Integrating Metaecosystem Theory with Ecological Stoichiometry

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DEDICATION

This document is dedicated my wonderful Vanessa, without whom I doubt this thesis would exist.

ABSTRACT

Extending and integrating ecological concepts and theories can provide new solutions for difficult ecological problems. The ecosystem concept and ecosystem ecology theory have seen important developments through the elaborations of metaecosystem theory, which extends the ecosystem concept through spatial flows of energy, materials and organisms between interconnected ecosystems, and ecological stoichiometry, which extends ecological energetics by examining multiple chemical balances of substances in ecological interactions. However, these two extensions of ecosystem ecology theory have not been brought together in any form. In this thesis, I first extend both ecological stoichiometry and metaecosystem theory, and then integrate them in order to clarify difficult ecological concepts and to provide new solutions to ecological problems.

My overall approach is to develop mathematical models to formally articulate ecological concepts such as nutrient colimitation, stoichiometric imbalances and metaecosystem connectivity within the frameworks of ecological stoichiometry and metaecosystem theory. First, I present a parameterized stoichiometric ecosystem model that examines the relationship between mechanisms and phenomenology of nutrient colimitation, and how the mechanisms may interact with stoichiometrically imbalanced trophic interactions. I show that there are no clear relationships between mechanisms and phenomena, and that the mechanisms of colimitation are key in determining ecological dynamics and functioning.

I then examine in a spatially-explicit model how the connectivity of a metaecosystem

and the relative movement rates of nutrients and organisms can drive dynamics of spatially perturbed metaecosystems. I show that the eigenvalues of the matrix that describes metaecosystem connectivity can be used to predict the spatial dynamics of a metaecosystem and the kinds of dynamics present depends heavily on relative movement rates.

Lastly, I bring metaecosystem theory and ecological stoichiometry together in a spatially-explicit stoichiometric metaecosystem model to examine how spatial flows of nutrients and organisms can act as a mechanism to cause nutrient colimitation at local and regional scales. The model indicates that nutrient colimitation can be caused by spatial flows and this mechanism can be used to explain many confounding patterns in colimited growth responses found in the empirical literature.

ABRÉGÉ

L'extension et l'intégration des théories et des concepts écologiques peuvent nous aider à trouver de nouvelles solutions pour des problèmes écologiques difficiles. Le concept de l'écosystème et la théorie des écosystèmes ont survécu à d'importants changements par l'élaboration de la théorie des métaécosystèmes, qui ajoute au concept de l'écosystème des flux d'énergie, de matériaux et d'organismes entre des écosystèmes liés ensemble, et la stoechiométrie écologique, qui étend la théorie énergétique des écosystèmes par l'inclusion de l'équilibre de plusieurs substances chimiques dans les interactions écologiques. Pourtant, ces deux extensions de la théorie des écosystèmes ne sont pas encore réunies. Dans ma thèse, j'étends la théorie des métaécosystèmes et la stoechiométrie écologique, et par la suite je les unis ensemble pour adresser des concepts écologiques difficiles et pour trouver des solutions aux problèmes écologiques.

La méthodologie pour aborder ces sujets consiste à développer des modèles mathématiques pour l'articulation des concepts écologiques comme la limitation du croissance par plusieurs nutriments, les déséquilibres stoechiométriques et la connectivité des méta- écosystèmes dans le cadre de la théorie des métaécosystèmes et la stoechiométrie écologique. Premièrement, je présente un modèle stoechiométrique d'un écosystème avec des paramètres pris d'un écosystème réel qui a pour but d'examiner les relations entre les mécanismes et les phénomènes de la limitation de la croissance par plusieurs nutriments. En plus, j'examine comment cette limitation peut inteágir avec les déséquilibres stoechiométriques entre les autotrophes et les herbivores.

Deuxièment, j'étudie avec un modèle spatial comment la connectivité d'un métaécosystème et les taux relatifs de mouvement des nutriments et des organismes peuvent diriger les dynamiques des métaécosystèmes perturbés. Je montre que les valeurs charactéristiques de la matrice qui décrit la connectivité du métaécosystème peuvent être utilisées pour prédire les dynamiques spatiales du métaécosystème et les types de dynamiques dépendent des taux relatifs de mouvement.

Finalement, j'unis la théorie des métaécosystèmes avec la stoechiométrie écologique dans un modèle qui contient un métaécosystème stoechiométrique. J'utilise ce modèle pour examiner si les flux de nutriments et des organismes peuvent agir comme un mécanisme de limitation de la croissance par plusieurs nutriments dans les écosystèmes locaux et les métaécosystèmes. Le modèle indique que la limitation de la croissance par plusieurs nutriments peut être causée par les flux spatiaux et ce mécanisme à la capacité d'expliquer plusieurs phénomèmes empiriques dans le domaine de la limitation par plusieurs nutriments.

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PREFACE

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Contributions of authors

I developed and organized all of the chapters presented in this thesis. In addition, I developed all of the models, analyzed them mathematically, wrote the Matlab and XPPAUT code necessary for performing numerical simulations and analyzed all the resulting data for each chapter. My co-supervisors F. Guichard and M. Loreau contributed to the development of the thesis by providing revisions for the chapters, academic mentorship and funding.

Thesis format and style

For this thesis, I am using the manuscript-based thesis format as I have three research chapters for which I am the primary author. In order to provide a coherent and logical whole, I have used connecting statements between each chapter. In order to improve the general look of the thesis, I have decided to use the APA citation style and bibliography throughout the document instead of formatting each chapter based on the journal that I have submitted it to. Since each of my research chapters contains a review of the literature in their introductions, my first chapter will be general introduction to the philosophical motivations underpinning this work and to present the overall themes of the thesis.

Novelty and impact of thesis research

Contributions from Chapter 1: Using the research traditions philosophical framework in order to argue for the rise, the decline and reemergence of the ecosystem ecology research tradition.

- Using the philosophical framework of the research tradition, I examine the history of the ecosystem concept and the research tradition that arose from it in order to better understand why it achieved such striking successes from the 1950s to 1970s, but fell on hard times after the International Biology Program ended. I am unaware of any other such analysis of ecological history using the research tradition framework

Contributions of Chapter 2: Clarifying difficulties surrounding the link between nutrient colimitation mechanisms and the colimited growth responses of autotrophs, and a demonstration of the importance of identifying the mechanisms of colimitation in understanding ecosystem dynamics and functioning.

- With the parameterized stoichiometric ecosystem model that I developed, I show a novel result that a colimited growth response found in nutrient addition experiments are not necessarily indicative of any mechanism of nutrient colimitation, suggesting that ecologists should be wary of drawing inferences about the presence of nutrient colimitation from nutrient addition experiments
- I also show for the first time that it is the mechanisms of nutrient colimitation that matter in stoichiometrically imbalanced trophic interactions, such that the mechanisms need to be the primary focus, not the growth responses.

Contributions from Chapter 3: Predicting ecosystem dynamics and stability from metaecosystem spatial structure and movement rate.

- With the one of the first spatially-explicit metaecosystem models formulated in the literature, I show the novel result that the eigenvalues of the connectivity matrix of the metaecosystem combined with their eigenvectors can be used to predict changes in dynamics and stability due to differences in movement rates of ecosystem components.
- An additional novel result is the demonstration that which eigenvalue is linked to the destabilization is dependent on the relative movement rates of the ecosystem components.

Contributions of Chapter 4: Integration of metaecosystem theory and ecological stoichiometry in order to show how spatial processes can lead to local and regional nutrient colimitation.

- By building a spatially-explicit stoichiometric metaecosystem model, I am one of first researchers to explicitly integrate the two theories within a single model.
- This model is the first model that I am aware of to show how nutrient colimitation can emerge only due to the movement of nutrients and organisms
- I also provide, for the first time, a mechanism of nutrient colimitation can could explain multiple confounding patterns seen in the nutrient addition literature

Chapter 1
GENERAL INTRODUCTION

On a pale blue dot with flecks of green and brown, fantastical things appear above, below and on its surface. The world is a great engine, churning out heat from its energy transformers of all shapes and sizes (Lotka, 1925). There are super-organisms everywhere that colonize, react and develop as they strive for their final climax (Clements, 1916). There are systems, embedded in one another from the atom to the ecosystem to the universe, that overlap, interlock and interact with one another (Tansley, 1935).

Ecologists of old used wild metaphors, speculative concepts and borrowed frameworks from more developed sciences to grapple with the unruly complexity of the world we live in. As their science has matured and grown, many of these concepts and ideas have been debated, refined, formalized and used as jumping off points for whole domains of ecological study and theory, including community and ecosystem ecology (McIntosh, 1985; Golley, 1993; Kingsland, 1995, 2005; Cuddington & Beisner, 2005). This is not to say that all ecologists are satisfied with how these concepts and their associated theories have developed, far from it (O'Neill, DeAngelis, Waide, & Allen, 1986; Peters, 1991; Shrader-Frechette & McCoy, 1993; Lawton, 1999; O'Neill, 2001; Ricklefs, 2008; Reiners & Lockwood, 2009). In contrast, other ecologists feel certain enough about the conceptual, empirical and theoretical progress observed in ecology that general theories and laws can be found (Turchin, 2001; Pickett, Kolasa, & Jones, 2007; Scheiner & Willig, 2008, 2011).

The major difficulty in deciding who is 'right' in these debates is the lack of clear philosophical, normative propositions that are shared between ecologists about what makes for good concepts and good theories. For example, Peters (1991) would only accept theories that make 'useful' predictions, while Reiners and Lockwood (2009) would accept a wide variety of theories that could just provide explanations. In addition, many ecologists are partisans of Kuhnian paradigms (e.g. Cuddington & Beisner, 2005; Pickett et al., 2007), which generally lack criteria for changes between them (Kuhn, 1970; Lakatos, 1970; Lakatos & Musgrave, 1970; Laudan, 1977). Therefore, it could be the case that ecological concepts and theories are adopted based on non-scientific reasons where 'anything goes' (Feyerabend, 1993).

In this general introduction, I will present my own views on how scientific concepts and theories evolve over time in order to better motivate the work done in this thesis. I follow this brief philosophical section by compactly examining the evolution of the ecosystem concept and its associated theories from its coining in 1935 up until the late 1970s, and I indicate how these developments can be viewed through a philosophical lens. This is followed by a concise examination of two extensions of the ecosystem concept and its theories: ecological stoichiometry and metaecosystem theory. Finally, I examine the potential of extending and integrating metaecosystem theory with ecological stoichiometry to explain and predict ecological problems by outlining my thesis (Figure 1.1).

Research Traditions, Conceptual Problems and Explanatory Unification

In their insightful book on using the philosophy of science to help improve our understanding of ecological theory, Pickett et al. (2007) propose that there are at least four 'paradigms' in ecology: 'Stuff' ecology, 'Thing' ecology, 'Now' ecology and 'Then' ecology. For the remainder of this introduction, I will focus only on the 'Stuff' and 'Thing' ecology paradigms.

The difficulty with the 'paradigms' is that they would share many phenomena within the same domain, i.e. the spatiotemporal scale and phenomena that the 'paradigm' is addressing (Pickett et al., 2007). This would mean that the paradigms would be, in some sense, competing with one another for adherents, which does not lend itself to a Kuhnian analysis (Lakatos, 1970; Laudan, 1977). Rather, the state of theory in ecology would be better represented through what have been described as 'research traditions' (Laudan, 1977).

A research tradition has certain central tenants about the world and gives rise to many allied theories, concepts and models, but is too general to be used to make explicit predictions or explanations (Laudan, 1977). For example, the 'general' theory for ecology proposed by Scheiner and Willig (2008) represents a research tradition for 'Thing' ecology, i.e. evolutionary, population and community ecology, broadly defined (Pickett et al., 2007). 'Stuff' ecology, which many associate with ecosystem ecology and biogeochemistry, would be a distinct research tradition with principles relating to fluxes and pools of material and energy (Pickett et al., 2007). This division of ecological research traditions has long been recognized, sometimes under the guises of biodemography and biogeochemistry (Hutchinson, 1948) or by population/community-ecosystem/process dichotomy (O'Neill et al., 1986; Pickett et al., 2007). Since 'Stuff' and 'Things' may be a bit vague, I will use population/community ecology as one research tradition and ecosystem ecology as the other research tradition for the remainder of the introduction.

The constitutive theories that are partially derived from these research traditions (only partially due to the need of other assumptions, concepts and methodologies to make the theory operational) are then used to solve 'problems' (Laudan, 1977). For instance, both food web theory (from the population/community ecology research tradition) and ecological energetics theory (from the ecosystem ecology research tradition) could be applied to solve an empirical problem, such as the eutrophication of Lake Winnipeg. These theories would then try to 'solve' the problem through the creation of models, experiments and other methods proscribed within their research tradition (Laudan, 1977). The way that research traditions would compete is through 'solving problems', such that scientists would pick and choose which research tradition to follow based on its problem-solving ability (Laudan, 1977).

However, not all problems are empirical. Many problems within science are conceptual, i.e. theories may be logically internally inconsistent or logically inconsistent with other theories within its domain or beyond its domain (Laudan, 1977). For example, Clements' successional theory relied in part on Lamarckian evolution, which was logically inconsistent with the broader understanding of evolutionary theory in the 1940s and caused conceptual problems for Clements' theory (Kingsland, 2005). Resolving conceptual problems is perhaps more important than solving empirical problems in ecology, as there is frequent conceptual confusion and vagueness within our discipline (O'Neill et al., 1986; Peters, 1991; Shrader-Frechette & McCoy, 1993; O'Neill, 2001; Pickett et al., 2007; Reiners & Lockwood, 2009).

For example, there has been frequent debates about what relationship, if any, exists between ecosystem complexity and ecosystem stability (Loreau, 2010). Because of the multitude of concepts related to 'stability', it was very difficult to evaluate whether certain models or experiments addressed the type of 'stability' proposed (Loreau, 2010). Only through strenuous theoretical work have these conceptual difficulties been resolved and clearer answers can be provided about how and when increases in ecosystem complexity could result in increased ecosystem stability (Loreau, 2010).

Therefore, I agree with Laudan (1977) that research traditions and the theories that constitute them are 'good' when they solve many 'empirical' problems while keeping any 'conceptual' problems to a minimum. Unfortunately, Laudan (1977) failed to mention how 'problems' are solved in science. My own position is that empirical and conceptual problems can both be solved when we can explain them through unifying our theories and research traditions (Kitcher, 1981, 1993; Maki, 2001; Pickett et al., 2007; Odenbaugh, 2011).

For example, Darwin's theory of natural selection uses minimal set of consistent principles in order to explain phenomena observed in palaeontology, anatomy and many other biological fields of study (Kitcher, 1993; Odenbaugh, 2011). Of course, full-blown unification is likely difficult in ecology, but piecemeal integration can help accelerate the synthesis between theories and their research traditions, hopefully resulting in better explanations of phenomena and less conceptual problems (Pickett et al., 2007; Loreau, 2010; Odenbaugh, 2011).

My goal for my thesis, then, is to help reduce some of the conceptual problems that are causing difficulties within ecological research traditions by integrating different theories together, in the hopes of providing stimulus for a future unification of the two major research traditions in ecology. Of course, it may be helpful to understand why we have two research traditions in the first place, which I investigate in the next section.

The Ecosystem: Concepts and Theories

> "The fundamental concept appropriate to the biome considered together with all the effective inorganic factors of its environment is the *ecosystem*, which is a particular category among the physical systems that make up the universe. In an ecosystem the organisms and the inorganic factors alike are *components* which are in relatively stable dynamic equilibrium. Succession and development are instances of the universal processes tending towards the creation of such equilibrated systems."
>
> Arthur G. Tansley in *The Use and Abuse of Vegetational Concepts and Terms*

Despite Tansley's argument for it being the appropriate fundamental concept in which to consider succession and other ecological phenomena, the ecosystem concept had an inauspicious start in ecology (Golley, 1993). The concept was barely used in its first few years of existence, and only became prevalent in the ecological literature after Eugene Odom's *Fundamentals of Ecology* was first published in 1953 (Golley, 1993; Kingsland, 2005). There are many reasons for its slow adoption, including the competing concepts of the *holocoen*, coined by entomologist Karl Friederichs, and the *biosphere*, which was proposed by Vladimir Vernadsky, the founder of biogeochemistry (Golley, 1993). But what may have been the main stumbling block for the concept was its lack of a theoretical foundation within ecology itself. Nowhere within Tansley's article can we find out how the components of the ecosystem interact in order to give rise to the properties such as a dynamically stable equilibrium of species within a defined area (Tansley, 1935). Without such an explanation, the concept lacked the necessary tools to solve the primary problem of ecology at the time, ecological succession (Kingsland, 2005).

This is in sharp contrast with the biotic community concept of Frederick Clements and his followers, which posited that the strong biological interactions of competition and facilitation gave rise to such a well-organized entity that it could be viewed as an organism and succession represented the development of that organism (Clements, 1916). One of Tansley's stated goals for the ecosystem concept was to replace the concept of biological community within the budding field of successional theory, as he viewed the biological community to be a wholly unsatisfactory concept as it lacked any consideration of inorganic processes and suggested the validity of certain vitalistic ideas in ecology (Tansley, 1935; Kingsland, 2005). He was also aware that succession did not necessarily lead to well-organized climax communities and abiotic factors could direct vegetational change, which left the successional theory of

Clements open to criticism from ecologists who promoted 'individualistic' views of plant community organization (Gleason, 1926, 1927).

It could be said that while Tansley's new concept of the ecosystem tried to alleviate certain conceptual problems of the biotic community and successional theory in general, it introduced new conceptual problems by having no explanation for how the abiotic and biotic components formed a system. Furthermore, Tansley was trying to use the ecosystem as a component of the population/community ecology research tradition, which generally focused on organisms and entities with similarities to organisms (i.e. biotic communities). The ecosystem, from this point of view, was ill-suited due to its abiotic components which may not be entities.

It did not have to be this way. A well-thought out and mathematically rigorous theory for a 'physical biology' had already been developed by Lotka (1925) and could have been used by Tansley to demonstrate the power of his concept. Unfortunately, Lotka's work was never fully integrated or acknowledged during the early development of the ecosystem concept (Golley, 1993). The concept had to be exhumed and developed by others.

The languishing of the ecosystem concept ended when Raymond Lindeman posthumously published his seminal paper, 'The Trophic-Dynamic Aspect of Ecology'. Within this paper, the link between the abiotic and biotic components was made explicit through the transfers of energy between biotic components with the original energy source being solar radiation (Lindeman, 1942). Furthermore, the ecosystem was then brought together with the idea of the lake as a fundamental ecological unit, such that its productivity, energy budgets and energy efficiencies all could be related to the succession of Cedar Bog Lake (Lindeman, 1942).

Hence, the ecosystem concept could now relate how the abiotic and biotic factors interacted to bring about succession, leading to immediate conceptual and theoretical advances (Lindeman, 1942). Furthermore, it represented the emergence of the ecosystem ecology research tradition and the beginnings of ecological energetics (Golley, 1993). This emergence was perhaps first recognized by Lindeman's supervisor, G. E. Hutchinson described Lindeman's work as being part of the *biogeochemical* approach to ecology (Hutchinson, 1948).

The next step in the development of the ecosystem concept occurred when Eugene Odum used it as the centralizing concept for his ecology textbook, the *Fundamentals of Ecology* (Golley, 1993; Kingsland, 2005). He emphasized that the ecosystem was the fundamental unit of ecological inquiry and began, with his brother Howard T. Odum, to study it as an entity in its own right (Odum, 1953; Golley, 1993; Kingsland, 2005). For example, they studied a reef ecosystem and measured its 'metabolism' by measuring changes in oxygen found in the waterflow (Odum & Odum, 1955).

Their emphasize on the flows of energy and materials in the ecosystem was also coupled to a cybernetic approach, which indicated that ecosystems had mechanisms to control these flows and this control was an emergent property of the ecosystem (Odum, 1969; Golley, 1993). Furthermore, a great deal of emphasis was placed on maximizing principles that ecosystems supposedly tried to meet, and thermodynamic principles became part of standard ecological practice (Odum, 1969). These ideas were not new, as Lotka (1925) emphasized the same aspects of ecological systems before the ecosystem concept was coined, but this represented the first systematization of the ecosystem ecology research tradition acceptable to many ecologists (Golley, 1993; Kingsland, 2005).

With the elaboration of this 'new ecology' or ecosystem ecology, the way the ecosystem concept was used changed. Ecosystems, under Odum's definition, were not only the abiotic components and biotic components within a given area, but they also required a flow of energy in order to give rise to characteristic trophic structures and material cycles (Odum, 1969). Ecosystems 'developed' through succession, and the major characteristics of this succession were increasing control of material cycles, increased biomass, increased species diversity and increased stability (or resistance to external perturbation) through increasingly strong biotic interactions (Odum, 1969). Therefore, a properly developed ecosystem was closed to material flows, highly structured and highly stable, which should give rise to very distinct entities (Odum, 1969). The parallels between Odum's concept of the ecosystem and the 'community as organism' concept of Clements are striking (Kingsland, 2005).

This change in the concept and its theoretical articulations were widely successful, especially within American ecology (Golley, 1993; Kingsland, 2005). The emphasis of flows of materials was aided by new technologies involving radioactive isotopes, such that many of the ecologists who adopted the ecosystem ecology research tradition were funded by Atomic Energy Commission and such funding helped spur further research (Golley, 1993). This new research tradition also used the latest advances in computing in order to compute the predictions of the cybernetic models proposed by Howard T. Odum and others (Golley, 1993). Furthermore, it provided new solutions to ecological problems by emphasizing the dynamical stability of ecosystems, such that resolving environmental issues required improving ecosystem functioning (Odum, 1969).

The apogee of the research tradition was the International Biology Program (IBP) in the 1970s, which was based upon the principles of the ecosystem ecology expounded by Odum and others (Golley, 1993). Involving nearly 1,800 scientists and five different biomes across the world, its goals were to significantly advance ecosystem ecology theory and practice (Golley, 1993). Unfortunately, no advance of theory occurred and various conceptual difficulties were becoming paramount (Golley, 1993; Kingsland, 2005; de Laplante, 2005).

A major conceptual problem concerned the methodology of studying ecosystems. According to Odum, teams of specialized scientists were needed to tackle ecological research (Odum, 1977). In contrast, many ecologists preferred to work individually with occasional collaborations, even during ecosystem studies (Golley, 1993). The relative success of the Hubbard Brook ecosystem study compared to that of the IBP was one of many studies that helped remove the allure of 'Big Ecology' by showing fundamental ecosystem studies could be done quasi-independently (Golley, 1993). Furthermore, projects like the IBP were costly and many government agencies stopped funding large ecosystem study projects, making team building difficult (Golley, 1993).

Another non-empirical problem for the theory was the training of ecosystem ecologists (Golley, 1993). Ecologists generally originate from biology departments in universities, and are therefore trained in plant and animal physiology, cell and molecular biology, genetics and other biological disciplines. However, this training leaves ecologists poorly prepared to deal with the abiotic components of the ecosystem (Golley, 1993). This fact could explain the shift towards a more biotic view of the ecosystem concept, particularly Eugene Odum's as he was trained in physiology (Golley, 1993).

In addition, the repurposing of the ecosystem concept led to a fundamental retrenchment in the scope of ecosystem ecology theory and difficulties in applying certain terms. Ecosystems could only be recognized if they were well-organized, closed to fluxes of organisms and materials, spatially homogeneous, stable and their species were substitutable for others of 'similar functionality' (Odum, 1969; O'Neill, 2001). Very few natural systems would actually meet all the criteria as many ecosystems are highly open to fluxes, are spatially heterogeneous and many of their species are not substitutable (e.g. Turner, 1989; O'Neill, 2001; Polis, Power, & Huxel, 2004). Furthermore, the stability of ecosystems was conceptually fraught, as what was 'stable' and what 'stable' meant were ambiguous (O'Neill, 2001).

There was also an ominous absence of evolutionary theory from the field (O'Neill, 2001; de Laplante, 2005), which was undergoing large advances due to the molecular revolution in biology (Olby, 1990). The use of evolutionary theory in order to explain problems in ecology helped renew the vitality of the population/community ecology research tradition as seen in the work of MacArthur and others (Cody & Diamond, 1975; Kingsland, 1995). Furthermore, the advances in molecular biology also led to the creation of new disciplines within the population/community ecology research tradition including population biology, ecological genetics and molecular ecology (e.g. Singh & Uyenoyama, 2004) With the major competitor on the upswing with new concepts, models, techniques and tools on the one hand, and the lack integration with evolutionary theory on the other, ecologists entering the field may have decided to not adopt the 'new ecology' of Odum as their research tradition (Laudan, 1977).

Finally, there were predictive failures, especially with the cybernetic and ecological energetic theories associated with Odum's conception of the ecosystem. The attempts to fully model ecosystems in the IBP with the cybernetic approach was viewed as unsuccessful, and energetic models were unable to explain a number of phenomena residing firmly within the ecosystem ecology research tradition such as the large mismatches in chemical compositions of organisms compared to their environments or the relative flows of energy through different trophic chains (Reiners, 1986; Golley, 1993). Furthermore, many of Odum's predictions about ecosystem development were shown to be incorrect by those working within the research tradition, generating greater uncertainty about the conceptual foundations of the research tradition and leading to new formulations of the ecosystem concept (O'Neill et al., 1986; Reiners, 1986).

A major property of these new concepts was an attempt to integrate various elements of the population/community ecology research tradition within the ecosystem concept. For example, the metabolic theory of ecology tries to go from basic physiological principles of metabolism to explaining ecosystem-level processes within the same framework (Brown, Gillooly, Allen, Savage, & West, 2004). Other formulations tried to move beyond the spatial assumptions of Odum's ecosystem concept, like landscape ecology (Turner, 1989, 2005). While many of the new formulations hold promise for potential integration between the ecological research traditions, I will be focusing on two for the remainder of this thesis: ecological stoichiometry and metaecosystem theory.

Ecological Stoichiometry and Metaecosystem Theory

One new formulation of the ecosystem concept brought to the fore the constraints of matter, rather than the constraints imposed by energy as Odum did (Reiners, 1986). Clearly, the circulation of matter had always been a part of ecosystem ecology, but much of this circulation was considered only in conjunction with energetics (e.g. Lindeman, 1942). Lotka (1925) did clearly differentiate the importance of matter separately from that of energy, with special emphasis on the stoichiometry of living things compared to that of the abiotic environment. Unfortunately, very little work followed Lotka's approach to matter in ecology outside of Redfield's fundamental work on C:N:P ratios in phytoplankton until the 1980s (Reiners, 1986; Sterner & Elser, 2002).

The fundamental insight gained by looking into the chemical compositions of organisms is how different they are compared to their surrounding environments, and how maintaining their compositions is of fundamental importance to organisms as maintaining these compositions are required for protein synthesis, DNA replication and many other essential biological processes (Reiners, 1986; Sterner & Elser, 2002). From this insight and from other assumptions derived from evolutionary biology, biochemistry and the law of conservation of matter, a number of key predictions emerge about elemental limitation of growth, recycling and depletion of nutrients, differences in interspecific competitive ability and global changes in biogeochemical cycles over evolutionary timescales (Reiners, 1986; Sterner & Elser, 2002).

Ecological stoichiometry, as this approach to the ecosystem ecology research tradition is called, brings multiple benefits to the ecosystem concept. For example, it allows for more abiotic components within the ecosystem to be explicitly considered, providing clearer understanding of the relationships and feedbacks between biotic and abiotic controls on biogeochemical cycles (Reiners, 1986; Sterner & Elser, 2002; Lenton & Klausmeier, 2007). In addition, by focusing on relative balances of chemical substances, it provides alternative mechanisms and theories to ecosystem energetics concerning the controls of ecosystem production and other ecosystem functions (Reiners, 1986; Sterner & Elser, 2002; Elser, Fagan, Kerkhoff, Swenson, & Enquist, 2010). Ecological stoichiometry also allows for ecologists to view the chemical stoichiometries of organisms to be one of their traits, which can be acted upon through natural selection and provides a vital link between evolutionary theory and the ecosystem concept (Elser, Dobberfuhl, MacKay, & Schampel, 1996; Elser, O'Brien, Dobberfuhl, & Dowling, 2000; Elser, Fagan, et al., 2010).

Because ecological stoichiometry resolved some of the conceptual issues within ecosystem ecology, it was widely adopted and applied to many new and novel phenomena, such as issues of food quality (Urabe & Sterner, 1996; Urabe, Kyle, et al., 2002), consumer-driven recycling (Elser & Urabe, 1999; Nugraha, Pondaven, & Treguer, 2010), food web dynamics (Andersen, Elser, & Hessen, 2004; Hall, 2009), plant competition (Daufresne & Hedin, 2005; Danger, Daufresne, Lucas, Pissard, &

Lacroix, 2008) and ecological succession (Litchman, Klausmeier, Miller, Schofield, & Falkowski, 2006; Marleau, Jin, Bishop, Fagan, & Lewis, 2011). Many of these studies also attempt to solve problems within the population/community ecology research tradition (Moe et al., 2005), which may allow for a future synthesis between the ecological research traditions through ecological stoichiometry (Sterner & Elser, 2002).

However, ecological stoichiometry did not respond to the problems of space and of scale that have loomed large over the entire domain of ecology for the past forty years (Levin, 1974; Levin & Paine, 1974; O'Neill et al., 1986; Wiens, 1989; Levin, 1992). Ecological systems, whether viewed as entities or processes, can be highly heterogeneous and scale-dependent in space (Wiens, 1989; Levin, 1992). How the major research traditions responded to this challenge differed.

Ecologists within the population/community ecology research tradition first developed the concept of the metapopulation (Levins, 1969; Hanski, 1999), which idealized a population of populations as living in discrete patches that either went extinct, were maintained or were newly colonized. This concept was refined through such extensions as local population densities, and then extended to the whole biotic community (Leibold et al., 2004). A major benefit of this approach has been its ability to help capture the dynamics driven by spatial flows of organisms and provide insight on the emergence of spatial patterning within ecological systems (Hanski, 1999; Leibold et al., 2004)

Researchers within the ecosystem ecology research paradigm, however, took a different approach by focusing primarily on the abiotic and biotic heterogeneity within a given area or landscape, which led to landscape ecology (Turner, 1989, 2005). Once again, the world is divide up into patches, but instead of focusing on organisms arriving, establishing and leaving, the landscape concept in ecosystem ecology focused on how the characteristics of each patch, such as productivity, suitability for organism x and so on, and the connectivity between the continuous patches drive ecosystem processes and maintain ecosystem functioning (Turner, 1989; Urban & Keitt, 2001; Turner, 2005).

While it has helped resolve some of the conceptual issues involved with spatial homogeneity in the ecosystem concept, the landscape concept is itself highly limited to a specific physical scale and its associated theories largely ignore dynamic flows of materials and organisms in space (Loreau, Mouquet, & Holt, 2003; Loreau, 2010). This is unfortunate as a very large body of empirical literature has demonstrated that the spatial flows of energy, materials and organisms across landscape and ecosystem boundaries can dramatically affect local populations, communities and ecosystem functions (Polis, Anderson, & Holt, 1997; Polis, Power, & Huxel, 2004).

In an attempt to bring a greater emphasis on spatial flows of energy, materials and organisms and to help a partial integration of ecological research traditions, at least in spatial ecology, the metaecosystem concept was introduced (Loreau, Mouquet, & Holt, 2003). The metaecosystem concept borrows from the metapopulation and metacommunity concepts their use of discrete patches, their focus on spatial flows and their flexible spatial scale, while it takes from landscape ecology its focus on the spatial distribution of abiotic factors and material cycling (Loreau, Mouquet, & Holt, 2003). This conjunction of two of the most important spatial theories of ecology has led to a number of new theoretical models that have demonstrated the explanatory power of the new concept and ecologists have begun testing these ideas in the field (Loreau, Mouquet, & Holt, 2003; Loreau & Holt, 2004; Leroux & Loreau, 2008; Gravel, Guichard, Loreau, & Mouquet, 2010; Gravel, Mouquet, Loreau, & Guichard, 2010; Marleau, Guichard, Mallard, & Loreau, 2010; Loreau, 2010; Massol et al., 2011; Largaespada, Guichard, & Archambault, 2012). In particular, this new body of theory has demonstrated the key role of nutrients in coupling ecosystems and how nutrient movement can drastically alter local ecosystem dynamics and functioning (Gravel, Guichard, et al., 2010; Gravel, Mouquet, et al., 2010; Marleau, Guichard, et al., 2010).

Nevertheless, metaecosystem theory is still lacks articulation in a number of areas including the presence of multiple limiting nutrients and somewhat more realistic spatial structures. Without extending metaecosystem theory in those directions, many ecologists may not see the utility in developing and testing the theory, especially when landscape ecology does provide detailed theoretical ideas about how the connectivity of habitats should impact ecosystem function and the persistence of populations in the environment (Urban & Keitt, 2001; Turner, 2005). Bringing such elements into metaecosystem theory would therefore help it compete with the landscape concept and perhaps lead to a future synthesis between the constitutive theories of spatial processes within the ecosystem ecology research tradition.

Since ecological stoichiometry lacks a spatial approach and metaecosystem theory has not examined in any great detail the effects of the spatial flows of multiple limiting nutrients, it seems that the two theories would be ripe for some sort of integration. Of course, such an undertaking requires some motivation as integration is not a simple matter, especially in modelling. One of greatest benefits to the traditional energetic approach to ecosystems is the linearity of processes, which led to easily testable predictions and simple conceptual models. In contrast, models with ecological stoichiometry are generally highly non-linear and involve positive feedback loops through recycling, making it more difficult to understand causation and to test against empirical data. Adding spatial dynamics on top of that generally leads to the loss of tractability and may limit our potential to 'solve' certain types of problems unless simplifying assumptions are made.

Therefore, there are tradeoffs not only within modelling itself (e.g. Levins, 1966), but at the level of theories and research traditions (Kuhn, 1970; Laudan, 1977; Feyerabend, 1993). For example, one can view the dynamics of succession as a simple, progressive process using Odum's ecosystem concept (Odum, 1969), with everything that does not fit no longer corresponds to succession, or one can use the modern view that the dynamics of succession are highly unpredictable and non-linear but covers most vegetational change (Walker & del Moral, 2003).

However, I am of the view that the costs of not integrating ecological stoichiometry and metaecosystem theory are greater than integrating them, and many other ecologists are also supportive of further integration between our theories and research traditions (Pickett et al., 2007; Scheiner & Willig, 2008; Loreau, 2010; Scheiner & Willig, 2011). In particular, I feel that the absence of spatial processes within ecological stoichiometry greatly hampers our ability to apply the framework in ecosystems with large nutrient inputs from surrounding ecosystems. With this settled, I now turn my focus to how I will extend and integrate ecological stoichiometry with metaecosystem theory.

Extending and Integrating: Outline of Thesis

In order to show the benefits of integrating ecological stoichiometry with metaecosystem theory, I need to show how this integration can 'solve' problems that the distinct theories could not. In this view, the primary goal of my thesis is to show the superior problem solving ability of the integration. The problem that I have chosen to investigate is nutrient colimitation, which has a number of definitions (Güsewell, Koerselman, & Verhoeven, 2003; Arrigo, 2005; Saito, Goepfert, & Ritt, 2008; Craine, 2009; Harpole et al., 2011). What is minimally required for nutrient colimitation is the presence of at least two potentially limiting nutrients, which means the concept naturally fits within the confines of ecological stoichiometry.

Therefore, in **Chapter 2**, I develop a stoichiometric ecosystem model that is parameterized using data from Mount St. Helens in order to clarify the concept and extend the problem solving abilities of ecological stoichiometry by looking at the relationship between local nutrient colimitation mechanisms and colimited growth responses in nutrient addition experiments, and to see how nutrient colimitation mechanisms interact with stoichiometrically imbalanced herbivory to alter ecosystem dynamics and functioning (Figure 1.1).

The above model ignores spatial processes that may influence nutrient limitation status in autotroph communities (Hagerthey & Kerfoot, 2005), and suggests a role for metaecosystem theory. However, that study noted that it was the spatial structuring of the nutrient flows that created spatial heterogeneity in the lake's autotroph community, which is currently absent from all previous theoretical treatments in metaecosystem theory. Because of this, I develop in **Chapter 3** a spatially structured metaecosystem model to look at how metaecosystem connectivity and differences in movement rates for the different ecosystem compartments can affect ecosystem dynamics, functioning and stability (Figure 1.1).

In **Chapter 4**, I bring ecological stoichiometry and metaecosystem theory together in a spatially structured, stoichiometric metaecosystem model in order to investigate the ability of spatial flows of nutrients and organisms to cause nutrient colimitation at local and regional scales, thereby demonstrating the benefits of integrating the two theories.

