *et al.* 2014). Therefore, spatial structure can help us predict nutrient co-limitation when spatial processes matter.

For trophic structure, models addressing nutrient co-limitation need to move beyond nutrient–autotroph interactions. Empirical and theoretical studies have shown that other trophic levels, such as herbivores and decomposers, can alter nutrient limitation status of autotrophs and help promote nutrient co-limitation at local scales (Daufresne & Loreau 2001; Grover 2004; Cherif & Loreau 2007, 2009, 2013; Trommer *et al.* 2012; Atkinson *et al.* 2013). Furthermore, these trophic levels may become co-limited themselves, which further requires an expansion of nutrient co-limitation theory beyond autotrophs (Marleau and Loreau, in revision; Sperfeld *et al.* 2012). Lastly, because the movement rates between trophic levels differ greatly, there could be opportunities to extend the effects of movement on nutrient co-limitation to multiple trophic levels (McCann *et al.* 2005).

Interpreting nutrient addition experiments through the lens of spatial processes

In a meta-analysis of 641 nutrient addition experiments carried out in terrestrial, aquatic and marine ecosystems, over 20% of studies showed no autotroph growth response and nearly 15% showed a negative growth response to nutrient additions (Harpole *et al.* 2011). The explanations provided by the authors ranged from limited statistical power to pH changes in the soil due to nutrient additions, but other possibilities are recipient-control of autotrophs and improved nutrient quality for herbivores (Gruner *et al.* 2008). However, a meta-analysis of autotroph growth responses to nutrient additions and herbivore removal experiments indicated that herbivores cannot, in many cases, exhibit any recipient control at local scales (Gruner *et al.* 2008). The lack of local recipient control would need to be present in the almost 18% of nutrient addition experiments, resulting in simultaneous co-limited growth responses in the autotroph biomass (Harpole *et al.* 2011).

Surprisingly, our model, which lacks many of the proposed mechanisms and processes invoked by Harpole *et al.* (2011) and Gruner *et al.* (2008), can explain all of the above empirical patterns through the differences in movement rates for nutrients and organisms. Because of the high movement rates of herbivores and limiting nutrients, but low movement rates of autotrophs, there is a decoupling of herbivory from the local autotroph biomass, which can break local recipient-control and allow ultimate co-imitation to occur (Gruner *et al.* 2008; Harpole *et al.* 2011). However, this does not happen everywhere in the meta-ecosystem due to the spatial heterogeneity in autotrophs, as in some ecosystems autotrophs will demonstrate no growth response or negative growth responses to nutrient additions (Harpole *et al.* 2011). In addition, our model can even demonstrate serial limitation at high movement rates of the originally 'non-limiting' nutrient (when at control nutrient levels), which also occurs in 22% of cases (Harpole *et al.* 2011).

Of course, it is unlikely that our proposed mechanisms of differences in movement rates can apply to all the cases examined by Harpole *et al.* (2011). Movement rates of herbivores are commonly larger than autotrophs (e.g McCann *et al.* 2005), but nutrient movement also needs to be high. The presence of transport mechanisms such as overland water flow, riverine movement, oceanic currents and wind that can lead to substantial cross-ecosystem transfer of nutrients at scales similar to herbivores do provide such movement rates (Sitters *et al.* 2015). Furthermore, there is evidence that nutrients can and do differ in their movement rates, such as N and P within soils, which can lead to patterns of proximate co-limitation seen in our model (Sitters *et al.* 2015).

Nevertheless, our model does show that these mechanisms could explain at least some of the observed empirical patterns observed in nutrient addition experiments. Furthermore, our model helps us understand why non-spatial expectations of the effects of herbivores on autotroph growth responses to nutrients may be violated despite functional responses that lead to recipient-control (Gruner *et al.* 2008). Our testing for spatial signatures in biomass responses, such as heterogeneity in biomass responses between test plots after nutrient addition that had similar community composition and abiotic characteristics before nutrient addition, would help evaluate the role spatial processes can play in structuring community properties in ecosystems and meta-ecosystems.

ACKNOWLEDGEMENTS

JNM was supported by an NSERC PGS-D2 and FQRNT B2. FG was supported by the Natural Science and Engineering Research Council (NSERC) of Canada. ML was supported by the TULIP Laboratory of Excellence (ANR-10-LABX-41).

AUTHORSHIP

JNM, ML and FG designed the study. JNM developed the models and performed the analysis. JNM wrote the first draft of the manuscript and all authors contributed substantially to the revisions.

REFERENCES

Arrigo, K. (2005). Marine microorganisms and global nutrient cycles. *Nature*, 437, 349–355.

Atkinson, C.L., Vaughn, C.C., Forshay, K.J. & Cooper, J.T. (2013). Aggregated filter-feeding consumers alter nutrient limitation: consequences for ecosystem and community dynamics. *Ecology*, 94, 1359–1369.

