SPATIOTEMPORAL VARIATION IN ECOSYSTEMS

PATTERNS OF SPATIOTEMPORAL VARIATION AS TOOLS FOR PREDICTING AND INFERRING ECOSYSTEM DYNAMICS

By MATTHEW P. HAMMOND, M.Sc

A Thesis Submitted to the School of Graduate Studies in Partial Fulfillment of the
Requirements for the Degree Doctor of Philosophy

McMaster University

McMaster University DOCTOR OF PHILOSOPHY (2015) Hamilton, Ontario (Biology)

TITLE: Patterns of spatiotemporal variation as tools for predicting and inferring ecosystem dynamics

AUTHOR: Matthew P. Hammond, M. Sc. (University of Otago, Dunedin, New Zealand)

SUPERVISOR: Dr. Jurek Kolasa

NUMBER OF PAGES: xvi, 216

LAY ABSTRACT

The physical and biological components of ecosystems are constantly in flux, varying in value among locations (spatially) and over time (temporally). This dynamism makes it difficult to predict current or future behaviours of ecological variables (e.g., population size). This thesis tests the potential of using spatial and temporal patterns to make inferences and predictions about changes in ecological systems. I tested three new theory-based tools in aquatic ecosystems, finding that: The size of temporal fluctuations in an ecosystem variable can be predicted from the size of value-differences among locations; spatial and temporal patterns can predict how a variable responds when isolated fragments of ecosystems are connected; and attributes of ecosystem variables (e.g., their stability) can indicate the likelihood of resources recurring in the same location. Findings show that new insight into spatial and temporal patterns can help prediction and management in complex landscapes.

ABSTRACT

Ecosystems and their components (e.g., organisms, physicochemical variables) are dynamic in space and time. This dynamism makes ecological change notoriously difficult to study and manage. This thesis therefore aims to develop new ways of using spatiotemporal information for inference and prediction. Applying theoretical and statistical concepts to patterns of spatiotemporal variation in aquatic ecosystems led to three discoveries that show promise as ecological applications. First, I show that temporal variability of an ecosystem process can be inferred from its spatial variability. This application may be the first quantitative form of the widely-used method, space-for-time substitution. Its use is supported by an analytical framework giving the conditions under which space is a good surrogate for time. Second, I demonstrate the use of spatiotemporal patterns to predict responses of variables when ecosystem fragments are connected. Connection leads to large shifts in spatiotemporal pattern and other response metrics (e.g., temporal variability) for variables showing asynchrony and concentration gradients among sites (e.g., populations). Meanwhile, these changes are minimal if variables exhibit synchrony and homogeneity across space (e.g., energetic variables). A final discovery is that temporal attributes like stability are strong predictors of persistent spatial variation – a pattern that reflects how reliably resource concentrations occur in the same locations. This finding suggests the potential of *time-for-space substitution*, where one or few well-resolved time series could be used to infer landscape patterns. All but one of the tested approaches were data efficient and broadly-applicable across ecosystems and ecological processes. They thus contribute new possibilities for prediction when data are scarce, as well as new perspectives on dynamics in multi-variable landscapes. Research here shows that work at the intersection of spatial and temporal pattern can strengthen the interpretation of ecosystem dynamics and, more generally, foster synthesis from populations to landscapes.

ACKNOWLEDGEMENTS

The following chapters were made possible by the kind support and efforts of many people. I am grateful to Jurek Kolasa for the opportunity to learn, to question and to explore the natural world. With his enthusiasm, guidance, steadfast support and friendship, it has been a rewarding adventure indeed. Jim Quinn, David Rollo, Clive Jones, Madhur Anand and Kevin McCann provided invaluable supervision and insight, for which I am very thankful. Juan Marquez, Luana Sciullo, Jimmy Li and numerous other lab members made the work lighter through their friendship, fun attitudes and inspiring thoughts. I am also grateful to numerous researchers and reviewers for their valuable feedback, which strengthened ideas and manuscripts. Thanks go to the many past (but not forgotten) volunteers that labored hour upon hour to compile rock pool and lake data that have proven so essential to my projects.

This thesis would not have been possible without the support of friends and family. I thank Gary and Jennifer Chiang for their cheerful and caring support throughout my studies. Deepest appreciation also goes to my parents, Marg and Ken, and siblings, Jeremy and Jenny, who have always been a source of strength, inspiration and encouragement. Finally, words cannot fully thank my wife Sarah for joining me on this adventure. Her support, patience, humour, and understanding have been a gift every step of the way.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF APPENDIX FIGURES

LIST OF TABLES

LIST OF APPENDIX TABLES

LIST OF ABBREVIATIONS AND SYMBOLS

CV	Coefficient of Variation
i or j	Landscape patch
k or l	Sampling time
$\mathrm{Cov}(X_i,X_j)$	Covariance of values in patches i and j
$\mathrm{Cov}(X_k,X_l)$	Covariance of values at times k and l
Var(X)	Variance of series with value X
SD(X)	Standard deviation of series with value X
m	Arithmetic mean
Y	Spatially-aggregated series (i.e., regional)
Z	Temporally-aggregated series
n	Number of observations
ANOVA	Analysis of Variance
MANOVA	Multivariate Analysis of Variance
φ_T	Index of inter-patch synchrony
φ_S	Index of persistence of spatial variation
LTER	Long-term Ecological Research program
NPP	Net primary productivity
GPP	Gross primary productivity
DO	Dissolved oxygen concentration
β_0	Y-intercept of a bivariate regression
b	Scaling exponent (slope on a log-log plot)
PSV	Spatiotemporal pattern of persistent spatial variation
C	Subscript denoting measurement from a connected system
U	Subscript denoting measurement from an unconnected system
CExp	Subscript denoting value expected, in a connected system, from change in mean
MS	Mean squares from ANOVA
η	Chemical hardness
ρ	Pearson correlation coefficient
OMI	Outlying Mean Index for estimating niche marginality
F	Test statistic of ANOVA
α	Alpha-level of statistical significance
$\mathrm{Var}_{s.pop}$	Spatial variance from different population sizes in occupied sites
$\mathrm{Var}_{s.occ}$	Spatial variance from occupancy patterns
τ	Autocorrelation time; a measure of temporal scale

DECLARATION OF ACADEMIC ACHIEVEMENT

I am the primary contributor to this thesis in terms of conceptual development, experimental work, data collation, analysis and writing. Dr. Jurek Kolasa supervised the work reported in Chapters 2-4, providing intellectual and technical guidance. Chapters 2 and 4 used some data not collected by myself: One public data set (North Temperate Lakes LTER), and one long-term data set collected by Dr. Jurek Kolasa and his colleagues (Jamaican rock pools). Drs. April Hayward and Ermias Azeria contributed the species body size and niche values used in Chapter 4.

CHAPTER 1.

SPATIOTEMPORAL DYNAMICS IN ECOSYSTEMS: CAUSES, CONSEQUENCES AND OPPORTUNITIES

This chapter and Chapter 5
adapted from a manuscript to be submitted to Oecologia *as a* Review and Synthesis *article*

Consider the swift transit of a rainstorm across the landscape which leaves some places sodden and others dry (Kumar and Foufoula-Georgiou 1993). This is one of countless examples of spatiotemporal dynamics, defined as a process of spatial and temporal change. Predicting and understanding these dynamics in nature has been a vital task in human societies. Traditional cultures passed down strategies for coping with spatial and temporal variation in food, climate and resources (Sluyter 1994, Berkes et al. 2000). Meanwhile, variation has been understood as an intrinsic feature of systems since at least the fifth century BCE with Heraclitus' maxim, "All things are in motion" (Plato and Jowett n.d.). Modern ecological research on spatiotemporal change began a century ago with Cowles' (1899) study of plant communities on the shifting sand dunes of Lake Michigan. Yet reconciling spatial and temporal change is still a major challenge.

Ecologists recognize that ecosystems vary across space and over time. This variation is often seen as unwanted and controlled by experimental design or statistical methods. But an increasing number of studies make spatiotemporal variation, and its underlying dynamics, their focus (Fig. 1.1a). These contributions make clear that spatiotemporal dynamics drive the functioning of most, if not all, biological (Spatiotemporal 2007), geological (Paine 1985) and ecological systems (Bascompte 1998, Liebhold et al. 2004, Rietkerk and van de Koppel 2008, Guichard and Gouhier 2014). Spatiotemporal research has reshaped our understanding of complex phenomena but has been criticized on two fronts; first as emphasizing theoretical patterns that do not resemble real ecological dynamics (Kareiva and Wennergren 1995, Guichard and Gouhier 2014) and, second, as interpreting patterns in natural ecosystems without adequate grounding in theory (McIntire and Fajardo 2009, Walker et al. 2010). There is, therefore, a pressing need to translate theoretical concepts into real-world applications.

My thesis aims to address this shortcoming by using theory to develop applications for making inferences or predictions from spatiotemporal data. This introductory chapter seeks to point out new opportunities for applications by: (1) Summarizing current lines of research, (2) identifying gaps with high potential for progress, and (3) proposing novel applications by way of hypotheses that are tested in the remaining chapters.

(1) Spatiotemporal dynamics: What is known?

Spatiotemporal research is burgeoning (Fig. 1.1a), but I am not aware of attempts to summarize and guide research across fields. Fig. 1.2 shows ten current or potential directions of spatiotemporal research. Directions differ from one another by emphasizing different stages of the process of spatiotemporal change. These stages are: (i) A variable (i.e., any measurable aspect of an ecological process) responds to the spatiotemporal environment which includes all biotic and abiotic conditions; (ii) these responses generate spatiotemporal dynamics; and (iii) spatiotemporal dynamics leave behind measurable patterns of spatiotemporal variation. Directions cover a range of research interests and can be seen as addressing the *causes, consequences* and *opportunities* of spatiotemporal dynamics (Fig. 1.1b), which are detailed below.

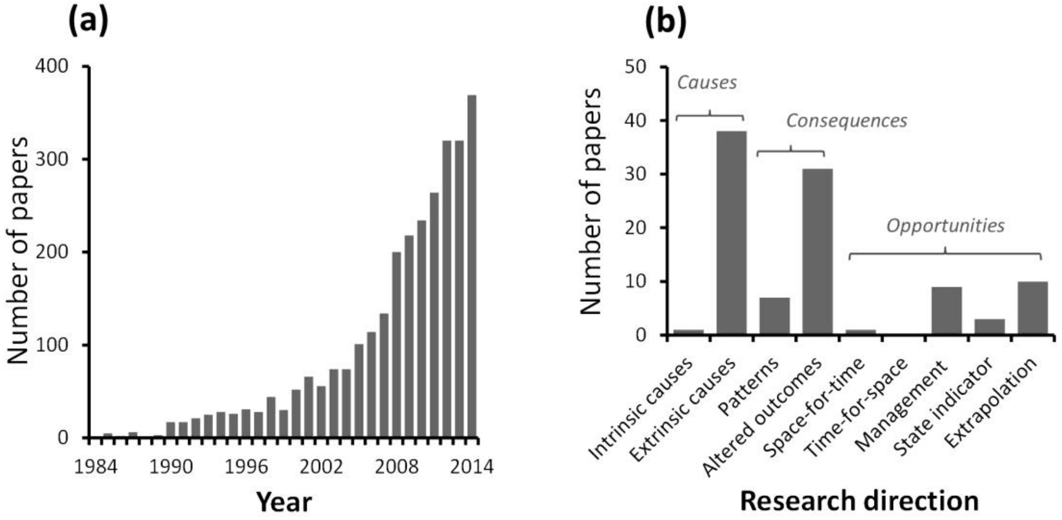


Figure 1.1. Spatiotemporal research trends as indicated by *Web of Science* citations, 2004-2014. (a) Accelerating growth in the number of spatiotemporal papers published in the ecological and environmental sciences. **(b)** Numbers of published papers, drawn from a random subset of 100, falling under research directions in Fig. 1.2 (see also main text) and corresponding to the causes, consequences and opportunities of spatiotemporal dynamics. Research directions are major research themes but are not exhaustive and, in particular, ignore studies targeting spatial or temporal variation alone. Note: Literature search on Web of Science (accessed Oct. 3rd, 2014) used the keyword “spatiotemporal” and included the fields of ecology, environmental science, oceanography, limnology, biodiversity conservation, forestry, fisheries and environmental studies. Studies were categorized based on stated aims.

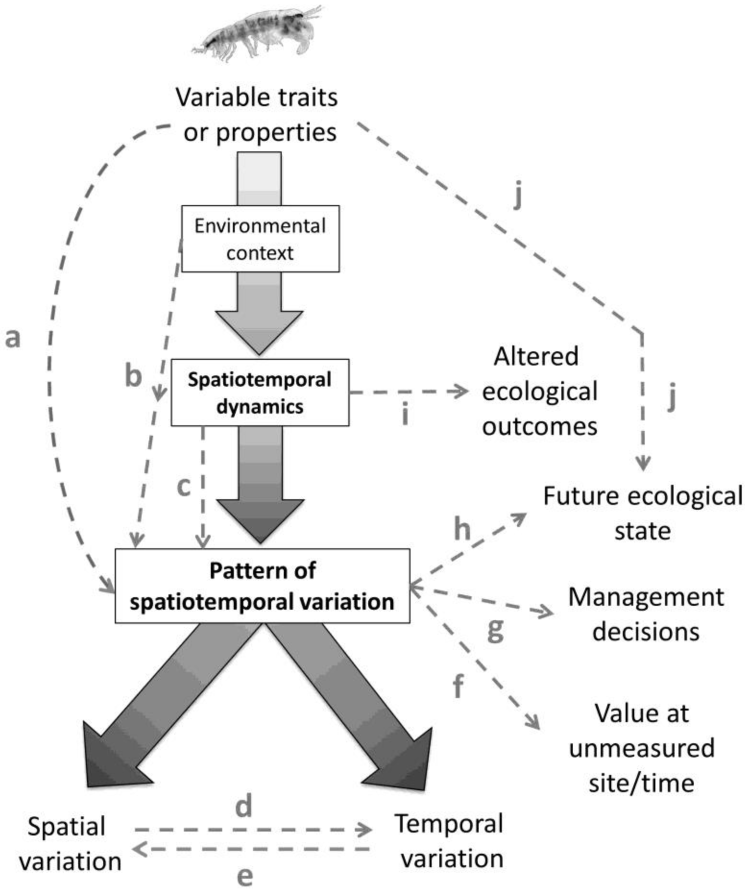


Figure 1.2. A visual summary of research directions involving spatiotemporal dynamics. Large arrows denote stages of spatiotemporal change in which: An ecosystem variable responds to the spatiotemporal environment (all biotic and abiotic factors); this response generates spatiotemporal dynamics; and spatiotemporal dynamics are detected as patterns of spatiotemporal variation. Patterns of spatiotemporal variation can, in turn, be broken down into spatial and temporal components of variation (see Fig. 1.3). Research directions (dashed arrows) focus on different stages of this process, and include: **(a)** Intrinsic causes (variable traits or properties that predispose them to certain spatiotemporal dynamics); **(b)** Extrinsic causes (external population, community or physicochemical drivers that cause spatiotemporal dynamics); **(c)** Patterns of spatiotemporal variation (variation in values as a result of spatiotemporal dynamics); **(d)** Space-for-time substitution (inference of temporal variation or sequence from spatial gradients); **(e)** Time-for-space substitution (inference of spatial variation from temporal variation); **(f)** Extrapolation (out-of-sample prediction of values based on observed spatiotemporal patterns); **(g)** Management decisions (using descriptions of spatiotemporal patterns to inform resource management); **(h)** Pattern-based state indicator (use of *a priori* spatiotemporal pattern to indicate likely ecosystem state after environmental change); **(i)** Altered outcomes (changes in ecological structure or functioning as a result of spatiotemporal dynamics); **(j)** Trait-based state indicator (use of *a priori* trait or property of a variable to indicate likely ecosystem state after environmental change).

Causes of spatiotemporal dynamics

Studies of *causes* aim to uncover mechanisms that create spatiotemporal dynamics (e.g., Saether et al. 1999) and account for the majority of research to date (Fig. 1b). Perhaps the ultimate cause of spatiotemporal dynamics is the architecture of ecological systems (Holling 1992): Sites typically differ in climate, geology and/or community composition and are subjected to time-dependent processes like disturbance and recovery (Turner and Chapin III 2005). These forces provide the fuel for dynamism at the ecosystem level while the dynamics of individual species, materials and energetic processes may or may not match those of the ecosystem. Dynamics of a given variable can usually be attributed to specific demographic, community and physicochemical causes (Table 1.1). Causal mechanisms can be extrinsic to a variable (research direction *b* in Fig. 1.2) as when climatic forcing causes synchronous change among mammal populations (Post and Forchhammer 2002). Or they may be intrinsic to a variable (research direction *a* in Fig. 1.2) as when demographic stochasticity causes asynchrony among bird populations (Saether et al. 2011). A particular challenge in applied ecology is to determine whether dynamics arise mostly from extrinsic drivers like environment (e.g., Fox et al. 2011), from intrinsic traits of variables like cycling of populations which promotes spatial synchrony (e.g., Becks and Arndt 2013) or from both (e.g., Estay et al. 2011).

Table 1.1. Documented causes of spatiotemporal dynamics and examples of resulting patterns of spatiotemporal variation. See Fig. 1.3 and main text for pattern definitions.

Cause	Mechanism of change	Resulting pattern	Author
Disturbance	Landscape structure and inter-patch differences in fuel type lead to spatial variation in fire frequency	Persistent spatial variation	Floyd et al. 2000
Demography	Demographic stochasticity spurs asynchrony among populations of rare birds	Ephemeral variation	Saether et al. 2011
Competition	Trade-off between competitive and dispersive abilities causes separation of species in space	Persistent spatial variation	Hassell et al. 1994
Facilitation	Facilitation in desert shrubs leads to stable vegetation patches	Persistent spatial variation	Tirado and Pugnaire 2003
Predation	Localized predation of fly larvae causes transient spatial patterns	Ephemeral variation	Tobin and Bjørnstad 2003
Resource distribution	Resource concentration leads to consistent aggregation of scavenging raccoons	Persistent spatial variation	Prange et al. 2004
Weather	Weather synchronizes caribou populations over large distances	Inter-patch synchrony	Post and Forchhammer 2002
Dispersal	Dispersal drives inter-patch synchrony of bird populations	Inter-patch synchrony	Paradis et al. 1999

Consequences of spatiotemporal dynamics

Studies of *consequences* ask how spatiotemporal dynamics lead to changes in ecological structure and functioning (e.g., Cottenie and De Meester 2004, McCauley et al. 2012). These studies show that, far from trivial noise, spatiotemporal dynamics impact multiple levels of ecological organization (Cushman 2010) by; (i) altering ecological outcomes; and (ii) determining the distribution of resources in space and time.

Altered ecological outcomes (research direction *i* in Fig. 1.2) refer to cases where spatiotemporal dynamics lead to different endpoints or states. In metapopulations, for instance, dispersal among discrete populations can ensure their persistence through “rescue effects.” These occur when immigrants from self-sustaining populations help to sustain moribund ones (Roff 1974, Brown and Kodric-Brown 1977, Hanski 1991, Gonzalez et al. 1998) and are essential for maintaining threatened populations (Hilderbrand 2003). Dispersal also underlies other important population phenomena like the synchronization of dynamics among patches (reviewed by Bjørnstad et al. 1999, Liebhold et al. 2004) and the existence of sink populations (Gonzalez and Holt 2002).

At higher levels of organization, metacommunity (Hanski 1991, Wilson 1992) and metaecosystem dynamics (Loreau et al. 2003) alter ecological outcomes by modifying the strength or nature of local interactions (Leibold et al. 2004). Huffaker's (1958) famous orange experiments, for instance, showed that mite populations persisted so long as prey could disperse to new patches (oranges) ahead of predators. Such dynamics are now thought to be major determinants of community structure (Cottenie and De Meester 2004), species coexistence (Ettema et al. 2000, Salomon et al. 2010) and species richness (Howeth and Leibold 2010, but see Limberger and Wickham 2012). At the ecosystem level, inter-patch movement appears equally essential for maintaining productivity, ecosystem services, and important physicochemical processes (Wetzel et al.

2005, Staddon et al. 2010, Garibaldi et al. 2011, Valett et al. 2014). Table 1.2 lists further examples of altered outcomes.

Table 1.2. Some population, community and ecosystem consequences of spatiotemporal dynamics.

Consequence	Mechanism/example	Author(s)
Persistence	Animal immigration into patches causes “rescue effects” that prevent local declines in abundance	Gonzalez et al. 1998
Source-sink dynamics	Movement from positively- (source) to negatively-growing (sink) populations allow occupancy and outbreaks in low quality habitats	Gonzalez and Holt 2002
Species richness	Differential dispersal of species creates spatial and temporal refugia from predation and competition, sustaining species richness	Ettema et al. 2000, Howeth and Leibold 2010
Environmental structure	Spatiotemporal pattern of disturbance creates habitat templet which, in turn, drives insect community composition and structure	Townsend et al. 1997
Altered productivity	Nutrient flux between ecosystems sustains higher levels of productivity	Helfield and Naiman 2001, Cloern 2007
Species distributions	Small game populations have higher temporal variability at range edges which increases local extinction and range contraction	Williams et al. 2003
Spatial insurance	Dispersal ensures stable ecosystem functioning by allowing replacement of locally-extinct species with functionally-similar ones	Staddon et al. 2010
Resource patterns	Habitat suitability and exploitation cause stable spatial patterns in commercial fish species	Morfin et al. 2012

The second major consequence of spatiotemporal dynamics is the distribution of energy, materials or organisms in space and time. This distribution is seen as a pattern of spatiotemporal variation – spatiotemporal pattern for short – resulting from the movements and interactions of variables within the landscape (research direction *c* in Fig. 1.2). Patterns are assessed from values at replicated sites and times, and reflect how spatial variation changes over time or, vice versa, how temporal variation differs from place to place (Larsen et al. 2001, Legendre et al. 2010). While purely descriptive studies are rare (Fig. 1.1b), all ecological variables display spatiotemporal variation at some spatial or temporal scale. Climate, for instance, may appear stable or spatially-uniform over small spatial and temporal scales but is variable at larger scales (e.g., Barnes et al. 2012).

Spatiotemporal patterns can take striking and intricate forms like travelling waves of populations (Ranta and Kaitala 1997), elongated invasion fronts (Eppinga et al. 2013) or stable spatial patterns (Rietkerk and van de Koppel 2008). Yet the bulk of natural patterns are of three basic types, which are relevant to the management of landscapes (Fig. 1.1). *Persistent spatial variation* occurs when spatial patterns are fixed or stable over time, as with consistent hotspots and coolspots of biomass or species richness (Santora and Veit 2013). Resources with this pattern can be found consistently in the same locations by managers or harvesters (e.g., Lucifora et al. 2011). *Inter-patch synchrony* occurs when temporal patterns are positively correlated among sites. This pattern reflects changes that are shared across a region (Post and Forchhammer 2002), and so is a concern for increasing variability and extinction risk of regional populations

(Heino et al. 1997, Hilderbrand 2003). Lastly, ephemeral patterns occur when temporal patterns differ among sites or spatial patterns differ among sampling times. These reflect populations or resources whose concentrations are not predictably tied to a particular location or time, and include challenging management scenarios like shifting mosaics of weather formations (Kumar and Foufoula-Georgiou 1993), pests (Aukema et al. 2008), disease epidemics (Grenfell et al. 2001) and migratory animals (Bull et al. 2013).

Opportunities offered by spatiotemporal dynamics

Studies of *opportunities* use information contained in patterns of spatiotemporal variation to make decisions, inferences, or predictions. Spatiotemporal patterns can inform management decisions (research direction *g* in Fig. 1.2) by giving insight into moving conservation targets (Doak et al. 2008, Bull and Bonsall 2010). For example, spread patterns of invasive species can suggest optimal control strategies (Pysek and Hulme 2005). Similarly, patterns can indicate where and when to monitor to best detect trends and thus help allocate effort (Urquhart et al. 1998, Larsen et al. 2001). Lastly, management efforts like prescribed fires and timber harvests can be adapted to emulate natural spatiotemporal patterns of disturbance (Landres et al. 1999, Long 2009).

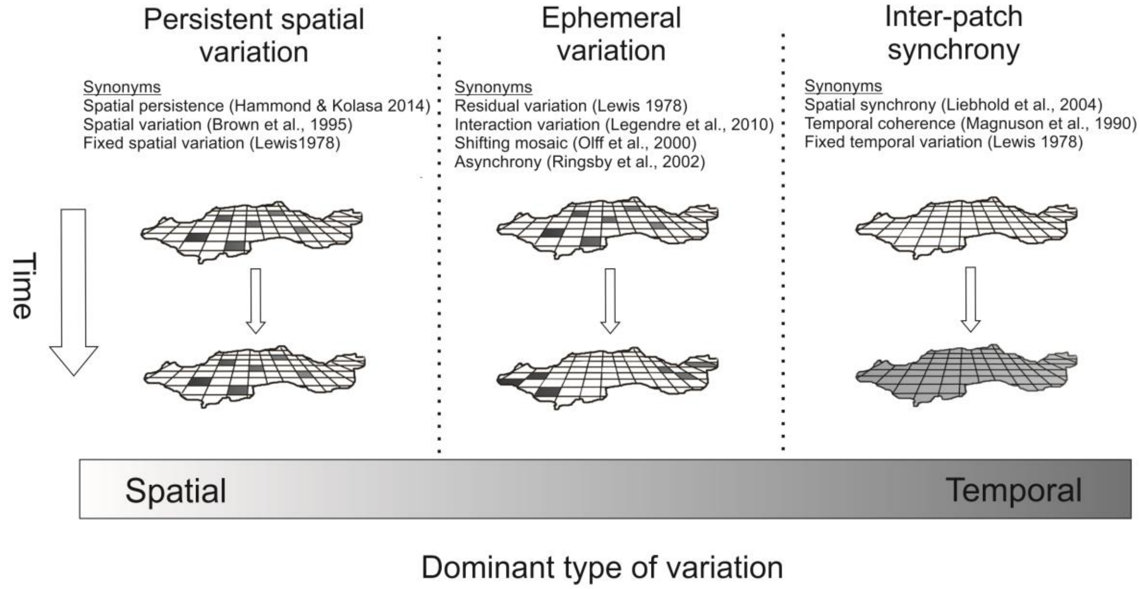


Figure 1.3. Basic types of spatiotemporal patterns that a variable - defined as any measurable aspect of an ecological process - can display. Left to right, patterns range from spatially-dominated in which spatial variation remains unchanged over time (persistent spatial variation) to temporally-dominated in which temporal variation is shared across sites (inter-patch synchrony. Ephemeral variation is an intermediate case in which temporal variation differs among sites or, viewed another way, spatial variation differs among sampling times. See main text for examples.