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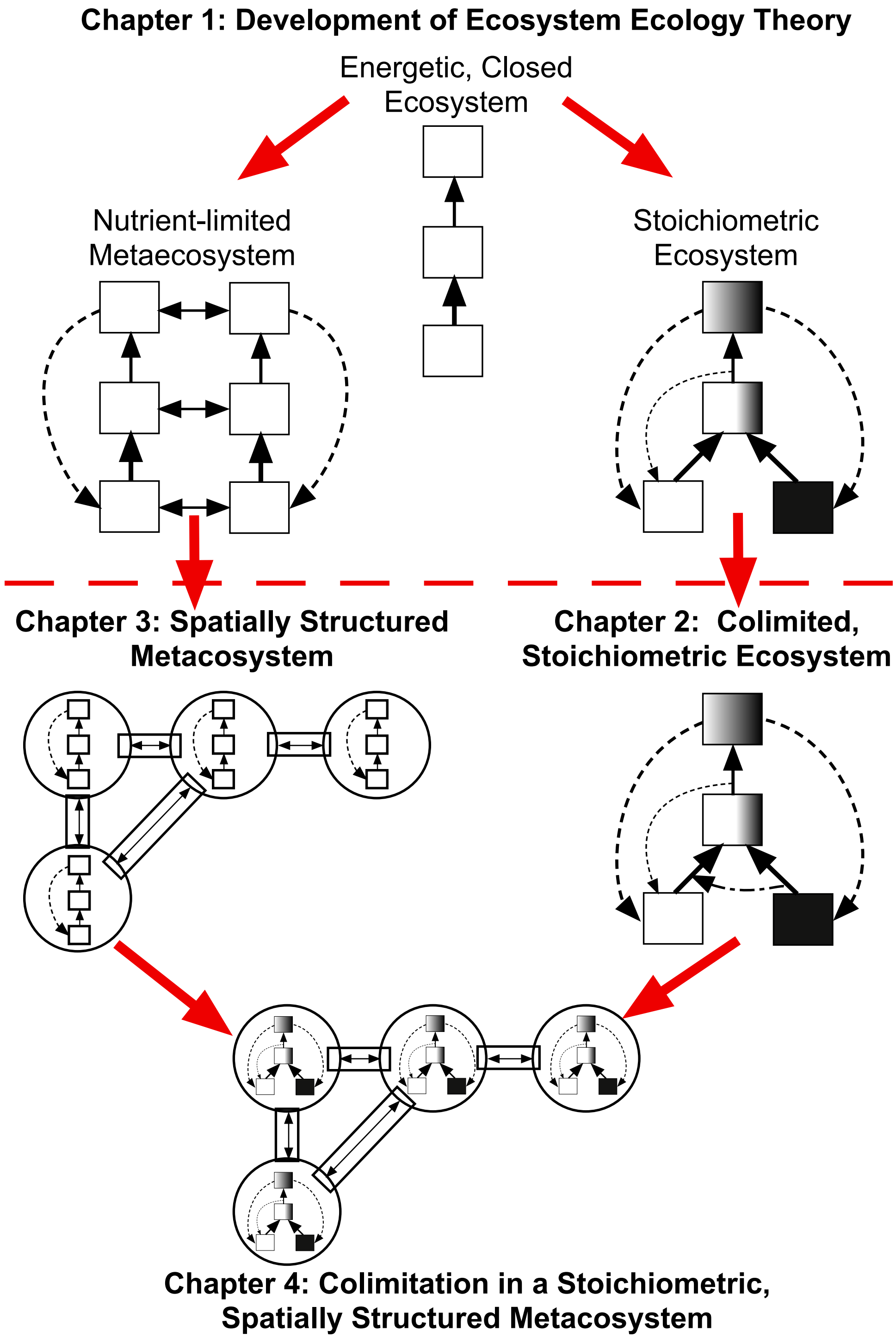
Table and Figure Captions

Figure 1.1: Outline of the thesis. In Chapter 1, I survey the development of ecosystem ecology theory and its evolution due to emergence of ecological stoichiometry and metaecosystem theory. In Chapter 2, I extend ecological stoichiometry by applying it to the problem of nutrient colimitation. In Chapter 3, I extend metaecosystem theory by looking at how spatial structure and differences in spatial flows between ecosystem compartments affect ecosystem dynamics and functioning. In Chapter 4, I integrate ecological stoichiometry and metaecosystem theory together in order to investigate if nutrient colimitation at local and regional scales can be

caused by spatial flows of nutrients and organisms.

Tables and Figures



Chapter 1: Development of Ecosystem Ecology Theory
Energetic, Closed
Ecosystem
Nutrient-limited
Metaecosystem
Stoichiometric
Ecosystem
Chapter 3: Spatially Structured
Metacosystem
Chapter 2: Colimited,
Stoichiometric Ecosystem
Chapter 4: Colimitation in a Stoichiometric,
Spatially Structured Metacosystem

Figure 1.1

Chapter 2
THE COMBINED EFFECT OF NUTRIENT COLIMITATION AND ECOLOGICAL STOICHIOMETRY ON ECOSYSTEM DYNAMICS AND FUNCTIONING

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Abstract

Recent experimental work has indicated that primary production in many ecosystems is limited by two or more nutrients (colimitation). The presence of colimitation in ecosystems suggests an important role of stoichiometric constraints on ecosystem processes beyond primary production, but little has been done to integrate colimitation into the larger framework of ecological stoichiometry. In this study, we present a general ecosystem model to examine different colimitation mechanisms and their interactions with stoichiometric imbalances between autotrophs and herbivores in order to elucidate impacts on ecosystem dynamics and functioning. Our results show that nutrient colimitation and stoichiometric imbalances can lead to declines in autotroph biomass with increasing nutrient availability, long-term transient cyclical dynamics and abrupt collapses of ecosystem production. Furthermore, the mechanisms of colimitation can lead to highly different ecosystem outcomes despite similarities in growth responses to nutrient additions, which indicates inadequacies of growth response-based definitions of colimitation. These results suggest that nutrient colimitation and stoichiometric imbalances are key mechanisms in determining ecosystem properties and need to be considered in our ecosystem management strategies.

Introduction

The relative abundance of elements or stoichiometry of an organism rarely matches the availability of those elements in the abiotic environment and can be significantly different from other organisms (Sterner & Elser, 2002). Because of the molecular and biochemical constraints on the creation of functional carbohydrates, lipids, nucleic acids and proteins within organisms, the elemental or stoichiometric mismatch between the resource and the consumer can control the consumer's growth (Lotka, 1925; Reiners, 1986; Sterner & Elser, 2002). While many elements may be in insufficient amounts for optimal growth of the consumer, there has long been a dominant view in ecology that the element which is least available relative to consumer demand should control the growth rate of the consumer, which is typically called 'Liebig's law of the minimum' (e.g. Redfield, 1958; Chapin, Matson, & Mooney, 2002). This principle of a single element being the primary controlling or limiting factor of growth has been extended beyond single organisms or species to whole communities of primary producers and to ecosystems (e.g. Martin, Gordon, & Fitzwater, 1991; Schindler et al., 2008).

However, this view has been challenged both on empirical and conceptual grounds. On the empirical side, a recent meta-analysis of 641 experimental studies involving nitrogen and phosphorus additions found primary producer communities are frequently limited in biomass growth by both elements, such that either the primary producers respond to either nutrient added independently or require both to be added simultaneously (Figure 2.1a; Harpole et al., 2011). On the conceptual side, ecologists have invoked a number of mechanisms that should lead to primary producer growth being limited by multiple elements (Figure 2.1b; Bloom, Chapin, & Mooney, 1985; Chapin, Bloom, Field, & Waring, 1987; O'Neill, DeAngelis, Pastor, Jackson, & Post, 1989; Chapin, Matson, & Mooney, 2002; Arrigo, 2005; Klausmeier, Litchman, & Levin, 2007; Danger, Daufresne, Lucas, Pissard, & Lacroix, 2008; Saito, Goepfert, & Ritt, 2008; Craine, 2009). These include i) abiotic supply rates of essential elements being extremely low (e.g. Arrigo, 2005), ii) different species in the community being limited by different elements (e.g. Arrigo, 2005; Danger et al., 2008), iii) the biochemical uptake and assimilation processes of one element within organisms can be helped by the presence of another element (e.g. Saito et al., 2008) and iv) the attempts of organisms to adapt to their external environments to achieve optimal or 'balanced' growth (Bloom et al., 1985; Abrams, 1987; Chapin, Bloom, et al., 1987; Chapin, Schulze, & Mooney, 1990; Gleeson & Tilman, 1992; Chapin, Matson, & Mooney, 2002; Klausmeier et al., 2007), though it should be noted that they are not mutually exclusive mechanisms (Figure 2.1b).

When the elements in question are essential nutrients such as nitrogen and phosphorus, ecologists talk about primary producers and other trophic levels as being colimited. However, there is no consistency in the literature about what 'nutrient colimitation' actually means. For some ecologists, if the biomass of a population increases more with the addition of two nutrients is greater than with the addition of either nutrient, then that population is colimited (e.g. Trommer, Pondaven, Siccha, & Stibor, 2012). For others, only if there is a positive biomass response to the simultaneous addition of both nutrients does nutrient colimitation occur (e.g. Güsewell, Koerselman, & Verhoeven, 2003). Neither of these definitions of nutrient colimitation is satisfactory, and Harpole et al. (2011) have attempted a synthesis of the various definitions presented in the literature to create two usable categories of colimitation, independent and simultaneous, for use in the field (Figure 2.1a).

However, these biomass response patterns are supposed to inform us of the underlying mechanisms, which then need to be incorporated into our models and theories (Harpole et al., 2011). A major concern is that these patterns do not correspond to any specific mechanisms and could easily be categorized as a 'special case' of 'Liebig's law of the minimum' (Harpole et al., 2011). If a pattern could be explained by a Droop or Tilman-like autotroph growth model (e.g. Droop, 1973; Tilman, 1982) that implements 'Liebig's law' through a minimum function, it is unclear there would be nutrient colimitation (Saito et al., 2008; Harpole et al., 2011). It could also be the case that the presence of a mechanism that clearly indicates a dependence of one nutrient on another may not lead to 'colimited' biomass response patterns.

Because of such concerns, we will be using a mechanistic definition of nutrient colimitation which differs somewhat from other ecologists who do not clearly delineate between 'Liebig's law' and nutrient colimitation (Saito et al., 2008). Nutrient colimitation occurs when the uptake or assimilation of one nutrient by an ecological entity (i.e. organism, population, community, ecosystem) is dependent on the presence of another nutrient. While similar to 'biochemical colimitation', this definition is expansive enough to include community and adaptive colimitation as both allow for the modification of nutrient uptake by the presence of another nutrient (Figure 2.1b Klausmeier et al., 2007; Danger et al., 2008).

Furthermore, the definition does allow us to rule out Tilman and Droop models as having a mechanism of colimitation (Figure 2.1b) and it should be able to accommodate different timescales of nutrient colimitation, be they proximate (short-term growth responses) or ultimate (changes in community structure) forms of limitation (Vitousek, Porder, Houlton, & A. 2010; Chapin, Matson, & Vitousek, 2011). A number of models with autotrophs having nutrient colimitation being implemented through such mechanisms have been produced and in some cases perform better at fitting data than a typical Droop or Tilman model (O'Neill et al., 1989; Pahlow & Oschlies, 2009; Poggiale, Baklouti, Queguiner, & Kooijman, 2010). What has not been explored in much detail (though see Poggiale et al., 2010) is how introducing nutrient colimitation mechanisms in ecosystem models will affect ecosystem dynamics and functioning, especially when interacting with stoichiometrically mismatched herbivores.

Previous studies have indicated that stoichiometric mismatches between herbivores and autotrophs can dramatically alter nutrient limitation status of the autotrophs, which can potentially alter ecosystem dynamics and functioning(Urabe & Sterner, 1996; Attayde & Hansson, 1999; Daufresne & Loreau, 2001; Grover, 2002, 2003, 2004; Andersen, Elser, & Hessen, 2004; Cherif & Loreau, 2007, 2009, 2013; Elser et al., 2010; Trommer et al., 2012). In one classic experiment, increasing the stoichiometric imbalance between herbivore and autotroph lead to the herbivores being surrounded by so many low quality algae that they exhibited barely any growth (Urabe & Sterner, 1996). Such imbalances, if sustained for a prolonged period, can easily lead to herbivore extirpation and potential food web collapse (Andersen et al., 2004). Nevertheless, herbivores can potentially mitigate such stoichiometric imbalances by altering the nutrient limitation status of the autotrophs through nutrient recycling (Daufresne & Loreau, 2001; Urabe, Elser, et al., 2002; Trommer et al., 2012).

Furthermore, the presence of herbivores should lead to different responses to nutrient additions by the autotrophs, especially when there are strong stoichiometric imbalances (Hall, Leibold, Lytle, & Smith, 2006; Diehl, 2007; Hall, 2009). Declines in autotroph biomass, rather than biomass increases or stability, can occur due to the stoichiometry of the autotrophs becoming closer to the stoichiometry of the herbivore with the nutrient addition (Hall et al., 2006). However, the previous studies have only investigated the response of autotrophs to herbivores with Droop or Tilman formulations for autotroph growth (Hall et al., 2006; Hall, 2009). Therefore, it is an open question if nutrient colimitation would reinforce or attenuate this effect of herbivores on autotrophs.

In this study, we evaluate the interactions between colimitation mechanisms and stoichiometric imbalances and investigate how they produce colimited biomass responses as well as impact the dynamics and functioning of ecosystems. To do so, we construct a general two nutrient-autotroph-herbivore ecosystem model that explicitly tracks the dynamics of nutrients inside the autotroph (primary producer) and herbivore communities and use this model to examine how colimitation and stoichiometric imbalances affect ecosystem persistence, the presence of oscillatory dynamics, as well as autotroph and herbivore biomass and production. Our results indicate that the incorporation of stoichiometric imbalances with colimitation can dramatically alter the dynamics and functioning of ecosystems. Familiar patterns of top-down control are skewed and sudden shifts in model behaviour can be observed, though this is strongly dependent on the colimitation mechanism. We conclude by examining how these results require new thinking about colimited ecosystems and the stoichiometric imbalances within them.

Methods

General Stoichiometric Ecosystem Model

Consider an ecosystem with two available inorganic nutrients that can potentially limit autotroph growth (R and S), autotrophs (X) with biomass B_X (in mol carbon) that uptake (F and U) these inorganic nutrients and herbivores (Y) with biomass B_Y (in mol carbon) hat in turn consume (W) the autotrophs, with no migration or immigration of autotrophs and herbivores (Figure 2.2). The internal stock per mol carbon of nutrient j for the autotrophs is then defined to be Q_{Xj}, which is the amount of nutrient j (in moles) per mol carbon. For our purposes, we will only track explicitly the dynamics of nutrients R and S in autotrophs (Q_{XR} and Q_{XS}) and in herbivores (q_{YR} and q_{YS}, which are regulated at a constant level).

The growth of the autotrophs (G) is determined by Q_{XR} and Q_{XS} as all other nutrients are assumed to be non-limiting (Figure 2.2a). The growth of the herbivore is determined by herbivory (W) and stoichiometric constraints (Z) (Figure 2.2a). Nutrients that are not assimilated into the biomass of the herbivores due to a stoichiometric imbalance between them and the autotrophs are excreted (C and D) and return to the available inorganic nutrient pools. The autotrophs and the herbivores suffer losses of nutrients due to mortality and non-mortality based losses such as shedding or leaf senescence (M and L, respectively), with some of those nutrients being recycled back into the inorganic nutrient pools. The pools of inorganic nutrients receive inputs (I and Φ) from numerous sources, such as atmospheric deposition (in terrestrial ecosystems) and upwelling (in aquatic ecosystems), and suffer losses (E and Δ) due to processes such as water runoff (in terrestrial ecosystems) and the sinking of organic matter (in aquatic ecosystems; Figure 2.2a).

With these assumptions, we have the following general system of equations for our model:

$$\frac{dR}{dt} = I(R) - E(R) - F(R, S, Q_{XR}, Q_{XS})B_X + \varepsilon_R M(B_X)Q_{XR} \tag{2.1a}$$

$$+ \chi_R L(B_Y)q_{YR} + C(Q_{XR}, Q_{XS}, B_X)B_Y$$

$$\frac{dS}{dt} = \Phi(S) - \Delta(S) - U(R, S, Q_{XR}, Q_{XS})B_X + \varepsilon_S M(B_X)Q_{XS} \tag{2.1b}$$

$$+ \chi_S L(B_Y)q_{YS}, + D(Q_{XR}, Q_{XS}, B_X)B_Y$$

$$\frac{dQ_{XR}}{dt} = F(R, S, Q_{XR}, Q_{XS}) - G(Q_{XR}, Q_{XS})Q_{XR} \tag{2.1c}$$

$$\frac{dQ_{XS}}{dt} = U(R, S, Q_{XR}, Q_{XS}) - G(Q_{XR}, Q_{XS})Q_{XS} \tag{2.1d}$$

$$\frac{dB_X}{dt} = G(Q_{XR}, Q_{XS})B_X - M(B_X) - W(B_X, B_Y) \tag{2.1e}$$

$$\frac{dB_Y}{dt} = Z(Q_{XR}, Q_{XS})W(B_X, B_Y) - L(B_Y) \tag{2.1f}$$

Where Z describes the stoichiometric imbalances between the autotroph and herbivores and modifies the growth of herbivores from consuming the biomass of autotrophs. Since the focus of our study is on nutrient colimitation and stoichiometric imbalances, we will be specifying simple functional forms for certain processes: nutrient inputs will be held constant, i.e. $I(R) = \Gamma$ and $\Phi(S) = \phi$, and losses of nutrients from compartments will be linear functions, i.e. $E(R) = \eta R$, $\Delta(S) = \delta S$, $M(B_X) = mB_X$ and $L(B_Y) = lB_Y$. Furthermore, we will be specifying a Lotka-Volterra functional response for herbivore consumption of autotrophs, i.e. $W(B_X, B_Y) = \omega B_X B_Y$.

Implementing colimitation mechanisms

There are a bewildering number of ways of implementing colimitation mechanisms in model ecosystems (e.g O'Neill et al., 1989; Gleeson & Tilman, 1992; Klausmeier et al., 2007; Saito et al., 2008; Poggiale et al., 2010). However, one can define two major types of biotic mechanisms, i.e. those that affect nutrient uptake and those that affect nutrient assimilation during growth (Figure 2.2b). Nutrient uptake of one limiting nutrient can be colimited when the uptake is at least partially dependent on the presence of another nutrient, such as in the case of phytoplankton carbon uptake which greatly increases in the presence of additional zinc (Saito et al., 2008). Furthermore, colimitation through nutrient uptake can possibly occur due to external nutrient availabilities or internal nutrient availabilities (Figure 2.2b). Colimitation through nutrient assimilation during growth can occur when limiting nutrients are partially substitutable (cobalt and zinc in phytoplankton) in cellular machinery or through other processes (Figure 2.2b; Saito et al., 2008).

For our purposes, we will use somewhat phenomenological modifications in order to add in colimitation, though some have been derived mechanistically (Pahlow & Oschlies, 2009; Poggiale et al., 2010). We do so for ease of comprehension, implementation and tractability. Furthermore, we will be using asymmetric colimitation for nutrient uptake (i.e. nutrient R affects S uptake, but not vice-versa) in order to emphasize the effects of the colimitation mechanism.

Before implementing a colimitation mechanism into nutrient uptake, the type of uptake function needs to be considered. For our purposes, we have decided to use modified Michaelis-Menten uptake kinetics that have a maximum uptake rate for nutrient j, v_j, and a half-saturation constant, K_j, but are also affected negatively by increasing internal nutrient stock of j. Therefore, without a colimitation mechanism, uptake for nutrients R and S can be described by the following equations:

$$F(R, S, Q_{XR}, Q_{XS}) = F(R, Q_{XR}) = \left(\frac{v_R R}{K_R + R}\right)\left(\frac{Q_{XR}^{\max} - Q_{XR}}{Q_{XR}^{\max} - Q_{XR}^{\min}}\right) \quad (2.2a)$$

$$U(R, S, Q_{XR}, Q_{XS}) = U(S, Q_{XS}) = \left(\frac{v_S S}{K_S + S}\right)\left(\frac{Q_{XS}^{\max} - Q_{XS}}{Q_{XS}^{\max} - Q_{XS}^{\min}}\right) \quad (2.2b)$$

To implement internal nutrient stock as a colimitation mechanism of nutrient uptake, we multiply the above uptake functions by a function that goes from 0 when the 'other' nutrient is at minimum levels in the autotroph to 1 when the other nutrient is at maximal levels in the autotroph:

$$F(R, S, Q_{XR}, Q_{XS}) = \left(\frac{v_R R}{K_R + R}\right)\left(\frac{Q_{XR}^{\max} - Q_{XR}}{Q_{XR}^{\max} - Q_{XR}^{\min}}\right)\left(\frac{Q_{XS} - Q_{XS}^{\min}}{Q_{XS}^{\max} - Q_{XS}^{\min}}\right) \quad (2.3a)$$

$$U(R, S, Q_{XR}, Q_{XS}) = \left(\frac{v_S S}{K_S + S}\right)\left(\frac{Q_{XS}^{\max} - Q_{XS}}{Q_{XS}^{\max} - Q_{XS}^{\min}}\right)\left(\frac{Q_{XR} - Q_{XR}^{\min}}{Q_{XR}^{\max} - Q_{XR}^{\min}}\right) \quad (2.3b)$$

To add colimitation through external nutrient concentration, we can modify the half-saturation constants by making them functions of the other nutrient (Poggiale et al., 2010):

$$\begin{aligned} F(R,S,Q_{XR},Q_{XS}) &= F(R,S,Q_{XR}) = \left(\frac{v_R R}{K_R(S)+R}\right)\left(\frac{Q_{XR}^{\max}-Q_{XR}}{Q_{XR}^{\max}-Q_{XR}^{\min}}\right) && \text{(2.4a)}\\ U(R,S,Q_{XR},Q_{XS}) &= U(R,S,Q_{XS}) = \left(\frac{v_S S}{K_S(R)+S}\right)\left(\frac{Q_{XS}^{\max}-Q_{XS}}{Q_{XS}^{\max}-Q_{XS}^{\min}}\right) && \text{(2.4b)}\\ K_R(S) &= K_R\frac{1+S}{S},\ K_S(R) = K_S\frac{1+R}{R} \end{aligned}$$

Without colimitation, we will use a Droop formulation for 'Liebig's law of the minimum' to model growth. We note that Saito et al. (2008) have argued that the Droop formulation itself is a colimitation mechanism ('type I' according to their schema), but we and other ecologists dispute such an assertion as any ecosystems demonstrating serial limitation would be considered colimited (e.g. Craine, 2009; Harpole et al., 2011). With a colimitation mechanism affecting growth, we will use a multiplicative formulation for growth (Saito et al., 2008). Therefore, we have the following expressions for G, the growth function of the autotrophs:

$$\begin{aligned} G(Q_{XR},Q_{XS}) &= \mu\min\left(1-\frac{Q_{XR}^{min}}{Q_{XR}}, 1-\frac{Q_{XR}^{min}}{Q_{XR}}\right) && \text{(2.5a)}\\ G(Q_{XR},Q_{XS}) &= \mu\left(1-\frac{Q_{XR}^{min}}{Q_{XR}}\right)\left(1-\frac{Q_{XR}^{min}}{Q_{XR}}\right) && \text{(2.5b)} \end{aligned}$$

Where μ is the theoretical maximum growth rate under no limitation. There does exist issues with the theoretical maximum growth rate formulation under serial limitation (Cherif & Loreau, 2010), though we will not address them here they are not the primary concern of this paper.

Stoichiometric constraints and imbalances

Both the autotrophs and the herbivores are under stoichiometric constraints with regards to their elemental compositions. The autotrophs have flexible stoichiometries that must remain within certain ranges to allow for their growth and assimilation of new nutrients, such that the internal stock of any nutrient j per mol C will have a minimum value, $Q_{Xj}^{\min}$, and a maximum value, $Q_{Xj}^{\max}$. For the herbivores, we have already indicated a fixed stoichiometry, which they regulate by excreting excess nutrients.

Because of the variability in the autotroph stoichiometry and the fixed stoichiometry of the herbivores, stoichiometric imbalances between the autotrophs and the herbivores are likely to occur (Figure 2.2b). They can occur if the autotrophs are relatively richer in R than herbivores, if autotrophs are relatively richer in S than herbivores or if autotrophs are relatively richer in both R and S than the herbivores. These three circumstances can be expressed through the use of a minimum function and leads to the following expression for Z:

$$Z(Q_{XR}, Q_{XS}) = \min\left(\frac{Q_{XR}}{q_{YR}}, \frac{Q_{XS}}{q_{YS}}\right) \tag{2.6}$$

If there is a perfect match in stoichiometry for the two nutrients ($Q_{XR} = q_{YR},\ Q_{XS} = q_{YS}$), then Z is equal to one and there is a perfect conversion of autotroph biomass to herbivore biomass. For our purposes, we will generally restrict the parameter ranges explored to a specific ecosystem where the autotrophs are much poorer in the limiting nutrient than the herbivore, thus Z will always be less than one (2.6) and (2.7) The stoichiometric mismatches lead to the recycling of the excess nutrients by the herbivores which are expressed in the following forms for C and D:

$$C(Q_{XR}, Q_{XS}, B_X) \;=\; \max\left(Q_{XR} - \frac{q_{YR}}{q_{YS}} Q_{XS}, 0\right) \omega B_X \tag{2.7a}$$

$$D(Q_{XR}, Q_{XS}, B_X) \;=\; \max\left(Q_{XS} - \frac{q_{YS}}{q_{YR}} Q_{XR}, 0\right) \omega B_X \tag{2.7b}$$

Model parameterization

Parameter values for the model were chosen to reflect elements of a colimited ecosystem found on Mount St. Helens, Washington, USA (Fagan, Bishop, & Schade, 2004; Gill et al., 2006; Apple, Wink, Wills, & Bishop, 2009; Bishop et al., 2010; Marleau, Jin, Bishop, Fagan, & Lewis, 2011). The plant community, which was initially dominated by *Lupinus lepidus*, has demonstrated strong nitrogen and phosphorus limitation, with asters such as *Hypochaeris radicata* greatly benefiting from the increases in nitrogen (Gill et al., 2006). In addition, there is strong evidence that the herbivore community is also limited by nutrients, particularly phosphorus (Fagan et al., 2004; Apple et al., 2009; Bishop et al., 2010). Furthermore, there are strong mismatches in the stoichiometry between the herbivores and autotrophs, making this an ideal system for the model to be applied to (Fagan et al., 2004).

For this study, we will only use parameters for a subset of the plant and herbivore communities. For the plants, we use *Hypochaeris radicata* as the representative autotroph in the ecosystem due to its high abundance and detailed data on its uptake kinetics (Schoenfelder, Bishop, Martinson, & Fagan, 2010; Marleau et al., 2011). For the herbivores, we chose the *Orthoptera* order as they are generalist herbivores that affect all of the autotroph community (Bishop et al., 2010). In particular, we use available parameters for *Anabrus simplex* as little is available on the elemental compositions of the other *Orthoptera* on Mount St. Helens. The parameters for the model can be found in Table 2.1.

We note that *Anabrus simplex* is much richer in nitrogen and phosphorus than *Hypochaeris radicata* and therefore should be limited by these nutrients rather than other nutrients (Table 2.1). We can therefore expect that both nutrients will not be recycled simultaneously by *Anabrus simplex.*

Model analysis

Our analysis of the above model can be separated into two parts. In the first part, we examine differences in growth responses of the autotrophs for the colimitation mechanisms in the absence of herbivores. We do so by numerically evaluating four different formulations of equation (2.1) (three colimitation mechanisms and one without colimitation mechanisms) at a control level of N and P input (I_c and Φ_c), at higher N input ($2I_c$ and Φ_c), at higher P input (I_c and $2\Phi_c$) and at higher input levels of both N and P ($2I_c$ and $2\Phi_c$). We then take the equilibrium values for autotrophs biomass for each nutrient input condition and normalize them by the control equilibrium values, such that the control value is always equal to 1. We also examined the effects of adding herbivores to the ecosystem on the growth responses to nutrient additions.

In the second section, we examine the biomass and production responses of autotrophs and herbivores to changes in nutrient levels with differing colimitation mechanisms. Autotroph production is defined by the growth function multiplied by autotroph biomass ($G(Q_{XR}, Q_{XS})B_X$), while herbivore production is defined as $Z(Q_{XR}, Q_{XS}, q_{YR}, q_{YS})W(B_X, B_Y)$, or herbivory modified by stoichiometric imbalance. However, at equilibrium, there can be simpler expressions for production at equilibrium, which will be seen below. Analytically, we examine certain equilibrium properties of the model in order to understand the roles played by stoichiometric imbalances and colimitation mechanisms. We complement this equilibrium analysis with numerical simulations of ecosystem dynamics using Matlab and the evaluation of the stability of those ecosystem dynamics using the bifurcation analysis software XPP AUT.

Results

Colimitation mechanisms can lead to a variety of growth responses

Depending on the control nutrient levels, the presence of a colimitation mechanism did not lead to a colimited biomass response for autotrophs and colimited biomass responses were observed with no colimitation mechanism whatsoever (Figure 2.3). At low levels of N and P input, all mechanisms lead to nitrogen-limited growth (Figure 2.3A). At high P input levels, only one type of colimitation mechanism, i.e. uptake of P is influence by external N concentrations, leads to a colimited growth response (Figures 2.3B and 2.3D). All other mechanisms demonstrate nitrogen-limited growth responses (Figures 2.3B and 2.3D). Over these three control conditions, very little differentiation exists between colimitation mechanisms except for one type of external uptake colimitation.

At high N and low P input levels, there is a wide variety of growth responses from the different mechanisms (Figure 2.3C). With no colimitation mechanism or with internal nutrient uptake colimitation mechanisms, autotrophs exhibits a simultaneous colimited growth response (Figure 2.3C). When autotrophs are modelled with a growth colimitation or nitrogen uptake being influenced by external P concentrations, we see growth responses match independent colimitation (Figure 2.3C). However, when P uptake is influenced by external N concentrations, we see nitrogen-limited growth responses (Figure 2.3C).

Based on the growth responses, there seems to be a clear indication that independent colimitation growth responses correspond to a colimitation mechanism (Figure 2.3). However, growth responses demonstrating simultaneous colimitation can be found without a mechanism at certain nutrient levels, which suggests that these growth responses should not be taken as indicative of a mechanism of colimitation (Figure 2.3C).

When herbivores are present in the ecosystem, there is generally negative growth responses to nutrient addition for autotrophs, while herbivore biomass responds to nitrogen addition (Figure A1). Intriguingly, slight independent colimitation can appear in herbivores, despite a lack of colimitation mechanism (Figure A1).

Interactions between nutrient colimitation and stoichiometric imbalances on equilibrium ecosystem properties

With an equilibrium that has both autotrophs and herbivores coexisting in the ecosystem, the biomass of autotrophs depends heavily on the stoichiometric imbalance between it and herbivores:

$$B_X^* = \frac{l}{\omega \min\left(\frac{Q_{XR}^*}{q_{YR}}, \frac{Q_{XS}^*}{q_{YS}}\right)} \tag{2.8}$$

Equation (2.8) indicates that the more the stoichiometric imbalance is reduced between autotrophs and herbivores, the lower the biomass for autotrophs. This result makes intuitive sense since, if the stoichiometric imbalance between herbivore and autotroph is smaller, the autotroph is more nutritious for the herbivore and more herbivore biomass can be produced per biomass of autotroph consumed, which leads to more herbivory on the autotrophs and less autotroph biomass at equilibrium.

The biomass of herbivores depends on the (co)limitation status of autotrophs at equilibrium:

$$B_Y^* = \frac{\mu \min\left(1 - \frac{Q_{XR}^{\min}}{Q_{XR}^*}, 1 - \frac{Q_{XS}^{\min}}{Q_{XS}^*}\right) - m}{\omega} \text{ or} \tag{2.9a}$$

$$B_Y^* = \frac{\mu\left(1 - \frac{Q_{XR}^{\min}}{Q_{XR}^*}\right)\left(1 - \frac{Q_{XS}^{\min}}{Q_{XS}^*}\right) - m}{\omega} \tag{2.9b}$$

Equation (2.9) indicates that the biomass of herbivores increases with increasing internal nutrient stocks (Q_{XR} and Q_{XS}) of autotrophs. The primary reason for this increase in herbivore biomass is the increase in autotroph biomass production with higher Q_{XR} and Q_{XS} values. The biomass production of autotrophs (Π_X) at equilibrium is also a function of internal nutrient stocks, though it is somewhat more complex:

$$\Pi_X = \mu \min\left(1 - \frac{Q_{XR}^{\min}}{Q_{XR}^*}, 1 - \frac{Q_{XS}^{\min}}{Q_{XS}^*}\right) B_X^* = \frac{l\mu \min\left(1 - \frac{Q_{XR}^{\min}}{Q_{XR}^*}, 1 - \frac{Q_{XS}^{\min}}{Q_{XS}^*}\right)}{\omega \min\left(\frac{Q_{XR}^*}{q_{YR}}, \frac{Q_{XS}^*}{q_{YS}}\right)} \text{ or} \tag{2.10a}$$

$$\Pi_X = \mu \left(1 - \frac{Q_{XR}^{\min}}{Q_{XR}^*}\right)\left(1 - \frac{Q_{XS}^{\min}}{Q_{XS}^*}\right) B_X^* = \frac{l\mu \left(1 - \frac{Q_{XR}^{\min}}{Q_{XR}^*}\right)\left(1 - \frac{Q_{XS}^{\min}}{Q_{XS}^*}\right)}{\omega \min\left(\frac{Q_{XR}^*}{q_{YR}}, \frac{Q_{XS}^*}{q_{YS}}\right)} \tag{2.10b}$$

Where equation (2.10a) represents equilibrium production if autotroph growth obeys Liebig's Law of the Minimum and equation (2.10b) is autotroph production is derived from colimited growth. One aspect concerning autotroph biomass production is that if autotroph growth and herbivore growth are limited by the same nutrient (R or S) as in (2.10a), then autotroph biomass production is constant. This result does not necessarily hold with (2.10b). In both cases, it is possible for increases or decreases in autotroph biomass production with changes in internal nutrient stock. The biomass production herbivores at equilibrium is just a function of its biomass multiplied by its lost rate l:

$$\Pi_Y^* = lB_H^* = l\frac{\mu \min\left(1 - \frac{Q_{XR}^{\min}}{Q_{XR}^*}, 1 - \frac{Q_{XS}^{\min}}{Q_{XS}^*}\right) - m}{\omega} \text{ or} \tag{2.11a}$$

$$\Pi_Y^* = lB_Y^* = l\frac{\mu \left(1 - \frac{Q_{XR}^{\min}}{Q_{XR}^*}\right)\left(1 - \frac{Q_{XS}^{\min}}{Q_{XS}^*}\right) - m}{\omega} \tag{2.11b}$$

Therefore, increases (or decreases) in herbivore biomass result in increases in herbivore production, which is not necessarily the case for autotrophs. While it is possible to derive expressions for Q_{XR}^* and Q_{XS}^*, they are much too complex to be interpreted here.

Abrupt changes and the emergence of oscillations in ecosystem biomass dynamics

The responses of autotrophs and herbivore biomass to increasing nitrogen input (Γ) are striking, with abrupt changes and the unexpected emergence of oscillations in biomass dynamics (Figure 2.4). Ecosystems modelled with no colimitation mechanism or with colimitation through external or internal P acting on N uptake all exhibit an initial gradual decline in autotroph biomass accompanied with a gradual increase in herbivore biomass with increasing Γ until Γ reaches a value that causes a collapse in autotroph biomass (Figure 2.4A). For values of Γ beyond that point, both autotroph and herbivore biomass oscillate around somewhat steady mean value of biomass, with the amplitudes of the oscillations ever increasing with greater Γ (Figure 2.4A).

For ecosystems with the other colimitation mechanisms, no similar collapse in autotroph biomass can be observed, but oscillations do occur after some threshold value of Γ (Figures 2.4B-2.4D). Instead of a collapse, there are declines from initial high values towards the mean autotroph biomass found at the onset of oscillations, with some declines being steeper than others Figures 2.4B-2.4D). While the biomass dynamics of herbivores are broadly similar between colimitation mechanisms, the growth colimitation mechanism does have a lower threshold Γ value for oscillations and a lower mean value for herbivore biomass at high Γ (Figure 2.4B).

