* figures
* latexifier le document
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1. **Introduction**

Paragraph 1: contribution of the resource-ratio theory to the understanding of coexistence

Paragraph 2: resource-ratio theory is essentially spatial, but has yet to integrate recent developments of metacommunity theory. Only a few amounts of papers deals with spatial exchanges of nutrients and organisms (Klausmeier; Basius). These studies concern the vertical distribution of biomass in the water column and do not provide a mechanistic understanding of dispersal impacts on coexistence.

Paragraph 3: objectives and approach

1. **Model description**

We consider a general metaecosystem model with nutrient recycling in a spatially heterogeneous landscape (Gravel et al. 2010). The model accounts for *n* different inorganic nutrients *Njx* (where *j* denotes a nutrient and *x* a locality) and is stoichiometrically explicit by maintaining mass balance for each of them. Local dynamics follow the ecosystem model of Daufresne and Hedin (2005). The dynamics of the primary producers *Pix* of species *i* are:

**EQ1**.



where *Gi* is the growth function describing the per capita uptake rate of the inorganic nutrients and *mi* is the mortality rate. The total biomass of the primary producer *i* consists of the sum of all the nutrients bounded in its biomass, which are allocated in a constant ratio (quota):

**EQ2.**



The growth function *Gi* depends on the stoichiometry of the inorganic nutrients and the primary producer specific demand. We assume that *Gi* follows a Liebig’s law of the minimum:

**EQ3.**



where *gij* represents the growth of the primary producer species *i* when limited by nutrient *j*. We do not specify at this point the shape of the functional response. We consider a simple diffusive (passive) dispersal between compartments *C* of the locality *x* and its adjacent locality *y*:

**EQ4.**



where *dC* is the diffusion rate of the compartment.

Dead organic matter is directly incorporated in the detritus compartment *Dix*, and then mineralized by decomposers at rate *r*:

**EQ5.**



We do consider similar recycling rates among the different nutrients to maintain the simplicity of the analysis, but it is possible to expand the model to account for differential recycling rates (see Daufresne and Hedin, 2005).

The dynamics of the inorganic nutrient concentration accounts for external inputs, losses, recycling of detritus *Dix*, consumption by primary producers *Pix* and diffusion among localities:

**EQ5**.



The inorganic nutrients are supplied to each locality via mineral alteration and atmospheric depositions at rate *Sjx*, and leached out of the system at rate *e*. A fraction *l* of the inorganic mineral is loss out of the system during the mineralization process.

1. **Graphical interpretation of resource ratio theory**

The conditions for coexistence among primary producer species competing for two resources is best understood using a graphical representation of the model. We first illustrate and derive tools to interpret the equilibrium state of the system with a single resident primary producer species at one locality and detritus mineralization. We will introduce dispersal for each compartment at the following section.

The external supply point *S* represents the equilibrium nutrient concentration in the system in absence of this primary producer (no consumption – FIG 1A). The zero net growth isocline (*ZNGIi*) represents the combination of the two nutrient levels (*Nj\*)* at which the primary producer growth is null. The growth of the primary producer is possible only if the supply point is located above the *ZNGIi*.

The use of vectors is a convenient tool to understand the dynamics of the system and the equilibrium state of the system. The mass balance constraint implies the system will satisfy the following conditions at equilibrium (assuming no dispersal):

EQ 6.

The condition 1 allows the definition of the species ZNGI on the two-dimensional space of nutrients. The condition 2 implies that the accumulation of dead organic matter equals the recycling rate for each detritus compartment. The condition 3 implies that the consumption of inorganic nutrients must equal the rate at which they are supplied. The primary producer consumes the two nutrients simultaneously, at the rate indicated by a consumption vector , where XXX. The slope of the consumption vector is equal to the quota of the primary producer. At equilibrium, the inorganic nutrient concentration is located along the ZNGI, at the point satisfying the following condition:

EQ6. 

where XXX is the inorganic nutrient supply vector, defined by XXX. In other words, the inorganic nutrient concentration corresponds to the location where the projection of the consumption vector crosses the supply point.

The mineralization of the detritus pool alters the equilibrium density of the primary producer, and thus of the inorganic nutrient consumption (Daufresne and Hedin, 2005). We must therefore consider an altered inorganic nutrient supply vector to balance the new consumption vector:

EQ 7.

where the new supply vector is XXX. The consumption vector therefore points toward a net nutrient supply point, which is new location is

EQ XXXX.

Note that the location of the net supply point will simply be a translation along the projection of the consumption vector in the situation where the mineralization of the detritus returns nutrients to the inorganic pool in the same proportion than they are sequestered in the biomass.