Spatiotemporal patterns can also be used for inference. One commonly-used approach is space-for-time substitution (Pickett 1989; research direction *d* in Fig. 1.2) which uses spatial variation to infer temporal variation under the assumption that they are equivalent. Its use in ecology parallels pioneering work in physics that estimated the temporal dynamics of electrons based on ergodic theory (reviewed in Paine 1985). Ecologists have applied a similar type of space-time correspondence at least since Watt's (1947) suggestion that community variation across space was a snapshot of sites at different stages of (temporal) development. Gradients of different-aged sites are now widely used to reconstruct long-term temporal dynamics such as succession (reviewed by Walker et al. 2010), changes in biodiversity (Blois et al. 2013), community responses to climate change (reviewed by Fukami and Wardle 2005) and soil development (Matamala et al. 2008, Walker et al. 2010). Yet space-for-time substitution has disadvantages. Most important of these is that a temporal sequence can only be accurately inferred from a spatial gradient when sites share similar environmental conditions and histories (Pickett 1989, Fukami and Wardle 2005, Jongejans and De Kroon 2005, Walker et al. 2010).

Inference from spatiotemporal patterns need not assume that spatial and temporal variation are equivalent. Some approaches assume only that temporal dynamics leave a characteristic imprint in spatial patterns (McIntire and Fajardo 2009). For example, ecologists have noted that slowly-changing processes tend to occur over larger spatial scales (Holling 1992, Steele et al. 1994). Though the mechanisms underlying this scaling relationship have been poorly studied, it has been used to infer the speed of change in different-sized habitats (Delcourt and Delcourt 1983). Many studies also use spatiotemporal patterns to diagnose intrinsic and extrinsic mechanisms of change (the reverse of research directions *a* and *b* in Fig. 1.2); attributing, for instance, population declines to weather or local habitat degradation (Morrison et al. 2010).

A final use of spatiotemporal patterns is in prediction, which is both a challenge and necessity for coping with global ecological change (Clark et al. 2001). Prediction often takes the form of extrapolation where values for unmeasured locations or times are predicted from observed spatiotemporal patterns (research direction *f* in Fig. 1.2). Species distribution models use this approach to predict the occurrence of at-risk species (reviewed by Elith and Leathwick 2009), while species richness may be predicted out-of-sample from species-time-area curves (Adler and Lauenroth 2003).

While models deliver precise forecasts of values of ecological variables (Mann et al. 1998, Aukema et al. 2008, Valett et al. 2014), ecologists often desire simple tools that predict responses to ecosystem change e.g., whether habitat fragmentation will destabilize populations (Coffman et al. 2001). In these cases, indicators can be useful in signaling a likely future state or dynamics according to *a priori* expectations. Some indicators are pattern-based (research direction *h* in Fig. 1.2) such as spatial patterns that indicate the approach to chaotic dynamics (Sole and Bascompte 1995) or sudden ecosystem transitions (Litzow et al. 2008, Dai et al. 2012a). Other indicators may be based on traits or properties of variables (research direction *j* in Fig. 1.2) such as using the spatial scale of species to predict responses to altered landscape connectivity (e.g., Uezu et al. 2005).

(2) Critical gaps in spatiotemporal research

Fig 1.1b shows that research on *opportunities* of spatiotemporal dynamics lags behind that of *causes* and *consequences* by ~15%, leaving gaps for new solutions to conservation challenges (Bascompte 1998, Liebhold et al. 2004, Carpenter 2013). In particular, three opportunities remain underexplored: Space-for-time substitution (*d* in Fig. 1.2), indicators of ecological state (*h* and *j* in Fig. 1.2), and time-for-space substitution (*e* in Fig. 1.2).

Space-for-time substitution is actually a relatively common practice and so may be underrepresented in the survey. It is, nevertheless, underexplored in one important sense: Space-for-time substitution has been a qualitative procedure to date, yielding only the sequencing and timing of events (i.e., a chronosequence). There are no quantitative alternatives that substitute spatial variance or Coefficient of Variation for its temporal equivalent. Progress towards this goal could lead to a new ways of extracting information from spatial data.

Indicators of future ecological states – such as ecosystem structure or dynamics – are also in their infancy. But recent interest in leading indicators of change (Carpenter et al. 2011, Dai et al. 2012b) suggests that they will be indispensable for monitoring and prediction. Indicators based on variable traits or properties may have the most scope for growth. While species traits like body size and trophic level can predict community structure (Jackson et al. 2001, White et al. 2007), the extent to which they predict responses to ecosystem change is unclear (but see Williams et al. 2010). But there is increasing evidence that intrinsic properties of variables, such as whether they are energetic or material, reveals much about their dynamics under a range of conditions (Leavitt et al. 2009, Vogt et al. 2011). However, these avenues need further work.

Lastly, time-for-space substitution is a novel, or at least very uncommon, direction of research (cf. Blois et al. 2013). As the converse of space-for-time substitution, it entails using the temporal pattern at a single site to infer spatial pattern. If sound, this application could help managers forecast the spatial distribution of energy, material or organisms from one or more well-resolved time series. Conceptually, this research direction fits well with a broader effort underway to discern how temporal processes like self-organization imprint on patterns in the landscape (Rietkerk and van de Koppel 2008, McIntire and Fajardo 2009).

The above research gaps may be best filled by applications that combine the advantages of theory and empirical observation (Bascompte 1998). Ideally, they will take the form of broadly-useful “rules of thumb” (Carr et al. 2010) that maximize predictive or inferential power while minimizing the need for exhaustive data collection. To be broadly-useful, applications will have to meet three criteria that reflect the practicalities of data collection and the diversity of ecological systems:

i) *An application must be data-efficient.* Many statistical methods, models and indicators are data-intensive even though data are sparse for most ecological systems. Long time series are especially rare, as well as revealing (Carpenter 2013). Researchers are thus increasingly looking to accessible alternatives like spatial data (Sole and Bascompte 1995, Carpenter 2013, Eppinga et al. 2013). Advanced statistical approaches have been called for to better probe patterns (Liebhold et al. 2004) and these are progressing rapidly (Legendre and Gauthier 2014). But opportunity remains for innovative and data-efficient approaches to spatiotemporal analysis.

ii) *An application must apply across systems.* Spatiotemporal applications are often developed and tested in narrow contexts, such as *in silico* or in a single system. This can be effective for developing local management solutions. But more enduring techniques are based on general patterns that apply to all types of ecological systems. The advantage of statistical- or theory-based general rules is that they can indicate the most likely outcome or pattern without the need to document and understand the many system-specific details.

iii) *An application must apply across types of ecological process.* An ecosystem includes “not only the organism-complex, but also the whole complex of physical factors” (Tansley 1935), but these components are rarely studied as an integrated whole. This separation risks an incomplete understanding because conclusions drawn from an organism-centric focus may differ from those drawn when abiotic variables are also considered (Massol et al. 2011, Leroux and Loreau 2011). Thus, rules that can account for both biotic and abiotic responses will be more realistic and should help to answer practical, ecosystem-level questions such as: How do different ecosystem services respond to changes in connectivity (Mitchell et al. 2013)? And, are some types of variables better for tracking the impacts of climate change (Adrian et al. 2009)?

(3) Hypotheses and tests for new spatiotemporal applications

This thesis aims to fill research gaps in the areas of inference and prediction of ecological dynamics. I evaluate the general proposition that applying theoretical and statistical concepts to spatiotemporal patterns will lead to new, broadly-useful ecological applications. This proposition is evaluated in the context of three spatiotemporal problems framed by the following hypotheses, a rationale for which is given at the beginning of each chapter:

- *Spatial variation can be a quantitative substitute for temporal variation* (Chapter 2)
- *Patterns of spatiotemporal variation can be used to predict responses to connecting ecosystem fragments* (Chapter 3)
- *Measurable properties of ecosystem variables help to predict the occurrence of persistent spatial variation* (Chapter 4)

To assess the real-world applicability of findings, I test hypotheses in up to three aquatic ecosystems of increasing ecological realism. These are:

Aquatic microcosms: A laboratory connectivity experiment tracked the dynamics of macroinvertebrates and ecosystem metrics for four months. It represents a small and rapidly-changing but controlled ecosystem that is closed to most external inputs.

Jamaican rock pools: 12 years of macroinvertebrate and environmental data from 49 coastal rock pools were used to represent a small, rapidly-changing and open ecosystem.

Wisconsin North Temperate Lakes (LTER): 30 years of macroinvertebrate, fish and environmental data from seven temperate lakes were used to represent a large, open ecosystem with multiannual rates of change comparable to many management scenarios.

Findings are evaluated, within chapters and in a final discussion chapter (Chapter 5), for their contribution to understanding and their applicability to other ecosystems. Applications will be judged to be of general and practical importance if they meet the above-listed criteria of a broadly-useful application. Results are anticipated to add to spatiotemporal research by: Describing rules of thumb through new conceptual, statistical and empirical approaches; documenting spatiotemporal patterns; enabling prediction when data are scarce; and providing new perspectives through work on understudied opportunities.

CHAPTER 2.

SPATIAL VARIATION AS A TOOL FOR INFERRING TEMPORAL VARIATION AND DIAGNOSING TYPES OF MECHANISMS IN ECOSYSTEMS

Adapted from
Hammond, M. P. and J. Kolasa. 2014. Spatial variation as a tool for inferring temporal variation and diagnosing types of mechanisms in ecosystems. PLoS One. 9(2): E89245.
DOI: 10.1371/journal.pone.0089245

HYPOTHESIS AND RATIONALE

Hypothesis tested: *Spatial variation can be a quantitative substitute for temporal variation*

Rationale: Spatial and temporal variation make up the two halves of spatiotemporal dynamics and are often studied separately. However, some approaches like space-for-time substitution (Pickett 1989) take advantage of the relationship between spatial and temporal variation by using the former as a surrogate for the latter. Space-for-time substitution is an essentially qualitative method, using spatial variation in the form of gradients of site age or disturbance to infer sequences of events (chronosequences; reviewed by Fukami and Wardle 2005, Walker et al. 2010). Surprisingly, the approach has ignored the *quantitative* differences of value among events (temporal variance). But it is possible to incorporate this quantitative aspect using ANOVA variance partitioning methods, which relate spatial and temporal variance. This study is an application of research direction *d* in Fig.1. 2.

ABSTRACT

Ecological processes, like the rise and fall of populations, leave an imprint of their dynamics as a pattern in space. Mining this spatial record for insight into temporal change underlies many applications, including using spatial snapshots to infer trends in communities, rates of species spread across boundaries, likelihood of chaotic dynamics, and proximity to regime shifts. However, these approaches rely on an inherent but undefined link between spatial and temporal variation. We present a quantitative link between a variable's spatial and temporal variation based on established variance-partitioning techniques, and test it for predictive and diagnostic applications. A strong link existed between spatial and regional temporal variation (estimated as Coefficients of Variation or CV's) in 136 variables from three aquatic ecosystems. This association suggests a basis for substituting one for the other, either quantitatively or qualitatively, when long time series are lacking. We further show that weak substitution of temporal for spatial CV results from distortion by specific spatiotemporal patterns (e.g., inter-patch synchrony). Where spatial and temporal CV's do not match, we pinpoint the spatiotemporal causes of deviation in the dynamics of variables and suggest ways that may control for them. In turn, we demonstrate the use of this framework for describing spatiotemporal patterns in multiple ecosystem variables and attributing them to types of mechanisms. Linking spatial and temporal variability makes quantitative the hitherto inexact practice of space-for-time substitution and may thus point to new opportunities for navigating the complex variation of ecosystems.

Keywords: Spatiotemporal; spatial; temporal; space-for-time; substitution; variation; variance; prediction; landscape; ecosystem; dynamics; synchrony; LTER; mechanism; stability; constancy

INTRODUCTION

The spatial texture of a landscape is a fundamental reflection of the ecological processes underpinning it. Thus, spatial distributions of population (Reed et al. 2000), geological (Barnes et al. 2012) and climatological variables (Leavitt et al. 2009) can reveal key details to investigators about the forces, operating over time, that forged them. Spatial patterns are *diagnostic* when they are used to uncover hidden mechanisms in the landscape, and *predictive* when they indicate the likely future behavior of a process. Ecology is full of examples of the former, diagnostic approach where spatial patterns are mined for evidence of mechanisms like dispersal, competition or environmental structuring (Seabloom et al. 2005, Fangliang et al. 2008, Burrows et al. 2009, Anderson et al. 2012). But the latter, predictive approach is also commonplace. Because obtaining long time series is difficult, inferring temporal patterns from spatial data is used in such varied contexts as: (i) chronosequences, where gradients of different-aged sites are used to track how a process (e.g., succession) changes from one state to another over time

(Pickett 1989, Fukami and Wardle 2005, Walker et al. 2010, Blois et al. 2013), (ii) boundary dynamics, where spatial snapshots can reveal the rate of species spread (Eppinga et al. 2013), (iii) complex dynamics, where spatial data help detect chaos (Sole and Bascompte 1995), and (iv) regime or phase shifts, where changes in spatial variation can expose the incipient reorganization of an ecosystem (Litzow et al. 2008, Guttal and Jayaprakash 2009, Dai et al. 2012).

Using spatial patterns to infer temporal patterns ("space-for-time substitution"; *sensu* (Pickett 1989)) or mechanisms quickly encounters the hard problem of interpreting dynamics (Marcos-Nikolaus and Martin-Gonzalez 2002, McIntire and Fajardo 2009). We, as others (Levin 1992, McIntire and Fajardo 2009), note that progress will require a deep understanding of what spatial patterns reveal about temporal patterns, and how these come together in the spatiotemporal patterns of landscapes. We further suggest that such insight will help both *predictive* and *diagnostic* efforts.

Here we focus on the variability of values over time (i.e., the inverse of stability (Lehman and Tilman 2000) or constancy (Grimm and Wissel 1997)) as opposed to properties like resistance or resilience (Grimm and Wissel 1997). We focus, therefore, on the dissimilarity of values and whether this variability (e.g., fluctuations in density) can be predicted from a snapshot of spatial variability. This application, in particular, would be useful given the rarity of long time series in ecology (Fukami and Wardle 2005), the widespread nature of anthropogenic impacts (Turner 2010), the increasing attention to ecological stability (Pimm 1984, Micheli et al. 1999, Lehman and Tilman 2000, Cottingham et al. 2001, Abbott 2011), and the need for clearer links between spatial and temporal concepts (Bolliger et al. 2007).

To our knowledge, no links explicitly tie the temporal and spatial variation of a variable. However, a theoretical foundation for doing so is available through ANOVA variance partitioning (Lewis 1978, Larsen et al. 2001, Legendre et al. 2010) because overall spatiotemporal variation can be broken down into its spatial and temporal components. Crucially, these components can be re-expressed in terms of temporal variance at the regional scale (i.e., spatially-aggregated at time *k*; given as Var(Y) where $\mathrm{Y_k} = \sum_{\mathrm{i=1}}^{\mathrm{n}} \mathrm{X_{ik}}$). This scale reflects the net sum of what occurs in all patches and thus reflects variation in resources and ecological functions at the landscape level. Our derivation makes regional temporal variance itself decomposable (Fig. 2.1A). Traditional variance partitioning methods, in contrast, only decompose total spatiotemporal variance. We show in Fig. 2.1A that regional temporal variance (Var(Y)) obeys a simple relationship with a spatial quantity - the sum of spatial variances measured at time *k* ($\sum \mathrm{var}(\mathrm{X_k})$). This relationship, in turn, is modified by two spatiotemporal patterns (Lewis 1978, Chesson 1985, Larsen et al. 2001, Legendre et al. 2010), *inter-patch synchrony* and *persistence of spatial variation* (Figs. 2.1 & 2.2; see Appendices A-C for derivation and details).

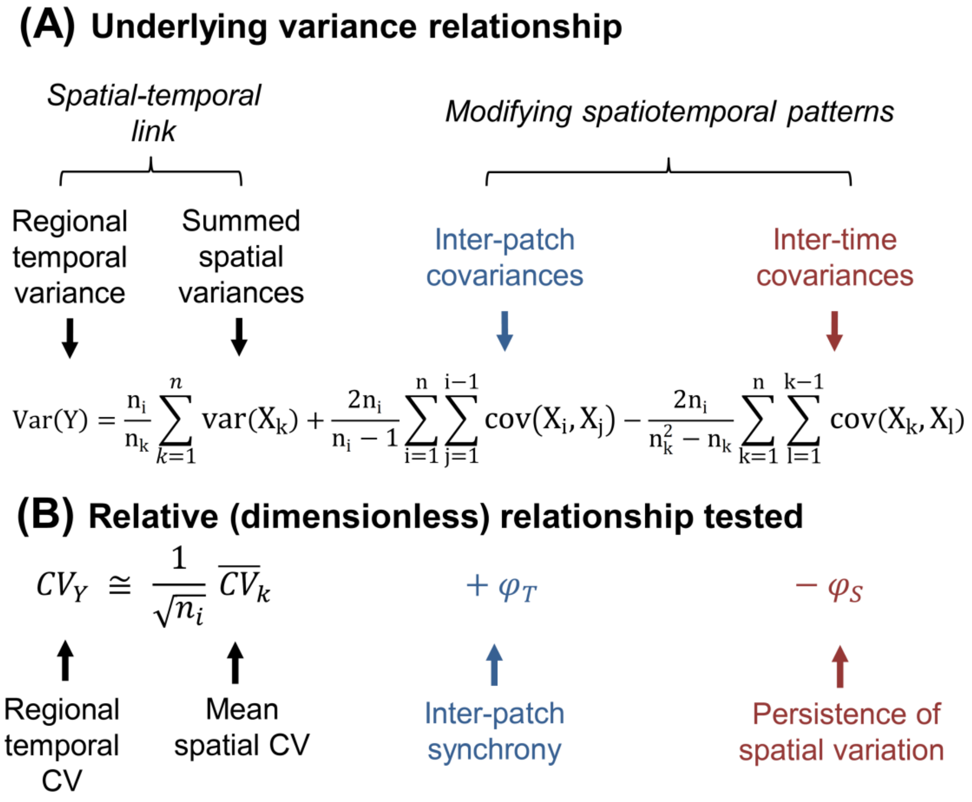


Figure 2.1. The spatial-temporal variability link. (A) We derived an analytical relationship linking regional temporal variance of a process (Var(Y)) to summed spatial variances at time k ($\sum\mathrm{var}(X_k)$). Inter-patch synchrony ($\sum\mathrm{cov}(X_i,X_j)$) and persistence ($\sum\mathrm{cov}(X_k,X_l)$) modify this link and lead temporal and spatial variance to scale as a function of number of patches (n_i) and time points (n_k) when these terms are zero. **(B)** We evaluate the usefulness, for prediction and description, of the corresponding (relative) relationship that uses dimensionless coefficients: Regional temporal CV (CV_Y), mean spatial CV ($\overline{\mathrm{CV}_k}$), and indices of synchrony (φ_T) and persistence (φ_S). While an exact solution exists (Eq. B.16, Appendix B), we use a more useful approximation, $CV_Y \cong (1/n_i^{1/2})\overline{\mathrm{CV}_k}$, that gives an expected temporal CV for a given spatial CV when synchrony and persistence are negligible (Eq. C.3, Appendix C).

Inter-patch synchrony (summed inter-patch covariances; $\sum \mathrm{cov}(X_i, X_j)$) refers to temporal changes that happen simultaneously in patches *i* and *j*. It is well known to boost temporal variation at the regional scale (Earn et al. 2000; e.g., widespread population decline during drought). On the other hand, *persistence of spatial variation* (summed inter-time covariances; $\sum \mathrm{cov}(X_k, X_l)$) - *persistence* for short - describes differences or gradients between patches *i* and *j* that are retained from time *k* to *l* (e.g., fixed or permanent differences between locations). Opposite in sign to synchrony, persistence is associated with lower temporal variance. This is because a pattern of spatial variation is retained over time only if most patches are relatively stable. Temporal variance thus depends critically on the balance of synchrony and persistence.

Implications of analytical framework

The relationship captured in Fig. 2.1A points out the basis for *predictive* applications like space-for-time substitution. It does so by showing that spatial and temporal variance will scale exactly (by a factor of n_i/n_k) for stochastic processes. Stochastic processes enable this because their values are uncorrelated between patches *i* and *j*, as well as between times *k* and *l*, and this sets synchrony and persistence terms to zero ($\sum \mathrm{cov}(X_i, X_j) = 0$, $\sum \mathrm{cov}(X_k, X_l) = 0$). This is a form of ergodicity (Paine 1985) that can be illustrated by an analogy. Imagine a seascape in which wave peaks are independent of each other: In this null case, wave amplitudes from trough to peak would be equally large or small whether waves were measured from a fixed point (i.e., waves passing over time) or from a transect across the seascape (i.e., a snapshot of waves across space). Our formulation merely adds that this match between temporal and spatial variability applies at the regional (seascape) scale as well as at the patch (wave) scale. Fig. 2.2 summarizes this

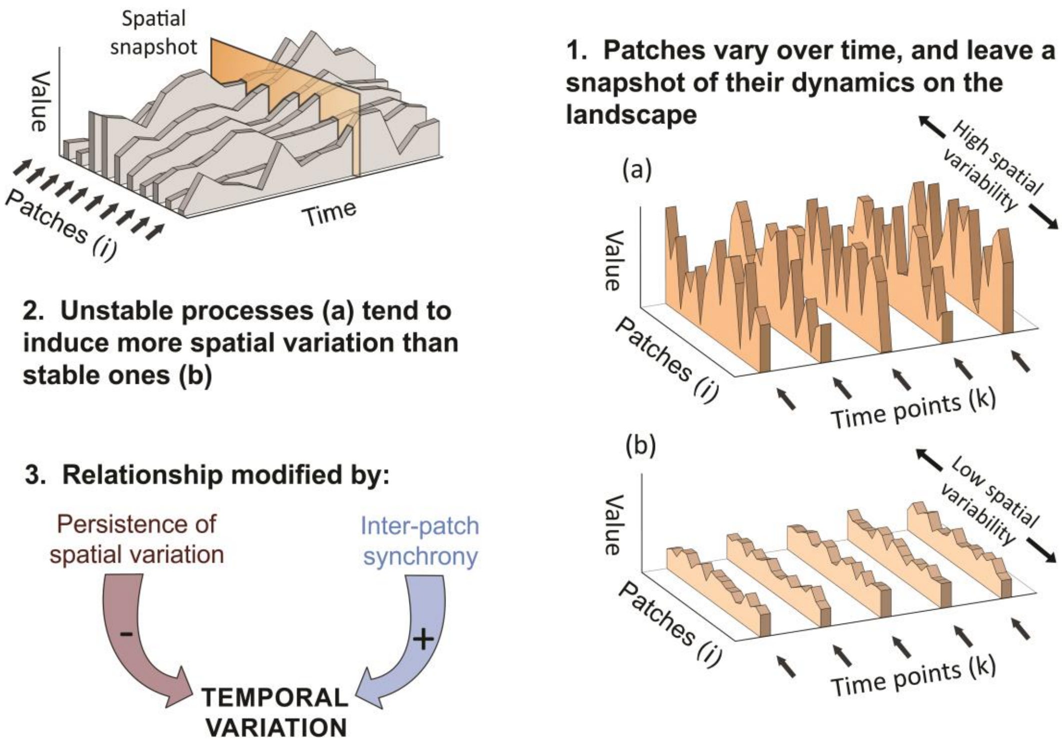


Figure 2.2. Spatial imprinting of ecosystem processes. Theorized mechanism by which temporal fluctuations of an ecosystem variable create spatial variability in the landscape. Fig. 2.1 indicates that spatial variability can be a quantitative proxy for temporal variability, but that substitutability is weakened by two modifying spatiotemporal patterns (inter-patch synchrony and persistence). It is unknown whether the link between spatial and temporal pattern is strong enough for substitution or whether it has diagnostic value for describing spatiotemporal patterns.

mechanism, showing how temporal fluctuations are recorded as spatial variability.

Diagnosis, where inferences are made about how patterns came about, may also be made possible by the analytical solution. This is because components of temporal variance from Fig. 2.1A also describe and summarize spatiotemporal patterns that are the net result of ecological mechanisms. Moreover, because these terms are linked to temporal variability, they may provide a new view of dynamics and their consequences for stability.

Because they are commonly used in ecology, we extended our analytical framework to include common indices (Fig. 2.1B) like the Coefficient of Variation (CV), and indices of synchrony (φ_T) and persistence (φ_S). We test the validity of these formulations and turn them to answering three questions: (i) Is the spatial CV of a landscape variable a meaningful proxy for its (regional) temporal CV? (ii) Under what conditions is it predictive? And (iii) what do departures from an exact match between spatial and temporal CV tell us about the forces shaping dynamics of variables? We apply our approach to 136 biotic and physicochemical variables from three landscape types: Laboratory arrays of connected aquatic microcosms (measured for 20 weeks), a natural array of Jamaican coastal rock pool ecosystems (13 years), and a set of seven lakes from the North Temperate Lakes LTER site (30 years). Results shed light on what real world inferences can be drawn when the relationship between spatial and temporal variation is known.

MATERIALS AND METHODS

Ethics statement

Invertebrate species were sampled with permission on land owned by University of West Indies (Discovery Bay Marine Lab) and are not protected by law. Laboratory experiments used invertebrate species that do not require permits or procedural approvals.