The onset of oscillations occurs due to a shift from nitrogen limitation to phosphorus limitation for herbivores, while the abrupt collapse in autotroph biomass requires a similar shift to occur for autotrophs in addition to that of herbivores (Figure B1). The restricted range of internal phosphorus stock for the autotroph and the lack of influence of increasing nitrogen on internal phosphorus stock promote the abrupt shift, such that if the nitrogen addition does alter internal phosphorus stocks, there will not be such a collapse. In addition, if these shifts did not occur, such that autotrophs and herbivores remained nitrogen-limited, then there would be no collapse nor any oscillations within the parameter ranges chosen (Figure B2). This is not to say the oscillations would never occur if only limited by nitrogen, as very large nitrogen inputs would eventually lead to complex eigenvalues as in similar predator-prey models (McCann, 2011).

Furthermore, there is no need for any recycling of nutrients for the oscillations to occur, but there does need to be upper limits on autotroph internal N and P concentrations (Figure B3). In addition, no oscillations or collapses in biomass dynamics can be observed at lower phosphorus input (ϕ), though there are significant differences between colimitation mechanisms in biomass responses to nitrogen enrichment (Figure B4).

The oscillations, which persist over extremely long time periods in the numerical simulations (over 30000 days), do not seem to be produced by a bifurcation according to numerical computation of the eigenvalues by AUTO (Figure B5). Rather, the oscillations emerge as real eigenvalues become complex and the real parts of these complex eigenvalues remain negative but approach zero as Γ increases. Therefore, the equilibrium solution is still locally stable, though the return time to this equilibrium is extremely long due to the real part of the dominant eigenvalue approaching zero (Figure B5). Hence, the oscillations are transients and over very long timescales, the oscillations should peter out.

Large differences in ecosystem production between colimitation mechanisms

The different colimitation mechanisms also lead to large differences in biomass production for autotrophs and herbivores (Figure 2.5). At relatively high ϕ, the colimitation mechanisms that lead to a collapse in autotroph biomass also lead to a collapse in autotroph production, but unlike biomass, production initially increases with increasing Γ (Figure 2.5A). Autotroph production for the growth and internal uptake (N on P) colimitation mechanisms show complex behaviour with increasing Γ, with an initial rise in production followed by a decline that levels offs and begins to slightly increase (Figure 2.5A). Ecosystems with external uptake (N on P) colimitation for autotrophs see a nearly monotonous increase in autotroph production with increasing Γ (Figure 2.5A). In contrast, herbivore production follows directly from its biomass, such that there are only relatively minor differences between colimitation mechanisms (Figure 2.5B).

At lower ϕ, there are marked differences between colimitation mechanisms in autotroph and herbivore production at low Γ values, though the differences diminish at higher Γ (Figures 2.5C-2.5D). However, the external uptake (P on N) colimitation mechanism maintains much higher autotroph production and lower herbivore production than all the other mechanisms over most of the Γ values explored (Figures 2.5C-2.5D).

Discussion

We have constructed a stoichiometric ecosystem model integrating colimitation mechanisms with stoichiometric imbalances and have evaluated their impacts on ecosystem dynamics and functioning. Furthermore, we have examined the relationship between colimitation defined by growth responses and colimitation mechanisms. Our results show that colimitation mechanisms interact with stoichiometric imbalances and cause large differences in expected autotroph and herbivore biomass dynamics and biomass production. In addition, at some control nutrient levels, distinctions between colimitation mechanisms can not be achieved by examining growth responses, while certain 'colimited' growth responses can be achieved without any colimitation mechanism whatsoever.

Colimitation: Growth responses or mechanisms?

As mentioned in the introduction, definitions abound about what colimitation is (Arrigo, 2005; Saito et al., 2008; Craine, 2009; Harpole et al., 2011). Broadly, the definitions may focus on the mechanisms that lead could lead to colimited growth responses (Arrigo, 2005; Saito et al., 2008) or on the growth responses themselves (Harpole et al., 2011). Since it is much more difficult to ascertain biochemical mechanisms than to perform nutrient addition experiments, field ecologists have focused on growth responses to determine colimitation and the impacts of other trophic groups on colimitation (e.g. Harpole et al., 2011; Trommer et al., 2012; Atkinson, Vaughn, Forshay, & Cooper, 2013).

There are difficulties with such an outcome-oriented definition, however, as our study shows. First, the nutrient levels found in ecosystems can mask the presence of colimitation mechanisms within the autotroph community, such that nutrient addition experiments can show no colimited growth responses in such ecosystems. Second, the presence of a colimited growth response is not indicative of the presence of a colimitation mechanism as defined here. In both these cases, the key insight is the importance of the external supply of nutrients. If the relative supplies of nutrients are close to the relative demands by the community, then a simultaneous or an independent colimitation growth response will occur. If the relative supplies of nutrients are not close to the relative demands, then single-nutrient responses will occur.

Lastly, the differences in the mechanisms, even when they do not show colimited growth responses when herbivores are absent, can cause substantial differences in biomass and biomass production when other trophic levels are present. Furthermore, all signs of nutrient limitation may be lost in the autotroph community due to the herbivory, which could help explain the prevalent lack of response of autotroph communities to nutrient addition experiments (Harpole et al., 2011).

This last point is especially important when bringing colimitation into the ecological stoichiometry framework (Sterner & Elser, 2002). Typically, colimitation is expressed in equations through external nutrient concentrations, which works well with nutrient addition experiments (O'Neill et al., 1989; Saito et al., 2008; Poggiale et al., 2010). However, these formulations do not take into account the internal nutrient stores which alter the autotroph uptake rates of nutrients and force limitations on the stoichiometric compositions of autotrophs (Newbery, Wolfenden, Mansfield,

& Harrison, 1995; Grover, 2002, 2003). As the internal nutrient stores also play a pivotal role in stoichiometric imbalances, their mechanistic role in colimitation should be addressed in greater detail.

With all this in mind, we recommend that ecologists use more mechanistic definitions of colimitation (e.g. Saito et al., 2008). However, such definitions will need to be expanded in order to take stoichiometric constraints and the potential effects of trophic interactions into account.

Collapses, declines and oscillations: deviations from single nutrient ecosystems

The combination of colimitation and stoichiometric imbalances in our ecosystem model leads to a number of deviations from previous predictions concerning the response of ecosystem compartments (i.e. autotrophs, herbivores) to increasing nutrient enrichment (e.g. Loreau, 2010). The most pronounced deviation is the unexpected collapse of autotroph biomass and production, which requires both stoichiometric imbalances and the presence of two limiting nutrients to occur, though no colimitation mechanism. With human activities altering the nutrient limitation status of autotroph communities through species loss (Millennium Ecosystem Assessment, 2005) and increasing atmospheric deposition of nitrogen (Elser et al., 2010), our model suggests that the collapse of ecosystem primary production should be considered seriously. It must be noted, however, that these collapses differ significantly from those found in other studies (e.g. Scheffer, 2009) as the system can be easily returned to the previous state and there are unambiguous signals of incoming collapse (Hastings & Wysham, 2010).

The primary signal of collapse is the decline of autotroph biomass with increasing nutrient enrichment, which is another important deviation from single-nutrient ecosystem models. Generally, when there is a form of top-down control (Fretwell, 1977) operating in an ecosystem model at equilibrium, the ecosystem compartment under top-down control will not respond to nutrient enrichment (Loreau, 2010). In our model and other models with flexible stoichiometry (e.g. Hall et al., 2006), there are instead continuing declines in the biomass of the autotrophs with increasing enrichment. This is because the stoichiometric imbalance between autotrophs and herbivores diminishes, leading to increased herbivore biomass and herbivory (Urabe & Sterner, 1996; Sterner & Elser, 2002). When nutrient enrichment no longer reduces the stoichiometric imbalance, no further declines in autotroph biomass occurs, which is highly-dependent on the colimitation mechanism that is present.

Another deviation regarding decline is in autotroph production. Previous work has shown that while nutrient enrichment does not benefit autotroph biomass, it does lead to increase autotroph production (Loreau, 2010). Here, we observe multiple instances where declines occur instead, though the magnitude of the declines depend on the colimitation mechanism at work. The declines are possible due to the strong interactions between colimitation and stoichiometric imbalances, which are expressed through the internal nutrient stocks of the autotrophs as seen in equation (2.10). Furthermore, because a nutrient can become non-limiting at high levels in stoichiometric models, unlike single-nutrient models, enrichment can stop affecting production completely.

However, that is only true if the system remains at equilibrium. For our model, high levels of 'non-limiting' nutrient seem to allow oscillations to emerge and amplify. Such a result was unexpected as traditional trophic food chain models require saturating, non-linear functional responses to generate oscillatory dynamics (e.g. Rosenzweig, 1971; Hastings & Powell, 1991) and models incorporating stoichiometry can reduce the possibility of oscillatory dynamics (Andersen et al., 2004; Stiefs, van Voorn, Kooi, Feudel, & Gross, 2010). Grover (2003) observed oscillations with non-saturating functional responses in the herbivore, but suggested that herbivore nutrient recycling would promote oscillatory dynamics, which we do not need in our model. Instead, our results support the idea that the oscillations are due to the change in nutrient limitation and the self-limitation in the nutrient uptake functions. The oscillations observed in our model are not stable, but are rather extremely long-lasting transients. However, such transient dynamics are at ecologically relevant timescales and indicate the importance of looking beyond equilibrium conditions in ecological systems (Hastings, 2004; Caswell, 2007; Hastings, 2010).

The overall implications are that nutrient colimitation and stoichiometric imbalances are important processes to consider in the construction of ecosystem models and are expected to cause significant deviations from single-nutrient or energetic models. Further work needs to be done in examining how to generalize the results beyond the specific functional forms provided here and to apply similar models to colimited ecosystems beyond Mount St. Helens.

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Table and Figure Captions

Table 2.1: The definitions and values of the Mount St. Helens ecosystem parameters with nitrogen (N) and phosphorus (P) being limiting nutrients

Figure 2.1: Relating phenomena to mechanisms in nutrient colimitation. *A* In field, nutrient colimitation is inferred by the growth responses of primary producers to additions of potentially limiting nutrients (R and S). Within the literature, the growth responses associated with serial limitation, independent colimitation and simultaneous colimitation have all been deemed to indicate colimitation, though serial limitation is not 'true' colimitation to many ecologists (e.g. Craine, 2009). *B* A number of mechanisms have been invoked to explain the phenomena. These mechanisms include i) insufficient abiotic supply of multiple limiting nutrients (circles), ii) different nutrients limiting the growth of different plant species within the community (species on left is limited by white nutrient, species on right is limited by black nutrient), iii) the requirement of one nutrient in the uptake or assimilation of another nutrient (black nutrient uptake receptor (black rectangle) only becomes active when a white nutrient binds its receptor (white rectangle)) and iv) species alter their stoichiometry and receptors adaptively (rectangles) to achieve balanced growth.

Figure 2.2: Conceptual model of a stoichiometric, colimited ecosystem with two limiting inorganic nutrients (R and S), an autotroph community and a herbivore community. *A* The autotroph and herbivore communities are characterized by their biomasses (B_X and B_Y, respectively) and their internal stocks of nutrients (Q_{XR} and

Q_{XS} for autotrophs, q_{YR} and q_{YS} for herbivores). The pools of inorganic nutrients receive inputs from non-specified sources (I and Φ) and the recycling of nutrients due to autotroph losses ($\epsilon_R M B_X Q_{XR}$ and $\epsilon_S M B_X Q_{XS}$), herbivore losses ($\chi_R L B_Y q_{YR}$ and $\chi_S L B_Y q_{YS}$) and stoichiometric imbalance between herbivores and autotrophs (CB_Y and DB_Y). The pools of inorganic nutrients lose nutrients either to inorganic pathways (E and Δ) or to autotroph nutrient uptake (FB_X and UB_X). The nutrients obtained by the autotroph community through uptake alter their internal stocks and influence the growth of autotroph (G) biomass. The autotrophs lose biomass either through intrinsic losses (MB_X) or through herbivory (W). The nutrients obtained through herbivory are partially assimilated based on the fixed internal nutrient stores (q_{YR} and q_{YS}) and thereby influence the growth of herbivore biomass (Z). The herbivores only suffer intrinsic losses (MB_Y). *B* How colimitation (blue) and stoichiometric imbalances (red) enter the model.

Figure 2.3: Models of colimitation mechanisms and the associated growth responses of autotrophs to nitrogen (N) addition (+N; diagonal lines bar), phosphorus (P) addition (+P; patterned bar), and to addition of both (+NP; white bar) at four different control (C; black bar) nutrient levels. *A* At low control N and P levels, all model formulations (with and without colimitation mechanisms) demonstrate nitrogen-limited growth responses. *B* At low control N and high P levels, all model formulations except external uptake colimitation (N influences P uptake), which shows slight independent colimitation growth response, show nitrogen-limited grow responses. *C* At high N and low P levels, there are a variety of growth responses: no colimitation

mechanism and both internal uptake colimitation mechanisms show a simultaneous colimited growth response, external uptake (P influences N uptake) and growth colimitation mechanisms show independent colimitation and external uptake colimitation (N influences P uptake) shows an nitrogen-limited growth response. *D* At high N and P levels, same responses as in *D*.

Figure 2.4: Changes in autotroph and herbivore biomass dynamics (minimum, mean and maximum values) across a nitrogen input (Γ) gradient for different colimitation mechanisms. In all cases, ϕ=2.871 x $10^{-}4$ μmol P/(L*day). Initial conditions for all simulations were R=0.002 mol N/L, S=0.001 mol P/L, Q_{XR}=0.0312 mol N/mol C, Q_{XS}=0.0014 mol P/mol C, B_X=1 mol C, B_Y = 0.5 mol C. *A* No colimitation mechanism. *B* Growth colimitation mechanism. *C* External colimitation mechanism (N on P). *D* Internal colimitation mechanism (N on P). Note that external and internal uptake (P on N) colimitation demonstrate dynamics identical to no colimitation mechanism (*A*).

Figure 2.5: Changes in autotroph (*A* and *C*) and herbivore (*B* and *D*) production across a nitrogen input (Γ) gradient for different colimitation mechanisms at two levels of phosphorus (ϕ; low ϕ is for panels *A* and *B*, high ϕ is for panels *C* and *D*) input. Values are averages taken from time series.

Tables and Figures

Table 2.1: The definitions and values of the Mount St. Helens ecosystem parameters used in this study with nitrogen (N) and phosphorus (P) being limiting nutrients. Ecosystem and *Hypochaeris* (autotrophs) data from Marleau, Jin, Bishop, Fagan, and Lewis (2011) and references wherein, though lower P values than within natural range are used for some simulations. *Anabrus* (herbivores) data from Pfadt (1994), Visanuvimol and Bertram (2010).

Parameter (unit)	Definition	Value
Γ (μmol N day^{-1} L^{-1})	Influx of available N into ecosystem	10 to 6000
ϕ (μmol P day^{-1} L^{-1})	Influx of available P into ecosystem	28.7 to 2830
η (day^{-1})	Efflux of available N from ecosystem	0.005 (free parameter)
δ (day^{-1})	Efflux of available P from ecosystem	0.005 (free parameter)
μ (day^{-1})	Maximum growth rate of *Hypochaeris* at infinite internal nutrients	0.352
m (day^{-1})	Mass-specific C loss rate of *Hypochaeris*	0.005
$Q_{XR}^{\max}, Q_{XR}^{\min}$ (mol N mol C^{-1})	Maximum and minimum internal N concentration of *Hypochaeris*	0.0509 (max), 0.0115 (min)
$Q_{XS}^{\max}, Q_{XS}^{\min}$ (mmol P mol C^{-1})	Maximum and minimum internal P concentration of *Hypochaeris*	1.7 (max), 1.13 (min)
v_R (mol N mol C^{-1} day^{-1})	Maximum N uptake rate	0.1272
v_S (mmol P mol C^{-1} day^{-1})	Maximum P uptake rate	0.348
K_R (μmol N L^{-1})	Half-saturation constant for N uptake	7
K_S (μmol P L^{-1})	Half-saturation constant for P uptake	0.7321
ϵ_R(-)	Proportion of N lost by *Hypochaeris* that is recycled	0
ϵ_S(-)	Proportion of P lost by *Hypochaeris* that is recycled	0
q_{YR} (mol N mol C^{-1})	Internal N concentration of *Anabrus*	0.19125
q_{YS} (mol P mol C^{-1})	Internal P concentration of *Anabrus*	0.00698
ω (mol C plant mol C herbivore^{-1} day^{-1})	*Anabrus* attack rate	0.0287
l (day^{-1})	Mass-specfic C loss rate of *Anabrus*	0.005
χ_R (-)	Proportion of N lost by *Anabrus* that is recycled	0
χ_S (-)	Proportion of P lost by *Anabrus* that is recycled	0

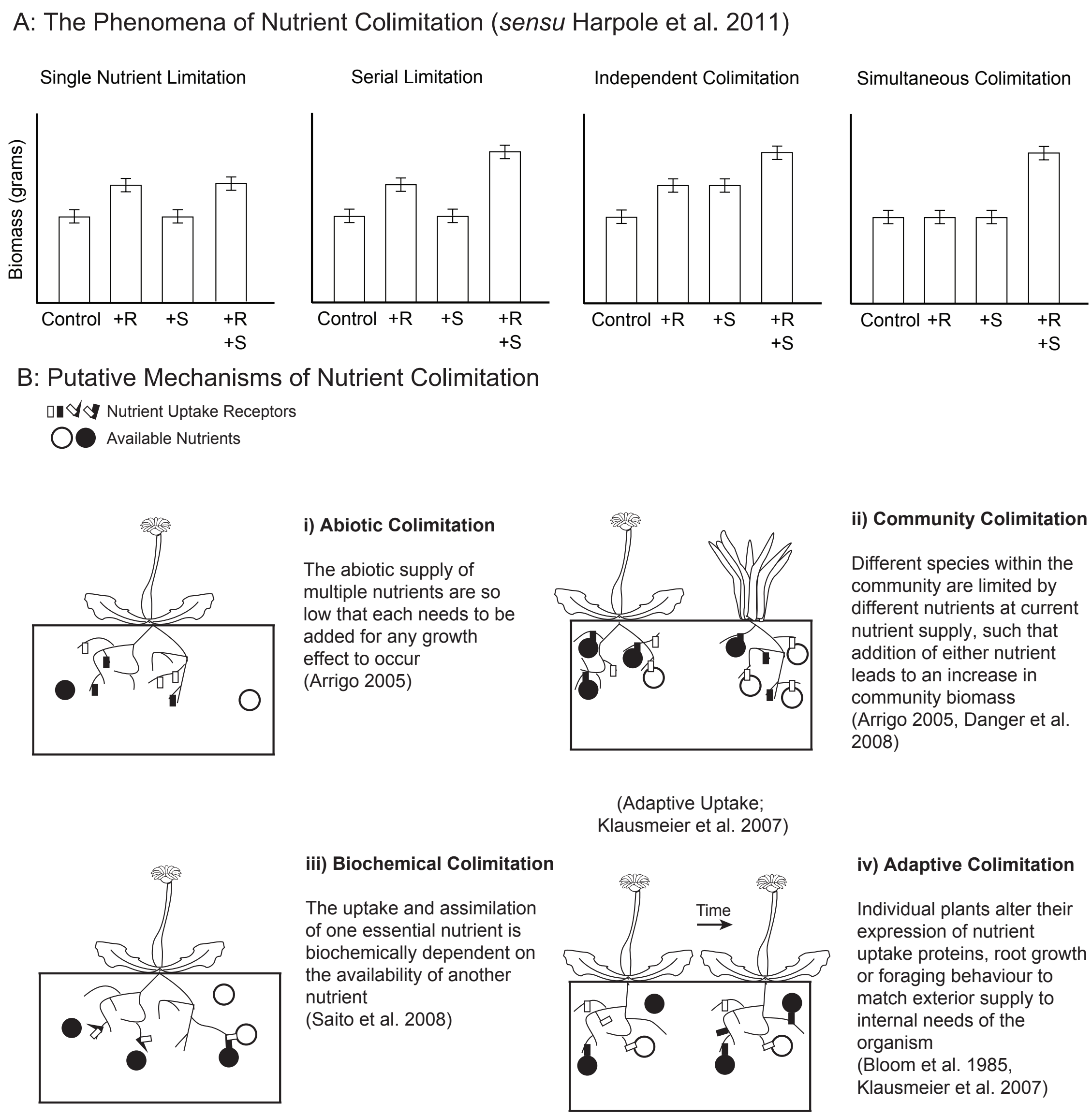

A: The Phenomena of Nutrient Colimitation (*sensu* Harpole et al. 2011)
Single Nutrient Limitation
Serial Limitation
Independent Colimitation
Simultaneous Colimitation
Biomass (grams)
Control
+R
+S
+R +S
B: Putative Mechanisms of Nutrient Colimitation
Nutrient Uptake Receptors
Available Nutrients
i) Abiotic Colimitation
The abiotic supply of multiple nutrients are so low that each needs to be added for any growth effect to occur (Arrigo 2005)
ii) Community Colimitation
Different species within the community are limited by different nutrients at current nutrient supply, such that addition of either nutrient leads to an increase in community biomass (Arrigo 2005, Danger et al. 2008)
(Adaptive Uptake; Klausmeier et al. 2007)
iii) Biochemical Colimitation
The uptake and assimilation of one essential nutrient is biochemically dependent on the availability of another nutrient (Saito et al. 2008)
Time
iv) Adaptive Colimitation
Individual plants alter their expression of nutrient uptake proteins, root growth or foraging behaviour to match exterior supply to internal needs of the organism (Bloom et al. 1985, Klausmeier et al. 2007)

Figure 2.1

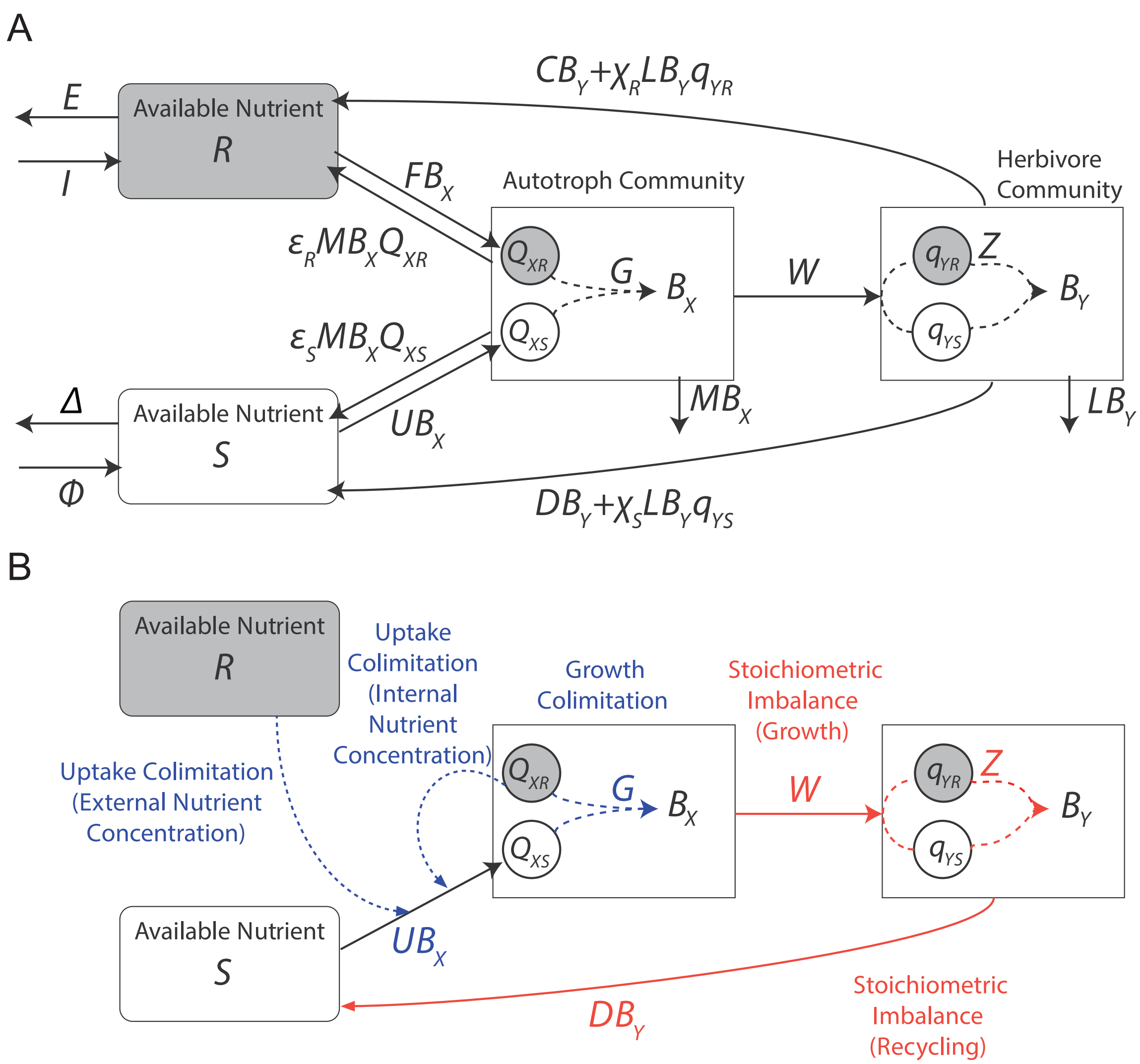

A
Available Nutrient
R
E
I
FB_X
CB_Y+χ_RLB_Yq_YR
ε_RMB_XQ_XR
Autotroph Community
Herbivore
Community
Q_XR
G
B_X
W
q_YR
Z
B_Y
ε_SMB_XQ_XS
Q_XS
q_YS
Δ
Available Nutrient
S
Φ
UB_X
MB_X
LB_Y
DB_Y+χ_SLB_Yq_YS
B
Available Nutrient
R
Uptake
Colimitation
(Internal
Nutrient
Concentration)
Growth
Colimitation
Stoichiometric
Imbalance
(Growth)
Uptake Colimitation
(External Nutrient
Concentration)
Q_XR
G
B_X
W
q_YR
Z
B_Y
Q_XS
q_YS
Available Nutrient
S
UB_X
DB_Y
Stoichiometric
Imbalance
(Recycling)

Figure 2.2

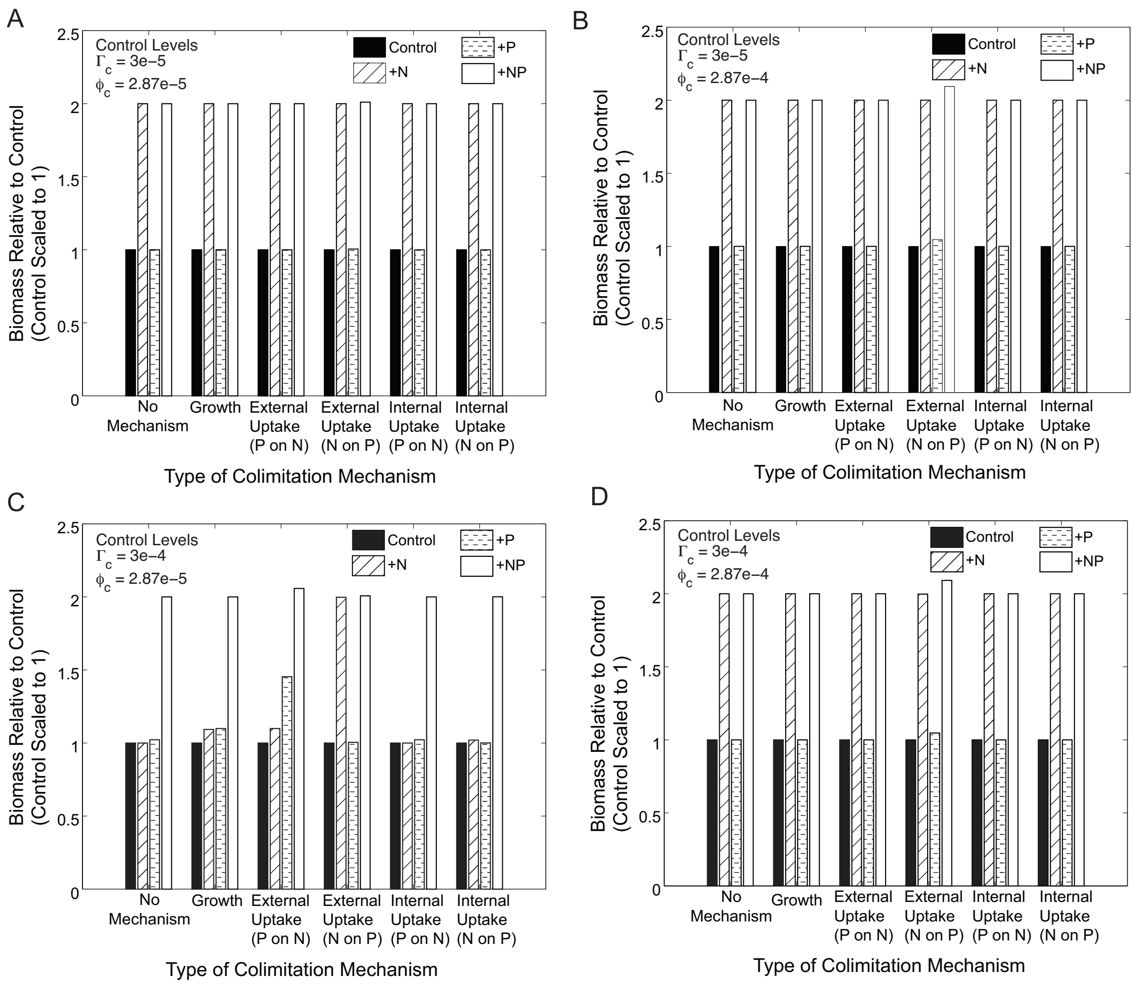

A
Control Levels
Γ_c = 3e−5
ϕ_c = 2.87e−5
Control
+N
+P
+NP
Biomass Relative to Control (Control Scaled to 1)
No Mechanism
Growth
External Uptake (P on N)
External Uptake (N on P)
Internal Uptake (P on N)
Internal Uptake (N on P)
Type of Colimitation Mechanism
B
Control Levels
Γ_c = 3e−5
ϕ_c = 2.87e−4
C
Control Levels
Γ_c = 3e−4
ϕ_c = 2.87e−5
D
Control Levels
Γ_c = 3e−4
ϕ_c = 2.87e−4

Figure 2.3

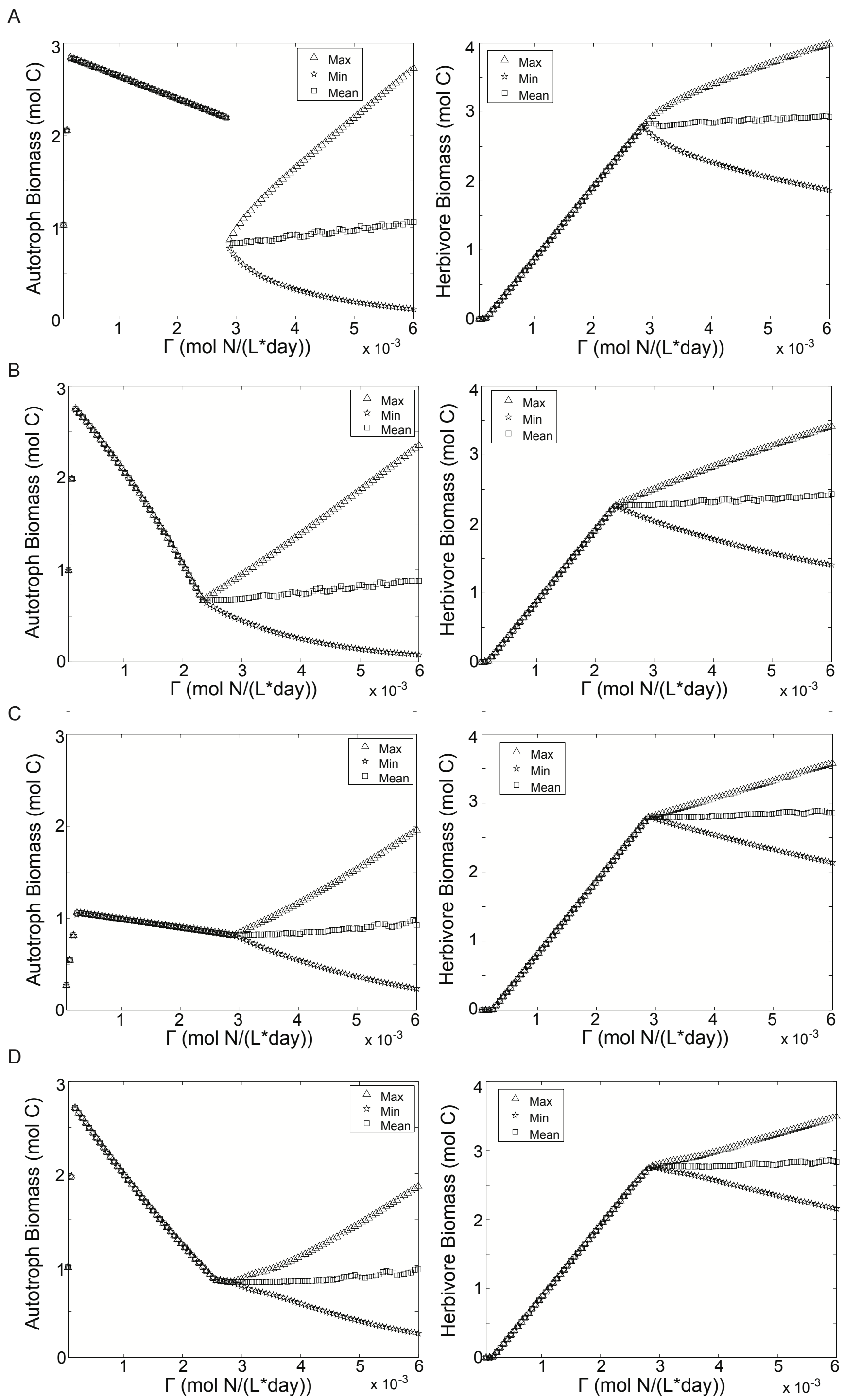

A
B
C
D
Max
Min
Mean
Autotroph Biomass (mol C)
Herbivore Biomass (mol C)
Γ (mol N/(L*day))
x 10^-3

Figure 2.4

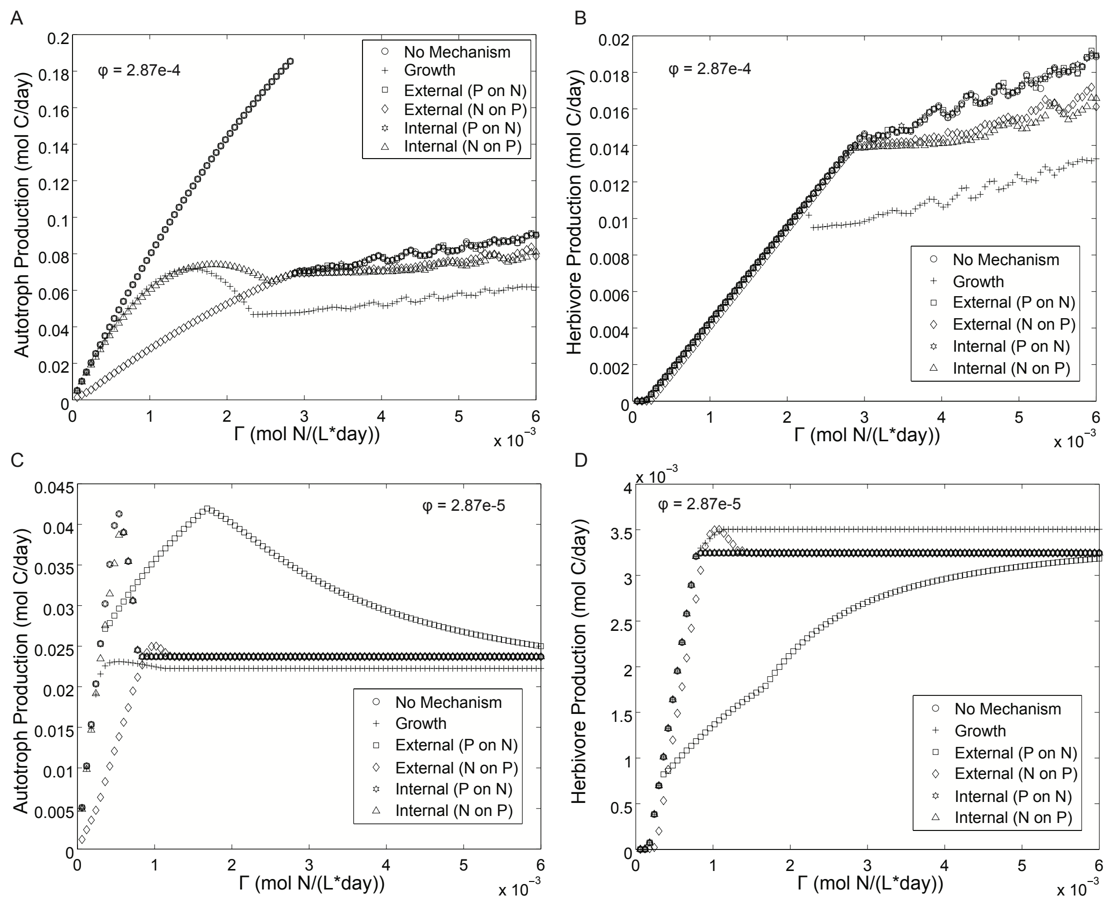

A
φ = 2.87e-4
No Mechanism
Growth
External (P on N)
External (N on P)
Internal (P on N)
Internal (N on P)
Autotroph Production (mol C/day)
Γ (mol N/(L*day))
x 10^-3
B
φ = 2.87e-4
Herbivore Production (mol C/day)
C
φ = 2.87e-5
Autotroph Production (mol C/day)
D
φ = 2.87e-5
Herbivore Production (mol C/day)
x 10^-3

Figure 2.5

Appendix A: The effects of herbivore presence on biomass responses to nutrient additions

In this section, we examine the role that herbivores plays in determining the growth responses of autotrophs to nutrient additions, as well as the growth responses of herbivores. Unlike in Figure 3, autotroph growth does not respond positively to nutrient addition as herbivores exerts severe top-down control on the autotroph population (Figure A1). Positive growth responses are found in herbivores, though they are typically limited to nitrogen addition except in two cases, one of which shows independent colimitation (Figure A1). This is quite unexpected as there is no obvious mechanism for the colimited growth response. However, since the autotrophs would show such a growth response without the presence of herbivores (Figure 2.3), it may be that the colimited growth response of autotrophs is transferred to the herbivores.