Bartels, P., Cucherousset, J., Steger, K., Eklöv P., Tranvik, L.J., Hillebrand, H. (2012). Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics. *Ecology*, 93, 1173–1182.

Cherif, M. & Loreau, M. (2007). Stoichiometric constraints on resource use, competitive interactions, and elemental cycling in microbial decomposers. *Am. Nat.*, 169, 709–724.

Cherif, M. & Loreau, M. (2009). When microbes and consumers determine the limiting nutrient of autotrophs: a theoretical analysis. *Proc. Biol. Sci.*, 276, 487–497.

Cherif, M. & Loreau, M. (2013). Plant-herbivore-decomposer stoichiometric mismatches and nutrient cycling in ecosystems. *Proc. Biol. Sci.*, 280.

Conley, D.J., Paerl, H.W., Howarth, R.W., Boesch, D.F., Seitzinger, S.P., Havens, K.E. *et al.* (2009). Controlling eutrophication: nitrogen and phosphorus. *Science*, 323, 1014–1015.

Craine, J.M. (2009). *Resource Strategies of Wild Plants*. Princeton University Press, New Jersey.

Danger, M., Daufresne, T., Lucas, F., Pissard, S. & Lacroix, G. (2008). Does Liebig's law of the minimum scale up from species to communities? *Oikos*, 117, 1741–1751.

Daufresne, T. & Hedin, L.O. (2005). Plant coexistence depends on ecosystem nutrient cycles: extension of the resource-ratio theory. *Proc. Natl Acad. Sci. USA*, 102, 9212.

Daufresne, T. & Loreau, M. (2001). Plant-herbivore interactions and ecological stoichiometry: when do herbivores determine plant nutrient limitation? *Ecol. Lett.*, 4, 196–206.

Elser, J.J., Bracken, M.E., Cleland, E.E., Gruner, D.S., Harpole, W.S. *et al.* (2007). Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol. Lett.*, 10, 1135–1142.

Elser, J.J., Andersen, T., Baron, J., Bergström A., Jansson, A., Kyle, M. *et al.* (2009). Shifts in lake n:p stoichiometry and nutrient limitation driven by atmospheric nitrogen deposition. *Science*, 326, 835–837.

Fagan, W.F. (2002). Connectivity, fragmentation, and extinction risk in dendritic metapopulations. *Ecology*, 83, 3243–3249.

Gravel, D., Guichard, F., Loreau, M. & Mouquet, N. (2010). Source and sink dynamics in metaecosystems. *Ecology*, 91, 2172–2184.

Grover, J.P. (2004). Predation, competition, and nutrient recycling: a stoichiometric approach with multiple nutrients. *J. Theor. Biol.*, 229, 31–43.

Gruner, D.S., Smith, J.E., Seabloom, E.W., Sandin, S.A., Ngai, J.T., Hillebrand, H. *et al.* (2008). A cross-system synthesis of consumer and nutrient resource control on producer biomass. *Ecol. Lett.*, 11, 740–755.

Güsewell, S., Koerselman, W. & Verhoeven, J.T.A. (2003). Biomass n:p ratios as indicators of nutrient limitation for plant populations in wetlands. *Ecol. Appl.*, 13, 372–384.

Hagerthey, S.E. & Kerfoot, W.C. (2005). Spatial variation in groundwater-related resource supply influences freshwater benthic algal assemblage composition. *J. N. Am. Benthol. Soc*., 24, 807–819.

Hanski, I. & Ovaskainen, O. (2000). The metapopulation capacity of a fragmented landscape. *Nature*, 404, 755–758.

Harpole, W.S., Ngai, J.T., Cleland, E.E., Seabloom, E.W., Borer, E.T., Bracken, M.E. *et al*. (2011). Nutrient co-limitation of primary producer communities. *Ecol. Lett*., 14, 852–862.

Howarth, R.W. (1988). Nutrient limitation of net primary production in marine ecosystems. *Annu. Rev. Ecol. Syst*., 19, 89–110.

Howarth, R.W. & Marino, R. (2006). Nitrogen as the limiting nutrient for eutrophication in coastal marine ecosystems: evolving views over three decades. *Limnol. Oceanogr*., 51, 364–376.

Jansen, V.A. & Lloyd, A.L. (2000). Local stability analysis of spatially homogeneous solutions of multi-patch systems. *J. Math. Biol*., 41, 232–252.

Keeling, M.J. & Eames, K.T.D. (2005). Networks and epidemic models. *J. R. Soc. Interface*, 2, 295–307.

Klausmeier, C.A., Litchman, E. & Levin, S.A. (2007). A model of flexible uptake of two essential resources. *J. Theor. Biol*., 246, 278–289.

Leroux, S.J. & Loreau, M. (2008). Subsidy hypothesis and strength of trophic cascades across ecosystems. *Ecol. Lett*., 11, 1147–1156.