Analytical relationship: Linking spatial and regional temporal variance

Values in a landscape vary over time (*k…n*), and across patches (*i…n*). These dimensions of variation both contribute to regional temporal variance, which is the variance of the spatially-aggregated time series (i.e., Var(Y) where $\mathrm{Y_k} = \sum_{\mathrm{i=1}}^{\mathrm{n}} \mathrm{X_{ik}}$). Spatial and temporal variation can be precisely linked through two mathematical truisms: (i) Spatial and temporal variances, estimated from the same site × time data matrix, are related by rules that underlie ANOVA variance partitioning and (ii) these variances, which capture variation at the aggregate scale for both time (i.e., Var(Y)) and for space (i.e., temporally-aggregated for patch *i*; Var(Z) where $\mathrm{Z_i} = \sum_{\mathrm{k=1}}^{\mathrm{n}} \mathrm{X_{ik}}$), can be further decomposed into variances and covariances of patches *i* and *j* or time points *k* and *l* (Feller 1950). See Appendix A for derivation. Var(Y) can thus be re-expressed as in Fig. 2.1A where; var(X_k) is the spatial variance at time *k*, cov(X_i,X_j) is the covariance of patch *i* with *j* (synchrony), and cov(X_k,X_l) is the covariance of time *k* with *l* (persistence of spatial variation). These three components of spatiotemporal pattern are consistent with prior theory and statistical concepts (Lewis 1978, Chesson 1985, Larsen et al. 2001, Legendre et al. 2010).

We converted the above analytical relationship into dimensionless quantities (Eq. B.16; Appendix B) – regional temporal CV (CV_Y), spatial CV (CV_k), and indices of synchrony (φ_T) and persistence (φ_S). While exact, this relationship does not yield a clear null relationship between CV_Y and spatial CV. We therefore used an approximation of it (Eq. C.3; Appendix C) that gives the expected value of temporal CV from spatial CV in the absence of synchrony or persistence (Fig. 2.1B). Temporal CV values calculated using this approximation were 94-98% correlated (1:1) with values from random number simulations where synchrony and persistence were close to zero. These null values, in turn, were used to plot the lines of "independent dynamics" in Figs. 2.4 and 2.5.

Data analysis

Biotic variables included population densities of invertebrate and fish species and ecosystem-level quantities like NPP, while physicochemical variables ranged from temperature and pH to ion concentrations (Appendix E). For each variable, we estimated all indices in Fig. 2.1B. Regional temporal CV was estimated as the quotient of the time series standard deviation and mean. Mean spatial CV of a variable was defined as the average of spatial CV's measured at time *k*. These were calculated either across the three microcosms of each experimental replicate, across 49 Jamaican rock pools, or across the seven LTER lakes. If a species was absent from all water bodies spatial CV could not be calculated for that time point. In these cases, mean spatial CV was calculated as an average of the time points in which it was present (mean frequency of occurrence = 65% of years).

We estimated inter-patch synchrony using a variance ratio φ_T (Loreau and de Mazancourt 2008) which is, roughly speaking, a ratio of aggregate (regional) to component variances:

$$\varphi_T = \frac{\mathrm{Var(Y)}}{(\sum \mathrm{SD}(X_i))^2} \qquad \text{Eq. 2.1}$$

where $SD(X_i)$ is the standard deviation of a patch. As patches synchronize, the value of φ_T grows from zero to one. The counterpart of inter-patch synchrony is persistence where, instead of temporal changes being similar from patch *i* to *j*, spatial differences are similar from time *k* to time *l*. We therefore estimated persistence with the spatial counterpart of φ_T, which we call φ_S. φ_S was calculated by replacing Var(Y) and $SD(X_i)$ in Eq. 2.1 with their spatial equivalents; the variance of the temporally-aggregated series (i.e., Var(Z)) and spatial standard deviation at time *k* ($SD(X_k)$). Analogous to φ_T, φ_S values increase from zero to one as differences among patches persist more through time.

We used General Linear Models (GLM) and multiple regression in Statistica v. 8.0 (StatSoft Inc., 2007) to predict regional temporal CV from mean spatial CV, φ_T, and φ_S (i.e., ~Fig. 2.1B). Temporal and spatial CV values were log transformed for analysis because, when plotted, they tended to form fan-shaped data clouds that were best described by power functions. We tested residuals of all analyses for normal distribution using Kolmogorov-Smirnov tests. Surfaces (Fig. 2.5) were fitted by distance-weighted least squares.

Microcosm connectivity experiment

We assembled replicate arrays of three × 700 mL aquatic microcosms. Each array contained community types that were relatively stable under laboratory conditions: (i) impoverished, containing ubiquitous microbes initially surviving in distilled water, (ii) phytoplankton and microbes, and (iii) 10 invertebrate species (cladocerans, ostracods) and phytoplankton and microbes. We arranged microcosms such that each initially contained a distinct community type, with all three types represented in an array.

Spatial exchange was manipulated by connecting component microcosms with clear Tygon® tubes. Treatments were: No connection among microcosms and bi-directional connection among all three microcosms. Connector tube diameters were increased by ~70% at week 10 of the 20-week experiment. Seven ecosystem-level variables were measured weekly in each microcosm of the array for 20 weeks using light-dark bottle methods, chlorophyll extractions and environmental sensor probes (Table E.1, Appendix E). Microcosm NPP data were rescaled, bringing the lowest value to zero to correct spatial and temporal CV’s for negative values.

Natural rock pool ecosystem

We collected data over thirteen annual surveys (1989-2002) in a Jamaican rock-pool system of 78 invertebrate species, dispersing among 49 rock pools. The system lies near Discovery Bay Marine Laboratory, University of the West Indies, on the northern coast of Jamaica (18°28' N, 77°25' W). Pools create a mosaic 25m in radius on a fossil reef no further than 10m from the ocean and have volumes ranging from 0.5 to 78.4 L. Pools are, on average, within 1m of the nearest neighbor and never more than 5 m away. Ocean tides occasionally flood a few of the most seaward pools. But most are refilled only by precipitation or, on some occasions, ocean spray. We treated the 49 pools as a single system linked by material fluxes and organism dispersal.

The 70+ invertebrate species in rock pools disperse predominantly by propagules transported via wind, ocean spray, animal vectors and, very occasionally, by overflow from neighboring pools after heavy rainfall (Sciullo and Kolasa 2012). Invertebrate species include: Ostracods (20 species), copepods (five species), cladocerans (five species), worms (15 species), aquatic insects (18 species) and other crustaceans (six species). Most species occurred rarely, some only once (for more details, see Pandit et al. 2009). We therefore confined all analyses, except for contributions of variance components (Fig. 2.6) to 26 common species and temperature, pH, salinity, dissolved oxygen, oxygen saturation, and chlorophyll-a.

Invertebrate densities were estimated for each pool as the number of animals in a 0.5 L sample of water, which was withdrawn after stirring the pool to dislodge organisms from rock walls and to homogenize contents. Each sample was filtered through 63 μm mesh to isolate invertebrates, which were immediately preserved in 50% ethanol. Community samples were sorted, identified to highest possible taxonomic resolution and counted by microscope.

Environmental variables like salinity and pH (Table E.2, Appendix E) were measured in each pool using multiprobe sondes (DataSonde, Yellow Springs Instruments, Yellow Springs, Ohio, USA or Hydrolab, Austin, Texas, USA) during biotic surveys for 6-11 of the survey years, depending on the variable.

Small rock pools occasionally dried up, preventing community sampling. These events were recorded as blank data entries, and were <10% of total observations. For our main analyses (Figs. 2.4-2.5), we replaced blank entries with zeroes, assuming that a desiccated pool harbored no living, adult invertebrates. To check if this assumption introduced bias, analyses were repeated using two alternative procedures; (i) leaving blank cells unchanged or (ii) interpolating by replacing blanks with the pool mean. All procedures produced similarly significant results indicating no major effect of our assumption. For abiotic variables, blank entries had no logical association with zero (e.g., desiccation does not suggest a 0°C temperature), so these cells were left blank.

North Temperate Lakes Long-Term Ecosystem Research Program

We used data from seven Wisconsin lakes (Allequash, Big Muskellunge, Crystal, Sparkling, Trout, Crystal Bog and Trout Bog), collected by the North Temperate Lakes Long-Term Ecological Research program. Lake data were obtained from a public database hosted by the North Temperate Lakes LTER, NSF, Center for Limnology, University of Wisconsin-Madison, available at http://lter.limnology.wisc.edu. We included up to 30 years of data from 60 biotic and abiotic variables across five datasets (Table E.2, Appendix E). The following datasets, collected and maintained by LTER associates, were used:

- Chemical limnology of primary study lakes: Major ions
- Chemical limnology of primary study lakes: Nutrients, pH and carbon
- Physical limnology of primary study lakes
- Pelagic macroinvertebrate abundance
- Fish abundance

Collection methods corresponding to datasets can be found as metadata on the online database (http://lter.limnology.wisc.edu). For fish data, only fyke net catches were used and were standardized by effort (i.e., catch per unit effort) to facilitate comparison. Values for a given lake were annual, obtained by averaging organism densities or physicochemical values across depths, across sampling dates and across stations. Density data were used to equalize the contribution from each lake because Trout Lake is up to 3200 times larger than other lakes, and therefore dominates the landscape spatiotemporal pattern. Results therefore emphasize patterns owing to ecological differences among lakes, rather than to lake size. Data are available from the LTER database or upon request from the authors.

RESULTS

Three quantities jointly accounted for 87-100% of a variable's regional temporal CV (Table F.1, Appendix F) - mean spatial CV, inter-patch synchrony $\varphi_{T,}$ and persistence φ_S. This result verifies that spatial and temporal CV's are related and substitutable to the degree that synchrony or persistence does not interfere. Perfect substitution occurs when values are uncorrelated between patches *i* and *j* and between times *k* and *l.* In this case, regional temporal CV is roughly $1/n_i^{1/2}$ times the mean spatial CV (Fig. 2.1B; Eq. C.3).

We verified the theoretical relationship between spatial and temporal CV with a null, stochastic model using values drawn from a uniform distribution with the same range as data from the microcosm experiment. We found that a stochastic variable, plotted as a point, lies within an "independent dynamics region" on a plot of spatial and temporal CV (Fig. 2.3A, Appendix D). It falls on a line of slope $\sim 1/n_i^{1/2}$ or ~1 on log-scales (Fig. 2.3C). Inter-patch synchrony (e.g., from climatic forcing) increases regional temporal variability, shifting a variable to an upper "synchrony region" of the plot (Fig. 2.3A). But the variable shifts to a lower, "persistence region" (Fig. 2.3A) when spatial gradients are retained over time (e.g., from patch-specific factors). Simulations could have used distributions other than uniform, but the use of these would not change the conclusion that the empirical relationship between spatial and temporal variability approaches the theoretical relationship when a process is uncorrelated in space and time. Nor would it change empirical findings, as simulated data were not used as benchmarks for assessing significance.

Simulations suggested that a range of plot patterns can emerge depending on the variables sampled and their spatiotemporal dynamics. First, weak or no linear association exists when variables' spatial and temporal CV's span only a narrow range and stochastic differences in synchrony and persistence create scatter (Fig. 2.3B). Second, strong linear association emerges if all landscape variables have stochastic behavior (black circles, Fig. 2.3C), similar degrees of inter-patch synchrony (blue circles, Fig. 2.3C) or similar degrees of persistence (red circles, Fig. 2.3C). The latter two cases occur because all points are equally displaced up or down from the independent dynamics region. Finally, regression slopes deviate from the expected slope of 1 when some variables display synchrony and others persistence to produce skew (Fig. 2.3D).

Significant linear regressions existed between spatial CV and regional temporal CV for real ecosystem variables (Fig. 2.4). In all three data sets, the most stable variables (e.g., hydrological and environmental variables) had low spatial variability, while unstable variables (e.g., species populations) were spatially patchy in the landscape (Fig. 2.4A-C).

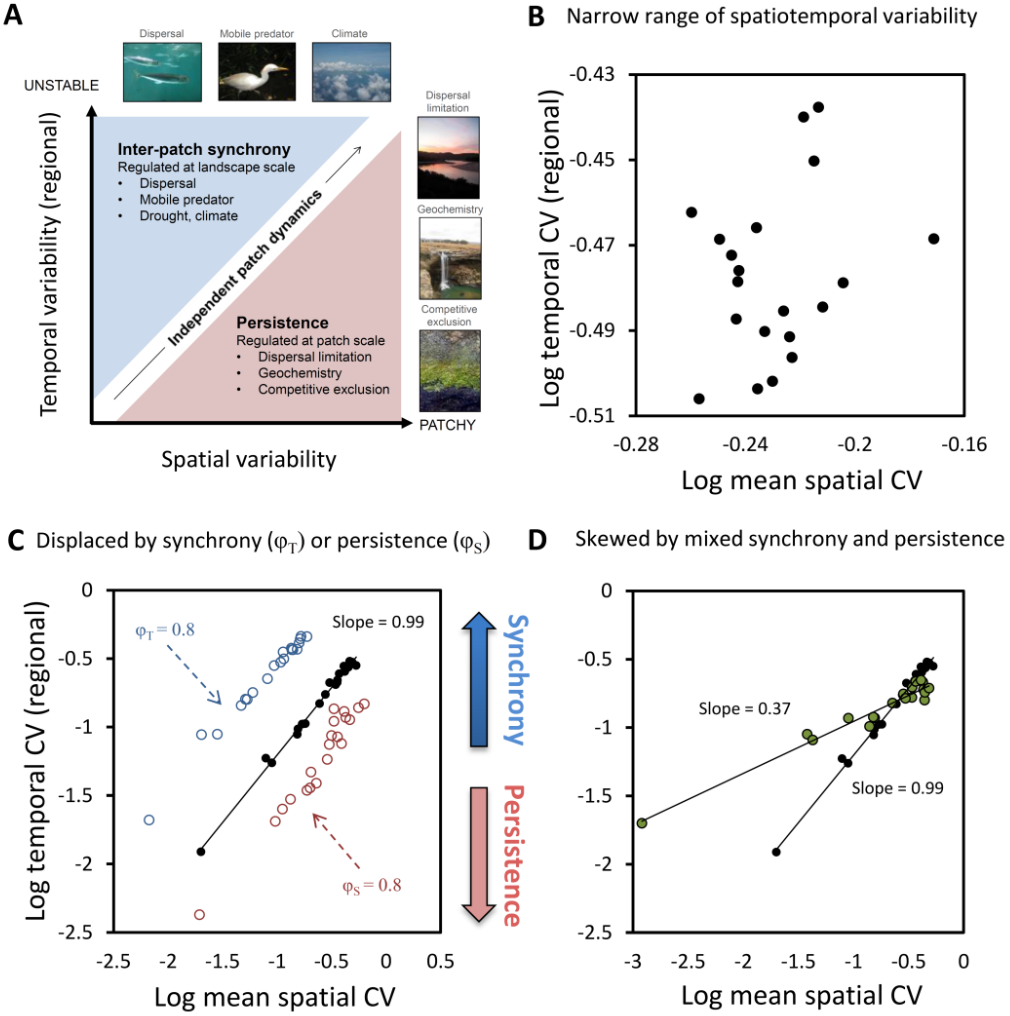


Figure 2.3. Anatomy of a plot between spatial and regional temporal variability. A simulation of ecosystem variables (points) in a three-patch mosaic plotted illustrated the behavior of a plot of their spatial and regional temporal CV's. **(A)** Three regions exist in which a variable, represented as a point, can fall; an "independent dynamics region" when values are independent between patches *i* and *j* and time points *k* and *l*, a "synchrony region" when inter-patch synchrony boosts temporal CV, and a "persistence region" when spatial gradients are retained over time; **(B)** Weak linear relationship when variables share similar spatiotemporal variability, leading to scatter from small differences in synchrony or persistence; **(C)** Strong linear relationships when variables differ in spatiotemporal variabililty and occupy the "independent dynamics region" (black circles), but also when all variables are equally dispaced by synchrony (blue circles) or by persistence (red circles); **(D)** Deviation of regression slope from ~1 (black circles) when variables change in synchrony or persistence as a function of variability. Here, a gradient exists from variables with low variability and synchrony to variables with high variability and persistence. Spatial CV values are means of spatial CV measured at time point *k*. Each point represents a variable and is a mean of ten replicate simulations.

Some statistical dependence exists in these plots because mean spatial CV and regional temporal CV are calculated from the same data matrix. However, results were almost perfectly conserved when a single sampling event (*k*) served to estimate spatial CV and predict subsequent (*k+1…n*) temporal CV (Fig. 2.4D-F). Results are also unlikely to have arisen from biased estimators, since trends were confirmed using several alternative indices (Table F.1, Appendix F).

Not all variables lay close to the independent dynamics region. This was reflected in regression slopes and intercepts (solid lines, Fig. 2.4) which departed from the independent dynamics case (dashed lines, Fig. 2.4). For instance, regression slopes for microcosms and rock pools were reduced because physicochemical variables (blue circles) at one end of the data cloud exhibited more inter-patch synchrony (Fig. 2.4A,B,D,E). Meanwhile, lake physicochemical variables showed considerable persistence, lowering temporal variability and steepening the slope (Fig. 2.4C,F). Though slopes and intercepts deviated from the independent dynamics region, r^2 values of 0.70-0.93 suggest that the rank order of variable's CV's was preserved. We do note some outliers, however, such as pH, Mg and Ca in the persistence region of Fig. 2.4C, F. Also, some variable types (e.g., species populations; red circles) had greater scatter. Overall, however, synchrony and persistence interfered relatively little with the scaling of spatial and temporal CV. Multiple-regression beta coefficients, for instance, revealed that temporal CV increased 2.9-6.2 times more with a variable's spatial CV than with its

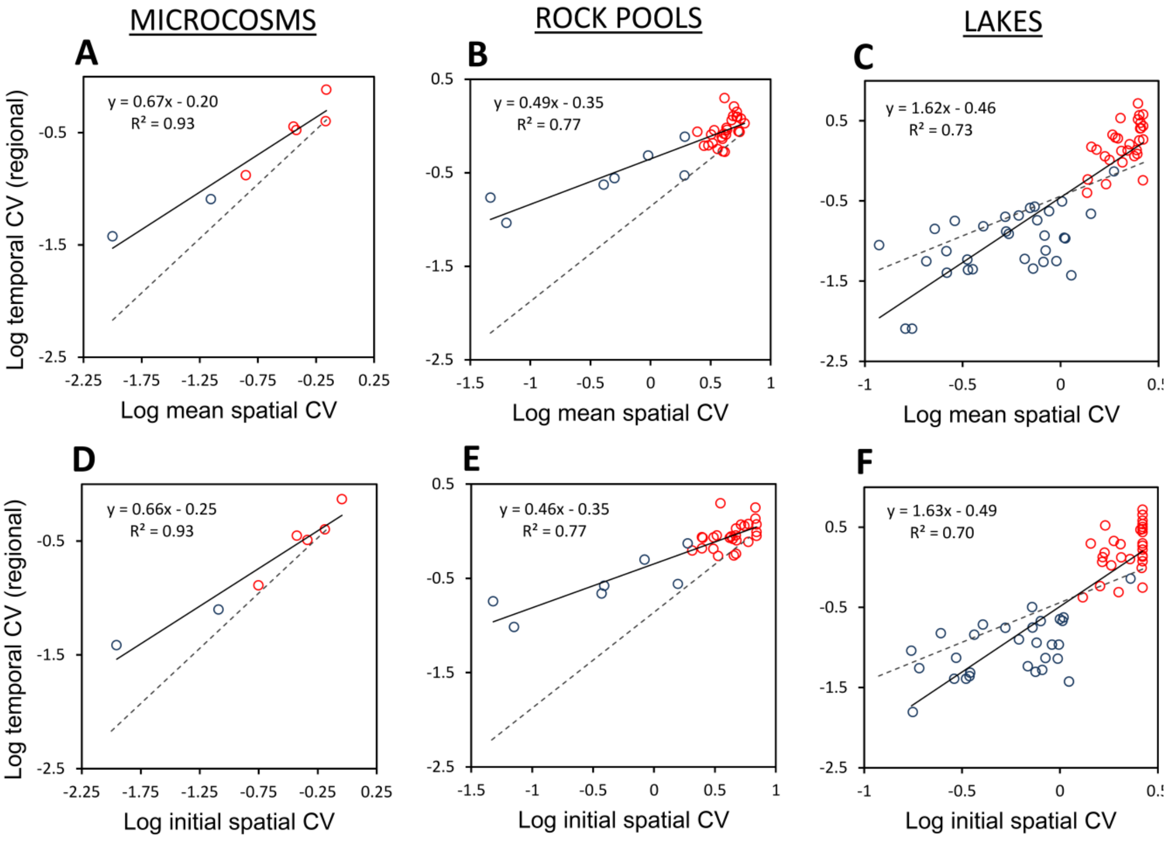


Figure 2.4. Empirical plots illustrating the link between spatial and temporal CV of ecosystem variables. The regional temporal CV of an ecosystem variable (point) was predictable from its spatial CV in microcosm (n = 7) **(A, D)**, rock pool (n = 33) **(B, E)**, and lake systems (n = 60) **(C, F)**. The predictive value of spatial variability was consistent in that linear associations emerged whether spatial variability was estimated as the mean of spatial CV's at time k **(A-C)**, or whether a spatial CV from an initial time point (k) was used to predict temporal CV of the remaining (k+1…n) time series **(D-F)**. Dashed lines denote the relationship expected for stochastic processes i.e., when values are independent across space and time. These were obtained by simulating random numbers with the same data range as empirical data sets. Abiotic variables (blue circles) were consistently more stable and less spatially patchy than biotic variables (red circles).

synchrony (Fig. 2.5).

Variables differed in the relative importance of spatial variability, synchrony or persistence to their landscape dynamics. We generated a fingerprint of these dynamics by normalizing the right hand terms of the variance equation (Fig. 2.1A) for each variable and then plotting them (Fig. 2.6). A division existed between biotic and physicochemical dynamics, and variables spread across several regions of the plot (quadrants A-D) corresponding to different spatiotemporal behaviors leading to temporal variability. Table 2.1 describes these modes of behavior in further detail and explores how they may arise in nature.

Species (blue points) clumped together, their population dynamics dominated by spatial variability with little synchrony or persistence (Fig. 2.6; intersection of quadrants A-D). Meanwhile, most atmospherically-driven processes (green points e.g., temperature, dissolved oxygen) were set apart by little persistence but were destabilized by synchrony (quadrant A). In contrast, many watershed-associated variables (black points e.g., ion concentrations) were characterized by persistence but little synchrony (quadrant B), a combination leading to lower temporal variability at the regional scale.

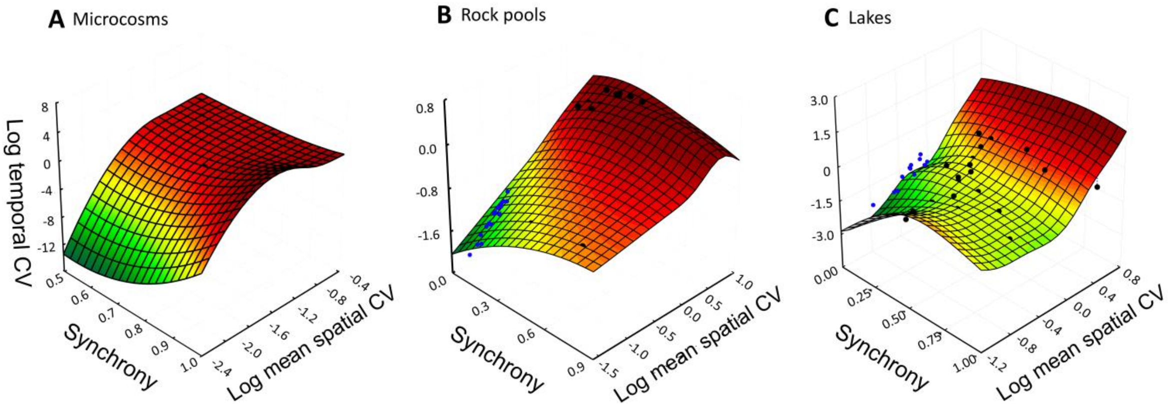


Figure 2.5. The modifying role of inter-patch synchrony. Relationship between spatial CV and regional temporal CV as modified by the degree of inter-patch synchrony in **(A)** microcosm, **(B)** rock pools and **(C)** lakes. Synchrony increased regional temporal CV relatively little over that explained by spatial CV. Black points = empirical variables, blue points = simulated, randomly-generated variables (n = 20; see Appendix D) to represent "independent dynamics region."