Table and Figure Captions

Figure A1: Models of colimitation mechanisms with the presence of herbivores and the associated growth responses of autotrophs and herbivores to nitrogen (N) addition (+N; diagonal lines bar), phosphorus (P) addition (+P; patterned bar), and to addition of both (+NP; white bar) at two different control (C; black bar) phosphorus levels. *A* At low control P levels, all model formulations (with and without colimitation mechanisms) demonstrate reduced autotroph growth with +NP addition and only one mechanism (growth) shows a positive growth response to a nutrient addition (+P). *B* At low P levels, all model formulations except external uptake colimitation (P influences N uptake), which shows serial limitation growth response, show nitrogen-limited grow responses for herbivores. *C* At high P levels, all model formulations (with and without colimitation mechanisms) demonstrate reduced autotroph growth with nutrient addition *D* At high P levels, all model formulations except external uptake colimitation (N influences P uptake), which shows an independent colimitation growth response, show nitrogen-limited grow responses for herbivores.

Tables and Figures

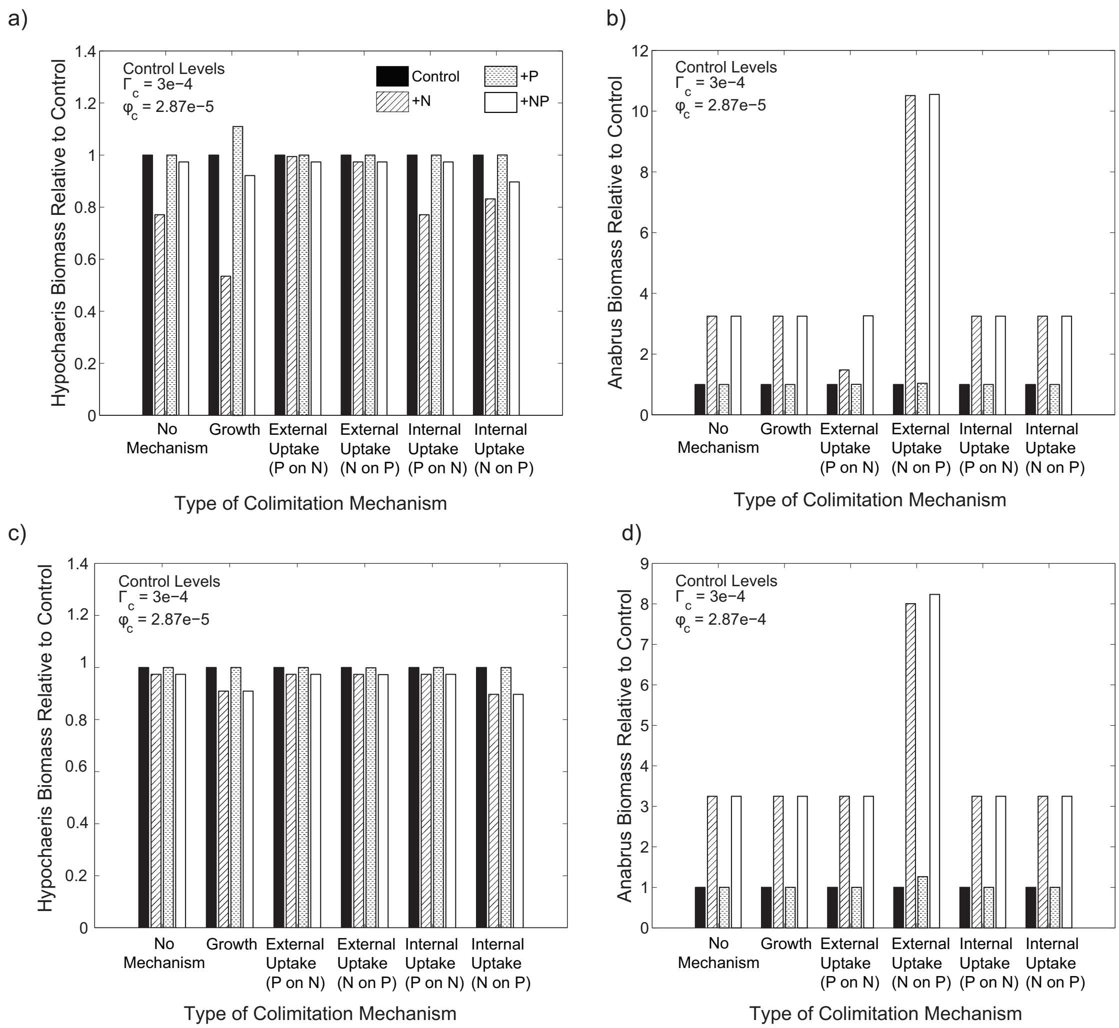

a)
Control Levels
Γc = 3e−4
φc = 2.87e−5
Control
+N
+P
+NP
Hypochaeris Biomass Relative to Control
No Mechanism
Growth
External Uptake (P on N)
External Uptake (N on P)
Internal Uptake (P on N)
Internal Uptake (N on P)
Type of Colimitation Mechanism
b)
Control Levels
Γc = 3e−4
φc = 2.87e−5
Anabrus Biomass Relative to Control
Type of Colimitation Mechanism
c)
Control Levels
Γc = 3e−4
φc = 2.87e−5
Hypochaeris Biomass Relative to Control
Type of Colimitation Mechanism
d)
Control Levels
Γc = 3e−4
φc = 2.87e−4
Anabrus Biomass Relative to Control
Type of Colimitation Mechanism

Figure A1

Appendix B: Further examination of the biomass dynamics: nutrient limitation, different nutrient levels and stability

In this section, we examined in greater detail the various components of the biomass dynamics, including changes in nutrient limitation and the local stability of the observed dynamics.

Nutrient limitation status changes and biomass dynamics

As indicated in the main text, the changes in nutrient limitation status of autotrophs and of herbivores correspond to shifts in biomass dynamics, especially with no colimitation mechanism. With somewhat 'high' levels of phosphorus input (ϕ), we initially have both autotrophs and herbivores being nitrogen-limited at low levels of nitrogen input Γ (Figure B1). As we increase Γ, we eventually see a shift in nutrient limitation, with phosphorus becoming the limiting nutrient for both autotrophs and herbivores, with the shift being extremely sudden for herbivores (Figure B1). This shift in nutrient limitation status occurs at the collapse of autotroph biomass and the onset of long-lasting transient oscillatory dynamics (Figure 4A).

Factors responsible for the oscillations

We subtly modified the model formulation with no colimitation mechanism by eliminating the stoichiometric imbalance between autotrophs and herbivores, allowing for no nutrient recycling. According to Grover (2003), herbivore nutrient recycling is key for the emergence of oscillations in his stoichiometric model. However, we still see oscillations in our model without herbivore nutrient recycling (Figure B3A). Rather, if we remove the maximum internal nutrient concentrations, we can eliminate the oscillatory dynamics found in the model (Figure B3B).

Changes in biomass dynamics at lower phosphorus availabilities

At low levels of phosphorus input, ϕ, autotrophs and herbivores do not exhibit oscillations in their biomass dynamics as nitrogen input, Γ, increases (Figure B4). Nevertheless, large differences in equilibrium levels of biomass can be observed across the nitrogen input gradient (Figure B4).

Stability of equilibrium solution: numerical bifurcation diagram

Using AUTO through XPPAUT, we generated bifurcation diagrams that numerically evaluate the stability conditions and eigenvalues of the model, which in this case has a growth colimitation mechanism. In all cases, the equilibrium remained stable over the values of Γ explored, though the dominant eigenvalue approaches zero with increasing Γ (Figure B5).

Table and Figure Captions

Figure B1: Limitation status of autotrophs (left) and herbivores (right) at different levels of nitrogen input Γ. Whatever line has the lowest value at a specific Γ indicates the limiting nutrient. Notice the abrupt shift near $\Gamma = 0.003$ mol N/(L*day).

Figure B2: Biomass dynamics of autotrophs and herbivores at different levels of nitrogen input Γ when autotrophs can only be limited by nitrogen. Notice the lack of oscillatory dynamics and the lack of sudden collapses in autotroph biomass.

Figure B3: Biomass dynamics of autotrophs (solid) and herbivores (dashed) with differences in model formulation in order to examine the existence of long-lasting transient oscillations. *A* No stoichiometric imbalance between autotrophs and herbivores allows for oscillations to occur. *B* No stoichiometric imbalance and the removal of maximum internal nutrient concentrations in the uptake functions eliminates the oscillations seen in the model.

Figure B4: Changes in autotroph and herbivore biomass dynamics across a nitrogen input (Γ) gradient for different colimitation mechanisms at $\phi = 2.871^{-5}$ mol P/(L*day). Note that internal uptake colimitation mechanisms have results similar to (a).

Figure B5: Bifurcation diagram for the model corresponding to Figure 2-3B. The thick solid line indicates that the solution, which is an equilibrium, is stable over all the values of Γ.

Tables and Figures

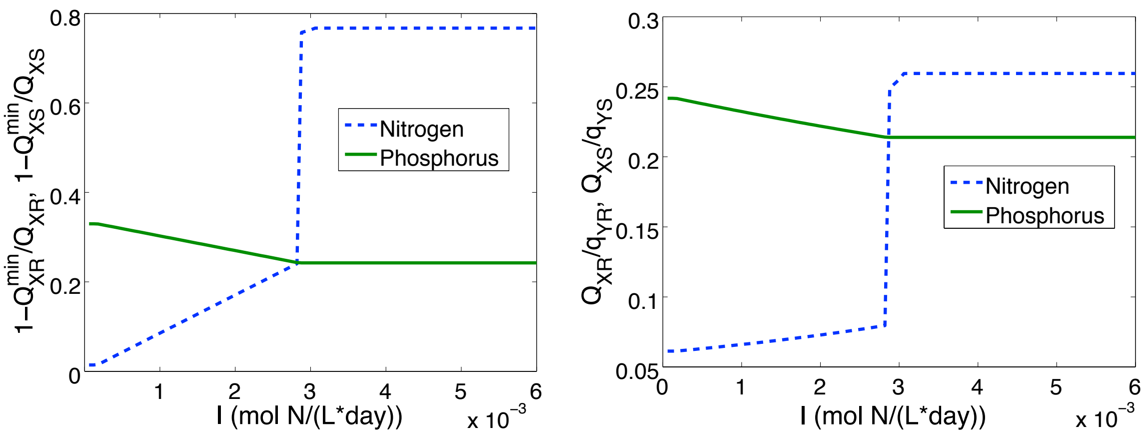


Figure B1

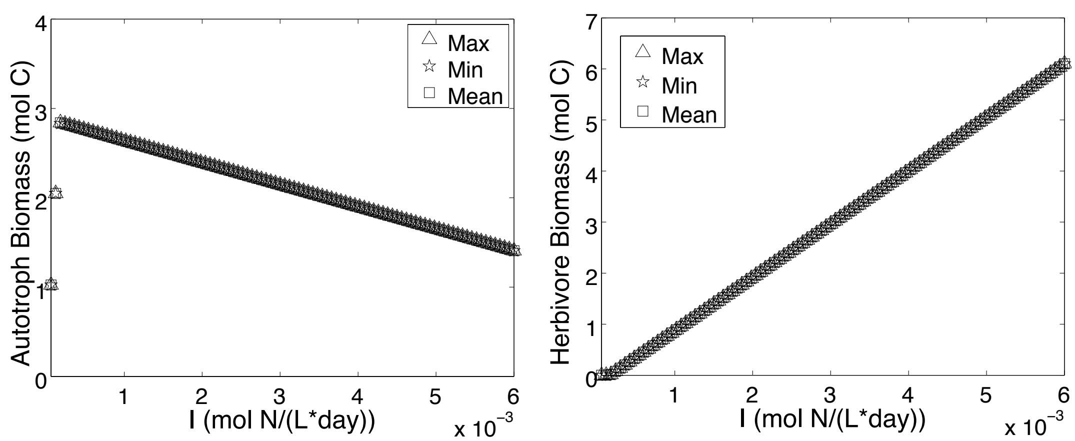


Figure B2

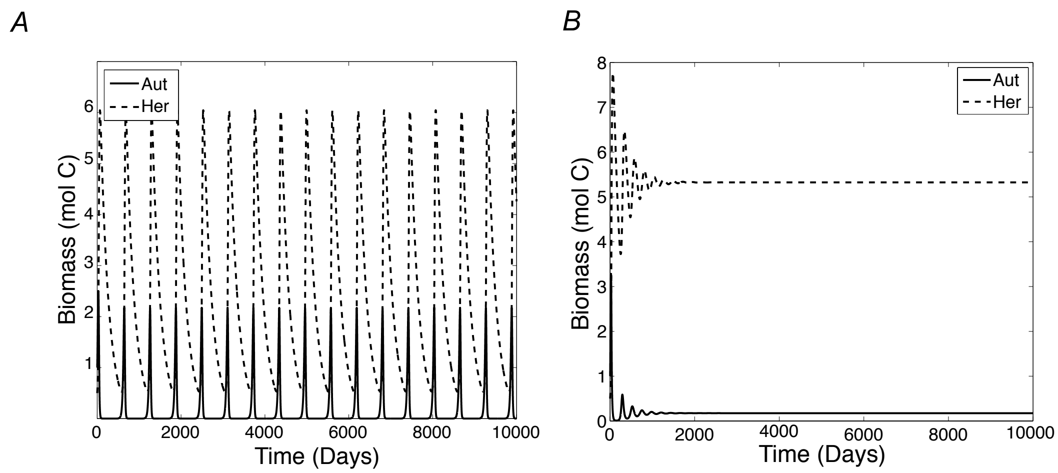
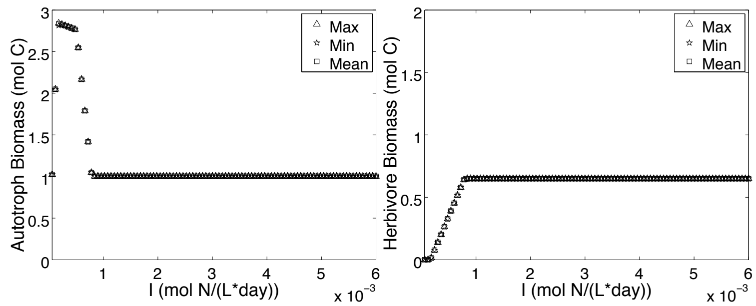
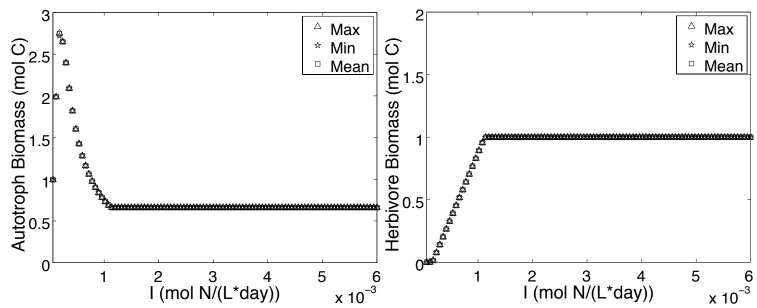

A
B
Aut
Her
Biomass (mol C)
Time (Days)
0
2000
4000
6000
8000
10000
1
2
3
4
5
6
7
8

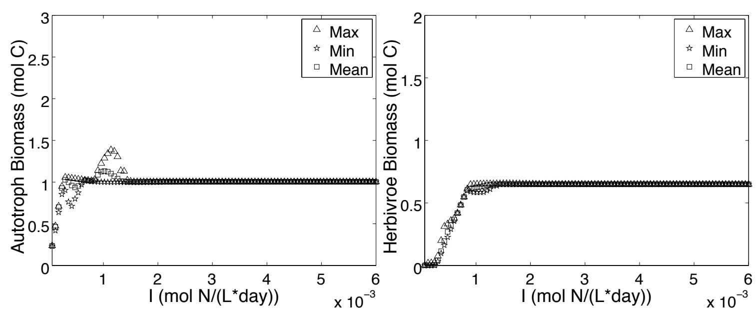
Figure B3



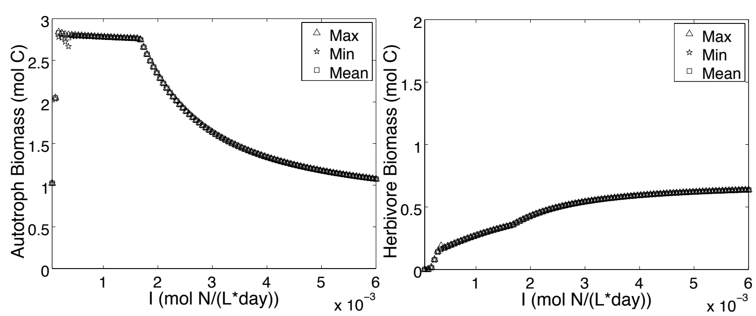
(a) No colimitation mechanism



(b) Growth colimitation mechanism



(c) External uptake (N on P) colimitation mechanism



(d) External uptake (P on N) colimitation mechanism

Figure B4

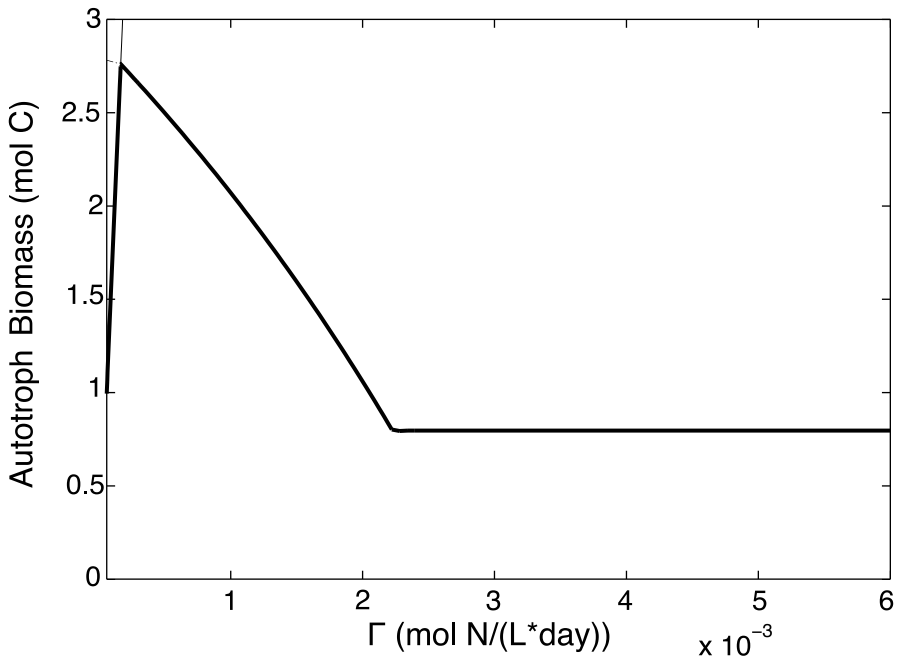


Figure B5

Connecting Statement

The major goal for the synthesis of ecological theories and research traditions is to provide solutions to problems that are not currently solvable or whose solution is incomplete by the distinct theories (Pickett, Kolasa, & Jones, 2007; Loreau, 2010). In chapter 2, I applied the framework of ecological stoichiometry through a stoichiometric ecosystem model in order to help clarify the concept of nutrient colimitation, which has been defined in a multitude of ways by different ecologists (Arrigo, 2005; Saito, Goepfert, & Ritt, 2008; Craine, 2009; Harpole et al., 2011). The main results from this model include the difficulties in associating nutrient colimitation mechanisms in the autotroph community with colimited growth responses observed in nutrient addition experiments and the vital importance of the identity of the mechanism when autotrophs interact with herbivores who are not in stoichiometric balance with the autotrophs.

However, the local mechanisms of colimitation that were used in this model were not capable of explaining many of the patterns observed in the literature, especially if herbivory is present (Harpole et al., 2011). One potential mechanism beyond the local mechanisms is the spatial flows of nutrients and organisms from other ecosystems, as these flows have been shown to have large impacts on ecosystem function (Polis, Anderson, & Holt, 1997; Polis, Power, & Huxel, 2004). Furthermore, the spatial positioning of those flows can lead to shifts in the identity of the limiting nutrient in autotroph communities within a relatively homogeneous environment such as a lake (Hagerthey & Kerfoot, 2005). In chapter 3, I develop a spatially-explicit metaecosystem model with one nutrient in order investigate how the spatial position of connected ecosystems and the spatial flows of nutrients and organisms between them can lead to changes in local and regional ecosystem dynamics and functioning.

Chapter 3
METAECOSYSTEM DYNAMICS AND FUNCTIONING ON FINITE SPATIAL NETWORKS

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Abstract

The addition of spatial structure to ecological concepts and theories has spurred integration between sub-disciplines within ecology, including community and ecosystem ecology. However, the complexity of spatial models limits their implementation to idealized, regular landscapes. We present a model metaecosystem with finite and irregular spatial structure consisting of local nutrient-autotrophs-herbi- vores ecosystems connected through spatial flows of materials and organisms. We study the effect of spatial flows on stability and ecosystem functions, and provide simple metrics of connectivity that can predict these effects. Our results show that high rates of nutrient and herbivore movement can destabilize local ecosystem dynamics, leading to spatially heterogeneous equilibria or oscillations across the metaecosystem, with generally increased metaecosystem primary and secondary production. However, the onset and the spatial scale of this emergent dynamics depend heavily on the spatial structure of the metaecosystem and on the relative movement rate of the autotrophs. We show how this strong dependence on finite spatial structure eludes commonly used metrics of connectivity, but can be predicted by the eigenvalues and eigenvectors of the connectivity matrix that describe the spatial structure and scale. Our study indicates the need to consider finite size ecosystems in metaecosystem theory.

Introduction

The concepts of the population, the community (Clements, 1916) and the ecosystem (Tansley, 1935) are fundamental to ecological understanding. In order to operationalize these concepts into usable components of theory, ecologists have added temporal, genetic and spatial structure to the concepts. The successful incorporation of space has led to metapopulation (Hanski, 1999), metacommunity (Leibold et al., 2004) and metaecosystem (Loreau, Mouquet, & Holt, 2003) theories, which have in turn spurred new experiments, observations and models and have renewed hope for the integration of community and ecosystem ecology through spatial structure (Polis, Power, & Huxel, 2004; Loreau, 2010; Massol et al., 2011).

Modifying population, community or ecosystem models to include space has been done through limiting cases such as two connected systems (e.g. Marleau, Guichard, Mallard, & Loreau, 2010; Gravel, Guichard, Loreau, & Mouquet, 2010), implicit space (e.g. Levins, 1969; K. S. McCann, Rasmussen, & Umbanhowar, 2005) or infinite continuous (Kot, Lewis, & van den Driessche, 1996; Ermentrout & Lewis, 1997) or discrete spatial domains (e.g. Gouhier, Guichard, & Gonzalez, 2010). These limiting cases can help us analyze spatial processes by simplifying the spatial structure. For example, analyzing the effects of the movement of nutrients on ecosystem dynamics and functioning in metaecosystems was simplified by using idealized spatial structures (Marleau et al., 2010; Gravel, Guichard, et al., 2010; Gravel, Mouquet, Loreau, & Guichard, 2010).

However, the spatial structure of ecological systems are finite and irregular (Turner, 1989; S. A. Levin, 1992; Durrett & S. Levin, 1994; Turner, 2005) and these finite, irregular features of the physical landscape can affect how organisms and materials are distributed across space by affecting both interactions and movement (Polis et al., 2004; Turner, 1989, 2005). Population persistence and dynamics are affected by realistic landscapes in metapopulation (Hanski & Ovaskainen, 2000; Fagan, 2002; Ovaskainen & Hanski, 2002; Ovaskainen & Hanski, 2003; Ovaskainen & Hanski, 2004), epidemic (Keeling & Eames, 2005) and predator-prey (Holland & Hastings, 2008) models, and metrics capturing these effects of the landscape (Hanski & Ovaskainen, 2000; Fagan, 2002; Ovaskainen & Hanski, 2002; Ovaskainen & Hanski, 2003; Ovaskainen & Hanski, 2004) on population persistence have been derived and related to landscape connectivity (e.g. Hanski & Ovaskainen, 2000; Urban & Keitt, 2001). What is lacking are equivalent metrics capturing the effects of spatial structure on ecosystem dynamics and functioning, which are likely to be affected by the different movement rates of organisms and materials.

The goal of our study is to fill this gap by expanding metaecosystem theory to include finite landscapes and to examine how the movement of organisms and materials interacts with landscape connectivity to impact the stability, dynamics and functioning of ecosystems. We do so by creating a metaecosystem model that consists of nutrient-autotroph-herbivore ecosystems that exchange materials and organisms, and has a spatial structure determined by a finite spatial network that mimics aspects of real landscapes.

Our results show that high nutrient and high herbivore movement rates can destabilize the metaecosystem and lead to spatially heterogeneous dynamics, but the destabilization and its associated dynamics are dependent on spatial structure and the autotroph movement. The effect of spatial structure is revealed by the 'scales of spatial interactions' (non-zero eigenvalues of the connectivity matrix) that emerge from the differences in connectivity between ecosystems, and which scale is associated with the destabilization can predict the dynamics seen in the metaecosystem. For example, the dynamics associated with small scales of spatial interaction have large oscillations in highly connected ecosystems, and smaller oscillations in less connected ecosystems. Furthermore, our analysis reveals how the scales of spatial interactions cannot be easily explained through other network connectivity metrics. In addition, the spatial structure of a metaecosystem can affect its primary and secondary productivity, indicating complex effects of spatial structure on ecosystem function. Our results provide new ways of integrating finite spatial structure into metaecosystem theories and of interpreting its impact on ecosystem function despite the complexity they introduce.

Methods : The metaecosystem model

Regional and local processes in metaecosystems

We modify a metaecosystem model (Marleau et al., 2010) to highlight the effects of spatial structure on metaecosystem dynamics and functioning. The model can be broken up into regional processes that connect ecosystems and local processes that describe the internal dynamics of the ecosystems (Figure 3.1). The regional processes are the movements of materials and organisms between the ecosystems, while the local processes are trophic and non-trophic interactions (nutrient recycling; Figure 3.1). As in previous work (Marleau et al., 2010), we limit our local ecosystems to one limiting nutrient R and we track the stocks of that nutrient in autotrophs A and herbivores H (Figure 3.1).

The movements of materials and organisms between ecosystems are determined by the connectivity matrix (**C**) and the movement matrix (**D**), which allows us to separate out the effect of spatial structure from the effects of movement rates (Jansen & Lloyd, 2000). The connectivity matrix is an n x n matrix, where n is the number of ecosystems in the metaecosystem, whose off-diagonal entries (i.e. $c_{ij}, i \neq j$) indicate the links between the different ecosystems. The diagonal entries (i.e. c_{ii}) represent the total number of connections that ecosystem i has, normalized by the total possible connections it could have. Because of certain beneficial properties for analysis (see Appendix A), we will consider only symmetric connectivity matrices (i.e. $c_{ij} = c_{ji}$) that allow for no loss of materials and organisms during movement between ecosystems (i.e. $\sum_{j=1}^{n} c_{ij} = 0$).

The movement matrix is a k x k matrix, where k is the number of ecosystem compartments in each ecosystem. The diagonal entries of the movement matrix are the movement rates of each compartment, while the off-diagonal entries would indicate cross-movement, which occurs when the movement of one ecosystem compartment (e.g. autotrophs) is dependent on another compartment (e.g. herbivores). However, we will not consider cross-movement in this study, making the movement matrix a 3 x 3 diagonal matrix with entries d_R, d_A and d_H, which are the movement rates of the limiting nutrient, the autotrophs and the herbivores, respectively.

At the local level, we have the available limiting nutrient R at the base of the ecosystem. It is supplied at a constant rate I from rock weathering and other abiotic sources and is lost at rate E proportional to its concentration in the medium (e.g. soil, water). Part of the available limiting nutrient R is assimilated into the autotrophs based on their uptake function $U(R, A)$, but this is balanced by nutrient recycling from autotroph losses $\epsilon M(A)$, herbivore losses $\chi L(H)$ and assimilation inefficiencies from herbivory $\gamma W(A, H)$. Autotroph nutrient stocks increase through the uptake function $U(R, A)$, but decrease through their intrinsic losses $M(A)$ and herbivory $W(A, H)$. Herbivore nutrient stocks increase through herbivory $(1-\gamma)W(A, H)$ and decrease through intrinsic losses $L(H)$.

Combining regional and local processes gives us the following system of ordinary differential equations:

$$\frac{dR_i}{dt} = I - ER_i - U(R_i, A_i) + \epsilon M(A_i) + \chi L(H_i) + \gamma W(A_i, H_i) + d_R \sum_{j=1}^{n} c_{ij} R_j \tag{3.1a}$$

$$\frac{dA_i}{dt} = U(R_i, A_i) - M(A_i) - W(A_i, H_i) + d_A \sum_{j=1}^{n} c_{ij} A_j \tag{3.1b}$$

$$\frac{dH_i}{dt} = (1-\gamma) W(A_i, H_i) - L(H_i) + d_H \sum_{j=1}^{n} c_{ij} H_j \tag{3.1c}$$

For analytic simplicity, we assume the parameters within the functions are the same across the metaecosystem (but see Appendix). While much of our mathematical analysis can be done with the functions of equation (3.1) (Appendix B), our numerical simulations require specified functions. We assume type II/Michaelis-Menten functional responses based on their widespread prevalence in plants (Bassirirad, 2000) and herbivores (Jeschke, Kopp, & Tollrian, 2004) for uptake, and density-independent losses for both the autotrophs and herbivores, which transform equation (3.1) into:

$$\frac{dR_i}{dt} = I - ER_i - \frac{\alpha_A R_i A_i}{\beta_A + R_i} + \epsilon m A_i + \chi l H_i + \gamma \frac{\alpha_H A_i H_i}{\beta_H + A_i} + d_R \sum_{j=1}^{n} c_{ij} R_j \quad (3.2a)$$

$$\frac{dA_i}{dt} = \frac{\alpha_A R_i A_i}{\beta_A + R_i} - m A_i - \frac{\alpha_H A_i H_i}{\beta_H + A_i} + d_A \sum_{j=1}^{n} c_{ij} A_j \quad (3.2b)$$

$$\frac{dH_i}{dt} = (1-\gamma) \frac{\alpha_H A_i H_i}{\beta_H + A_i} - l H_i + d_H \sum_{j=1}^{n} c_{ij} H_j \quad (3.2c)$$

Where α_A and α_H are maximum uptake rates, β_A and β_H are the half-saturation constants and m and l are density-independent loss rates.

Effects of spatial structure on metaecosystem stability

The metaecosystem model presented above can exhibit a wide range of dynamical behaviour, even when no movement occurs (Marleau et al., 2010). However, our focus is on how metaecosystem stability is modulated by its spatial network structure. As in Marleau et al. (2010), we use movement parameters to perturb the metaecosystem, allowing us to highlight spatial processes instead of local processes.

For simplicity, we restrict ourselves to parameter ranges that allow a unique stable equilibrium when there are no regional processes (but see Appendix). In other words, each ecosystem in the metaecosystem will be in the same state if no nutrients and no organisms are moving between them. If we add regional processes, each ecosystem will return to this state after perturbations as long as the Jacobian matrix describing the dynamics of the whole metaecosystem at the spatially homogeneous equilibrium state has only eigenvalues with negative real parts. This Jacobian matrix, which would normally be a $3n$ x $3n$ matrix, can be broken up into n matrices of the following form (Jansen & Lloyd, 2000):

$$\mathbf{V}(i) \;=\; \mathbf{J} + \lambda_i \mathbf{D} \tag{3.3}$$

Where $\mathbf{J}$ is the Jacobian matrix of a local ecosystem without regional processes and λ_i is the ith eigenvalue of the connectivity matrix $\mathbf{C}$ (Appendix B). If each $\mathbf{V}(i)$ matrix has eigenvalues, ϕ_{ik}, with negative real parts, then each ecosystem will return to its original equilibrium state after perturbation.

The stability of the ecosystem equilibrium is lost when the real part of at least one eigenvalue ϕ_{ik} of one of the $\mathbf{V}(i)$ matrices becomes positive (bifurcates) as the movement rates of the nutrients and organisms change. Such bifurcations can lead to (i) spatially heterogeneous equilibria (Appendix B), with individual ecosystems at different equilibrium values, which can include some local ecosystems having no autotrophs, or (ii) spatially heterogeneous oscillations across individual ecosystems (Marleau et al., 2010). The minimum, positive movement rates necessary to cause the bifurcations are defined as the minimum critical movement rates, $d_X^{\mathrm{min},c}$, where $X = R, H$, as autotroph movement cannot cause a bifurcation. The critical minimum herbivore movement rate, $d_H^{\mathrm{min},c}$, is associated with spatially heterogeneous equilibria, while the critical nutrient movement rate, $d_R^{\mathrm{min},c}$, is associated with spatially heterogeneous oscillations. Our analysis will focus on the spatially heterogeneous oscillations to compare to previous work (Marleau et al., 2010).

Scales of spatial interaction in metaecosystems

The non-zero eigenvalues of the connectivity matrix play an important role in creating spatial heterogeneity (equation (3.3)), just like the dominant eigenvalue

($\lambda_1 = 0$) of any connectivity matrix represents the dynamics without spatial structure (Jansen & Lloyd, 2000). These eigenvalues represent how the spatial structure of the metaecosystem influences the response of the ecosystems to perturbations. In equilibrium contexts, they are the equivalent of the wave number or spatial frequency in reaction-diffusion models, which indicates the spatial scale of perturbations to the equilibrium (Jansen & Lloyd, 2000). This spatial scale of interaction between the ecosystems is thus key in predicting the ability of a perturbation to propagate across a metaecosystem through movement of individuals and matter (Okubo & S. A. Levin, 2001).

Therefore, we define a scale of spatial interaction to be a non-zero eigenvalue λ_i of the connectivity matrix C, with more negative eigenvalues representing smaller spatial scales. For convenience, we order the non-zero eigenvalues from largest (i.e. less negative) to smallest (i.e. most negative) such that $\lambda_2 \geq \lambda_3 \geq ... \geq \lambda_n$, such that we go from large scales of spatial interaction to the smallest. Each metaecosystem could have multiple, unique (up to $n - 1$, excluding λ_1) scales of spatial interaction, each corresponding to an eigenvalue that lies between 0 and -2 (Appendix A).

