# The importance of the spatial configuration of the landscape in terrestrial nutrient cycling: A theoretical model treatment

# La importancia de la configuración especial del paisaje en los ciclos de nutrientes terrestres: Un acercamiento de modelación teórico

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Por

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Director de Tesis:

Prof. Víctor H. Marín

# FACULTAD DE CIENCIAS

# UNIVERSIDAD DE CHILE

# INFORME DE APROBACION

# TESIS DE DOCTORADO

Se informa a la Escuela de Postgrado de la Facultad de Ciencias que la Tesis de Doctorado presentada por el candidato.

**Matthew Morris Yarrow**

Ha sido aprobada por la comisión de Evaluación de la tesis como requisito para optar al grado de Doctor en Ciencias con mención en Ecología y Biología Evolutiva, en el examen de Defensa Privada de Tesis rendido el día 29 de enero del 2010.

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## Matthew M Yarrow

He encontrado una falta de integración en el área de sobreposicion entre la ecología de los ecosistemas y la ecología del paisaje. Esta zona de sobreposicion puede facilitar una mejor comprensión del movimiento y transformacion de los nutrientes en los paisajes terrestres. Mi investigación doctoral se basa en un enfoque teórico que puede generar hipótesis verificables en terreno. En el futuro, me gustaría seguir explorando los aspectos espaciales de los ciclos de nutrientes. Además, quiero trabajar hacia una ciencia integrada que puede entregar herramientas útiles para los planificadores y tomadores de decisiones.

I have found a lack of integration in the area of overlap between ecosystem ecology and landscape ecology. At the same time, this area of overlap can provide a better understanding of how nutrients move and cycle in terrestrial landscapes. My doctoral research is based on a theoretical approach that can generate field-testable hypotheses. Moving forward, I would like to continue exploring the spatial aspects of nutrient cycles. In addition, I want to work to an integrated science that can provide useful tools to planners and decision-makers.

**Revistas Academicas**

Yarrow M, Marin V et al. (2009) The ecology of *Egeria densa* Planchon (Liliopsida: Alismatales): A wetland ecosystem engineer? Revista Chilena de Historia Natural.

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**Capitulos en Libros**

Yarrow M. M., Torres M.A. (2008) The ecological and cultural landscape of the Aysén River basin. En: Neves R, Baretta J and Mateus M (eds). Perspectives on Integrated Coastal Zone Management in South America, IST Press, Lisbon, Portugal (ISBN:978-972-8469-74-0).

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**Presentaciones en Congresos**

Chambel-Leitão P, Yarrow M (2007) Simulating *Nothofagus* forests in the Chilean Patagonia: a test and analysis of tree growth and nutrient cycling in SWAT. 4th International SWAT Conference, Delphi, the Netherlands.

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# Resumen de la Tesis en Español

En la actualidad, varias disciplinas de las ciencias ecológicas y físicas incluyen ciclos de nutrientes como un área clave de investigación. Esto ha llevado a una situación en que los distintos enfoques, basados en divergentes constructos teóricos, han sido aplicados estudiar el mismo conjunto de fenómenos. En la segunda edición del libro Ecological Understanding, Pickett y colegas (2007) afirman que la teoría es "quizás la herramienta más importante para la integración de la ecología." En este contexto, es esencial tomar medidas deliberadas para promover la integración de los conceptos teóricos actualmente empleados en el estudio de los ciclos de nutrientes. Esta tesis contiene tres capítulos – cada uno organizado como un artículo científico – que se enfocan en la integración teórica y el estudio de los aspectos espaciales de los ciclos de nutrientes. En el cuarto capítulo se presenta una discusión de estos temas basada en los resultados de un modelo hecho para esta tesis.

El capítulo uno propone que se cree una teoria 'puente' que una los pertinentes constructos teóricos de diferentes subdisciplinas relacionadas con los ciclos de nutrientes y por lo tanto promover la integración y el entendimiento. El dominio de esta nueva teoría ha sido definida de una manera que intenta limitar los fenómenos esenciales de interés, pero permite el uso de numerosos niveles de organización y escalas espacio-temporales. Conceptos y constructos teóricos de diversas subdisciplinas de la ecología se describen brevemente como relevantes y potencialmente útiles en la teoría 'puente'. Las preguntas fundamentales descritas en

este capítulo puedan ayudar a perfeccionar esta teoría en desarrollo, dando informacion sobre cuales componentes teóricos se pueden agregar o quitar. Cabe señalar que las subdisciplinas pertinentes se intersectan fuertemente en torno al concepto de cuencas, por lo tanto este concepto puede ser un punto de partida en el desarrollo teórico. Un proximo paso seria un marco que vincule los conceptos teóricos relacionados con los fenómenos de interés. Una vez que este marco comienze a tomar forma, la creación de modelos específicos para el dominio de la teoría "puente" será más sencillo y fructífero.

Después de revisar algunos modelos que han contribuido al desarrollo teoríco, el capítulo dos describe los conceptos y las ecuaciones detrás de LaNuM (Landscape Nutrient Model), un modelo simple que simula el comportamiento de los ciclos de nutrientes en los paisajes terrestres. LaNuM fue concebido como una herramienta que se utilizará en el desarrollo de la teoría en el espacio de intersección entre la ecología del paisaje, la ecología del ecosistemas y la biogeoquímica. LaNuM fue desarrollado utilizando un enfoque de modelación teórico que tiene como objetivo 1) el uso de modelos simples para generar y revisar las hipótesis y 2) examinar las consecuencias de la hipótesis sobre la estructura del modelo, la complejidad, y sus fundamentos conceptuales. En LaNuM se han incorporado de manera simple los ciclos de nitrógeno y fósforo así como un "nutriente hipotético" que sirvió de modelo nulo. Se presentan los resultados de un análisis de sensibilidad y se compara con un modelo descrito por Gergel (2005).

El capítulo tres describe la configuración y los resultados de un experimento de modelacion utilizando LaNuM. Las cinco hipótesis examinadas están basadas en tres factores principales: el grado de contagio del paisaje, la configuración topográfica de los paisajes, y el grado de infiltración de agua y nutrientes a la capa subterráneo. Las hipótesis fueron las siguientes:

1. La importancia de la configuración de las fuentes y los sumideros en los paisajes alcanza un peak de entre 55-70% de fuente cubierta.

2. Un contagio mayor dará lugar a un mayor nivel de importancia de la configuración del paisaje.

3. La topografía de forma 'S' disminuirá la velocidad de los flujos cerca del fondo del paisaje, favoreciendo la formación de células de sumidero.

4. La topografía de forma 'V' alterará significativamente la matriz de correlación entre las metricas del paisaje y las cargas de nutrientes (en comparación con la topografia uniforme).

5. A medida que los flujos subterraneos aumentan, el patrón que el paisaje superficial imparte a los nutrientes subterraneos se reduce.

Resultados de las simulaciones hechas con LaNuM muestran que la hipótesis uno es verdadera, con algunas excepciones. Los peak de la varianza de las cargas de nutrientes hipotéticos se ajustan al rango en el porcentaje del paisaje cubierto por células de fuentes propuesta por Gergel (2005). Los peak de varianza para los ciclos de nitrógeno y fósforo en la mayoría de los grupos en el diseño experimental estaban dentro de este rango. La hipótesis dos resultó ser cierto para todas las formas de nutrientes. El aumento en el contagio del paisaje estimuló la aparición del peak de varianza de las cargas de N y P. Hipótesis tres también es cierta. Ocurrió la formación de las células de tipo sumidero en la zona ribereña de la topografia de forma 'S' (véase la Figura 3.14 del capítulo 3). La matriz de correlaciones entre las metricas del paisaje y de las cargas de nutrientes de la topografía de forma 'V' en comparación con la topografía uniforme cambio (Hipótesis cuatro). Sin embargo, la mayoría de los cambios en la correlación de Spearman fueron menores. La hipótesis cinco no parecía ser verdadera para los nutrientes hipotéticos subterráneos. Ninguna de las formas de P o N subterráneos presentaron curvas de varianza. Así, más simulaciones tendrían que llevarse a cabo para proporcionar una respuesta satisfactoria.

En el capítulo cuarto se resumen los capítulos anteriores y se presenta una discusión que indica cómo los resultados de las simulaciones LaNuM profundizan el conocimiento en el área descrito en el capítulo uno. Se discute la relación entre el umbral de percolación, las métricas del paisaje, y el comportamiento de las cargas de nutrientes. Se muestra cómo los resultados de LaNuM han ayudado a delimitar un espacio conceptual en el que se espera que la heterogeneidad espacial sea un factor importante para explicar los flujos de nutrientes que salen de un paisaje. Este espacio está organizado a lo largo de varias dimensiones que se identifican en la tabla siguiente. El análisis de los resultados muestra que el acercamiento hacia el punto de máxima importancia (alta varianza de cargas) de una dimensión puede estimular la aparición del peak de la varianza, incluso si la posición a lo largo de las otras dimensiones no es la óptima.

| Dimensión | La importancia de la configuración espacial es mayor cuando: |
|---|---|
| La fuerza de los procesos fuente y sumidero | Los procesos fuente y sumidero son fuertes y constantes en el tiempo |
| Porcentaje del paisaje como fuente | La cobertura de los fuentes en el paisaje es intermedio → 55% - 70% |
| El grado de contagio | El grado de contagio es alto |
| Importancia relativa de los flujos superficiales con respecto a los flujos subterráneos | La infiltración de nutrientes es limitada (flujos superficiales son mas importantes) |

En última instancia, LaNuM ha demostrado ser una buena herramienta para el desarrollo de la teoría. En el futuro podría ser modificado y utilizado para continuar la refinacion de las hipótesis y la evaluacion de la utilidad de los conceptos teóricos. Tambien se podría utilizar como una herramienta para poner a prueba los índices funcionales de la configuración del paisaje.

# Chapter 1 *AN EXAMINATION OF THE THEORETICAL DIVIDE BETWEEN ECOSYSTEM AND LANDSCAPE ECOLOGY: ELEMENTS FOR A "BRIDGE" THEORY*

## Abstract

Ecosystem and landscape ecology share a significant area of overlapping domain in terms of (1) spatial and temporal scales, (2) focus on the relation between pattern and process, (3) use of systems theory, (4) focus on fluxes of materials, energy, and information within and between systems, and (5) embrace of human activity and socioeconomics as integral part of scope. Although the domains overlap, the theory corresponding to this space is incomplete. This chapter considers a subset of the overlap between ecosystem and landscape ecology: aquatic and terrestrial nutrient cycles. A "bridge" theory that can unite relevant theoretical constructs and thus promote integration and understanding is proposed. The domain of this theoretical space is described and critical questions and concepts are identified. Additionally, some of the tools and approaches to theoretical development in this area are outlined. The phenomena broached by this "bridge" theory are especially suited to exploration through modeling and thus attention is paid to the topic of modeling and theory development. Promoting integration of theory in this area of overlap will not only satisfying ecologists' desire to fill in gaps in the ecological research agenda, but hopefully provide tools and guidance for natural resource management.

## Introduction

At the beginning of this new century, it is common to comment on the complexity of ecological systems, especially when considered as interlinked with social systems. If a given study system includes physical, chemical, biological, economic, and social components that have formed under singular historic conditions, then understanding – not to mention managing – such complexity becomes a formidable task (Pickett et al. 2001, Alberti et al. 2003, P. M Groffman et al. 2004). Under those conditions, theoretical models become important as a way to delineate a study system, suggest which processes might be important in driving and maintaining system dynamics, and to focus investigation on components or processes that can be most fruitful (Weiner 1995). However, numerous authors have criticized ecological theory as not being sufficiently predictive nor useful to management (Møller and Jennions 2002, Sagoff 2004, Groffman et al. 2006, Krebs 2006). While there may be merits in considering some issues raised by these authors, the approach here is to examine the theoretical constructs near the convergent zones in the continuing trend toward integration of ecological subdisciplines. In other words, in new interdisciplinary areas of study (e.g. ecohydrology), although theory is expected to be immature it is nevertheless critical to orient and integrate research efforts.

An example of where the overlap between subdisciplines has promising potential involves (1) ecosystem ecology, which looks at processes resulting in flows of energy, nutrients and information, (2) landscape ecology with its focus on structures and spatial configurations and (3) biogeochemistry with a focus on nutrient cycles (Figure 1.1). Ecosystem ecology is the older cousin of landscape ecology: Tansley first defined the ecosystem in 1935, Lindeman's seminal study on the trophic dynamics in Cedar Bog Lake came in 1942. Ecologists such as the Odum brothers, Gene Likens and F. Herbert Bormann explored theoretical and empirical approaches to ecosystem ecology, contributing to the maturity of the subdiscipline (Odum 1957, Odum et al. 1962, Bormann and Likens 1967). The term "landscape ecology" was first used in 1939 by German biogeographer Carl Troll (Turner 2005a). However, for the next four decades, landscape ecology spread little outside Europe and was primarily associated with land planning. As a result, it was generally not considered part of the discipline of ecology (Forman and Godron 1981, Kareiva 1994, Turner 2005a). In 1926, VI Vernadsky coined the term "biogeochemistry" to describe the subdiscipline of geochemistry that deals with the chemical components of life (Gorham 1991). Although it is a highly interdisciplinary field, biogeochemistry overlaps significantly with ecosystem ecology, notably in the study of nutrient cycling (Grimm et al. 2003, Likens 2004). In most of the following discussion, the study of nutrient cycling is considered an aspect of ecosystem ecology.

Why is this area of disciplinary overlap of interest? Nutrients can be viewed as a currency used and manipulated by both relatively "undisturbed" ecosystems and by humans in agricultural or urban systems (Vitousek et al. 1997a). That nitrogen and phosphorus can greatly affect water quality and food-web dynamics in fresh and salt-water aquatic systems underscores the importance of understanding nutrient cycles not as a-dimensional "black boxes", but as a series of flows and processes occurring throughout a given landscape (Johnson and Gage 1997, Jones et al. 2001). This chapter attempts to synthesize existing theory where the above-mentioned ecologicalsubdisciplines overlap. Some of the tools and approaches to theoretical development in these areas are outlined. Finally, the domain of this theoretical space is described and critical questions and concepts are identified.

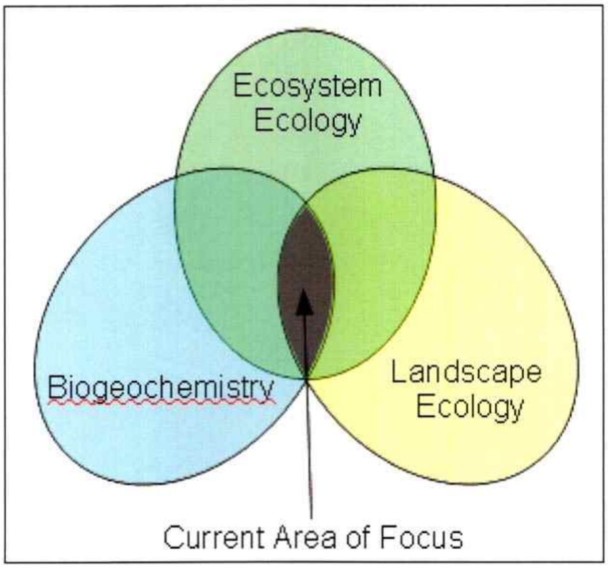

Figure 1.1: Venn diagram showing area of subdiscipline overlap addressed in this thesis. Notice that all overlap between biogeochemistry and landscape ecology occurs in the context of ecosystem ecology.

### Role of Theory and Modeling

As this chapter considers theoretical constructs in different ecological subdisciplines, it is appropriate to briefly comment on the role of theory in ecology and its relation to modeling. Theory is often thought of as a rather monolithic system of statements, laws or principles that have explanatory power and that have been confirmed by experimentation and observation (Oxford English Dictionary 1989). Some authors have required that theory be capable of making falsifiable predictions (Peters 1991). Others see theory as a tool for integration that aids in the linking of theoretical constructs and allows a "dialogue" between concepts and empirical knowledge (Pickett et al. 2007). However, many ecologists see their discipline as lacking a general or integrative theory such as those found in the physical sciences (Lawton 1999, Scheiner and Willig 2008). There have been attempts at creating a unified ecological theory or a set of general laws (Allen and Hoekstra 1993, Lawton 1999, Scheiner and Willig 2008). But perhaps ecological theory is best portrayed as fragmented with most theory coalescing within specific subdisciplines. In between these subdisciplines, there are usually gaps in understanding because (1) there has been inadequate theoretical integration and links between theoretical components in two subdisciplines are missing or (2) the domains of theory developed within subdisciplines do not overlap and thus certain phenomena lack cohesive theory (Pickett et al. 2007).

The idea that theory can be portrayed as a nested hierarchy is useful in the context of this chapter. Scheiner and Willig (2008) describe different levels on which theoretical constructs can be developed: (1) the level of general theory – where fundamental principals relating to an entire scientific disciple are enunciated; (2) the level of constituent theories – where the domain is more specific to a subdiscipline; and (3) the model level – where predictions and causal relations are most often dealt with. The notion of the ontogeny of theory is also a useful idea in examining the subject matter of this chapter (Pickett et al. 2007). The philosophy of science often examines complete or mature theories, while it is common in newer subdisciples or those treating complex middle-number systems for the associated theory to be relatively incomplete (Malanson 1999). Pickett and colleagues (2007) state that theory changes along three axis: completeness, development, and integration. An immature theory maybe missing critical components, have components that are vague and need further development, or be lacking critical connections with other theoretical constructs. If this is the case, subjecting theory to rigorous testing is not appropriate because it may lead to the dismissal of potentially useful theoretical tools (Pickett et al. 2007).

Models are an integral part of theory and the process of theoretical development. In general, models are important in formulating new questions and hypotheses, clarifying what are or are not critical features of complex natural system, exploring the dynamics of systems that are too large or difficult for a empirical experimental approach, exploring issues related to scaling and extrapolation in ecology, and setting preferences for empirical research (May 1981, With 1997, Malanson 1999, Urban 2005, Scheiner and Willig 2008). It must be noted that models are metaphorical descriptions of the material world; models can closely approximate scientific observations, but a model is always a simplification based on assumptions. Modeling efforts in ecology have been criticized on many fronts, a small sample: for being too far removed from empirical data, for being too simple, for being too complex, for being impossible to verify, for being hard to parameterize, for the issue of equifinality (Oreskes et al. 1994, Weiner 1995, Van-nes and Scheffer 2005). However, models have played a central role in the creation and refinement of theory (Caswell 1988, Pickett et al. 2007). In fact, it is by embracing the examination of model assumptions that much ecological theory can emerge. By looking at model behavior when different assumptions are made and by trying to identify those assumptions necessary to recreate certain dynamics, ecologists can use models to gain understanding (Allen et al. 2001, Ives and Agrawal 2005). Whether verbal models, conceptual models, or any in a large range of mathematical models, model building consists of a few common steps: determining system components, choosing interactions of interest between these components, specifying the mechanisms and/or drivers of these interactions, identifying missing information, specifying key assumptions, exploring model behavior, and potentially simplifying or adding to the model in order to improve model performance (Heemskerk et al. 2003, Jørgensen 2002). The area outlined in Figure 1.1, is especially suited to exploration through modeling because of the inherent spatial heterogeneity, the numerous processes contained in nutrient cycles, and the range of valid spatiotemporal scales for studying the phenomena of interest.

### Divide between ecosystem and landscape ecology

The role of space and the impact of spatial heterogeneity on ecological processes is the defining feature of landscape ecology (Turner 2005b). Although spatial heterogeneity has always been recognized by ecologists, it has historically been peripheral to ecosystem ecology and modeling (Kareiva 1994, Running and Gower 1991). Ecosystems are often delineated as homogeneous within their boundaries; typical examples are lakes, wetlands, or watersheds (Bormann and Likens 1967, Lindeman 1942). This difference in the treatment of spatial heterogeneity represents the central divide between ecosystem and landscape ecology. Other dividing lines exist, however. Especially during its early years, landscape ecologists examined either single species or species interactions to a great extent than other ecological phenomenon (Kareiva 1994, With and Crist 1995, Forman 1995). Ecosystems ecologists have often had a dismissive view of population studies given that populations of particular species are often incorporated conceptually in high level components in ecosystem models and thereby have limited importance (deLaplante

2009, Holling 1992). Below is a brief review of the theory and approaches to the study of ecology associated with these two subdiscplines.

There are several divergent theoretical and methodological pathways within ecosystem ecology (McIntosh 1985). One looks at food webs, trophic dynamics and the associated fluxes of biomass and energy within an ecosystem (Carpenter et al. 2001, Emmett Duffy et al. 2003). This area of investigation overlaps significantly with community ecology (Holling 1992). Another major area of investigation involves biogeochemical cycles. The range of scales is tremendous: from very localized nutrient sources or sinks to the global carbon cycle (Cramer et al. 2001, Harms and Grimm 2008). With the Hubbard Brook Experimental Forest, Likens and other scientists demonstrated the value of an ecosystem approach based on small watersheds (Bormann and Likens 1967, Likens 2004). Starting with an assumption that the stream associated with a watershed represents the main exit point for water and nutrients and that precipitation and nutrient deposition was readily quantifiable, Likens and Bormann used a mass balance approach to examine the impacts of different treatments on nutrient cycles. This approach has since been adapted to watershed modeling and is used globally as an effective means of integrating human and ecological systems and evaluating management strategies (Alexander et al. 2002a, Band et al. 2001, Wade et al. 2005). The use of models has allowed researchers to examine the spatial characteristics of ecosystem processes in watersheds in a way that is infeasible in empirical studies. Nevertheless, the incorporation of concepts and theory from landscape ecology has been gradual (Turner 2005b). Many models are built to consider the effects of different landuses on nutrient exports in a lumped or statistical manner, rather than explicitly examining the role of spatial patterns (Beven 1997, Caraco et al. 2003, Grizzetti et al. 2005, Neitsch et al. 2002).

A third area of ecosystem ecology focuses on behavior of complex systems. Significant theoretical development has occurred in the decades since EP Odum's (1969) seminal paper on ecosystem development. General systems theory, hierarchy theory, thermodynamics, network theory, information theory, self-organization and emergence are just some of the theoretical approaches that have been integrated into ecosystem ecology (Kay and Regier 2000, Müller 1997, Ulanowicz 2004, Marín 1997). Many of these approaches are of utility when attempting to work with complex systems that combine geophysical, ecological, and socioeconomic components (Alberti et al. 2003, Pickett et al. 2001). Ecosystem ecology has been successful in conceptually simplifying or distilling complex systems through (1) a focus on fluxes of materials and energy instead of individuals or populations, (2) a holistic focus on emergent phenomena, and (3) incorporating the idea of "constraints" that derives from hierarchy and information theory (Jørgensen and Fath 2004, Ulanowicz 2004, Yarrow and Marín 2007). However, it is worth noting that this work on complex systems has effectively transported the ecosystem concept to a new paradigm – one based on the idea that ecosystems are self-organizing open systems that can exhibit stability around local attractors, but are not inherently stable (Kay and Regier 2000, O'Neill 2001). Gone is the idea that there is a "balance of nature" where a closed-system ecosystem closely orbits a certain equilibrium point (WU and Loucks 1995). As part of this paradigm shift, ecosystems boundaries are now more frequently viewed as spatially open and the "black box" has opened to reveal internal spatial heterogeneity (O'Neill 2001). As a result, ecosystems as conceptual constructs are now better suited to being studied using approaches derived from landscape ecology.

Despite the explosion of work in landscape ecology since the early 1980's, the theory accompanying landscape ecology is uneven and some is in the initial stages of theoretical ontogeny (Pickett et al. 2007, Turner 2005a). In fact, it appears to be a common impression among landscape ecologists themselves that the subdiscipline lacks a core set of principles and theory that distinguish it from other subdisciplines (Friedman 2006). Landscape ecology is actually full of theoretical constructs, but it is an open question as to how integrated and useful they are in fostering new understanding. Theory has made little headway in predicting landscape patterns due to the many factors in pattern formation and the centrality of contingency. And theory addressing ecosystem process and their interaction with landscape pattern is in its infancy and is still considered to be a research frontier (Lovett et al. 2005, Turner 2005b).

As landscape ecology became incorporated into the discipline of ecology, many existing theoretical concepts lent themselves to this fresh spatial perspective. For example, the study of metapopulations had been initiated with a spatially implicit model by Richard Levins in 1969, but when it integrated into landscape ecology its utility and use increased (Hanski and Gilpin 1991). Issues related to scale, a perennial theme in ecology, were swiftly applied to landscape ecology (Levin 1992, Turner et al. 1989a). The theory of island biogeography also had an implicit spatial dimension that could be easily explored in the context of landscape ecology – although it was quickly realized that it is not directly applicable to patches (Forman and Godron 1981, MacArthur and Wilson 1967). However, landscape ecology did arrive with some basic conceptual models of spatial heterogeneity across landscapes – chiefly the patch/matrix model (Forman and Godron 1981). Thus, an early assumption was that spatial heterogeneity was best approached by defining discrete, crisp patches. Only recently are methods for dealing with landscape gradients being introduced to landscape ecologist (McGarigal et al. 2009).

I have argued that theoretical work on ecosystem process from the perspective of landscape ecology was limited, although this was recognized early on as a potential area of research (Forman and Godron 1981). Nevertheless, some work has been done and it is instructive to mention it here. Weins and colleagues (1985) produced a paper on boundary dynamics in landscapes that explicitly included processes and fluxes typically considered in ecosystem ecology. They formulated a conceptual model that connected boundary location with underlying landscape characteristics (e.g. edaphic), disturbance regimes, and fluxes of organisms, energy and materials. Ultimately these authors saw boundaries as a key to understanding ecosystems in a spatially-explicit way. Although it provided a foundation, this paper did not ultimately stimulate a cohesive body of theory relating to boundary systems; this is shown by several papers by Cadenasso and colleagues that purported to establish a framework for ecological boundary theory (Cadenasso et al. 2003). In general, an understanding of the lateral fluxes between ecosystems (both terrestrial and aquatic) in a landscape has remained elusive (Turner 2005b).

**Box 1: Ecohydrology: an evolving discipline.**

Ecohydrology is a new field arising principally from the discipline of hydrology and dedicated to the study of the mutual interaction between the hydrological cycle and ecosystems (Bond 2003). Given the centrality of the watershed (a landscape delineated using topography) as unit of analysis in ecohydrology and the common use of 3-D modeling within watershed hydrology, it appears that landscape ecology can play a vital role in this new discipline by supporting the coupling of ecological and hydrological models (Schröder 2006). Landscape ecology and hydrology both utilize the concept of connectivity – a functional connectedness between landscape elements that is a feature of a whole landscape, and where the scale of the landscape is determined by the movement of an organism or material flux in question (Tischendorf and Fahrig 2000, With et al. 1997). Hydrologic connectivity is the "water-mediated transfer of matter, energy and/or organisms within or between elements of the hydrologic cycle" (Pringle 2003). Different processes within nutrient cycles are often closely related to one of these concepts, e.g. the flushing of $NO_3$-N from a hillside will depend on the hydrologic connectivity between a given soil layer, the aquifer below it and the hyporheic zone of the river corridor. The degree to which connectivity will be an important factor in water and nutrient flows depends largely on the degree to which landscape and hydrologic connectivity has been severed or affected by human activities (Pringle 2003). Although the domain of ecohydrology is broader than the space delineated in Figure 1.1, the connections with biogeochemistry, landscape ecology and ecosystem ecology are notable. It is important to consider ecohydrology in this analysis of the theoretical overlap between landscape and ecosystem ecology. In order to justify a distinct "bridge theory" between these 3 ecological subdisciplines it will eventually be necessary to have enough novel theory/ questions/ and approaches to maintain separateness from ecohydrology.

## Utility of bridging divide between ecosystem and landscape ecology

Ecosystem and landscape ecology share a significant area of overlapping domain in terms of (1) spatial and temporal scales ranging from very small (e.g. biogeochemical hotspots and landscapes as they appear to insects) to very large (e.g. major river basins), (2) focus on the relation between pattern and process, (3) use of systems theory, such as hierarchy theory used to order units of study, (4) focus on fluxes of materials, energy, and information within and between systems, (5) embrace of human activity and socioeconomics as integral part of scope, (6) incorporation of abiotic components and associated fields such as geomorphology, geochemistry, and hydrology, (7) their role in land management and conservation (Crist et al. 1992, McClain et al. 2003, Alberti et al. 2003, Turner 2005b, Groffman et al. 2004). Although the domains of these subdisciplines overlap, the theory corresponding to this space is incomplete. This chapter considers a subset of the overlap between ecosystem and landscape ecology: aquatic and terrestrial nutrient cycles. Promoting integration of theory in this area of overlap will not only satisfying ecologists' desire to fill in gaps in the ecological research agenda, but hopefully provide tools and guidance to a series of management issues (Brett et al. 2005, Lovett et al. 2005).

Humans now dominate landscapes, transforming the landscape according to a variety of economic activities, transportation needs, and dwelling patterns (Vitousek et al. 1997). Biogeochemical cycles, especially the N cycle, have been heavily modified by human activities in many parts of the world (Vitousek et al. 1997a, Hooda et al. 2000, Naiman and Turner 2000). Potential feedback from human modification of nutrient cycles toward human society itself has generated many empirical studies and simulation models in the last 4 to 5 decades (Johnes 1996, Heathwaite et al. 2005). Nonetheless our understanding is limited due to the complexity of these cycles in changing environments and the numerous valid spatial and temporal scales of study. Clearly theoretical and methodological contributions to the study of nutrient cycles in landscapes can immediately contribute to applications aimed at reducing and mitigating human impact. Given the nature of the problem, approaches will have to be interdisciplinary and multi-scaled.

Ultimately, the utility of bridging the divide between ecosystem and landscape ecology by embracing the overlap in domain will be that certain weakness in each discipline will become active areas of research and innovation. In the case of ecosystem ecology, landscape ecology can provide tools and theory that can potentially contribute to: (1) dealing with difficulties in delineating an ecosystem in a landscape (once the phenomena of interest is established), (2) the incorporation of spatial heterogeneity within a given ecosystem as a way to understand the mechanisms behind certain emergent phenomena such as critical thresholds (O'Neill 2001), (3) an understanding of changes in connectivity between ecosystem components through time. One the other hand, ecosystem ecology can contribute to landscape ecology by (1) indicating which processes might be dominant in a system and therefore important to locate on a landscape, (2) suggesting theory that might help explain observed self-organization and pattern formation, and (3) providing indices of ecosystem development, information, and cycling, that could be generated across space thereby allowing direct comparison between metrics based on structure and those characterizing process in the same system or context.

### Tools and strategies of bridging the divide

This section focuses on existing tools and strategies that through a change of focus or the incorporation of new patterns and processes can help in the development of theory in the area of overlap between the subdisciplines.

### Landscape metrics and spatial statistics

Whereas ecosystem ecology has several indices that distill ecosystem processes or indicate emergent phenomena (Jørgensen et al. 2000, Ulanowicz 2004, Odum 1988), landscape ecology has hundreds of landscape metrics that purport to measure an important facet of landscape pattern (Hargis et al. 1998, Riitters et al. 1995, Mander et al. 2005). Landscape metrics have drawn on percolation theory, information theory, and fractal geometry (Li 2000, Metzger and Décamps 1997, O'Neill et al. 1988) FRAGSTATS, an academic computer program, has become the primary repository of landscape metrics (McGarigal and Marks 1995). Most metrics associated with FRAGSTATS either measure composition or configuration of landscape patterns. The former looks at the diversity and quantity of patch types, the later refers to the placement or spatial character of patches within a landscape. These metrics can be fed into statistical model to explore the phenomenological connection between pattern and process. Metrics based on configuration of elements are theoretically sensitive to specific arrangements of patch types in a landscape. So, for example, structural connectivity depends on the spatial configuration of patches in the landscape (e.g. vicinity of barriers); the dispersal behavior of organisms changes with landscape configuration and is sensitive to the grain of the landscape (Baguette and Van Dyck 2007).