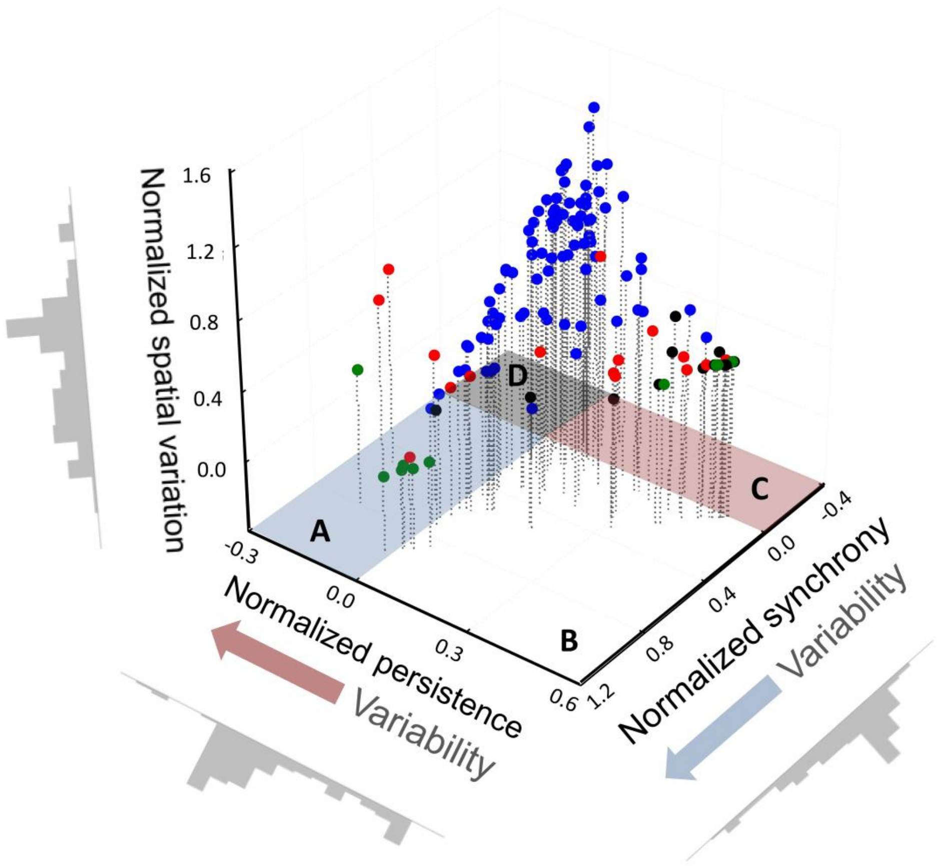


Figure 2.6. Patterns of spatiotemporal variation underlying the temporal variability of ecosystem variables. Temporal variance of an ecosystem variable can be decomposed into contributions of spatial variation, synchrony and persistence using the terms in Fig. 2.1A. These contributions were plotted against one another after being normalized as proportions of their sum. Variables (points) were assigned to *a priori* groupings based on their likely genesis and mode of regulation, where blue points = species populations, green = atmospheric, red = non-population biotic, black = watershed. n = 136, and includes an additional 36 rare rock pool species that were excluded from earlier analyses due to sparseness of data. Points scatter across theorized modes of dynamics described in Table 2.1: **A** = destabilized by synchrony, **B** = stabilized by persistence, destabilized by synchrony, **C** = stabilized by persistence, **D** = stabilized by compensatory dynamics, **Intersection of A-D** = stabilized by asynchrony. Gray histograms show frequency distributions for each component of temporal variance.

Table 2.1. Theorized modes of dynamics in landscape variables, their effect on regional temporal variation, and ecological examples. Modes reflect different mixtures of inter-patch synchrony and persistence, and correspond to regions of Fig. 2.6, where variables from three natural ecosystems are plotted by their spatiotemporal patterns.

Graph region	Synchrony / persistence	Dominant effect on temporal variation	Ecological scenario
A	High / Low	Destabilized by synchrony	Local factors less important, landscape-scale factors synchronize dynamics. E.g., synchrony of isolated mammal populations via weather (Post and Forchhammer 2002)
B	High / High	Stabilized by persistence and destabilized by synchrony	Local factors establish permanent spatial gradients, landscape-scale factors synchronize dynamics. E.g., synchrony of source-sink fish populations via dispersal (Isaak and Thurow 2006)
C	Low / High	Stabilized by persistence	Local factors establish permanent spatial gradients, dynamics differ among sites. E.g., stable spatial distributions of organisms across habitats (Morfin et al. 2012)
D	Low / Low	Stabilized by compensatory dynamics	Dynamics negatively correlated from time to time, site to site. E.g., spatiotemporal refugia of competing soil nematodes (Ettema et al. 2000)
Intersection of A,B,C,D	Zero / Zero	Stabilized by asynchrony	Dynamics appear stochastic, independent from time to time, site to site. E.g., settlement of broadcast oceanic larvae (Siegel et al. 2008)

DISCUSSION

Spatial signatures of temporal variability

Variables from three aquatic ecosystems showed a striking and tight correspondence between their regional temporal CV and mean spatial CV. This trend may be considered predictive because it held even when the spatial CV was known from only one time point. Moreover, trends emerged in ecosystems ranging from large to small, and from tropical to temperate, suggesting a potentially general and widespread phenomenon. Applying a space-time correspondence follows more than a century of studies involving substitution (Cowles 1899, Pickett 1989, Fukami and Wardle 2005, Walker et al. 2010), but our formulation extends usefulness in two ways; (i) it is quantitative in the form of equations in Fig. 2.1 rather than qualitative (e.g., chronosequence studies; see Paine 1985 for critical review) and (ii) the logic applies equally when substituting CV's of a single variable or when plotting many ecosystem variables for a multivariate view of landscape variation.

Tight linear dependence between spatial and temporal CV's likely owes to two reasons: First, when dynamics are stochastic or independent, variation in space roughly matches that in time as in ergodicity. Thus small fluctuations in time render equally small fluctuations across space. Second is the empirical observation that the factors that theoretically interfere with this correspondence - synchrony and persistence - do so little, at least when using the CV. While variables can lie anywhere on the plot (shifted up the y-axis by synchrony, down by persistence; Fig. 2.3C), they adhered more to the "independent dynamics" region than being shifted (Fig. 2.5). This makes sense in that a variable (e.g., a population) with low temporal CV in each patch will still be relatively stable regionally even when patches partially synchronize. This, in turn, registers as a low spatial CV because of how small temporal fluctuations beget small spatial variation (Fig. 2.2). There are exciting hints that this type of correspondence also applies to other temporal properties, such as recovery time or deterministic chaos, that leave a telling trace of their temporal dynamics in space (Sole and Bascompte 1995, Dai et al. 2012).

Analytical solutions and simulations show that spatial CV has value as a signature of temporal variability under certain conditions. When values of a variable are relatively uncorrelated in time and space (e.g., Fig. 2.4A), the temporal CV can be recovered with an analytical approximation (Fig. 2.1B; Eq. C.3). Accuracy wanes when ecological forces synchronize patches and shift the variable into the synchrony region of the plot (Fig. 2.3) where spatial CV underestimates temporal CV. Here, synchrony simultaneously boosts temporal variability and lowers spatial variability by aligning the peaks and troughs of fluctuations. Accuracy is also lower when ecological forces cause spatial gradients to persist through time and shift a variable into the persistence region of the plot (Fig. 2.3). Here, spatial variability exists, but it is created by patches that are stable over time.

Having shown that spatial CV is an accurate proxy for temporal CV when values are uncorrelated among locations and among times, it follows that quantitative substitution will work best when dynamics are effectively stochastic in space and time. This assumption will often not hold in nature (e.g., when climate swings induce synchrony). And whether it does hold will likely depend on the types of variables chosen (fast or slow, broad-scale or fine-scale) as well as the spatial and temporal sampling scales (Table 2.2). For instance, spatially-autocorrelated variables may have low spatial variability relative to their temporal variability. Conversely, temporally-autocorrelated variables may have high spatial variability relative to temporal variability.

Even when the assumption of independent values in time and space does not hold, however, regressions suggest that the rank order of temporal CV's (e.g., highest to lowest) might still be recovered from spatial CV's for qualitative substitution. This should be possible when: (i) All variables are thought to be synchronized or persistent to the same degree (Fig. 2.3C), (ii) they smoothly intergrade from synchrony to persistence (Figs. 2.3D; 2.4C,F), and/or (iii) the distorting effect of synchrony and persistence can be estimated and corrected for (Table 2.2). Thus, the link between spatial and temporal variation may be valuable for understanding when CV's are interchangeable, and how to interpret them when they are not.

Some variable types may be better suited to substitution than others. Interestingly, species populations (Fig. 2.4; red circles) illustrated a tradeoff between precision and accuracy. Precision to distinguish species with high versus low temporal CV's using spatial CV's was weak. This was for the sampling reasons that species had a limited range of variability (i.e., range of CV's < scatter) or possibly greater measurement error; or for the ecological reason that they differed in synchrony or persistence which created scatter. Such differences can occur when species respond even slightly differently to the spatial over the temporal environment (Jongejans and De Kroon 2005). But on the other hand, accuracy was probably higher for species because these variables lay closer to the independent dynamics line than physicochemical variables.

Results captured strong associations between spatial and temporal CV when data were separated by one time point (Fig. 2.4C-F) or were overlapping (Fig. 2.4A-C). Future work must address how far into the future a spatial CV can be a proxy for temporal CV. Additional error will certainly accrue for substitution if unexpected events alter a variable's temporal variability in ways not indicated by its initial spatial variability. The exact impact of this non-stationarity, however, is a matter of scale and of research question asked. For instance, high resolution prediction of single-species dynamics following a stochastic disturbance (e.g., forest fire) may be untenable if the disturbance drastically alters variability, synchrony or spatial persistence. But spatial CV should be a rough proxy – either quantitative or qualitative – for regional temporal CV under the ecological and sampling conditions in Table 2.2.

Table 2.2. Conditions under which the spatial variability of an ecological process is a precise or accurate substitute for its regional temporal variability.

Condition	Description	Substitution	Requirements	Ecological scenario
Independent dynamics	Values must be reasonably assumed independent from place to place, time to time	Spatial and temporal CV values roughly interchangeable (see Fig. 2.1B)	Scale of process ≤ scale of measurement in both space and time	Isolated communities with fast dynamics; intercontinental, long-term comparisons
Constant levels of synchrony or persistence across variables	Spatiotemporal behavior (e.g., synchrony) that is shared by all variables shifts all points equally on plot (Fig. 2.3C). Values shifted by a constant	Order (rank) of temporal CV's is conserved among variables	Approximately equivalent spatiotemporal behavior among variables	Variables similarly shaped by spatial constraints (e.g., microclimates) or by landscape-scale temporal shocks (e.g., weather)
Mixed synchrony and persistence of known magnitude	Variables differ in their synchrony and persistence (Fig. 2.3D), but degree of divergence is known and corrected for	Temporal CV value or order (rank) can be back-calculated	Estimates of synchrony and/or persistence; Fairly stationary dynamics	Variables responding differentially to spatiotemporal variation in the landscape with synchrony or persistence

Diagnostic signatures of complex dynamics

The terms of Fig. 2.1 also allowed a window into diagnosing landscape dynamics. Ecosystems conceal ecological information in an eclectic range of spatiotemporal patterns (Kareiva and Wennergren 1995, Bascompte 1998). Populations of exploited species (Erisman et al. 2012), biodiversity hotspots (Rutledge et al. 2001), harmful algal blooms (Edwards et al. 2012), pest outbreaks (Aukema et al. 2008) and wildfires (Senici et al. 2010) all display complex patterning in space and time. A range of analyses, as well as spatial and time series statistics, explore these patterns by examining underlying frequencies (e.g., spectral and wavelet analysis; Michele and Bernardara 2005, Grenfell et al. 2001) and patterns of correlation (e.g., correlograms; Ranta et al. 1997), or by fitting predictive models (e.g., autoregressive; Crabtree et al. 2009). Such approaches decompose spatiotemporal patterns, but do not link them to temporal variation as does our framework. Nonetheless, other procedures might provide profitable statistical extensions in the future.

We used plots of spatial versus temporal CV's as convenient and unique summaries of landscape dynamics (Fig. 2.4). Some variables occupied the synchrony region (above dashed line), others the persistence region (below dashed line). Such a mixture may be typical when a wide array of ecosystem processes is sampled. These mixtures left their mark on regression slopes. Slopes <1 in Fig. 2.4A-B show that abiotic variables in microcosms and rock pools were more stable, but also more prone to synchrony, than populations. Y-intercepts also changed to the degree that multiple variables displayed synchrony or persistence. These therefore offer multivariate indices of the degree of synchrony (β_0 > expected) or persistence (β_0 < expected) experienced by a landscape (Fig. 2.3C). Such plots may be fruitful ground for streamlined comparisons of landscapes containing diverse variables and dynamics, like pre-and post-disturbance ecosystems.

The components of temporal variance themselves – spatial variance, synchrony and persistence (Fig. 2.1A) – may also prove useful for describing patterns and mechanisms driving temporal variation. As we have seen, spatial variance can signal instability at the local, patch scale e.g., from demographic (Watson et al. 1984), community (Jiang and Pu 2009), natural enemies (Vogwill et al. 2009), spatial (Abbott 2011) or local environmental causes (Table G.1, Appendix G). Synchrony, in turn, indicates landscape-scale causes of variation like dispersal (Dey and Joshi 2006, Vogwill et al. 2009) or weather (Paradis et al. 1999, Liebhold et al. 2004). Finally, persistence points to the existence of long-term differences in mean value or state among patches, such as regulation by local communities or physical conditions. Combined, these components of variation gave an alternative view of dynamics.

Fine distinctions emerged when all elements of Fig. 2.1A were normalized to create a fingerprint or signature of dynamics. The grouping of variables controlled by different parts of the biosphere, like the atmosphere (e.g., temperature, dissolved oxygen) and the watershed (e.g., pH, ion concentrations), suggests that unique signatures may exist for types of ecological processes. Potential may thus exist for predicting the likely dynamics of a variable based on its type (e.g., atmospheric). Meanwhile, the breadth of spatiotemporal behaviors seen suggests a range of spatial variation, synchrony and persistence combinations leading to temporal variation in nature. Our framework may be useful for cataloguing these types of spatiotemporal dynamics in ecosystems (e.g., Table 2.1), and for making broad-stroke inferences about spatiotemporal mechanisms e.g., population rescue effects (Blasius et al. 1999, Abbott 2011), predator-prey cycles (Tobin and Bjørnstad 2003), species coexistence (Hassell et al. 1994, Ettema et al. 2000), and invasive species spread (Pysek and Hulme 2005).

CONCLUSIONS

Unexplained variation is common in nature, both across heterogeneous landscapes and over timespans of interest. By illustrating the link between spatial and temporal variation, we bring more clarity to the problems of *prediction* and *diagnosis* from spatial or spatiotemporal patterns. More work is needed to test the limits of prediction across scales, variables and ecosystem types. Yet, indications here suggest usefulness in; substituting spatial for temporal variability (either quantitatively or qualitatively), judging when substitution will not work, and interpreting the manifold changes of multivariate landscapes. Such efforts are hoped to add momentum towards the Rosetta Stone of landscape and ecosystem ecology, in which process and mechanism may be deeply and easily discerned from landscape pattern (Keitt and Urban 2005).

ACKNOWLEDGEMENTS

K. Abbott, P. Abrams, M. Anand, S. Carpenter, L. Dai, C. Jones, K. McCann, T. Parker, J. Quinn, D. Rollo, D. Vasseur, R. Vogt, D. Waring, J. Wu and several anonymous reviewers provided comments on the manuscript. We also thank the North Temperate Lakes LTER and Discovery Bay Marine Lab as data sources.

REFERENCES

Abbott, K. 2011. A dispersal-induced paradox: Synchrony and stability in stochastic metapopulations. Ecology Letters 14:1158–1169.

Anderson, K. E., F. M. Hilker, and R. M. Nisbet. 2012. Directional biases and resource-dependence in dispersal generate spatial patterning in a consumer-producer model. Ecology Letters 15:209–217.

Aukema, B. H., A. L. Carroll, Y. Zheng, J. Zhu, K. F. Raffa, R. D. Moore, K. Stahl, and S. W. Taylor. 2008. Movement of outbreak populations of mountain pine beetle: Influences of spatiotemporal patterns and climate. Ecography 31:348–358.

Barnes, J. B., T. A. Ehlers, N. Insel, N. Mcquarrie, and C. J. Poulsen. 2012. Linking orography, climate, and exhumation across the central Andes. Geology 40:1135–1138.

Bascompte, J. 1998. Spatiotemporal patterns in nature. Trends in Ecology and Evolution 13:173–174.

Blasius, B., A. Huppert, and L. Stone. 1999. Complex dynamics and phase synchronization in spatially extended ecological systems. Nature 399:354–359.

Blois, J. L., J. W. Williams, M. C. Fitzpatrick, S. T. Jackson, and S. Ferrier. 2013. Space can substitute for time in predicting climate-change effects on biodiversity. Proceedings of the National Academy of Science 110:9374–9379.

Bolliger, J., H. H. Wagner, and M. G. Turner. 2007. Identifying and quantifying landscape patterns in space and time. Pages 177–194 *in* F. Kienast, O. Wildi, and S. Ghosh, editors. A changing world: Challenges for landscape research. Springer.

Burrows, M. T., R. Harvey, L. Robb, E. S. Poloczanska, N. Mieszkowska, P. Moore, R. Leaper, S. J. Hawkins, and L. Benedetti-Cecchi. 2009. Spatial scales of variance in abundance of intertidal species: Effects of region, dispersal mode, and trophic level. Ecology 90:1242–1254.

Chesson, P. L. 1985. Coexistence of competitors in spatially and temporally varying environments: A look at the combined effects of different sorts of variability. Theoretical Population Biology 287:263–287.

Cottingham, K. L., B. L. Brown, and J. T. Lennon. 2001. Biodiversity may regulate the temporal variability of ecological systems. Ecology Letters 4:72–85.

Cowles, H. C. 1899. The ecological relations of vegetation on the sand dunes of Lake Michigan. Botanical Gazette 27:167–202.

Crabtree, R., C. Potter, R. Mullen, J. Sheldon, and S. Huang. 2009. A modeling and spatio-temporal analysis framework for monitoring environmental change using NPP as an ecosystem indicator. Remote Sensing of the Environment 113:1486–1496.

Dai, L., K. S. Korolev, and J. Gore. 2012. Slower recovery in space before collapse of connected populations. Nature 496:355–358.

Dey, S., and A. Joshi. 2006. Stability via asynchrony in Drosophila metapopulations with low migration rates. Science 312:434–436.

Earn, D. J. D., S. A. Levin, and P. Rohani. 2000. Coherence and conservation. Science 290:1360–1364.

Edwards, M., D. G. Johns, S. C. Leterme, E. Svendsen, and A. J. Richardson. 2012. Regional climate change and harmful algal blooms in the northeast Atlantic. Limnology and Oceanography 51:820–829.

Eppinga, M. B., C. A. Pucko, M. Baudena, B. Beckage, and J. Molofsky. 2013. A new method to infer vegetation boundary movement from “snapshot” data. Ecography 36:622–635.

Erisman, B., O. Aburto-oropeza, C. Gonzalez-abraham, I. Mascarenas-Osorio, M. Moreno-Baez, and P. A. Hastings. 2012. Spatio-temporal dynamics of a fish spawning aggregation and its fishery in the Gulf of California. Nature Scientific Reports:1–11.

Ettema, C. H., S. L. Rathbun, and D. C. Coleman. 2000. On spatiotemporal patchiness and the coexistence of five species of Chronogaster (Nematoda: Chronogasteridae) in a riparian wetland. Oecologia 125:444–452.

Fangliang, H., P. Legendre, and J. V Lafrankie. 2008. Distribution patterns of tree species in a Malaysian tropical rain forest. Journal of Vegetation Science 8:105–114.

Feller, W. 1950. An introduction to probability theory and its applications. Page 461. Wiley, New York.

Fukami, T., and D. A. Wardle. 2005. Long-term ecological dynamics: Reciprocal insights from natural and anthropogenic gradients. Proceedings of the Royal Society B 272:2105–2115.

Grenfell, B. T., O. N. Bjornstad, and J. Kappey. 2001. Travelling waves and spatial hierarchies in measles epidemics. Nature 414:716–723.

Grimm, V., and C. Wissel. 1997. Babel, or the ecological stability discussions: An inventory and analysis of terminology and a guide for avoiding confusion. Oecologia 109:323–334.

Guttal, V., and C. Jayaprakash. 2009. Spatial variance and spatial skewness: Leading indicators of regime shifts in spatial ecological systems. Theoretical Ecology 2:3–12.

Hassell, M. P., H. N. Comins, and R. M. May. 1994. Species coexistence and self-organizing spatial dynamics. Nature 370:290–292.

Isaak, D. J., and R. F. Thurow. 2006. Network-scale spatial and temporal variation in Chinook salmon (Oncorhynchus tshawytscha) redd distributions: Patterns inferred from spatially continuous replicate surveys. Canadian Journal of Fisheries and Aquatic Sciences 296:285–296.

Jiang, L., and Z. Pu. 2009. Different effects of species diversity on temporal stability in single-trophic and multitrophic communities. The American Naturalist 174:651–659.

Jongejans, E., and H. De Kroon. 2005. Space versus time variation in the population dynamics of three co-occurring perennial herbs. Journal of Ecology 93:681–692.

Kareiva, P., and U. Wennergren. 1995. Connecting landscape patterns to ecosystem and population processes. Nature 373:299–302.

Keitt, T. H., and D. L. Urban. 2005. Scale-specific inference using wavelets. Ecology 86:2497–2504.

Larsen, D. P., T. M. Kincaid, S. E. Jacobs, and N. S. Urquhart. 2001. Designs for evaluating local and regional scale trends. BioScience 51:1069–1078.

Leavitt, P. R., S. C. Fritz, N. J. Anderson, P. A. Baker, T. Blenckner, L. Bunting, J. Catalan, D. J. Conley, W. O. Hobbs, E. Jeppesen, A. Korhola, S. McGowan, K. Ruhland, J. A. Rusak, G. L. Simpson, N. Solovieva, and J. Werne. 2009. Paleolimnological evidence of the effects on lakes of energy and mass transfer from climate and humans. Limnology and Oceanography 54:2330–2348.

Legendre, P., M. De Caceres, and D. Borcard. 2010. Community surveys through space and time: Testing the space-time interaction in the absence of replication. Ecology 91:262–272.

Lehman, C. L., and D. Tilman. 2000. Biodiversity, stability, and productivity in competitive communities. The American Naturalist 156:534–552.

Levin, S. A. 1992. The problem of pattern and scale in ecology: The Robert H. MacArthur Award lecture. Ecology 73:1943–1967.

Lewis, W. M. 1978. Comparison of temporal and spatial variation in the zooplankton of a lake by means of variance components. Ecology 59:666–671.

Liebhold, A., W. D. Koenig, and O. N. Bjørnstad. 2004. Spatial synchrony in population dynamics. Annual Review of Ecology, Evolution and Systematics 35:467–490.

Litzow, M. A., J. D. Urban, and B. J. Laurel. 2008. Increased spatial variance accompanies reorganization. Ecological Applications 18:1331–1337.

Loreau, M., and C. de Mazancourt. 2008. Species synchrony and its drivers: Neutral and nonneutral community dynamics in fluctuating environments. The American Naturalist 172:E48–E66.

Marcos-Nikolaus, P., and J. M. Martin-Gonzalez. 2002. Spatial forecasting: Detecting determinism from single snapshots. International Journal of Bifurcation and Chaos 12:369–376.

McIntire, E. J. B., and A. Fajardo. 2009. Beyond description: The active and effective way to infer processes from spatial patterns. Ecology 90:46–56.

Michele, C. De, and P. Bernardara. 2005. Spectral analysis and modeling of space-time rainfall fields. Atmospheric Research 77:124–136.

Micheli, F., K. L. Cottingham, J. Bascompte, O. N. Bjørnstad, G. L. Eckert, J. M. Fischer, T. H. Keitt, B. E. Kendall, J. L. Klug, and J. A. Rusak. 1999. The dual nature of community variability. Oikos 85:161–169.

Morfin, M., J.-M. Fromentin, A. Jadaud, and N. Bez. 2012. Spatio-temporal patterns of key exploited marine species in the Northwestern Mediterranean Sea. PLoS One 7:1–14.

Paine, A. D. M. 1985. “Ergodic” reasoning in geomorphology: Time for a review of the term? Progress in Physical Geography 9:1–15.

Pandit, S., J. Kolasa, and K. Cottenie. 2009. Contrasts between habitat generalists and specialists: An empirical extension to the basic metacommunity framework. Ecology 90:2253–2262.

Paradis, E., R. Baillie, W. J. Sutherland, and R. D. Gregory. 1999. Dispersal and spatial scale affect synchrony in spatial population dynamics. Ecology Letters 2:114–120.

Pickett, S. T. A. 1989. Space-for-time substitution as an alternative to long-term studies. Pages 110–135 Long-term studies in ecology: Approaches and alternatives.

Pimm, S. L. 1984. The complexity and stability of ecosystems. Nature 307:321–326.

Post, E., and M. C. Forchhammer. 2002. Synchronization of animal population dynamics by large-scale climate. Nature 420:168–71.

Pysek, P., and P. E. Hulme. 2005. Spatio-temporal dynamics of plant invasions: Linking pattern to process 1. Ecoscience 12:302–315.

Ranta, E., V. Kaitala, and P. Lundberg. 1997. The spatial dimension in population fluctuations. Science 278:1621–1623.

Reed, D. C., P. T. Raimondi, M. H. Carr, and L. Goldwasser. 2000. The role of dispersal and disturbance in determining spatial heterogeneity in sedentary organisms. Ecology 81:2011–2026.

Rutledge, D. T., C. A. Lepczyk, J. Xie, and J. Liu. 2001. Spatiotemporal dynamics of endangered species hotspots in the United States. Conservation Biology 15:475–487.

Sciullo, L., and J. Kolasa. 2012. Linking local community structure to the dispersal of aquatic invertebrate species in a rock pool metacommunity. Community Ecology 13:203–212.

Seabloom, E. W., O. N. Bjørnstad, B. M. Bolker, and O. J. Reichman. 2005. Spatial signature of environmental heterogeneity, dispersal, and competition in successional grasslands. Ecological Monographs 75:199–214.

Senici, D., H. Y. H. Chen, Y. Bergeron, and D. Cyr. 2010. Spatiotemporal variations of fire frequency in central boreal forest. Ecosystems 13:1227–1238.

Siegel, D. A., S. Mitarai, C. J. Costello, S. D. Gaines, B. E. Kendall, R. R. Warner, and K. B. Winters. 2008. The stochastic nature of larval connectivity among nearshore marine populations. Proceedings of the National Academy of Sciences 105:8974–9.

Sole, R. V, and J. Bascompte. 1995. Measuring chaos from spatial information. Journal of Theoretical Biology 175:139–147.

Tobin, P. C., and O. N. Bjørnstad. 2003. Spatial dynamics and cross-correlation in a transient predator–prey system. Journal of Animal Ecology 72:460–467.

Turner, M. G. 2010. Disturbance and landscape dynamics in a changing world. Ecology 91:2833–2849.