Each scale of spatial interaction has an associated eigenvector that can provide information on the amplitudes and frequencies of the emergent spatial perturbation. For finite metaecosystems observed here, the eigenvectors would be associated with the oscillations within the individual ecosystems. The signs of the elements of the eigenvector indicate the synchrony between ecosystems, and their relative magnitudes represent the amplitudes of fluctuations in an ecosystem (Appendix C). Combined, these tools can help us examine the temporal and spatial stability of finite-size metaecosystems, though such information is of limited value for scales of spatial interaction that are repeated as the associated eigenvectors can offer different predictions.

Previous work on metapopulations showed the effect of the dominant eigenvalue of the connectivity matrix, which should represent the shortest scale of spatial interaction (λ_n; Ovaskainen & Hanski, 2002; Ovaskainen & Hanski, 2003; Ovaskainen & Hanski, 2004). Here we examine the general relationship between the scales of spatial interaction and our critical movement rates to discern which eigenvalues of the connectivity matrix play a role in determining metaecosystem stability.

Metaecosystem dynamics and functioning

We use our general model (equation (3.1)) to quantify the critical minimum movement rates that capture the shift from spatial homogeneity to spatial heterogeneity. We also use numerical simulations of our specified model equations (3.2) to detail the dynamics of individual ecosystems within the metaecosystem across critical movement rates for stability. We illustrate our results with 5 by 5 connectivity matrices with equal link density, but differing spatial network structure. In addition, we examined how the spatial scale of interaction associated with the spatial heterogeneity can determine metaecosystem dynamics by altering the movement rate of the autotrophs.

The implication of dynamical responses to movement for metaecosystem function are assessed by measuring the average primary and secondary production at the metaecosystem level for increasing rates of nutrient movement (d_R) in metaecosystems with differing network structures. Average primary and secondary production was measured by evaluating U and $(1-\gamma)W$ over 5000 time steps, respectively. In addition, we compare the rankings of network structures for primary and secondary production across scales of spatial interactions causing metaecosystem destabilization.

Relating network connectivity properties to scales of spatial interaction

Landscape ecology and network theories have produced a number of metrics to characterize connectivity. We use our model to determine if the scales of spatial interaction are related to two common metrics of connectivity associated with network stability: link density and maximum node degree. There are other metrics available (Urban & Keitt, 2001), but we focus on these metrics in order to capture metaecosystem-level connectivity with a single number for use in prediction.

Link density is the number of links divided by the number of nodes in the network, which in our case is the number of ecosystems in the metaecosystem. Maximum node degree is the number of links found at the most connected node in the network. For our purposes, we derived a relative scale of maximum node degree that goes from 0 (minimum) to 1 (maximum; Appendix A).

We used randomly generated 694071 30 by 30 connectivity matrices to discern if any or all of these connectivity measures can predict the scales of spatial interaction and provided a link between metaecosystem properties and connectivity (Appendix A).

Results

Metaecosystem stability: the interaction between movement and spatial structure

We first analyze the stability of the spatially homogeneous metaecosystem following its perturbation by the movement of nutrients and other organisms. We derive functions of critical movement rates corresponding to a transition from a spatially homogeneous ecosystem state throughout the metaecosystem to one with significant spatial heterogeneity (Appendix B):

$$d_H^c(\lambda_i) = \frac{-\mathbf{det}(\mathbf{J}) + \lambda_i d_R j_{23} j_{32}}{\lambda_i((j_{11} + \lambda_i d_R)(j_{22} + \lambda_i d_A) - j_{12} j_{21})} \tag{3.4a}$$

$$d_R^c(\lambda_i) = \frac{-B(\lambda_i, d_A, d_H) - \sqrt{B(\lambda_i, d_A, d_H)^2 + 4\lambda_i^2(j_{22} + \lambda_i(d_A + d_H))C(\lambda_i, d_A, d_H)}}{-2\lambda_i^2(j_{22} + \lambda_i(d_A + d_H))} \tag{3.4b}$$

Where j_{lk} is the row l and column k element of Jacobian matrix $\mathbf{J}$, $\mathbf{det}(\mathbf{J})$ is the determinant of the Jacobian matrix, and B and C are complex functions of movement rates and of eigenvalues of the connectivity matrix (Appendix B). From these functions, we derive the minimum movement rates required to create spatial heterogeneity for given movement rates and a given connectivity matrix:

$$d_H^{\min,c} = \min(d_H^c(\lambda_2), d_H^c(\lambda_3), ..., d_H^c(\lambda_n)) \tag{3.5a}$$

$$d_R^{\min,c} = \min(d_R^c(\lambda_2), d_R^c(\lambda_3), ..., d_R^c(\lambda_n)) \tag{3.5b}$$

Where n is number of patches in the metaecosystem, which means there is only a finite number $(n-1)$ of non-zero eigenvalues for a specific connectivity matrix. Furthermore, the number of unique non-zero eigenvalues can range from 1 to $n-1$, which means that few scales of spatial interaction (i.e. few unique λ_i) can be present even in large n metaecosystems.

The relationship between the scales of spatial interaction (λ_i) and the minimum critical movement rates ($d_H^{\mathrm{min},c}$ and $d_R^{\mathrm{min},c}$) depends strongly on the movement rate of autotrophs (d_A; Figure 3.2). When d_A is low, $d_H^c(\lambda_i)$ and $d_H^c(\lambda_i)$ decrease with decreasing λ_i (Figures 3.2a-3.2b). Therefore, for a given metaecosystem, the value of λ_n (the shortest scale of spatial interaction) determines the minimum critical movement rates at low d_A (Figures 3.2a-3.2b). Since metaecosystems with high maximum node degree and high link density have smaller λ_n, metaecosystems with greater connectivity, according to those metrics, are more easily destabilized by nutrient and herbivore movement at low d_A (Figures 3.3a-3.3b).

At higher d_A values, $d_H^c(\lambda_i)$ and $d_H^c(\lambda_i)$ show a parabolic relationship with λ_i, such that minima are reached at intermediate values of λ_i (Figures 3.2c-3.2d). For a given metaecosystem, this can lead to either a longer scale of spatial interaction (e.g. λ_{n-1}) determining the minimum critical movement rates or it can result in no destabilization being possible as the λ_i's all lead to negative $d_R^{min,c}$ and $d_H^{min,c}$ values (Figures 3.2c-3.2d). In other words, metaecosystems lacking longer scales of spatial interaction will not be destabilized at high d_A. Therefore, all the scales of spatial interaction would need to be evaluated to determine the stability, not just the shortest (Figures 3.2c-3.2d). However, network connectivity metrics provide little guidance in predicting what scales of spatial interaction to expect at given connectivity levels and hence provide little help in determining metaecosystem stability (Figures 3.3c-3.3d).

Metaecosystem dynamics: dependence on scale of spatial interaction and spatial structure

The realized dynamics of local ecosystems after metaecosystem destabilization depend on their spatial structure and the scales of spatial interaction (Figure 3.4; see Appendix D for parameter values). If the destabilization is associated with the shortest scale of spatial interaction, λ_n, the ecosystems with higher node degree (and with neighbours with higher node degree) within the metaecosystem have greater amplitude oscillations than ecosystems with lower node degree (Figures 3.4a-3.4b). As the node degree of each ecosystem depends directly on network structure, metaecosystems with different network properties display different synchrony patterns between ecosystems (Figures 3.4a-3.4b). In particular, ecosystems with the same connectivity properties (e.g. node degree and node degree of immediate neighbours) exhibit synchronized and identical oscillations (Figures 3.4a-3.4b). These dynamics can be seen even with spatially heterogeneous nutrient supplies or high nutrient supplies that lead to local oscillations without movement (Appendix E).

When the scales of spatial interaction between ecosystems are longer (e.g. λ_{n-1}), the resulting dynamics are more complex (Figures 3.4c-3.4d). For example, it is possible for central ecosystems within the network to be barely affected by the instability, while the outer ecosystems show large and anti-phase oscillations (Figure 3.4c). Or there can be little discernible pattern in the spatial distribution of oscillations across the metaecosystem (Figure 3.4d). Furthermore, ecosystems with similar connectivity properties no longer demonstrate synchronized dynamics nor do they necessarily oscillate at the same amplitude as they did at shorter scales of spatial interaction (Figures 3.4c-3.4d).

The dynamics shown above can, in certain cases, be predicted through the eigenvectors associated with the scales of spatial interaction (Appendix D). For example, metaecosystems with the same scale of spatial interaction and the same associated eigenvector will have the same spatial and temporal dynamics close to $d_R^{min,c}$ (Figure C.1). However, the predictive ability of the eigenvectors weaken as the movement rates increase beyond $d_R^{min,c}$. The reason for this is that the other scales of spatial interaction could destabilize the metaecosystem at the new higher rates of movement independently of the original destabilizing scale and their contributions to the dynamics become significant (Appendix C).

Metaecosystem production

The differences in metaecosystem dynamics due to spatial structure lead to differences in metaecosystem functioning (Figure 3.5). When small scale interactions cause the spatially homogeneous equilibrium to lose stability, both primary and secondary production generally increase with increasing nutrient movement (Figures 3.5a-3.5b). The specific network structures show differences in terms of their production, with the network with the highest maximum node degree consistently having the highest production at all levels of nutrient movement rate (Figures 3.5a-3.5b).

Similar to the results involving metaecosystem dynamics, the destabilization associated with large scale interactions results in patterns in metaecosystem production that differ from those associated with small scale interactions (Figures 3.5c-3.5d). Both primary and secondary production show small, non-monotonic increases with increasing nutrient movement relative to the equilibrium case (Figures 3.5c-3.5d). Furthermore, the network with highest maximum node degree consistently has the lowest primary production, which is in opposition to the small scale spatial interaction case, though it does not always hold for secondary production (Figures 3.5c-3.5d).

Discussion

Our analysis reveals that non-zero eigenvalues of the connectivity matrix describing the finite spatial structure of the metaecosystem, and hence multiple scales of spatial interaction, can determine metaecosystem stability and productivity in response to increasing movement of matter and organisms. We also show how the scales of spatial interactions driving the loss of metaecosystem stability can predict the distribution of dynamical regimes among local ecosystems. The study of finite-size landscapes escapes predictions relating ecosystem dynamics to the dominant scales of spatial interaction and made under the assumption of infinite or well-mixed space. Our results demonstrate the importance of multiple scales of interactions for resolving the complex response of stability and productivity to fluxes of matter and individuals across metaecosystems of finite size.

Scales of spatial interaction: the importance of finite space in ecological models

Our study uses the non-zero eigenvalues and eigenvectors of the connectivity matrix to help characterize the spatial structure of metaecosystems. These eigenvalues represent the scales of spatial interaction between local ecosystems, indicate how the ecosystems will respond to perturbations and each of them can lead to the destabilization of metaecosystesms. In addition, these eigenvalues are not well predicted by other measures of spatial structure commonly used in ecology, which makes them a novel tool for research (Turner, 1989, 2005). Furthermore,wWhen modelling multi-level movement models, the need to examine all scales of spatial interaction leads to the inadequacy of two-patch (e.g. Marleau et al., 2010) and infinite domain (e.g. Ermentrout & Lewis, 1997) models to capture these critical elements of spatial structure.

Two-patch models can be represented by a connectivity matrix with a single eigenvalue or scale of spatial interaction (e.g. Marleau et al., 2010). This makes the two-patch model similar to a fully connected network as every ecosystem is connected to every possible neighbour and its results do not scale up when networks are not fully connected. In constrast, models of infinite domain can be formulated to contain all possible scales of spatial interaction such that movement could always destabilize them if destabilization is possible (Jansen & Lloyd, 2000). The issue here is that metapopulations, metacommunities and metaecosystems are not infinite in size, but finite (Leibold et al., 2004; Massol et al., 2011; Hanski & Ovaskainen, 2000; Fagan, 2002; Holland & Hastings, 2008). Such finite size leads to a limited number of associated scales of spatial interaction where perturbations can manifest and destabilize metaecosystems at equilibrium. Therefore, infinite domain models may predict that a perturbation will destabilize an ecological system, while a more realistic finite network model will predict its stability.

Unequal movement rates of materials and of organisms across landscapes

Spatial instabilities are produced and their impacts on dynamics and functioning are modulated through the unequal movement of nutrients and of organisms (Jansen & Lloyd, 2000; Okubo & S. A. Levin, 2001; Rietkerk & van de Koppel, 2008). Our study shows how multiple scales of spatial interaction resulting from such movement are determined by the spatial structure of the metaecosystem. Our model predicts that if the shortest scale of spatial interaction drives destabilization, increasing connectivity (i.e. the link density or the maximum node degree of the metaecosystem) can further promote instabilities. However, increasing the movement rate of the autotrophs allows for longer scales of spatial interaction to have a dominant destabilizing role, which then results in the relationship between instabilities and connectivity to be highly irregular.

Interactions between the structure and rates of movement have profound implications for ecosystem functioning. The loss of regional stability driven by spatial structure and movement rates leads to the emergence of source-sink ecosystems for autotrophs (Gravel, Guichard, et al., 2010; Loreau, Daufresne, et al., 2013) and to increased productivity at the regional level. However, the production gains are offset by increases in variability at local and regional scales, which may lead to local loss of autotrophs and herbivores (Marleau et al., 2010). Our results support the importance of integrating movement properties of ecosystem compartments to the spatial structure of landscapes.

Our analysis emphasizes the importance of unequal movement across ecosystem compartments. Other efforts to discern the importance of movement on community and ecosystem processes have postulated that spatial structure could be subsumed through the coupling of fast moving, high trophic level organisms, which would have the strongest support in marine ecosystems (K. S. McCann et al., 2005; Rooney, K. S. McCann, Gellner, & Moore, 2006; Rooney, K. S. McCann, & Moore, 2008). However, coupling can occur at all trophic levels, and we predict that even limited movement can have large impacts on dynamics, functioning and stability. The study of differential movement in finite-size ecosystems should allow for greater integration between food web and landscape ecology (Loreau, Mouquet, & Holt, 2003; Polis et al., 2004; Massol et al., 2011).

Our model has several limitations with regards to the unequal movement rates of materials and of organisms that should be addressed in future studies. First, the impacts of cross-diffusion were ignored, even though herbivores can serve as vectors for autotroph movement (e.g. Fuller & del Moral, 2003). Second, adding another autotroph or herbivore with a different movement rate should be explored in order to determine how this can impact dynamics, functioning and stability. Lastly, we recognize that ecosystems are not immobile spatial patches, but are spatially distributed and formed through the interactions between their biotic and abiotic components (Massol et al., 2011; Jones, Lawton, & Shachak, 1994). Given these features of natural ecosystems, our study reinforces the notion that more research is needed to understand the impacts of connectivity on communities and ecosystems if we are to develop better conservation strategies (Chetkiewicz, St Clair, & Boyce, 2006; Gonzalez, Rayfield, & Lindo, 2011). Our study points towards the multiple scales over which ecosystems interact across landscapes as a tool to predict and understand their complex dynamics.

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Table and Figure Captions

Figure 3.1 : Conceptual diagram for a general metaecosystem model. Local ecosystems (circles) have internal dynamics based on trophic (solid black arrows) and non-trophic (dashed black arrows) interactions between ecosystem compartments, which in this case are a limiting nutrient (R), autotrophs (A) and herbivores (H). Local ecosystems form a metaecosystem through the movement of materials and organisms, which is determined by the connectivity matrix **C** and the movement matrix **D**. The connectivity matrix indicates how the ecosystems are connected to one another (blue boxes), while the movement matrix gives the movement rates of each ecosystem compartment (red two-headed arrow). Without a connection specified by the connectivity matrix, materials and organisms cannot move between ecosystems (black X).

Figure 3.2 : Relationships between the scales of spatial interaction (λ_i) and the minimum critical movement rates of nutrients ($d_R^{\min,c}$) and of herbivores ($d_H^{\min,c}$) for given metaecosystems (blue and red inset) as described by equations (3.4) and (3.5) at different autotroph movement rates (d_A). $d_R^{\min,c}$ is determined by evaluating $d_R^c(\lambda_i)$ (black line) at all the scales of spatial interaction the metaecosystem (blue and red vertical lines) and taking the smallest value of d_R found (blue and red horizontal lines). The procedure is identical for $d_H^{\min,c}$. Note that for the blue metaecosystem, $\lambda_5 = \lambda_4 = \lambda_3 = \lambda_2$.

(a) and (b) At low d_A, $d_R^{\min,c}$ and $d_H^{\min,c}$ are determined by λ_5, the shortest scale of spatial interaction, for both metaecosystems. (c) and (d) At higher d_A, there are no positive $d_R^{\min,c}$ and $d_H^{\min,c}$ values for the blue metaecosystem due to lack of longer scales of spatial interaction, while $d_R^{\min,c}$ and $d_H^{\min,c}$ are determined by λ_4, the second shortest scale of spatial interaction, for the red metaecosystem.

Figure 3.3 : Relationships between network connectivity measures and the scales of spatial interaction in randomly generated 30 by 30 connectivity matrices. (a) Higher link density is somewhat associated with more negative values for the shortest scale of spatial interaction (λ_n), though there is a good deal of variability. (b) Higher maximum node degree is tightly associated with more negative values for the shortest scale of spatial interaction (λ_n). (c) Higher link density is associated with more negative (i.e. shorter) scales of spatial interaction, but the ranges are very large at any given link density level. (d) Higher maximum node degree allows for more (shorter) negative scales of interaction, which matches with (b), but provides little insight on the location of the longer scales of spatial interaction for a given maximum node degree for a metaecosystem.

Figure 3.4 : The effects of metaecosystem network structure on local ecosystem dynamics after the local equilibrium solution is destabilized by high nutrient movement. The colours of the graphic insets indicate which time series is to be found in the local ecosystem, which means if two local ecosystems share the same colour, they have the same temporal dynamics. With d_A equal to zero, the two metaecosystem configurations ((a) and (b)) show large oscillations in their most connected ecosystems, though the patterns differ greatly between them. With d_A equal to 0.045, metaecosystems ((c) and (d)) continue to show oscillations, but the most centralized ecosystems no longer show the highest amplitude oscillations; however, the temporal and spatial dynamics differ greatly between them.

Figure 3.5 : The effects of metaecosystem network structure on autotroph and herbivore productivity where the total number of links between ecosystems are equal, nutrient movement (d_R) is used to perturb the metaecosystem and with no autotroph movement ($d_A = 0$; (a) and (b)) and relatively high autotroph movement ($d_A = 0.045$; (c) and (d)). In all cases, the average of ten simulations were used to reduce the effects of time series truncation on the overall results. Both (a) autotroph and (b) herbivore productivity increase with increasing nutrient movement with no autotroph movement, though the differences between networks are large. When autotroph movement is high, (c) autotroph and (d) herbivore productivity still increase with increasing nutrient movement, but the relative rankings of the networks is drastically different.

Tables and Figures

$$\begin{array}{cc} & \begin{array}{cccc} \text{1} & \text{2} & \text{3} & \text{4} \end{array} \\ C= & \begin{pmatrix} -0.33 & 0.33 & 0 & 0 \\ 0.33 & -0.67 & 0.33 & 0 \\ 0 & 0.33 & -0.67 & 0.33 \\ 0 & 0 & 0.33 & -0.33 \end{pmatrix} \end{array}$$

$$D=\begin{pmatrix} 0 & 0 & 0 \\ 0 & 0 & 0 \\ 0 & 0 & d_H \end{pmatrix}$$

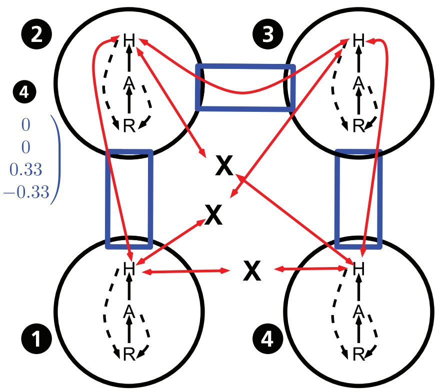
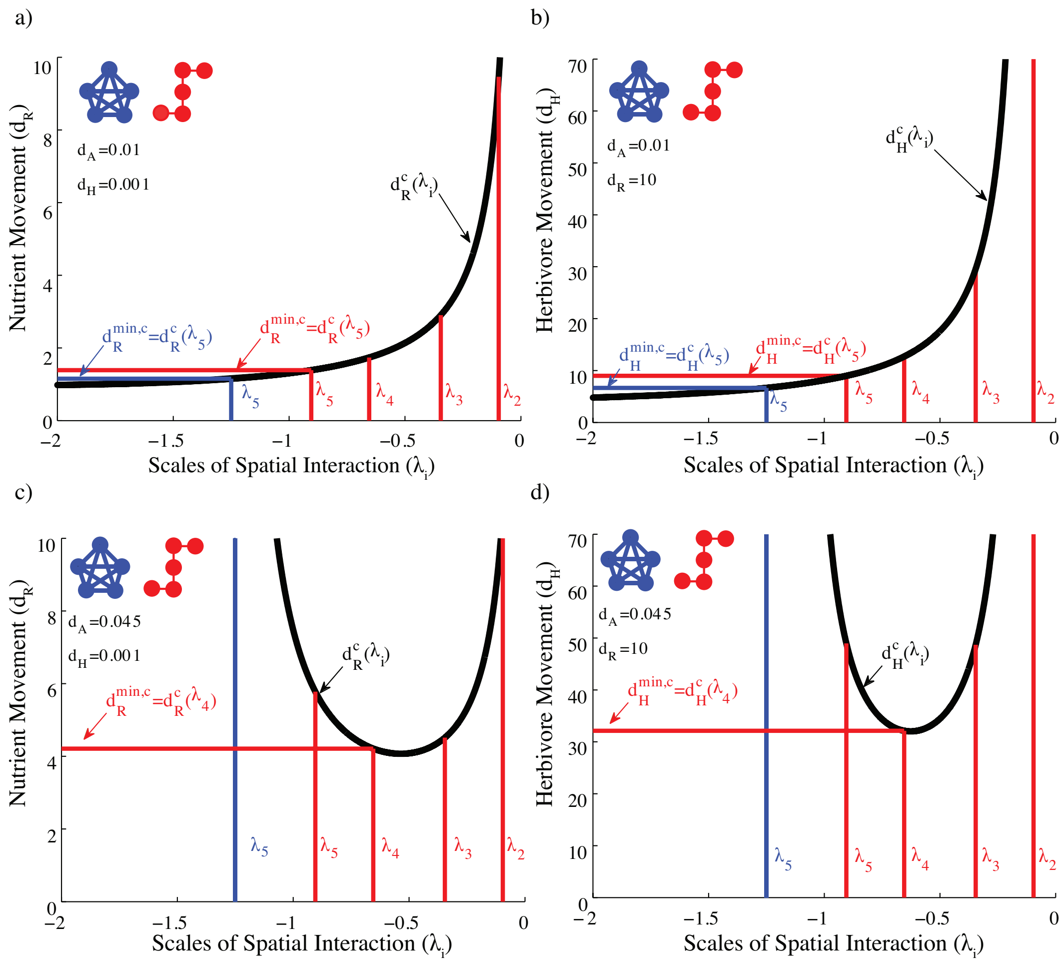
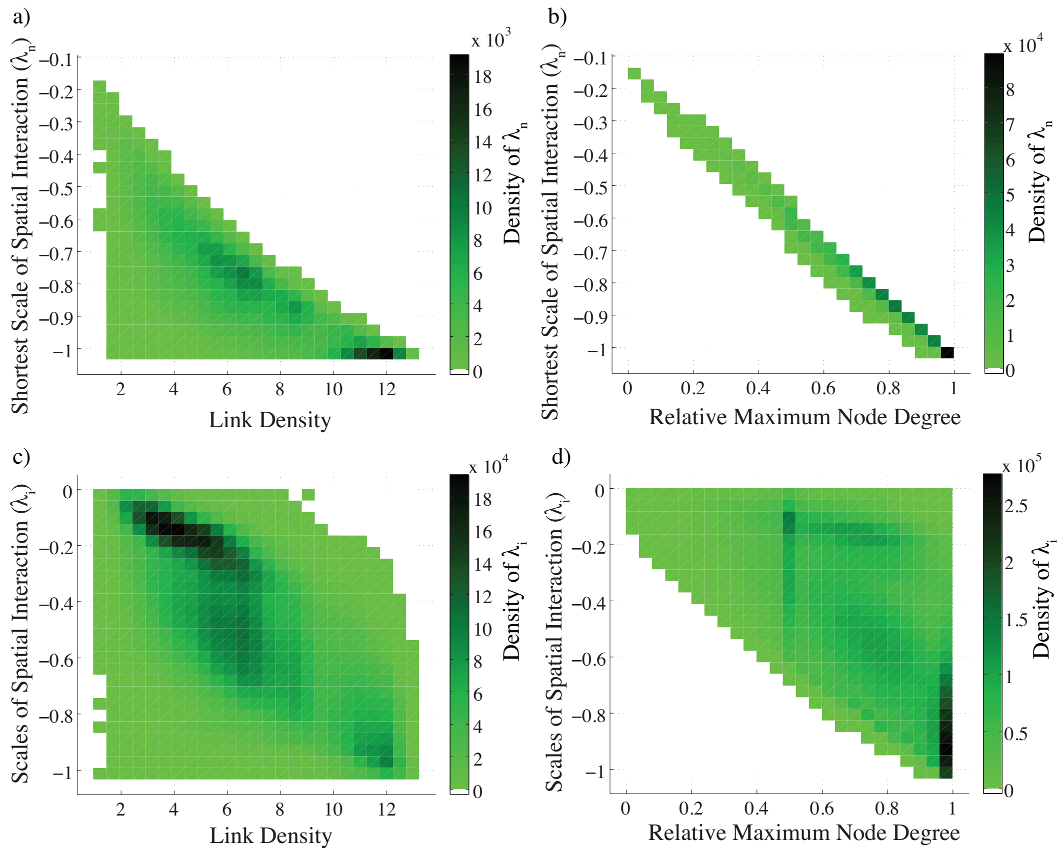


Figure 3.1



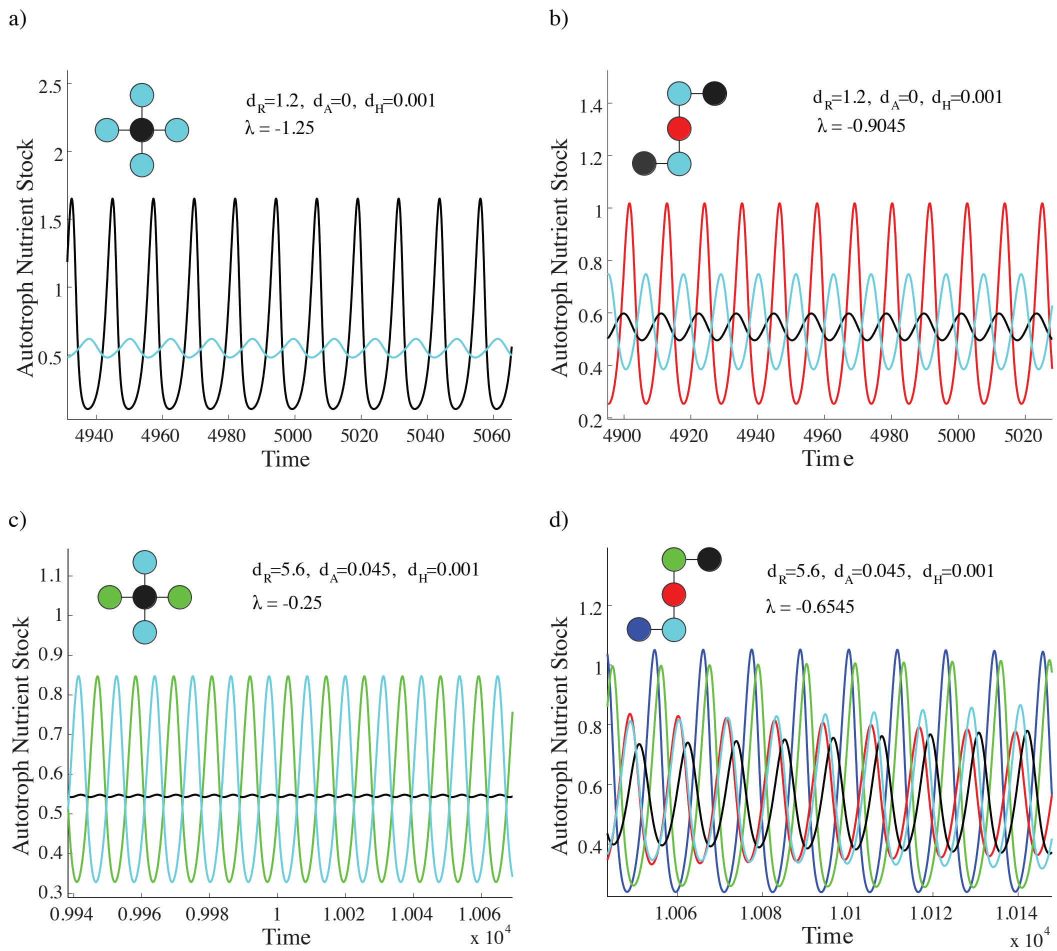
a)
b)
c)
d)
Nutrient Movement (d_R)
Herbivore Movement (d_H)
Scales of Spatial Interaction (λ_i)
d_A=0.01
d_H=0.001
d_R=10
d_A=0.045
$d_R^c(\lambda_i)$
$d_H^c(\lambda_i)$
$d_R^{min,c}=d_R^c(\lambda_5)$
$d_H^{min,c}=d_H^c(\lambda_5)$
$d_R^{min,c}=d_R^c(\lambda_4)$
$d_H^{min,c}=d_H^c(\lambda_4)$
λ_5
λ_4
λ_3
λ_2

Figure 3.2



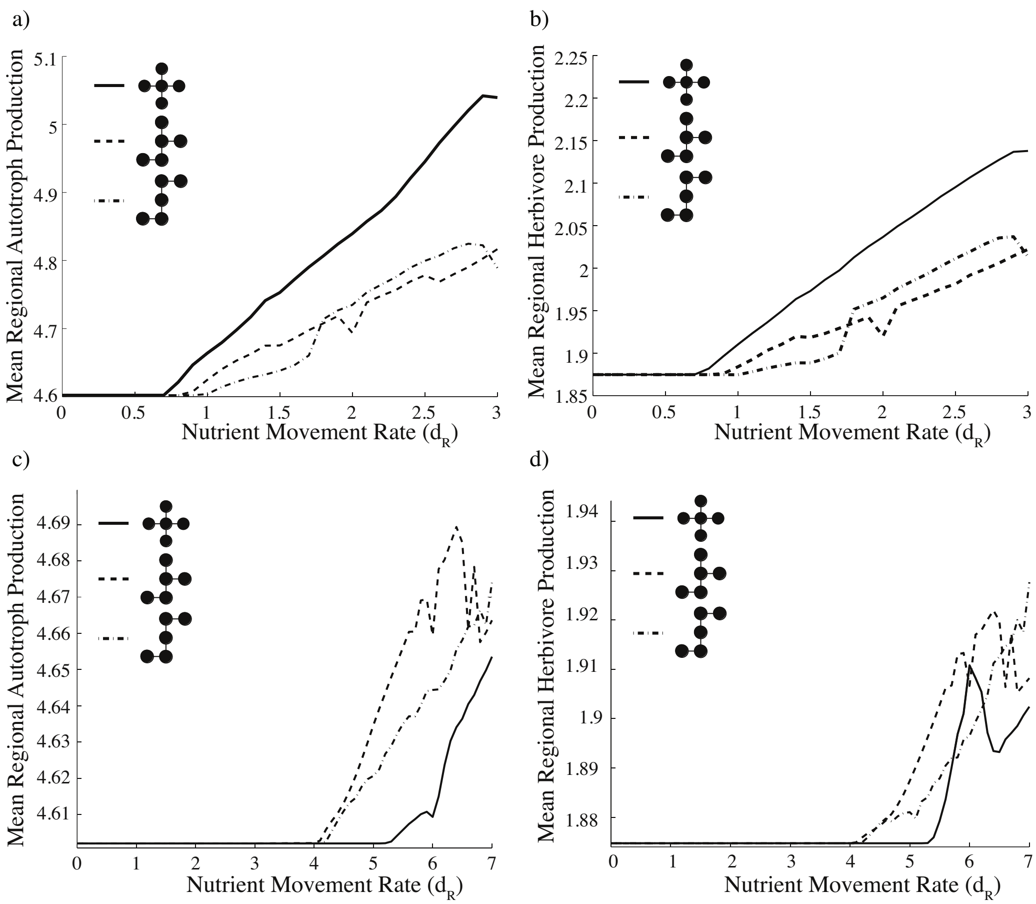
a)
b)
c)
d)
Shortest Scale of Spatial Interaction (λ_n)
Link Density
Density of λ_n
x 10^3
Relative Maximum Node Degree
x 10^4
Scales of Spatial Interaction (λ_i)
Density of λ_i
x 10^5

Figure 3.3



a)
d_R=1.2, d_A=0, d_H=0.001
λ = -1.25
Autotroph Nutrient Stock
Time
b)
d_R=1.2, d_A=0, d_H=0.001
λ = -0.9045
Autotroph Nutrient Stock
Time
c)
d_R=5.6, d_A=0.045, d_H=0.001
λ = -0.25
Autotroph Nutrient Stock
Time
x 10^4
d)
d_R=5.6, d_A=0.045, d_H=0.001
λ = -0.6545
Autotroph Nutrient Stock
Time
x 10^4

Figure 3.4



a)
Mean Regional Autotroph Production
Nutrient Movement Rate (d_R)
b)
Mean Regional Herbivore Production
Nutrient Movement Rate (d_R)
c)
Mean Regional Autotroph Production
Nutrient Movement Rate (d_R)
d)
Mean Regional Herbivore Production
Nutrient Movement Rate (d_R)

Figure 3.5

Appendix A: Properties of the connectivity matrix

The connectivity matrices used in our paper have the following properties: 1) they have only real eigenvalues, 2) the largest eigenvalue is zero and corresponds to the no movement case, and 3) the eigenvalues of any connectivity matrix will be constrained between 0 and -2. The first property is assured by the connectivity matrix being symmetric. The second property is derived from the condition that $\sum_{j=1}^{n} c_{ij} = 0$.

The third is due to the normalization of the connectivity matrix, which forces the off-diagonal entries to be equal to $1/(n-1)$. The sum of the off-diagonal entries of one row can, at most, be equal to one. The Gershgorin Circle theorem states that the eigenvalues of any complex matrix must reside within discs in the complex plane with radius equal to the sum of the off-diagonals of each column and each disc is centred at the diagonal entry. As the connectivity matrices used here are real symmetric matrices, the eigenvalues must lie on the real line section from $-(\sum_{j\neq i} c_{ij}) + c_{ii}$ to $(\sum_{j\neq i} c_{ij}) + c_{ii}$. But this is simply $2c_{ii}$ to 0. Since the most negative value possible for c_{ii} is -1, all eigenvalues for any of the connectivity matrices used in this paper must lie within [-2,0].

Since our connectivity matrices represent spatial networks, we can also derive network connectivity properties from them. For our purposes, we derived a formula for maximum node degree, which determines the connectivity of the most connected node in the network with n nodes:

$$\omega(n, \delta) = max(\frac{\delta_i - 2}{n - 3}), \ n \geq 4 \quad \text{(A1)}$$

Where δ_i is the number of links connected to node i. This formula provides a relative scale for maximum node degree which varies from 0 (least possible number of connections for most connected node) to 1 (most possible number of connections for most connected node).