Loreau, M., Mouquet, N. & Holt, R.D. (2003). Metaecosystems: a theoretical framework for a spatial ecosystem ecology. *Ecol. Lett*., 6, 673–679.

Loreau, M., Daufresne, T., Gonzalez, A., Gravel, D., Guichard, F., Leroux, S.J. *et al*. (2013). Unifying sources and sinks in ecology and earth sciences. *Biol. Rev*., 88, 365–379.

Low-Decarie, E., Fussmann, G.F. & Bell, G. (2014). Aquatic primary production in a high-co2 world. *Trends Ecol. Evol*., 29, 223–232.

Marleau, J.N., Guichard, F., Mallard, F. & Loreau, M. (2010). Nutrient flows between ecosystems can destabilize simple food chains. *J. Theor. Biol*., 266, 162–174.

Marleau, J.N., Guichard, F. & Loreau, M. (2014). Metaecosystem dynamics and functioning on finite networks. *Proc. Biol. Sci*., 281, 2013–2094.

Massol, F., Gravel, D., Mouquet, N., Cadotte, M.W., Fukami, T. & Leibold, M.A. (2011). Linking community and ecosystem dynamics through spatial ecology. *Ecol. Lett*., 14, 313–323.

McCann, K.S., Rasmussen, J.B. & Umbanhowar, J. (2005). The dynamics of spatially coupled food webs. *Ecol. Lett*., 8, 513–523.

Michalak, A.M., Anderson, E.J., Beletsky, D., Boland, S., Bosch, N.S., Bridgeman, T.B. *et al*. (2013). Record-setting algal bloom in lake erie caused by agricultural and meteorological trends consistent with expected future conditions. *Proc. Natl Acad. Sci. USA*, 110, 6448–6452.

O'Neill, R.V. (2001). Is it time to bury the ecosystem concept? (With full military honors, of course!). *Ecology*, 82, 3275–3284.

O'Neill, R.V., DeAngelis, L.D.Pastor, J.J., Jackson, B.J., Post, W.M. (1989). Multiple nutrient limitations in ecological models. *Ecol. Model*., 46, 147–163.

Ovaskainen, O. & Hanski, I. (2002). Transient dynamics in metapopulation response to perturbation. *Theor. Popul. Biol*., 61, 285–295.

Polis, G.A., Power, M.E. & Huxel, G.R. (2004). *Food Webs at the Landscape Level*. University of Chicago Press, Chicago.

Saito, M., Goepfert, T. & Ritt, J. (2008). Some thoughts on the concept of colimitation: Three definitions and the importance of bioavailability. *Limnol. Oceanogr*., 53, 276–290.

Schindler, D.W. (2012). The dilemma of controlling cultural eutrophicaion of lake. *Proc. Biol. Sci*., 279, 4322–4333.

Schindler, D.W. & Hecky, R.E. (2009). Eutrophication: more nitrogen data needed. *Science*, 324, 721–722.

Schindler, D.W., Hecky, R.E., Findlay, D.L., Stainton, M.P., Parker, B.R.., Paterson, M.J. *et al*. (2008). Eutrophication of lakes cannot be controlled by reducing nitrogen input: Results of a 37-year whole-ecosystem experiment. *Proc. Natl Acad. Sci. USA*, 105, 11254 –111258.

Sitters, J., Atkinson, C.L., Guelzow, N., Kelly, P. & Sullivan, L.L. (2015). Spatial stoichiometry: cross-ecosystem material flows and their impact on recipient ecosystems and organisms. *Oikos*, 124, 920–930.

Sperfeld, E., Martin-Creuzburg, D. & Wacker, A. (2012). Multiple resource limitation theory applied to herbivorous consumers: Liebig's minimum rule vs. interactive co-limitation. *Ecol. Lett*., 15, 142–150.

Sterner, R.W. (2008). On the phosphorus limitation paradigm for lakes. *Int. Rev. Hydrobiol*., 93, 433–445.

Trommer, G., Pondaven, P., Siccha, M. & Stibor, H. (2012). Zooplankton-mediated nutrient limitation patterns in marine phyoplankton: an experimental approach with natural communities. *Mar. Ecol.-Prog. Ser*., 449, 83–94.

Vitousek, P.M., Porder, S., Houlton, B.Z. & Chadwick, O.A. (2010). Terrestrial phosphorus limitation: mechanisms, implications and nitrogen-phosphorus interactions. *Ecol. Appl*., 20, 5–15.

Wolfe, A.P., Baron, J.S. & Cornett, R.J. (2001). Anthropogenic nitrogen deposition induces rapid ecological changes in alpine lakes of the colorado front range (USA). *J. Paleolimnol*., 25, 1–7.

SUPPORTING INFORMATION

Additional Supporting Information may be downloaded via the online version of this article at Wiley Online Library (www.ecologyletters.com).

Editor, Robert Sterner
Manuscript received 4 May 2015
First decision made 10 June 2015
Manuscript accepted 17 July 2015