Vogwill, T., A. Fenton, and M. A. Brockhurst. 2009. Dispersal and natural enemies interact to drive spatial synchrony and decrease stability in patchy populations. Ecology Letters 12:1194–1200.

Walker, L. R., D. A. Wardle, R. D. Bardgett, and B. D. Clarkson. 2010. The use of chronosequences in studies of ecological succession and soil development. Journal of Ecology 98:725–736.

Watson, A., R. Moss, P. Rothery, and R. Parr. 1984. Demographic causes and predictive models of population fluctuations in Red Grouse. Journal of Animal Ecology 53:639–662.

CHAPTER 3.

SPATIOTEMPORAL PATTERNS AS PREDICTORS OF DYNAMIC CHANGE FROM CONNECTING ECOSYSTEM FRAGMENTS

Adapted from

Hammond, M. P. and J. Kolasa. Spatiotemporal patterns as predictors of dynamic change from connecting ecosystem fragments

Submitted to *Oecologia* on January 30th, 2015

HYPOTHESIS AND RATIONALE

Hypothesis tested: *Patterns of spatiotemporal variation can be used to predict responses to connecting ecosystem fragments*

Rationale: Spatiotemporal dynamics are common in populations and physicochemical variables after a change in landscape structure. Physical connection of ecosystem fragments, for instance, initiates a process of spatiotemporal change that tends to synchronize fluctuations and homogenize spatial variation among sites (e.g., Lecomte et al. 2004, Fox et al. 2013). Variables driven by regional-scale factors tend to be nearly maximally synchronous and homogenous (Lecomte et al. 2004), implying that they will not increase further with connection. In contrast, variables driven by local-scale factors often display asynchrony and differences among sites (Ims and Andreassen 2005), implying the possibility of larger increases in synchrony and homogeneity. Because these spatiotemporal changes manifest in a number of response metrics (e.g., temporal variation), they must be captured with suitable graphical and statistical summaries as are developed here. This study tests pattern- and trait-based indicators of future ecological dynamics, represented by research directions *h* and *j* in Fig. 1.2.

ABSTRACT

Landscape modifications like fragmentation and reconnection spark a process of spatiotemporal change that impacts populations, communities and ecosystems. Unraveling and predicting how landscape modification alters dynamics like temporal variability remains a major research focus. But few findings apply to the full complement of variables in ecosystems. We tested whether spatiotemporal pattern (which reflects the balance of regional and local dynamics) could predict the responses of ten ecosystem variables to physical connection of aquatic microcosms. Connection caused rapid shifts in spatiotemporal pattern as spatial gradients were equalized, consistent with those predicted by a conceptual framework. Spatiotemporal shifts manifested at local and regional scales as changes in mean, temporal variation and covariation between patches, which we partitioned with a novel statistical framework. While seeming idiosyncratic, these responses were highly predictable ($r^2 = 0.66$-0.92) from a variable's spatiotemporal pattern in the unconnected treatment: Variables with high inter-patch synchrony underwent the least change in mean and covariation while variables with pronounced spatial gradients saw the largest changes in temporal variation. Responses also mapped well onto distinctions between energetic, material and population/biotic variables. Results suggest regularities where synchrony indicates diffuse dynamics that are insensitive to connection and size of spatial gradient indicates the potential for local change when dissimilar patches mix. Findings may help to simplify

the task of predicting changes in the dynamics of multiple variables in impacted landscapes.

Keywords: Variability, variation, connectivity, corridor, spatiotemporal, synchrony, microcosm, fragmentation, ecosystem, spatial

INTRODUCTION

Processes like fragmentation, afforestation and the use of wildlife corridors commonly change the structural connectivity or continuity of habitat patches (*sensu* Taylor and others 2006). Such landscape modifications often spark a process of spatiotemporal change in communities and ecosystems that has far-reaching consequences. Increased connectivity can, for instance, stabilize populations and boost species richness and can enhance productivity, nutrient cycling and service provisioning (Wetzel et al. 2005, Richardson et al. 2009, Garibaldi et al. 2011). While much is known about these effects and their causal mechanisms, predicting the response of a given variable (defined as a measurable aspect of an ecological process) to connection remains a challenge.

Predicting connectivity responses is essential for anticipating the changes in abundance or variability (in space and time) of ecological resources that come with landscape alteration (Ellis et al. 2010). To achieve this level of prediction, simplifying and synthetic rules are needed that apply across populations and communities (Ellis et al. 2010) as well as to physicochemical variables (e.g., Mitchell et al 2013; Valett et al 2014). This endeavour is complicated by the fact that structural connectivity may enhance movement for some variables but not others (Clevenger and Waltho 2000, Mitchell et al. 2013). Yet recent findings show generalities, for example that patterns and scales of organism movement can predict connectivity responses (Haddad 1999, D'Eon et al. 2002, Uezu et al. 2005). We extend this notion and test the idea that spatiotemporal patterns, which reflect the relative importance of regional or local factors (Ims and Andreassen 2005), can indicate the connectivity responses of variables. But first we constrain the problem with a conceptual and graphical framework of the possibilities for spatiotemporal change.

Conceptual and graphical framework

If connection leads to reorganization, a shift will be seen in a variable's spatiotemporal pattern from unconnected to connected treatments. This shift can be plotted using variance components from ANOVA with space and time as random factors, as in Fig. 3.1. Components correspond to *fixed spatial, fixed temporal* and *remainder variation* (Lewis 1978) and serve to summarize a variable's spatiotemporal pattern (grey point, Fig. 3.1). When *fixed spatial variation* accounts for most variation, persistent spatial variation occurs in which there is unevenness among site means (bottom right, Fig. 3.1). When *fixed temporal variation* accounts for most variation, synchrony occurs in which fluctuations are positively correlated among patches of similar mean (top left, Fig. 3.1). Finally, when *remainder variation* dominates, the pattern is one of asynchrony among

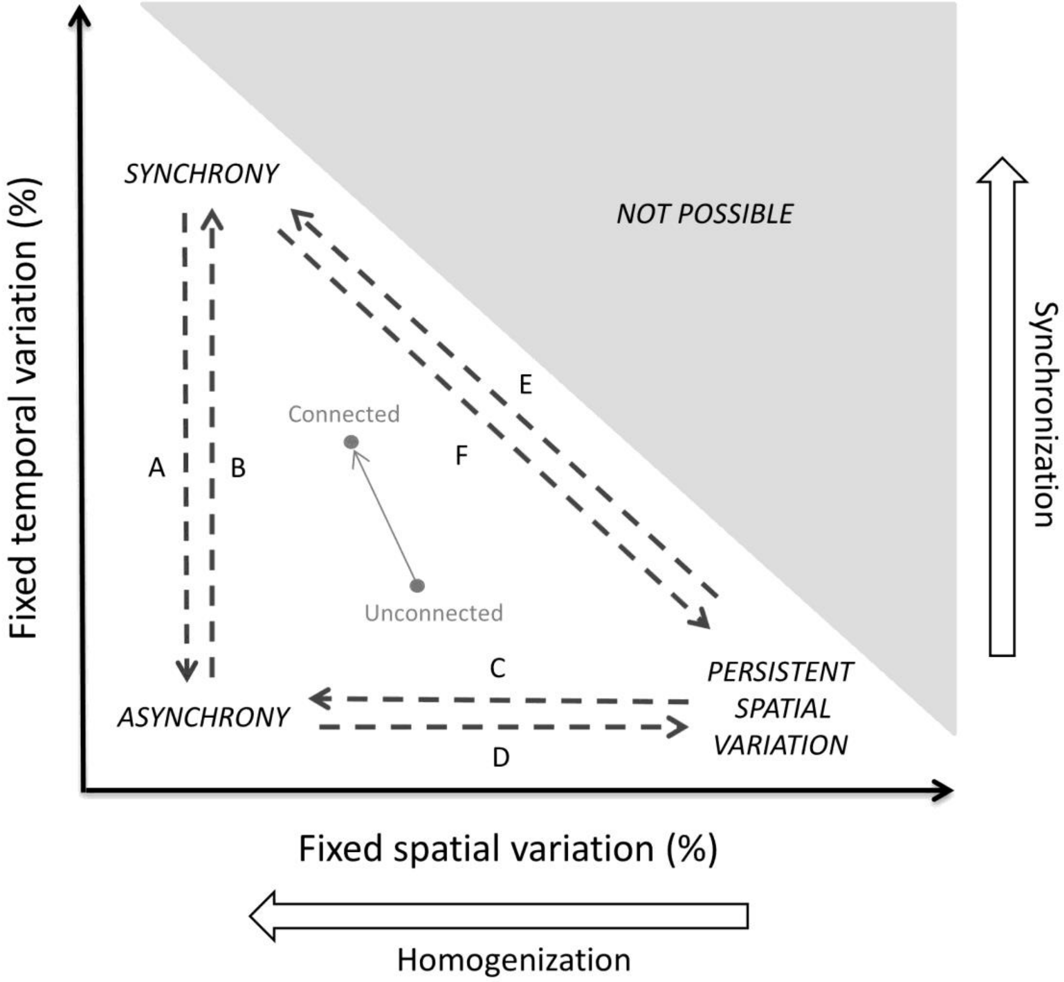


Figure 3.1. Changes in spatiotemporal pattern possible from connecting ecosystem fragments. Plotting an ecosystem variable (point) by its spatial and temporal variance components positions it according to its spatiotemporal pattern, which can include synchrony, asynchrony or persistent spatial variation. If structural connection changes the variable's spatiotemporal pattern, the point will shift from an "Unconnected" to a new "Connected" position. The grey arrow portrays the magnitude and direction of change, while broken arrows denote the various changes in spatiotemporal pattern possible, described further in Table 3.1. The null expectation is for connection to homogenize and synchronize patches, driving points towards the upper left, synchrony region.

patches, also called ephemerality (bottom left, Fig. 3.1). Any transformation of the unconnected pattern into another pattern by connection is conveniently reflected in a shift in position on the plot, indicated by grey arrows (Fig.3.1).

What spatiotemporal changes are possible with structural connection? At least six changes in spatiotemporal pattern can occur, as shown by arrows at the transitions between different patterns in Fig. 3.1. Examples of these transitions can also be found in nature (Table 3.1). Importantly, despite the range of possibilities, two types of change may be expected more often than others (see Appendix H for discussion):

(1) *Homogenization* (arrow C in Fig. 3.1), where movement reduces unevenness among sites by causing their means to converge (see Fig. H.1 for illustration) and;

(2) *Synchronization* (arrow B in Fig. 3.1), where movement brings out-of-step fluctuations into step such that they are positively correlated across patches (see Fig. H.2).

Homogenization and synchronization occur when movement that equalizes patches is high and local responses (e.g., to pH or predation) that cause patches to diverge are low (cf. Earn et al 2000; Cazelles et al 2001; Ims and Andreassen 2005). These conditions will not always be met; for instance, responses to the local environment may override the homogenizing effect of dispersal (Cottenie and De Meester 2004) and chaotic dynamics may prevent synchrony (Becks and Arndt 2013). But conditions for homogenization do appear to be common in natural systems. Many energetic and material variables (e.g., weather, solute concentrations) diffuse from high to low concentration or mix readily across space, all of which tend to homogenize differences among sites (Mahadevan 2005). For biotic or population variables, dispersal that is (positive) density-dependent or simply prodigious can equalize population sizes (e.g., Lecomte et al 2004). Moreover, movement from high to low concentration appears to be common in animals (Matthysen 2005) and passively-transported propagules (e.g., Di Franco et al 2012).

Synchronization of fluctuations also occurs over a wide range of situations (Cazelles et al. 2001, Becks and Arndt 2013). Among other causes, it is induced by (positive) density-dependent (Lecomte et al. 2004) or fitness-dependent movement (Ruxton and Rohani 1999) or even density-independent movement of sufficient magnitude (Münkemüller and Johst 2008). Movement is not always synchronizing (e.g., Ims and Andreassen 2005), but research to date suggests that it may be more often than not. It thus provides a reasonable null case with which to compare actual responses of variables to connection.

Variables that homogenize and synchronize easily when connected (e.g., those with diffusive movement) will reflect the combined pulls of arrows B and C (arrow E, Fig. 3.1), shifting towards the top left of the diagram. The line tracing this or any other transition (grey line, Fig. 3.1) provides useful diagnostic information about the response of a variable to connection. First, the length of the line indicates the amount of *change in spatiotemporal pattern* due to connection, ranging from zero percent, when a variable has no response, to its maximum when its response follows arrow E or F in Fig. 3.1. Second, the slope of the line indicates the rate at which spatial differences (i.e., concentration gradients) are converted into synchrony when connectivity is increased.

Table 3.1. Types of spatiotemporal change possible for an ecosystem variable in response to structural connection. Types of change correspond to arrows in Fig. 3.1 and differ in the magnitude of spatiotemporal pattern change (arrow length).

Type of change	Description	Magnitude of pattern change	Example
No change	Spatiotemporal pattern remains the same	Small to none	No or lagged response (Ims and Andreassen 2005)
A	Desynchronize fluctuations in patches	Intermediate	Dispersal desynchronizes fly populations (Dey and Joshi 2006)
B	Synchronize fluctuations in patches	Intermediate	Synchronization of bacterial populations (Vogwill et al. 2009)
C	Reduce unevenness among patches	Intermediate	Homogenization of salmon population sizes (Einum et al. 2008)
D	Increase unevenness among patches	Intermediate	Concentration of solutes along lake chains (Soranno et al. 1999)
E	Reduce unevenness and synchronize patches	Large	Homogenization and synchronization of lizard populations (Lecomte et al. 2004)
F	Increase unevenness and desynchronize patches	Large	Nutrient concentration in marsh islands (Wetzel et al. 2005)

Other response metrics and hypotheses

Spatiotemporal reorganization that accompanies connection will likely register as changes in more traditional response metrics. Temporal variance is one such metric that reflects the variation of ecological resources over time, and when measured at the regional scale (i.e., aggregated patches) contains information about regional- and local-scale change. We therefore use a novel statistical decomposition that breaks down percent change in regional temporal variance into three relative measures of local and regional change (Table 3.2): (1) Δ covariability - the magnitude of synchronous change between patches *i* and *j*, (2) Δ variability - the magnitude of change in the variability of patch *i*, and (3) Δ mean – the magnitude of change in the mean value of patch *i*. The advantage of these measures lies in tracking several responses to connection with a consistent family of dimensionless indices.

We test the following hypotheses suggested by our synthetic framework by comparing connected and unconnected treatments of aquatic laboratory microcosms:

1) Variables will reflect, to varying degrees, the null tendency towards homogenization and synchronization with arrows pointing to the top left of Fig. 3.1.

2) Variables lying in the synchrony region (Fig. 3.1, top left) are close to maximum homogenization and synchronization, and so will undergo little change in spatiotemporal pattern and response metrics with connection.
3) Variables lying in the persistent spatial variation region (Fig. 3.1, bottom right) are far from maximum homogenization and synchronization, and so will undergo more change in spatiotemporal pattern and response metrics.
4) Energetic variables will undergo less connective change than biotic and material variables because they equilibrate easily across space even when structural connectivity is low and have weak responses to local conditions in patches.

Findings present a new view of spatiotemporal change caused by structural connection and help to link the properties of variables to their potential dynamic responses.

METHODS

Connectivity experiment and ecosystem measurements

We assembled three aquatic communities from species that had co-occurred stably in cultured laboratory populations. Communities were: (1) Ubiquitous microbes retained in distilled laboratory water, (2) phytoplankton and microbes, and (3) ~10 species of invertebrates (cladocerans, ostracods), phytoplankton and microbes. The short lifespans of organisms (< 2 months) meant that the experiment included several generations.

The three communities were distributed into an array of 3 × 700 mL microcosms, with one community type per microcosm. This set-up mimicked natural spatial heterogeneity with significant differences among microcosms within an array (MANOVA $F = 41.78$, $p < 0.0001$; significant differences for 9 of 10 variables). In a connected treatment (12 replicate arrays), microcosms in an array were connected with 30 mm of clear 10 mm diameter Tygon® tubes. In an unconnected treatment (9 replicate arrays), spatial exchange was prevented by blocking connection tubes with aquarium grade silicone. Connector tube diameter was increased by 70% in week 10 of the 20 week experiment, aiming to compare the effects of a connection event with the effects of separate connectivity treatments. Unfortunately, the manipulation was confounded by the extinction of species over time and is thus not considered further.

Ten community and ecosystem variables, measured weekly, were categorized as energetic (e.g., temperature), material (e.g., dissolved oxygen), biotic (e.g., net primary productivity) or population (e.g., *Daphnia* density). Ecosystem respiration, net primary productivity (NPP) and gross primary productivity (GPP) were measured using light/dark bottles (Wetzel and Likens 1991) of a homogenized community sample, incubated for three hours *in situ* in a sealed, lightproof or clear 25 mL glass vial. Microcosm dissolved oxygen concentration and temperature were measured with an ExStik® DO600 probe (Waltham, Massachusetts, USA). Phytoplankton densities were estimated as chlorophyll a (*Chl a* hereafter) in a 12 mL water sample, concentrated onto a 1.1 µm glass micro-fibre filter, boiled in 2.5 mL of 95% ethanol for 20 minutes, extracted for 24 hours, and measured on a BioTek Synergy 2 microplate reader (Warren 2008). Picoplankton/particulate density was estimated as the spectral absorption at 550 nm of 2 mL of microcosm water filtered through a 1.1 µm micro-fibre filter. *Daphnia*, ostracod and total invertebrates were counted from digital photographs. To distinguish invertebrates from background, a homogenous, 25 mL sample of microcosm water was photographed twice, five seconds apart, in a shallow eye glass dish. One image was then subtracted from the other using Image J software (National Institute of Health, v. 1.46r) to obtain a derived image of only live, moving invertebrates.

Data pre-treatment: Removing trend and restoring spatial structure

We focused on short-term fluctuations by removing temporal autocorrelation (trend). This was done by first-differencing time series values ($X_k \ldots X_n$) of each microcosm using the operation $X_{k+1} – X_k$ (Hsieh et al. 2005). First-differencing effectively removes the mean value of a time series and, when applied across microcosms, eliminates any spatial structure arising from differences in mean among microcosms. To restore this structure, we added a constant to each time series value that was equal to the mean removed by first-differencing. The constant was (m_o - m_d), where m_o and m_d are the means of the original and first-differenced series, respectively. This operation yields a final series for each microcosm that has a mean identical to the original series and minimal autocorrelation. Zeros representing the extinction of organisms (*Daphnia*) from an entire array were removed. We repeated analyses on undifferenced data to check for any autocorrelated responses to connection. Appendix I reports representative time series from the ten study variables.

Description of spatiotemporal patterns

We described spatiotemporal patterns of each variable in each microcosm array with the three variance components from a random effects ANOVA with site and time as factors (Lewis 1978). Components are: *Fixed spatial*, *fixed temporal* and *remainder variation* (see Introduction for details). Small negative components were set to zero as is convention. Each component was expressed as a percentage of the sum of components. Shifts in spatiotemporal pattern were plotted on axes of percent fixed spatial and fixed temporal variation. Change in spatiotemporal pattern (the lengths of arrows in Figs. 3.1, 3.3) was calculated as the hypotenuse of a Pythagorean triangle with side lengths corresponding to changes in y- and x-values.

Decomposing % change in regional variance

Structural connection can alter many facets of dynamics that are quantified by various metrics. Below, we present a new method that partitions four main components of change from the difference in temporal variance between connected and unconnected systems (see Appendix J for derivations).

Regional temporal variance $Var(Y)$ is the variance of the spatially-aggregated time series Y i.e., $Var(X_i, + X_j \ldots X_n)$ where i and j are patches. Its value is a result of: (1) Variability of the regional series Y, (2) temporal variability of component patches i, (3) covariability, that is the relative amount of synchronous change between patches i and j and (4) the mean of regional series Y because variance depends on the mean (Taylor 1961). While the Coefficient of Variation (CV) can estimate quantities 1-3, it can be biased (McArdle et al. 1990, Proulx et al. 2010) and removes but does not index quantity 4. However, if we consider a difference between two variances, e.g., from a connected and unconnected landscape, we can estimate how much of this difference arises from changes in quantities 1-4. This works by comparing observed values of variances and covariances to those expected if connection *changed only the mean*.

The variance expected from a change in mean is calculated from a statistical rule: Multiplying series values X by a constant k yields a new mean of km and a new variance of $k^2Var(X)$ (Kilpatrick and Ives 2003). Now consider an unconnected system with mean m_U whose values change by k upon connection. The new connected mean m_C is km_U. Rearranging gives $k = m_C/m_U$, and since the new variance is k^2 times the original, unconnected variance $Var(Y)_U$, the expected connected variance $Var(Y)_{CExp} = (m_C/m_U)^2Var(Y)_U$. Comparing the observed connected variance $Var(Y)_C$ to this null value, we know that: (1) Means alone have changed if observed $Var(Y)_C$ = expected $Var(Y)_{CExp}$ (Fig. 3.2a), (2) variability has increased if $Var(Y)_C > Var(Y)_{CExp}$ (Fig. 3.2b), and (3) variability has decreased if $Var(Y)_C < Var(Y)_{CExp}$ (Fig. 3.2c). Meanwhile, the difference between expected variance $Var(Y)_{CExp}$ and unconnected variance $Var(Y)_U$ serves as an index of change in mean (Table 3.2; Appendix J).

Values expected for mean-only change can be calculated for summed patch variances ($\sum var(X_i)$) and summed inter-patch covariances ($\sum cov(X_i, X_j)$) because these are also a function of k. Subtracting these values from observed values allows the difference between two regional variances to be split further into the contributions of patches and their covariation (Fig. 3.2d). Table 3.2 reports these formulas standardized to the unconnected regional variance. The result is dimensionless indices - Δ *regional variability,* Δ *mean*, Δ *patch variability*, and Δ *covariability* - that sum to percent change in regional variance.

Indices were calculated for each variable from treatment group means of variances and covariances. Indices showed no evidence of bias by the mean (Appendix K) which often plagues variability indices (McArdle et al. 1990). Because our indices work only on the difference between two variances, we used the CV^2 of Proulx and others (2010) and its components for two-tailed t-tests between treatment groups, though these showed some signs of mean bias (Appendix M).

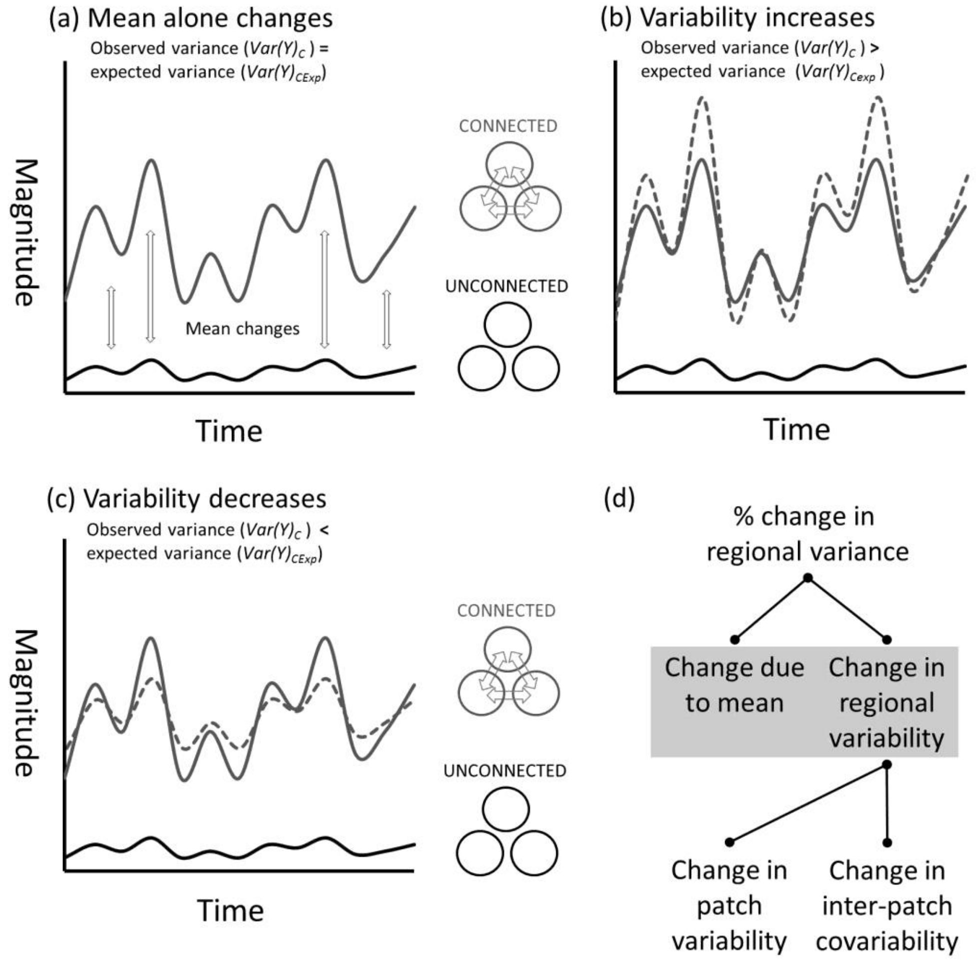


Figure 3.2. Decomposing a change in regional variance, from an unconnected system (lower, black line) to a connected one (upper, gray lines), into changes in mean and variability; solid gray line shows expected values. (a) If mean alone changes upon connection, observed connected variance $Var(Y)_C$ will equal the theoretical value $Var(Y)_{CExp}$.**(b)** If $Var(Y)_C > Var(Y)_{CExp}$, then variability has increased. Larger positive differences indicate larger increases in variability. **(c)** If $Var(Y)_C <$ $Var(Y)_{CExp}$, then variability has decreased. More negative differences indicate larger decreases in variability. **(d)** Scheme for derived dimensionless indices (Table 3.2) that partition % change in regional variance into sources of change. Gray box denotes sources shown in a-c

Table 3.2. Decomposition of % change in regional variance into contributing sources of change. Table reports dimensionless indices of sources plus related indices from Proulx and others (2010). Sources are quantified by comparing observed connected variances with those expected if means alone, and not variability, changed with connection. Symbols: Var(Y) = regional variance; $\sum \mathrm{var}(X_i)$ = summed patch variances defined as $\sum_{\mathbf{i=1}}^{\mathbf{n}} \mathbf{var}(\mathbf{X_i})$; $\sum \mathrm{cov}(X_i, X_j)$ = summed inter-patch covariances defined as $\sum_{\mathbf{i=1}}^{\mathbf{n}} \sum_{\mathbf{j=1}}^{\mathbf{i-1}} \mathbf{cov}(\mathbf{X_i}, \mathbf{X_j})$. Sub-scripts: C = connected; U = unconnected; CExp = connected value expected from change in mean. See Appendix J for derivations.