There is also a distinction to be made between structural and functional indices, with functional indices indicating the importance of a given ecosystem function (Mander et al. 2005). Functional metrics have been used to evaluate the relative condition of water resources at a regional scale (Jones et al. 2001). A recent paper, and surprisingly the only one found that applies FRAGSTATS metrics to water quality and measures of material transport, compared 7 metrics to data on BOD7, total-N and total-P from 24 watersheds. The results showed that land-cover was a better predictor of water quality, but that edge density increased with total-N export and Chemical Oxygen Demand (COD) had a negative and significant association with complex landscape structure (low Contagion and high mean shape index) (Uuemaa et al. 2007). The directional leakiness index (DLI) is a functional metric conceived of as a measure of the retention of resources such as soil and water in arid grasslands (Ludwig et al. 2002). This index considers the percent cover, number, size, shape, spatial arrangement and orientation of vegetation patches; the directionality is used only if there is a clear wind or topography gradient. Unlike most simple landscape metrics, an index like the DLI combines information about land cover in a landscape with a data about a directional driver (e.g. water and wind). The result is a measure of a directional source-sink dynamic that is based on a pre-classified raster image. Ludwig and colleagues extended their index twice; however given the unique ability of this index to calculate the relative magnitude of lateral flows in a patchy environment, it is surprising similar strategies have been rare to nil (Ludwig et al. 2007, 2006).

### Neutral Landscape Models

One way the relationship between landscape process and patterns can be tested is if the expected pattern in the absence of the process is known (Gardner et al. 1987). Neutral landscape models (NLMs) are the product of a random process in which all other physical and biological factors are excluded. NLMs have two main purposes: (1) to determine the extent to which landscape structure deviates from some theoretical spatial distribution and (2) to predict how ecological processes, such as animal movement, and nutrient transport and transformation are affected by a known spatial structure (With 1997). Gardner used percolation theory as a way to randomly generate neutral models and test the idea that a random square landscape would "percolate" – achieve complete connectivity from one side of the landscape to the other – near the critical probability pc = 0.5928 (Gardner et al. 1987). Using NLMs, With and King (2001) explored critical thresholds in simulated species' response to landscape structure. The fecundity of simulated species was differently sensitive to patch edges and patch area creating cases where the simulated landscape would become a sink or source. The results indicated that rules of thumb about the percent of habitat in a landscape required for the reproductive success of a given species should be avoided, as this number can vary widely depending on life history traits. In another study, these authors found that in a spatially-explicit community model, landscape structure (high patch aggregation and connectivity) does not determine the emergence of community structure, but organized communities are inevitable in highly structured landscapes; communities in intermediate structure tended to have the highest species richness (With and King 2004). Similar methods have been used in questions addressing ecosystem processes. A spatially explicit individual-based model approach (cellular automata) was used to explore the interaction between landscape pattern and the functioning of nitrogen fixing and non-fixing components of a simulated ecosystem (Jenerette and Wu 2004). Beginning with random landscapes, the model eventually produced self-organized spatial patterns of vegetation functional types. Because ecosystem processes (fixation and utilization of N in the landscape) was slower than community dynamics (change in plant functional type), different behavior appeared at the local vs landscape scales. Using N amendments to test for nutrient limitation, local nitrogen limitation was observed, but at broader scales the evidence of limitation disappeared due to spatial heterogeneity in the supply and utilization of nitrogen. The approach to theoretical development seen in these examples is to create simple but spatially-explicit models with clear assumptions relating to a particular theme in ecology. Clear patterns that form in either landscape structure or in the location or magnitude of a given process become hypothesis that can be tried in real world systems or linked to existing theoretical constructs as a way to integrate theory.

### Models and modeling strategies

Modeling can be considered a tool that allows for the examination of system properties (Jørgensen 2002). Because theory itself is a system of theoretical constructs, it is clear that models can play an important role in developing and testing theories. There are two fundamental categories of models for theory development. The first type – the theoretical model — is usually highly abstract and generally quite simple. Theoretical models can include static graphical representations or concept maps, to analytical models using one or more mathematical equations, to system or functional models that often lump internal components (Pickett et al. 2007). The goal is not to attempt to reproduce behavior of specific systems, rather to examine model behavior as a consequence of assumptions about model structure, equations, and complexity. In fact, the process of translating theoretical constructs into mathematical models can help translate verbal models into predictive theories (Weiner 1995). Such models aid in generating hypotheses that are strongly connected to theory. The second category includes more complex physically-based models that are often calibrated to reproduce the behavior of material systems (Rykiel, Jr. 1996). These models can be used to test hypotheses when empirical tests are infeasible or costly. The catch is that the models themselves are essentially hypothesis about the structure of complex systems and thus the problem of the 'double doubt' emerges (Jørgensen 2002).

There has been a long-running discussion about the tradeoffs between model complexity and the ability to predict or produce system behavior (Jackson et al. 2000, Jørgensen 2002). A specific example is the debate about the utility of different types of models in predicting nutrient and erosion loads at the watershed level: spatially explicit models or simple aggregated empirical models (Gergel 2005, Jetten et al. 2003). In many cases simple, spatially-aggregated models predict nitrogen loads in larger watersheds better than complex physically-based models (Caraco et al. 2003). However, it is clear that the spatial configuration of landscape elements can influence ecosystem processes (Turner 2005b). The dualistic nature of this debate (simple and phenomenological vs. complex and mechanistic) distracts us from what is often the case: combining or iterating between different types of models and empirical data can create a much greater degree of certainty in the results than one approach by itself (Scheffer and Carpenter 2003). As an example, Marín and colleagues (Marín et al. 2009) used a simple-biology model combined with experimental data and long-term climate data to explain the occurrence of a regime shift in a wetland system. In support of theory development, modeling methodologies can be combined iteratively so as to benefit from the strengths of different modeling approaches. An example can be seen in Figure 1.2.

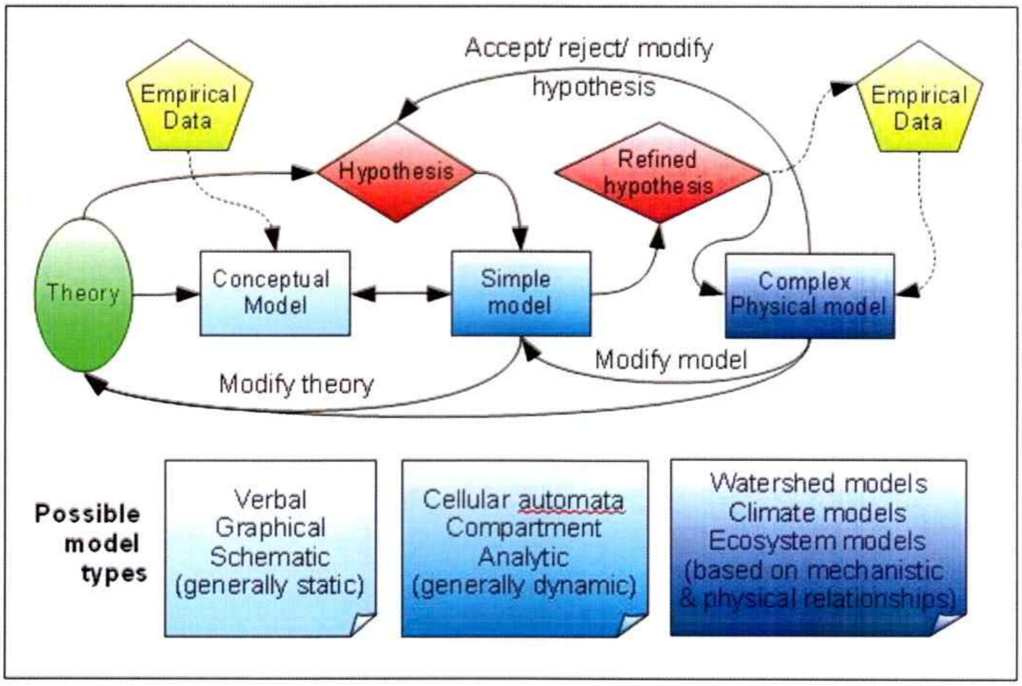

Figure 1.2: An iterative modeling methodology for the development of theory

The validation of models in ecology has gotten a lot of attention in the literature (Marín et al. 2009, Oreskes et al. 1994, Rykiel, Jr. 1996). Although Oreskes and colleagues (Oreskes et al. 1994) asserted that validation is impossible on philosophical grounds, it is still ubiquitous in ecological modeling. Certainly, the comparison of model output with empirical data is critical to lend credibility to most system-specific models (Rykiel, Jr. 1996). However, does validation play a role in highly abstract theoretical models? According to Caswell (Caswell 1988), theoretical problems have a "legitimate, objective existence in ecology". Without getting into the philosophical issues surrounding the suggestion that theory has an objective existence, Caswell's point is that theory is a legitimate subject of ecology in and of itself. In this context, it would be unreasonable to expect theoretical models to be validated with data sets from particular ecological systems. According to Rykiel (Rykiel, Jr. 1996), models that are created for working on theoretical problems including exploration, initial development of new theoretical constructs and new perspectives do not require validation. However, such models still need to be evaluated for internal mathematical consistency and undergo sensitivity analysis. Furthermore there are many tests that can be used to evaluate how they compare to existing understanding of the phenomena in question. Some examples: tests against other models, qualitative comparison of visual information from other systems (e.g. time series), occurrence of particular events during simulation, and the tracing of the behavior of internal variables to see if it corresponds to known behavior in other systems (Rykiel, Jr. 1996).

## Fundamentals of a "bridge" theory

The previous sections have described the divide between the theoretical basis of landscape and ecosystem ecology. Although several disciplines (e.g. ecohydrology, landscape ecology, biogeochemistry) have identified nutrient cycles and their spatial dynamics as a worthy areas of research, an effort to create an explicitly interdisciplinary theoretical framework will likely stimulate faster advances in understanding. An integrative theory will allow scientists in different fields to share a set of common concepts and research questions and help in the synthesis of results coming from many different methodologies.

### Defining the domain

The creation of an elaborated theoretical framework to bridge the divide between ecosystem and landscape ecology is beyond the scope of this chapter. However, I take the first steps in this direction by proposing a domain for what I will informally call the "bridge theory" that attempts facilitate theoretical integration between the subdisciplines in question. The domain of a theory outlines the scope in terms of spatiotemporal scale, phenomena of interest, and levels of organization where the phenomena are observed or controlled (Pickett et al. 2007). The following addresses each component of the theoretical domain.

Phenomena: (1) spatial patterns of nutrient concentration or mass across terrestrial and aquatic landscapes and how these patterns change with time; (2) patterns of biogeochemical processes, i.e. heterogeneity of their occurrence and rates in space and time; (3) biological, physical, chemical, hydraulic, climatic and socioeconomic and political drivers[1] of nutrient cycle dynamics.

Levels of Organization: In bridging the theory of ecosystem and landscape ecology, it follows that concepts will be integrated that were formulated at the ecosystem and landscape levels of organization. However, it is appropriate that the primary level of organization is this new bridge theory be the watershed (catchment). This is because: (1) ecosystem ecologists often use the watershed as an operational definition for the more abstract ecosystem concept (Bormann and Likens 1967); (2) the watershed is easily viewed as a landscape delineated topographically; (3) as a concept, the watershed is hydrologically connected and integrates internal processes; and (4) the watershed is multi-scalar concept (Tague 2009). In some instances, however,

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[1] The Millennium Ecosystem Assessment definition of a driver is any natural or human-induced factor that directly or indirectly causes a change in an ecosystem (Nelson et al. 2006)

addressing the phenomena in question will require the consideration of components on a variety of ecological levels of organization from specific populations (e.g. nitrogen-fixers, salmon) to the biosphere where phenomena like global warming and the C cycle are understood in their entirety (Helfield and Naiman 2001, Jenerette and Wu 2004, Vitousek et al. 1997b). A complicating factor is that different disciplines have different organizational hierarchies. In catchment hydrology, a typical organizational hierarchy would be soil block, patch, hillside, catchment, basin (Tague 2009). In political science, governmental entities can operate at different geographical levels: local, regional, national, and international. The associated laws and regulations also occur at different levels of organization, e.g., from local zoning laws to international environmental treaties (Clark et al. 2000, Nelson et al. 2006). Once the scale of the particular phenomenon of interest and the relevant drivers are selected, the levels of organization from associated disciplines can be selected.

Scales: The bridge theory described here is temporally and spatially multi-scalar. The primary level of organization is the watershed, which can vary spatially from hectares to millions of square kilometers. If the goal is to identify mechanisms, smaller spatial scales may be needed, while in other applications the constraints of global phenomena may drive the patterns and processes in question. Temporally, precipitation and biogeochemical hot moments are among the key processes that can occur on the scale of minutes to days (McClain et al. 2003). On the other end of the temporal spectrum, human land-use change and climate will influence nutrient cycles, leading to periods of time in the 10s to 100s of years. Most events occurring on geological time constrain the patterns and processes of nutrient cycles in the landscape but are not direct drivers of behavior.

### Fundamental Questions

Fundamental questions can be posed that address the foundation of this "bridge" theory. Such questions serve to refine and change a developing theory (Pickett et al. 2007). Because the "bridge" theory is in its initial stages, the most useful questions will deal with which theoretical components should be added or rejected from the theory. Questions can help in understanding which components of the theory can be borrowed or adapted from existing theory and in what cases new components will need to be created. What follows is a list of questions aimed at stimulating discussion on the domain, structure, and function of the theory.

- When is spatial heterogeneity an important factor in explaining nutrient flows in terrestrial landscapes?
- If spatial heterogeneity is important, which measures of spatial pattern are related to fluxes of different nutrient forms?
- How do patterns in nutrient distribution arise from processes?
- How does hydraulic connectivity change with scale? And how does this affect nutrient flux?
- How are nutrient cycles affected by hydrological extremes (drought and flooding)?
- What landscape characteristics are related to riparian function?

- Can understanding the functional implications of landscape composition and configuration enlighten how humans interact with landscapes?
- Can the location and timing hot spots and hot moments be predicted through modeling? What kinds of models are most effective in a given biogeographical context?
- To what extent are hot spots and hot moments associated with ecological boundaries?
- When are different models of spatial heterogeneity (patch mosaic vs. surfaces of continuously changing variables) appropriate in understanding the feedback loop with process location and rate?
- How does the spatial scale of landscape pattern identification change watershed model predictions?
- Are particular processes in nutrient cycles associated with spatial pattern at a characteristic scale?
- How can the ecosystem concept of functional groups be used in a heterogeneous landscape? Can such a concept aid in understanding biogeochemical processes in a landscape?
- Can threshold behavior in hydrology and nutrient loading be detected in different kinds of systems? How does landscape configuration impact the likelihood that threshold behavior will occur?
- Can thermodynamic theory via an examination of gradients and fluxes in a landscape illuminate how fluxes impact spatial heterogeneity?

- What is the impact of preferential hydraulic pathways (fractures, rills, and gullies) on ecological or biogeochemical processes?
- When do stream/river ecosystems play an important role in nutrient transformation/cycling? When are stream/river ecosystems essentially conduits for nutrient transport?
- What is the role of organisms in nutrient transport across landscapes? Do any general patterns emerge in terms of the impact of organisms on nutrient concentrations and export?
- What controls the location and duration of nutrient sinks in a landscape? What are potential consequences of human manipulation of nutrient sinks as a way to control nutrient exports?

### Theoretical Concepts

Given that a theory is a *system of conceptual constructs that organizes and explains phenomena*, it is important to begin identifying concepts and constructs that can be used in the "bridge" theory (Pickett et al. 2007). Many of these are inherited from other disciplines. Because of this, the basic assumptions associated with them will also be mentioned. The concepts mentioned are all complex and fairly well developed; they are often used as the sole theoretical framework for specific projects. The proposition made here is that to work in the domain of the "bridge" theory, they should all be taken into consideration as sources theoretical guidance. This will stimulate a process of integration – essentially the building of a framework to order these concepts (and others) so that links between them are clear and so they can be readily used to create models. The following list is by no means complete, but is intended to give a sense of the theoretical breadth that a coalescing "bridge" theory could draw upon.

Patch mosaics: A concept with deep roots in ecology, but now fundamentally associated with landscape ecology. The concept is that ecological systems can be viewed as a hierarchical system of patches that differ is size, shape, and community composition (WU and Loucks 1995). Assumptions include: a fairly "crisp" expression of spatial heterogeneity on various scales; the patch structure appearing at a given spatial scale will have importance for a large set of ecological phenomena; patches have high internal structural homogeneity and a set of processes that occur on that scale.

Ecological boundary: Posits the boundary as a critical component of landscapes. A boundary has structural characteristics that impact the type and rate of flow of energy, materials, organisms and information that may flow through it (Cadenasso et al. 2003, Yarrow and Marín 2007). Assumptions: like patch mosaics, assumes the landscape is made up of fairly discrete patches; boundaries are highly functional component of landscapes; delineation based on vegetation structure is valid even if studying boundary function.

Landscape gradients: This is essentially an alternative to the patch mosaic model of landscape heterogeneity. Heterogeneity is viewed as change in the intensity of each variable across the landscape. This creates a three-dimensional surface of any ecological, edaphic or geomorphologic attribute of interest (McGarigal et al. 2009).

Assumptions: gradients can often lead to a better understanding of landscape processes than the patch mosaic model, remote sensing (the main source of gradient data) captures system attributes relevant to the phenomena of interest.

Ecosystem stoichiometry: Characteristic ratios between elements determine the basic stoichiometry for different level of ecological organization (e.g. organism to biosphere). Looking at the causes and consequences of relative stoichiometric ratios in different ecosystems across a landscape can illuminate the functional connections (Schade et al. 2005). Assumptions: community-level models of resource competition are applicable to ecosystems; functional delineation of ecosystems in a landscape is repeatable in different settings; and ecosystem biomass production is always linked to stoichiometry.

Watershed concept: The watershed acts to integrate the hydrologic and nutrient cycles and is a good level of organization in which to use mass balance equations to study the impact of manipulations within the watershed on nutrient budgets (Bormann and Likens 1967). Assumptions: groundwater flows and aquifer recharge are relatively unimportant; other landscape fluxes not mediated by water are relatively unimportant.

Networks: Graph theory is a method of research for understanding the structure and emergent properties of a system that is characterized as a network, i.e. a system of nodes and links. It is compatible with a range of theoretical concepts in ecology such as resilience, connectivity, ascendancy, and flows of energy and information (Janssen et al. 2006, Jørgensen and Fath 2006, Urban and Keitt 2001). Assumptions: landscapes can be represented as fairly discrete patches, requires assumptions about the importance of attributes selected to make up network structure.

Source/Sink dynamics: An approach to the study of fluxes of organisms or materials across a landscape. Allows for a simple representation of how system functions are distributed in space and can aid in management decision. Assumptions: sources and sinks of a given entity can be clearly identified in space; a high degree of connectivity between sources and sinks underlies the observed dynamics.

## Conclusion

The focus of this chapter has been the study nutrient cycles in the landscape. Several disciplines have already started to converge on this topic and the associated set of ecological problems (which include geological, hydrological, economic, and social components). There is no overarching theory in place that has the integrative framework necessary to guide this fundamentally interdisciplinary research. Instead, many theoretical fragments of different stages of maturity have some bearing on the area of interest. This chapter proposes that a "bridge" theory can unite relevant theoretical constructs from different subdisciplines and thus promote integration and understanding. The domain of this new theory has been defined in a way that attempts to limit the essential phenomena of interest, but that allows the use of numerous levels of organization and spatiotemporal scales. In the past, the subdisciplines in ecology have been organized around these levels of organization, such that as one moves up or down the hierarchy, the theoretical framework also changes. One consequence is that although the subdisciplines often share questions, different theoretical concepts lead to approaches that do not necessarily inform each other (Pickett et al. 2007). Thus, the role of the bridge theory would be to promote common understanding of theoretical concepts and provide a framework that could readily incorporate knowledge and understanding generated by a range of approaches carried out on a range of scales. The watershed concept is a construct where the relevant subdisciplines intersect strongly and thus can be a point of departure in theoretical development. Further work should involve the development of the framework that can link the concepts mentioned above as they relate to the phenomena of interest. Once this framework begins to take shape, the creation of models specific to the domain of the "bridge" theory will be more straightforward and fruitful. At this juncture, it is impossible to state with certainty whether the "bridge" theory described here will in fact occupy a distinct space in the increasingly crowded field of interdisciplinary disciplines that draw on ecological theory. However, by considering the domain outlined above as a valid area of study that requires theoretical integration, the objective is avoid stagnation on the edges of current theoretical domains.

# Chapter 2 THE LANDSCAPE NUTRIENT MODEL (LANUM): A THEORETICAL MODEL FOR EXAMINING THE SPATIAL ASPECTS OF NUTRIENT CYCLES

## Abstract

Nutrient cycles tie together relatively "undisturbed" ecosystems and human-dominated agricultural or urban systems (Grimm et al. 2005, Hatt et al. 2004, Johnes and Heathwaite 1997). A number of disciplines (e.g. ecohydrology, landscape ecology, ecosystem ecology, and biogeochemistry) have approached different aspects of nutrient cycles leading to a somewhat fragmented literature. One area requiring a deeper understanding and theoretical framework is the study of lateral fluxes between ecosystems (both terrestrial and aquatic) in a landscape (Turner et al. 1989b, Turner 2005b). In fact, there is no comprehensive theoretical basis for understanding when spatial heterogeneity will be an important factor in nutrient transport across landscapes (Gergel 2005). Given the importance of nutrient cycling in agriculture, water quality problems, and land planning, this appears to be a serious oversight.

Discussing the structure and development of theories in ecology, Pickett et al. (Pickett et al. 2007) attest to the central role that modeling can play in theoretical development. This chapter is based on the idea that in order for abstract models to have utility in ecology, they need to be tied to important theoretical questions. A simple simulation model of landscape nutrient cycles (LaNuM), which builds on the work of Gergel

(2005), is presented in this article. The model allows users to examine several potentially important factors in the quest to understand when spatial configuration of terrestrial landscape elements affects nutrient loading to streams or rivers. A conceptual theoretical model, used to guide the construction of LaNuM, is also presented. After describing the internal structure of LaNuM, a sensitivity analysis is carried out and the model is compared to Gergel's as a way to analyze its utility as a theoretical tool. The results of simulations run in LaNuM are presented in the next chapter.

## Introduction

With the human domination of the biosphere, ecological science has been forced to address socioeconomic dynamics such as urbanization, landuse, and pollution (Vitousek et al. 1997b). Nutrient cycles tie together relatively "undisturbed" ecosystems and human-dominated agricultural or urban systems (Grimm et al. 2005, Hatt et al. 2004, Johnes and Heathwaite 1997). Despite the importance of nutrient cycles as a subject of research and the target of management practices, there is little in the theoretical realm that guides understanding of the relation between landscape structure and nutrient flows and transformations (Turner 2005b). Although models have been used extensively in examining specific study systems, they have not yet contributed significantly to the theory behind the spatial aspects of nutrient cycling. This chapter presents a tool (LaNuM) that has utility in filling this void.

Two kinds of models have dominated examinations of nutrient export from hillsides and watersheds: export coefficient models (Caraco et al. 2003, Johnes 1996), and complex watershed models (Arnold and Fohrer 2005, Krysanova et al. 1998, Alexander et al. 2002b). Although watershed models are of varying complexities and approach spatial heterogeneity in different ways (from distributed to lumped), they often used physically-based equations to simulate a variety of hydrological, meteorological, and ecological processes (Tague and Band 2001, Tague 2005). Export coefficient models are spatial implicit, i.e. they group all landuse of a given type and apply an export coefficient (Johnes 1996). In the area between these two extremes, there appears less empirical or predictive modeling, yet this is perhaps the most fertile territory for theoretical or "heuristic" models (Gergel 2005, Soranno et al. 1996, Weller et al. 1998, Jenerette and Wu 2004). An analysis of these models created a context for a simple spatially-explicit model like LaNuM.

(Soranno et al. 1996) noted that one drawback of export coefficient models is the assumption of a linear relationship between the area of distinct landuses and phosphorous (P) loading. Phosphorous loading is often dominated by P that is attached to sediment (Sharpley et al. 1994). Thus, source areas that have high connectivity to the stream network, often via overland flow, will tend to drive P loading (Gburek et al. 2000). By adding the length of the flow paths from source areas to the stream network and a transmission coefficient to account for transformation and retention of P along these flowpaths, Soranno and colleagues created a simple model that included essential spatial information. The results showed that this new P-flux model, after calibration, could provide a better fit to empirical data from agricultural watersheds in Wisconsin, than the export-coefficient model. The approach here is to condense spatial information into one variable (flow path length) that can be used in a simple model.

Other efforts have taken a more detailed approach to the study of critical nutrient source areas and the associated flow paths. (Heathwaite et al. 2005) describe the "TopManage" tool which uses detailed topographic data (1m or below) to create risk maps of surface and subsurface runoff in a particular study area. This information can then be combined with indexes that characterize the potential for nutrient export from source areas. The P-index is one such index that incorporates P inputs as fertilizer and management actions such as tillage (Sharpley 1995).

Weller et al. (1998), using a simple model of riparian buffers, examined the effects of variation in buffer width and continuity on nutrient loading. The authors note in their introduction that empirical evidence as to the effectiveness of buffer retention is mixed and often scale-dependent. The model they construct is based on a simple hillside scenario of contributing grid cells passing fluxes of water and materials (modeled together) to a riparian buffer that varies in width. The material flux (transmission) through the buffer decreases exponentially with buffer width. These authors compare constant width buffers with a Poisson width distribution over different cell transmission values. The authors conclude that the effect of buffer width variability is most important for highly retentive buffers that are narrow. With this combination of factors (narrow and retentive) great variation in the results of empirical studies would be expected unless width and gap frequency were taken into account. The authors conclude with a statement to the effect that a simple model is an appropriate tool for examining the interaction between spatial heterogeneity and ecosystem function given that it can provide basic understanding and testable hypotheses (Weller et al. 1998).

Jenerette and Wu (2004) developed a cellular automata ecosystem model to explore the interaction between landscape pattern and the functioning of nitrogen fixing and non-fixing components. Cellular automata are spatially explicit models where locally interacting entities can develop complex spatial patterns at larger scales (Wootton 2001). In the case of the model created by Jenerette and Wu, the model produced self-organized spatial patterns of vegetation functional types when initialed with simple random landscapes. During the simulations, nutrient limitation was evaluated by adding N to the landscape. Interestingly, local nitrogen limitation was observed, but at broader scales the evidence of limitation disappeared due to spatial heterogeneity in the supply and utilization of nitrogen. The appeal to this kind of modeling is that the rules and assumptions applied at the local level can be quite simple and easily understandable. Thus, it is a good way to explore how assumptions might affect system behavior at several scales.

The model created by Gergel (Gergel 2005) follows in this tradition of using simple models with some degree of spatial distribution to examine processes and patterns in the landscape. Beginning with randomly generated, 100 x 100 grid grid cells neutral landscape models (NLMs), Gergel modeled uni-directional flows of nutrients across the landscape. The binary landscape was composed of source and sink cells whose relative "strength" in terms of nutrient output vs. uptake was varied under different scenarios. Only surface fluxes of nutrients were modeled and there was no transformation processes that would alter the behavior of the nutrient as it moved across the landscape. Outputs from the landscape were collected at the bottom of the landscape (conceptually the interface with an aquatic system). Gergel compared the mean and variance in loading of the hypothetical nutrient while varying the source:sink ratio in the landscape. A peak in the variance of nutrient loading was used to indicate the importance of spatial configuration (calculated for 10,000 random landscapes with the same source:sink ratio). Two major questions were explored with this model: (1) Under what conditions might the arrangement of land cover types in a landscape be more important than the area of each type?, and (2) How does heterogeneity in source output at different scales impact the utility of landscape indicators? Gergel concluded that landscape indicators that characterize spatial configuration would be most helpful in watersheds containing an intermediate ratio of sources:sinks. As source output becomes greater than sink uptake, the peak variance shifts to a lower source:sink ratio. Gergel also presents some hypothesis that could be evaluated empirically. Because of the simplicity and clarity of this model, I use it here as a point of comparison for LaNuM. However, LaNuM incorporates more of the complexity encountered in empirical studies of nutrient cycling. Specifically, LaNuM includes nitrogen and phosphorus cycles and allows them to interact with three potentially important factors that control nutrient cycling at the landscape level: (1) different landscape patterns, especially increased contagion, (2) subsurface and surface landscape flows, and (3) more complex topography.

### Conceptual Model

Conceptual models are often employed as a way to clarify the system in question and the factors that control its behavior (Delgado et al. 2009, Heemskerk et al. 2003). Controlling factors can be located within the system as mechanisms or above the level of the system as constraints (Cadenasso et al. 2006, Wu and David 2002). Because the current modeling exercise addresses the development of theory, a first step to creating a conceptual model was to place LaNuM in a conceptual framework (Figure 2.1). Further information on the theoretical foundations of the subdisciplines included in Figure 2.1 can be found in Chapter One.

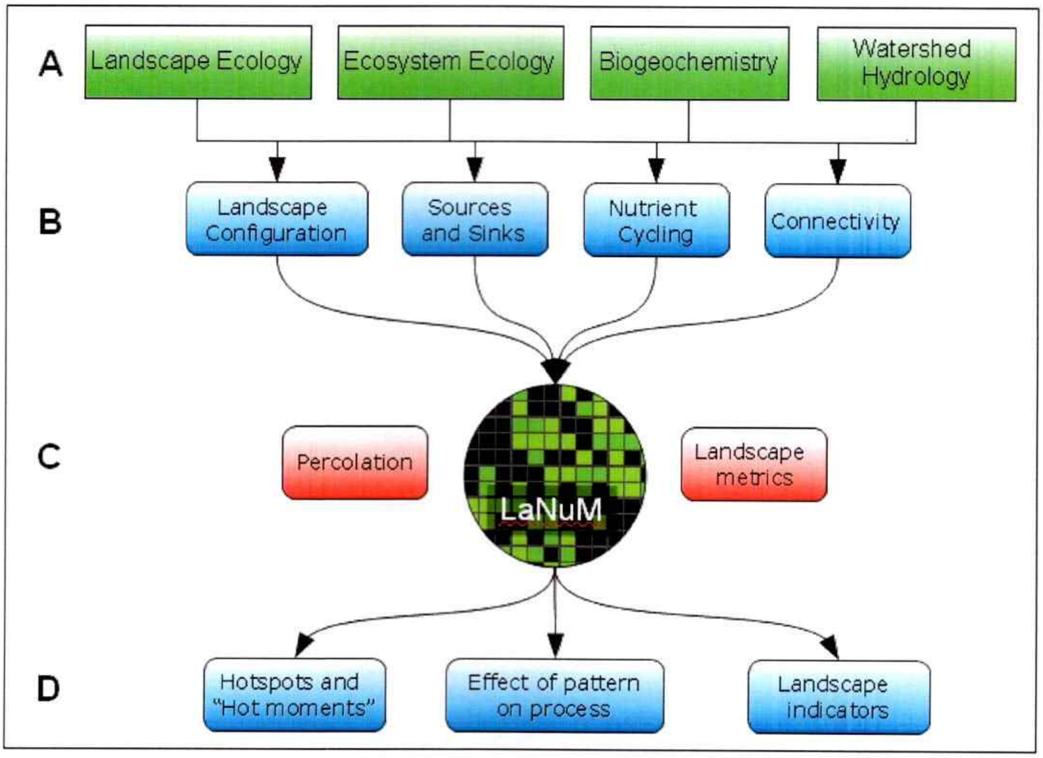


Figure 2.1: Conceptual framework of the LaNuM model. Level A: the subdisciplines from which theoretical constructs and tools are utilized; Level B: Some essential theoretical concepts that were used in model construction; Level C: the model itself shares a level with tools and concepts that can be used to understand model behavior; Level D: model results will potentially contribute to the theory behind these concepts/tools.