Appendix B: Derivations for stability conditions for equation (1)

General local ecosystem model

Let R be the amount of available inorganic nutrient, let A be the nutrient R stock in the autotrophs that are limited by nutrient R and let H be the nutrient R stock in the herbivores that consume autotrophs. The ecosystem dynamics can be described by the following system of equations:

$$\frac{dR}{dt} = F(R,A,H) = I - ER - U(R,A) + \epsilon M(A) + \chi L(H) + \gamma W(A,H) \quad \text{(B1a)}$$

$$\frac{dA}{dt} = G(R,A,H) = U(R,A) - M(A) - W(A,H) \quad \text{(B1b)}$$

$$\frac{dH}{dt} = K(R,A,H) = (1-\gamma)W(A,H) - L(H) \quad \text{(B1c)}$$

Let us assume that there exists an equilibrium in the positive (R,A,H) octant and call it Q. The local stability of Q can be deduced through the use of the Jacobian matrix:

$$\mathbf{J} = \begin{pmatrix} \frac{\partial F}{\partial R} & \frac{\partial F}{\partial A} & \frac{\partial F}{\partial H} \\ \frac{\partial G}{\partial R} & \frac{\partial G}{\partial A} & \frac{\partial G}{\partial H} \\ \frac{\partial K}{\partial R} & \frac{\partial K}{\partial A} & \frac{\partial K}{\partial H} \end{pmatrix} = \begin{pmatrix} j_{11} & j_{12} & j_{13} \\ j_{21} & j_{22} & j_{23} \\ j_{31} & j_{32} & j_{33} \end{pmatrix} \quad \text{(B2)}$$

Where the j_{ik} parameters represent the effect of an increase in ecosystem compartment k at equilibrium on ecosystem compartment i. For example, j_{21} is the effect of increasing available nutrient R on autotroph nutrient R stock at equilibrium. Generally, it is assumed that any increase in limiting nutrient should increase autotroph biomass (and hence nutrient stock), which means that for most ecosystem models j_{21} has a positive value. Similar derivations of the signs for the j_{ik} parameters in the Jacobian can be done, but will not be discussed in detail here. Q is locally stable if the following three conditions are met:

$$-\mathbf{tr}(\mathbf{J}) > 0 \tag{B3a}$$

$$-\mathbf{det}(\mathbf{J}) > 0 \tag{B3b}$$

$$-\mathbf{tr}(\mathbf{J}) * (\mathbf{J_{11}} + \mathbf{J_{22}} + \mathbf{J_{33}}) > -\mathbf{det}(\mathbf{J}) \tag{B3c}$$

Where **tr** and **det** are the trace and determinant of the matrix, respectively, while $\mathbf{J_{11}}$, $\mathbf{J_{22}}$ and $\mathbf{J_{33}}$ are the cofactors of the Jacobian matrix. In terms of the j_{ik} parameters:

$$\begin{aligned}
\mathbf{tr}(\mathbf{J}) &= j_{11} + j_{22} + j_{33} \\
\mathbf{det}(\mathbf{J}) &= j_{11}(j_{22}j_{33} - j_{23}j_{32}) - j_{12}(j_{21}j_{33} - j_{23}j_{31}) + j_{13}(j_{21}j_{32} - j_{22}j_{31}) \\
\mathbf{J_{11}} &= j_{22}j_{33} - j_{23}j_{32} \\
\mathbf{J_{22}} &= j_{11}j_{33} - j_{13}j_{31} \\
\mathbf{J_{33}} &= j_{11}j_{22} - j_{12}j_{21}
\end{aligned}$$

For the first condition to be met, it requires at least one compartment to experience self-limitation in growth at equilibrium, and that self-limitation needs to be stronger than any positive feedbacks found in the other compartments. The second and third conditions are too complex to understand biologically without some knowledge of the signs of j_{ik} parameters.

For the purposes of our study, we will be assuming that j_{11}, j_{12} and j_{23} will be negative while j_{13}, j_{21}, j_{22} and j_{32} will be positive at equilibrium Q. Furthermore, we assume that j_{31} and j_{33} will be equal to zero at equilibrium Q. While some of these assumptions can be relaxed to achieve similar results in the derivation of the critical movement rates (d_R^c and d_H^c), the assumptions made here allow for a clearer presentation of the derivations.

Using the information about the signs of the Jacobian matrix elements and the stability conditions in equation (B3), we can derive the following relationships between the j_{ik} that ensure the equilibrium Q will be locally stable:

$$|j_{11}| > j_{22} \tag{B4a}$$

$$|j_{11}j_{23}| > |j_{13}j_{21}| \tag{B4b}$$

$$j_{11}(-j_{11}j_{22} + j_{12}j_{21}) + j_{13}j_{21}j_{32} > |j_{22}(j_{23}j_{32} - j_{11}j_{22} + j_{12}j_{21})| \tag{B4c}$$

A wide array of functional forms can achieve such relationships at equilibrium, including the specified functional forms found in equation (3.2). Our interest lies in how the addition of movement and spatial structure to the local ecosystem model can destabilize the equilibrium Q without any changes to the j_{ik} parameters.

General metaecosystem model

For the general metaecosystem model, we recall equation (3) from the main text:

$$\mathbf{V}(i) = \mathbf{J} + \lambda_i \mathbf{D}$$

For the spatially homogeneous solution to hold across the metaecosystem, i.e. all ecosystems are at equilibrium Q, all the eigenvalues of each matrix $\mathbf{V}(i)$ must have negative real parts. For this to be the case, the conditions described in equation (B3) must hold for each $\mathbf{V}(i)$. We therefore have:

$$-\mathbf{tr}(\mathbf{V}(i)) = -\mathbf{tr}(\mathbf{J}) - \lambda_i(d_R + d_A + d_H) > 0 \tag{B5a}$$

$$\begin{aligned} -\mathbf{det}(\mathbf{V}(i)) = -\mathbf{det}(\mathbf{J}) + j_{23}j_{32}\lambda_i d_R - \\ \lambda_i d_H((j_{11} + \lambda_i d_R)(j_{22} + \lambda_i d_A) - j_{12}j_{21}) > 0 \end{aligned} \tag{B5b}$$

$$-\mathbf{tr}(\mathbf{V}(i) * (\mathbf{V_{11}} + \mathbf{V_{22}} + \mathbf{V_{33}}) > -\mathbf{det}(\mathbf{V}(i)) \tag{B5c}$$

Note that the inequality in (B5a) will always be satisfied as λ_i must be equal to or less than zero. Therefore, only inequalities (B5b) and (B5c) can be violated. From inequality (B5b), we can quickly derive a value of d_H at which the inequality will no longer hold by setting the left-hand size of the inequality to zero:

$$\begin{aligned} & -\mathbf{det}(\mathbf{J}) + j_{23}j_{32}\lambda_i d_R - \lambda_i d_H((j_{11} + \lambda_i d_R)(j_{22} + \lambda_i d_A) - j_{12}j_{21}) = 0 \\ \Leftrightarrow \quad & \lambda_i d_H((j_{11} + \lambda_i d_R)(j_{22} + \lambda_i d_A) - j_{12}j_{21}) = -\mathbf{det}(\mathbf{J}) + j_{23}j_{32}\lambda_i d_R \\ \Leftrightarrow \quad & d_H = \tfrac{-\mathbf{det}(\mathbf{J}) + j_{23}j_{32}\lambda_i d_R}{\lambda_i((j_{11} + \lambda_i d_R)(j_{22} + \lambda_i d_A) - j_{12}j_{21})} \end{aligned}$$

From the above derivation, we can define the critical herbivore movement rate function, which is a function of λ_i:

$$d_H^c(\lambda_i) = \frac{-\mathbf{det}(\mathbf{J}) + j_{23}j_{32}\lambda_i d_R}{\lambda_i((j_{11} + \lambda_i d_R)(j_{22} + \lambda_i d_A) - j_{12}j_{21})} \tag{B6}$$

When d_H is above a positive minimum critical herbivore movement rate (equation (3.5)), we have spatially heterogeneous equilibria occurring throughout the metaecosystem (Figure

From inequality (B5c), it is possible to derive a value of d_R at which the inequality no longer holds, though the derivation is much more involved:

$$
\begin{aligned}
&-\mathbf{tr}(\mathbf{V}(i) * (\mathbf{V_{11}} + \mathbf{V_{22}} + \mathbf{V_{33}}) + \mathbf{det}(\mathbf{V}(i)) = 0 \\
\Leftrightarrow &(-\mathbf{tr}(\mathbf{J}) - \lambda_i(d_R + d_A + d_H)) * (v_{22}v_{33} - j_{23}j_{32} + \\
&(j_{11} + \lambda_i d_R)v_{33} + (j_{11} + \lambda_i d_R)v_{22} - j_{12}j_{21}) + \\
&\mathbf{det}(\mathbf{J}) - j_{23}j_{32}\lambda_i d_R + \lambda_i d_H((j_{11} + \lambda_i d_R)(j_{22} + \lambda_i d_A) - j_{12}j_{21}) = 0 \\
\Leftrightarrow &- \lambda_i^2(v_{22} + v_{33})d_R^2 + (-2\lambda_i j_{11}(v_{22} + v_{33}) + \\
&\lambda_i(j_{12}j_{21} - v_{22}^2 - 2v_{22}v_{33} - v_{33}^2))d_R + \\
&(-j_{11}^2(v_{22} + v_{33}) + j_{11}(j_{12}j_{21} - v_{22}^2 - 2v_{22}v_{33} - v_{33}^2) + \\
&v_{22}(j_{12}j_{21} + j_{23}j_{32} - v_{22}v_{33}) + v_{33}(j_{23}j_{32} - v_{22}v_{33}) + j_{13}j_{21}j_{32}) = 0 \\
\Rightarrow &d_R = \frac{-B - \sqrt{B^2 + 4\lambda_i^2(v_{22} + v_{33})C}}{-2\lambda_i^2(v_{22} + v_{33})} \\
&B = B(\lambda_i, d_A, d_H) = -2\lambda_i j_{11}(v_{22} + v_{33}) + \lambda_i(j_{12}j_{21} - v_{22}^2 - 2v_{22}v_{33} - v_{33}^2) \\
&C = C(\lambda_i, d_A, d_H) = -j_{11}^2(v_{22} + v_{33}) + j_{11}(j_{12}j_{21} - v_{22}^2 - 2v_{22}v_{33} - v_{33}^2) + \\
&v_{22}(j_{12}j_{21} + j_{23}j_{32} - v_{22}v_{33}) + v_{33}(j_{23}j_{32} - v_{22}v_{33}) + j_{13}j_{21}j_{32}
\end{aligned}
$$

Where $v_{22} = j_{22} + \lambda_i d_A$ and $v_{33} = \lambda_i d_H$. From the above derivation, we can define the critical nutrient movement rate function, which is a function of λ_i:

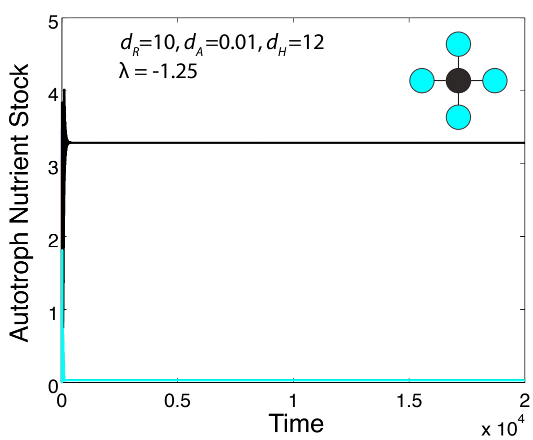
$$
\begin{aligned}
d_R^c(\lambda_i) \;=\; &\frac{-B(\lambda_i, d_A, d_H)}{-2\lambda_i^2(j_{22} + \lambda_i(d_A + d_H))} - \\
&\frac{\sqrt{B(\lambda_i, d_A, d_H)^2 + 4\lambda_i^2(j_{22} + \lambda_i(d_A + d_H))C(\lambda_i, d_A, d_H)}}{-2\lambda_i^2(j_{22} + \lambda_i(d_A + d_H))}
\end{aligned} \tag{B7}
$$

The general dynamics that occur after the minimum critical movement rate are spatially heterogeneous equilibria (Figure B1a) and spatially heterogeneous oscillations (Figure B1b; same as Figure 4a in main text).

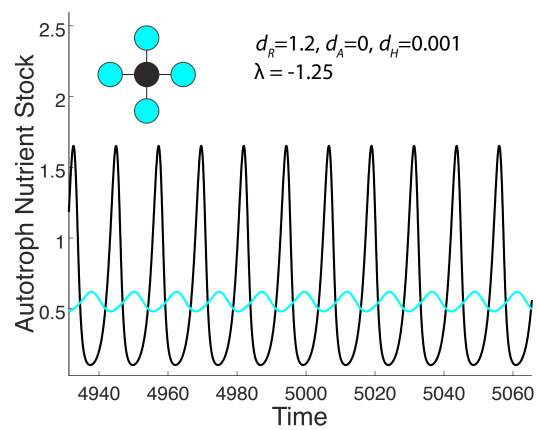
Table and Figure Captions

Figure B1: The types of dynamics that occur beyond the minimum critical movement rates. (a) After d_H is increased past $d_H^{min,c}$, the metaecosystem displays spatially heterogeneous equilibria. (b) After d_R is increased past $d_R^{min,c}$, the metaecosystem displays spatially heterogeneous oscillations.

Tables and Figures



(a)



(b)

Figure B1

Appendix C: Eigenvalues and eigenvectors of connectivity matrices

Each eigenvalue of a connectivity matrix is associated with its own eigenvector. For example, all the connectivity matrices presented in this study have a 0 eigenvalue, which is always associated with the $n \mathbf{x} 1$ eigenvector with entries all equal to 1. Eigenvectors can be used to predict the dynamics that emerge after the destabilization that is associated with its eigenvalue. For each network configuration found in Figure C1, it is the most negative eigenvalue that leads to the destabilization at the rate of nutrient movement presented. The eigenvector associated with the most negative eigenvalue in each of the four configurations (a-d) is :

$$\mathbf{v_a} = \begin{pmatrix} -0.22 \\ -0.22 \\ -0.22 \\ 0.89 \\ -0.22 \end{pmatrix}, \ \mathbf{v_b} = \begin{pmatrix} 0.89 \\ -0.22 \\ -0.22 \\ -0.22 \\ -0.22 \end{pmatrix}, \ \mathbf{v_c} = \begin{pmatrix} 0 \\ -0.20 \\ 0.20 \\ -0.68 \\ 0.68 \end{pmatrix}, \ \mathbf{v_d} = \begin{pmatrix} 0.20 \\ -0.34 \\ -0.70 \\ 0.42 \\ 0.42 \end{pmatrix} \qquad \text{(C1)}$$

The magnitudes of the entries indicate how much a local ecosystem will oscillate, while the signs of the entries indicate whether the oscillations are in phase with one another. For example, in $\mathbf{v_a}$, one ecosystem will have very large oscillations that are out of phase with the smaller oscillations of the other four ecosystems, which is what occurs in metaecosystem dynamics near the critical nutrient movement rate (Figure C1a). Similar results hold for the other metaecosystem networks (Figure C1b-C1d).

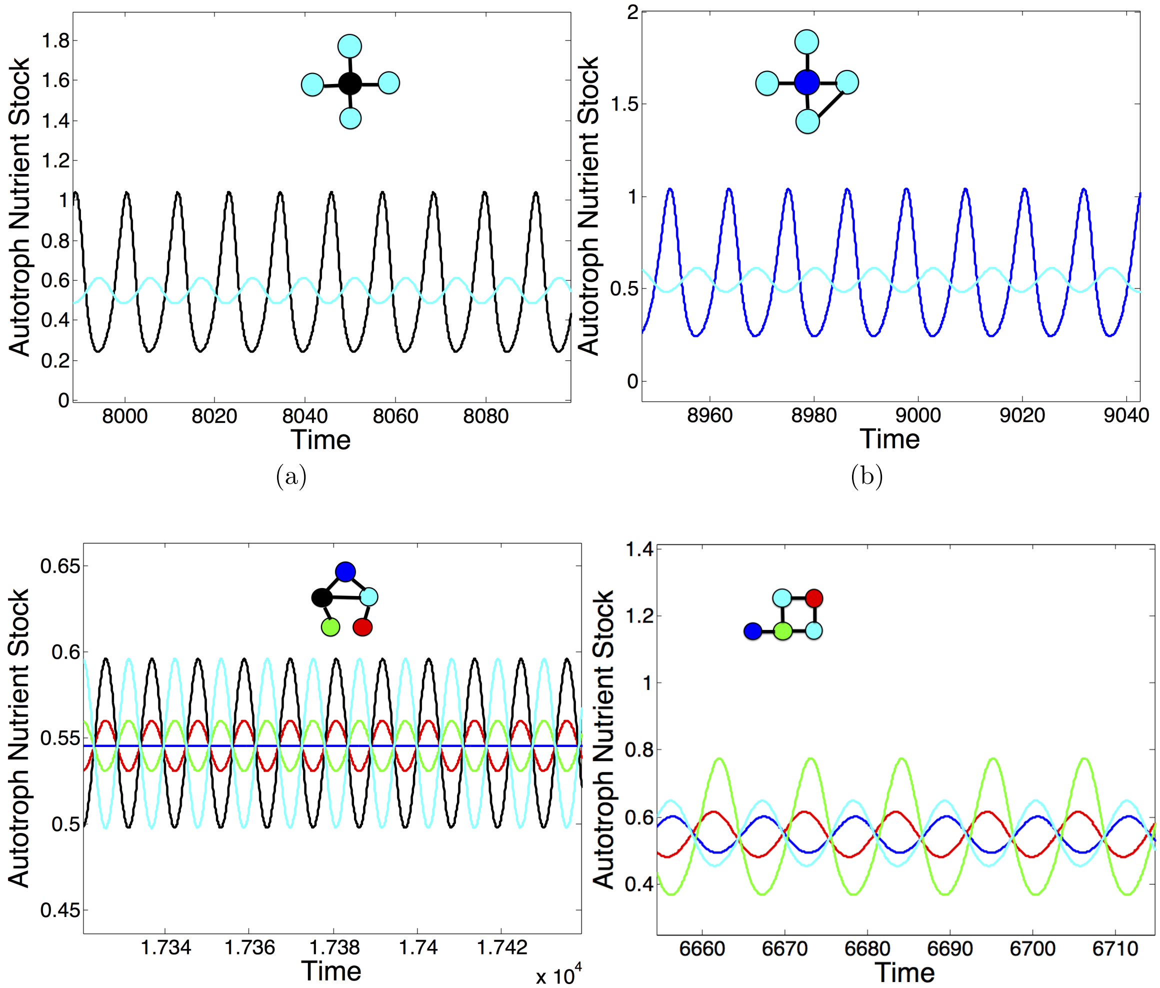
These predictions can fail when the nutrient movement rate is increased far beyond the critical nutrient movement rate (Figure C2). They fail because the other eigenvalues, and their associated eigenvectors, can influence metaecosystem dynamics. This occurs when nutrient movement is strong enough to destabilize the metaecosystem through at least one of the other eigenvalues, independently from the most negative eigenvalue. In other words, as the nutrient movement rate increases, multiple scales of spatial interaction operative to produce unpredictable dynamics both locally and regionally. This lack of predictive ability will also occur when eigenvalues are repeated: each eigenvalue will have a distinct eigenvector, such that even though there is only one 'scale' which is causing the instability, multiple eigenvectors will be associated with the instability. Therefore, multiple eigenvectors will influence the dynamics instead of just one in the case of unique eigenvalues.

Table and Figure Captions

Figure C1: The effects of metaecosystem network structure on local ecosystem dynamics after the local equilibrium solution is destabilized by a nutrient movement rate just above the critical nutrient movement rate ($d_R = 0.84$). The colours of the graphic insets indicate which time series is to be found in the local ecosystem, which means if two local ecosystems share the same colour, they have the same temporal dynamics. The temporal dynamics for all network configurations are predicted by eigenvectors associated with the most negative connectivity matrix eigenvalue.

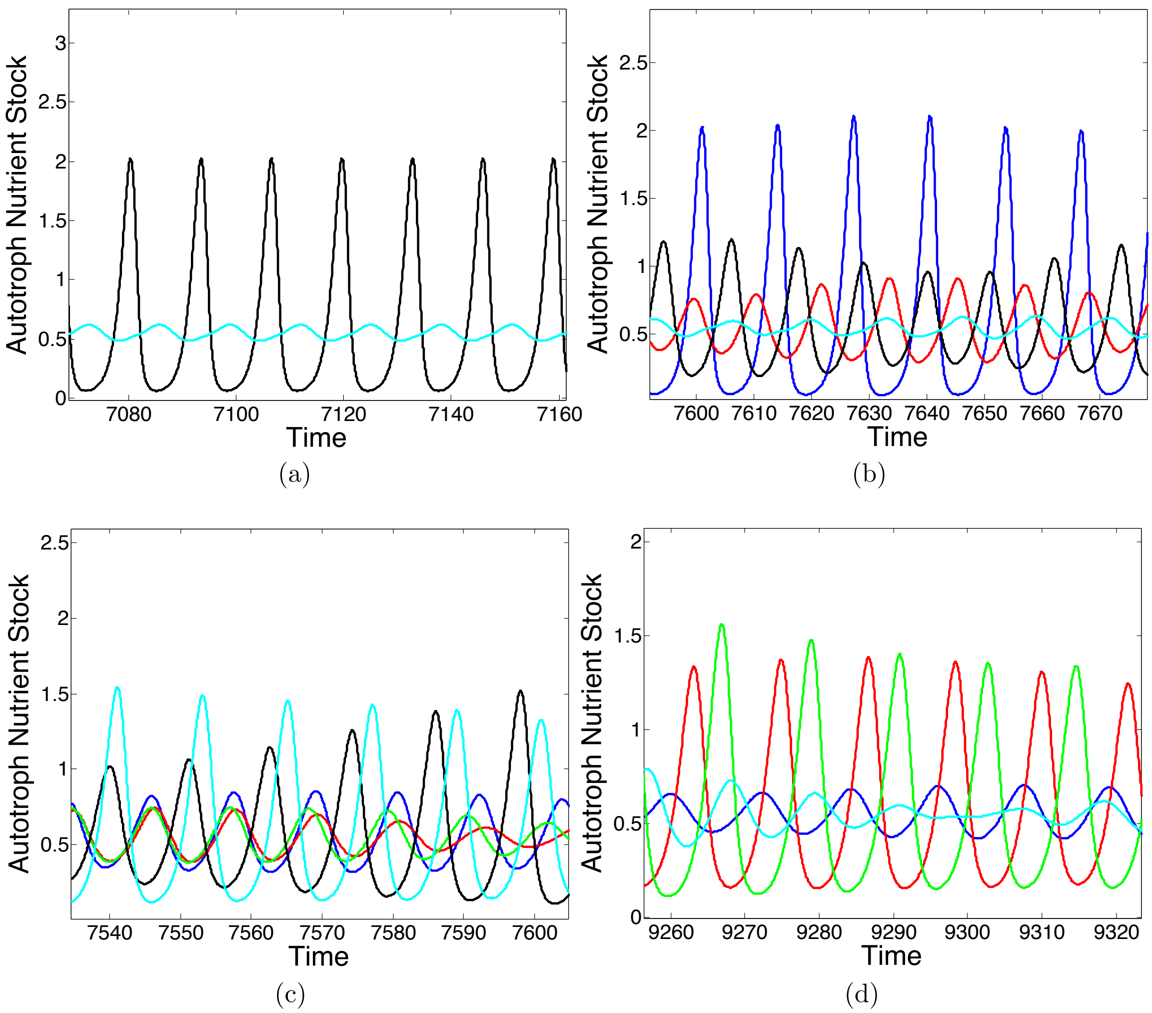
Figure C2: The effects of metaecosystem network structure on local ecosystem dynamics after the local equilibrium solution is destabilized by a nutrient movement rate far above the critical nutrient movement rate ($d_R = 1.5$). The colours of the graphic insets indicate which time series is to be found in the local ecosystem, which means if two local ecosystems share the same colour, they have the same temporal dynamics. The temporal dynamics for three of the four network configurations are not predicted by eigenvectors associated with the most negative connectivity matrix eigenvalue.

Tables and Figures



(a) (b) (c) (d)

Figure C1



Autotroph Nutrient Stock
Time
(a)
Autotroph Nutrient Stock
Time
(b)
Autotroph Nutrient Stock
Time
(c)
Autotroph Nutrient Stock
Time
(d)

Figure C2

Appendix D: Parameter values used to generate figures

For all figures, we used the same set of parameters for all non-movement related parameters. The values are $I = 2$, $E = 0.4$, $\alpha_A = 2$, $\beta_A = 0.5$, $\epsilon = 0$, $\chi = 0$, $m = 1$, $l = 0.5$, $\alpha_H = 6$, $\beta_H = 6$ and $\gamma = 0$.

Appendix E: Relaxing assumptions used for the analytical results

Within the Methods section, we invoked a number of simplifying assumptions in order to derive equations 4 and 5, and Figure 2 in the main text. These assumptions included that parameters within local ecosystems are identical and that the chosen parameters would lead to identical equilibria in the absence of spatial flows in order to obtain a spatially homogeneous solution, which is required for the derivations. However, many of the results are robust to the relaxation of these strict assumptions. For example, allowing for spatial heterogeneity in nutrient supply ($I_i \neq I_j$, for all i, j) such that each local ecosystem reaches its own unique equilibrium still results in qualitatively similar spatial dynamics (Figure E1). The situation differs slightly if the spatially homogeneous solution is a stable limit cycle, as the bifurcation of the dynamics is more complex (Figure E2). However, we still see spatial dynamics that match our expectations from the eigenvector and eigenvalue of the connectivity matrix, such that the most connected ecosystem exhibits larger amplitude oscillations and the other four ecosystems have synchronized dynamics after destabilization by spatial flows (Figure E2).

We can also combine spatially heterogenous attractors together such as a stable limit cycle with spatially heterogeneous equilibria due to spatial heterogeneity in nutrient supply ($I_i \neq I_j$, for all i, j; Figure E3). While there are initially substantial differences between ecosystems, relatively low amounts of nutrient movement leads to progressive homogenization of the metaecosystem, leading to similar equilibria being found across the metaecosystem at intermediate nutrient movement rates

(Figures E3A-E3C). However, high amounts of nutrient movement still leads to spatial dynamics that match our expectations from the eigenvector and eigenvalue of the connectivity matrix, though with some variation between ecosystems that are synchronized (Figure E3D). This exploration of the robustness of our results signals that they can hold over many different parameter ranges and in spatially heterogeneous environments.

Table and Figure Captions

Figure E1: The effects of spatial heterogeneity in nutrient supply (I varies from 1.9 to 2 in the local ecosystems) on the local ecosystem dynamics after the local equilibria solutions are destabilized by nutrient movement at (A) low and (B) high autotroph movement rates. Note how the synchrony of the dynamics match those found in Figure 4 of the main text.

Figure E2:The effects of higher nutrient supply ($I = 2.2$) on the local ecosystem dynamics (A) before and (B) after the local limit cycle solutions are destabilized by nutrient movement at low autotroph movement rates. Note how the synchrony of the dynamics after perturbation are similar to those found in Figure 4 of the main text.

Figure E3: The effects of spatial heterogeneity in nutrient supply (I varies from 1.8 to 2.2 in the local ecosystems) on the local ecosystem dynamics with (A) no movement, (B) low nutrient movement rates, (C) intermediate nutrient movement rates and (D) high. (A) With no nutrient movement, there is one ecosystem with a stable limit cycle, while the others are at different stable equilibria (not seen in autotrophs due to top-down control). (B) Low movement rates allow for small oscillations to occur across the metaecosystem. (C) Intermediate movement rates lead to the elimination of the oscillations as the nutrient levels are homogenized across the metaecosystem at a level that leads to stable equilibrium. (D) High movement rates lead to the destabilization of the stable equilibrium found in (C). Note how the synchrony of the dynamics after perturbation are similar to those found in Figure 4 of the main text.

Tables and Figures

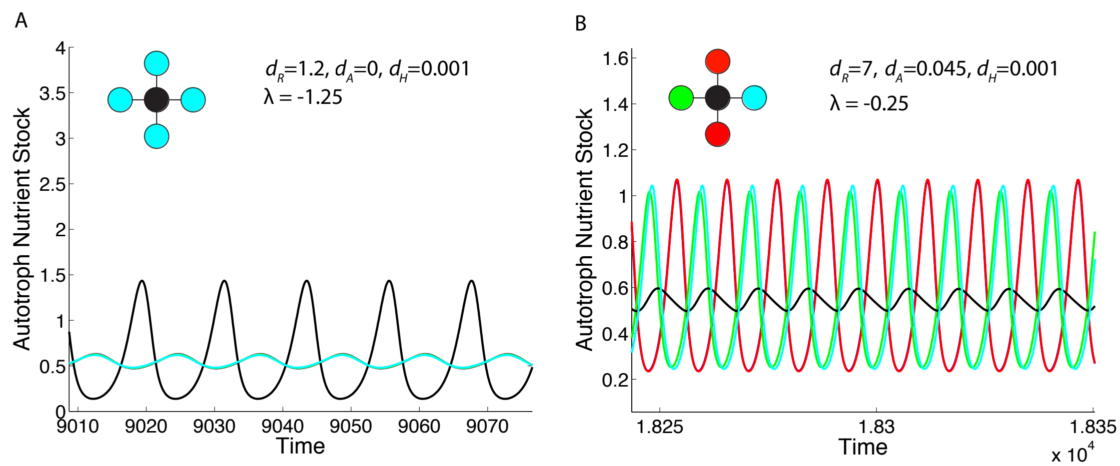


Figure E1

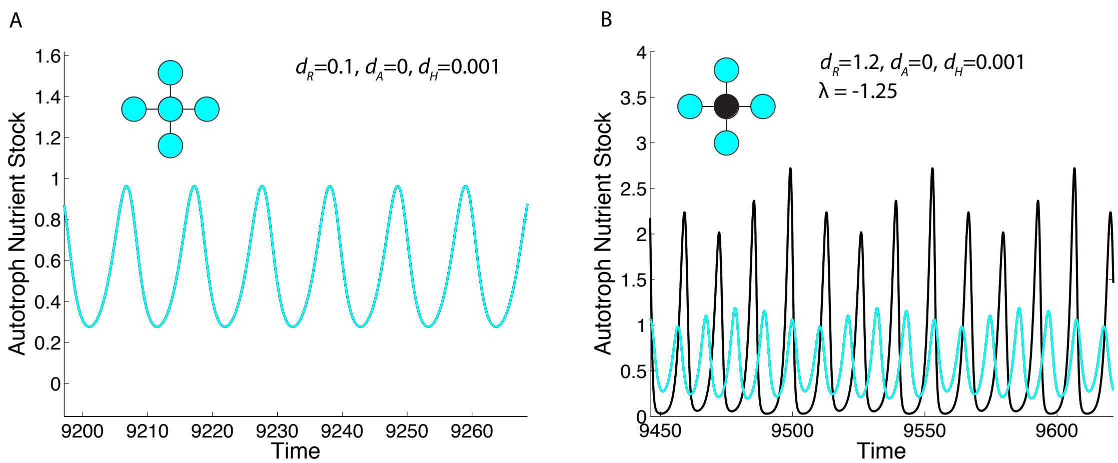
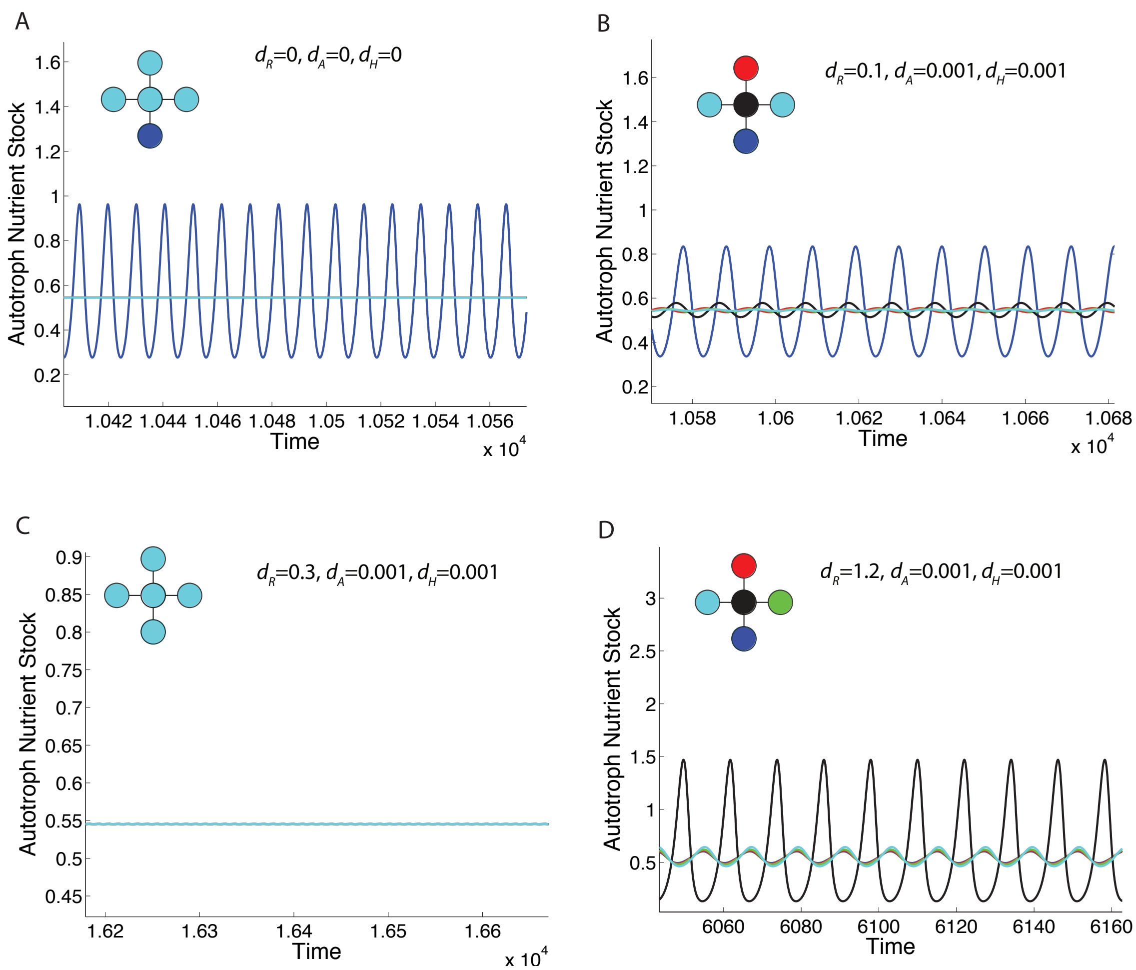

A
Autotroph Nutrient Stock
Time
d_R=0.1, d_A=0, d_H=0.001
B
Autotroph Nutrient Stock
Time
d_R=1.2, d_A=0, d_H=0.001
λ = -1.25

Figure E2



A
d_R=0, d_A=0, d_H=0
Autotroph Nutrient Stock
Time
x 10^4
B
d_R=0.1, d_A=0.001, d_H=0.001
Autotroph Nutrient Stock
Time
x 10^4
C
d_R=0.3, d_A=0.001, d_H=0.001
Autotroph Nutrient Stock
Time
x 10^4
D
d_R=1.2, d_A=0.001, d_H=0.001
Autotroph Nutrient Stock
Time

Figure E3

Connecting Statement

In Chapter 2, I indicated the utility of the framework of ecological stoichiometry to address the problem of nutrient colimitation, but indicated that there were some limitations in only exploring local mechanisms for colimitation and a need to look at spatial flows and structure. In Chapter 3, I show that the spatial flows of nutrients and organisms and the spatial structure of a metaecosystem can control the resulting dynamics and functioning at local and regional scales. Furthermore, I show that by using the eigenvalues of the connectivity matrix that described the spatial structure of the metaecosystem, I could predict some of the dynamics observed, though it depended heavily on the movement rates of nutrients and organisms.

In Chapter 4, I bring these two approaches together in order to investigate if the spatial flows of nutrients and organisms can be a mechanism for nutrient colimitation at local and regional scales, and if it can help explain certain patterns found in the empirical literature (Harpole et al., 2011).

Chapter 4
EMERGENCE OF NUTRIENT COLIMITATION IN STOICHIOMETRIC METAECOSYSTEMS

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Status: In preparation

Abstract

Extending and integrating ecological concepts and frameworks can provide new insights on difficult ecological problems. In this study, we investigate integrating metaecosystem theory together with ecological stoichiometry in order to clarify the difficult concept of nutrient colimitation by examining if the movement of organisms and nutrients can generate colimited growth responses at different scales and ecosystems with differing local limitation status. We do so by creating a stoichiometric metaecosystem model composed of two limiting nutrients, autotrophs and herbivores that have different movement rates between the interconnected ecosystems. Our results show that nutrient colimitation can emerge in metaecosystems despite no local mechanisms for nutrient colimitation due to different movement rates between herbivores, autotrophs and nutrients. Furthermore, the type of colimitation present depends on the movement rates of the nutrients and the spatial structure of the metaecosystem. These results suggest that spatial processes such as movement between ecosystems can be a potential mechanism for nutrient colimitation at local and regional scales, and can help explain previously anomalous results in the colimitation literature.

Introduction

The concept of the ecosystem, at certain points of its historical development, invoked spatial closure, spatial homogeneity and a focus on energetics (O'Neill, DeAngelis, Waide, & Allen, 1986; Golley, 1993; O'Neill, 2001). The narrowing of the ecosystem concept aided ecologists to establish the ecosystem as a fundamental unit of investigation and produced tremendous theoretical and empirical progress in the relatively nascent field of ecosystem ecology (O'Neill et al., 1986; Golley, 1993; Kingsland, 2005). However, many ecosystems are excluded from such a concept due to their lack of closure to spatial fluxes, their spatial heterogeneity and the numerous limiting factors other than energy regulating their functioning (O'Neill et al., 1986; Reiners, 1986; Polis, Anderson, & Holt, 1997; Polis, Power, & Huxel, 2004; O'Neill, 2001).