Source of change	**Index formula**	**Description**	**Related index**
% change in regional variance	$\frac{\mathrm{Var(Y)_C} - \mathrm{Var(Y)_U}}{\mathrm{Var(Y)_U}} \cdot 100$	Includes effects of changes in mean, patch variances and covariances	
Δ regional variability	$\frac{\mathrm{Var(Y)_C} - \mathrm{Var(Y)_{CExp}}}{\mathrm{Var(Y)_U}} \cdot 100$	Change in pure regional variability i.e., beyond that expected from change in mean	CV^2
Δ patch variability	$\frac{\sum \mathrm{var(X_i)_C} - \sum \mathrm{var(X_i)_{CExp}}}{\mathrm{Var(Y)_U}} \cdot 100$	Change in pure variability of patches	Variance CV
Δ covariability	$\frac{2\left(\sum \mathrm{cov}(X_i, X_j)_C - \sum \mathrm{cov}(X_i, X_j)_{CExp}\right)}{\mathrm{Var(Y)_U}} \cdot 100$	Change in pure covariability among patches	Covariance CV
Δ mean	$\frac{\mathrm{Var(Y)_{CExp}} - \mathrm{Var(Y)_U}}{\mathrm{Var(Y)_U}} \cdot 100$	Variance change attributable to difference in mean. Equals % change in squared means.	

RESULTS

Structural connection initiated major shifts in spatiotemporal patterns. These shifts were in the direction of homogenizing site differences and synchronizing fluctuations in all variables but temperature, which underwent the opposite to a small degree (Fig. 3.3). The greatest change in spatiotemporal pattern (arrow length in Fig. 3.3) occurred in variables that had high fixed spatial variation in an unconnected system. This relationship explained 97% of variation, indicating that it was the presence of spatial gradients that drove responses to connection (Fig. L.1, Appendix L). In addition to magnitude of change, variables differed in rates of spatiotemporal change (slope of arrows, Fig. 3.3). The energetic variable of temperature had a large slope (-1.57), a value consistent with rapid synchronization as spatial gradients were equalized. Material variables had intermediate slopes and rates (dissolved oxygen = -0.71; particulate = -0.51). Biotic and population variables had the smallest slopes and rates (GPP = -0.20; Respiration = -0.41; *Daphnia* = -0.49; Ostracods = -0.11; Total inverts = -0.14). Only NPP had an anomalously large slope (-2.18).

Changes in spatiotemporal patterns were significantly correlated with changes in all response metrics (Table L.1, Appendix L). 90% of ecosystem variables underwent significant changes in regional variability, patch variability, inter-patch covariability, or local mean (Appendix M). However, variables displayed complex mixtures of these changes with some increasing and some decreasing with connection. These varied responses were effectively summarized by decomposing % change in regional variance into its components (Fig. 3.4).

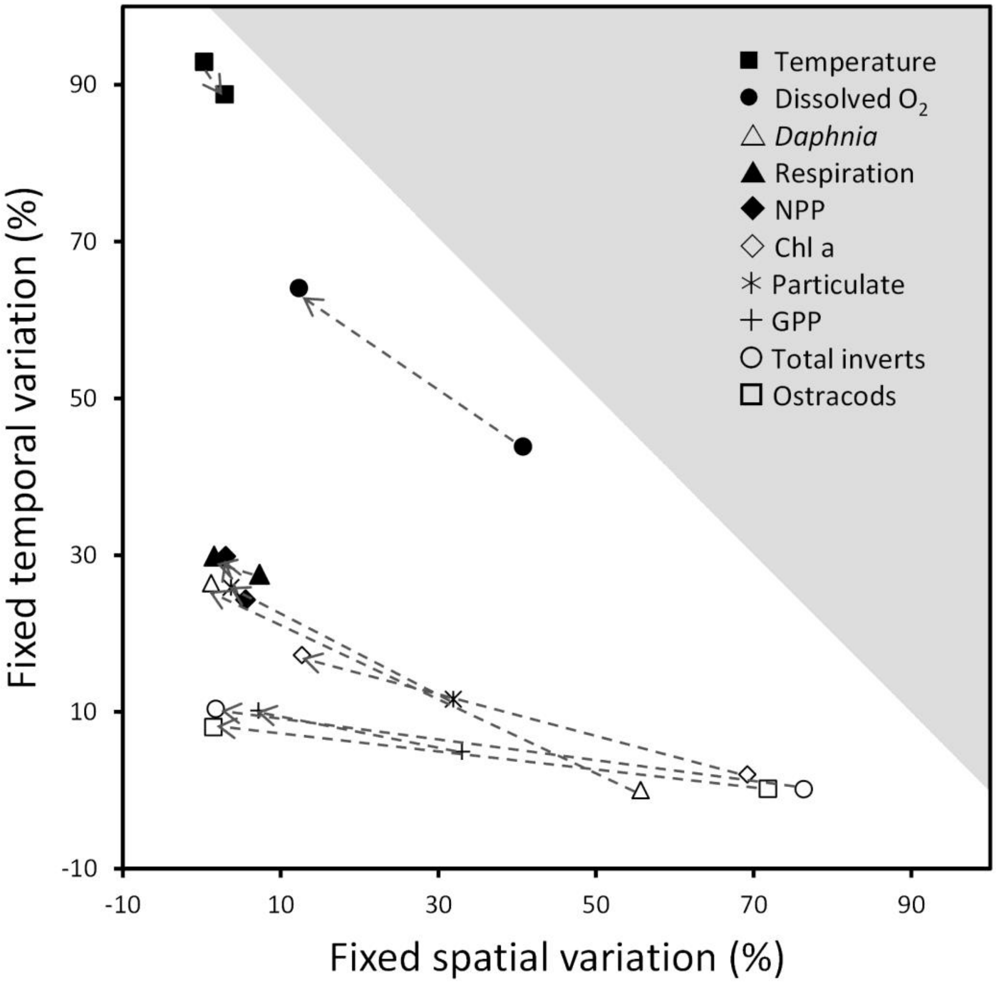


Figure 3.3. Changes in spatiotemporal patterns of ecosystem variables due to structural connection. Each arrow traces a shift in spatiotemporal pattern for a single variable, pointing from unconnected to connected treatment values (= treatment means). See Fig. 3.1 for more detail.

Population variables (*Daphnia*, ostracods, total invertebrates and chlorophyll a) had the largest jumps in mean density, patch variability and covariability with connection (Fig. 3.4). This coincided with rapid increases in density (1.5- to 9-fold) over initial values during the first six weeks of the experiment (see Appendix I for time series). Energetic and material variables had weaker responses, some of which were nonetheless significant (Appendix M).

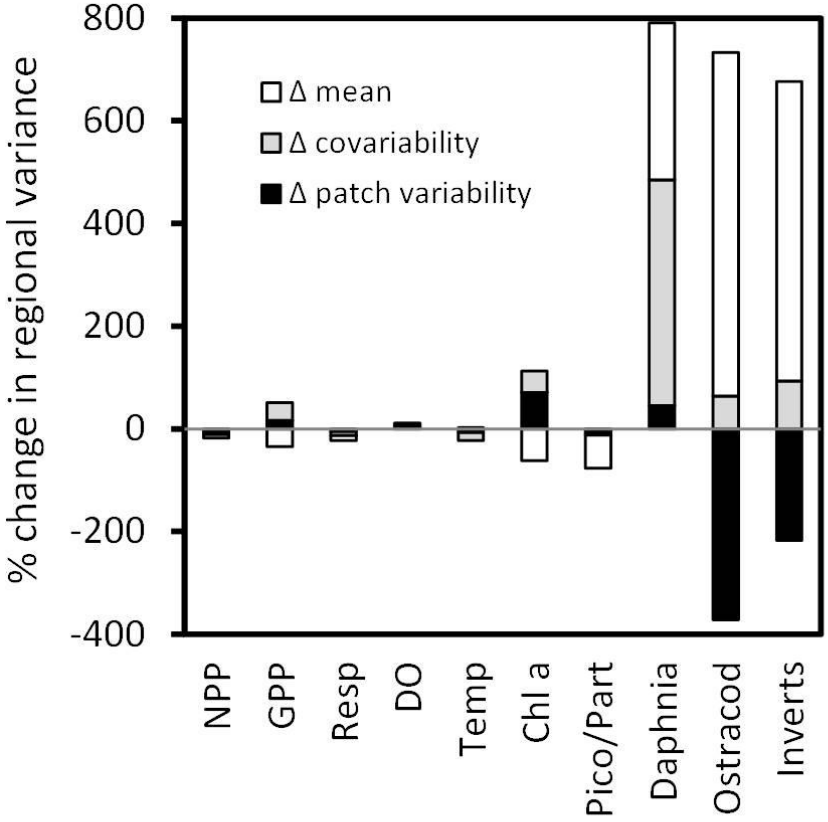


Figure 3.4. Response profiles of ten ecosystem variables to microcosm connection. Bars show contributions of Δ mean, Δ patch variability, and Δ covariability (Table 3.2) to % difference in regional variance between unconnected and connected treatments. Positive values indicate a connection response that increased regional variance, and negative values a response that decreased regional variance.

Changes in mean, variability and covariability were largely predictable from a variable's spatiotemporal pattern in an unconnected system. Those variables with high fixed temporal variation (e.g., temperature, dissolved oxygen) saw the least change in covariability (Fig. 3.5a) and local mean when connected (Fig. 3.5c) while biotic variables with low fixed temporal variation saw large changes (Fig. 3.5a,c). Because the axes of Fig. 3.5a are statistically dependent, we confirmed this result with an alternate method that scaled independent synchrony estimates for unconnected and connected treatments (Fig. N1, Appendix N). Consistent with findings in Fig. 3.3, variables with high fixed spatial variation in unconnected systems experienced the most change in patch variability, while those with weak spatial gradients experienced little to no change (Fig. 3.5b).

Results were robust in that similar trends were found in undifferenced data but disappeared when data were randomized (Appendices O, P). Indices from Table 3.2 used were also found to perform well, being unbiased by the mean (Appendix K).

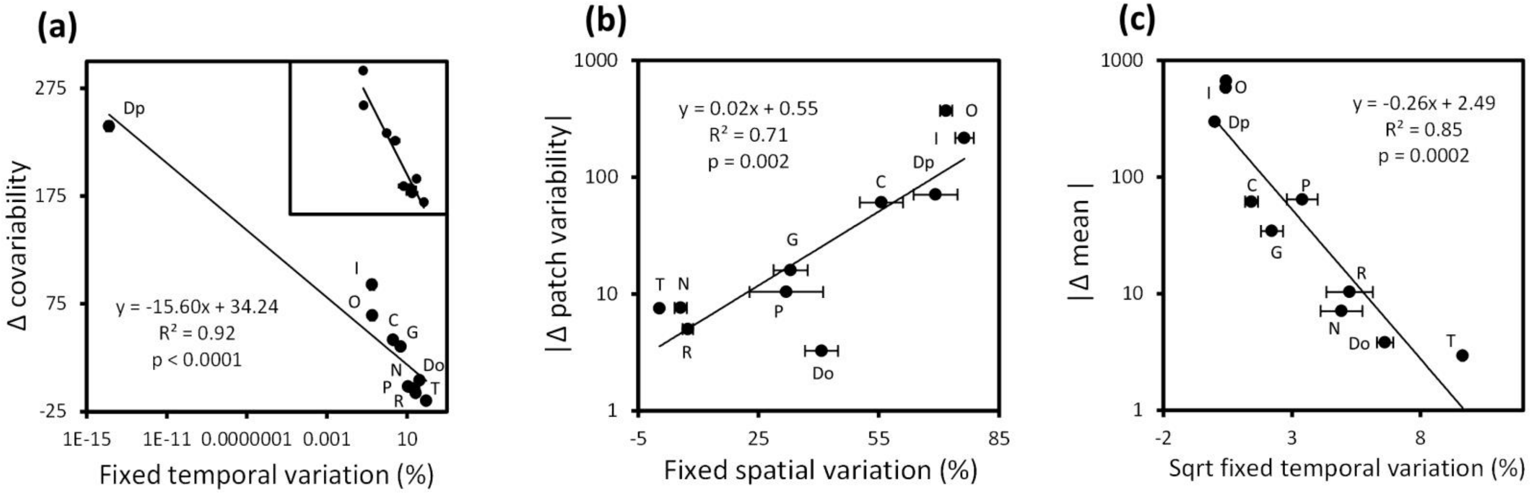


Figure 3.5. Predictors of connection responses in ecosystem variables. (a) Variables (points) with dynamics dominated by fixed temporal variation (high inter-patch synchrony) in unconnected systems responded least in terms of covariability of patches. Inset: Plot with influential data point removed. **(b)** Fixed spatial variation in unconnected systems was associated with transient, spatiotemporal responses to connection, which led to large increases or decreases in variability (note absolute values on y-axis) at the patch scale. **(c)** Variables with high fixed temporal variation also exhibited less change in mean value from connection. Variables are labelled as follows: Dp = Daphnia; I = Total invertebrates; O = Ostracods; C = Chlorophyll a; G = GPP; N = NPP; Do = Dissolved oxygen; P = picoplankton/particulate; R = Respiration; T = temperature. Note logarithmic scales.

DISCUSSION

Results underscore the diversity of dynamic changes that occur when ecosystem fragments are connected (Figs. 3.3, 3.4). This diversity highlights the difficulty of predicting responses to landscape change in multiple ecosystem variables (Uezu et al. 2005, Mitchell et al. 2013), which is needed for basic understanding and ecosystem-level management (Ellis et al. 2010). However, findings also uncovered regularities in variable responses that may enhance prediction.

Responses to connection would seem idiosyncratic, differing across variables and between response metrics as is found in many communities and ecosystems (e.g., D'Eon et al 2002; Howeth and Leibold 2010; Gilbert-Norton et al 2010). But viewed through the coarser lens of spatiotemporal pattern, ecosystem variables reflected the tendencies for site differences to be homogenized and temporal fluctuations to be synchronized (arrows B and C in Fig. 3.1). This support for our first hypothesis suggests an 'attractor' – a pull towards synchrony and spatial homogeneity – that may guide the connectivity responses of many ecosystem variables. Homogenization and synchronization occur under limited conditions, namely when movement equalizes patches faster than responses to local biotic and environmental conditions cause them to diverge (see Appendix H). Interestingly, even variables that underwent explosive growth upon colonizing new patches (e.g., *Daphnia*, ostracods) showed some deflection towards synchrony and homogeneity, suggesting that variables not conforming to the null expectations in Fig. 3.1 may be exceptional.

Exceptional variables for which connection is not homogenizing and synchronizing are likely to have certain types of movement and dynamics. For instance, movement that is unidirectional (e.g., fluvial or colluvial) or from low to high concentration will tend to desynchronize fluctuations or reinforce differences among sites (arrows A, D, F in Fig. 3.1; Table 3.1). This result may also occur in variables with chaotic or strong responses to local conditions that amplify fluctuations or source-sink patterns upon connection (Roy et al. 2005, Becks and Arndt 2013). It is possible that such outliers might be anticipated from known movement behaviours (e.g., aggregating) or from indicators of dynamics (e.g., reactivity; Neubert et al 2009).

Predictors of connectivity responses

Strong links between a variable's spatiotemporal pattern and its response to connection supported our second and third hypotheses, and suggested potential for pattern-based prediction of responses. Variables close to the attractor changed the least in spatiotemporal pattern, local mean and covariability (Figs. 3.3, 3.5). Fig. 3.5a suggests that variables with high spatial synchrony are least susceptible to further changes in covariation, which agrees with observations in other systems. Fox et al (2013) showed that synchrony saturates with dispersal such that more synchronous metapopulations have less scope for increased synchrony. Corridor studies show that structural connections do not enhance the movements of wide-ranging organisms (e.g., Haddad 1999; Gilbert-Norton et al 2010), also suggesting limits to further synchronization.

The level of functional connectivity and reactivity to local patch conditions can be seen as predisposing variables to spatiotemporal patterns and to the connection responses in Fig. 3.5a (Appendix H). For instance, variables like temperature have high functional connectivity (synchrony-promoting) relative to reactivity (synchrony-disrupting) and so display high synchrony even in unconnected systems (Ims and Andreassen 2005). These properties also increase the likelihood that such variables will undergo weak connection responses (see Fig. 3.5c). There are two reasons this. First, connection should not increase inter-patch movement much if it is already high, and so will not lead to increased synchrony. Second, connection should not incur strong local responses (e.g., chaotic) if reactivity is already low, and so will not decrease synchrony either.

The presence of spatial concentration gradients was also a strong predictor of the amount of spatiotemporal reorganization following connection (Fig. L.1, Appendix L).This agrees with the notion that concentration gradients create potentials for ecological change and that these potentials are realized by cross-gradient fluxes (Müller 1998). We found that change in temporal variability did indeed increase with the size of spatial gradient (Fig. 3.5b). However, spatial gradient size predicted only the absolute magnitude of change in variability and not whether variability increased or decreased. Mechanistic detail might, therefore, help to fill in these details.

Concentration gradients could have spurred changes to local dynamics in two ways: First, a gradient is thermodynamically unstable (Müller 1998) and any homogenizing movement that equalizes it will also alter spatial and temporal patterning. Second, movement introduces particles to patches that differ in density and possibly environmental conditions, inducing responses like the explosive growth of *Daphnia* populations. Either way, variables that build up measureable spatial gradients would be more prone to spatiotemporal change. Exceptions would be those variables, perhaps the "slow" variables like bedrock composition or soil organic matter, for which connection does not rapidly equalize gradients and/or lead to local responses.

Though our microcosm system was spatially-heterogeneous, work remains to evaluate connectivity responses in more complex spatial and temporal environments. It is known that high spatial heterogeneity in environmental conditions can disrupt synchronization (Peltonen et al. 2002) while environmental fluctuations in time are commonly synchronizing (e.g., Post and Forchhammer 2002). The magnitude of such environmental effects will clearly depend on the sensitivity of a particular variable to spatial or temporal heterogeneity. But provided these departures are small compared to differences in responses among variables, variation around the relationships in Fig. 3.5 should remain negligible. Datasets covering structural changes in large, natural ecosystems would provide an ideal test of robustness.

Responses of energetic, material and biotic variables

Consistent with our fourth hypothesis, population or biotic variables underwent the largest changes in pattern and response metrics followed by material and energetic variables. Though we cannot be certain without measuring fluxes, differing movement patterns and local responses among variables can account for contrasting responses to connection. First, connections are more likely to enhance functional connectivity and movement for population variables than for energetic variables. This is because energetic variables often have already high degrees of functional connectivity through thermal fluxes mediated by the atmosphere (Adrian et al. 2009). Second, population and biotic variables are generally more reactive to local conditions than physical variables, typically undergoing non-linear responses (Hsieh et al. 2005). Connections are expected to trigger these large responses by allowing subsidies into patches and delivering organisms to new patches (e.g., Leroux and Loreau 2011).

Differences of slope in Fig. 3.3 support the idea of intrinsic differences among variables. The generally steep slopes of energetic and material variables were consistent with spatial gradients being rapidly converted into synchronous fluctuations upon connection. Though, connection had the opposite effect on temperature than expected, desynchronizing and increasing heterogeneity among patches. This result could be a random effect of location on the lab bench. In contrast, population variables had shallow slopes reflecting homogenization but only partial synchronization. *Daphnia* populations proved to be a mild exception due to cyclic dynamics which facilitate synchronization (Grover et al. 2000, Becks and Arndt 2013). The intermediate slopes and connectivity responses of aggregate ecosystem variables (GPP, ecosystem respiration, but not NPP) perhaps reflects a dampened response due to averaging of responses of contributing variables (cf. Vogt et al 2011).

A hierarchy of connectivity responses, from energetic to population, agrees with theory on the transit of energy through ecosystems (Leavitt et al. 2009, Vogt et al. 2011). These studies suggest that local processing (e.g., within-lake) increases along a continuum of energetic to material variables, and that this constraint shapes spatiotemporal patterns. Our results reinforce that the intrinsic properties of ecosystem variables (e.g., functional connectivity) are potent drivers of spatiotemporal pattern, and add that these same properties predispose variables to certain connectivity responses. Variable type may thus be another indicator of potential for change due to landscape alteration.

CONCLUSIONS

Results support the idea that spatiotemporal patterns can predict responses to connection in multiple ecosystem variables and circumvent, to a reasonable degree, knowledge of mechanisms. Predictors of connectivity effects – including inter-patch synchrony, the strength of spatial gradients, and the type of ecosystem variable – show promise for suggesting potential for change in impacted landscapes, but require further evaluation in natural ecosystems.

ACKNOWLEDGEMENTS

This work was supported by a Natural Sciences and Engineering Research Council of Canada Discovery Grant (JK). We thank J. Wilson for equipment use, and M. Anand, S. Hammond, K. McCann, C. Jones, J. Quinn, D. Rollo and two anonymous reviewers for valuable feedback. Experiments comply with all ethical guidelines and laws in the country of work.

REFERENCES

Adrian, R., C. M. O’Reilly, H. Zagarese, S. B. Baines, D. O. Hessen, W. Keller, D. M. Livingstone, R. Sommaruga, D. Straile, E. Van Donk, G. a Weyhenmeyer, and M. Winder. 2009. Lakes as sentinels of climate change. Limnology and Oceanography 54:2283–2297.

Becks, L., and H. Arndt. 2013. Different types of synchrony in chaotic and cyclic communities. Nature communications 4:1359.

Cazelles, B., S. Bottani, and L. Stone. 2001. Unexpected coherence and conservation. Proceedings of the Royal Society B 268:2595–2602.

Clevenger, A. P., and N. Waltho. 2000. Factors influencing the effectiveness of wildlife underpasses in Banff National Park, Alberta, Canada. Conservation Biology 14:47–56.

Cottenie, K., and L. De Meester. 2004. Metacommunity structure: Synergy of biotic interactions as selective agents and dispersal as fuel. Ecology 85:114–119.

D’Eon, R. G. D., S. M. Glenn, I. Parfitt, and M. Fortin. 2002. Landscape connectivity as a function of scale and organism vagility in a real forested landscape. Conservation Ecology 6:10.

Dey, S., and A. Joshi. 2006. Stability via asynchrony in Drosophila metapopulations with low migration rates. Science 312:434–436.

Earn, D. J. D., S. A. Levin, and P. Rohani. 2000. Coherence and conservation. Science 290:1360–1364.

Einum, S., K. H. Nislow, S. Mckelvey, and J. D. Armstrong. 2008. Nest distribution shaping within-stream variation in Atlantic salmon juvenile abundance and competition over small spatial scales. Journal of Animal Ecology 77:167–72.

Ellis, A. M., T. Václavík, and R. K. Meentemeyer. 2010. When is connectivity important? A case study of the spatial pattern of sudden oak death. Oikos 119:485–493.

Fox, J. W., G. Legault, D. A. Vasseur, and J. A. Einarson. 2013. Nonlinear effect of dispersal rate on spatial synchrony of predator-prey cycles. PloS one 8:e79527.

Di Franco, A., G. Coppini, J. M. Pujolar, G. a De Leo, M. Gatto, V. Lyubartsev, P. Melià, L. Zane, and P. Guidetti. 2012. Assessing dispersal patterns of fish propagules from an effective mediterranean marine protected area. PloS one 7:e52108.

Garibaldi, L. a, I. Steffan-Dewenter, C. Kremen, J. M. Morales, R. Bommarco, S. a Cunningham, L. G. Carvalheiro, N. P. Chacoff, J. H. Dudenhöffer, S. S. Greenleaf, A. Holzschuh, R. Isaacs, K. Krewenka, Y. Mandelik, M. M. Mayfield, L. a Morandin, S. G. Potts, T. H. Ricketts, H. Szentgyörgyi, B. F. Viana, C. Westphal, R. Winfree, and A. M. Klein. 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. Ecology letters 14:1062–72.

Gilbert-Norton, L., R. Wilson, J. R. Stevens, and K. H. Beard. 2010. A meta-analytic review of corridor effectiveness. Conservation Biology 24:660–8.

Grover, J. P., D. McKee, S. Young, H. C. J. Godfray, and P. Turchin. 2000. Periodic dynamics in Daphnia populations: Biological interactions and external forcing. Ecology 81:2781–2798.

Haddad, N. M. 1999. Corridor use predicted from behaviors at habitat boundaries. The American Naturalist 153:215–227.

Howeth, J., and M. Leibold. 2010. Species dispersal rates alter diversity and ecosystem stability in pond metacommunities. Ecology 91:2727–2741.

Hsieh, C., S. M. Glaser, A. J. Lucas, and G. Sugihara. 2005. Distinguishing random environmental fluctuations from ecological catastrophes for the North Pacific Ocean. Nature 435:336–340.

Ims, R. A., and H. P. Andreassen. 2005. Density-dependent dispersal and spatial population dynamics. Proceedings of the Royal Society B 272:913–918.

Kilpatrick, A. M., and A. R. Ives. 2003. Species interactions can explain Taylor's power law for ecological time series. Nature 422:65–68.

Leavitt, P. R., S. C. Fritz, N. J. Anderson, P. A. Baker, T. Blenckner, L. Bunting, J. Catalan, D. J. Conley, W. O. Hobbs, E. Jeppesen, A. Korhola, S. McGowan, K. Ruhland, J. A. Rusak, G. L. Simpson, N. Solovieva, and J. Werne. 2009. Paleolimnological evidence of the effects on lakes of energy and mass transfer from climate and humans. Limnology and Oceanography 54:2330–2348.