Once a conceptual model is constructed and arrows placed to represent flows, biological interactions or other linkages, they can be used to generate hypothesis and as a template for the creation of more complex models (Groffman et al. 2004). Figure 2.2 presents a conceptual model that shows LaNuM's focus on how source and sink dynamics can influence nutrient outputs. Important factors included in the model include (1) variability of landscape patterns (random versus fractal NLMs), (2) surface vs. subsurface flows, (3) topographic variability and its effect on landscape context, and (4) a nutrient cycles that can vary in a landscape.

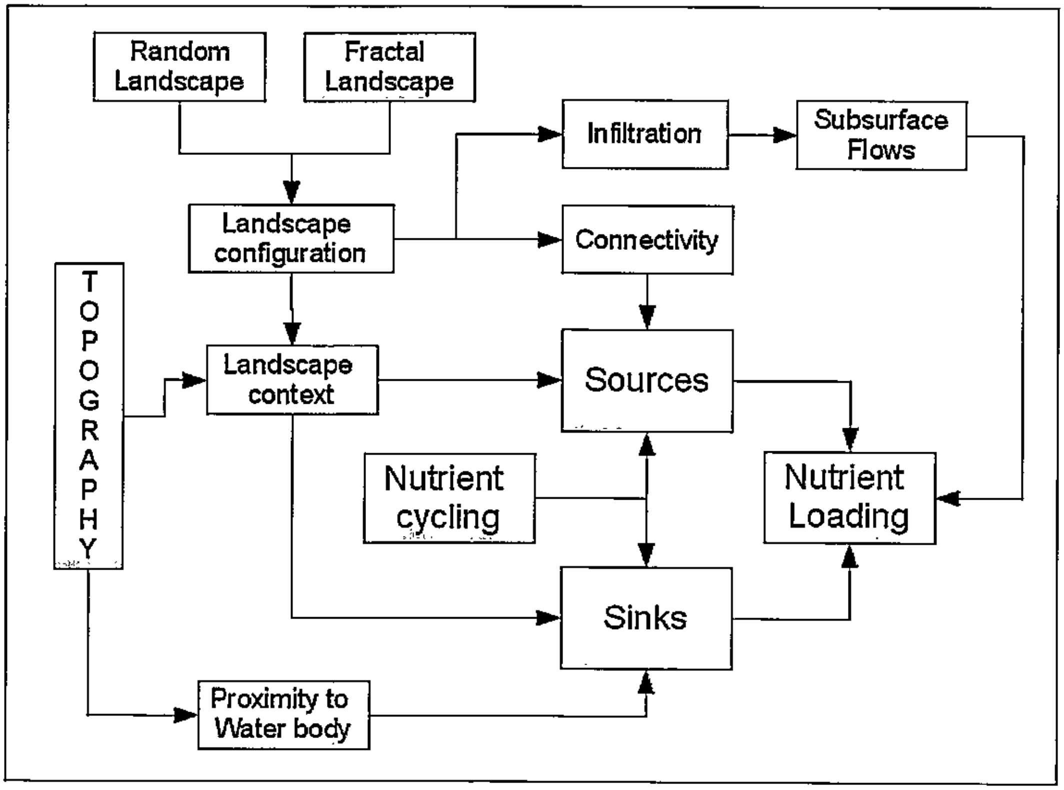


Figure 2.2: Conceptual model used to guide the building of LaNuM.

Once a conceptual model is constructed and arrows placed to represent flows, biological interactions or other linkages, they can be used to generate hypothesis and as a template for the creation of more complex models (Groffman et al. 2004). Figure 2.2 presents a conceptual model that shows LaNuM's focus on how source and sink dynamics can influence nutrient outputs. Important factors included in the model include (1) variability of landscape patterns (random versus fractal NLMs), (2) surface vs. subsurface flows, (3) topographic variability and its effect on landscape context, and (4) a nutrient cycles that can vary in a landscape. The conceptual model postulates that landscape configuration will determine the connectivity of source patches which contributes to nutrient loading. In the conceptual model, sinks are controlled by the landscape context (i.e. local patterns around the phenomena of interest), as well as by nutrient cycling. More specifically, sinks are hypothesized to have more influence on nutrient loading near the water body and in landscapes where flow paths converge before arriving at the water body. In this way, themes such as riparian function can be examined with LaNuM. The pattern in this model begins with a series of random or fractal NLMs of landcover type. Because nutrient cycles and hydrologic connectivity differ according to landcover type, patterns will emerge in nutrient and water mass in a landscape. Finally, temporal patterns in nutrient loading will likely be found. Process rates will depend on the patterns of nutrients and water. Cadenasso and colleagues (Cadenasso et al. 2006) conceptualize the biocomplexity of a system on three axes: how structural elements are arranged (heterogeneity), how system components interact (connectivity) and how they change through time (contingency). LaNuM has a high spatial heterogeneity, medium-to-high connectivity, and low contingency. The low contingency is due to the fact that rain is the only purely stochastic process modeled, and that the patterns of sources and sink in the landscape do not feedback to influence the landscape composition and configuration.

### Simulation Model – LaNuM

The Landscape Nutrient Model (LaNuM) is a simple spatially-explicit model for exploring the relation between landscape configuration and nutrient loading to bodies of water. It has been coded in C++ and has a graphical user interface (GUI) that allows for visualization of water and nutrient in landscapes as the simulation runs. The model can record output by iteration in a .csv file; it also calculates a core set of landscape metrics which can be output in a separate file.

LaNuM builds upon the work of Gergel (2005). Using a similar "heuristic" model framework, Gergel examined the importance of space in controlling the export of a theoretical nutrient from NLMs. This hypothetical nutrient had only one form and traveled only across the surface of the landscape. In fact, Gergel's model did not model the flow of water, only the nutrient. LaNuM expands on Gergel's model to include simple nitrogen and phosphorus cycles as well as a hypothetical nutrient. The idea is that P and N cycles are distinct and thus may not react in a uniform way to changes in landscape configuration (McClain et al. 1998). Whereas the use of a simple hypothetical nutrient may point to the utility of using landscape indicators of nutrient loading from terrestrial landscapes, more complex nutrient cycles may exhibit behavior not easily interpreted through the use of indices and metrics. Nutrient cycle processes and nutrient flows can exhibit different rates when near the surface as compared with deeper soil layers (Haag and Kaupenjohann 2001). In order to consider these differences in the LaNuM model, the soil profile was divided into two simple layers. Conceptually, the surface layer is relatively shallow and contains the bulk of vegetation roots and biological activity. On the other hand, the deeper layer is not directly influenced by the vegetation and can present a distinct roughness coefficient to simulate different soil textures in the two layers.

Watershed hydrology can be extremely complex – this is evidenced by the number of models created to capture certain process behaviors (Aksoy and Kavvas 2005, Merritt et al. 2003). The strategy in creating LaNuM was to include a general description of basic hydrological processes, without including the specific details of interactions that would require site-specific data (Merritt et al. 2003). An attempt was made to include the most important factors for each process and then to group the remaining in one lumped parameter. This phenomenological approach avoids complex equations for evapotranspiration, sediment generation, and infiltration. This represents a large assumption, given that many complex equations give rise to non-linear behavior. However, this approach does allow the user to quickly adjust different processes relative to each other and to readily interpret which processes are driving results.

### Hydrology/sediment/vegetation equations

The hydrological component of the model drives the nutrient flows across the landscape. The rate of water flow and direction are in turn determined by a DEM (Digital Elevation Model). From any given cell on the landscape, water can flow to any of the 8 neighboring cells that have a lower elevation. In this way, there are several possible flow paths from each cell. This corresponds to the multiple flow direction model (Freeman 1991) instead of the D-8 model where only the steepest flow path carries water and materials out of a cell (Wilson et al. 2007). The D-8 model does not allow for divergent flow in a landscape and also tends to produce many parallel flow paths in flat areas. Nevertheless, no single flow routing algorithm is ideal for all situations (Wilson et al. 2007). The multiple flow direction algorithm is deemed acceptable for this model because it allows for flows to disperse across a landscape to a greater degree than the D-8, effectively integrating landscape processes. The slopes derived from the DEM apply both to the surface and subsurface layers. Figure 2.3 shows how water moves in the model landscape.

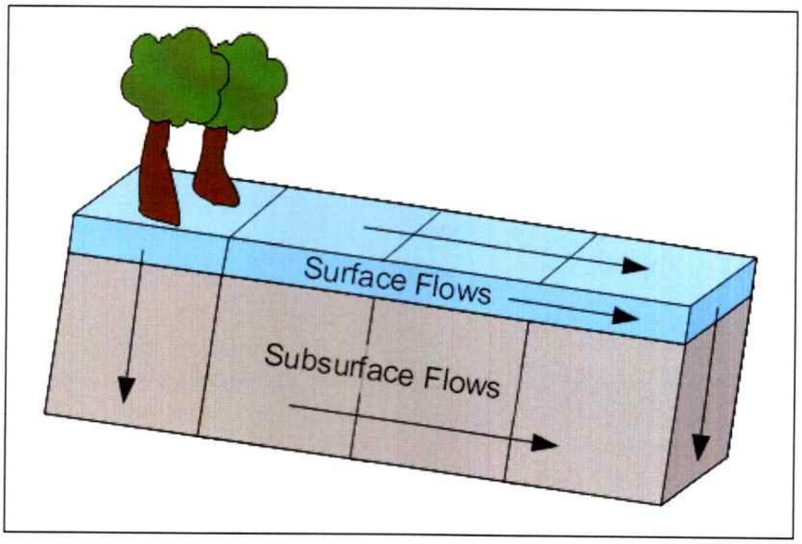


Figure 2.3: Schematic drawing of landscape flows.

**Lateral flow** is the movement of water down slope within the surface or subsurface soil layers. Different flow rates can be set for each layer via a distinct rate coefficient.

(1) $$F_{ij} = k_{FL} \cdot slp \cdot W_{ij}$$

where $F_{ij}$ = flow of water from cell $ij$; $W_{ij}$ = water in cell ij; $slp$ = slope; $k_{FL}$ = coefficient of lateral flow.

**Infiltration** carries water from the surface layer to the subsurface layer, this in turn drives the movement of nutrients to the subsurface layer. The infiltration equation:

$$I_{ij} = W_{ij} \cdot \begin{cases} k_{iv} & \text{If } veg_{ij} \geq 1 \\ k_{im} & \text{If } veg_{ij} = 0 \end{cases} \tag{2}$$

where $Iij$ = infiltration of water from cell ij; $Wij$ = water in cell ij; $vegij$ = presence of vegetation; $ki$= coefficient of infiltration (subscript $v$ for vegetation, $m$ for matrix)

**Precipitation** is based on an equation from the SWAT model that is calculated with the exponential distribution (Neitsch et al. 2002). The user can set the probability of a wet day following a dry day and of a wet day following a wet day in addition to the average amount of precipitation per iteration. The precipitation generation equation is as follows:

$$R = \mu_m(-\ln(rnd))^{rexp} \tag{3}$$

where $R$ = precipitation; $\mu m$ = average monthly precipitation; $md$ = random number; $rexp$ = parameter between 1-2 (default 1.4).

**Uptake by vegetation** extracts water from the surface layer when vegetation is present (when the cover class is one or greater) different uptake parameters could be easily assigned to each cover class by modifying source code, but this option is not built into the GUI. The equation is as follows:

$$U_{ij} = W_{ij} \cdot k_U \cdot veg_{ij} \tag{4}$$

$U_{ij}$ = uptake of water by vegetation in each cell, $W_{ij}$ is the water content of the surface layer, $k_U$ is the uptake coefficient, and $veg_{ij}$ is the presence of vegetation.

**Erosion** is difficult to calculate in a theoretical model. The equation listed here is an adaptation of the RUSLE (Revised Universal Soil Loss Equation) from the SWAT model (Neitsch et al. 2002). This equation is only partially implemented in the current version LaNuM. This is because some of the parameters required for this empirical erosion equation have no direct parrellel in LaNuM. For example, RUSLE includes a peak runoff rate parameter, however because there is no way to easily calculate this within LaNuM, this factor is set to unity. A simple equation that generates sediment erosion using slope, water flow and an adjustable rate coefficient was also included in LaNuM, however the RUSLE is capable of generating more realistic nonlinear output to changing slope or flow. The version implemented in LaNuM is as follows:

$$sed = 11.8(Q_s \cdot area)^{0.56} \cdot K \cdot C \cdot LS \tag{5a}$$

where *sed* = daily sediment production; *Qs* = volume of the runoff; *area* = area of pixel; *K* = erodibility factor (USLE); *C* = land use factor (USLE); *LS* = topographic factor (USLE). The K and C factors are given by the user. The LS factor is given by the following equations:

(5b) $$LS = \left(\frac{Lpix}{22.1}\right)^{m} \cdot \left(65.41 \cdot \sin^2(\alpha) + 4.56 \cdot \sin\alpha + 0.065\right)$$

(5c) $$m = 0.6 \cdot \left(1 - \exp\left[-35.835 \cdot slp\right]\right)$$

(5d) $$slp = \tan\alpha$$

where: *Lpix* is the length of the pixel in meters, *m* is an exponential term, *α* is the angle of the slope, *slp* is the slope of the pixel expressed as rise over run. Note that in considering the the length of the pixel as the length of the hill slope an underestimation of sediment yield may occur at smaller pixel sizes. This may be of importance in comparing runs at different pixel sizes. If this is the case, a further simplication is

(5e) $$sed = slp_{ave} \cdot q_{pix} \cdot k_{sy}$$

where: $slp_{ave}$ is the average slope of pathways leading out of the cell, $q_{pix}$ is the total flow out of the cell, and $k_{sy}$ is the sediment yield coefficient.

### Hypothetical nutrient equations

**Movement of hypothetical nutrients in the landscape**: this equation controls movement in surface and subsurface layers as well as infiltration. However, each of these processes can take a different coefficient. The equation is as follows:

(6)
$$F_{HN} = k_{HN} \cdot Q \cdot HN_{i\,j}$$

*where* $F_{HN}$ = Flow of hypothetical nutrients; $k_{HN}$ = flow rate parameter; Q = water flow; $HN_{ij}$ = hypothetical nutrient in a given cell

**Source/sink dynamics of hypothetical nutrients** follow a simple set of rules. Vegetation class zero is considered to be the source class, so if veg=0 then for each iteration a user-specified amount of hypothetical nutrient is added to that cell. If the value of the cell is greater or equal to 1, then a user-specified amount of hypothetical nutrient is removed from the cell (as long as the remaining amount does not go negative). The equation is as follows:

(7)
$$HN_{ij} = \begin{cases} HN_{t-1} - 2, & veg_{ij} = 1 \\ HN_{t-1} + 2, & veg_{ij} = 0 \end{cases}$$

*where* $HN_{ij}$ = hypothetical nutrients in cell ij; $veg_{ij}$ = presence of vegetation.

### Phosphorus cycle equations

Effort was made to simplify these cycles into their essential forms which might exhibit different behavior in the landscape (Viney et al. 2000). At each iteration, the model calculates nutrient flows from each cell to neighboring cells. Then, nutrient cycle processes occur within each cell, allowing nutrients to move between chemical forms. The phosphorus cycle is condensed into two main forms each of which has a surface and subsurface pool: soluble P and insoluble/organic P. The net P desorption/mineralization balance is the main cycling equation. The rest of the flows describe the movement of P into and out of landscape cells. The organic/adsorbed P can only move in a landscape when it is carried with eroding soil. Thus, the subsurface pool of organic P is stationary while soluble P can move with surface water *and* subsurface water flows. Figure 2.4 shows the P cycle as implemented in LaNuM.

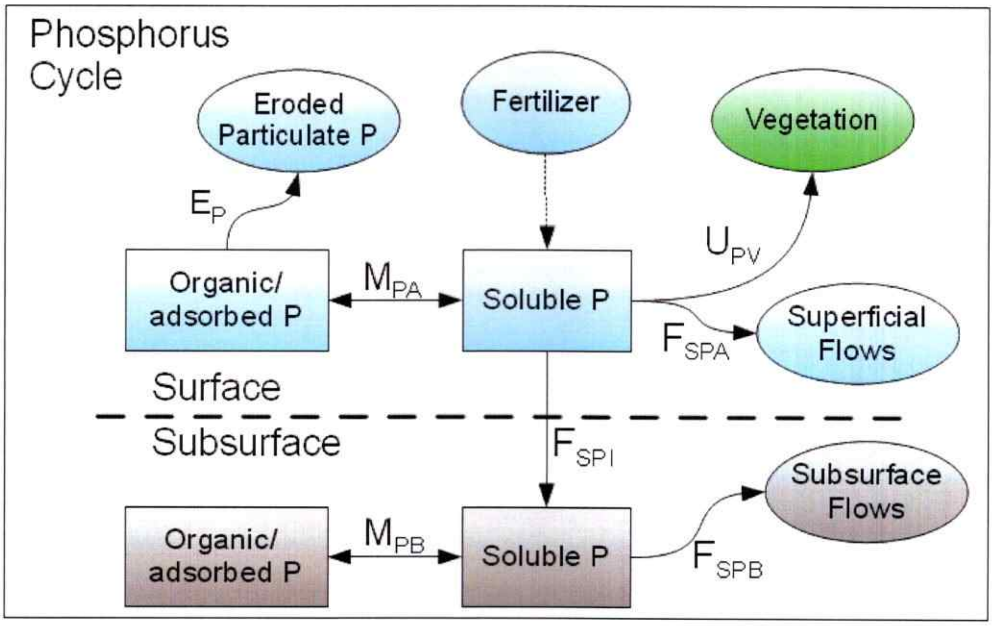


Figure 2.4: Phosphorus pools and processes used in LaNuM

**Movement of soluble P** is the movement of soluble P both in the surface and subsurface layers. The coefficient can be varied to account for different rates of movement. The equation is as follows:

(8)
$$F_{PS} = k_{PS} \cdot Q \cdot P_S$$

where $F_{PS}$ = Flow of soluble P; $k_{PS}$ = flow rate parameter; $Q$ = water flow; $P_S$ = Soluble P.

**Net P desorption/ mineralization** represents the net movement between the organic/absorbed P pool and the soluble P pool. Viney and colleagues (Viney et al. 2000) consider it a reasonable assumption to set the mineralization rate parameter equal to 1.The equation is as follows:

(9)
$$M_P = k_{MP} \frac{1}{r+1} (P_O - rP_S)$$

where *MP* = net mineralization *r* = P retention index; *kMP* = mineralization rate parameter; *PO* = Organic/adsorbed P; *PS* = Soluble P.

**Plant uptake of soluble P** is a simple equation controlled by a rate parameter:

(10) $$U_{PV} = k_{UP} \cdot Veg_{ij}$$

where $U_{PV}$ = uptake by plants; $k_{UP}$ = uptake rate constant; $Veg_{ij}$ = the presence of vegetation.

**Movement of particulate P** is movement of P in the organic/absorbed pool. It only occurs in the surface layer as that is where erosion occurs. The equation is as follows:

(11) $$E_P = 0.001 P_{NS} \cdot \frac{sed}{area_{pix}} \cdot ER_P$$

where *sed* = sediment flow; $P_{NS}$ = Particulate P in the surface layer; $area_{pix}$ = pixel or cell area; $ER_P$ = P enrichment ratio

### Nitogen cycle equations

The nitrogen cycle contains three main forms, each of which has a surface and subsurface pool: nitrate, ammonium, and organic N. Processes occurring as part of the N cycle are: mineralization, nitrification, denitrification and uptake by vegetation. Nitrogen can move via runoff, erosion of organic N, and infiltration. Figure 2.5 shows the N cycle as implemented in LaNuM.

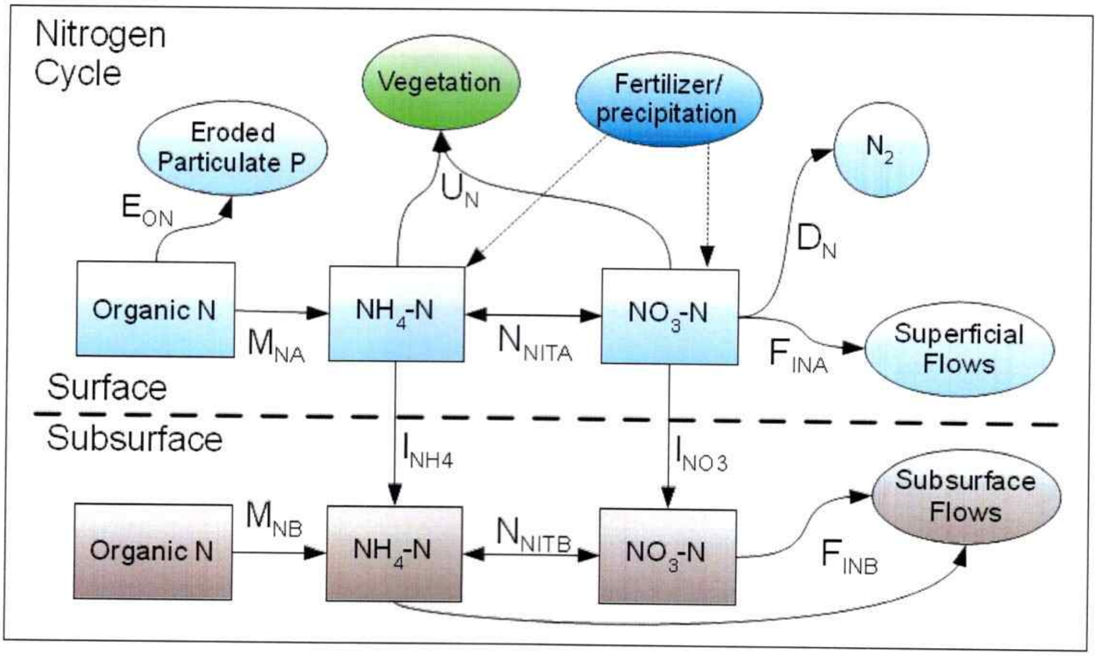


Figure 2.5: Nitrogen pools and processes used in LaNuM

**Movement of inorganic nitrogen** is a simple equation from Viney et al. (2000). The equation is as follows:

$$F_{IN} = k_{IN} \cdot Q \cdot IN \tag{12}$$

where $F_{IN}$ = Flow of inorganic N ; $k_{IN}$ = flow rate parameter; $Q$ = water flow; $IN$ = inorganic N (either $NO_3$-N or $NH_4$-N)

**Movement of Organic N** is based on an equation incorporated into the SWAT model (Neitsch et al 2002). The equation is as follows:

(13) $$E_N = 0.001 N_{ON} \cdot \frac{sed}{area_{pix}} \cdot ER_N$$

where *sed* = sediment flow; $N_{ON}$ = Organic nitrogen in surface layer; $area_{pix}$ = pixel or cell area; $ER_N$ = N enrichment ratio.

**Nitrification** is a simple equation from Viney et al. (2000). The equation is as follows:

(14) $$N_{Nit} = k_{Nit} \cdot N_{NO4}$$

where $N_{Nit}$ = nitrification; $k_{Nit}$ = nitrification rate constant; $N_{NH4}$ = Soil ammonium pool

**Net mineralization of organic nitrogen** derives from an equation from Viney et al. (2000). This process only ocurrs if the current volume of water in the surface soil layer is greater than or equal to 50% of maximum potential water in the surface layer. The equation is:

(15) $$M_N = k_{MN} \cdot N_O$$

where $M_N$ = mineralization; $k_{MN}$ = mineralization rate; $N_O$ = Organic nitrogen pool in the soil.

**Denitrification** derives from an equation from Viney et al. (2000). This process only ocurrs if the current volume of water in the surface soil layer is greater than or equal to 90% of maximum potential water in the surface layer. The equation is as follows:

(16)
$$D_N = k_{DM} \cdot N_{NO3}$$

where $D_N$ = denitrification; $k_{MN}$ = denitrification rate constant; $N_{NO3}$ = Soil nitrate pool.

### Landscape Metrics

Landscape metrics are used to distill potentially complex landscape patterns to one dimension -- thereby simplifying analysis and interpretation. If a metric can be tied to a certain landscape process, then it has potential as a rapidly derived indicator of hard-to-measure biogeochemical processes across space (Gergel et al. 2002, Johnson and Gage 1997). In dealing with landscape metrics, it is often customary among landscape ecologists to separate composition from configuration. Composition refers to both the total number of landscape cover classes and their relative proportions; configuration refers to the spatial pattern of patches in a landscape (McGarigal and Marks 1995). LaNuM defines patches as grid cells of a particular class that are within the threshold of the eight neighest-neighbors. This definition of patch correspond to the multiple flow direction model that is used to generate water and nutrient flows based on a DEM. Class-level metrics focus on each class individually and are useful when the user is interested in the pattern of a particular cover class. Landscape-level metrics consider all cover classes in a landscape. The landscape metrics that have been coded into LaNuM are described below:

## Class-level metrics

**Cell Count**: The number of cells of a given class in the landscape. Total area of each class is easily obtained by multiplying by cell area.

**Percentage of Landscape**: Simply, the percentage of the landscape area occupied by each class.

**Number of Patches**: The patch count of each land cover class.

**Edge Count**: This metric is a tally of all the edges surrounding the patches of each class type. Cell edges internal to a patch are not included.

**Core Count**: This metric is a tally of the number of cells of each class that are surrounded on all sides by the same class type.

**Edge Density**: The edge count for a given class divided by the area of the landscape.

**Mean Fractal Dimension**: The fractal dimension is a measure of the complexity of patch shape. This index is characterized at the patch-level and presented here as the mean for all patches of a cover class. The appeal of fractal analysis is that it can be applied to spatial features over a wide variety of scales (McGarigal and Marks 1995).

**FD Standard Deviation**: This index is characterized at the patch-level and presented here as the standard deviation for all patches of a cover class. Higher standard deviations indicate a diversity of patch shapes; lower deviations indicate a uniformity of patch shape.

**Largest Patch Index (LPI):** The area of the largest patch of each class divided by the area of the landscape.

**Aggregation Index (AI):** A measure of the aggregation of the focal class type. It is computed as a percentage based on the ratio of the observed number of like adjacencies, to the maximum possible number of like adjacencies given the proportion of a given class in the landscape (McGarigal and Marks 1995).

**Connectance Index**: Whereas AI is based on cell adjacencies, the connectance is a measure of aggregation or functional connectance between patches of a given class. The user specifies the distance threshold below which patches are considered to be connected. Connectance is reported as a percentage of the maximum possible connectance given the number of patches (McGarigal and Marks 1995).

**Percolating Class**: This index is 1 when one patch of the given class has at least one common edge along the vertical and horizontal edges of the landscape. The index equals zero if this condition is not met. Percolation is an indicator of a high level of connectivity within the cover class of interest (Gardner et al. 1989).

### Landscape-level metrics

**Landscape Cell Count**: A tally of cells in the landscape; it is used to calculate area.

**Vegetated Area**: This is the area of cover classes represented by an integer > zero.

**Number of Patches**: The patch count of all patches in the landscape.

**Leakiness Index**: The leakiness index (LI) was designed with reference to savanna landscapes as an indicator of how much landscapes leak vital system resources such as rainwater, nutrients and soil (Ludwig et al. 2007). LI is an interesting index to consider in the context of the problem of nutrient loading from terrestrial landscapes, as it not only considers the proportion of vegetation cover and its configuration, but directionality of fluxes.

**Contagion Index**: Contagion refers to the tendency of patch types to be spatially aggregated; that is, to occur in large, aggregated or "contagious" distributions. It is based on the probability of finding a cell of type i next to a cell of type j. This index was proposed first by O'Neill et al. (1988) and has subsequently been widely used.

**Aggregation Index**: The aggregation index (AI) is a measure of the aggregation of all cover classes in the landscape. It is computed as a percentage based on the ratio of the observed number of like adjacencies, to the maximum possible number of like adjacencies for the entire landscape(McGarigal and Marks 1995).

**Connectance Index**: The connectance is a measure of aggregation or functional connectance between patches of a given class. The connectance index at the landscape level is essentially the weighted average of (CI) at the class-level.

**Percent of Like Adjacencies**: This metric is the sum of the diagonal elements (i.e., like adjacencies) of the adjacency matrix divided by the total number of adjacencies. A landscape containing greater aggregation of patch types (e.g., larger patches with compact shapes) will contain a higher proportion of like adjacencies than a landscape containing disaggregated patch types (e.g., smaller patches and more complex shapes). In contrast to the contagion index, this metric measures only patch type dispersion, not interspersion (McGarigal and Marks 1995).

**Simple Riparian Index**: This matrix selects the cells that represent the lowest 20% of the elevation range of the landscape. The index returns the proportion of these cells that represent class zero (the nutrient source class). Given the assumption that the areas adjacent to water bodies exert a greater control on nutrient exports, this index is expected to have a positive correlation with nutrient loading.

**Percolating Landscape**: This index is 1 when at least one of the cover class types in the landscape is percolating.

### Sensitivity analysis

(Rykiel, Jr. 1996) stated that models created for theoretical exploration do not require validation in the sense of recreating the behavior observed in a particular system. However, theoretical or heuristic models still need to be evaluated for internal mathematical consistency and undergo sensitivity analysis. In the case of LaNuM, each model process in the landscape was checked by looking at the inputs and outputs to a cell when that process was activated. This manual approach to validating the internal consistency of the computer code was useful, but impossible to perform throughout the hyper-dimensional parameter space. Thus, a sensitivity analysis was used to explore the parameter space more completely and to establish which parameters had the greatest impact on model output. Sensitivity analyses based on variance or sampling (e.g. Monte Carlo methods) have the advantage of being able to quantify interactions between model parameters (Saltelli et al. 2008). However, these methods are generally very computationally expensive. Because the objective here is a qualitative yet global look at the importance of the different LaNuM parameters a modification of Morris' 1991 elementary effects sensitivity measure is used (Campolongo et al. 2007). Morris' method uses *r* trajectories (often between 10 and 50) in input parameter space; the starting point for each trajectory is random (Morris 1991).

Campolongo and colleagues (Campolongo et al. 2007) introduce a method that selects *r* trajectories from a large pool of random trajectories in order to maximize their dispersion in the input space. Two sensitivity measures are described by Morris (Morris 1991): (1) $\mu$ – the mean of the elementary effects for an input parameter assesses the overall influence of this factor on output, and (2) $\sigma$ - the standard deviation of the elementary effects is an estimate of the factor's higher order effects, i.e. non-linear and/or due to interactions with other factors (Campolongo et al. 2007). Normally, both of these measures are used to rank input parameters acording to their effect on model output, so as to avoid errors involved in using only $\mu$. A revised measure ($\mu^*$) is an estimate of the mean of the absolute values of the elementary effects and can be used by itself to rank input parameters (Campolongo et al. 2007).

The sensitivity analysis was carried out using the sensitivity R package (Pujol 2008). Forty parameters from LaNuM that are adjustable via the GUI were implemented using the Morris experimental design with modifications by Campolongo et al. (2007). The number of trajectories used was $r$=20, selected from a pool of 200 trajectories. Uniform distributions were used for each paramerter; most of the parameters tested were rate parameters ranging from 0 to 1. The same random landscape with equal percentage of vegetated and non-vegetated cells was used in all simulations and the initial cell water and nutrient contents were also held constant. Sensitivity measures were calculated for the following outputs: surface and subsurface water, surface and subsurface hypothetical nutrient, surface and subsurface nitrate, surface and subsurface ammonium, surface organic nitrogen, surface and subsurface soluble phosphorus, and surface non-soluble phosphorus. Results for water flows and hypothetical nutrients can be seen in Figures 2.6 and 2.7, respectively. Results for N and P output are shown in Tables 2.1 and 2.2. The last column in these tables is the sum of inverse rankings for each parameter. Higher values reflect higher rankings and importance to more than one output.