The location of the net nutrient supply point is crucial to understand coexistence. The criteria for coexistence in the classical resource-ratio theory is that the supply point must be located between the projection of the consumption vectors of the competing species (FIG 1B) and that species are more limited (higher N\*) by the resource they consume the most (in other words, the species with the uppermost ZNGI also has the steepest consumption vector). The addition of nutrient recycling alters this condition, the altered nutrient supply point must be located between the projection of the consumption vectors (Daufresne and Hedin, 2005).

1. **Analysis of metaecosystem dynamics**

In this section we will analyse the impacts of spatial flows between two local ecosystems on the equilibrium inorganic nutrient concentration in the presence of a single resident primary producer. We focus on the location of the net supply point because it is central to understand invasion conditions and thus coexistence in both locations. We will study each spatial flow independently and finish with the analysis of a special case where spatial flows and nutrient recycling promote unstable coexistence (alternate stable states) between two competing species. The analysis is essentially derived from a graphical interpretation of equilibrium vectors and supported by the mathematical analysis of the model.

* 1. **Case 1: Detritus diffusion**

Because we assume passive diffusion, the detritus will flow from the most productive location to the least productive one. The equilibrium total biomass of the producer at a location, and consequently the detritus biomass producer, is easily found on the two-dimensional space of nutrients. The biomass will be proportional to the distance between the net supply point and the equilibrium inorganic nutrient concentration (in absence of diffusion). For instance, at Fig 2, the equilibrium producer and detritus biomass will be larger at the blue location than the red location. Diffusion between the two locations have an averaging effect, meaning that it will tend to homogenize the detritus compartments from the two locations. The movement of the net supply point is still however along the projection of the consumption vector because the two nutrients are exchanged between the location exactly in the same proportion they are consumed. The equilibrium inorganic nutrient concentration thus remains unchanged by spatial flows of detritus, and consequently coexistence is neither promoted or impeded by detritus flows.

This result is easily shown with a simple derivation of the model. The equation X tells us that the displacement of the supply point of nutrient *j* at location *x* is:

EQX

And consequently, the slope of the change (see Fig 1) is:

EQX

which corresponds to the slope of the consumption vector. The spatial flow of detritus could thus promote unstable coexistence if the displacement of the net supply point from the original supply point is crossing the projection of an inferior competitor or alternatively it could lead to competitive exclusion in the opposite situation (See below)

* 1. **Case 2: Nutrient dispersal**

The impact of nutrient dispersal is somewhat more complicated because the two nutrients are not necessarily exchanged in the same ratio between the two locations. The results differ if the primary producer is limited by the same nutrient in the two locations, or by different nutrients, but the general principal remain the same (Fig 3): each of the inorganic nutrient will flow from the location with highest concentration to the lowest and this will result in a spatial homogeneization of the net supply points (they will get closer in the two-dimensional space). In the situation where the same nutrient is limiting the producer at the two locations (Fig. 3A), the location with the highest supply rate of the non-limiting nutrient will be the net exporter of that nutrient and the other location will be the net importer. Consequently the net supply point, the equilibrium nutrient concentration and the biomass will be more similar with increasing diffusion. In the situation where different nutrients are limiting the producer in the two locations, one nutrient will be exported (the non-limiting one) and one nutrient will be imported (the limiting one) at each location. Diffusion will also homogenize all compartments in this situation.

The solution to the situation of nutrient dispersal is more complicated than for detritus, but still interpretable. In this situation, the displacement of the net supply point relative to the original supply point is:

EQX

And thus the slope of the change for the supply point at location *x* is:

EQX.

It is not possible to derive an instructive solution for the equilibrium nutrient concentration and producer densities in the two locations. This solution however simplifies considerably in the simpler, but still informative, situation where there is not nutrient recycling:

EQX.

This equation is not complete in absence of the equilibrium nutrient concentrations, but these could be easily obtained from a graphical interpretation of equilibrium states (such as Fig 3). It however confirms the above interpretation of source and sink dynamics (Gravel et al. 2010): the slope of the change will be positive (enrichment for both nutrients) when the focal location is a sink for both nutrients and negative when the location is a sink for one nutrient and a source for the other.