In order to incorporate these features into a more comprehensive ecosystem concept, two main extensions have been developed and explored. The first extension of the ecosystem involves adding spatial processes in order to evaluate the effects of fluxes across ecosystem boundaries or to consider the impacts of spatial heterogeneity on ecosystem functioning (Polis, Anderson, & Holt, 1997; Polis, Power, & Huxel, 2004; Turner, 2005). The inclusion of space can be expressed either through the landscape concept (Turner, 1989, 2005), which emphasizes spatial heterogeneity in abiotic and biotic components of ecosystems at the regional scale, or the metaecosystem concept (Loreau, Mouquet, & Holt, 2003), which focuses on spatial fluxes between coupled ecosystems. Both approaches have demonstrated that spatial heterogeneity and fluxes can affect ecosystem dynamics, persistence and productivity

(Polis, Power, & Huxel, 2004; Leroux & Loreau, 2008; Gravel, Guichard, Loreau, & Mouquet, 2010; Gravel, Mouquet, Loreau, & Guichard, 2010; Marleau, Guichard, Mallard, & Loreau, 2010; Massol et al., 2011).

The second extension of the ecosystem concept brought the multiple limiting factors, particularly nutrients, into focus and brought out significance of the relative ratios (stoichiometry) of these nutrients in ecological interactions (Reiners, 1986; Sterner & J. J. Elser, 2002). This renewed focus on the balances of limiting nutrients, which was presented much earlier by Lotka (1925), led to the foundation of modern ecological stoichiometry framework (J. J. Elser, Fagan, Denno, et al., 2000; Sterner & J. J. Elser, 2002; Vrede, Dobberfuhl, Kooijman, & Elser, 2004; J. J. Elser, Fagan, Kerkhoff, Swenson, & Enquist, 2010). As with the addition of spatial processes, the incorporation of multiple limiting nutrients led to new insights in ecosystem dynamics, functioning and persistence (Daufresne & Loreau, 2001a; Sterner & J. J. Elser, 2002; Andersen, Elser, & Hessen, 2004; Daufresne & Hedin, 2005; Cherif & Loreau, 2009, 2013; Marleau, Jin, Bishop, Fagan, & Lewis, 2011).

However, there is severe lack of theoretical integration between the two extensions, leaving it an open question how differences in local and regional processes for multiple limiting nutrients can affect ecosystems (Massol et al., 2011). The few theoretical studies that have considered multiple limiting nutrients in a spatially explicit context have de-emphasized nutrient movement in favour of other trophic levels (Miller, Kuang, Fagan, & Elser, 2004; Kato, Urabe, & Kawata, 2007) or lack explicit nutrient stoichiometry and nutrient cycling (Ryabov & Blasius, 2011). Since the movement of limiting nutrients can lead to spatiotemporal instabilities across a metaecosystem that lead to important effects on ecosystem functioning and the susceptibility of metaecosystems to such instabilities are dependent on nutrient cycling, incorporating these aspects is vital for our understanding of ecosystems (Marleau, Jin, et al., 2011).

Such an integration can lead to new explanations of unresolved phenomena and clarification of concepts (Pickett, Kolasa, & Jones, 2007). One ecological field in need of clarification is the complex topic of nutrient colimitation, or the limitation of growth by multiple nutrients (Arrigo, 2005; Saito, Goepfert, & Ritt, 2008; Craine, 2009; Harpole et al., 2011). There are disagreements about what constitutes nutrient colimitation (Güsewell, Koerselman, & Verhoeven, 2003; Saito et al., 2008; Harpole et al., 2011), there are different metrics used to quantify it (Güsewell et al., 2003; Harpole et al., 2011) and there are a multitude of proposed mechanisms to generate it (Arrigo, 2005; Saito et al., 2008).

The most prevalent way of detecting nutrient colimitation is to observe a colimited growth response of autotrophs in nutrient addition experiments, such that either autotroph biomass increases only with the addition of both nutrients (i.e. independent colimitation) or the addition of either nutrient increases autotroph biomass (i.e. independent colimitation, Harpole et al., 2011). When such a response is observed, ecologists usually infer that some sort of local mechanism is responsible for the growth response, be it community complementarity in nutrient uptake, biochemical nutrient dependencies or other potential processes (Arrigo, 2005; Saito et al., 2008; Craine, 2009; Harpole et al., 2011). In previous work, we showed by using a stoichiometric ecosystem model that such inferences are unwarranted and that the identity of a nutrient colimitation mechanism can drastically alter predictions about ecosystem dynamics and functioning in response to nutrient enrichment because of trophic interactions (Marleau and Loreau, in review).

However, there is a significant gap in the literature when it comes to non-local mechanisms for nutrient colimitation, despite growing awareness that nutrient inputs and trophic interactions cross ecosystem boundaries (O'Neill, 2001; Loreau, Mouquet, & Holt, 2003; Polis, Power, & Huxel, 2004; Massol et al., 2011). One study demonstrated that within a single lake, there was spatial heterogeneity in fluxes of ground water that greatly differed in N:P ratios, which lead to autotroph assemblages indicative of either P or N limitation depending on their location in the lake (Hagerthey & Kerfoot, 2005). Such heterogeneity in nutrient limitation should indicate that the lake's autotroph community is limited by multiple nutrients over the whole lake, despite not necessarily demonstrating a colimited growth response in each local sampling site. Furthermore, the above study suggests that purely spatial processes could drive local autotroph community nutrient limitation (Hagerthey & Kerfoot, 2005).

In this study, we use a stoichiometric metaecosystem model to investigate if the movement of organisms and nutrients can lead to nutrient colimitation within a system dominated by the trophic interactions between autotrophs and herbivores, which we quantify by examining the local and metaecosystem responses of autotrophs to both long-term and short-term additions of nutrients. Furthermore, we assume in the model that there are no local mechanisms of nutrient colimitation and all model parameters are identical within local ecosystems. While the conditions are strict, the model demonstrates that if the movement of nutrients and organisms combined with the trophic interactions can break the symmetry of dynamics between local ecosystems, the autotrophs in local ecosystems can be limited by different nutrients at equilibrium. Furthermore, enrichment of the two nutrients across the metaecosystem can lead to positive growth responses to both nutrients, indicating the validity of the spatial fluxes as drivers of nutrient colimitation.

Methods

General Model Development

Our model is based on a hierarchy of processes and scales within a metaecosystem (Figure 4.1). 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 (Figure 4.1A). The biomass of the autotroph can be expressed as the sum of the total amount of each nutrient 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 (Figure 4.1A; 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; Figure 4.1A):

$$q_k = \frac{P_k}{\sum_{k=1}^{l} P_k},\ \rho_k = \frac{\Theta_k}{\sum_{k=1}^{l} \Theta_k} \tag{4.1}$$

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, O (Figure 4.1A-B). To simplify our model analysis, we will assume that the quotient of other nutrients is the same for herbivores and autotrophs (i.e. $q_O = \rho_O$). In addition, we will be assuming for the rest of the paper that herbivores are richer in S 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 (Figure 4.1B). The growth of autotroph biomass is determined by three processes: growth due to nutrient uptake, $U(R,S)$, intrinsic losses, MX, where M is constant, and herbivory, $H(X)Y$ (Figure 4.1B). Growth due to nutrient uptake obeys Liebig's Law of the Minimum and follows Michealis-Menten kinetics, which leads to the following equation:

$$U(R,S) = \min\left(\frac{u(R)}{q_R}, \frac{u(S)}{q_S}\right) = \min\left(\frac{V_R R}{q_R(K_R+R)}, \frac{V_S S}{q_S(K_S+S)}\right) \quad (4.2)$$

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 (Figure 4.1B). For the rest of this study, the herbivore will have a Type II functional response:

$$H(X) = \frac{\alpha X}{\beta + X} \quad (4.3)$$

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 ($\bar{\gamma} H(X)Y$, $\bar{\gamma} = q_R - \rho_R \gamma$; Figure 4.1B). 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 Δ and nutrient uptake ($q_S U(R,S)$; Figure 4.1B).

At the metaecosystem level, two different elements link local ecosystems together. The diffusive movement of nutrients (d_R and d_S), of autotrophs (d_X) and of herbivores (d_Y) connect the local ecosystems, if such connections exist (Figure 4.1C). 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 (Figure 4.1D). The size of the connectivity matrix is n x n, where n is the total number of local ecosystems in the metaecosystem. 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 utilize 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 metaecosystem:

$$\frac{dR_i}{dt} = I - ER_i - q_R U(R_i, S_i)X_i + \epsilon_R q_R M X_i + \chi_R \rho_R L Y_i + \bar{\gamma} H(X_i)Y_i + d_R \sum_{j=1}^{n} c_{ij} R_j \tag{4.4a}$$

$$\frac{dS_i}{dt} = \Phi - \Delta S_i - q_S U(R_i, S_i)X_i + \epsilon_S q_{XS} M X_i + \chi_S \rho_S L Y_i + d_S \sum_{j=1}^{n} c_{ij} S_j \tag{4.4b}$$

$$\frac{dX_i}{dt} = U(R_i, S_i)X_i - MX_i - H(X_i)Y_i + d_X \sum_{j=1}^{n} c_{ij} X_j \tag{4.4c}$$

$$\frac{dY_i}{dt} = \gamma H(X_i)Y_i - LY_i + d_Y \sum_{j=1}^{n} c_{ij} Y_j \tag{4.4d}$$

Note that the model parameters are the same across the metaecosystem, such that in the lack of spatial processes there would be no differences in the dynamics of the local ecosystems. Furthermore, we will be generally restricting our focus on parameter values that allow for a stable equilibrium which allows the coexistence of autotrophs and herbivores.

Distinguishing Measures of Nutrient Colimitation

In order to investigate how the movement of nutrients and organisms can be a mechanism of nutrient colimitation, we have to be precise in how we measure nutrient colimitation. In this study, we will use two main measures: the uptake ratios of autotrophs in local ecosystems and the biomass responses of autotrophs at local and metaecosystem scales.

As mentioned previously, autotrophs within a local ecosystem can only be limited by one nutrient at a time because of the presence of the minimum function in equation (4.2). 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 biomass response in the autotrophs, while a pulse of the other nutrient would not. Therefore, without any spatial processes, the expectation each local ecosystem will see the same instantaneous biomass response to one nutrient, which is determined by the following ratio:

$$
\begin{aligned}
\left(\frac{q_S}{q_R}\right)\left(\frac{u(R_i)}{u(S_i)}\right) &> 1 \\
\Rightarrow \frac{u(R_i)}{u(S_i)} &> \frac{q_R}{q_S}
\end{aligned}
\tag{4.5}
$$

In words, the above condition implies that if relative ratio of $R{:}S$ uptake is greater than the stoichiometric $R{:}S$ ratio in the autotrophs, then instantaneous autotroph biomass response is S-limited in ecosystem i. If the ratio of $R{:}S$ uptake is less than the stoichiometric $R{:}S$ ratio in the autotrophs, then instantaneous autotroph biomass growth is 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, then ecologists would be able to detect instantaneous biomass responses for the autotrophs for both nutrients within the metaecosystem. 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 colimitation at the metaecosystem scale, but not at the local ecosystem scale when the local autotrophs differed in their R:S uptake ratios at equilibrium. Because of the metric used, we will call this form of nutrient colimitation in a metaecosystem 'spatial uptake colimitation' and we detect it by determining if at least one local ecosystem differs in its instantaneous nutrient limitation status. In addition, the presence of spatial uptake colimitation within a metaecosystem could also suggests changes in the autotroph community composition, though not in this model (Wolfe, Baron, & Cornett, 2001; Hagerthey & Kerfoot, 2005; J. Elser et al., 2009).

Another metric that can be used to detect nutrient colimitation 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 colimitation, then according to this metric we should see colimited growth responses of autotrophs, such as independent or simultaneous colimitation, at the local ecosystem and/or metaecosystem scale after the set time period. Therefore, we do detect such an increase, we will say that 'biomass response colimitation' has occurred.

The relationship between the two metrics or types is not simple. In this model, it is not possible for a local ecosystem to demonstrate nutrient colimitation for instantaneous autotroph growth, but a local ecosystem could display long-term biomass response colimitation due to the movements of nutrients and organisms. In addition, a metaecosystem that displays spatial uptake colimitation may or may not demonstrate biomass response colimitation at the metaecosystem scale, as processes beyond autotroph responses to nutrients regulate autotroph biomass. These metrics of nutrient colimitation are distinct and need to be considered separately.

Model Analysis

Our investigation into colimitation at local ecosystem and metaecosystem scales utilizes both analytical and numerical techniques to discern the importance of movement in generating colimitation. 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 equation (4.4) 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 4.1.

Within those ranges, we investigate whether spatial uptake and biomass response colimitation may emerge due to the spatial processes through the use of numerical simulations. To test for biomass response colimitation, we perform a simulation of a factorial nutrient addition experiment through increasing nutrient input levels by 50% from a control level. Within these same experiments, we also examine if spatial uptake colimitation is occurring after nutrient additions by measuring the number of S-limited ecosystems within the metaecosystem. 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 metaecosystem will affect both growth response and spatial uptake colimitation. All numerical simulations are performed using Matlab and the ode package.

Results

Expectations from a metaecosystem 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 increase in nutrient inputs as long as the equilibrium remains stable (Appendix A). This result is easily seen from the expression for autotroph biomass at equilibrium:

$$X^* = \frac{\beta L}{\frac{q_S}{\rho_S}\alpha - L} \tag{4.6}$$

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 4). 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 biomass response colimitation at either local or metaecosystem scales.

The 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 limitation status of the whole metaecosystem when there is no movement between ecosystems (Appendix 4). This result means that spatial uptake colimitation is also not possible without the local ecosystem equilibrium becoming destabilized.

For the local ecosystem equilibrium to become destabilized through the movement of nutrients and organisms, the certain movement rates must be large while others remain small. In particular, the movement rates of the herbivores and the limiting nutrient at equilibrium must be large in order for there to be heterogeneous equilibria throughout the metaecosystem, while the movement rate of autotrophs remains small (Appendix A; Marleau, Guichard, & Loreau, 2014). The movement rate of the non-limiting nutrient at equilibrium has no impact on the stability of the equilibrium (Appendix 4). For the remainder of this paper, we will assume that S is limiting at the spatially homogeneous equilibrium.

Emergence of nutrient colimitation through movement

When we add sufficient movement of herbivores and nutrient S to the metaecosystem (Appendix A), we can detect the emergence of both types of colimitation in response to nutrient additions (Figure 4.2). For a fully connected ecosystem (Figure 4.2D), we can observe that at the metaecosystem scale, simultaneous biomass response colimitation for autotrophs can occur (Figure 4.2A). Furthermore, the local ecosystems differ in their limitation status for autotrophs, which indicates spatial uptake colimitation (Figure 4.2B).

At the level of the local ecosystems, the response to nutrient additions is mixed (Figure 4.2C). For this parameter set and metaecosystem connectivity, the autotrophs of two of the ecosystems display strong simultaneous colimited biomass responses, while the other ecosystems see large reductions in autotroph biomass with nutrient additions (Figure 4.2C). The differences in the ecosystem responses is driven by the initial conditions, such that the ecosystems with the low autotroph biomass would change if different initial conditions are used (compared Figure 4.2C with Figure 4.3C). However, the overall effect of two ecosystems with increases in autotroph biomass and three with a decrease is insensitive to the initial conditions. To achieve understanding of this result, it is required to look at the other ecosystem compartments across the metaecosystem (Figure 4.3).

The spatial heterogeneity that exists for autotrophs is also present for the other ecosystem compartments, to a much lesser degree (Figure 4.3). In particular, the herbivores and available nutrient S display very small differences over the metaecosystem, which is due to their very high movement rates (Figures 4.3B and 4.3D). The high diffusive movement rates of the herbivores is especially important, as the herbivores will leave the high autotroph ecosystems to colonize the low autotroph ecosystems (Figure 4.3D). The autotrophs, on the other hand, have low diffusive movement and that leads to autotroph biomass being barely exchanged between ecosystems, which helps generate the spatial heterogeneity through a Turing-like mechanism and local ecosystem colimited growth responses (Figure 4.3C).

This spatial segregation of the autotrophs then leads to the spatial patterning of the nutrients across the metaecosystem, but the relative movement rates of S and R determine the spatial heterogeneity (Figures 4.3A and 4.3B). Nutrient S is able to reduce the negative effect of the autotrophs on local availability through diffusion and helps sustain the high autotroph biomass found in certain ecosystems due to random initial conditions (Figure 4.3B). Nutrient R, whose movement rate is lower by an order of magnitude, cannot diffuse fast enough between ecosystems and its availability decreases greatly, causing ecosystems with the highest autotroph biomass to become R limited (Figure 4.3A). This leads to the spatial uptake colimitation as the ratios of R to S must differ between local ecosystems and leads to the patterns seen in Figure 4.2B.

However, the above differences in local ecosystems nutrient limitation caused by fast diffusing S nutrients and slower moving R nutrients does not provide any insight on the positive biomass response to the addition of both nutrients at the metaecosystem scale.

Nutrient colimitation is dependent on movement rates and metaecosystem connectivity

In order to explain the colimited biomass response at the metaecosystem level, it is necessary to alter the movement rate of nutrient R (d_R; Figure 4.4). When there is no movement of nutrient R, we see only a weak colimited growth response at the metaecosystem level (Figure 4.4A). This result occurs despite spatial uptake colimitation and the presence of colimited biomass responses at the level of the local ecosystems (Figures 4.4B-4.4C).

Increasing the movement rate of nutrient R results in an increasingly strong colimited biomass response at the metaecosystem level and it also results in the elimination of spatial uptake colimitation at high d_R (i.e. all local ecosystems have the same limitation status at equilibrium; Figures 4.4A-4.4B). Furthermore, at high d_R, the biomass responses of the local ecosystems to the increase in both nutrients leads to one ecosystem demonstrating a very large increase in autotroph biomass, while all the others show a large decline in autotroph biomass (Figure 4.4D). However, the increased movement in nutrient R allows for more nutrient R to reach the autotrophs whose biomass is no longer strictly controlled by herbivores as indicated by equation

(4.6) in the spatially homogeneous case, leading to greater metaecosystem autotroph biomass than when d_R is lower (Figure 4.4A). Increasing d_R even further can allow for serial colimitation to appear, with S being the 'primary limiting' nutrient (Figure B1).

We also controlled for metaecosystem connectivity in order to discern how much of this behaviour is driven by the movement rates compared to the other potential spatial variables (Figure 4.5D). Using a linear arrangement of ecosystems in the metaecosystem managed to alter many of the effects of increasing d_R, but both types of colimitation still occurred (Figure 4.5). For example, there is only a limited increase metaecosystem autotroph biomass with the addition of both nutrients, even at large d_R values (Figure 4.5A). In addition, the range of d_R values that allow for spatial uptake colimitation is much more limited (Figure 4.5B). 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 metaecosystems (Figure 4.5C).

Discussion

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

Nutrient colimitation at local scales: limitations of local processes to explain patterns

Ecologists have proposed a number of mechanisms to explain the persistent patterns of nutrient colimitation in autotroph biomass responses observed in nutrient addition experiments (Arrigo, 2005; Danger, Daufresne, Lucas, Pissard, & Lacroix, 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, Litchman, & Levin, 2007). While the effectiveness of these mechanisms to generate colimited biomass responses and the ability to distinguish the mechanisms through colimited biomass responses are open questions (Marleau and Loreau, in review), it is clear that ecologists are looking at local processes to explain the patterns observed in ecosystems.

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, Power, & Huxel, 2004; Leroux & Loreau, 2008; Gravel, Guichard, et al., 2010; Massol et al., 2011; Loreau, Daufresne, et al., 2013). For example, our study adds to this literature by further demonstrating that local nutrient limitation status of autotrophs, which can alter the autotroph community composition (e.g. Wolfe et al., 2001; Hagerthey & Kerfoot, 2005), can be determined by the movements of herbivores and and limiting nutrients between locally identical ecosystems. Furthermore, examining nutrient limitation at only local scales could give false impressions about the limiting nutrients at the metaecosystem scale, as local ecosystems showed both R-limited uptake and S-limited uptake such that autotroph nutrient uptake was colimited spatially. This emergent form of colimitation could only be examined through explicit analysis of spatial processes.

Our results also indicate that colimited biomass responses for autotrophs at local scales can also be generated through spatial processes, even without any of the proposed local mechanisms for nutrient colimitation. This result raises a danger to one of the main recommendations from previous studies, which were to integrate local nutrient colimitation mechanisms into ecosystem models based on autotroph-only models and the ubiquity of colimited autotroph biomass responses (Danger et al., 2008; Harpole et al., 2011). But as we have shown, colimited biomass responses in local ecosystems may have nothing to do with the local processes operating in the ecosystem, but are rather driven by spatial processes. Therefore, adding putative nutrient colimitation mechanisms to models, especially when we have difficulty identifying the mechanisms that drive colimited biomass responses (e.g. Marleau and Loreau, in review), 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 (Saito et al., 2008, p. e.g.).

Linking nutrient colimitation to spatial and trophic structure

Two key insights brought by integrating metaecosystem theory with ecological stoichiometry in this model are the importance of trophic interactions and of spatial structure in generating nutrient colimitation at local ecosystem and metaecosystem scales. Without the presence of multiple ecosystems connected through the movement of nutrients, autotrophs and herbivores that had large differences in their movement rates, neither type of nutrient colimitation could occur in the model. However, even greater insights can be achieved by plumbing deeper into the connections between spatial structure, trophic structure and nutrient colimitation.

For spatial structure, we provided a clear signal that the presence of spatially heterogeneous nutrient limitation of autotrophs and of strong colimited biomass responses at the metaecosystem was dependent on the connectivity of the metaecosystem, which is in line with other studies on spatial structure's effects on metapopulations (Hanski & Ovaskainen, 2000; Ovaskainen & Hanski, 2002; Fagan, 2002; Keeling & Eames, 2005). However, it is possible to go farther than just dependence. In other work, we have shown that the eigenvalues of the connectivity matrix, which defines the connection of the metaecosystem, can be used in conjunction with their eigenvectors to predict relative biomass of organisms in the metaecosystem (Marleau, Guichard, & Loreau, 2014). Since in our model, high autotroph biomass indicates biomass response colimitation in the local ecosystem, we could predict which local ecosystems should display nutrient colimitation (with certain caveats, see Marleau, Guichard, & Loreau, 2014). Therefore, spatial structure can help us predict nutrient colimitation when spatial processes matter.

For trophic structure, models addressing nutrient colimitation need to move beyond simple nutrient-autotroph interactions. Numerous empirical and theoretical studies have indicated that other trophic levels, such as herbivores and decomposers, can significantly alter nutrient limitation status of autotrophs and even help promote nutrient colimitation at local scales (Daufresne & Loreau, 2001b; Grover, 2004; Cherif & Loreau, 2007, 2009, 2013; Trommer, Pondaven, Siccha, & Stibor, 2012; Atkinson, Vaughn, Forshay, & Cooper, 2013). Furthermore, these trophic levels may end up colimited themselves, which further requires an expansion of nutrient colimitation beyond autotrophs (Marleau and Loreau, in review; Sperfeld, Martin-Creuzburg, & Wacker, 2012). Lastly, because the movement rates between trophic levels differ greatly, there could be opportunities to extend the effects of movement on nutrient colimitation to multiple trophic levels (McCann, Rasmussen, & Umbanhowar, 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 ecosystem, over twenty percent of studies showed no autotroph biomass response and nearly fifteen percent showed a negative biomass response to nutrient additions (Harpole et al., 2011). The explanations provide by the authors ranged from statistical power limitations to pH changes in the soil due to nutrient additions, but one of the possibilities is 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 can, in many cases, not exhibit any recipient control at local scales (Gruner et al., 2008). The lack of local recipient-control would also need to be present in the almost eighteen percent of nutrient addition experiments resulting in simultaneous colimited 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 local autotroph biomass, which can break local recipient-control and allow for simultaneous colimited biomass responses (Gruner et al., 2008; Harpole et al., 2011). However, this does not happen everywhere in the metaecosystem due to the spatial heterogeneity in autotrophs, as in some ecosystems autotrophs will demonstrate no biomass response or negative biomass responses to nutrient additions (Harpole et al., 2011). In addition, our model can even demonstrate serial limitation (*sensu* Harpole et al. (2011)) at high movement rates of the originally 'non-limiting' nutrient at control nutrient levels, which also occurs in twenty-two percent 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), as there may not be sufficient differences in movement to obtain the desired spatial heterogeneity. 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 biomass responses to nutrients may be violated despite functional responses that lead to recipient-control (Gruner et al., 2008). Overall, we would suggest that 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 metaecosystems.

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Table and Figure Captions

Table 4.1 : The definitions and values of the ecosystem parameters used in the Figures

Figure 4.1 : Hierarchy of processes and scales within the metaecosystem model. *A* at the level of the autotrophs and herbivores, we see that there biomasses (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), we can derive a relationship with biomass, such that it is equal to q_kX (or ρ_kY), where q_k (or ρ_k) is the portion of element k in a unit of biomass. *B* At the local ecosystem level, the biomasses of the autotrophs and the herbivores are determined by the flows of elements entering and leaving compartments. Abiotic elemental nutrient inflows (I and Φ) and outflows (E and Δ) provide the available nutrients needed for autotroph growth (q_RU and q_SU), which provide the nutrients for herbivore growth (γH). Some of the biomass lost by autotrophs (M) and herbivores (L) is recycled ($\epsilon_R q_R M$, $\epsilon_S q_S M$, $\chi_R \rho_R L$ and $\chi_S \rho_S L$), as is nutrients not utilized due to stoichiometric imbalance ($\bar{\gamma} H$). *C* At the level of two connected ecosystems, nutrients and organisms move diffusively between the ecosystems at their own rates (d_R, d_S, d_X and d_Y). *D* At the metaecosystem level, the connections between ecosystems are determined by the off-diagonal elements of the connectivity matrix (c_{ij}). Ecosystems without connections do not have nutrients and organisms move between them, even at positive movement rates.

Figure 4.2 : The emergence of colimitation 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 metaecosystem scale, there is simultaneous

colimitation growth response to the addition of nutrients when movement is present, while no response is observed without movement. B The metaecosystem also exhibits metaecosystem colimitation with the addition of both nutrients when movement is present, while no such colimitation is observed absent movement. C At the local ecosystems, there is both growth response colimitation and collapses in autotroph biomass when movement is present, but no such responses without movement. D Diagram indicating the metaecosystem connectivity used in the simulations.

Figure 4.3 : 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 destabilize the spatially homogeneous solution, and the movement rates and the metaecosystem connectivity are the same as in Figure 4.2. The relatively strong discrepancies of R availability and of autotroph biomass and the relatively small discrepancies of S availability and of autotroph biomass between local ecosystems can be explained by their relative movement rates. The large movement rates of nutrient S and herbivores allows for a relatively even distribution across the metaecosystem, but the small movement rates of nutrient R and autotrophs makes their compartments more isolated from the rest of the ecosystem. These differences in movement rates allows for spatial heterogeneity to emerge, with certain ecosystems maintaining large autotroph biomass while others have very little because herbivore biomass is no longer dictated by local autotroph biomass due to large movement rates. The differences in autotroph biomasses then leads to differential pressures on nutrients in local ecosystems, with S availability being maintain by influxes from other ecosystems, while R availability declines due to lack of movement between ecosystems. All these effects

together give rise to metaecosystem colimitation and both local and metaecosystem growth response colimitation.

Figure 4.4 : The effects of changing nutrient R's movement rate (d_R) on the local ecosystem and metaecosystem responses to nutrient additions. *A* At the metaecosystem level, the colimited growth response becomes much stronger as d_R increases, such that there is more than a 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 growth responses of autotrophs to the addition of both nutrients in local ecosystems at low d_R show four ecosystems exhibiting colimited growth responses, while one ecosystem had a collapse of its autotrophs. *D* The growth responses of autotrophs to the addition of both nutrients in local ecosystems at high d_R show only one ecosystem showing an impressive colimited growth response, while the other ecosystems see their autotroph biomass collapse.

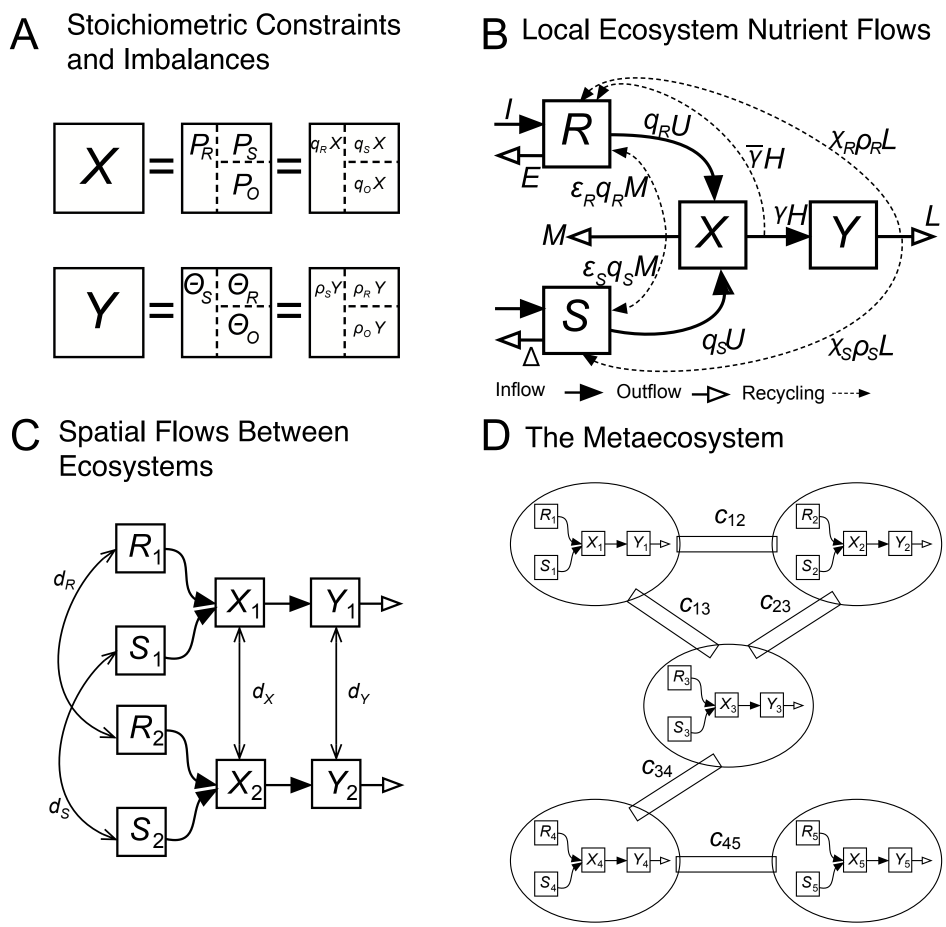
Figure 4.5 : The effects of changing metaecosystem connectivity on the local ecosystem and metaecosystem responses to nutrient additions. *A* At the metaecosystem level, the colimited growth response do not become much stronger as d_R increases, unlike in Figure 4.4. *B* The number of ecosystems limited 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. *C* The growth responses of autotrophs to the addition of both nutrients in local ecosystems with nutrient R movement show three ecosystems exhibiting colimited growth responses, while two ecosystems show a slight decline in their autotrophs. *D* Diagram indicating the

metaecosystem connectivity used in the simulation of Figure 4.5.