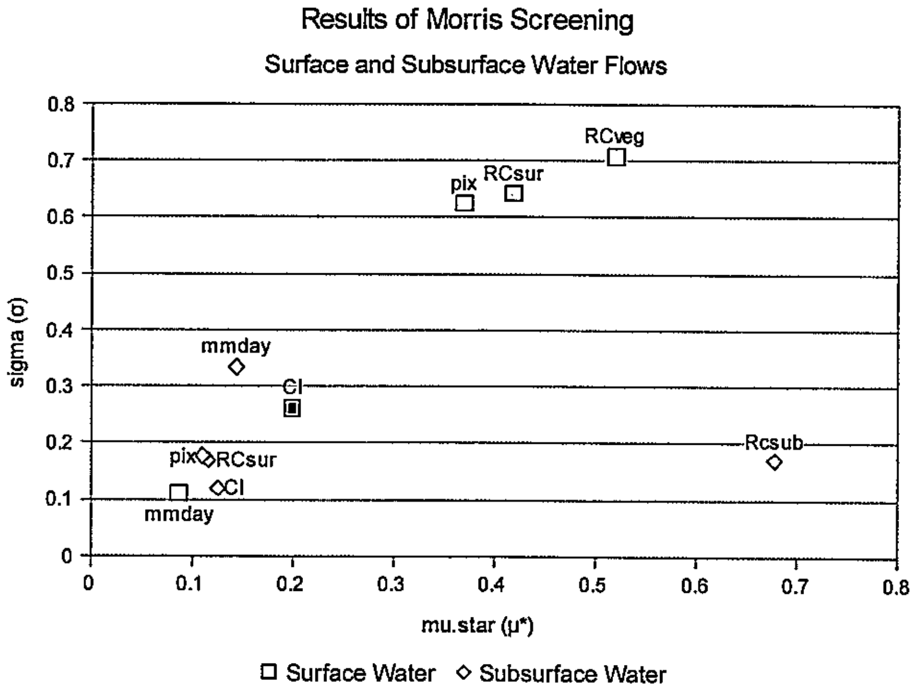


Figure 2.6: Results of Morris Screening method for surface and subsurface water.

The results are generally in agreement with the design philosophy behind LaNuM: model processes are most sensitive to the rate coefficients included in the principal equations. Other parameters affecting a given output are often related to water flow or nutrient transformations. Organic N and non-soluble P are most sensitive to the erosion parameters. The subsurface outputs are sensitive to parameters that control processes rates on the surface, indicating that landscape patterns can potentially affect subsurface flow patterns. It fits with the model logic that subsurface parameters have no effect on surface output. Because water is apportioned across the landscape according to grid cell size, this parameter affects surface water outputs significantly, however this effect does not seem to propagate to the nutrient cycles.

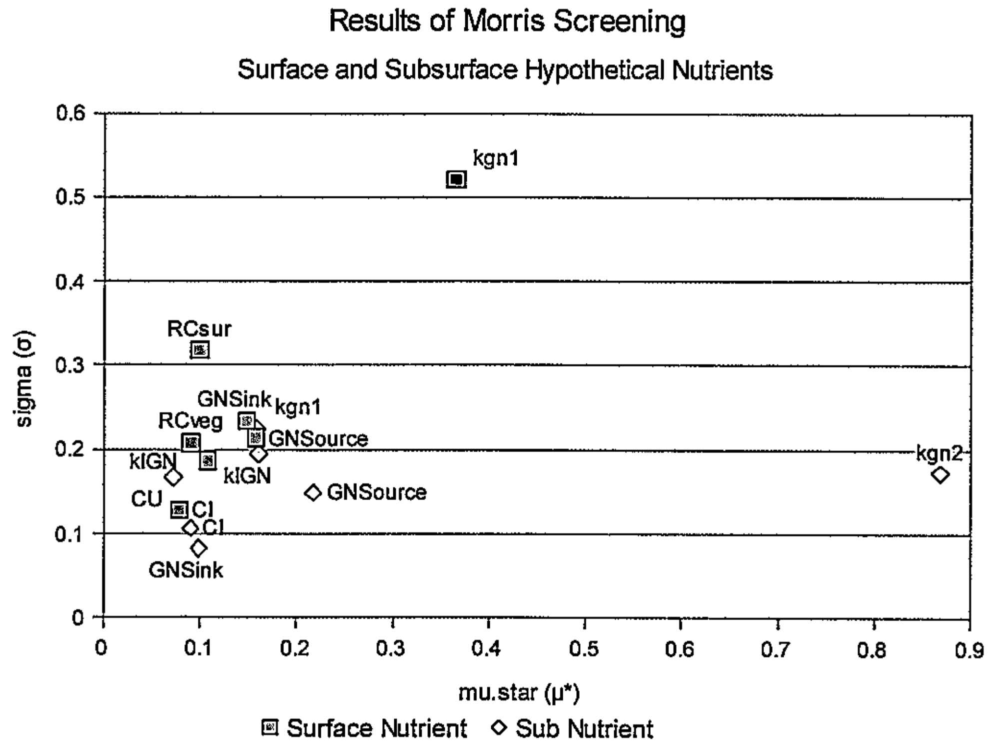


Figure 2.7: Results of Morris Screening method for surface and subsurface hypothetical nutrients (based on Gergel's 2005 heuristic model).

In Figure 2.7, the hypothetical nutrient surface flow coefficient (*kgn1*) has a high sigma value indicating that there are significant non-linearities and interactions with other factors. In fact, it makes sense that the amount of hypothetical nutrients added and removed from source and sink cells (*GN Source* and *GN Sink* parameters) would interact strongly the surface nutrient flow rate parameter. In a similar fashion, the water runoff coefficients for vegetated and non-vegetated cells (*RCveg* and *RCsur*) in Figure 2.6, have high sigma values and likely interact with each other in determining surface water output. Most of the forty parameters are key to determining at least one output. However, none of the output variables show much sensitivity to *pWD* and *pWW*, respectively the probability of a wet day following a dry day and of a wet day following a wet day. This indicates that the temporal rainfall pattern is not as important as the average amount of rain that fall on the landscape.

The sensitivity analysis indicates that the assumptions made in setting up the model carry through to the model output. In other words, there are no parameters that overwhelmingly control the water and nutrient outputs and the main parameters are associated with assumptions made in choosing the equations. The analysis also did not show many parameters that can be fixed or simplified (with the exception of PWD and pWW). The model seems to function even in the more extreme regions of the parameter space. In the future, most parameters will be held at moderate values while those being tested will be preturbed. It is important to note that organic N and non-soluble P are quite sensitive to the RUSLE erosion parameters. This may indicate that a simpler equation could be used or that close attention be paid to these parameters when setting up a simulation so that too much erosion doesn't occur. One interesting tendency is for subsurface output to be moderately sensitive to surface flow and nutrient processing parameters. The consequences of this will be explored in future work.

Table 2.1: Morris Screening Results for LaNuM Nitrogen Output

| Parameter | Description | Surface NO3 | Sub NO3 | Surface NH4 | Sub NH4 | Surface Organic N | Sum of Inverse Rankings |
|---|---|---|---|---|---|---|---|
| nitsubNH4 | NH4 Surface Flow | | 9 | 1 | 3 | | 1.44 |
| kNH4A | NH4 Sub Nitrification | | 5 | | 1 | | 1.2 |
| K | Soil Erodibility Factor | | | | | 1 | 1 |
| kNO3B | NO3 Sub Flow | | 1 | | | | 1 |
| NO3upmat | NO3 Uptake Matrix | 1 | | | | | 1 |
| CI | Water Infiltration | | 2 | 8 | 6 | 9 | 0.9 |
| minOrgN | Organic N Mineralization | | 3 | 6 | 7 | 4 | 0.89 |
| NH4upveg | NH4 Uptake (vegetation) | 7 | 9 | 2 | | | 0.75 |
| nitsurNH4 | NH4 Surface Nitrification | 4 | | 4 | 5 | | 0.7 |
| RCveg | Surface Runoff (veg) | 8 | | 5 | 8 | 5 | 0.65 |
| kNO3A | NO3 Surface Flow | 2 | 8 | | | | 0.63 |
| RCsur | Surface Runoff Matrix | | | 7 | 9 | 3 | 0.59 |
| NH4upmat | NH4 Uptake Matrix | 5 | | 3 | | | 0.53 |
| kINH4 | NH4 Infiltration | | 6 | 9 | 4 | | 0.53 |
| C | USLE Management | | | | | 2 | 0.5 |
| kNH4B | NH4 Sub Flow | | | | 2 | | 0.5 |
| denitNO3 | NO3 Denitrification | 3 | | | | | 0.33 |
| pix | Cell size | 10 | | 10 | | 8 | 0.33 |
| RCsub | Subsurface Lateral Flow | | 4 | | | | 0.25 |
| ERN | N enrichment factor | | | | | 6 | 0.17 |
| NO3upveg | NO3 Uptake (vegetation) | 6 | | | | | 0.17 |
| kINO3 | NO3 Infiltration | | 7 | | | | 0.14 |
| mmday | Average Rainfall (per t) | | | | | 7 | 0.14 |

### Comparison to Gergel's model

A set of LaNuM simulations were created to correspond to the baseline run in Gergel's (2005) paper. The LaNuM model was parameterized to turn off the new functionality, such as subsurface flows. By attempting to replicate Gergel's results, LaNuM's basic functionality can be evaluated. It should be noted that in this basic setup, LaNuM differs from Gergel's model in that (1) a multiple flow algorithm is used in LaNuM rather than uni-directional flows, (2) water flows drive nutrient flows instead of nutrients moving directly across the landscape, (3) rainfall is a stocastic process in LaNuM. One thousand five hundred random neutral landscape models (50x50 pixels) were generated for each source:sink ratio; the percent source cover varied from 0% to 100% at intervals of 5%. The results (see Figure 2.9) were compared to a figure in Gergel (2005) – reproduced here as figure 2.8.

Table 2.2: Morris Screening Results for LaNuM Phosphorus Output

| Parameter | Description | Surface Soluble P | Sub Soluble P | Surface Non-soluble P | Sum of Inverse Rankings |
|---|---|---|---|---|---|
| kSP1 | Soluble P Surface Flow | 1 | 5 |  | 1.2 |
| kSP2 | Soluble P Sub Flow |  | 1 |  | 1 |
| C | USLE Management |  |  | 1 | 1 |
| ERP | P Enrichment Factor | 10 | 2 | 3 | 0.93 |
| SPupmat | Soluble P Uptake Matrix | 2 | 10 | 10 | 0.7 |
| CI | Water Infiltration | 5 | 3 | 7 | 0.68 |
| RCsur | Surface Runoff Matrix | 4 | 6 | 4 | 0.67 |
| SPupveg | Soluble P Uptake Matrix | 3 | 9 | 8 | 0.57 |
| K | Soil Erodibility Factor |  |  | 2 | 0.5 |
| RCveg | Surface Runoff Matrix | 6 |  | 5 | 0.37 |
| kISP | Soluble P Infiltration | 9 | 4 |  | 0.36 |
| minOrgP | Organic P Mineralization | 8 |  | 6 | 0.29 |
| CU | Water Uptake (vegetation) | 7 | 8 |  | 0.27 |
| RCsub | Subsurface Lateral Flow |  | 7 |  | 0.14 |
| pix | Cell size |  |  | 9 | 0.11 |

The general pattern of a peak in variance in nutrient loading at 65% source cover is clear in the LaNuM output. This variance in loading among the NLM replicates with the same source:sink ratio is caused by the configurations of sources and sinks in the random landscapes. Thus, there is a good correspondance between LaNuM and Gergel's Model. It is interesting to note that the peak in loading variance is not as smooth as in Gergel's model. This could be due to the model differences described above or to the sample size. Here 1500 landscapes were used for each data point compared with 10,000 in Gergel's model.

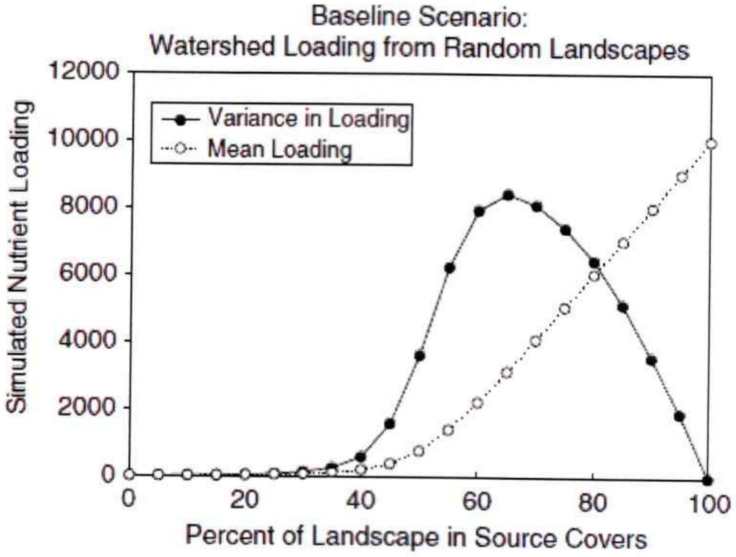


Figure 2.8: A reproduction of Figure 3 from Gergel (2005) for comparison with Figure 2.9.

### Conclusion

This chapter has presented LaNuM, a new tool for the exploration of the importance of the spatial configuration of terrestrial landscape elements in determining nutrient loading to streams or rivers. The modeling approach employed here has been to utilize phenomenological equations to include additional process that can occur in the landscape. A downloadable version of LaNuM will be available at http://antar.uchile.cl. In the next chapter, LaNuM will be used to examine different topographic models, surface and subsurface landscape flows, distinct N and P cylces, and different kinds of NLM (with a greater degree of landscape contagion). In addition, LaNuM calculates some key landscape metrics which will facilitate a search for patterns between metric values and nutrient loadings. The ultimate goal was to build on the work by Gergel (2005), generating a bridge over the gap in theory between landscape and ecosystem ecology.

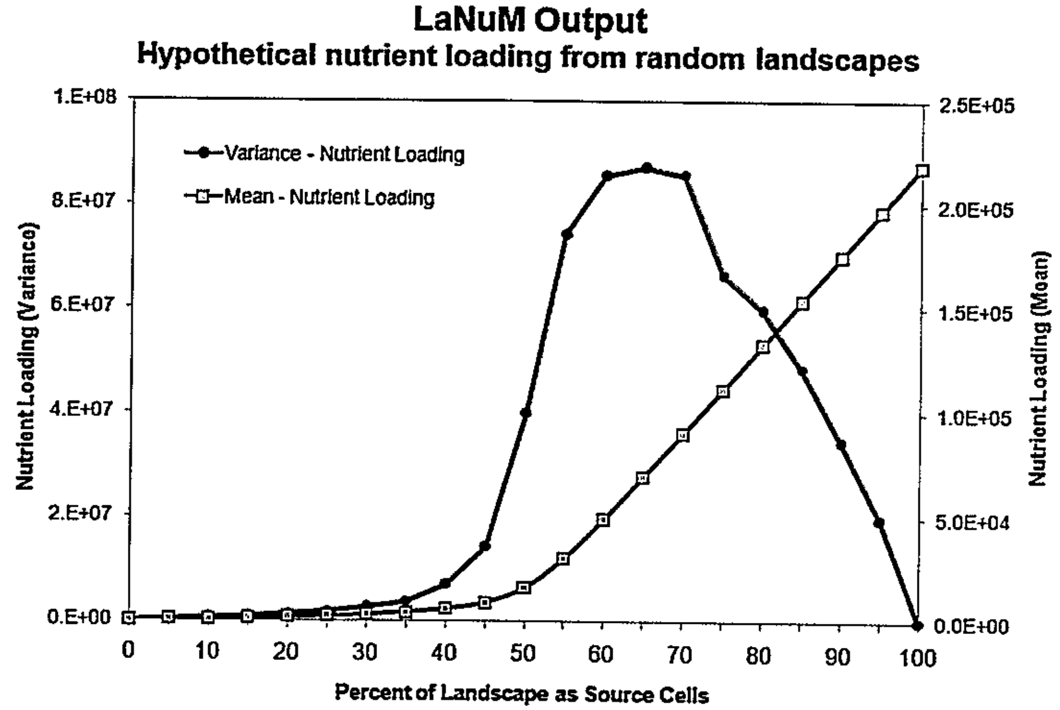


Figure 2.9: Results of LaNuM for the hypothetical nutrient simulations set up by Gergel (2005). The graph shows the mean and variance in loading from random landscapes. The variance in loading among 1500 replicates at each percent source is an indicator of the importance of landscape configuration on nutrient loading.

# Chapter 3 EXPLORING THE IMPORTANCE OF LANDSCAPE CONFIGURATION IN NUTRIENT TRANSPORT: LANDSCAPE NUTRIENT MODEL (LANUM) RESULTS

## Introduction

There is increasing recognition of the importance of spatial heterogeneity in the analysis of nutrient cycles in landscapes. Nutrient transformation and transport are key ecosystem processes that tie together ecology, biogeochemistry, fluvial geomorphology, and land use planning and management. Yet understanding of the interaction between landscape pattern and nutrient cycles and export is still fragmented and incomplete. The nature of this subject matter is complex, interdisciplinary, multi-scalar, and fairly intractable to comprehensive large-scale empiricism. Thus, there is a need to approach it from a range of perspectives and with a range of strategies and tools. This paper takes a theoretical modeling approach, in which potentially important controls on terrestrial nutrient transport are examined using a simple spatially-explicit simulation model. Previous work has begun to explore the spatial aspects of nutrient cycles, but some of the most basic questions remain unanswered in a comprehensive and satisfying way. One central question is: under what contexts can we expect that landscape configuration will be important in explaining processes associated with nutrient cycles? The answer has the potential to inform land management, conservation, and pollution mitigation as well as help focus and direct future ecological research.

One approach toward answering this question is to deepen theoretical understanding by connecting and synthesizing pre-existing concepts and by searching for general patterns that can later be tested in the field. The work of Gergel (2005), Weller et al. (Weller et al. 1998), and Jenerette and Wu (Jenerette and Wu 2004) provide some examples of this theoretical modeling. Gergel found that the variance in nutrient loading of a hypothetical nutrient consistently reached a peak and then declined as the proportion of nutrient sources in a landscape increased from 0 to 1. Depending on the relative strength of nutrient sources and sinks, this peak moved somewhat in the range between 55% - 70% source cover (Gergel 2005). The existence of this peak in variance when all other factors were held constant was significant as an overall measure of the importance of landscape configuration (a concept that is difficult to quantify in a general sense). In an attempt to further this work I asked: Does this peak in variance hold for simple N and P cycles in different topographic contexts with a range of landscape patterns? In essence, I propose testing the universality of this variance peak as a way to further understanding about the connection between landscape configuration and nutrient cycling.

Nutrient loads are commonly linked landscape pattern through the use of metrics and indicators(Kearns et al. 2005, Gergel et al. 2002). However, pattern-based landscape metrics often cannot be consistently interpreted in different landscapes and their sensitivity to spatial resolution can lead to spurious conclusions (Uuemaa 2005). In this chapter I compare some common landscape metrics with LaNuM nutrient output; in the discussion, I examine what underlies the behavior of metrics in LaNuM and suggest a role for theoretical models in the development functional indices.

The source-sink dynamics model in population ecology has been heavily utilized in empirical research, has inspired development of theory and has been integrated with landscape ecology concepts (Pullium 1988, With and King 2001). In contrast, the source-sink behavior of flows of materials in landscapes has not been placed in a firm theoretical context. A spatially–explicit source-sink approach to the study of nutrient cycles is one potential framework that could help bring together concepts currently isolated along disciplinary lines. Some source-sink approaches to nutrient transport have been published, yet much remains to be done (Gergel 2005, Jenerette and Wu 2004, Creed et al. 1996, Weller et al. 1998). In this chapter, I compare the original maps loaded into LaNuM with the results of a cell-by-cell nutrient balance. The results indicate that topographic position influences the rearrangement of actual sources and sinks on the landscape.

## Nutrient cycles and Parameterization of LaNuM

LaNuM is a simple simulation model of landscape nutrient cycles (LaNuM), which allows users to examine several potentially important factors in the quest to understand when spatial configuration of terrestrial landscape elements affects nutrient loading to streams or rivers. The conceptual basis and model structure was described in detail in an earlier work (Chapter 2 of this thesis). LaNuM is currently setup to model binary landscapes, i.e. landscapes with two cover classes. Binary landscapes are often used in modeling sources/sink dynamics and when using a matrix/patch model of the landscape (Bender et al. 2003, With et al. 1999, With and King 2001). In this paper, we take a flexible source-sink approach. For the hypothetical nutrient (based on (Gergel

2005) source-sink status is programmed directly – source cells give off nutrients and sink cells absorb them. For the nitrogen and phosphorus cycles, the source cells are conceived of as a productive land use classes such as rangeland or agriculture. The sink class is conceived of as a forested or other cover type that absorbs nutrients and has a tight internal nutrient cycle. Thus, with the P and N cycles, the source and sink cells are not established a priori. Rather, depending on cover class, each cell is parameterized to give it a propensity to be source or sink.

Although LaNuM is a theoretical or "heuristic" model that does not attempt to reproduce the behavior of a particular system, careful consideration was made in parameterizing the model. The main objective was to look at how landscape configuration influences nutrient loading and how this might change in different topographical contexts and with varying importance of subsurface flowpaths. Thus, the absolute value of nutrient outputs and processing rates is of less concern than the relative magnitudes. Measures of N and P cycles in different forested ecosystems or watersheds are presented in Table 3.1. The nitrogen cycle in forests has been studied extensively. From the four examples in Table 3.1, it is clear that on a yearly basis N input and output are 2 to 3 orders of magnitude greater than the N stored in the system. The two watersheds downwind from urban and agricultural areas (Hubbard Brook and Höglwald) show elevated levels of nitrogen deposition (Aber et al. 2003, Perakis and Hedin 2002, Gundersen et al. 2006).

Table 3.1: Nitrogen and Phosphorus budgets for four forested systems (kg ha-1 yr-1). References: (Binkley et al. 1992, Bormann et al. 1977, Campbell et al. 2000, 2004, Kreutzer et al. 2009, Likens et al. 1970, Oyarzun et al. 1998, Perez et al. 2003, Vann et al. 2002, Yanai 1992)

| **Study Site** | **Hubbard Brook, New Hampshire** | **Höglwald, Germany** | **Southern Chile** | **Cascade Head, Oregon** |
|---|---|---|---|---|
| **N Cycle** | Northern Temperate Hardwood Forest | 100-yr-old Spruce Plantation | Old-growth forests | 80-yr-old Conifer-Alder Forest |
| Uptake by Vegetation | 79.6 | 145 | 16.5 | 82.6 |
| Deposition | 20.7 | 16 | 6 | 2.9 |
| Mineralization | 69.9 | 512 | 21.6 | |
| Denitrification | 6 | 10 | 0.2 | 0.14 |
| $NO_3$- stream export | 3.1 | 21 | 0.6 | 35.8 |
| $NH_4$+ stream export | 1.7 | <1 | 0.3 | 3.6 |
| Organic Nitrogen (export) | 1.4 | – | 5.2 | 10.6 |
| Total N pools | 5258 | 10507 | 4400 | 821§ |
| $NO_3$- export after clear-cut | 104 -147 | | | |
| **P cycle** | | | | |
| Uptake by Vegetation | 9.62 | | 8.14 | 9.3 |
| Deposition | 0.04 | | 0.18 | 0.1* |
| Net Mineralization | 5.63 | | | |
| Particulate P (Stream) | 0.01 | | | |
| Disolved P (Stream) | 0.01 | | | |
| Total P (Stream) | | | 0.04 | |
| Leaching | 0.3 | | | 0.03* |
| Total P pools | 1756 | | 130 | 86.3§ |

§ Vegetation and forest floor only – doesn't not include soil; * Forests in Washington State (Compton and Cole 1998)

According to Gundersen et al. (2006), when N deposition and litterfall exceed forest vegetation demand for nitrogen nitrate leaching may exhibit threshold behavior. It is also worth noting that the dominant nitrogen form in stream water is not consistent across different ecosystems and geographic contexts. In the examples from the Northern Hemisphere, nitrate is the most plentiful N output, while the organic forms of N are most plentiful in streams from Southern Chile (Perakis and Hedin 2002). In forest systems, most phosphorus is bound up in organic compounds or immobilized in the soil matrix. In addition, very little phosphorus is deposited via precipitation or exported in stream water (Bünemann and Condron 2007, Yanai 1992). There are several soil P classification schemes and associated terminology; here we follow the operational definition proposed by Haygarth and colleagues (Haygarth et al. 2000): reactive P, unreactive P and total P. Many studies of forested watersheds indicate that unreactive P is a larger export as compared to reactive P. In a study in two ~60km$^2$ forested watersheds in Canada, (Cooke and Prepas 1998) show that the average total phosphorus (0.07 kg ha-1 yr-1) is 3.5 times the dissolved reactive P. A study of five watersheds in Georgia with 50% or over forest cover had an average total P (0.64 kg ha-1 yr-1) 4.4 times greater than the reactive P (Feyereisen et al. 2008). A regression analysis using 685 watersheds around the world indicates that in three biomes (Boreal, Temperate Coniferous, and Temperate Deciduous Forest) the percent forest cover in a watershed is negatively related to P loads (Alvarez-Cobelas et al. 2009).

There is great heterogeneity in grassland nutrient cycles, with climate, intensity of landuse and management, species composition, soil characteristics and geomorphology being some of the most important underlying factors (Brye et al. 2002, Bünemann and Condron 2007, Burke et al. 1998, Owens et al. 2003, de Willigen et al. 2007). There has been a substantial amount of work documenting how nitrate leaching increases in grasslands with higher grazing pressure, fertilizer inputs, or cover of N-fixing species (Owens et al. 2003). After reviewing the relevant literature, Di and Cameron (2002) concluded that the potential for nitrate to leach into groundwater and to streams was least in forests and increased in the following order: cut grasslands < grazed pastures < arable cropping < ploughed pastures. In production cropping systems, N is often amended to the soil at a rate of 200 kg ha-1 yr-1, which can contribute to N leaching rates frequently above 50 (and occasionally above 100) kg ha-

1 yr-1 (Di and Cameron 2002). Some example nutrient budgets are presented in Table 3.2.

Table 3.2: Nitrogen and Phosphorus budgets for Chaparral, Pasture and Prairie (kg ha-1 yr-1).

| | **Chaparral California USA** | | **Managed Pasture X Region Chile** | | **Pasture Ohio USA** | **Prairie Wisconsin USA** |
|---|---|---|---|---|---|---|
| | Nitrogen | Phosphorus | Nitrogen | Phosphorus | Phosphorus | Nitrogen |
| Live plants (Pool) | 417.2 | 28.9 | | | | |
| dead wood (Pool) | 62.8 | 4.6 | | | | |
| litter (Pool) | 205.0 | 6.0 | | | | |
| Deposition | 2.6 | | 5.4 | 0.5 | 0.5 | 10.7 |
| Fertilizer | 0.0 | 0.0 | 67.5 | 40.0 | 65.3 | 0 |
| N mineralization | | | 303.5 | | | -1.6 |
| Plant uptake | 99.6 | 4.5 | 500.3 | 64.9 | | 28.4 |
| Sediment Flux | | | | | 1.9 | |
| Subsurface flow | | | | | 0.4 | |
| Surface runoff | | | | | 1.9 | |
| Loss to Stream | 0.3 | 0.1 | 17.2 | 0.01 | 4.2 | 0.1 |
| Reference | Schlesinger 1997 | | Alfaro et al. 2009 | | Owens 2003 | Brye et al. 2003 |

Phosphorus is often applied in agroecosystems in the range between 20 and 50 kg P ha-1 yr-1 (Haygarth et al. 2005). Given that P is readily adsorbed to sediment particles, surface P transport pathways are strongly associated with erosion processes (Bowes et al. 2003, Gburek and Sharpley 1998). Indeed, there has been much attention paid to "critical source areas" of P in agricultural watersheds and the corresponding surface transport pathways (Gburek et al. 2000, Quinn et al. 2008, Sharpley 1995). P export from irrigated dairy pastures has been shown to reach 10-20 kg ha-1 yr-1 (Drewry et al. 2006). On the other hand, in systems where there is continuous vegetation cover throughout the year, erosion is limited and P export to aquatic systems is frequently below 1 kg P ha-1 yr-1 (Haygarth et al. 1998). P leaching has not been considered an important transport, but through-soil transport is beginning to be recognized as a potentially important pathway, especially in soils with preferential flowpaths (McGechan et al. 2005). It is clear that grasslands being used for productive purposes can be net sources of nutrients. Although in any given watershed, sources and sinks can occur in a variety of land use types; the above discussion about nutrient cycling and transport in grasslands and forests provides some empirical basis for the source-sink approach considered here.

### Factors considered in LaNuM

The main objective of this work was to examine how landscape configuration might influence nutrient loading and how this might be influenced by the hydrogeomorphological context. In Gergel's 2005 paper on nutrient loading using a simple "heuristic" model, only random landscapes were used. Although random landscapes are appropriate for testing the null hypothesis that landscape pattern arises from random processes, as a template for landscape simulation models they are limited. Comparisons between maps derived from remote sensing of the earth's surface and random maps show clear differences (Li et al. 2004, Pearson and Gardner 1997). However, it is worth noting that simple random maps become harder to distinguish from actual maps when the cover class of interest passes a percolation threshold and the degrees of freedom available for dissimilarity in landscape pattern decreases (Gardner et al. 1987). There are a variety of other types of neutral landscape models based on theoretical distributions; here we use the midpoint displacement algorithm (as implemented in the program QRULE) which generates multifractal maps (Gardner 1999). This algorithm allows the selection of *H*, a parameter that determines fractal dimension (*D*=3-*H*) (Saupe 1998). Effectively, as *H* is adjusted from 0 to 1, the landscape cover classes become more aggregated, i.e. contagion increases (Figure 3.1). Because the goal was to examine under what conditions landscape configuration is important in determining nutrient loading, a wide array of landscape patterns should be introduced into the model. The contagion of the landscape is thus a factor with three levels: random, moderately aggregated fractal landscape, and highly aggregated landscape. The working hypothesis was that greater contagion will lead to a higher level of importance of landscape configuration. This is because as the contagion of the landscape increases, the location of each "clump" or large patch should have a greater relative impact on nutrients exiting the landscape as compared to the smaller patches in the random map. As a map moves away from a completely random distribution, the percolation threshold decreases which should moves the peak in variance of nutrient loads to a lower *p* (proportion of landscape covered by class of interest) (Gardner et al. 1987, Gergel 2005). The degree to which the peak in nutrient loads observed by Gergel using random landscapes holds true for other types of neutral landscapes can be used to indicate the degree of universality of the working hypothesis.