* 1. **Case 3: Producer dispersal**

The dispersal of the primary producer has two effects on the equilibrium states of the metaecosystem. First, because there is a transfer of biomass from the most productive to the least productive location, it has an enrichment effect exactly the same as we observed above for the diffusion of the detritus. But the most fundamental effect, and consequent for spatial dynamics and competitive interactions, is the source-sink dynamics and alteration of competitive hierarchies (Loreau and Mouquet, 1999). Because producers are leaving the source patch at rate XXX, the net effect is similar to an inflated mortality rate. It thus decreases the equilibrium population size (condition X) and consequently increases the inorganic nutrient availability. In other words, the N\* for the limiting resource will increase in the source patch. Alternatively, it will decrease in the sink patch. We see this effect on the graphical representation of the dynamics as lateral movements of the ZNGI.

Again, the solution for the equilibrium states under producer dispersal is too complicated to be informative. But we could still obtain interpretable results with the assistance of the graphical representation of the metaecosystem dynamics. First, we need to specific a functional response for nutrient uptake by primary producer. For simplicity, without loss of generality, we will assume a simple linear functional response of the form XXX. Solving EqX for the equilibrium nutrient availability, we find:  
  
EQ XXX

It is easy to see the impact of source and sink dynamics on the equilibrium N\* from this equation. The difference between producer densities will take a positive value for a source (by definition, Px>Py) and consequently the N\* will increase. At the opposite, the N\* will decrease for a sink where the difference is negative (Px<Py). Paradoxally, source and sink dynamics will heterogenize the ZNGI of the species across the landscape (Fig 4), which homogenizes the overall competitivity of the species at the regional scale (Mouquet and Loreau, 2002). It is thus difficult to see any general trend on coexistence, producer dispersal could either promote or prevent coexistence at the local scale. But eventually it will reduce coexistence at the regional scale, which will feedback at the local scale (Mouquet and Loreau, 2002; Mouquet et al. 2006).

* 1. **Alternate stable states**

Diffusion of the detritus is a special case that could lead to alternate stable states. It is particular with respect to other spatial flows because it contributes to the displacement of the supply point, but it does not affect the equilibrium inorganic nutrient concentration (see above). Consequently, as the supply point moves from the original location to the net location with increasing dispersal and the build up of the detritus pool, it could cross the projection of the consumption vector of an inferior competitor (Fig 5). If such situation happens, locally stable coexistence could occur (local stability was confirmed by numerical analysis). Coexistence is however not globally stable, as it is not possible for the inferior competitor to invade when the superior competitor is resident. This situation is best exemplified by Fig 5. We see on that figure that both species will be able to develop a sustained population at both locations. In absence of detritus dispersal, however, only the red species will be able to invade both locations when the other species is resident. The blue species will not be able to invade the patch 2 because the equilibrium nutrient concentration is below its ZNGI. Detritus dispersal moves the location of the supply points, and consequently the net supply point of location 2 in presence of the blue species crosses the projection of the consumption vector of the red species. In this situation, if the red species invade, the availability of the nutrient 2 will be held constant (because of the blue species limitation) and the availability of the nutrient one will decrease to eventually reach the point where the two ZNGIs cross. Coexistence at this location could stand small perturbations but not large ones. There thus two alternate locally stable states: one with coexistence of both species and one with only the red species. We could also think about a situation where both supply points lie outside the triangle made by the projection of the consumption vectors and detritus dispersal bring them within it. Three alternate stables would be possible in this situation.

FIGURE LEGENDS

**Figure 1.** Graphical interpretation of the resource-ratio theory for a single location. The panel A) schematizes the equilibrium state of the system with a single resident primary resident population. Nutrient recycling moves the location of the supply point, from location S to the location S’. At equilibrium, the consumption vector is opposed to a net nutrient supply vector. The location of the equilibrium nutrient concentration will only be affected if the slope of the net supply vector is different of the slope of the consumption vector. Panel B) illustrates the conditions for coexistence. A second species could invade the system if its ZNGI is below the equilibrium nutrient concentration in the presence of the resident. The equilibrium nutrient concentration would thus be found at the crossing of the two ZNGIs. Stable coexistence will occur if the location of the net supply points is found between the projection of the two consumption vectors and if each species is more limited by the nutrient it requires the most (in other words, if the slope of the consumption vector increases as the ZNGI moves up and left).

**Figure 2.** Impacts of detritus dispersal on the equilibrium states of the metaecosystem with a single resident primary producer species.

**Figure 3.** Impacts of inorganic nutrient dispersal on the equilibrium states of the metaecosystem with a single resident primary producer species.

**Figure 4.** Impacts of primary producer dispersal on the equilibrium states of the metaecosystem with a single resident primary producer species.

**Figure 5.** Detritus dispersal could potentially lead to alternate stable states, including locally stable coexistence and locally stable dominance of a single primary producer species.

FIGURES