Tables and Figures

Table 4.1: The definitions and values of the ecosystem parameters used in the Figures

Parameter (unit)	Definition	Value Used
I (gram R day^{-1} L^{-1})	Influx of available R into ecosystem	1 and 1.5
Φ (gram S day^{-1} L^{-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 gram of autotroph biomass	0.4
q_S (gram S per gram of autotroph biomass)	Proportion of S that makes up 1 gram 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 L^{-1})	Half-saturation constant for R uptake	0.5
K_S (gram S L^{-1})	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 gram of herbivore biomass	0.38
ρ_S (gram R per gram of herbivore biomass)	Proportion of S that makes up 1 gram 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



A Stoichiometric Constraints and Imbalances
B Local Ecosystem Nutrient Flows
Inflow
Outflow
Recycling
C Spatial Flows Between Ecosystems
D The Metaecosystem

Figure 4.1

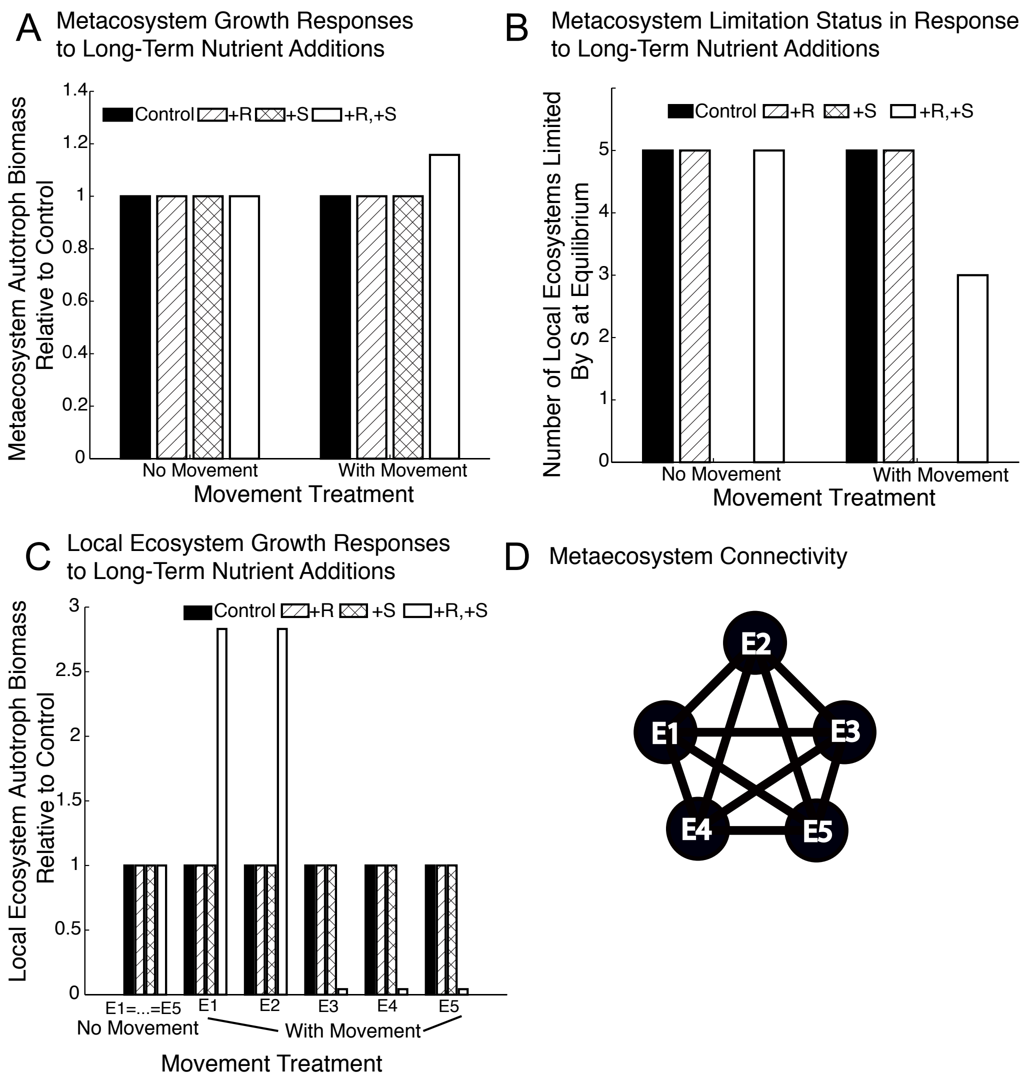

A
Metacosystem Growth Responses
to Long-Term Nutrient Additions
Metaecosystem Autotroph Biomass
Relative to Control
Control
+R
+S
+R,+S
1.4
1.2
1
0.8
0.6
0.4
0.2
0
No Movement
With Movement
Movement Treatment
B
Metacosystem Limitation Status in Response
to Long-Term Nutrient Additions
Number of Local Ecosystems Limited
By S at Equilibrium
Control
+R
+S
+R,+S
5
4
3
2
1
0
No Movement
With Movement
Movement Treatment
C
Local Ecosystem Growth Responses
to Long-Term Nutrient Additions
Local Ecosystem Autotroph Biomass
Relative to Control
Control
+R
+S
+R,+S
3
2.5
2
1.5
1
0.5
0
E1=...=E5
E1
E2
E3
E4
E5
No Movement
With Movement
Movement Treatment
D
Metaecosystem Connectivity
E2
E1
E3
E4
E5

Figure 4.2

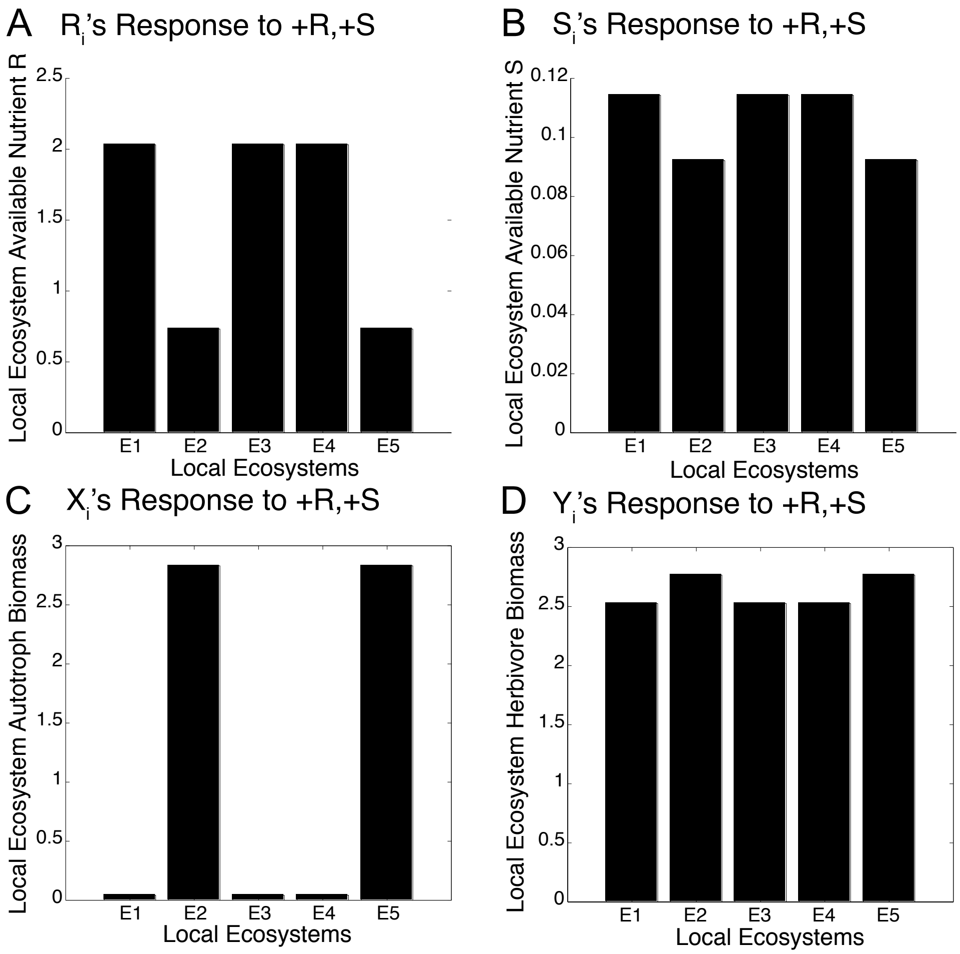

A R_i's Response to +R,+S
Local Ecosystem Available Nutrient R
Local Ecosystems
E1 E2 E3 E4 E5
B S_i's Response to +R,+S
Local Ecosystem Available Nutrient S
Local Ecosystems
C X_i's Response to +R,+S
Local Ecosystem Autotroph Biomass
Local Ecosystems
D Y_i's Response to +R,+S
Local Ecosystem Herbivore Biomass
Local Ecosystems

Figure 4.3

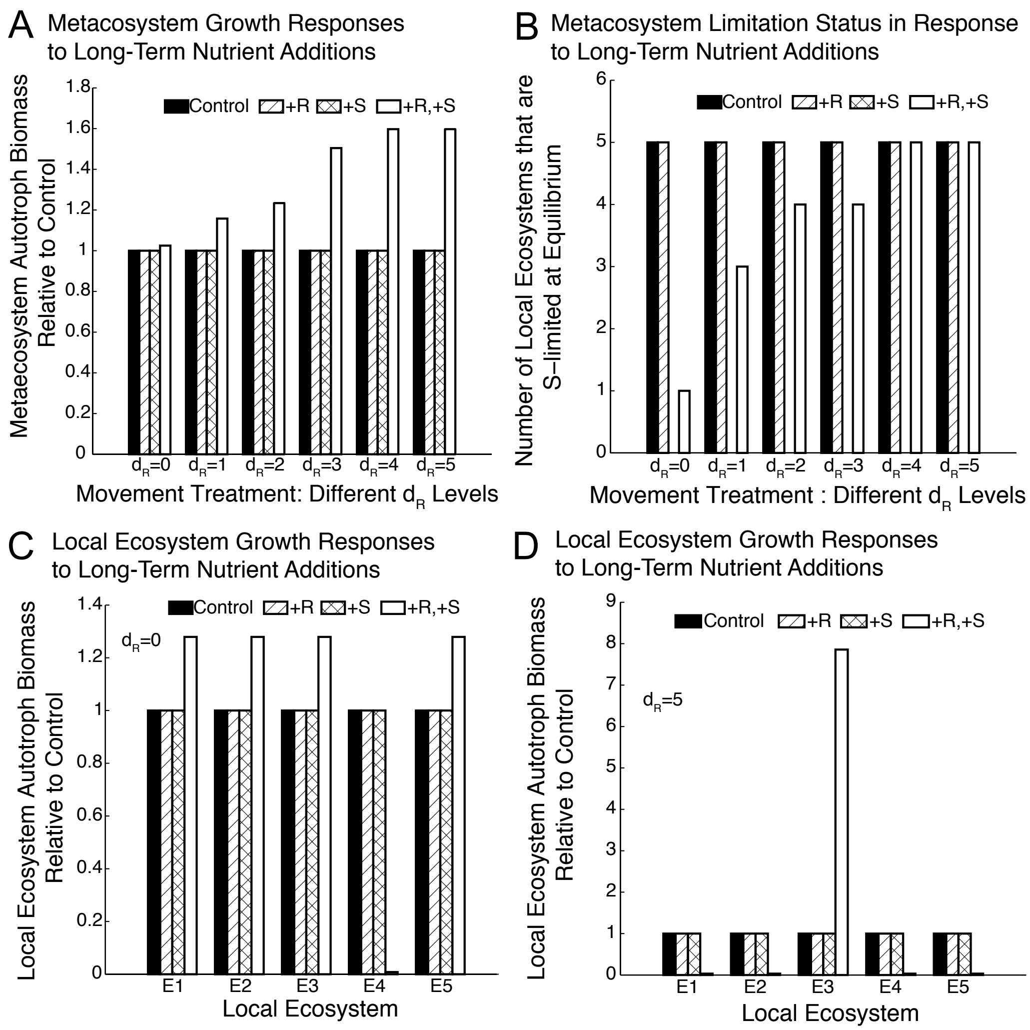

A Metacosystem Growth Responses
to Long-Term Nutrient Additions
Metaecosystem Autotroph Biomass
Relative to Control
Control +R +S +R,+S
Movement Treatment: Different d_R Levels
B Metacosystem Limitation Status in Response
to Long-Term Nutrient Additions
Number of Local Ecosystems that are
S–limited at Equilibrium
Movement Treatment : Different d_R Levels
C Local Ecosystem Growth Responses
to Long-Term Nutrient Additions
Local Ecosystem Autotroph Biomass
Relative to Control
d_R=0
Local Ecosystem
D Local Ecosystem Growth Responses
to Long-Term Nutrient Additions
d_R=5
Local Ecosystem

Figure 4.4

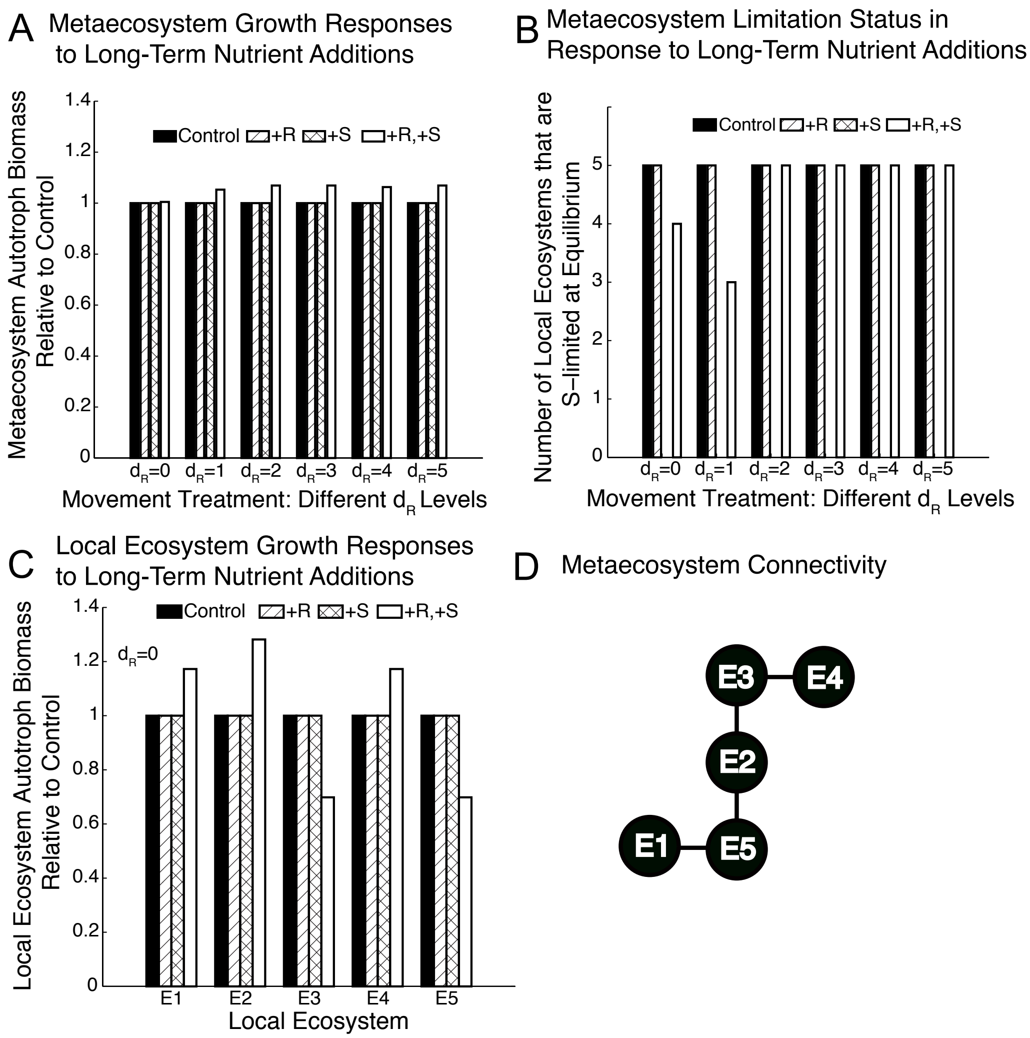

A Metaecosystem Growth Responses to Long-Term Nutrient Additions
Metaecosystem Autotroph Biomass Relative to Control
Control +R +S +R,+S
Movement Treatment: Different d_R Levels
B Metaecosystem Limitation Status in Response to Long-Term Nutrient Additions
Number of Local Ecosystems that are S-limited at Equilibrium
Control +R +S +R,+S
Movement Treatment: Different d_R Levels
C Local Ecosystem Growth Responses to Long-Term Nutrient Additions
Local Ecosystem Autotroph Biomass Relative to Control
Control +R +S +R,+S
d_R=0
E1 E2 E3 E4 E5
Local Ecosystem
D Metaecosystem Connectivity
E3 E4 E2 E1 E5

Figure 4.5

Appendix A: Equilibria, Local Stability Conditions and Diffusion-Induced Instabilities

In this section, we present the various equilibria that are present in equation (4.4) when there is no movement between ecosystems, determine their local stability conditions and examine how diffusion-induced instabilities can occur for the two nutrients-autotroph-herbivore equilibria in a local ecosystem. The first equilibrium of note is the two nutrients-no autotrophs-no herbivore equilibrium, which we label E_0. The equilibrium values for R, S, X and Y at E_0 are:

$$E_0 = E_0(R^0, S^0, X^0, Y^0) = \left(\frac{I}{E}, \frac{\Phi}{\Delta}, 0, 0\right) \tag{A1}$$

Because of the use of the minimum function in the autotroph nutrient uptake functions, there exists two equilibria that have only the two nutrients and the autotrophs in the ecosystems at equilibrium, E_{1R} and E_{1S}. The equilibrium with the autotrophs limited by R, E_{1R}, has the following values for R, S, X and Y:

$$\begin{aligned} E_{1R}(R^{1R}, S^{1R}, X^{1R}, Y^{1R}) \quad = \quad & \left(\frac{q_R M K_R}{V_R - q_R M}, \frac{\Phi - q_S(\epsilon_S - 1)MX^{1R}}{\Delta},\right. \\ & \left.\frac{I - ER^{1R}}{q_R(1-\epsilon_R)M}, 0\right) \end{aligned} \tag{A2}$$

Equilibrium E_{1S} is similar to E_{1R}:

$$E_{1S}(R^{1S}, S^{1S}, X^{1S}, Y^{1S}) = \left(\frac{I - q_R(\epsilon_R - 1)MX^{1S}}{E}, \frac{q_S M K_S}{V_S - q_S M}, \frac{\Phi - \Delta S^{1S}}{q_S(1-\epsilon_S)M}, 0\right) \tag{A3}$$

As with the case of only having the autotrophs as the only biotic compartment present in the local ecosystem, there are two equilibria that exist when there are two nutrients, autotrophs and herbivores all present in the local ecosystem. We define E_{2R} to be the equilibrium of the local ecosystem when herbivores are present and the autotrophs are R limited, while E_{2S} represents the case when autotrophs are S limited at equilibrium. However, for both equilibria, the equilibrium value of autotroph biomass is the same:

$$X^* = X^{2R} = X^{2S} = \frac{\beta L}{\gamma\alpha - L} \tag{A4}$$

For E_{2R}, the rest of the equilibrium values are:

$$\begin{aligned}
R^{2R} &= \frac{B + \sqrt{B^2 + 4Eq_R C}}{2Eq_R} \\
B &= Iq_R - Eq_R K_R - (1-\epsilon_R)q_R^2 MX^* + (\bar{\gamma} + \gamma\chi_R\rho_R - q_R)(V_R X^* - MX^* q_R) \\
C &= K_R(Iq_R - (1-\epsilon_R)q_R^2 MX^* - MX^* q_R(\bar{\gamma} + \gamma\chi_R\rho_R - q_R) \\
Y^{2R} &= \frac{\gamma}{L}\left(\frac{V_R R^{2R} X^*}{q_R(K_R + R^{2R})} - MX^*\right) \\
S^{2R} &= \frac{\Phi - q_S \frac{V_R R^{2R} X^*}{q_R(K_R + R^{2R})} + \epsilon_S q_{XS} MX^* + \chi_S\rho_S LY^{2R}}{\Delta}
\end{aligned} \tag{A5}$$

For E_{2S}, the rest of the equilibrium values are:

$$\begin{aligned}
S^{2S} &= \frac{B + \sqrt{B^2 + 4\Delta q_S C}}{2\Delta q_S} \\
B &= \Phi q_S - \Delta q_S K_S - (1-\epsilon_S)q_S^2 MX^* + (\gamma\chi_S\rho_S - q_S)(V_S X^* - MX^* q_S) \\
C &= K_S(\Phi q_S - (1-\epsilon_S)q_S^2 MX^* - MX^* q_S(\gamma\chi_S\rho_S - q_S) \\
Y^{2S} &= \frac{\gamma}{L}\left(\frac{V_S S^{2S} X^*}{q_S(K_S + S^{2S})} - MX^*\right) \\
R^{2S} &= \frac{I - q_R \frac{V_S S^{2S} X^*}{q_S(K_S + R^{2S})} + \epsilon_R q_{XR} MX^* + \chi_R\rho_R LY^{2S} + \bar{\gamma} H(X^*) Y^{2S}}{E}
\end{aligned} \tag{A6}$$

To evaluate the local stability of the above equilibria, we have to compute the Jacobian matrix for the system of equations (4.4) that define the model. The general Jacobian, without specifying which nutrient is limiting autotrophs at equilibrium, is:

$$\mathbf{J} = \begin{pmatrix} j_{11} & j_{12} & j_{13} & j_{14} \\ j_{21} & j_{22} & j_{23} & j_{24} \\ j_{31} & j_{32} & j_{33} & j_{34} \\ 0 & 0 & j_{43} & j_{44} \end{pmatrix} \tag{A7}$$

$$= \begin{pmatrix} -E-q_R U_R X & -q_R U_S X & -q_R U(R,S)+\epsilon_R q_R M+\bar{\gamma} H_X Y & \chi_R \rho_R L+\bar{\gamma} H(X) \\ -q_S U_R X & -\Delta-q_S U_S X & -q_S U(R,S)+\epsilon_S q_S M & \chi_S \rho_S L \\ U_R X & U_S X & U(R,S)-M-H_X Y & -H(X) \\ 0 & 0 & \gamma H_X Y & \gamma H(X)-L \end{pmatrix}$$

Where $U_R = \frac{\partial U(R,S)}{\partial R}$, $U_S = \frac{\partial U(R,S)}{\partial S}$ and $H_X = \frac{\partial H(X)}{\partial X}$. Because of the minimum function present in $U(R,S)$, only one of U_R and U_S will be non-zero at any equilibrium. For example, if we assume that U_R is non-limiting at equilibrium, which is the case for the control nutrient levels in the main text, we have the following Jacobian matrix:

$$\mathbf{J_S} = \begin{pmatrix} -E & -q_R U_S X & \frac{-q_R}{q_S} u(S)+\epsilon_R q_R M+\bar{\gamma} H_X Y & \chi_R \rho_R L+\bar{\gamma} H \\ 0 & -\Delta - q_S U_S X & -u(S)+\epsilon_S q_S M & \chi_S \rho_S L \\ 0 & U_S X & \frac{u(S)}{q_S} - M - H_X Y & -H \\ 0 & 0 & \gamma H_X Y & \gamma H - L \end{pmatrix} \tag{A8}$$

Where H is $H(X)$. The lack of other entries along the first column of $\mathbf{J_S}$ results in $-E$ to always be one of the eigenvalues of the Jacobian matrix, and since it is negative, it has no impact on the local stability of any of the equilibria. Hence, the first column and first row of $\mathbf{J_S}$ can be removed, giving the following reduced 3 x 3

Jacobian matrix to evaluate local stability:

$$\mathbf{J}_{\mathbf{No\ R}} = \begin{pmatrix} -\Delta - q_S U_S X & -u(S) + \epsilon_S q_S M & \chi_S \rho_S L \\ U_S X & \frac{u(S)}{q_S} - M - H_X Y & -H(X) \\ 0 & \gamma H_X Y & \gamma H(X) - L \end{pmatrix} \tag{A9}$$

From $\mathbf{J}_{\mathbf{No\ R}}$, we can derive the local stability of any equilibrium where the autotrophs are S-limited. For E_0 with S-limitation, it is stable if and only if $u(S^0) < q_S M$, which means that autotrophs do not uptake sufficient nutrient S to maintain positive biomass in face of continual biomass losses. If the condition does not hold, then E_{1S} exists and E_{1S} will be stable if and only if $\gamma H(X^{1S}) < L$, which means herbivores do not consume sufficient autotroph biomass to maintain positive biomass with continual herbivore biomass losses occurring. If the previous condition does not hold, then E_{2S} exists. Similar conditions hold for E_{1R} and E_{2R}.

The local stability of E_{2S} is lost through local processes due to a Hopf bifurcation (the other losses of stability involve lack of existence of E_{2S}) if if the following inequality is violated:

$$-(j_{22} + j_{33})(-j_{43}j_{34} + j_{22}j_{33} - j_{23}j_{32}) - j_{22}j_{34}j_{43} + j_{24}j_{32}j_{43} > 0 \tag{A10}$$

The Hopf bifurcation is possible because j_{33} is positive due to the saturation of the herbivore's uptake. Under certain parameter combinations, such as very high Φ values, j_{33} is sufficiently positive to violate the above inequality and oscillations will occur in the local ecosystem.

Adding the movement of nutrients and organisms to create the metaecosystem leads to some changes in the stability conditions of the spatially homogeneous equilibrium E_{2S} (or E_{2R}). Instead of having a single set of eigenvalues associated with the Jacobian matrix $\mathbf{J}$, we have n sets of eigenvalues associated with matrices $\mathbf{V(i)}$ (Marleau, Guichard, & Loreau, 2014). The matrices $\mathbf{V(i)}$ are composed of the Jacobian matrix $\mathbf{J}$ plus the movement matrix, which has d_R, d_S, d_X and d_Y on the diagonals and zeros everywhere else, which is multiplied by one of the eigenvalues of the connectivity matrix, which is composed of the elements c_{ij} (Marleau, Guichard, & Loreau, 2014).

Since the movement matrix is a diagonal matrix, it does not add any elements to the off-diagonal elements in $\mathbf{J_S}$, such that $\mathbf{V_i}$ matrices evaluated at E_{2S} can be reduced to 3 x 3 matrices. Because of this, the derivation of critical movement rates is identical to Marleau et al. (in review) and we will only restate the critical herbivore movement rate needed for spatially heterogeneous equilibria to occur if E_{2S} is stable without movement:

$$d_Y^c(\lambda_i) = \frac{-\mathbf{det}(\mathbf{J_{No\ R}}) + j_{34}j_{43}\lambda_i d_S}{\lambda_i((j_{22} + \lambda_i d_S)(j_{33} + \lambda_i d_X) - j_{23}j_{32})} \tag{A11}$$

The key thing to note from the above equation is that d_S must be large and d_X must not be too large, otherwise all the d_Y^c values will be negative and destabilization of the spatially homogeneous equilibrium cannot occur (Marleau, Guichard, & Loreau, 2014).

Appendix B: Increasing d_R to even higher levels

In this section, we show the effect of increasing d_R from 6 to 9 for the same parameter ranges in Figure 4. As can be seen in Figure B1A, the colimited growth response at the metaecosystem scale eventually gives way to a serially-limited growth response, *sensu* Harpole et al. (2011), with nutrient S being 'primarily' limiting. Within the local ecosystems when $d_R = 9$, we can see a variety of growth responses to R additions, with some ecosystems showing opposite responses to S addition and $R + S$ addition (Figure B1B).

Table and Figure Captions

Figure B1 : The effects of changing nutrient R's movement rate (d_R) on the local ecosystem and metaecosystem responses to nutrient additions at high d_R. *A* At the metaecosystem level, the colimited growth response does not increase as d_R increases, but the metaecosystem does show a S-limited growth response at the highest d_R values. *D* The growth responses of autotrophs to the addition of both nutrients in local ecosystems at the highest d_R, $d_R = 9$ show only one ecosystem showing an impressive colimited growth response, while the other ecosystems see their autotroph biomass collapse. Furthermore, two ecosystems show positive responses to S additions, while three ecosystems collapse with S additions.

Tables and Figures

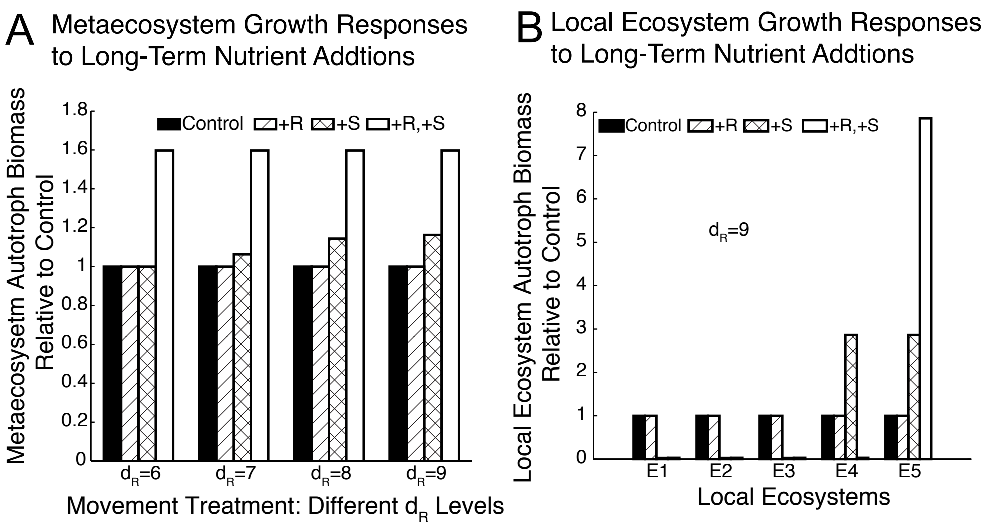

A
Metaecosystem Growth Responses to Long-Term Nutrient Addtions
Control
+R
+S
+R,+S
Metaecosysetm Autotroph Biomass Relative to Control
1.8
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
d_R=6
d_R=7
d_R=8
d_R=9
Movement Treatment: Different d_R Levels
B
Local Ecosystem Growth Responses to Long-Term Nutrient Addtions
Control
+R
+S
+R,+S
d_R=9
Local Ecosystem Autotroph Biomass Relative to Control
8
7
6
5
4
3
2
1
0
E1
E2
E3
E4
E5
Local Ecosystems

Figure B1

Chapter 5
GENERAL CONCLUSIONS

In the eyes of many ecologists, only by integrating our 'paradigms' of population/community ecology with ecosystem ecology can we possibly solve the dire problems facing humanity in the 21st century (Pickett, Kolasa, & Jones, 2007; Loreau, 2010b; Loreau, 2010a; Scheiner & Willig, 2011). For example, the theory of biodiversity and ecosystem functioning has shown how much can be gained by realizing the commonalities between the research traditions, rather than what drives them apart (Loreau, Naeem, & Inchausti, 2002; Naeem, Bunker, Hector, Loreau, & C. 2009; Loreau, 2010b; Loreau, 2010a). However, some philosophers of ecology and ecologists are not convinced and argue that synthesis and integration between research traditions are not possible (Cooper, 2003; Reiners & Lockwood, 2009). I side with the ecologists who want to build closer links and unify ecology, but I do agree that we must show what can be gained through integration, synthesis and potentially unification, as some losses are likely to occur in any such project (Kuhn, 1970; Laudan, 1977; Feyerabend, 1993).

This is why I have worked these past seven years within ecological frameworks and theories that have promised to bring together the disparate fields of ecology under the same roof (Marleau, Guichard, Mallard, & Loreau, 2010; Marleau, Jin, Bishop, Fagan, & Lewis, 2011). The promise of ecological stoichiometry and metaecosystem theory lie in their ability to span across levels of biological organization as well as spatial and temporal scales (Sterner & Elser, 2002; Loreau, Mouquet, & Holt, 2003). By having such a large range of applicability, they offer us the opportunity to solve more ecological problems than ever before, but we must put in the work to make sure we do not create conceptual problems during their implementations.

In this thesis, I have tried to demonstrate how such implementations can be done and how we can use these theories and frameworks to answer problems that bedevil us. In Chapter 1, I used the philosophical framework of research traditions and the problem solving motive for science as a way to understand what succeeded and what failed within the research tradition of ecosystem ecology, which came about from the ecosystem concept originally proposed by Tansley. One of the great successes of ecosystem ecology during its apogee was its ability to derive a great number of predictions from a fairly unified view of ecology, where energy fluxes controlled all important ecosystem processes. One of its greatest failings was its inability to accommodate any sort of heterogeneity in organisms, in dynamics and in space, which left it vulnerable to many critiques as its predictions failed to be validated by those within the research tradition. The successful theories that have emerged from its fall as the dominant research tradition have made such heterogeneity an essential part of their assumptions (Turner, 1989; Sterner & Elser, 2002; Loreau, Mouquet, & Holt, 2003).

For ecological stoichiometry, the heterogeneity lies in the relative imbalances of chemical substances in the soil relative to autotroph demand, and in the autotroph relative to herbivore demand and so on up the trophic levels (Sterner & Elser, 2002). One of the consequences of these imbalances is nutrient limitation of growth, which can occur at any trophic level, but is especially observed in plants (Urabe & Sterner, 1996; Vitousek, 2004; Cherif & Loreau, 2007). However, more and more studies have demonstrated that multiple nutrients can be limiting growth at the same time, which requires an explanation (Arrigo, 2005; Saito, Goepfert, & Ritt, 2008; Craine, 2009; Harpole et al., 2011).

In Chapter 2, I developed a stoichiometric model that was parameterized by data from a colimited plant community on Mount St. Helens to clarify the differences between the mechanisms of nutrient colimitation and the phenomena of nutrient colimitation, which are usually presented as colimited growth responses to nutrient addition experiments (Harpole et al., 2011). I also investigated whether the colimitation mechanism used affected ecosystem dynamics and functioning compared to other mechanisms when the autotrophs experienced stoichiometrically imbalanced herbivory. My results clearly demonstrate that inferences to colimitation mechanisms could not be drawn from colimited growth responses, and the mechanism of colimitation could completely alter expectations about ecosystem dynamics and primary production. The second result also upends certain expectations from the literature on increases in primary production with increasing nutrient enrichment (Loreau, 2010b).

However, the above model was not able to reproduce a colimited growth response of autotrophs while herbivores were present for the parameter ranges investigated in Chapter 2, which does not match well with the empirical literature on growth responses to nutrient additions (Gruner et al., 2008; Harpole et al., 2011). This result is caused by strong top-down control exerted by the herbivores in the local ecosystem. Therefore, another mechanism would be needed to generate colimited growth responses. One possibility is heterogeneous spatial fluxes entering by specific points into the local ecosystem, which has been shown to alter nutrient limitation statuses of autotroph communities (Hagerthey & Kerfoot, 2005). Metaecosystem theory is capable of handling spatial fluxes, but needed to be extended to include spatial structure, which I did in Chapter 3 by developing a spatially structured metaecosystem model.

In Chapter 3, I demonstrate that the spatial structure of the metaecosystem helps determine the local ecosystem dynamics found after spatial perturbations. Furthermore, the effect of spatial structure is modulated by the movement rates of the ecosystem components, especially that of the autotrophs. I also discovered that in a number of cases, the relative magnitudes and spatial synchrony of the ecosystem dynamics could be predicted from the eigenvalue of the connectivity matrix associated with the movement rate necessary to destabilize the spatially homogeneous solution. To highlight the importance of these eigenvalues, I coined the term 'scale of spatial interaction', for the eigenvalues represent the spatial scale at which the destabilization occurred. Only because of the finite spatial scale used in the model did I discover these properties, which helps reinforce the importance of finite space in modelling (Durrett & Levin, 1994).

With the results of Chapter 2 and 3 in tow, I finally addressed whether or not spatial fluxes of nutrients and organisms could act as a mechanism for colimitation. I did so with a spatially structured, stoichiometric ecosystem model with top-down control of autotroph growth at the spatially homogeneous equilibrium and no local mechanisms of nutrient colimitation. The answer is a resounding yes. Colimited growth responses could be found at both local and regional scales, and spatially heterogeneity in nutrient limitation for local autotroph communities also occurred. Furthermore, the mechanism of spatial fluxes could explain many of the patterns seen in the empirical literature of nutrient additions (Gruner et al., 2008; Harpole et al., 2011). In addition, these results should give pause to ecologists who were planning on adding local mechanisms of colimitation to their models because of colimited growth responses, as the mechanism need not be local in nature.

The overall result of the thesis is that the integration of ecological stoichiometry with metaecosystem theory did lead to more problem solving ability in this case than with just ecological stoichiometry.

Where do we go from here?

Integrating biodiversity

The major limitation of this thesis is the lack of biodiversity at any of the trophic levels. We know that species within trophic levels can differ in their stoichiometry, their consumption rates of food/nutrients, their movement rates and a number of other characteristics (e.g. Sterner & Elser, 2002; Grover, 2003; McCann, Rasmussen, & Umbanhowar, 2005). We also know that these traits likely lead to many of the complementarity effects that lead to increases in ecosystem functioning with increasing biodiversity (Loreau, Naeem, & Inchausti, 2002; Naeem et al., 2009; Loreau, 2010b). Of course, implementing full food webs within the modelling framework shown in this paper is not possible if any sort of tractability is desired.

I suggest that future work be focused on developing tactical models which slightly extend certain aspects of the model found in Chapter 4. The first such tactical change should be the addition of a second autotroph. Exploring how the movement rates of the two autotroph species and the other trophic levels could be used to promote coexistence at when competitive exclusion is expected would be a worthwhile investigation. A similar analysis could also be performed with two herbivores with one autotroph, once again to examine coexistence mediated through spatial processes. Both of these models would be somewhat complex, but the bifurcation points are still tractable and insights from the connectivity matrix would still be applicable.

However, the analysis should move beyond just species coexistence and contribute to the growing field of biodiversity and ecosystem functioning (Loreau, Naeem, & Inchausti, 2002; Naeem et al., 2009; Loreau, 2010b). The effects of increasing biodiversity in the presence of multiple trophic levels on ecosystem functioning is unclear (Loreau, 2010b). Adding relevant spatial structure and movement rates may aid ecologists in understanding how biodiversity affects the whole food web, not just the autotrophs.

Once again, tactical models could be developed as extensions of Chapter 4. For example, the addition of multiple autotrophs with differing stoichiometries could be used to investigate the potential complementarity in productivity between the autotroph species despite certain similarities in other physiological parameters. Furthermore, the movement rates of the autotrophs may lead to complementarity effects to emerge at the metaecosystem level, while such effects may be absent locally, just as in the case with nutrient colimitation.

Bringing theory to the field

While I did use empirical data to parameterize my model in Chapter 2 and considered empirical implications of my theoretical work in all the research chapters, there are still questions about how to implement field and experimental studies to test the results of this thesis. Furthermore, how the theoretical results can influence the management of ecological systems needs to be emphasized.

For all the research chapters, I would suggest experimental studies to test the theoretical predictions be done with algae, their herbivores and potentially higher trophic levels, as such experimental systems have already been successfully used before in dispersal studies (e.g. Vasseur & Fox, 2009) and in ecological stoichiometric studies (e.g. Urabe & Sterner, 1996; Trommer, Pondaven, Siccha, & Stibor, 2012). In addition, the nutrient colimitation mechanisms of algae have been well-documented in the literature (e.g. Saito et al., 2008), which should allow for simple experimental set-ups compared to terrestrial systems were the nutrient colimitation mechanisms are poorly understood. Also, controlling the spatial fluxes of the different organisms and nutrients as well as the spatial structure of the 'ecosystems' may be easier in aquatic mediums than terrestrial mediums.

For field studies wishing to elucidate whether or not the spatial mechanisms for spatial pattern formation, ecosystem functioning or nutrient colimitation proposed in this thesis are occurring, researchers will need to focus on the fluxes of biomass, not just the movement rates. For example, even if organisms may move very rapidly between ecosystems, the fluxes of the biomass relative to the stocks may be small. In such a case, the mechanisms invoked here would not be operational as substantial fluxes of biomass or materials such as nutrients are required for changes in local ecosystem and metaecosystem processes. In addition, the effect of the mechanisms should cease if the spatial links between ecosystems are broken, such that installing barriers between 'ecosystems' or study plots may provide clues about their presence.

The implications of my theoretical results for the management of ecological systems are generally focused towards landscape management and nutrient loading in the environment. The additions of nutrients to agricultural ecosystems can alter nutrient availability for generations (MacDonald & Bennett, 2009). The excess nutrients which the local ecosystems cannot absorb through productivity can then leach into neighbouring ecosystems, leading to long-term spatial patterning of communities across the metaecosystem and alterations in nutrient limitation (Albert et al., 2010). My theoretical work help to provide a foundation for understanding how the spatial structure of a metaecosystem can lead to the spatial patterning observed and to changes in nutrient limitation status across it. In addition, the theory can also provide insights in mitigating the effects of nutrient enrichment across a metaecosystem by altering the connectivity of the metaecosystem.

For example, in Chapter 4, it was observed that reducing the linkages between ecosystems resulted in no biomass increase in autotrophs at the metaecosystem level when nutrients where added, which is desired in many aquatic ecosystems. Better understanding of the spatial processes in metaecosystems, as provided here, should help us better manage interconnected ecosystems and allow us to improve ecosystem functioning.

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