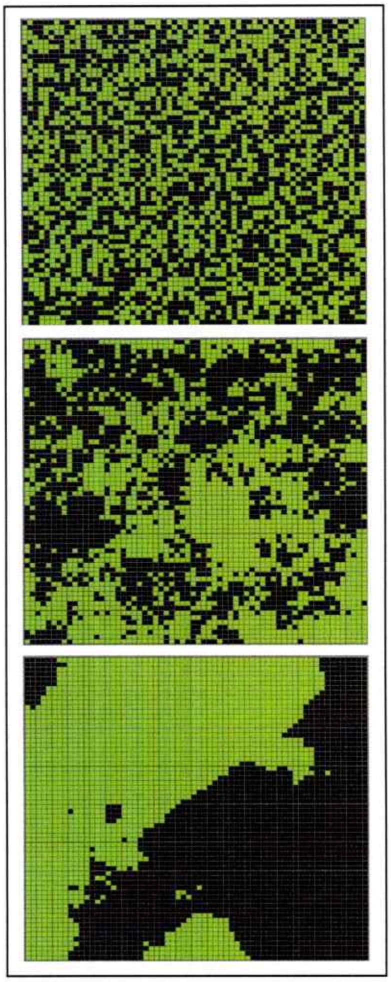


Figure 3.1: Examples of neutral landscape models: Top - random map; Middle - multifractal map (*H*=0); Bottom - multifractal map (*H*=1)

A second factor to be examined is how different topographic settings might affect the relationship between landscape metrics and nutrient loadings. In LaNuM, topography provides the basis for flows of water and nutrients across the landscape. The complexity and multi-scalar nature of landscape flowpaths and biogeochemical hotspots and hot "moments" may preclude a simple set of rules about how nutrient cycling and transport in different geomorphologic contexts (Harms and Grimm 2008, Richardson et al. 2007, Zehe and Sivapalan 2009). Nevertheless, given the need to create better metrics or indicators for landscape processes, it is worthwhile to explore, via theoretical models, whether associations between landscape pattern and nutrient loading change notably in different topographical contexts. Beaujouan et al. (2002) parameterized a hydrological/ nitrogen transport model for a small watershed in France and then introduced a set of hypothetical contrasting morphologies. They discovered that the model produced distinct results for the location and magnitude of denitrification as a result of changing the geomorphology of the model. This simple experiment indicated that residence time was more important than nitrogen concentration in controlling denitrification rates. Furthermore, although converging flowpaths concentrate flows in a small area – which underlies a temporal uniformity in denitrification rates – during times of high precipitation, it was the parallel flow topographies with larger set of downhill receiving cells that could quickly increase denitrification rates (Beaujouan et al. 2002).

The study of the effect of geomorphology on nutrient cycles overlaps with interesting work by stream ecologists and fluvial geomorphologists. Thorp and colleagues recently presented a "riverine ecosystem synthesis" based on Vanotte's River Continuum

Concept, Mongomery's process domains, Poole's hierarchical stream corridor patch dynamics, among other concepts (Montgomery 1999, Poole et al. 2004, Thorp et al. 2006). Process domains – defined as delineable areas at different spatial scales with distinct sets of geomorphic processes – provide a conceptual tool that might be used to create stereotypes of different geomorphological settings (Montgomery 1999). For example, in terms of nutrient cycling, much work has been done on riparian areas as highly functional elements of watersheds (Naiman et al. 2005, Peterjohn and Correll 1984). On the other hand, steep areas of hillslopes drive water flowpaths and erosional processes, favoring a distinct set of nutrient transport and cycling processes (Montgomery 1999).

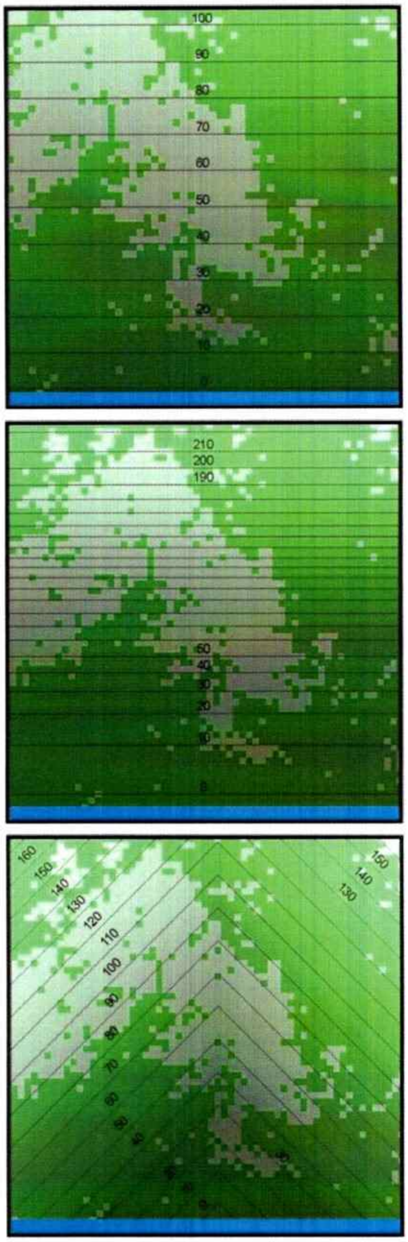


Figure 3.2: Examples of topographic models used with LaNuM: Top – uniform slope; Middle – S-shaped slope; Bottom – V-shaped watershed. Direction of flow is from top to bottom; the lines represent contour intervals of ten vertical units.

Three hypothetical elevation models were used in LaNuM (Figure 3.2). The first was a uniform slope that is similar to what Gergel used in her 2005 paper. The second was an "S-shaped" slope based on a sigmoid function. The idea is that this model would create a band with fast lateral flow and a "valley floor" area near the bottom edge of the landscape with slower flows. The third elevation model was V-shaped and tended to concentrate flows as they move toward the bottom of the landscape. This model is somewhat analogous to a headwater stream where local elevation minima concentrate runoff and eventually a channel forms. There has been no attempt in LaNuM to create channelized flow, however. As compared to the uniform topography, the S-shaped model slows down flows near the bottom of the landscape. It is hypothesized that this will favor the formation of sink cells, either through increased denitrification or by trapping and slowing nutrient forms as they move downhill. The V-shaped model creates different flow patterns from the uniform slope. It is hypothesized that this will significantly alter the correlation matrix between landscape metrics and nutrient loads.

Landscape metrics generally attempt to quantify landscape patterns on the surface of terrestrial systems. Myriad remote sensing products are available that are easily utilized in metric calculation (Power et al. 2005). Thus, in the attempt to find a relationship between landscape structure and nutrient loading, many authors assume the importance of surface or shallow subsurface flowpaths (Allan et al. 1997, Uuemaa et al. 2007). Granted different landuse types are known to affect infiltration rates, nutrient leaching and runoff (Caraco et al. 2003, Drewry et al. 2006). However, as the prevalence of lateral ground water flow in a terrestrial system increases, one can hypothesize that the "stamp" that surface vegetation patterns can impart to the nutrient content of soil water becomes less pronounced. In LaNuM, water and nutrients can enter into a subsurface layer where they pass unaltered below the surface layer to the receiving aquatic system. The third factor is the level of infiltration to this subsurface layer that is allowed to occur in the model.

## Methods

### Model Simulations

The Landscape Nutrient Model (LaNuM) is a simple spatially-explicit model for exploring the relation between landscape configuration and nutrient loading to bodies of water. A factorial experimental simulation design was created with three main factors: landscape contagion, topographic complexity, and subsurface flow. Each factor had three levels for a total of 27 groups. Within each group a fourth factor was considered: the percent of landscape cells designated as source. The percent source cells was varied from 0% – 100% with intervals of 5%. For each combination of these factors, 200 landscapes with a dimension of 64 x 64 pixels were randomly generated using the QRULE program (Gardner 1999). The subsurface flow factor was controlled by manipulating the infiltration coefficient; the three levels corresponded to no subsurface flow ($CI = 0$), moderate subsurface flow ($CI = 0.12$) and high subsurface flow ($CI = 0.36$). Because the generated landscapes are identical when the source cells make up 0% or 100% of the landscape, only one set of simulations (instead of three for each level of the landscape contagion factor) was carried out in these situations. In all, LaNuM was run 106,200 times for 130 iterations (~ 2x the linear dimension of the landscape). Landscape metrics were also generated for each unique landscape.

### Source-sink behavior in LaNuM

The LaNuM model is based on a source-sink approach in which an initial pattern of sources and sinks is introduced into the model by way of binary neutral landscape model (NLM). Class 0 was parameterized to be a source of N and P while Class 1 was parameterized to a sink (or at have a tighter internal nutrient cycling). Class 0 received small inputs of N and P every 10 iterations to simulate fertilization in agricultural or urban land uses. Both classes received N input through wet deposition and denitrification could occur in cells of either class. Vegetation in Class1 could uptake inorganic N and P forms between 25-40% faster than in Class 0 and slower surface water flow in Class 1 slowed export. Infiltration was identical for both classes. The simulations began with a significant amount of nutrients in the landscape in organic/immobilized forms. Thus, although each class had a propensity to act as a source or sink, its actual behavior over the course of the simulations was not determined *a priori*. A balance calculation for each nutrient in each cell was carried out at the end of each simulation and this provided the basis for a reclassification of source and sink cells in the landscape. Because many cells ended up exhibiting very weak source or sink behavior, a "neutral" class was established to group those cells with N and P balances close to zero. Each cell in the landscape was tallied according to its source-sink status before and after the simulation creating a 2x2 matrix (2x3 with neutral cells). From this matrix, the overall "accuracy" can be determined by dividing the values in the diagonal by the total number of entries. An accuracy of 1 would indicate that the spatial locations of sources and sinks had not changed over the course of the study. Change in the classification of cells is simply one minus accuracy. Because neutral cells were included in the matrix, when these make up a large proportion of the landscape, the accuracy decreases significantly.

### Statistical analysis

The primary objective of the statistical analysis was to explore the impact and interaction of the three primary factors on nutrient loading. Secondarily, the landscape metrics were analyzed as to their ability to show nutrient loading in different contexts. The factorial simulation design was implemented as a way to partition the variance in nutrient loading according to the different factors. A MANOVA method was attempted as a way to gain understanding of how factors interact to produce high nutrient loads. However, after examining the output data, it became clear that the basic parametric assumption of homogeneity of variances and covariances did not hold within the output dataset. In addition, some of the nutrient forms presented aberrations from normal distributions. Figure 3.3 shows the case for surface and subsurface nitrate loads. ANOVA and MANOVA are generally considered robust to some violations of assumptions (Zar 1999). As heterogeneity of variance increases, so does the ANOVA Type I error rate. Although many tests for this assumption are available, many are too conservative and may not be of much use

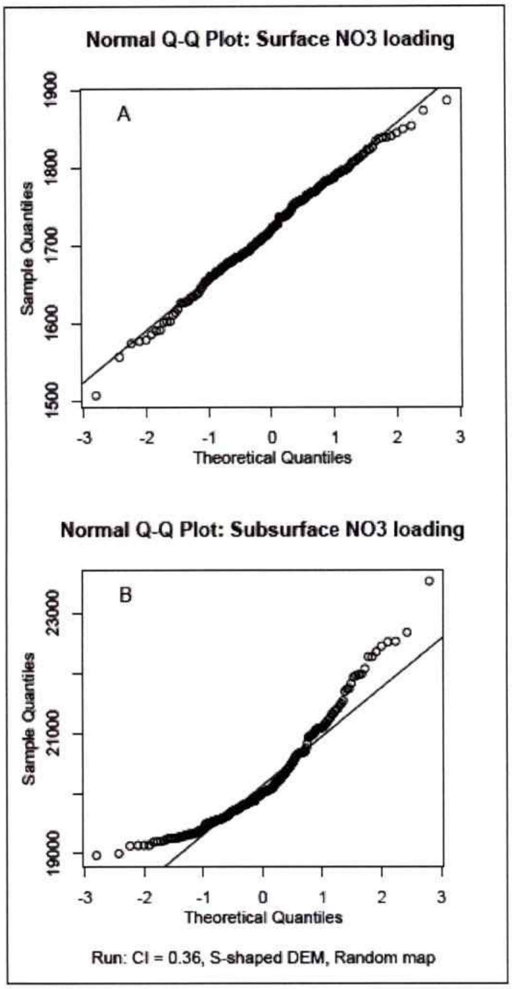


Figure 3.3: Normal quantile-quantile plot showing a normal distribution for surface NO3 while subsurface NO3 shows a negatively skewed distribution.

(McGuinness 2002). Box's M statistic was used to test for homogeneity of covariance matrices. A Box's M test was applied in R to the surface nutrient forms for all groups for $p$ = 65% of landscape cover (R Development Core Team 2009). The null hypothesis of the test for homogeneity of covariance was that the covariance matrices are equal (Timm 2002). The results of Box's M test clearly indicate a violation of the heterogeneity of variance assumption (Box' M, $X^2 = 46959.4$, $df = 546$, $p = 0$). Logarithmic and square root transformation of the data did not significantly improve the results of Box's M test and the Levene's tests.

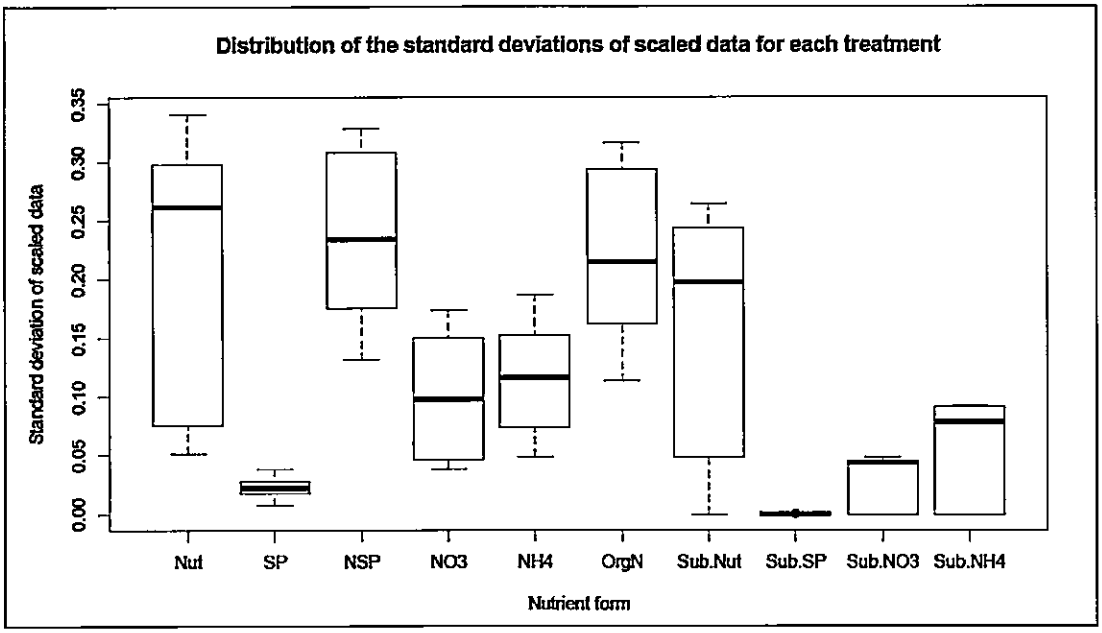


Figure 3.4: Distribution of standard deviation for scaled nutrient loading outputs. The nutrient forms beginning on the left with surface loads: theoretical nutrient, soluble phosphorus, non-soluble phosphorus, nitrate, ammonium, organic nitrogen, followed by subsurface forms.

In order to better understand the variance in the data, a standard deviation plot was constructed with the data from source cover $p$ = 65%. The data for each nutrient form in each group were scaled using by dividing column data by the root-mean-square for that column. Then standard deviations for each group were calculated by nutrient form and displayed as a distribution in Figure 3.4. It is interesting to note that for this p, the hypothetical nutrient has the greatest range of variance and the larger relatively large values (i.e. high inter-group variability). The organic forms of P and N have similar distributions, as do the surface nitrate and ammonium forms. Soluble P loadings show very little difference between groups and are generally very low. Figure 3.4 provides an understanding of where in the nutrient loading space the highest variance is found.

Non-metric Multidimensional Scaling (NMDS) is an ordination method based on dissimilarity between pairs of objects. It is used to find an ordination which maximizes agreement (or minimizes stress) between the distances between all pairs of objects (often ecological sites) are in rank-order agreement with their dissimilarities (given by a user defined metric) (Minchin 1987). Being a non-metric analysis, NMDS does not make assumptions about the response function of the variables used in the dissimilarity index and the underlying gradients. However, the application of this method can be complicated by an *a priori* determination the number of dimensions of the solution and the fact that the iterative algorithm used can become trapped in local minima (Kenkel and Orloci 1986). The R package 'vegan' was used to carry out the NMDS ordination (Oksanen et al. 2009). Screen plots were used to select the dimensionality of the analysis by plotting dimension number against stress. Stress is defined by the monotonic regression of distance on dissimilarity and provides a measure of the goodness of fit (Figure 3.5). The non-metric stress measure ($R^2$) and the linear fit based on correlation analysis ($r^2$) reported in Figure 3.5 show a high goodness of fit, indicating that further iterations were not necessary. The Bray – Curtis distance index was recommended by Michin (1987) as more useful in the context of

NMDS than Euclidean distance. Although an unconstrained ordination technique, environmental vectors can be fitted to the ordination plot to aid in interpretation. This process also generates squared correlation coefficients ($r^2$) for each vector and the significance of these values can be assessed by permutations of the environmental variable (Oksanen et al. 2009).

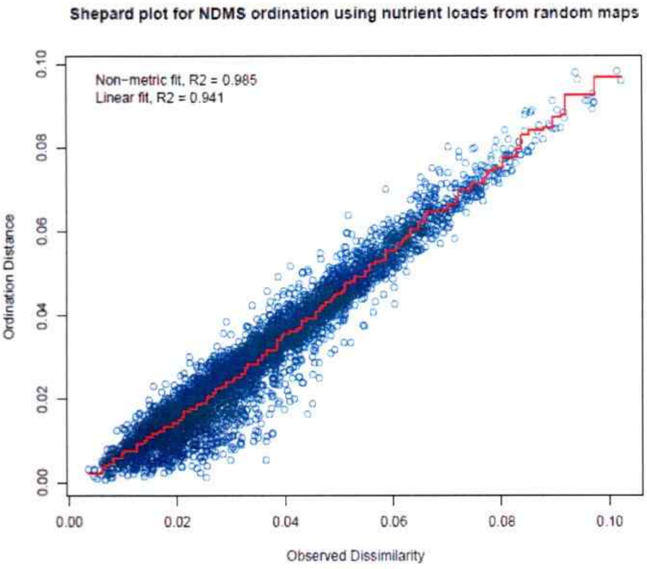


Figure 3.5: Shepard plot for NDMS ordination using data from a simulation with random maps, uniform DEM and 65% source cover. The non-metric $R^2$ is 0.0985.

Non-metric Multidimensional Scaling (NMDS) is an ordination method based on dissimilarity between pairs of objects. It is used to find an ordination which maximizes agreement (or minimizes stress) between the distances between all pairs of objects (often ecological sites) are in rank-order agreement with their dissimilarities (given by a user defined metric) (Minchin 1987). Being a non-metric analysis, NMDS does not make assumptions about the response function of the variables used in the dissimilarity index and the underlying gradients. However, the application of this method can be complicated by an *a priori* determination the number of dimensions of the solution and the fact that the iterative algorithm used can become trapped in local minima (Kenkel and Orloci 1986). The R package 'vegan' was used to carry out the NMDS ordination (Oksanen et al. 2009).

Screen plots were used to select the dimensionality of the analysis by plotting dimension number against stress. Stress is defined by the monotonic regression of distance on dissimilarity and provides a measure of the goodness of fit (Figure 3.5). The non-metric stress measure ($R^2$) and the linear fit based on correlation analysis ($r^2$) reported in Figure 3.5 show a high goodness of fit, indicating that further iterations were not necessary. The Bray – Curtis distance index was recommended by Michin (1987) as more useful in the context of NMDS than Euclidean distance. Although an unconstrained ordination technique, environmental vectors can be fitted to the ordination plot to aid in interpretation. This process also generates squared correlation coefficients ($r^2$) for each vector and the significance of these values can be assessed by permutations of the environmental variable (Oksanen et al. 2009).

Due to the non-normality and heterogeneity of variance in the dataset, the relation between different variables was assessed primarily with the Spearman Rank Order Correlation. Without making assumptions about the relationship between any two variables, the Spearman coefficient assesses how well they can be described by a monotonic function. The degree of correlation (and thus redundancy) between the landscape metrics included in LaNuM is assessed. The literature suggests that the correlation between pattern metrics and processes in different landscapes may not hold when the amount of habitat of interest ($p$) changes (Gardner et al. 1987, Gergel et al. 2002). Thus, we looked at the significance of correlation while varying $p$ of the source class.

## Results

### Overall Nutrient Loading

The three main factors examined in this study can have an important effect on the magnitude and variance of nutrient loading. However, it appears the effects are variable among the different nutrient forms. The hypothetical nutrient can be thought of as a null model of nutrient cycling. It is unreactive (doesn't change forms), but is influenced by the source-sink patterns and flowpaths in the landscape. Because of this, it can serve as a useful basis of comparison for the other nutrient forms. Table 3.3 presents the median and standard deviations for loadings of the hypothetical nutrient for all simulations (i.e. the median value of the set of simulations with varying p within each cell of the experimental design).

Table 3.3: Median ± standard deviation of hypothetical nutrient loading.

| Hypothetical Nutrient Loads | | Subsurface Flow (F3) | F2: Topography | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | Uniform | | S-curve | | V-shaped | |
| | | | Nutrient | Sub. Nut. | Nutrient | Sub. Nut. | Nutrient | Sub. Nut. |
| F1: Landscape Contagion | Fractal *H* = 0 | CI=0 | 520 ± 141 | 0 ± 0 | 479 ± 134 | 0 ± 0 | 503 ± 125 | 0 ± 0 |
| | | CI=0.12 | 349 ± 106 | 215 ± 40 | 327 ± 102 | 195 ± 38 | 321 ± 90 | 209 ± 42 |
| | | CI=0.36 | 212 ± 70 | 431 ± 73 | 203 ± 68 | 392 ± 70 | 178 ± 58 | 400 ± 75 |
| | Fractal *H* = 1 | CI=0 | 966 ± 314 | 0 ± 0 | 908 ± 306 | 0 ± 0 | 910 ± 270 | 0 ± 0 |
| | | CI=0.12 | 663 ± 238 | 352 ± 93 | 631 ± 233 | 322 ± 87 | 592 ± 195 | 338 ± 86 |
| | | CI=0.36 | 399 ± 151 | 689 ± 168 | 385 ± 147 | 636 ± 159 | 328 ± 124 | 638 ± 157 |
| | Random | CI=0 | 191 ± 17 | 0 ± 0 | 180 ± 16 | 0 ± 0 | 227 ± 19 | 0 ± 0 |
| | | CI=0.12 | 139 ± 14 | 92 ± 4 | 134 ± 14 | 84 ± 4 | 152 ± 14 | 102 ± 6 |
| | | CI=0.36 | 100 ± 11 | 208 ± 8 | 98 ± 11 | 192 ± 8 | 94 ± 9 | 213 ± 11 |

The hypothetical nutrient presents come clear patterns in behavior: (1) there is a tendency of both surface and subsurface nutrient loads to increase in both magnitude and variance as the level of contagion in the landscape is increased, (2) the dominance of surface or subsurface loading is sensitive to the infiltration parameter, (3) the effect of topography on loading is not pronounced; however, both the S-shaped and V-shaped topographies have a clear tendency to export less nutrients that the uniform model, (4) relative to the fractal landscapes, the variation in export from the random landscape is significantly less.

Nitrate presents a marked contrast from the behavior of the hypothetical nutrient (Table 3.4). First, the relative magnitudes of surface loadings are remarkably constant between the levels of landscape contagion. However the standard deviation values are consistently higher for surface $NO_3$, than for the other landscapes. The infiltration rate (*CI*) appears to have little effect on surface $NO_3$, although there is a small but consistent tendency for the subsurface $NO_3$ loads to increase when $CI = 0.36$. A curious result is the effect of the V-Shaped topography in reducing $NO_3$ loads. This is opposed to the hypothetical nutrient where no significant differences in loading between the S-shaped and V-shaped topographies.

Table 3.4: Median ± standard deviation of surface and subsurface nitrate loading.

| Surface and Subsurface NO3 loading | | Subsurface Flow (F3) | F2: Topography | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | Uniform | | S-curve | | V-shaped | |
| | | | NO3 | Sub NO3 | NO3 | Sub NO3 | NO3 | Sub NO3 |
| F1: Landscape Contagion | Fractal ($H = 0$) | CI=0 | 156 ± 14 | 0 ± 0 | 160 ± 14 | 0 ± 0 | 111 ± 10 | 0 ± 0 |
| | | CI=0.12 | 162 ± 15 | 2031 ± 98 | 162 ± 16 | 1989 ± 92 | 115 ± 11 | 1519 ± 66 |
| | | CI=0.36 | 154 ± 15 | 2046 ± 93 | 153 ± 15 | 2011 ± 87 | 109 ± 11 | 1527 ± 65 |
| | Fractal ($H = 1$) | CI=0 | 160 ± 22 | 0 ± 0 | 165 ± 25 | 0 ± 0 | 114 ± 16 | 0 ± 0 |
| | | CI=0.12 | 168 ± 27 | 2033 ± 99 | 169 ± 28 | 1990 ± 92 | 119 ± 19 | 1522 ± 66 |
| | | CI=0.36 | 161 ± 28 | 2051 ± 94 | 160 ± 28 | 2016 ± 88 | 115 ± 20 | 1531 ± 66 |
| | Random | CI=0 | 157 ± 7 | 0 ± 0 | 160 ± 8 | 0 ± 0 | 112 ± 5 | 0 ± 0 |
| | | CI=0.12 | 163 ± 6 | 2031 ± 98 | 162 ± 6 | 1989 ± 91 | 116 ± 5 | 1519 ± 66 |
| | | CI=0.36 | 154 ± 6 | 2046 ± 92 | 153 ± 6 | 2012 ± 86 | 110 ± 4 | 1527 ± 65 |

Table 3.5 presents the surface forms of the phosphorus cycle. The non-soluble form of phosphorus is closely associated with sediment transport (Baldwin et al. 2002). Thus the difference between the topographies was expected with the organic or non-soluble forms. However, it is remarkable the difference between the S-shaped topography and the other two. The S-shaped elevation has the steepest absolute slope of the three; however, the slowing of surface water, as it reached the flatter portion, appears to have an outsized effect on non-soluble P loading. A counterintuitive pattern appears in the soluble P loads: there is a small increase in loading as the infiltration coefficient increases drawing water from the surface flows. Because the non-soluble P is negatively associated with infiltration, at high infiltration rates, it remains in the landscape slowly mineralizing and increasing the overall amount of soluble P. Overall, the higher variation in non-soluble P loading as compared to soluble P indicates that the landscape configuration has a greater impact on this form.

Table 3.5: Median ± standard deviation of surface soluble and non-soluble phosphorus loading.

| Surface Soluble and Non-soluble P loading | | Subsurface Flow (F3) | F2: Topography | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | Uniform | | S-curve | | V-shaped | |
| | | | Soluble P | NSP | Soluble P | NSP | Soluble P | NSP |
| F1: Landscape Contagion | Fractal (*H* = 0) | *CI* = 0 | 268 ± 6 | 940 ± 243 | 295 ± 4.6 | 259 ± 70 | 186 ± 5.4 | 1093 ± 278 |
| | | *CI* = 0.12 | 279 ± 4.3 | 588 ± 163 | 299 ± 5.2 | 142 ± 40 | 195 ± 3.7 | 715 ± 197 |
| | | *CI* = 0.36 | 287 ± 4.5 | 370 ± 109 | 300 ± 5.8 | 80 ± 23 | 201 ± 3.1 | 461 ± 134 |
| | Fractal (*H* = 1) | *CI* = 0 | 265 ± 6.7 | 1154 ± 376 | 297 ± 8.2 | 295 ± 103 | 184 ± 6 | 1338 ± 439 |
| | | *CI* = 0.12 | 278 ± 5.1 | 712 ± 247 | 301 ± 9.7 | 158 ± 56 | 194 ± 3.8 | 865 ± 300 |
| | | *CI* = 0.36 | 287 ± 6.5 | 438 ± 157 | 302 ± 10.6 | 88 ± 32 | 201 ± 4.2 | 546 ± 195 |
| | Random | *CI* = 0 | 269 ± 5.7 | 875 ± 124 | 295 ± 2.3 | 252 ± 43 | 187 ± 4.9 | 1014 ± 139 |
| | | *CI* = 0.12 | 281 ± 3.9 | 551 ± 89 | 299 ± 2.2 | 140 ± 26 | 195 ± 3.5 | 668 ± 105 |
| | | *CI* = 0.36 | 288 ± 2.9 | 352 ± 64 | 300 ± 2.4 | 80 ± 16 | 202 ± 2.5 | 437 ± 78 |

To further explore the relation between landscape configuration and nutrient loading, a series of graphs comparable to those featured in Gergel's 2005 paper were produced. Gergel's work showed that the variance in nutrient loading of a hypothetical nutrient consistently reached a peak between 55% - 70% source cover (Gergel 2005). Figure 3.6 shows surface and subsurface hypothetical nutrient export from the three levels of landscape contagion. Immediately noticeable is the variance peak at 60% - 70% source cover in every plot. In the case of the uniform topography, the mean and variance for both surface and subsurface loads are small until about 45% source cover. As the landscape nears the percolation threshold – the point where 1 patch spans a random square lattice such as a random map enhancing connectivity – the variance explodes upward. Gardener and others have researched the impact of this threshold ($p = 0.5928$) on other properties of neutral landscape maps. For example, above p=0.3, the number of patches in a random landscape declines as pixels begin to group together. The coefficient of variation, however, increases, reaching a peak near the percolation threshold (Gardner et al. 1987). For the hypothetical nutrient in a random landscape, source cell export is rapidly absorbed by neighboring sink cells with *p* is small. The greater variability of landscape pattern as *p* approaches the percolation threshold effectively opens up nutrient flowpaths that can overpower the buffering effect of the sink cells. The almost linear nature of the mean nutrient export curve after *p*=50 in Figure 3.6A, indicates a direct relationship between the addition of source cells to the landscape and increased nutrient loading.

The almost mirror-image pattern of surface and subsurface means and variance for the hypothetical nutrient was not expected, especially at higher landscape contagion

(Figure 3.6). To some extent, this outcome is an artifact of the simplicity of the LaNuM model. Infiltration occurs at a constant rate evenly across the landscape. Thus, what enters the subsurface layer is a reflection of nutrient and water content on the surface. In the absence of input from the surface (and assuming some previous water and nutrient content), outflow from the subsurface layer would not exhibit this peak in variance. This indicates that the configuration of patches on the surface can create patterns of water and nutrient concentrations that propagate downward and laterally, persisting even though they are no longer influenced by the surface pattern.

The fractal landscapes in Figure 3.6 follow the same overall pattern as the random landscapes, but variance begins to increase at a lower source cover. In Figure 3.6E, the variance is already headed steeply upward at 15% source cover. The effect is that the area under the variance curve expands. In addition, although the magnitude of mean loading does not change dramatically between level of landscape contagion, the variance does, as is seen the re-scaling of the of the secondary y axis. This lends strong support to the hypothesis that greater contagion will lead to a higher level of importance of landscape configuration in controlling nutrient output.