Lecomte, J., K. Boudjemadi, F. Sarrazin, K. Cally, and J. Clobert. 2004. Connectivity and homogenisation of population sizes: An experimental approach in Lacerta vivipara. Journal of Animal Ecology 73:179–189.

Leroux, S. J., and M. Loreau. 2011. Dynamics of reciprocal pulsed subsidies in local and meta-ecosystems. Ecosystems 15:48–59.

Lewis, W. M. 1978. Comparison of temporal and spatial variation in the zooplankton of a lake by means of variance components. Ecology 59:666–671.

Mahadevan, A. 2005. Spatial heterogeneity and its relation to processes in the upper ocean. Pages 165–182 *in* G. M. Lovett, M. G. Turner, C. G. Jones, and K. C. Weathers, editors. Ecosystem function in heterogeneous landscapes. Springer, New York.

Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. Ecography 28:403–416.

McArdle, B. H., K. J. Gaston, and J. H. Lawton. 1990. Variation in the size of animal populations: Patterns, problems and artefacts. Journal of Animal Ecology 59:439–454.

Mitchell, M. G. E., E. M. Bennett, and A. Gonzalez. 2013. Linking landscape connectivity and ecosystem service provision: Current knowledge and research gaps. Ecosystems 16:894–908.

Müller, F. 1998. Gradients in ecological systems. Ecological Modelling 108:3–21.

Münkemüller, T., and K. Johst. 2008. Spatial synchrony through density-independent versus density-dependent dispersal. Journal of biological dynamics 2:31–9.

Neubert, M., H. Caswell, and A. R. Solow. 2009. Detecting reactivity. Ecology 90:2683–2688.

Peltonen, M., A. Liebhold, O. Bjornstad, and D. Williams. 2002. Spatial synchrony in forest insect outbreaks: Roles of regional stochasticity and dispersal. Ecology 83:3120–3129.

Post, E., and M. C. Forchhammer. 2002. Synchronization of animal population dynamics by large-scale climate. Nature 420:168–71.

Proulx, R., C. Wirth, W. Voigt, A. Weigelt, C. Roscher, S. Attinger, J. Baade, R. Barnard, N. Buchmann, F. Buscot, N. Eisenhauer, M. Lange, A. Milcu, P. A. Niklaus, Y. Oelmann, S. Rosenkranz, and M. Vicky. 2010. Diversity promotes temporal stability across levels of ecosystem organization in experimental grasslands. PLoS One 5:1–8.

Richardson, J. S., Y. Zhang, and L. B. Marczak. 2009. Resource subsidies across the land-freshwater interface and responses in recipient communities. River Research and Applications 26:55–66.

Roy, M., R. D. Holt, and M. Barfield. 2005. Temporal autocorrelation can enhance the persistence and abundance of metapopulations comprised of coupled sinks. The American naturalist 166:246–61.

Ruxton, G., and P. Rohani. 1999. Fitness-dependent dispersal in metapopulations and its consequences for persistence and synchrony. Journal of Animal Ecology 68:530–539.

Soranno, P. A., K. E. Webster, J. L. Riera, T. K. Kratz, J. S. Baron, P. A. Bukaveckas, G. W. Kling, D. S. White, N. Caine, R. C. Lathrop, and P. R. Leavitt. 1999. Spatial variation among lakes within landscapes: Ecological organization along lake chains. Ecosystems 2:395–410.

Taylor, L. R. 1961. Aggregation, variance and the mean. Nature 189:732–735.

Taylor, P., L. Fahrig, and K. A. With. 2006. Landscape connectivity: A return to basics. Pages 29–43 *in* K. Crooks and M. Sanjayan, editors. Connectivity Conservation. Cambridge.

Uezu, A., J. P. Metzger, and J. M. E. Vielliard. 2005. Effects of structural and functional connectivity and patch size on the abundance of seven Atlantic Forest bird species. Biological Conservation 123:507–519.

Valett, H. M., F. R. Hauer, and J. a. Stanford. 2014. Landscape influences on ecosystem function: Local and routing control of oxygen dynamics in a floodplain aquifer. Ecosystems 17:195–211.

Vogt, R. J., J. A. Rusak, A. Patoine, and P. R. Leavitt. 2011. Differential effects of energy and mass influx on the landscape synchrony of lake ecosystems. Ecology 92:1104–1114.

Vogwill, T., A. Fenton, and M. A. Brockhurst. 2009. Dispersal and natural enemies interact to drive spatial synchrony and decrease stability in patchy populations. Ecology Letters 12:1194–1200.

Warren, C. R. 2008. Rapid measurement of chlorophylls with a microplate reader. Journal of Plant Nutrition 31:1321–1332.

Wetzel, P. R., A. G. Van Der Valk, S. Newman, D. E. Gawlik, T. T. Gann, C. A. Coronado-molina, D. L. Childers, and F. H. Sklar. 2005. Maintaining tree islands in the Florida Everglades: Nutrient redistribution is the key. Frontiers in Ecology and the Environment 3:370–376.

Wetzel, R. G., and G. E. Likens. 1991. Limnological analyses. Page 391. Second edition. Springer-Verlag, New York.

CHAPTER 4.

PREDICTING THE OCCURRENCE OF PERSISTENT HOTSPOTS IN ECOSYSTEM VARIABLES

Adapted from

Hammond, M. P. and J. Kolasa. Predicting the occurrence of persistent hotspots in ecosystem variables

Submitted to *Oikos* on December 1st, 2014

HYPOTHESIS AND RATIONALE

Hypothesis tested: *Measurable properties of ecosystem variables help to predict the occurrence of persistent spatial variation*

Rationale: Spatiotemporal dynamics can generate many shifting or static patterns. One common pattern is seen when variables exhibit hotspots of concentration in the landscape (Brown et al. 1995, Ives and Klopfer 1997, Santora and Veit 2013). This is a pattern of persistent spatial variation (see Fig. 1.3). Predicting the occurrence of this pattern is difficult because it is a product of spatial and temporal patterns that can relate differently to explanatory variables. A novel variance decomposition can overcome this problem by breaking persistent spatial variation into its component spatial and temporal patterns. Subsequent tests can then identify which properties of variables (e.g., temporal variability, niche breadth) can predict these component patterns and, in turn, persistent spatial variation of ecological resources. This study therefore tests trait- or property-based indicators of spatiotemporal pattern (research directions *h* and *j* in Fig. 1.2) as well as an application of time-for-space substitution (research direction *e*).

ABSTRACT

Ecological resources (e.g., organisms, carbon sinks) exhibit spatial heterogeneity within landscapes. While spatial variation has been studied extensively, the pattern of hotspots and coolspots persisting over time – called persistent spatial variation (PSV) – has not. Yet this pattern imparts key information about whether resources will be found consistently in certain locations or vary unpredictably. Because of these management implications, anticipating whether an ecosystem variable will display PSV would be valuable. We tested whether the occurrence of PSV can be predicted from attributes of variables (e.g., niche breadth, abundance, temporal scale). By measuring PSV as the F-value in an Analysis of Variance comparing sites, we could decompose PSV into a spatial and temporal component: *Spatial variation* of site mean values and *stability* of time series at each site. This step allowed us to test whether variable attributes predicted the spatial component, the temporal component or PSV itself in temperate lakes and tropical coastal rock pools. We found PSV to be highly predictable (R^2 = up to 0.80) from an estimate of stability taken at a single site, as well as from other factors related to stability like: Whether a variable was environmental (stable, slow rate of change) or biotic (unstable, fast rate of change) or whether a variable is an aggregate of other variables. Niche position only modestly predicted the *spatial variation* component of PSV. Meanwhile, abundance stabilized population dynamics, increased site occupancy and decreased spatial variation, which had the net effect of increasing PSV. We conclude that PSV can be surprisingly-well predicted from simple temporal indicators (e.g.,

stability at a single location) and that pattern-based indicators may prove useful for predicting the distribution of resources in space and time when data are scarce.

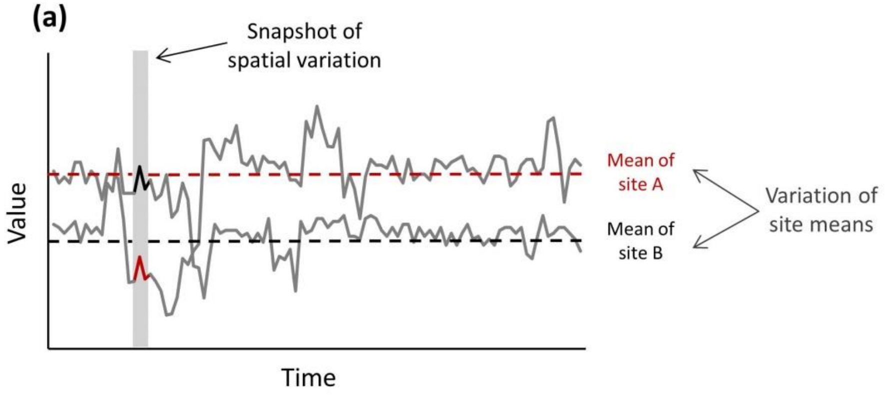
INTRODUCTION

Hotspots of abundance, biodiversity and biogeochemistry (e.g., Vandergast et al. 2008, Timilsina et al. 2013, Santora and Veit 2013) are part of the spatial heterogeneity of landscapes. Ecologists have long studied spatial variation as a measure of heterogeneity and have sought to predict the occurrence of hotspots both within a species' range and in absolute space (Sagarin and Gaines 2002a, Guisan and Thuiller 2005). Less studied is whether such concentrations of energy, organisms, or materials will recur consistently over time, which is a special case of spatial variation (Brown et al. 1995, Ives and Klopfer 1997). Yet knowing whether certain sites are reliably high-value is essential for conserving resources like exploited organisms or biodiversity (Santora and Veit 2013).

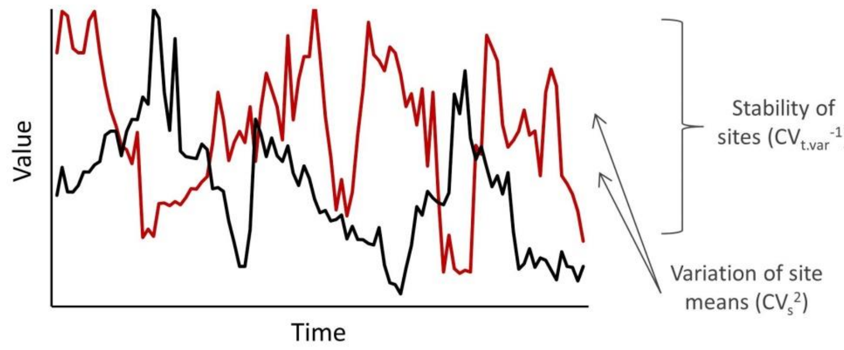
The temporal consistency of hotspots and coolspots is not discernable when spatial variation is studied over short timescales (Fig. 4.1a; e.g., Sagarin and Gaines 2002b). Over longer timescales, differences in site means signal that some locations have, on average, higher values than others (Fig. 4.1a; e.g., Brown et al. 1995). But this information also provides limited insight into whether high- and low-value sites remain so over time. For instance, it is possible for a typically low-value site to regularly have higher values than a typically high-value site (Fig. 4.1b). A pattern that does capture the consistency of values in sites, however, is fixed or *persistent spatial variation* (Lewis

1978, Hammond and Kolasa 2014) in which value differences among sites persist over the timescale of study (Fig. 4.1c). We refer to it as PSV hereafter. While a small number of studies have focused on this aspect of spatial variation (e.g., Brown et al. 1995, Ives and Klopfer 1997), research has not addressed the basic questions of: Which variables - defined as any measurable aspect of an ecological process - will display PSV? And, can this tendency be readily predicted?

Predicting the occurrence of PSV is challenging for ecological and statistical reasons. The main ecological challenge is that many variable-specific and interacting mechanisms can lead to spatial variation. Such mechanisms include; responses to the spatial and temporal environment (Brown et al. 1995, Ives and Klopfer 1997) or to disturbance (Tamburello et al. 2013); population or community interactions (Lecomte et al. 2004); and self-organization via feedbacks (Jackson et al. 2014). The existence of multiple ecological pathways to the same pattern makes mechanistic understanding a demanding task. But recent work suggests that system-specific, mechanistic detail may be unnecessary for prediction where generic properties of variables correlate well with spatial variation. For instance, spatial patterns in abundance and occupancy are correlated with species traits like niche breadth (Hurlbert and White 2007), dispersal ability (Lees and Peres 2009) and local density (Hurlbert and White 2007). Meanwhile, there is evidence that a variable’s identity as energetic or material determines its spatiotemporal pattern (Vogt et al. 2011).



(b) Non-persistent spatial variation



(c) Persistent spatial variation

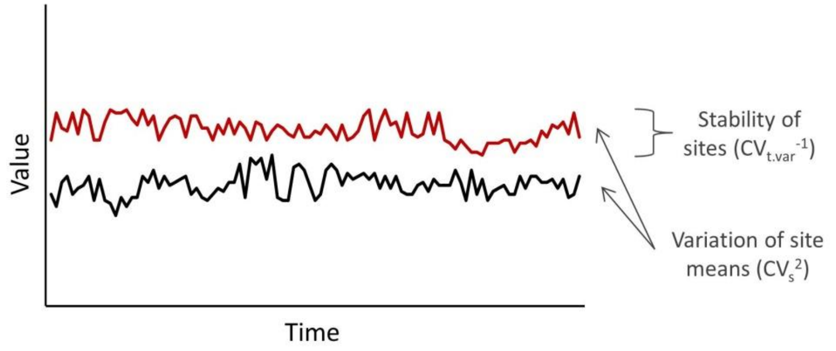


Figure 4.1. Types of spatial variation for two (hypothetical) sites sampled over time. **(a)** Spatial variation can reflect either short-term differences from a snapshot in time or long-term differences in which the mean value of site A > site B. **(b)** Spatial variation is non-persistent when unstable temporal dynamics or similar site means cause site B to occasionally have higher values than site A even though it has the lesser mean. **(c)** But spatial variation is persistent when high stability of sites or large differences in means causes site A to consistently and reliably have higher values than site B.

The second challenge to prediction is that there are statistical impediments, but these should ultimately be easier to overcome than ecological challenges. Specifically, PSV is difficult to predict from properties of variables because it is not a single pattern. Rather, it is a composite of two main constituent patterns: (1) *Spatial variation* in value among sites and (2) *stability* of individual sites in the sense that time series values are relatively constant. The result is that there are multiple pattern combinations that lead to similar levels of PSV. For instance, the same value of PSV in productivity could reflect either large value differences among sites (e.g., vegetated versus bare patches in deserts) or small differences among sites that are stable over time (e.g., shaded versus exposed slopes in tropical forests).

Distinguishing between these constituent patterns is vital because they represent two very different causes of PSV: Large value differences among sites suggests the importance of underlying spatial gradients in community or environmental conditions, whereas high stability indicates the importance of temporal attributes like disturbance rate, resistance and resilience. From an applied perspective, the dual nature of PSV suggests that no predictors (e.g., traits) will be able to accurately predict the occurrence of PSV unless they can account for both its spatial and temporal causes. Statistical decomposition of the pattern into its constituent parts may help this effort by: (1) Establishing a framework for breaking an important yet complex pattern into more interpretable parts, (2) allowing tests of which properties of variables predict PSV or, failing that, its constituent patterns, and (3) providing a conceptual basis for understanding how known causes lead to PSV in nature.

Persistent spatial variation in ecosystem variables – A general framework

We developed a quantitative framework that captures a total of four spatial and temporal components of PSV. It is based on the F-value of a one-way Analysis of Variance (ANOVA) comparing site means (i.e., mean of site i versus j obtained by averaging values over times k and l), which is a simple measure of persistent spatial variation. When F is large, PSV is high because values are consistently higher at some sites than others over the duration of study. When F is small, sites overlap in value and do not differ consistently. F is decomposed from mean squares into patterns of *spatial variation* and *stability* (Eq. 4.1). Here, *spatial variation* corresponds to among-site variation ($MS_{\text{among sites}}$) while *stability* is represented by within-site variation ($MS_{\text{within sites}}$). Importantly, Eq. 4.1 shows how F can be rewritten as the product of relative, dimensionless indices CV^2_s, $CV_{t.var}^{-1}$ and the ratio of the number of temporal and spatial observations (n_k and n_i, respectively; see Appendix Q for derivation):

$$F = \frac{MS_{\text{among sites}}}{MS_{\text{within sites}}} = CV_s^2 \cdot CV_{t.var}^{-1} \cdot \frac{n_k}{n_i} \qquad \text{Eq. 4.1}$$

$$CV_s^2 = \frac{\mathrm{Var}(\overline{Y}_i)}{\overline{\overline{Y}}_i^2} \qquad \text{Eq. 4.2}$$

$$CV_{t.var}{}^{-1} = \frac{\overline{Y}_K^2}{\sum_{i=1}^{n} \mathrm{var}_i} \qquad \text{Eq. 4.3}$$

CV^2_s is a spatial, squared-Coefficient of Variation where $\mathrm{Var}(\overline{Y}_i)$ is the variance of site means $\overline{Y}_i$ and $\overline{\overline{Y}}_i^2$ is the squared mean of $\overline{Y}_i$ (Eq. 4.2). It grows as *spatial variation* among sites increases. $CV_{t.var}^{-1}$ is the reciprocal of Proulx et al.'s (2010) temporal Variance CV where var_i is the temporal variance of site i and $\overline{Y}_K^2$ is the squared mean of the regional temporal series (Eq. 4.3). It increases with the *stability* of sites.

CV^2_s can be decomposed further because its numerator $\mathrm{Var}(\overline{Y}_i)$ integrates two sources of variation among sites. The first source we term *population variance* ($Var_{s.pop}$) which arises when populations in occupied sites (i.e., extant populations) differ in size. The second we call *occupancy variance* ($Var_{s.occ}$) which arises from zero counts due to site absences (i.e., "holes" or distributional gaps in the data matrix). These two sources of spatial variation are rarely considered simultaneously (but see He and Gaston 2003). But they can be approximated and additively partitioned from $\mathrm{Var}(\overline{Y}_i)$ using standard variance decomposition techniques (Sokal and Rohlf 1981, p. 216; see Appendix Q for derivation), to yield the following components that make up F:

$$\mathrm{F} = \left(\frac{\mathrm{Var_{s.occ}}}{\overline{\overline{Y}}_i^2} + \frac{\mathrm{Var_{s.pop}}}{\overline{\overline{Y}}_i^2}\right) \cdot \mathrm{CV_{t.var}}^{-1} \cdot \frac{n_k}{n_i} \qquad \text{Eq. 4.4}$$

where $\mathrm{Var_{s.pop}}/\overline{\overline{Y}}_i^2$ and $\mathrm{Var_{s.occ}}/\overline{\overline{Y}}_i^2$ are dimensionless indices of the population and occupancy components of CV^2_s that we call *relative population* and *relative occupancy variance*, respectively. Significantly, the indices described above enable comparison of F components among variables of differing mean or measurement scale.

Uncovering data-efficient predictors of persistent spatial variation

We hypothesize that simple trait- or property-based indicators can predict the occurrence of PSV or its constituent patterns in an ecosystem variable. While many factors might correlate, individually or in combination, with PSV or its components, we tested a subset that includes:

Stability and temporal scale: We predict that more stable variables, having higher $CV_{t.var}^{-1}$, will exhibit higher PSV. This effect should be greater for “slow” variables that have timescales on the order of millennia (e.g., rock weathering) than for faster variables like population parameters. This is because rates, and possibly magnitudes, of change are smaller for slow ecological processes that vary over timescales much longer than the period of observation.

Species traits: We predict that larger-bodied aquatic organisms will exhibit more pronounced spatial variation (CV^2_s) because they lack the long-distance motility of smaller-bodied organisms (Beisner et al. 2006). This tendency should, in turn, enhance PSV. Meanwhile, species at latitudes close to their range limits and at high trophic levels should show less PSV because of the lower stability ($CV_{t.var}^{-1}$) typical of marginal and high trophic populations (Curnutt et al. 1996, Voigt et al. 2003). Lastly, we suggest that high fecundity species should have more PSV by maintaining more stable population sizes.

Niche breadth and marginality: We predict that species with narrow environmental niches or those adapted to atypical (marginal) habitats will be intolerant of conditions at many sites (Hanski 1982). Such species should therefore exhibit more PSV due to site absences (increasing CV^2_s) and possibly also due to higher stability if their populations thrive in environmental conditions at occupied sites (increasing $CV_{t.var}^{-1}$).

Abundance: Abundance could plausibly affect both the spatial and temporal components of PSV. In space, if locally-abundant species occupy more sites (Hurlbert and White 2007), they may have lower $Var_{s.occ}$ and CV^2_s by minimizing occupancy gaps. Abundant species could also occur disproportionately at some sites or have different dispersal rates which would affect population sizes in occupied sites (Hanski 1982), and thus $Var_{s.pop}$ and CV^2_s. In time, abundance could increase $CV_{t.var}^{-1}$ if it stabilizes local dynamics by reducing the effect of processes like demographic stochasticity (Ballantyne and Kerkhoff 2007). Eq. 4.1 implies that the effect of abundance on PSV is a net result of how abundance affects the spatial and temporal components of PSV. These spatial and temporal effects can be quantified by scaling the means and variances from the terms of Eqs. 4.2-4.4 (see Appendix R and Methods).

We test the above predictions and framework over a wide range of physicochemical and populations variables in temperate lakes and tropical coastal rock pools. Findings help to interpret and predict one of the most common patterns in nature.

METHODS

Data

Wisconsin lakes – North Temperate Lakes LTER

We used data from seven temperate lakes in Wisconsin, US (Allequash, Big Muskellunge, Crystal, Sparkling, Trout, Crystal Bog and Trout Bog; 46°N, 89°W). Data were collected by the North Temperate Lakes Long-Term Ecological Research program (North Temperate Lakes LTER, NSF, Center for Limnology, University of Wisconsin-Madison), and can be found online with collection methods at http://lter.limnology.wisc.edu. We included up to 30 years of data from 60 biotic and abiotic variables across five datasets:

- Chemical limnology of primary study lakes: Major ions
- Chemical limnology of primary study lakes: Nutrients, pH and carbon
- Physical limnology of primary study lakes
- Pelagic macroinvertebrate abundance
- Fish abundance

We used annual values for each lake, obtained by averaging organism densities or physicochemical values across depths, across sampling dates and across stations within a lake (see Hammond and Kolasa 2014 for details).

Jamaican coastal rock pools

We collected data over fourteen annual surveys (1989-2003) in a system of 49 coastal rock pools near Discovery Bay Marine Laboratory, University of the West Indies, on the northern coast of Jamaica (18°28' N, 77°25' W). Pools within a 25m radius are linked by physicochemical fluxes and organism propagules transported by wind, ocean spray, animal vectors and overflow after heavy rainfall (Sciullo and Kolasa 2012). Most of 78 recorded invertebrate species occur rarely. We therefore analyzed only the 36 most common species plus temperature, pH, salinity, dissolved oxygen, chlorophyll-a and turbidity. Further system and sampling details can be found in Hammond and Kolasa (2014).

Rock pools could not be sampled when they dried up and were recorded as blank data entries (<10% of total observations). We analyzed species data both with blank entries and with blank entries replaced by zeros which assumes that no living, adult invertebrates occur in a dry pool. Both analyses gave similar results and conclusions, and we present results from the data with zeros-added. For physicochemical variables, we interpolated blank entries with the mean of adjacent temporal observations.

Analyses

Partitioning persistent spatial variation into its components

Persistent spatial variation (PSV) was calculated for each variable as its F-value and its components calculated according to terms in Eq. 4.4 (derived in Appendix Q). Our framework is reminiscent of a model proposed by He and Gaston (2003) linking abundance, occupancy and spatial variance, but differs mainly by being a statistical decomposition rather than a theoretical model.

We partitioned spatial variance of site means $\mathrm{Var}(\overline{\mathrm{Y}}_{\mathrm{i}})$ into its components (Eq. 4.4) by the following three steps: (1) Sites were assigned to two groups: 'Unoccupied' if a species did not occur at a site over the study period or 'occupied' if it occurred once or more. (2) Two variance components were calculated from one-way ANOVA formulae for unbalanced designs in Sokal and Rohlf (1981). Components were: (i) Variance between the occupied and unoccupied group which estimates variation from occupancy patterns and; (ii) variance within the occupied and unoccupied group. Because all values within the unoccupied group are zero, variation within the group is zero and variance component (ii) can be attributed solely to variation within the occupied group (see Appendix Q). Variance component estimates were set to zero if negative and were omitted if a group was too small for calculation. (3) Variance components were expressed as a proportion of their total and multiplied by $\mathrm{Var}(\overline{\mathrm{Y}}_{\mathrm{i}})$ to obtain two variances that sum to the original sample variance. These were $\mathrm{Var}_{\mathrm{s.pop}}$ for variance among occupied sites and $\mathrm{Var}_{\mathrm{s.occ}}$ for variance owing to the presence of unoccupied sites.

Our variance estimates could be subject to 'zero-inflation' in which rare species are erroneously counted as absent (zero) when they are actually present (Martin et al. 2005). This is a common source of uncertainty, but it would little affect our conclusions because we are not interested in true population sizes. Rather, we are interested the ability of managers to find organisms or resources at a given site using standard methods which have detection bias. Furthermore, false zeros should be limited given that; we excluded the rarest rock pool species from analysis and most lake species were relatively common in samples; and we declared a species absent from a site only if it was undetected at all sampling times (n_k = 13-30).