In Figure 3.7, the loads of surface nitrate and ammonium are compared across levels of landscape contagion. One difference with the hypothetical nutrient is that the variance curves for $NO_3$ and $NH_4$ are less defined in the random landscape and begin to form clearer peaks at the highest level of contagion. Although LaNuM was parameterized so that the two classes would have a propensity to be net sources or sinks, their actual behavior can be affected by slope, proximity to sources or sinks in an uphill direction, or landscape context (i.e. near the top of the hillside or in lower, convergent flow areas). It is probably a lack of a defined source-sink dynamic that gives rise to graphs such a 7b, where $NH_4$ variance remains relatively constant until well after the percolation threshold. In fact, in random landscapes, ammonium appears relatively insensitive to landscape configuration. However, as contagion increases the variance peak reemerges. Another difference with the hypothetical nutrient plots is that the increase in mean loading has a definitively linear appearance. This would indicate that when sink cells are in the majority, they are not removing a substantial amount of these nutrient forms and thereby lowering the slope of the mean loading curve. The nitrogen cycle in LaNuM was parameterized to reflect the relatively slow process rates (as compared to the total N pool in the landscape). In addition, both surface and subsurface cells began simulations with initial cell content. If more mobile forms such as nitrate or soluble P flow out of the landscape, they can be replaced through mineralization of the organic forms. Nevertheless, it is notable that despite major differences with the hypothetical nutrient, the variance peak does appear in both of these nutrient forms.

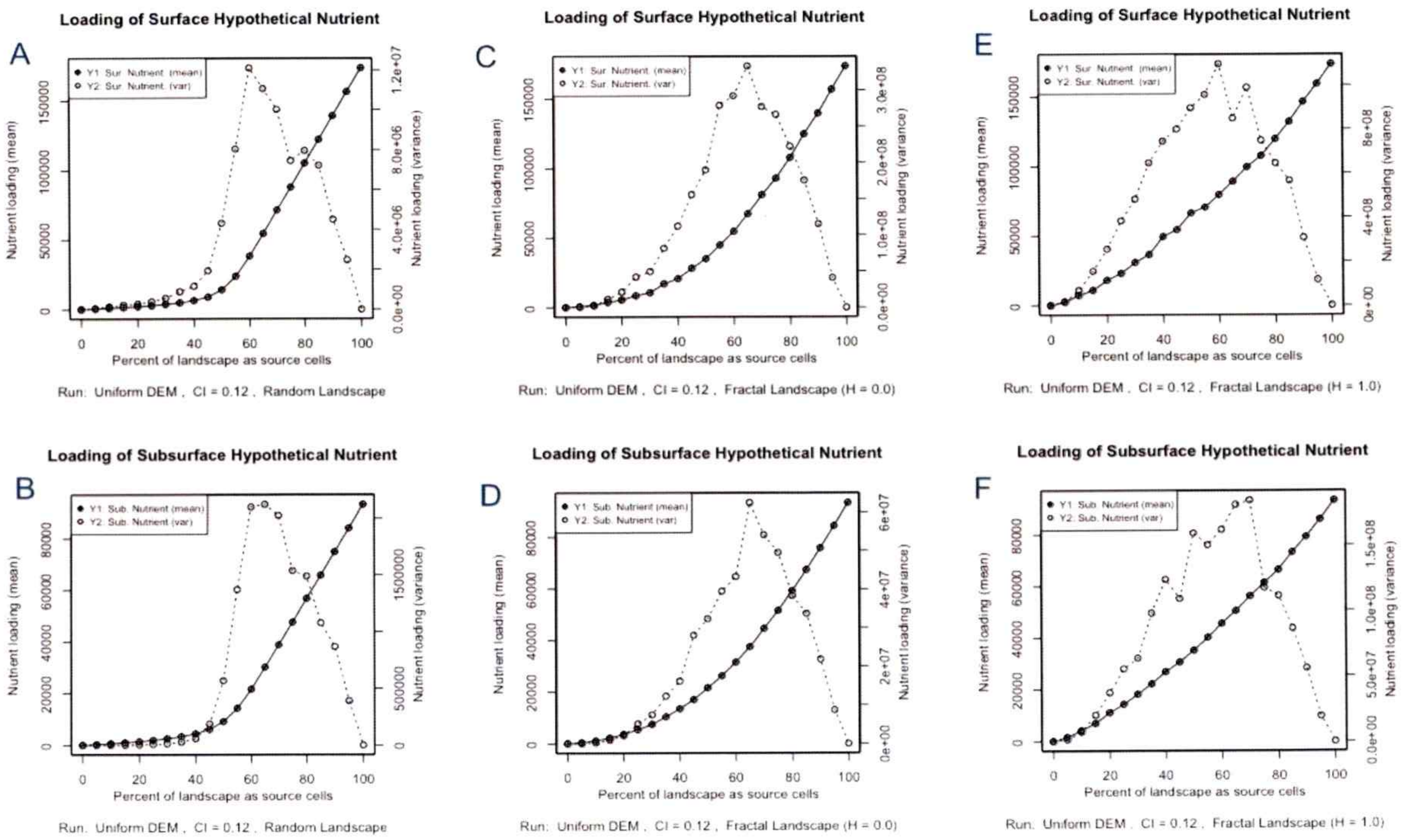


Figure 3.6: Plots of surface and subsurface hypothetical nutrient loading. The level of landscape contagion increases from left to right.

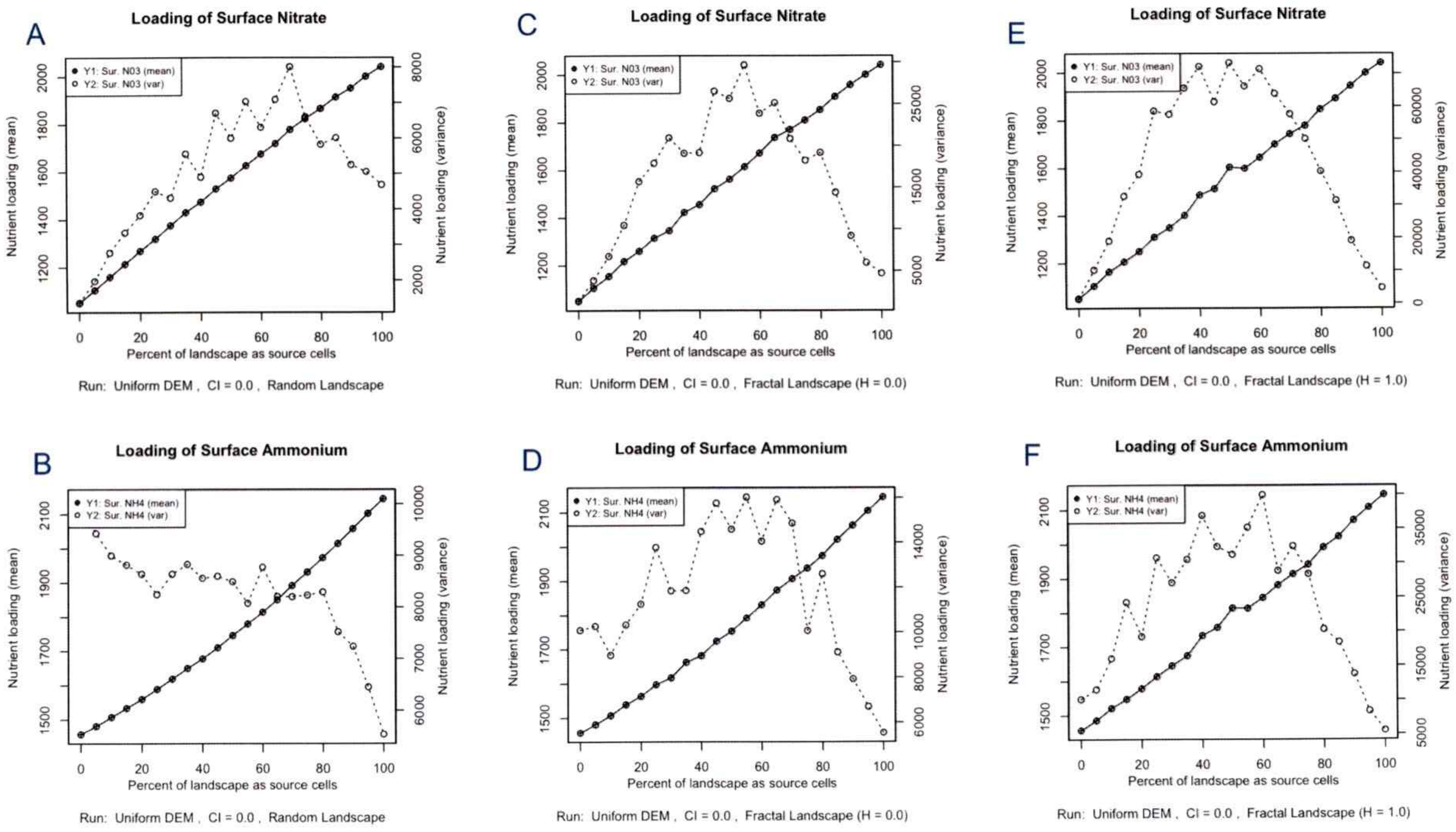


Figure 3.7: Surface NO3 and NH4 loading. The level of landscape contagion increases from left to right.

For most nutrient forms, the coefficient of infiltration did not affect the shape of the variance curve, only the relative magnitudes of loading and variance. However, the response of soluble P to an increase in the coefficient of infiltration from *CI*=0 to *CI* = 0.36 was unexpected. In Figure 3.8A, both the variance and mean present a linear response to increasing source cover in the landscape. This indicates that a source-sink dynamic was not present. In Figure 3.8B, a peak in variance is present, albeit small in magnitude. It is presumed that the slower surface flow due to higher infiltration creates a situation were non-soluble P erodes at a much lower rate. When non-soluble P leaves a cell at a greater rate than soluble P, the sorption equation that governs net desorption/mineralisation shifts toward the net adsorption/ immobilization of soluble P. In this way, the source cell of non-soluble P might become net sinks for soluble P.

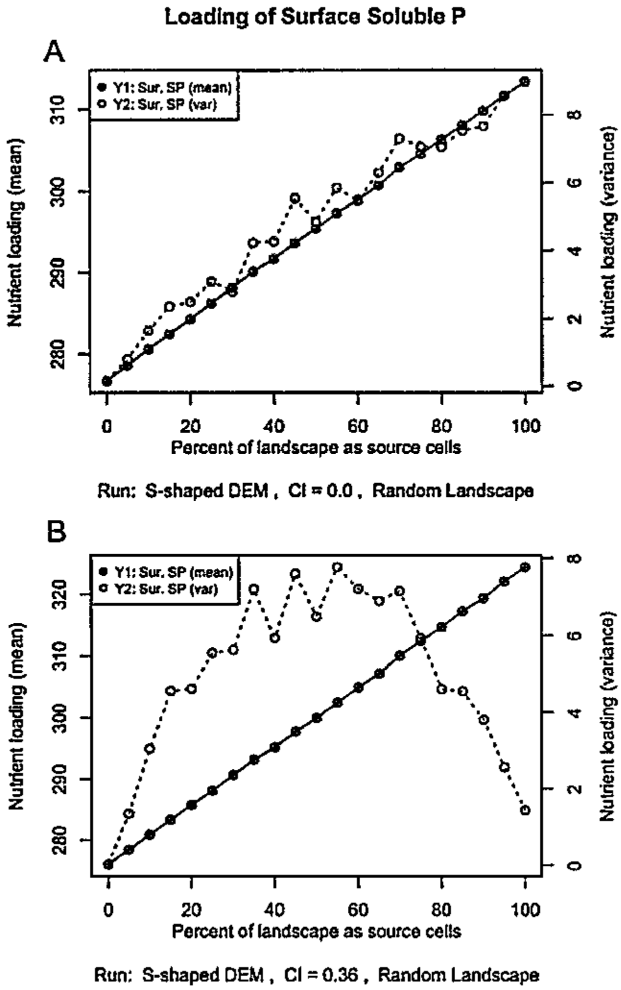


Figure 3.8: Divergent surface soluble P behavior at two levels of infiltration.

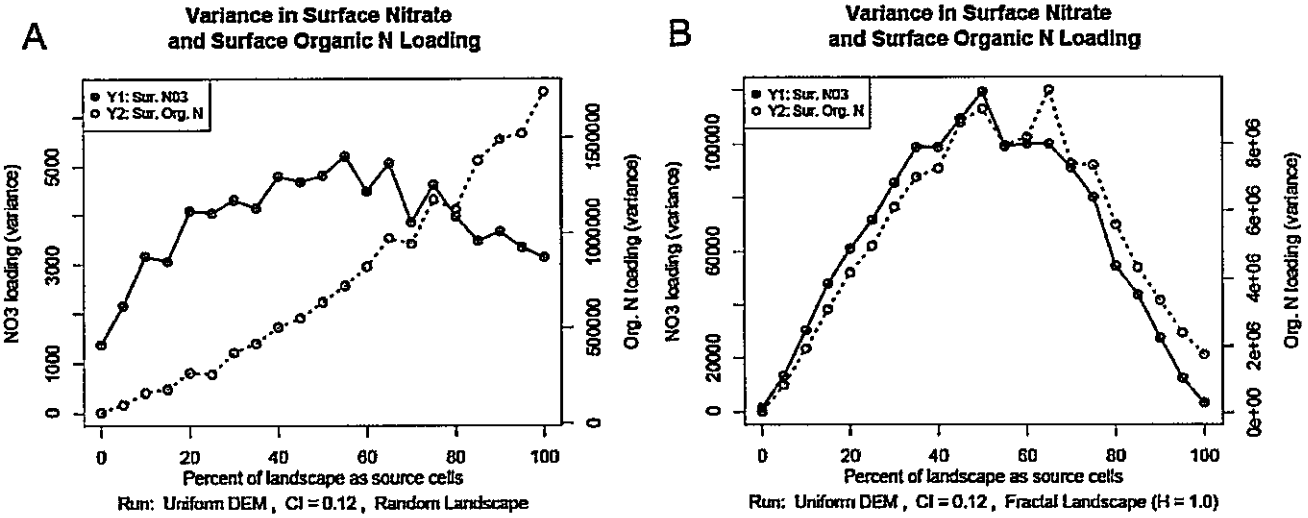


Figure 3.9: Variance in Nitrate and Organic N loading at different levels of contagion.

A comparison of the behavior of soluble versus organic or insoluble nutrient forms in LaNuM shows some notable differences. In Figure 3.9, the variance curves of nitrate and organic N are compared. When the landscapes are random, the nitrate shows a relatively flat variance curve, indicating that the landscape configuration has a minor effect on loading. The variance curve of organic N is directly tied to the mean (not shown) and indicates that the landscape configuration is not important in determining nutrient loading. However, as the landscape contagion increases, both N forms exhibit a variance curve that peaks between 50% and 65% source cover (Figure 3.9B). This shows that in landscapes where sources and sinks are highly aggregated, the configuration of these few patches is critical in determining N loading in LaNuM. At low contagion, it is important to specify the nutrient form in order to understand loading behavior, but at high contagion, it may be possible to lump all N forms due to a similar response to changing *p*.

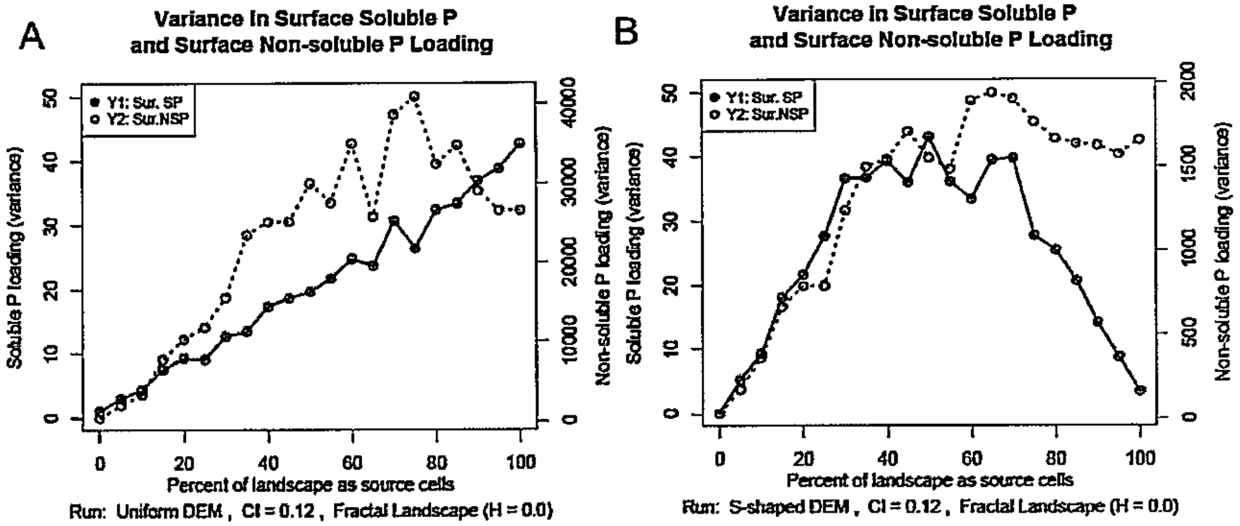


Figure 3.10: Variance in loading for P and NSP with two different topographies

In general, the different topographical models examined do not impact the form of the mean and variance curves. However, the results presented in Figure 3.10 present some limited evidence that topography can influence the shape of the variance curve. In Figure 3.10A, the soluble P variance curve is linear, but changes in Figure 3.10B when the model is run with the S-shaped DEM. It is not clear whether this change is because the S-shaped DEM increases surface soluble P loading overall, whether it is due to an acceleration of flows in the middle of the landscape and deceleration of flows in the "riparian" area, or whether it derives from an interaction between the soluble and non-soluble P forms.

Finally, it is interesting to note that while variation in subsurface loading of the hypothetical nutrient mirrors that of the surface, this is not the case with the N or P cycle. Figure 3.11 shows the case with surface and subsurface nitrate. The surface form has a clear variance peak near 45% source cover, while the subsurface loading has a relatively constant variation. This indicates that the surface source-sink signal is not readily apparent in the subsurface loading.

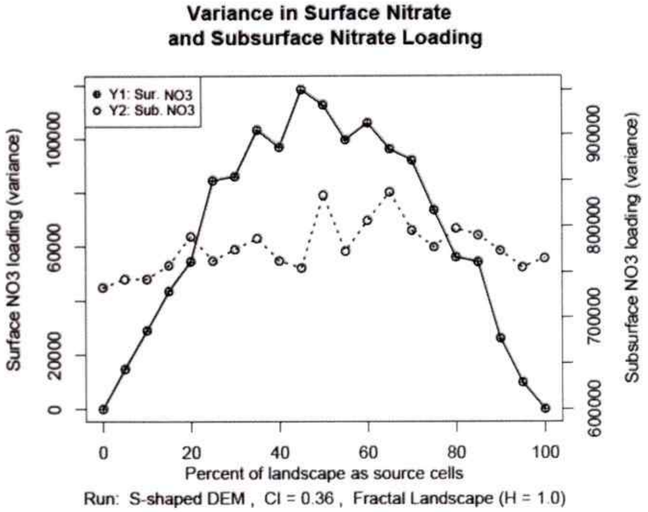
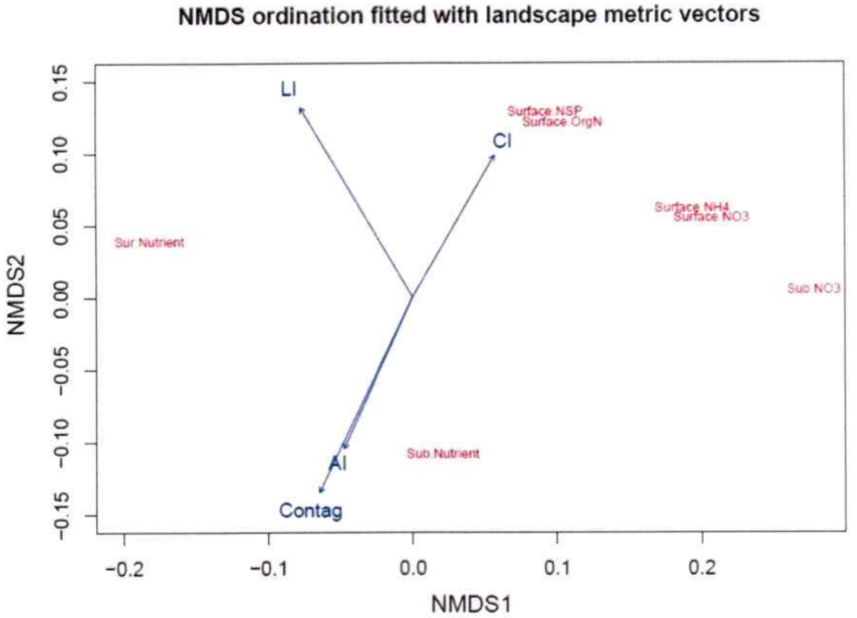


Figure 3.11: Variance in surface and subsurface $NO_3$ loading

## NMDS Ordination and Landscape Metrics

The NMDS ordination essentially provides a map of the distance (dissimilarity) between the export patterns of the different nutrient forms. The distances in a NMDS ordination are intuitive, i.e. the shortest distance between two mapped objects is a straight line between them. The ordination provides another way of viewing the difference (and similarity) between the nutrient forms. The top ordination in Figure 3.12 includes the hypothetical nutrient forms. A selection of landscape-level metrics was fitted as vectors in ordination space. The surface hypothetical nutrient was separated primarily along the first NMDS dimension from the N and P forms. The distance of the hypothetical forms suggests that the patterns in their behavior are, in fact, quite distinct from the N and P cycles. The two insoluble nutrient forms (organic N and non-soluble P) grouped very close together. This is understandable given that the primary export mechanism for both of these forms in LaNuM is overland flow with sediment erosion. NO3 and NH4 also group together reflecting that the same form of equation governs their export (the main difference being parameterization).



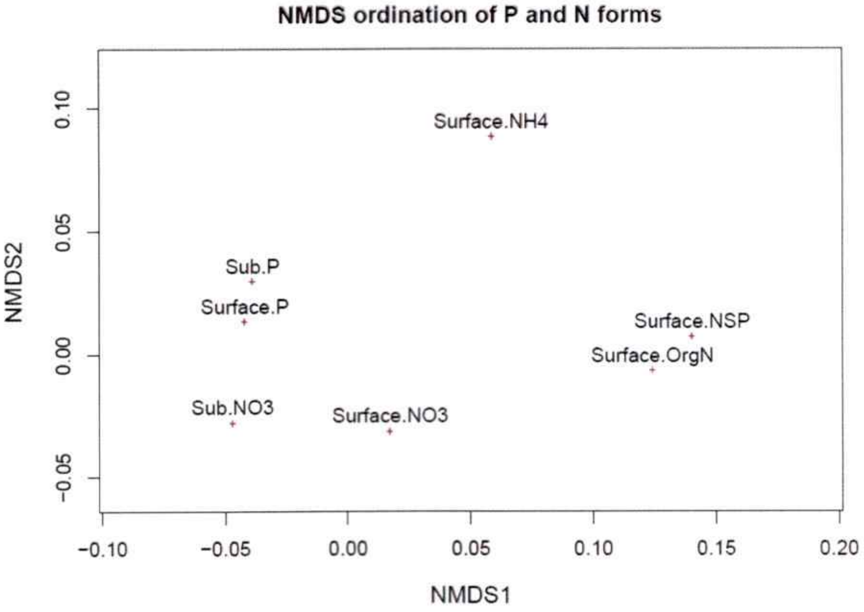


Figure 3.12: NMDS Ordination results.

The fitted landscape metrics point in the direction of most rapid change in value; their lengths are proportional to the correlation with the ordination (Okasanen et al. 2009). Several of the landscape metrics are highly correlated in ordination space. In fact, aggregation index (AI) and contagion were both left in figure 3.12 even though they are redundant. The connectance index appears to be highly negatively correlated with contagion and AI. Organic N and non-soluble P are strongly associated with the connectance index while the subsurface hypothetical nutrient is positively associated with AI and contagion. The leakiness index (LI) describes a somewhat different set of variation in ordination space, distinct from the other three indices. This is interesting given that LI was designed as a functional index based on both on land cover and topography. The lower part of Figure 3.12 is a separate ordination after dropping the two hypothetical nutrient outputs. It clearly separates the organic from inorganic forms; differences between surface and subsurface forms, however, do not appear to be as great as might be surmised given that surbsurface flows are not directly affected by landscape pattern in LaNuM. The correlation values and significance levels for different landscape metrics fitted to the NMDS ordination can be seen in Table 3.6.

The riparian index returns the proportion of cells in class zero (the nutrient source class) for the lowest 20% of the topography. The degree of correlation with the ordination, indicates that the area proximal to where the nutrient leave the landscape is able to describe much of the difference between the nutrient forms. Spearman rank correlation analysis was carried out to assess redundancy between metrics and to see which metrics could serve as indicators of nutrient loading.

Table 3.6: Results of fitting metrics to NMDS ordination. First two columns give the cosines of the vectors, $r^2$ is the squared correlation coefficient. Significance levels are based on random permutations of the data in R.

| Metric Name | NMDS1 | NMDS2 | $r^2$ | Pr(>r) | Significance |
|---|---|---|---|---|---|
| Riparian Index (Land) | -0.5 | 0.87 | 0.908 | 0.001 | *** |
| Core count (Source) | -0.39 | -0.92 | 0.73 | 0.001 | *** |
| Leakiness Index (Land) | -0.51 | 0.86 | 0.699 | 0.001 | *** |
| Aggregation Index (Source) | -0.41 | -0.91 | 0.679 | 0.001 | *** |
| Contagion (Land) | -0.43 | -0.9 | 0.67 | 0.001 | *** |
| Largest Patch Index (Source) | -0.45 | -0.89 | 0.53 | 0.001 | *** |
| Edge Count (Source) | 0.38 | 0.93 | 0.42 | 0.001 | *** |
| Connectance Index (Sink) | 0.48 | 0.88 | 0.408 | 0.001 | *** |
| Percent like adjacencies (Land) | -0.41 | -0.91 | 0.402 | 0.001 | *** |
| Connectance Index (Land) | 0.5 | 0.86 | 0.386 | 0.001 | *** |
| Aggregation Index (Land) | -0.41 | -0.91 | 0.3946 | 0.001 | *** |
| Edge Count (Sink) | 0.45 | 0.89 | 0.38 | 0.001 | *** |
| Core count (Sink) | 0.43 | 0.9 | 0.379 | 0.001 | *** |
| Largest Patch Index (Sink) | 0.29 | 0.96 | 0.334 | 0.001 | *** |
| Patch count (Source) | 0.66 | 0.75 | 0.248 | 0.001 | *** |
| Patch count (Sink) | -0.51 | -0.86 | 0.22 | 0.001 | *** |
| Aggregation Index (Sink) | 0.44 | 0.9 | 0.22 | 0.001 | *** |
| Connectance Index (Source) | -0.72 | -0.7 | 0.18 | 0.001 | *** |
| Fractal dimension (sdv) (Sink) | 0.09 | -1 | 0.049 | 0.001 | ** |
| Mean fractal dimension (Sink) | 0.07 | -1 | 0.04 | 0.01 | * |
| Mean fractal dimension (Source) | 0.35 | -0.94 | 0.02 | 0.14 | |
| Percolation (Source) | 1 | -0.01 | 0.01 | 0.24 | |

Significance Codes: *** 0.001; ** 0.01; * 0.05

Table 3.7 shows correlation between metrics for the moderately aggregated multifractal landscapes (*H*=0). It turns out that the metrics in Table 3.6 that are highly correlated with the NMDS ordination are, in general, highly intercorrelated. This can complicate a clear analysis. Many studies have assessed the redundancy between metrics and either eliminated highly correlated metrics or used principle component analysis and similar methods to reduce the dimensionality of the analysis (Cushman et al. 2008, Kearns et al. 2005, Riitters et al. 1995). The riparian and leakiness indices are positively associated with the amount of area covered by source cells and the percolation of the source class, but negatively associated with the number of patches of the source class. This is likely because patch number often peaks when the proportion of source cells on the landscape is still low (Gardner et al. 1987).

Table 3.7: Spearman rank correlation analysis between landscape and class-level metrics for moderately aggregated multifractal landscapes ($H$=0). Percent of landscape as source cells varied between 5% and 95% ($n$ = 19). Values in italics were significant at $p < 0.05$; values in bold represent Spearman rho values >0.6. (C0=source class; C1 = sink class; L =landscape level)

| Landscape Metrics | CONTAG (L) | AGGREG (L) | CONNECT (L) | Riparian (L) | Leakiness (L) | Tot_Area (C0) | Patch# (C0) | CORE (C0) | Mean_FD (C0) | StDv_FD (C0) | EDGE (C0) | AGGREG (C0) | CONNECT (C0) | Perc (C0) | Patch# (C1) | EDGE (C1) | CORE (C1) | Mean_FD (C1) | StDv_FD (C1) | LPI (C1) | AGGREG (C1) | CONNECT (C1) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| AGGREG (L) | 0.87 | 1.0 | | | | | | | | | | | | | | | | | | | | |
| CONNECT (L) | 0.08 | 0.46 | 1.0 | | | | | | | | | | | | | | | | | | | |
| Riparian (L) | 0.00 | 0.01 | -0.01 | 1.0 | | | | | | | | | | | | | | | | | | |
| Leakiness (L) | 0.10 | 0.19 | 0.13 | 0.92 | 1.0 | | | | | | | | | | | | | | | | | |
| Tot_Area (C0) | -0.01 | 0.01 | 0.01 | 0.93 | 0.89 | 1.0 | | | | | | | | | | | | | | | | |
| Patch# (C0) | -0.34 | -0.39 | -0.23 | -0.65 | -0.65 | -0.72 | 1.0 | | | | | | | | | | | | | | | |
| CORE (C0) | 0.32 | 0.48 | 0.29 | 0.79 | 0.85 | 0.85 | -0.80 | 1.0 | | | | | | | | | | | | | | |
| Mean_FD (C0) | -0.43 | -0.61 | -0.52 | 0.07 | -0.08 | 0.05 | 0.10 | -0.27 | 1.0 | | | | | | | | | | | | | |
| StDv_FD (C0) | -0.52 | -0.56 | -0.19 | -0.39 | -0.46 | -0.45 | 0.75 | -0.66 | 0.35 | 1.0 | | | | | | | | | | | | |
| EDGE (C0) | -0.86 | -0.99 | -0.45 | 0.07 | -0.11 | 0.07 | 0.34 | -0.42 | 0.61 | 0.54 | 1.0 | | | | | | | | | | | |
| AGGREG (C0) | 0.49 | 0.72 | 0.54 | 0.56 | 0.67 | 0.61 | -0.78 | 0.91 | -0.43 | -0.71 | -0.68 | 1.0 | | | | | | | | | | |
| CONNECT (C0) | -0.29 | 0.00 | 0.51 | -0.06 | 0.00 | -0.05 | 0.06 | 0.03 | -0.27 | 0.17 | 0.01 | 0.11 | 1.0 | | | | | | | | | |
| Perc (C0) | -0.11 | -0.08 | 0.02 | 0.81 | 0.77 | 0.85 | -0.64 | 0.67 | 0.01 | -0.32 | 0.16 | 0.45 | -0.03 | 1.0 | | | | | | | | |
| Patch# (C1) | -0.39 | -0.38 | -0.25 | 0.60 | 0.47 | 0.67 | -0.49 | 0.47 | 0.36 | -0.19 | 0.42 | 0.19 | -0.01 | 0.65 | 1.0 | | | | | | | |
| EDGE (C1) | -0.87 | -0.99 | -0.45 | -0.11 | -0.29 | -0.11 | 0.44 | -0.56 | 0.60 | 0.58 | 0.97 | -0.76 | 0.03 | 0.00 | 0.32 | 1.0 | | | | | | |
| CORE (C1) | 0.33 | 0.44 | 0.28 | -0.79 | -0.65 | -0.86 | 0.52 | -0.49 | -0.36 | 0.18 | -0.51 | -0.18 | 0.13 | -0.79 | -0.75 | -0.35 | 1.0 | | | | | |
| Mean_FD (C1) | -0.43 | -0.59 | -0.57 | -0.16 | -0.24 | -0.14 | 0.37 | -0.45 | 0.35 | 0.48 | 0.61 | -0.62 | -0.14 | 0.02 | 0.09 | 0.59 | -0.20 | 1.0 | | | | |
| StDv_FD (C1) | -0.40 | -0.39 | -0.23 | 0.30 | 0.22 | 0.41 | -0.26 | 0.21 | 0.33 | -0.03 | 0.44 | -0.02 | 0.06 | 0.46 | 0.77 | 0.35 | -0.55 | 0.36 | 1.0 | | | |
| LPI (C1) | 0.14 | 0.14 | 0.09 | -0.89 | -0.81 | -0.96 | 0.73 | -0.76 | -0.16 | 0.41 | -0.22 | -0.50 | 0.05 | -0.85 | -0.78 | -0.05 | 0.92 | 0.03 | -0.52 | 1.0 | | |
| AGGREG (C1) | 0.50 | 0.71 | 0.55 | -0.56 | -0.36 | -0.61 | 0.21 | -0.15 | -0.56 | -0.07 | -0.75 | 0.20 | 0.18 | -0.57 | -0.75 | -0.64 | 0.90 | -0.40 | -0.58 | 0.72 | 1.0 | |
| CONNECT (C1) | -0.29 | -0.01 | 0.36 | 0.06 | 0.15 | 0.09 | -0.03 | 0.17 | -0.08 | 0.13 | 0.01 | 0.18 | 0.27 | 0.12 | 0.23 | -0.02 | 0.01 | -0.17 | 0.28 | -0.09 | 0.09 | 1.0 |
| Perc (C1) | -0.10 | -0.13 | 0.01 | -0.86 | -0.84 | -0.85 | 0.73 | -0.80 | 0.07 | 0.47 | 0.05 | -0.59 | 0.04 | -0.83 | -0.59 | 0.22 | 0.70 | 0.04 | -0.40 | 0.85 | 0.44 | -0.03 |

Interestingly, the connectance index and fractal dimension are generally not highly correlated with other metrics and may describe independent components within the data. Fractal dimension is a measure of patch shape, which is unlikely to directly impact nutrient loadings. The connectance index measures the number of functional joinings between patches – in this case if patches are separated by only one cell. When the leakiness index is calculated using the V-shaped DEM, Spearman rank correlation with other metrics decrease. For example, the correlation with the total area of the source class decreases from 0.89 in when using uniform topography to 0.78 using the V-shaped DEM.

Several metrics were highly correlated with LaNuM nutrient loads. Table 3.8 shows the Spearman rank correlations for the uniform DEM with a medium infiltration (*CI*=0.12). The riparian index and the leakiness index are excellent indicators of nutrient loading. Aggregation index and percolation also have a high level of correlation with nutrient output. Despite evidence that surface and subsurface nutrient forms have distinct behavior (e.g. Figure 3.11), subsurface nutrients in Table 3.8 have high correlations with certain metrics. Compared to other nutrient forms, the subsurface ammonium output shows an inverse correlatation with metrics. A negative correlation between subsurface $NO_3$ and ammonium loads is due to the nitrification equation in LaNuM. This differs from the surface layer, where the number and relative location of source cells in a landscape drive ammonium and nitrate loading in a similar way. The Spearman rho decreases notably when random lanscapes or landscapes with a given percentage of source cells are compared to nutrient loading. For example, when random landscapes with ~60% source cells were used in the correlation analysis, only the hypothetical nutrient was correlated with a rho value greater than 0.61 (contagion: 0.83, source area: 0.83, aggregation index-source class: 0.79).

Table 3.8: Spearman rank correlation analysis between landscape metrics and LaNuM nutrient output for highly aggregated multifractal landscapes (*H*=1). Percent of landscape as source cells varied between 5% and 95% (*n* = 19). Values in italics were significant at $p < 0.05$; values in bold represent Spearman rho values >0.6. (C0=source class; C1 = sink class; L =landscape level; Sur = surface; Sub = subsurface, HN = hypothetical nutrient)

| Metrics | Sur HN | Sur P | Sur NSP | Sur NO3 | Sur NH4 | Sur OrgN | Sub HN | Sub P | Sub NO3 | Sub NH4 |
|---|---|---|---|---|---|---|---|---|---|---|
| CONTAG (L) | 0.14 | 0.11 | 0.07 | 0.07 | 0.05 | 0.07 | 0.14 | 0.11 | 0.00 | -0.01 |
| AGGREG (L) | 0.13 | 0.13 | 0.07 | 0.07 | 0.04 | 0.07 | 0.12 | 0.12 | 0.08 | -0.14 |
| Riparian (L) | 0.95 | 0.86 | 0.91 | 0.91 | 0.94 | 0.91 | 0.90 | 0.89 | 0.74 | -0.53 |
| Leakiness (L) | 0.96 | 0.88 | 0.94 | 0.94 | 0.93 | 0.94 | 0.95 | 0.93 | 0.83 | -0.72 |
| Patch# (C0) | -0.71 | -0.66 | -0.61 | -0.61 | -0.61 | -0.61 | -0.69 | -0.68 | -0.61 | 0.46 |
| StDv_FD (C0) | -0.57 | -0.39 | -0.41 | -0.41 | -0.40 | -0.41 | -0.52 | -0.43 | -0.25 | 0.22 |
| EDGE (C0) | 0.15 | 0.20 | 0.25 | 0.25 | 0.27 | 0.25 | 0.18 | 0.20 | 0.29 | -0.24 |
| AGGREG (C0) | 0.89 | 0.84 | 0.87 | 0.87 | 0.86 | 0.87 | 0.93 | 0.87 | 0.80 | -0.75 |
| CONNECT (C0) | -0.22 | -0.17 | -0.19 | -0.19 | -0.18 | -0.19 | -0.19 | -0.19 | -0.15 | 0.11 |
| Perc (C0) | 0.83 | 0.87 | 0.83 | 0.83 | 0.83 | 0.83 | 0.83 | 0.88 | 0.87 | -0.73 |
| Patch# (C1) | 0.46 | 0.31 | 0.39 | 0.39 | 0.41 | 0.39 | 0.50 | 0.33 | 0.36 | -0.22 |
| StDv_FD (C1) | 0.39 | 0.40 | 0.51 | 0.51 | 0.45 | 0.51 | 0.43 | 0.45 | 0.57 | -0.65 |
| EDGE (C1) | -0.54 | -0.55 | -0.50 | -0.50 | -0.47 | -0.50 | -0.55 | -0.56 | -0.52 | 0.54 |
| AGGREG (C1) | -0.87 | -0.83 | -0.86 | -0.86 | -0.88 | -0.86 | -0.93 | -0.83 | -0.75 | 0.64 |
| CONNECT (C1) | 0.27 | 0.33 | 0.26 | 0.26 | 0.29 | 0.26 | 0.27 | 0.31 | 0.34 | -0.35 |
| Perc (C1) | -0.85 | -0.87 | -0.87 | -0.87 | -0.87 | -0.87 | -0.85 | -0.87 | -0.87 | 0.50 |

### Source-Sink Dynamics

The amount of change in source-sink configuration varied greatly with the degree of landscape contagion from the original map to the post-simulation nutrient balance. Figure 3.13 shows this pattern for the nitrogen cycle; the P cycle follows a similar pattern. The arrangement of sources and sinks on random maps changed very little over the course of the simulations in LaNuM, while the highly aggregated landscapes (Fractal, *H* = 1) showed a significant amount of change, especially at high and low source cover. The variation between the 20 replicates was also much greater for this type of landscape, indicating the relative position of the patches in the original map affected how much the source-sink configuration would change over the course of the simulation.

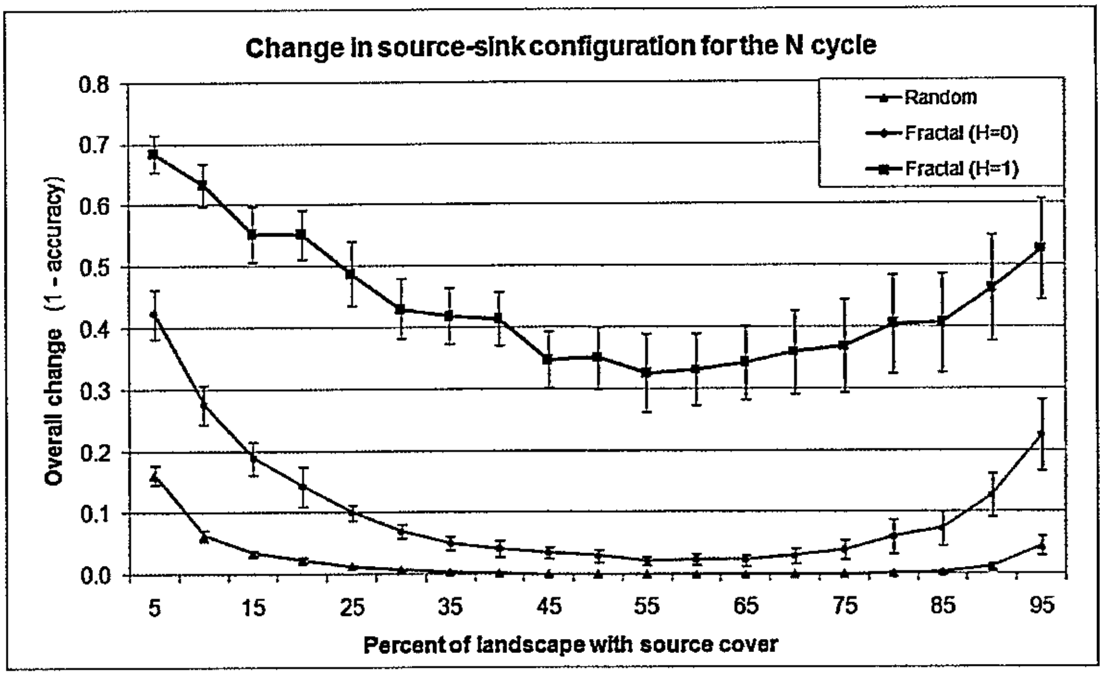


Figure 3.13: Change from the original map to post-simulation source-sink classification. Data are from simulations with the uniform DEM. Error bars represent 1 standard deviation (*n* = 20 maps)

It is interesting that the greatest change in source-sink pattern occurs at the extremes of source coverage in the landscape. Keeping mind that LaNuM was not parameterized in such a way to force source-sink behavior, it appears landscapes with minimal coverage of one of the classes tend to foster behavior associated with the other class. This leads to the idea that when the landscape has close to equal proportion of sources to sinks, it is somehow more stable. In fact, averaging over all landscape types and topographies for the N and P cycles, both nutrients have a peak in accuracy at 55% source cover.

A course-grain analysis of changes in source-sink position in the landscape from the original map to the post-simulation classification was done by comparing the entire landscape with the lower fourth (that portion most proximal to where nutrients exit the landscape). This lower portion is conceptually equivalent to the riparian zone and it would be expected that in the case of the S-shaped topography the lower slope would stimulate conversion of cell to the sink class. The percent of this "riparian zone" covered by sink cells is compared in Figure 3.14 to the entire landscape for the S-shaped and uniform topography and for medium and high landscape contagion. It is evident that the S-shaped topography underlies most of the increase in sinks on the landscape. This topography also gives rise to a clear increase in riparian zone sink cells as compared to the entire landscape. This is not the case with the uniform topography where the content of sinks in the riparian zone is not significantly different from the landscape as a whole. Thus, it appears that topography represents a significant control on the source-sink function of cells in the landscape irrespective of their initial parameterization as sources and sinks. This has potentially important consequences for how land use and land cover maps are interpreted. For example, the export coefficient model bases prediction of nutrient export from a watershed on the coverage of each land use type multiplied by an export coefficient (Caraco et al. 2003, Johnes and Heathwaite 1997). At large spatial scales this approach has been effective. However, for smaller watersheds, incorporating information about landscape position and flowpaths may help improve results (Beaujouan et al. 2002, Caraco et al. 2003).

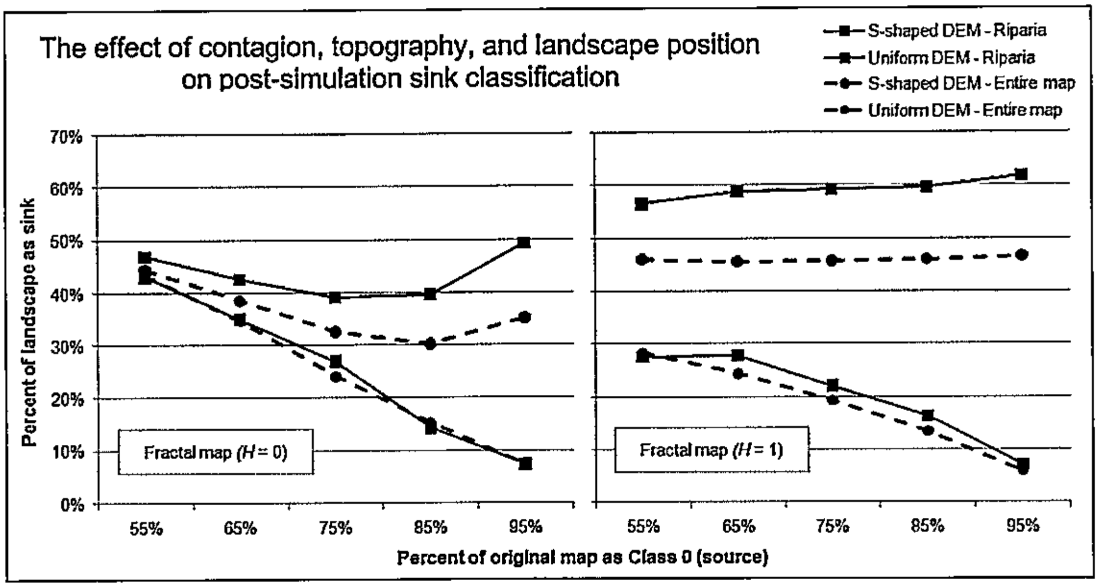


Figure 3.14: The effect of landscape context (riparia vs. entire landscape), topography, and contagion on the amount of functional nitrogen sink cells in the landscape.

In LaNuM, the rates of several hydrological and nutrient cycling processes abruptly change at the boundary between source and sink patches. Flows with a characteristic relative concentration of nutrient forms enter a new "processing regime" as they cross a boundary. Figure 3.15 shows the magnitudes of the source and sink effects for one highly contagious landscape. It is clear that the boundary between source and sink patches concentrates strong source and sink behavior. The core areas of the larger patches have behavior that is close to neutral. This suggests that flows in the interior of each class reach a sort of equilibrium as they move downslope – the nutrients increase or decrease until they balance the processing rates of that class. This behavior is quite interesting considering the simplicity of the model and it shows that LaNuM and similar models are fertile ground for trying to connect landscape pattern and process.

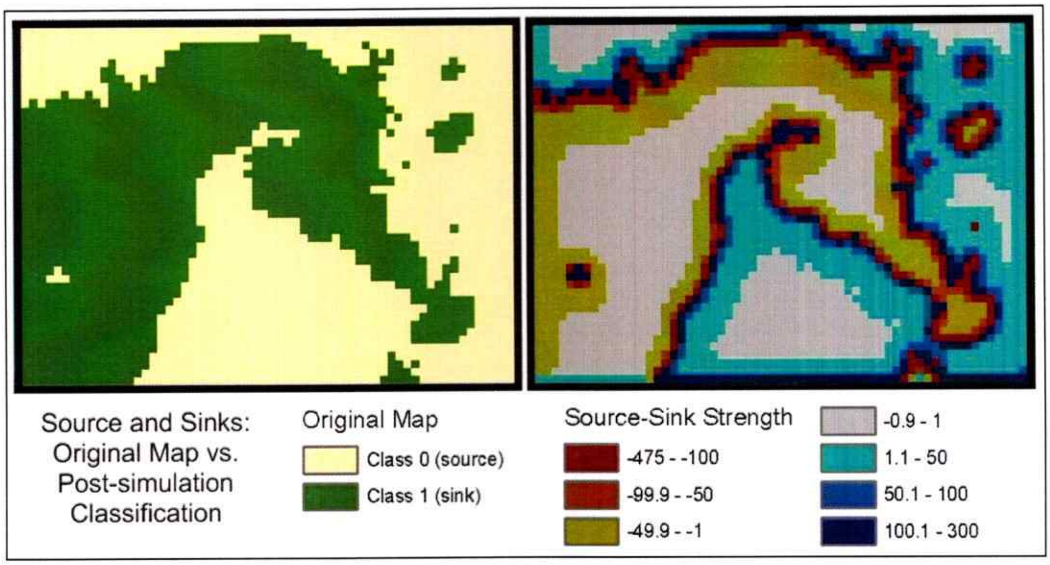


Figure 3.15: A comparison between the pattern of the original map and the nutrient balance output for nitrogen. Source-sink strength is the final balance in a given cell after 130 iterations. This example is a multifractal map ($H = 0$) run with uniform topography.

## Discussion and Conclusion

Simple theoretical models can be used to explore the influence of different factors on the behavior of a simulated system. In this way, hypothesis can be generated or honed. We began with the hypothesis that the importance of the configuration of sources and sinks in landscapes reaches a peak between 55-70% source cover (Gergel 2005). As in Gergel's work, this variance peak was used as an overall measure of the importance of landscape configuration. LaNuM was created as a tool to examine the importance of landscape configuration by allowing users to vary several factors simultaneously, specifically: landscape contagion, subsurface flow rate and topography context. Analyzing nutrient output for simulations at each combination of factor levels, it is clear that each of these factors can have an influence on the magnitude of nutrient loading. For example, the S-shaped topography lowered organic nutrient loads, while the V-shaped topography seemed to decrease inorganic nutrient loads (Table 3.5).

However, the landscape contagion factor had the greatest impact on the shape of the nutrient loading variance peak. Increasing the contagion increased the magnitude of nutrient loading variance and spread the variance peak toward the extreme values of $p$. In other words, increasing contagion lowered kurtosis of the loading variance curve. This can be seen in Figure 3.6.

The hypothetical nutrient is useful as a kind of null model of nutrient behavior in a landscape. Source and sinks for the unreactive hypothetical nutrient were of an equal magnitude. Figure 3.6 shows how surface and subsurface behavior of the hypothetical nutrient is similar as the landscape contagion changes. Similar patterns were produced with the other topographical models. The high kurtosis of the variance peak in Figure 3.6A leads to the conclusion that landscape configuration is very important over a limited range of source cover. Conversely, it indicates that if the proportion of source cells in the landscape ($p_s$) < 0.55, the spatial aspects of the landscape are perhaps relatively unimportant in the study of nutrient loading. As the variance curve expands laterally with increasing contagion, it indicates that spatial configuration may be important at lower $p_s$ such as 0.3. The occurrence of a hypothetical nutrient variance peak ~65% source cover for all levels of the simulation design gives support to the hypothesis that landscape configuration is a critical determining factor of nutrient loads near this $p_s$. It suggests that if nutrient sources and sinks in a landscape have fairly strong and consistent process rates, this type of variance peak should be observed. This indicates that empirical research should make note of which nutrient cycling processes are dominant in a landscape under particular conditions. A consistent set of dominant processes could allow a nutrient cycle to be simplified such that a source-sink approach is meaningful.

We also compared simple N and P cycles with the hypothetical nutrient described by Gergel. LaNuM was parameterized in such a way that the relative rate of internal processes corresponded to the range of values found in the scientific literature. This resulted in a greater variability of loading patterns and, in some cases, to situations where no clear source-sink behavior was taking place. For example, when random landscapes were used in simulations, ammonium, soluble P, non-soluble P, and organic N did not present variance loading peaks. This suggests that the difference in spatial configuration among the random landscapes was not enough to elicit the behavior seen with the hypothetical nutrient. As contagion increased, the variance peak emerged in all the surface N and P nutrient forms. However, subsurface N and P forms did not present clear loading variance peaks, even at the highest level of contagion. This suggests that if source and sink dynamics are not very strong, subsurface nutrient exports will not be sensitive to landscape configuration but rather to nonspatial aspects such as landscape composition. Thus, one conclusion from the work with LaNuM is that in most cases the overall importance of landscape configuration for N and P depends on 1) the level of landscape contagion, and 2) the relative contribution of surface and subsurface flows to overall loading. There may be situations (not modeled here) where sources and sinks have high processing rates that may lead to situations where the leaching of N and P is effectively controlled by surface patterns (as seen in the behavior of the hypothetical nutrient). For example, agriculture and urban land uses can be strong and consistent sources of N and P, while wetlands and remnants of old-growth forest can be consistent nutrient sinks (Alberti 2005, Haygarth 2005).

It was suggested in the introduction that because topography controls the flow of water in a landscape, the process domain concept might be employed in the study of spatial aspects of nutrient cycles. Tables 3.4 and 3.5 make clear that topography influences total nutrient loading, but how does topography interact with spatial configuration? The results indicate that the differences between the 3 hypothetical elevation models did not consistently alter the loading variance peak. The one exception is shown in Figure 3.10. It may be that more complex topography, such as found in mountainous regions, would alter the variance curve to a greater extent. However, the main reason that the variance peak is only slightly affected by topography is because in LaNuM landscape configuration is independent of the topography used. This assumption allowed us to separate the effects of these two factors. However, in most watersheds the distribution of land cover classes is not independent of topography.

The V-shaped model creates different flow patterns as compared to the uniform slope. Essentially, diagonal flow from each side of the landscape toward the center is favored. This did change the correlation matrix between landscape metrics and nutrient loads when compared to the uniform topography, as stated in the hypothesis. However, most of the changes in Spearman's rank correlation coefficient ($r_s$) were minor. A greater change in the correlation matrix was expected. Interestingly, the surface soluble P did experience a noticeable drop in overall correlation with the suite of metrics. The overall loading of this nutrient form was lower for the V-shaped DEM. The longer flowpaths in the V-shaped DEM affected soluble P to a greater extent compared to other nutrient forms because of the small lateral flow coefficient.

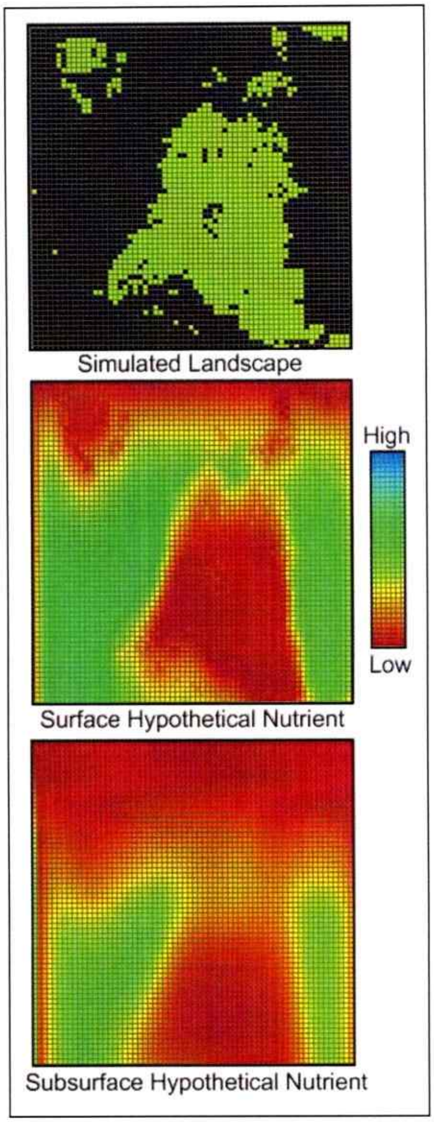


Figure 3.16: From the GUI of LaNuM: surface and subsurface flows of the hypothetical nutrient in an aggregated landscape.

The level of infiltration of water and nutrients to the subsurface layer in LaNuM did not greatly alter the shape of the loading variance curves for the surface nutrient forms. The one exception appears in Figure 3.8, where the bi-directional equation that governs sorption and mineralization of P can create different source-sink behavior in a cell depending on the relative concentrations of soluble and non-soluble P. In the case of the hypothetical nutrient, patterns of surface sources and sinks can be seen in the subsurface layer (Figure 3.16). This kind of behavior was not evident with the N and P cycles given that sources and sinks 1) had much lower process rates and 2) sources and sink behavior did not necessarily correspond to the simulated landscape map. An unexpected result was that several landscape metrics were highly correlated with subsurface loading. Thus, although at a given $p_s$, variation in landscape configuration does not seem to influence subsurface N and P output, when metrics are calculated and compared to nutrient loading over the entire range of $p_s$, strong correlative associations between subsurface nutrients and metrics are apparent. Further work can be done in examining the behavior of surface and subsurface flows. For example, subsurface return flow could be coded into LaNuM, allowing subsurface water and nutrients to return to the surface at the bottom of steep slopes. This would enhance the sink behavior of the "riparian" area, i.e. the topographically lowest area of the landscape. Preferential flowpaths either as impervious surface or macropore flow through the soil profile can change the way nutrients "encounter" the spatial configuration of a landscape (Asano et al. 2006, Harms and Grimm 2008, McGechan et al. 2005). Such flowpaths might also be coded into LaNuM in a simple yet conceptually compelling way.

### Functional indices

Functional indices can help bridge the gap in understanding between the patterns measured by landscape metrics and the processes that interact with them (Müller 2005, Turner 2005b). Functional indices include the location-weighed landscape index (Chen et al. 2009), the phosphorus index (Sharpley 1995), and the nitrogen source and flushing indices (Creed and Band 1998).

The leakiness index (LI) is one of the more developed functional indices and has shown promise in empirical studies of semi-arid systems (Bautista et al. 2007, Ludwig et al. 2007, 2002). The leakiness index is based on a map of vegetation cover and a DEM. Computations begin at the highest cells in the landscape and descend toward the lowest. At each step, the flow values from higher cells are multiplied by the potential loss of sediment – which is a negative exponential function based on vegetation cover. The result is then scaled by the minimum and maximum LI values (Ludwig et al. 2007). The calculation of LI was coded into LaNuM and the results are instructive. LI had some of the highest Spearman's rank correlation values when compared to nutrient loads. What is interesting is that the shapes of the mean LI and standard deviation curves in Figure 3.17 closely resemble the mean and variance curves for nutrient exports. This mean curve moves from an exponential shape for the random landscape to linear for the highly contagious landscapes. Furthermore, the variation in the index at a given percent source cover presents a unimodal peak. The main difference is that this peak is very skewed toward 100% source cover in the case of random landscapes. Given that this index has a similar variance structure to nutrient exports its ability to predict nutrient loads modeled with LaNum is not surprising. But it suggests that metric selection can be improved by examining their response to a series of NLMs. For example, Figure 3.18 shows the behavior of the contagion index. As a landscape-level index it measures the aggregation of both source

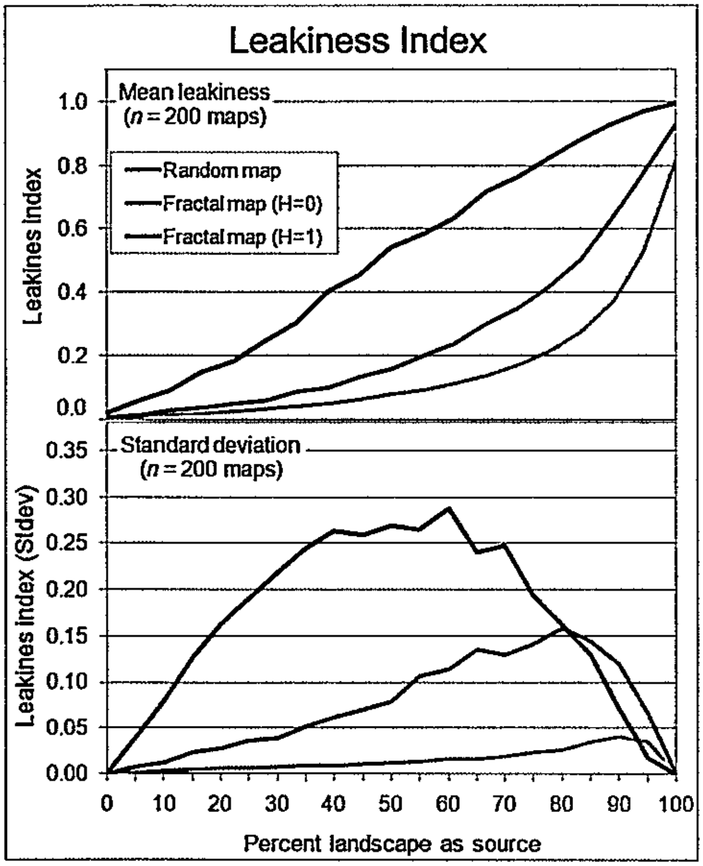


Figure 3.17: Mean and standard deviation of the leakiness index for three levels of landscape contagion

and sink classes and therefore increases as either class approaches 100% cover. The variation is actually bi-modal, peaking between 10-20% source cover and then again between 80-90% source cover. In the context of LaNuM modeling, it is apparent why contagion is not a useful metric for predicting nutrient loads.

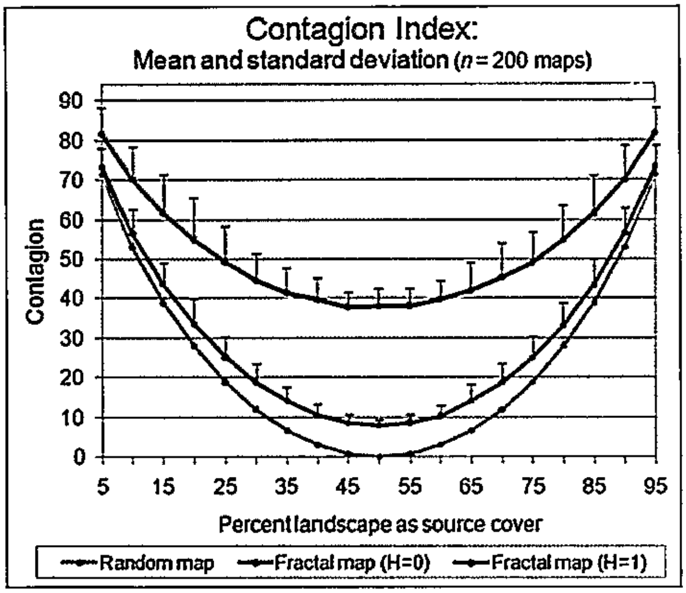


Figure 3.18: Mean and standard deviation of the contagion index for three levels of landscape contagion. Error bars represent standard deviation.

In creating and improving upon functional metrics, it is important to establish which processes are relevant in the system of interest, the dynamics of the process, and what factors constrain or drive those processes (Müller 2005). In the case of nutrient transport and cycling in the landscape, it is essential to consider both the underlying drivers and the mechanisms of nutrient transport. The success of LI in this context stems from the algorithm that estimates flow direction and magnitude from a DEM; essentially, the topography is the driver of landscape flows. Mechanisms such as overland flow in areas of bare ground or higher infiltration due to increased soil porosity associated with vegetation are captured by the LI with a non-linear equation that describes interaction of water and sediment flow with vegetation (Bautista et al. 2007). Topography is the common denominator for watershed hydrologists and geomorphologists studying flowpaths and erosion and biogeochemists studying nutrient cycling and the location of hotspots. Several indices based on topography have been created that characterize wetness across the landscape, hydrological connectivity, sediment erosion, topographic convergence, ground water flow, and even denitrification potential (Bogaart and Troch 2006, Grabs et al. 2009, Lane et al. 2009, Sørensen et al. 2006, Montgomery 2003, Beaujouan et al. 2002). The ubiquity of topographic data sets, and the breadth of relevant information to nutrient transport and processing that can be derived, indicate the utility of basing functional indices on DEMs. Soil and vegetation patterns interact with the topography to control and constrain the hydrologic functioning and transport of water, nutrients and sediment (Zehe and Sivapalan 2009).

Functional indices that attempt to measure critical nutrient processes will require integration of tools and theory from the ecological disciplines mentioned at the outset with those of hydrology and geomorphology. A theoretical model like LaNuM can be used to make progress on two fronts. First, functional indices are often tailored to a specific process or sets of processes (e.g P mobilization and transport in the P index). Understanding when certain controlling factors will be important in the process being measured is critical. For example, Gergel (2005) suggested (and it was corroborated here through LaNuM modeling) that the utility of landscape configuration metrics is dependent on the percent of source cover in the landscape. A theoretical modeling approach can contribute to functional index development by indicating under what combination of factors certain behavior may emerge and when certain factors can be ignored. Second, LaNuM and other relatively simple spatially-explicit models can be used to test the behavior of existing indices under a wide variety of conditions, i.e.

through the use of different parameter sets and NLMs. The source of unexpected behavior of the indices can be more readily traced in a simple model.

In summary, the peak in nutrient loading variance noted by Gergel (2005) is evident in the results of simulations with simple N and P cycles. Landscape contagion increases the overall magnitude of variance and widens the variance curve. The random landscapes failed to produce consistent and clear variance peaks in the different forms of P and N. However, intermediate and highly aggregated landscapes produced variance peaks in all the surface N and P forms. The exception is soluble P which exhibits unexpected interactions with topography and infiltration. Because maps derived from remote sensing are typically more aggregated than random maps, the failure of random landscapes to produce nutrient loading variance peaks does not require a major qualification of the universality of the variance peak and its ramifications for landscape configuration and nutrient cycling. In general, infiltration and topographic setting did not greatly affect the shape of the variance curve although they did have a significant effect on the magnitude of nutrient loading. Thus, the results of the LaNuM simulations show that the hypothesis that landscape configuration is an important factor in determining nutrient loads when source cells make up 55%-70% is robust to different landscape patterns and geomorphological contexts. A major area that remains to be explored is to what extent subsurface flows can reduce the importance of surface landscape configuration. Does the rate of source and sink processes have to be high in order for subsurface flows to reflect the surface pattern? Often practitioners of landscape ecology assume certain land cover classes will be sources or sinks. Results from a comparison of original binary maps and the post-simulation cell-based nutrient balance has indicated that topographic setting represents a significant control on the source-sink function of cells in the landscape, irrespective of their initial identity as sources and sinks. Finally, it is worth noting how a simple model like LaNuM can serve as a virtual laboratory for understanding the link between landscape pattern and process and a tool for developing metrics that can measure some aspect of this link.

# Chapter 4 *GENERAL DISCUSSION*

## Introduction

LaNuM, a simple simulation model of landscape nutrient cycles, was conceived of as a tool to be used in the development of theory in the overlapping space between landscape ecology, ecosystem ecology and biogeochemistry. LaNuM was developed using a theoretical modeling approach which aims to further theoretical development by 1) using simple models to generate and revise hypotheses and 2) examining the consequences of assumptions made about model structure, complexity, and conceptual underpinnings. This chapter summarizes the results obtained with the LaNuM model indicates how the results can contribute to the development of theory in this space of disciplinary overlap. But first I review the salient ideas from Chapters 1 and 2.

## Elements of a bridge theory

Nutrient cycles are not a new subject of scientific investigation (Gorham 1991). However, there is much that is not understood about how nutrient cycles vary in space and time and how biological, physical, chemical, hydraulic, climatic and socioeconomic factors interact to control cycling and transport rates. The role that nitrogen and phosphorus play in water quality problems and their ability to impact ecosystem functions and services underscores their importance as subject of inquiry (Carpenter et al. 1998). In fact, nutrients can be viewed as a currency used and manipulated by both relatively "undisturbed" ecosystems and by humans in agricultural or urban systems (Vitousek et al. 1997a). Currently, several disciplines in the ecological and physical sciences include nutrient cycles as a key area of investigation. This has led to a situation where distinct approaches, based in divergent theoretical constructs, have been brought to bear on the same set of phenomena. In the second edition of their book Ecological Understanding, Pickett and colleagues (2007) state that theory is "perhaps the most important tool for integration in ecology." In this context, it is essential to take deliberate steps to promote integration of the theoretical concepts currently employed in the study of nutrient cycles. In Chapter 1, I proposed that a "bridge" theory could unite relevant theoretical constructs from different disciplines and thus promote integration and understanding.

The first step toward developing this bridge theory involved a review of approaches employed by ecosystem ecology and landscape ecology in the study of nutrient cycling. It was clear from delving into the related literature that a conspicuous divide has separated these two subdisciplines of ecology, due in large part to their focus on different levels of the organizational hierarchy in ecology – landscape ecologists looked primarily at population dynamics, while ecosystems ecologists studied their namesake. Although the study of ecosystem process from the spatially-oriented perspective of landscape ecology was recognized early on as a potential area of research (Forman and Godron 1981), recent reviews of the state of landscape ecology bemoan that too little integration between processes and spatial patterns has occurred (Turner 2005b, Wu and Hobbs 2002). Both of these subdisciplines would gain from integration of theory: landscape ecology would benefit from the rich and diverse strands of ecosystem theory while ecosystem ecology would gain tools that could inform the opening of "black-boxes" when internal heterogeneity was strongly related to important ecosystem processes. The spatially-explicit study of nutrient cycles represents a proving ground for the integration of theoretical concepts from these subdisciplines.

A next step was to define the domain of this bridge theory. My strategy was to limit the essential phenomena of interest, but that allows the use of numerous levels of organization and spatiotemporal scales. The phenomena of interest was defined in the following way: (1) spatial patterns of nutrient concentration or mass across terrestrial and aquatic landscapes and how these patterns change with time; (2) patterns of biogeochemical processes, i.e. heterogeneity of their occurrence and rates in space and time; (3) biological, physical, chemical, hydraulic, climatic and socioeconomic and political drivers of nutrient cycle dynamics. Subsequently, fundamental questions were posed that address the foundation of this bridge theory. Such questions serve to refine a developing theory (Pickett et al. 2007). Questions can help in understanding which components of the theory can be borrowed or adapted from existing theory and in what cases new components will need to be created.

Continuing to build this idea of a bridge theory, I began to identify concepts and constructs from a variety of subdisciplines that could prove useful in the study of the spatial aspects of nutrient cycles. Brief descriptions were given of the following concepts: patch mosaics, ecological boundaries, landscape gradients, ecosystem stoichiometry, the watershed concept, networks and source-sink dynamics. The list is intended to give a sense of the theoretical breadth that a coalescing "bridge" theory could draw upon. Ultimately, the concepts that seem appropriate will need to be integrated into a theoretical framework that can order in such a way that links between them are clear and so they can be readily used to create models.

Elsewhere in the text of Chapter 1, I addressed the importance of modeling to the development of theory. Scheiner and Willig (2008) describe three hierarchical levels of theory: (1) the level of general theory – where fundamental principals are enunciated; (2) the level of constituent theories – where the domain is specific to a subdiscipline; and (3) the model level – where predictions and causal relations are most often dealt with. In beginning to describe theory that can bridge the gap between subdisciplines, this third level is a good place to start. Many existing theoretical concepts belong to this level and modifying them and integrating them represents a bottom-up approach to the ontogeny of theory. Modeling intersects directly with theory-building: models are important in formulating new questions and hypotheses, clarifying what are or are not critical features of complex natural system, exploring the dynamics of systems that are too large or difficult for a empirical experimental approach, and setting preferences for empirical research (May 1981, With 1997, Malanson 1999, Urban 2005, Scheiner and Willig 2008).

There is a long-running debate over whether simple and phenomenological or complex and mechanistic models are best able to describe or predict the behavior of a given system. I point out that this debate distracts us from what is often the case: combining or iterating between different types of models and empirical data can create a much greater degree of certainty in the results than one approach by itself. A conceptual model was presented that shows how modeling methodologies can be combined iteratively in support of the development of theory. Using LaNuM in an iterative modeling strategy along with a physically-based spatially-explicit eco-hydrological model like RHESSys (Regional Hydro-Ecologic Simulation System) would be a way of testing hypotheses and gaining insight into the spatial dynamics of nutrient cycling processes (Tague and Band 2004).

By proposing a domain for theory that could bridge the gap between disciplines my goal is to identify a spatially-oriented approach to nutrient cycling as valid area of study that is currently lacking a cohesive theoretical framework. The primary objective is to avoid stagnation on the edges of current theoretical domains. One way forward is to provide examples of integration of theoretical concepts that come from different disciplines. Eventually, the development of a framework that can link the concepts mentioned in Chapter 1 as they relate to the phenomena of interest might be attempted.

### Design of a theoretical model: LaNuM

Continuing with the theme of modeling approaches to the development of theory, I introduce the Landscape Nutrient Model (LaNuM) in Chapter 2. LaNuM belongs to a class of simple simulation models used to generate and revise hypotheses. While there was no attempt to model the patterns observed in specific watersheds, an effort was made to parameterize the model in such a way that the relative process rates corresponded to the range of values seen in the scientific literature. Insight can be gained not just from analyzing the modeled nutrient outputs, but from looking for patterns in model behavior and linking them to aspects of model structure, complexity, and conceptual underpinnings.

Theoretical or "heuristic" models that examine the interaction between pattern and process can be seen as occupying the area between complex, data intensive watershed models and simple empirical models like the export coefficient model (Caraco et al. 2003). I describe several models that fit this description, including a simple model of riparian buffers that was used to examine the effects of variation in buffer width and continuity on nutrient loading (Weller et al. 1998). Another interesting modeling effort was based on a cellular automata ecosystem model and used to explore the interaction between landscape pattern and the functioning of nitrogen fixing and non-fixing components (Jenerette and Wu 2004). However, it was the model created by Gergel (Gergel 2005) that provided direct inspiration for the creating of LaNuM. Gergel's approach was simple yet capable of demonstrating the importance of landscape configuration on nutrient loading. The model was based on binary random maps that were assigned a fixed source or sink behavior. Her use of the loading variance curve (over percent of landscape as source cover) as an indicator of the importance of landscape configuration on nutrient loading was appealing in its simplicity, its ability to integrate the configuration of numerous landscape, and its ease of interpretation. Two major questions were explored with this model: (1) Under what conditions might the arrangement of land cover types in a landscape be more important than simple measures of landscape composition? and (2) How does heterogeneity in source output at different scales impact the utility of landscape indicators? Gergel concluded that landscape indicators that characterize spatial configuration would be most helpful in watersheds containing an intermediate ratio of sources:sinks.

Before constructing LaNuM, I completed two conceptual modeling exercises: 1) the placement of LaNuM in a conceptual framework that includes essential theoretical concepts that were used in model construction, and 2) the creation of a conceptual model that shows LaNuM's focus on how source and sink dynamics can influence nutrient outputs. Factors that were hypothesized to affect the source-sink dynamic were included. I approached the construction of LaNuM conscious of the balance between increasing model complexity in order to more accurately reproduce certain processes and simplicity as a means to facilitate direct connections between assumptions and model behavior. The following processes and functions coded into LaNuM were considered important in the exploration of landscape configuration, source-sink dynamics and nutrient loading:

1) A simple nitrogen cycle model with $NO_3$, $NH_4$, organic N and transformation processes allowing movement from one nutrient form to another.
2) A simple phosphorus cycle with two forms: soluble and non-soluble P
3) Landscape water flows as the transport mechanism of nutrients
4) Sediment erosion as a way to simulate organic nutrient transport
5) The ability to model flows using any topographic model
6) The ability to introduce any land cover map into the model (not just NLMs)

7) A subsurface layer allowing leaching of inorganic nutrient forms

8) The calculation of landscape metrics for each landscape modeled.

9) The ability to visualize movement in the landscape using a GUI

10) The ability to do sensitivity analyses & batch runs using the command prompt

These characteristics of LaNuM were not (as far as I am aware) part of Gergel's model. Taken together they make for a flexible model that is able to simulate a variety of landscape types in a variety of topographic contexts with different varying surface:subsurface flow ratios. Chapter 2 describes the equations that govern landscape flows and nutrient cycling. Nutrient cycling equations come primarily from Viney et al. (2000). Precipitation and erosion equations come primarily from the SWAT model (Neitsch et al. 2002).(Viney et al. 2000) The rate of water flow and direction are based on the multiple flow direction model (Freeman 1991). Numerous landscape metrics are coded into LaNuM, most coming from FRAGSTATS documentation (McGarigal and Marks 1994). The leakiness index was adapted from Ludwig et al. (2007) and the percolation index from Gardner (1987). After describing the internal structure of LaNuM, a sensitivity analysis is carried out. The results of this analysis are generally in agreement with the design philosophy behind LaNuM: that model processes be most sensitive to the rate coefficients included in the principal equations. Finally, LaNuM output (the hypothetical nutrient) is compared to Gergel's results as a way to analyze its utility as a theoretical tool.

### LaNuM modeling

Simple theoretical models can be used to explore the influence of different factors on the behavior of a simulated system. Chapter 3 presents the experimental modeling design and the principal results from using LaNuM as a theoretical model. The point of departure was the hypothesis that the importance of the configuration of sources and sinks in landscapes reaches a peak between 55-70% source cover (Gergel 2005). Part of the ontogeny of theory involves enunciating hypotheses that may have some widespread relevance and then honing them. Rigorous testing of hypothesis before they reach a certain level of maturity may lead to the rejection of ideas with real utility (Pickett et al. 2007). A nutrient loading variance peak appears when one compares binary landscapes parameterized as sources and sinks over the entire range of *P* (the proportion of the class interest in the landscape). The unique properties of random landscape maps (e.g abrupt percolation threshold), compromise the generality of conclusions that are reached when using them in modeling exercises. Thus, a core objective of this research was to probe and hone Gergel's hypothesis. This involved examining under what conditions the loading variance peak appeared or disappeared. Ultimately, this has provided a more nuanced view as to when landscape configuration is important in determining nutrient loading.

The design had three main factors with 3 levels each. Within each level, a series of 200 landscapes were run in LaNuM for each 5% change in source cover class. Landscape contagion was a factor with three levels: random, moderately aggregated fractal landscape, and highly aggregated landscape. Topography was the second factor with three hypothetical elevation models as levels: a uniform DEM, an S-shaped DEM, and a V-shaped DEM. The third factor was relative flow rate of subsurface flows as controlled by the infiltration coefficient, also with three levels: zero, 0.12, and 0.36. Overall, the degree to which the peak in nutrient loads holds true for other types of neutral landscapes and topographic settings can be used to indicate the degree of universality of the variance peak as measure of the importance of spatial configuration. Below I reiterate the hypotheses proposed before running LaNuM simulations and elaborate on the results. The following section presents more detailed results and their ramifications.

### Hypotheses

1) The importance of the configuration of sources and sinks in landscapes reaches a peak between 55-70% source cover.
2) Greater contagion will lead to a higher level of importance of landscape configuration.
3) The S-shaped DEM will slow down flows near the bottom of the landscape favoring the formation of sink cells.
4) The V-shaped DEM flow patterns will significantly alter the correlation matrix between landscape metrics and nutrient loads (as compared to the uniform DEM).
5) As the prevalence of subsurface water flow increases, the pattern "stamp" that surface vegetation patterns impart to subsurface nutrient will decrease.

Hypothesis one, which was derived from Gergel (2005), was found to be true, with a few exceptions. The variance peaks of the hypothetical nutrients conformed to this range. Variance peaks for N and P cycles in most groups in the experimental design did fall in this range. However, one caveat is that with only 200 landscapes per simulation, the variance curves are somewhat jagged in appearance. Thus a peak may fall outside of this range, but the overall area under the variance curve is centered in this range. The second exception is that maps with the highest level of contagion tend to produce wide curves that look to be centered around 50% source. For those cases where the peak was located out of the range, the discrepancy was minimal.

Hypothesis two is true for all nutrient forms. The increase in contagion not only stimulated the appearance of the loading peak (as compared to the random landscape) in N and P forms, but independent of the shape of the variance curve, mean loading increased significantly.

Hypothesis three was also true. The formation of sink cells in the "riparian" zone of the model is shown in Figure 3.14 in Chapter 3. Table 3.5 has mean and standard deviation values for non-soluble P showing that loadings are greatly reduced when the S-shaped DEM is used.

Hypothesis four was false. The correlation matrix between landscape metrics and nutrient loads of the V-shaped DEM when compared to the uniform topography did in fact change. However, most of the changes in Spearman's rank correlation coefficient were minor.

Hypothesis five appeared not to be true for the subsurface hypothetical nutrient. None of the P or N forms presented variance curves for their subsurface forms. Thus, further simulations would have to be carried out to provide a satisfactory answer. In order to stimulate a variance curve in the subsurface N and P forms, a different parameter set would have to be used in order to stimulate the strength of the source-sink dynamics.

## LaNuM modeling results and theoretical considerations

### Landscape Contagion

LaNuM results showed that the degree of aggregation of patch types (what I termed "contagion" although it wasn't based on the contagion index) had an important impact on the loading variance curves. First of all, the random landscapes did not produce the expected loading variance curve for all forms of N and P, except surface $NO_3$. This indicates that overall N and P loads were not sensitive to configuration of sources and sinks in the landscape. The parameterization of LaNuM was based on the relative N and P transport and transformation rates culled from the literature and thus could be seen as somewhat conservative. In contrast, the hypothetical nutrient was parameterized to have strong and invariable sources and sinks. The $NO_3$ variance peak in random landscapes may have been due to differences between the different forms deriving from the simple N cycle coded in LaNuM: only $NO_3$ is directly available for denitrification. There are a few ramifications of this result for random landscapes: 1) differences in spatial configuration between random NLMs are minor when considering the source-sink dynamics of slow-cycling nutrients; 2) strong sink uptake and source output of nutrients is required to produce a clear variance curve.

Landscapes of an intermediate contagion level produced variance peaks in the surface N forms. The surface soluble P did not form a clear variance peak except in one case (under the topography section below). However, the fact that the soluble P variance curve sits above the 1:1 diagonal at intermediate source cover indicates that spatial variability may be inflating these variance values. The non-soluble P form had variance peaks that were incompletely formed – indicating that landscape configuration was playing a role in loading, but that the other stochastic process in the model, rainfall, was also contributing to the variance curve. The variance curve of the hypothetical nutrient continued to peak at 65% source cover, but the curve was wider – indicating that spatial configuration was affecting total loading at a lower percentage of source cells. The N cycle variance curves had a jagged appearance when source and sink patches were at intermediate relative abundance. This variability could be due to the small sample size; each combination of factors had 200 replicate landscapes, while Gergel used 10,000.

Highly aggregated landscapes produced clear variance peaks in all surface nutrient forms except soluble P, which did not produce a clear variance curve on a uniform DEM with zero infiltration. However, soluble-P did form loading variance peaks at other levels of topography and infiltration. All variance curves produced with the highly aggregated landscapes had low kurtosis. This shows that as the variance curve expands laterally with increasing contagion, the spatial configuration becomes an important control on loading for most of the range of source cover. In fact, only above 85% source cover and below 15% source cover could the effect of spatial configuration be considered relatively unimportant for N export. It is important to note that as contagion increases the mean loading stays constant while the peak variance values increase significantly, by a factor of 2.5 – 4, depending on the nutrient form. Although the hypothetical nutrient produced variance curves with a high kurtosis as compared to the N and P forms, the trend toward higher variance and wider variance curves holds true.

The change in loading variation in response to increasing landscape aggregation is associated with a key property of NLMs – the percolation threshold. In random binary landscapes, half of the landscapes will percolate (full connectivity of the cover class of interest between top and bottom of landscape) when $p$ = 593% of the map (Gardner et al. 1987). In landscapes of higher contagion the threshold can change somewhat. However, the main difference, as evident in figure 4.1, is that the frequency distribution becomes gentler with increasing contagion meaning that from 20% to about 85% source cover, some portion of highly aggregated NLMs would be on either side of the percolation threshold.

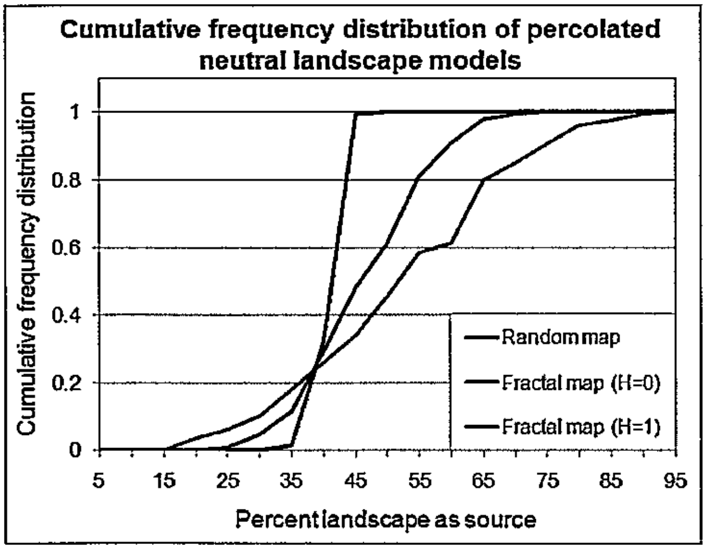


Figure 4.1: Cumulative frequency distribution of percolated landscapes by contagion level.

Because the behavior of landscape metrics often changes significantly near the percolation threshold, we would expect heterogeneity in percolation status for this wide range of source cover to underlie significant differences in pattern (Gardner et al. 1989). This in turn underlies the increase in overall loading variance and the decrease in kurtosis of the variance curves.

**Conclusions about landscape contagion:**

- Gergel's hypothesis of a variance peak at intermediate relative abundances of source and sink patches does not hold for the N and P cycles on random landscapes.
- The conditions under which random landscapes can give rise to a loading variance peak appear to be very limited. Strong, invariable source-sink behavior is required along with the absence of any other sources of variation.
- At an intermediate level of contagion, the N cycle is clearly controlled by spatial configuration for intermediate source coverage, while the P cycle shows some influence of spatial configuration but not a clear peak indicative of the importance of spatial configuration.
- High levels of contagion produce large, wide variance curves, with the hypothetical nutrient having a higher kurtosis than N and P forms. This leads to the conclusion that landscape configuration is very important over a wide range of source cover and, conversely, that only at extreme relative source and sink abundances does spatial configuration become irrelevant in the prediction of nutrient loading.
- Landscape percolation is an underlying driver of variability in spatial configuration at intermediate relative abundances of source and sink, and the change in the

cumulative frequency distribution at high contagion can explain why the nutrient loading variance curve has a lower kurtosis.

### Topography

Three topographic models were used in the LaNuM simulations. The uniform slope is the simplest and used as a baseline for comparison with the S-shaped and V-shaped DEMs. Mean loading of the hypothetical nutrient was not significantly different between the topographic models. For $NO_3$, mean loadings were ordered in this way: U-DEM ≈ S-DEM > V-DEM. For soluble P: S-DEM > U-DEM >> V-DEM, however this order is reversed for non-soluble P and organic N: V-DEM > U-DEM >> S-DEM. Given that the differences between these models in overall slope and complexity were minimal, it is clear that topography is an important control over mean loading, both by influencing rates of water flow and the associated nutrients and by placing constraints on soil wetness which in turn affects bacteria-mediated nutrient transformations like denitrification (Beaujouan et al. 2002, Florinsky et al. 2004) It is also readily apparent that the mean loading pattern is essentially reversed in organic nutrient forms as compared to inorganic forms. This difference stems from the fact that the main transport mechanism for organic and immobilized forms is sediment erosion that responds in a non-linear fashion to runoff. The effect of topography on total N or P (as opposed to one nutrient form) is more complex given the distinct behavior of soluble and insoluble forms.

In general, the different topographical models do not influence the shape of the loading variance curves. This indicates that topography does not significantly change the way the nutrient flows respond to different spatial configurations of sources and sinks, at least at this level of simplification. However, soluble P, which did not readily respond to increasing landscape contagion in terms of the shape of its variance curve, did form a variance peak when simulated using the S-shaped DEM (but not the V-shaped DEM). In LaNuM, soluble P is similar to $NO_3$ in terms of equations governing its movement and uptake by vegetation. However, there is a two-way sorption equation that governs transformation into the non-soluble form. It is presumed that since the low slope in the "riparian" area of the S-shaped DEM effectively traps non-soluble P this stimulates greater mineralization and eventually higher soluble P export.

### Conclusions about topography

- When landscape configuration varies independently from topography (not a realistic assumption for many watersheds), topography does not significantly interact with the way nutrient flows respond to the spatial configurations of sources and sinks.
- Determining the overall influence of topography on nutrient loading is complicated by divergent responses from organic and inorganic nutrient forms.
- In the case that a nutrient cycle has forms with distinct responses to topographic controls and there is a two-way transformation process between these forms, the likelihood of interaction between topography and spatial configuration of sources and sinks increases.
- Despite the complexity of incorporating topographic measures into functional indices (see previous two points), this is a promising area of investigation because topography ultimately drives landscape flows of water and nutrients in most

terrestrial systems. Incorporating information about the drivers of transport processes into indices can improve the ability of spatial metrics to predict nutrient loading. And perhaps just as importantly, the interpretation of these indices will be easier because a conceptual connection has already been posited about the influence of spatial pattern on process.

### Surface vs. subsurface flows

For most nutrient forms, the coefficient of infiltration did not affect the shape of the variance curve, only the relative magnitudes of loading and variance. As in the case of topography, this indicates that the different levels of infiltration and subsurface flow do not significantly interact with the way surface nutrient flows respond to the spatial configurations of sources and sinks. The hypothetical nutrient shows an intriguing pattern in its subsurface loading for all landscapes and topographical models: a variance peak appears that mirrors the shape of the surface variance peak. This indicates that the configuration of patches on the surface can create patterns of water and nutrient concentrations that propagate downward and laterally, persisting even though they are no longer influenced by the surface pattern. This pattern of reflection of variance structure to the subsurface flows was not seen in the N and P cycles. In LaNuM, organic and immobilized forms don't move in the subsurface compartment. As a result, the relative concentration of soluble and non-soluble forms on the surface is affected as the insoluble forms leach to the subsurface layer. Some evidence described in Chapter 3 shows that this mechanism is behind the appearance of a variance peak in surface soluble P when infiltration is increased.

By definition, infiltration controls the relative importance of surface versus subsurface flowpaths. Thus, when infiltration is high, the pattern of loading variance of the combined surface and subsurface forms may cease to show the impact of landscape configuration. A combination of variance pattern for surface and subsurface $NO_3$ showed that a significant amount of noise from the subsurface output was superimposed on the variance peak lowering its value as an indicator of the importance of spatial configuration.

### Conclusions about infiltration and subsurface flows

- In general, the introduction of subsurface flows in this conceptual model did not impact the shape of the variance curve for surface flows. Thus if the goal of a study is to relate spatial configuration to surface runoff or shallow lateral flow (within the root zone), the relative magnitude of surface versus subsurface flows should be irrelevant.
- In conditions where infiltration occurs rapidly relative to surface runoff and soil water moves toward the bottom of the landscape with little direct interaction with the terrestrial ecosystems, the overall influence of spatial configuration on nutrient loading is expected to be minimal. However, this depends on the degree of internal cycling in the terrestrial system. Tight nutrient cycles tend to immobilize mobile nutrient forms through uptake by soil microbes or vegetation.
- In systems with uniform infiltration and subsurface flow and a strong source-sink dynamic on the surface, spatial patterns of nutrient content will propagate to the subsurface layer, tending to become more diffuse with time.

## Final Conclusion

After the above discussion, I now answer directly the central question of this thesis:

*When is spatial heterogeneity an important factor in explaining nutrient flows in terrestrial landscapes?*

LaNuM results indicate that spatial heterogeneity is important over a similar range of source cover as that found by Gergel (2005). Gergel found that heterogeneity in the strength of source and sink functions of cells in the landscape changed the loading variance peak from the baseline scenario value of 65% source cover to a range of 55%-75% source cover. The work presented here shows that this widening of the range where the variance peak of nutrient loading occurs can result from increasing landscape contagion. What underlies this behavior? First, increasing landscape contagion is associated with a decrease in the abruptness with which NLMs percolate. Because the contagion of land use maps is typically greater than for random NLMs the results obtained from NLMs with intermediate to high contagion are more likely to correspond to what might be found via empirical research (Nagaike and Kamitani 1999).

LaNaM results have helped delineate a conceptual space in which spatial heterogeneity is expected to be an important factor in explaining nutrient flows and loading. This space is organized along several dimensions (Table 4.1). Analysis of the results shows that movement along one dimension toward the point of maximum importance (high loading variance) can stimulate the appearance of the variance peak, even if the position along the other dimension is not optimal.

Table 4.1: Dimensions describing importance of spatial configuration to nutrient loading

| Dimension | Importance of spatial configuration is highest when: |
|---|---|
| Strength of the source and sink processes | Source-sink processes are strong and constant in time |
| Percent of landscape as source cells | Source coverage is intermediate range = 55% - 70% |
| Degree of landscape contagion | Contagion is high |
| Relative importance of surface flows to subsurface flows | There is limited infiltration of nutrients |

There are several interesting topics that could be broached with LaNuM in the future. The first involves introducing preferential surface or subsurface flowpaths into the model. This would likely disrupt the current source sink dynamics observed in the model; however, new patterns occurring at faster temporal scales would be introduced. The main questions would be: How does the proportion of flows that enter preferential pathways affect the loading variance and the ability of landscape metrics to predict loading? To what extent does the sequential order of source and sink patches through which the flowpath passes determine nutrient loads? Another area ripe for investigation involves phenomena that emerge from a simple set of equations and rules that drive landscape flows and nutrient cycling. One such phenomenon is the appearance of areas of high source or sink processing near the boundaries between the two classes (Figure 4). What are the assumptions in particular that underlie this behavior? How do boundary phenomena change with topography? Another possibility is to convert LaNuM into a true cellular automaton, where each cell would change state (and thus its nutrient cycling parameterization) based on certain rules about the nutrient concentrations and water necessary to sustain a heavily vegetated system (Jenerette and Wu 2004). A major focus would be to see how landscape pattern and composition evolves from the original landscape map and how this might respond to the factors already incorporated in the model. Furthermore, the existence of critical thresholds in source-sink behavior deriving from the percolation threshold or the behavior of the cellular automata might be examined (Groffman et al. 2006). Finally, as mentioned above, work with LaNuM might support the development of functional indices that relate landscape pattern and process.

The exploration of the variance peak in nutrient loading using the LaNuM model allowed the development of a more nuanced understanding of when spatial configuration of source-sink patches might be an important control on nutrient loads leaving a landscape or watershed. The importance of landscape contagion on the shape and magnitude of the variance peak was clearly established. Most landscapes with a significant amount of human influence will have levels of patch aggregation much higher than the simple random map. Most landscapes will likely present levels of aggregation and contagion between the two levels of fractal maps used here. Thus it is reasonable to hypothesize that although variance peaks for N and P did not readily appear with random maps, they should appear data sets from empirical watershed studies. The inclusion of subsurface flows did not disrupt the source-sink dynamics on the surface, however if the amount of nutrients and water leaving a system via baseflow becomes larger than the surface flow, the presence of a peak in combined loading variance will be very sensitive to the strength of the source-sink behavior on the surface and the "tightness" of surface nutrient cycles. The lateral spread of the variance peak with increasing landscape contagion indicates that spatial configuration should be important in controlling nutrient loading over a wide range of source-sink relative abundance. Although limits to the universality of the variance peak were identified, the fact that this peak occurred in simple N and P cycles over a range of variation in topographical settings and subsurface flow magnitudes points to its potential value as a universal measure of the importance of spatial configuration on nutrient loading.

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