Stability and temporal scale

To test whether a single stability estimate could predict F for the whole landscape, we estimated stability at a single site - the largest water body in the lake or rock pool system – using the inverse of the Coefficient of Variation (Lehman and Tilman 2000). We used the largest water body for estimates because large water bodies may generally have the most data from being recreationally- and commercially-important and/or regularly-censused. If a species did not occur in the largest lake or pool, we estimated stability from the lake or pool in which it was most abundant. We also estimated skewness of time series values as above using the Fisher-Pearson coefficient (G_1). This statistic captures the relative frequency of extreme observations that may reduce stability.

The temporal scale of a variable represents the slowness of its rate of change in a time series (e.g., trend versus rapid fluctuation). We measured this quantity as autocorrelation time τ. It is defined as $-1/\ln(\rho)$, where ρ is the lag-1 autocorrelation estimated with Pearson's correlation coefficient (Dai et al. 2012). Because τ is undefined for negative autocorrelation, we followed Dai et al. (2012) and set these values to zero.

We then averaged across lakes or pools to obtain the mean autocorrelation time for a variable.

Chemical hardness (η) is a measure of chemical reactivity derived from Hard and Soft Acids and Bases (HSAB) theory. It is estimated as the resistance of atoms or molecules to change in the number of electrons (Parr and Pearson 1983). It may thus indicate the prospects for being conserved at stable concentrations in the environment. Soft chemical species (low η) are reactive with large radii, low charge density and high polarizability. Hard species (high η), in contrast, resist change or deformation through small ionic radii, high charge density and weak polarizability. We compiled hardness estimates from the literature for as many lake ions – or closely-related chemical species as substitutes – as possible (Appendix S).

Species traits

Species traits of lake fish included body size or mass, range size and latitudinal limits, trophic level, fecundity and minimum population doubling time. Data were obtained for as many species as possible from *Fishbase* (Froese and Pauly 2014), an online database found at www.fishbase.org. Rock pool invertebrates lack such detailed published data. Thus only body size could be tested as a predictor of PSV.

Niche breadth and marginality

We measured niche position and breadth with OMI (Outlying Mean Index) Analysis, which is an abundance-weighted eigenanalysis approach (Doledec et al. 2000). This multivariate analysis measures niche position as 'marginality', which is the difference between the average habitat conditions used by a species and the average habitat conditions across the landscape. It thus indicates a species' tendency to occupy atypical habitat. A second measure, 'tolerance', indexes niche breadth as the amount of environmental variation experienced by a species given its distribution (Doledec et al. 2000, Hurlbert and White 2007). Marginality and tolerance values were calculated from lake and rock pool means of environmental and species data. Data were analyzed using the *ade-4* package in *R*.

Abundance and mean-variance scaling

The components of F (Eqs. 4.1-4.4) are ratios of variances to squared-means. Ratio values thus depend on how variance (s^2) scales with the mean (m), which is described by the power law, $s^2 = am^b$. If b, estimated as the regression slope of logged means and variances, is less than two, larger species populations experience less variation relative to the mean (Ballantyne and Kerkhoff 2007). If $b > 2$, larger populations experience more variation relative to the mean. Thus, all else equal, abundance will increase F under two conditions: (i) When $b < 2$ for plots of mean and temporal variance, abundance is stabilizing and the $CV_{t.var}^{-1}$ component of F is larger for abundant species, or (ii) when b >

2 for plots of mean and spatial variance, abundance increases spatial variation and the CV^2_s component of F is larger for abundant species. We estimated regression slopes from mean-variance plots and tested whether they diverged from the null expectation b = 2 with a t-ratio, calculated as: (best fit b – 2)/standard error of b.

Predictors of F were tested individually using linear regression and in combination using multiple regression in Statistica 8.0 (StatSoft Inc., 2007). We built full and reduced models using standard and backward stepwise multiple regression, respectively. Because the latter is prone to bias (Flom and Cassel 2007), we used it to build support for the results of full, standard models. Appendix T shows that both methods gave highly comparable results.

RESULTS

F, our measure of persistent spatial variation (PSV), was significant in most variables (Fig. 4.2). But PSV was more pronounced in environmental variables than biotic variables (t = 9.07, $p < 0.0001$; Fig. U.1, Appendix U). Environmental variables like pH and temperature had high $CV_{t.var}^{-1}$ values indicating that PSV arose from stability of individual sites (Fig. 4.2b,d). Meanwhile weathered rock products (e.g., Ca, Mg) and biologically-cycled elements and stocks (e.g., NO_3, C, Chl a) had greater spatial variation (Fig. 4.2b). Species tended to be both unstable and exhibit considerable spatial variation among sites (e.g., rock bass, *Mysis;* Fig. 4.2c). However, variables that were aggregate measures were more stable than their components. For instance, $CV_{t.var}^{-1}$ and F were greater for: Total organism density than mean density of species; total *Chaoborus* density than either of its life stages; species richness than mean occupancy of species; total N than NO_3 or NH_4; total organic C than the dissolved fraction; and conductivity than contributing ions.

PSV peaked in slow, autocorrelated variables (Fig. 4.3a,b). In lakes, these slow variables were non-reactive (conservative) ions which meant that F was also predictable from the chemical hardness of an ion (Fig. U.2, Appendix U). Surprisingly, stability measured at one site predicted 59-80% of variance in F (Fig. 4.3c,d). Time series skewness also significantly and negatively correlated with F (ρ = -0.39 to -0.72).

PSV increased with species abundance at the local or regional scale (Lakes – $R^2 = 0.24$, F = 9.91, p = 0.004; Rock pools – $R^2 = 0.36$, F = 19.73, $p < 0.0001$). In lakes, this effect was due to abundance enhancing stability. This was indicated by a mean-variance scaling slope $b < 2$ that shows temporal variances growing more slowly than the mean (Fig. 4.4a), resulting in abundant species having lower variation relative to the mean and thus higher stability (Eq. 4.3). Meanwhile, a slope indistinguishable from two indicated spatial variance among site growing in step with the mean (Fig. 4.4a) such that spatial variation (CV^2_s) did not change with abundance. In rock pools, abundance increased F because it stabilized temporal variances (b = 1.73; Fig. 4.4d) which more than offset its opposing effect of reducing spatial variation (b = 1.86).

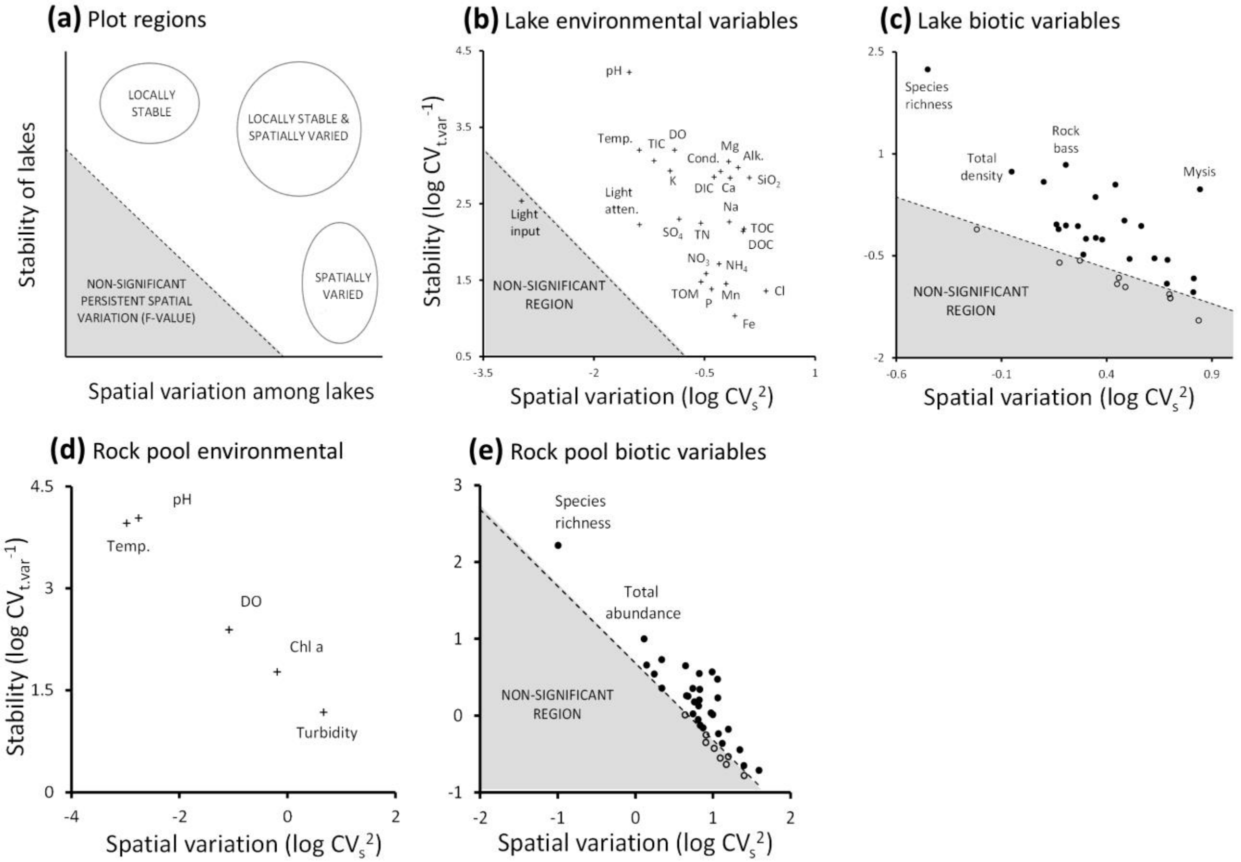


Figure 4.2. Dynamics underlying persistent spatial variation in ecosystem variables.
(Continued on next page)

Figure 4.2 (continued). (a) A plot of two components of PSV, spatial variation among sites and stability of sites, creates four regions of dynamics into which an ecosystem variable (point) can fall: (i) A *Non-significant PSV* region where limited spatial variation and/or low temporal stability cause F-values to fall below the critical value for significance ($\alpha = 0.05$), (ii) a *spatially varied* region where spatial variation is largely responsible for PSV, (iii) a *locally stable* region where temporal stability of local dynamics is responsible for PSV, and (iv) a *locally stable and spatially varied* region where both factors drive PSV. In practice, we found that plots can show negative trends (e.g., panel e) when a variable's spatial and temporal variation are similar (i.e., ergodic) and are standardized to the same overall mean (Eq. 4.4). Environmental and biotic variables from Wisconsin lakes **(b, c)** and from Jamaican rock pools **(d, e)** ranged widely across the four regions of dynamics. The non-significant region is not drawn for panel d because variables differed in the number of temporal observations, and thus critical F-values. Variables and their abbreviations are listed in Appendix V.

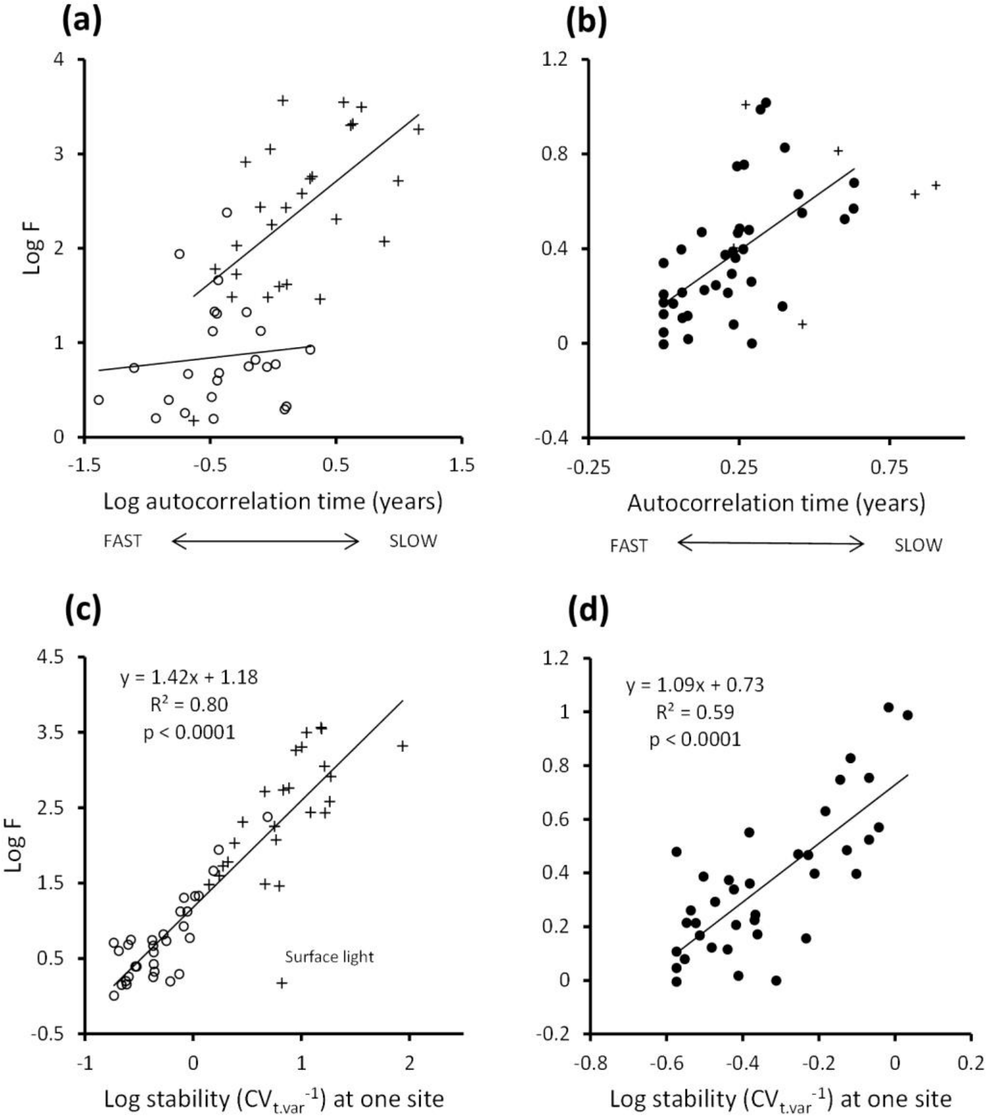


Figure 4.3. Temporal scale and stability as predictors of PSV. Variables (points) with slow response times exhibited more PSV, measured as F, than those with faster. Significant relationships existed **(a)** among lake environmental variables (R^2 = 0.35, F = 13.11, p = 0.001; crosses) and biotic variables (R^2 = 0.19, F = 6.82, p = 0.015; circles), and **(b)** among rock pool biotic variables (R^2 = 0.36, F = 19.95, p < 0.0001; circles) but not among rock pool environmental variables (crosses). PSV also related strongly to a variable's stability (CV^{-1}) measured at just one location in the landscape for; **(c)** lake environmental and biotic lake variables (with one removed outlier based on Cook's D, surface light intensity), and **(d)** biotic rock pool variables. Rock pool data were ln(x+1) transformed before plotting in panel b**.**

Abundance also affected the two components of spatial variance; *population* and *occupancy variance.* While abundance did not affect population variance in lakes (Fig. 4.4b), it did reduce occupancy variance (Fig. 4.4c) as more abundant species occupied more sites ($R^2 = 0.46$, $F = 24.97$, $p < 0.0001$). In rock pools, abundance increased population variance slightly (Fig. 4.4e) and decreased occupancy variance (Fig. 4.4f) with the latter again coinciding with a positive abundance-occupancy relationship ($R^2 = 0.68$, $F = 74.58$, $p < 0.0001$).

Species traits of environmental tolerance, fecundity, maximum age, maximum mass, minimum population doubling time and distance from range limit did not significantly predict PSV or its components. However, niche marginality (OMI) of a species predicted spatial variation (CV^2_s) in both systems (Fig. 4.5a,b), though not F itself. This effect was driven in lakes by the positive association between niche marginality and variation in population size among occupied sites (Fig. 4.5c).

Only a small subset of traits or variable properties was necessary to predict PSV well. Full and reduced multiple regression models (Tables T.1, T.2; Appendix T) showed that multiple predictors were significant in rock pool species (niche marginality and stability) and lake environmental variables (stability and autocorrelation time). But in most cases stability measured at one site was the only significant factor and always explained the most variation in F.

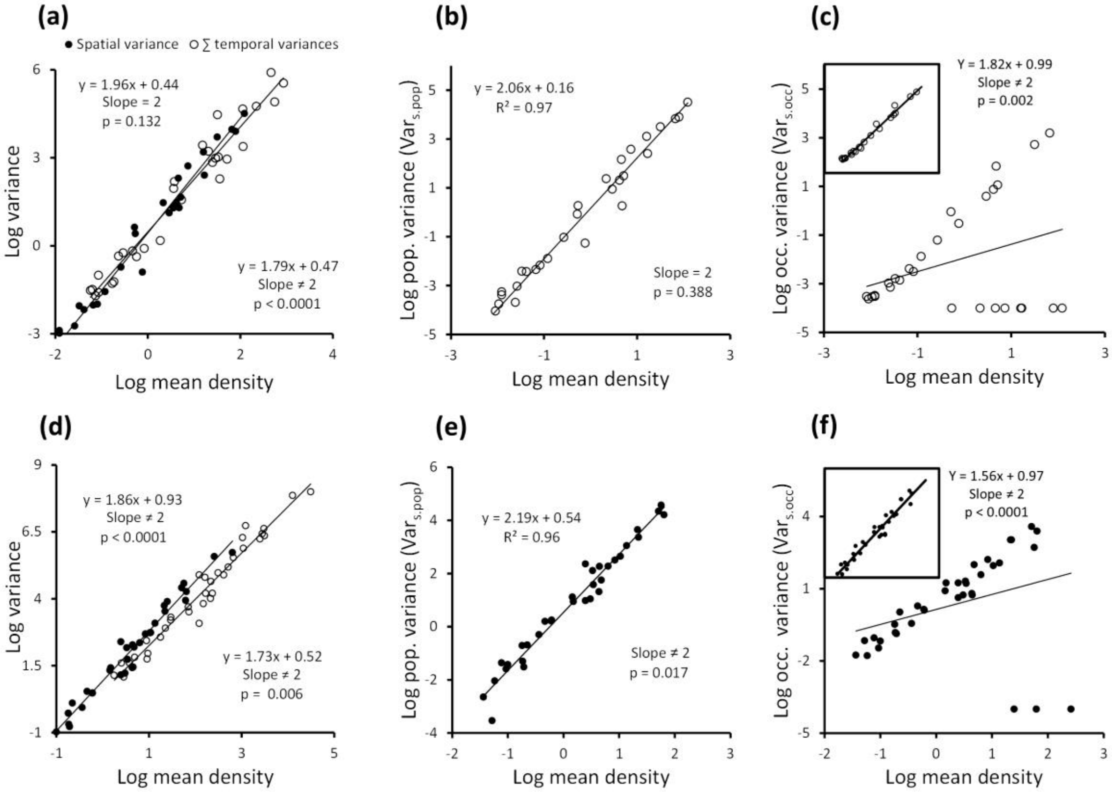


Figure 4.4. Mean-variance scaling for components of PSV. In lake species, mean density enhanced PSV through its components: **(a)** The scaling slope (b < null slope of 2) indicated that density stabilized the temporal component of PSV, the summed temporal variances, but did not affect the spatial variance of site means (b = 2). **(b)** Density did not affect that part of spatial variance arising among extant populations ($\mathrm{Var}_{s.pop}$; b = 2). But, **(c)** it did strongly reduce spatial variance arising from occupancy patterns. This effect was made noisy by several abundant species that occupied all lakes, thus minimizing occupancy variance, but was clear (b < 2) when these influential points were removed (inset). Density also enhanced PSV in rock pool species: **(d)** This is because, even though density somewhat reduced spatial variance (b < 2), the effect was overwhelmed by strong stabilizing of temporal variances (b << 2). **(e)** Density accentuated spatial variance among extant populations (b > 2), but **(f)** again strongly reduced spatial variance from occupancy patterns (b << 2) when species with full occupancy were removed (inset). Variances are scaled against their corresponding mean in Eq. 4.2-4.3, which is either the mean of site means ($\overline{\overline{\mathrm{Y}}}_i$) or the regional temporal mean ($\overline{\mathrm{Y}}_K$).

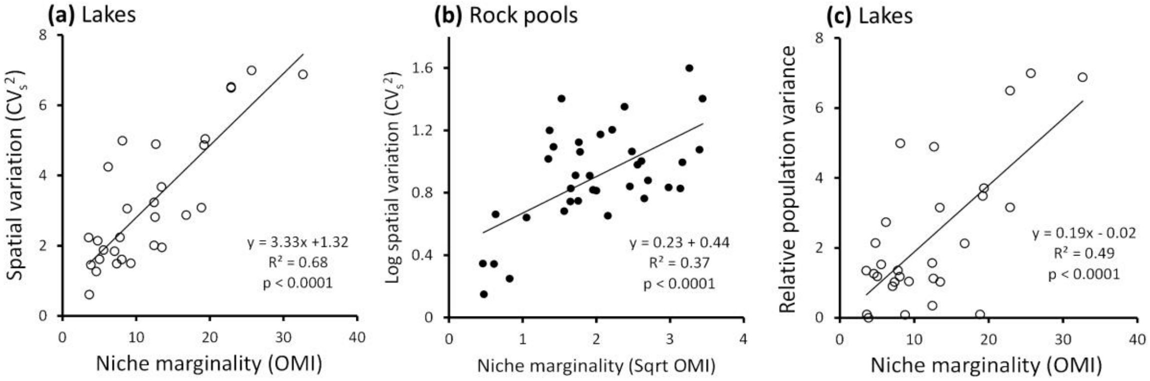


Figure 4.5. Niche predictors of PSV. Niche marginality significantly predicted the spatial variation (CV_s^2) component of PSV in lake species **(a)** and rock pool species **(b)**. **(c)** In lakes, species with high niche marginality also tended to exhibit high variation among extant populations, as measured by relative population variance.

DISCUSSION

Our results offer practical insight into the occurrence of a common but understudied landscape pattern: persistent spatial variation (PSV). Findings are novel in that they use a framework for breaking down PSV - a complex of superimposed sub-patterns and causes - into its constituent patterns of variation. This simplifying step allowed us to, first, uncover patterns of resource distribution in different types of ecosystem variables and, second, to expose a powerful class of traits or properties that predict PSV (Fig. 4.6).

PSV has major implications for anticipating the accessibility of resources in space and time. For instance, high levels of PSV in environmental variables suggest that physicochemical resources recur more consistently at sites than do biotic resources. This greater reliability appears to stem from the higher stability (Fig. 4.2) and slower rates of temporal change (Fig. 4.3a,b) in environmental variables, as exemplified by conservative ions. These temporal properties boost the stability term of Eq. 4.1 and, in turn, increase PSV even when spatial variation is relatively small (Fig. 4.2). In contrast, fish and invertebrate populations had relatively high spatial variation; but low stability and fast rates of change reduced PSV to low levels. The low stability and PSV seen in biotic variables might be expected in other systems since dynamics of populations are more non-linear than those of physical variables (Hsieh et al. 2005). These non-linearities can include amplification or attenuation of environmental noise (Orland 2003) and transient dynamics (Hastings 2004).

The sharp distinction between environmental and biotic variables suggests that PSV can be predicted based on variable-type. However, environmental variables that interact strongly with biotic dynamics may be exceptions. These variables had levels of PSV, stability and spatial variation comparable to biotic variables and included total organic matter, N, P, Mn and Fe. Dynamics of these materials and elements are either directly tied biological processes (e.g., organic matter, N, P) or are indirectly regulated by changes in redox chemistry from metabolism (e.g., Mn, Fe; Wetzel 2001, p. 303). Yet surface light intensity also had low PSV (Fig. 4.2b, 4.3c) even though it interacts weakly with biotic processes. We believe it to belong to an exceptional class of energetic, atmospheric variables that have little spatial variation and exhibit synchrony among locations (Vogt et al. 2011).

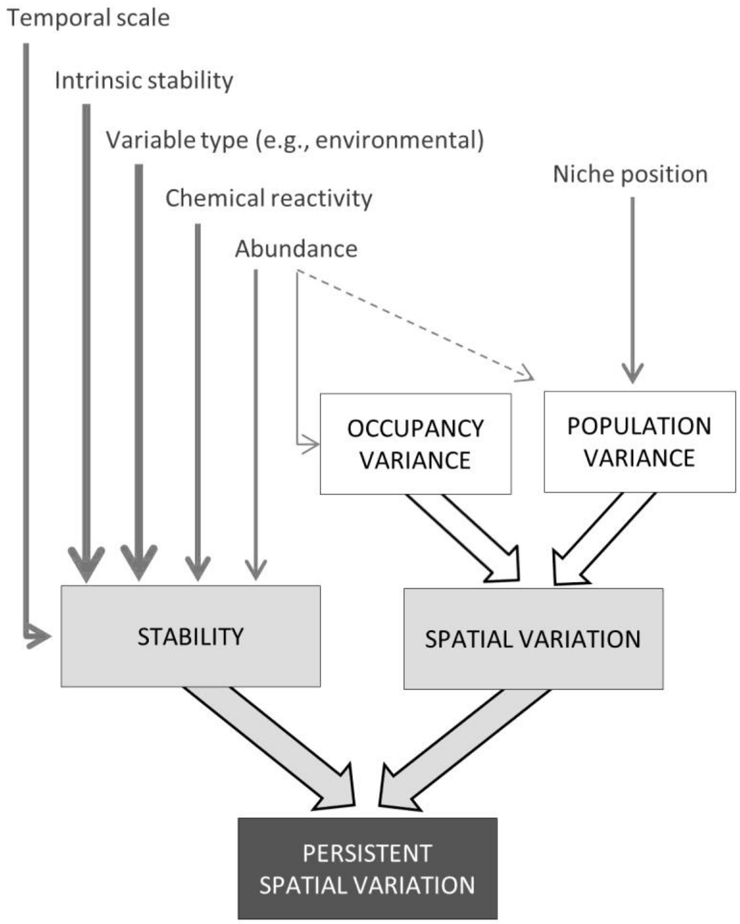


Figure 4.6. Visual summary of factors found to predict PSV and its component patterns. Arrow thickness corresponds to the explanatory power (variance explained) of the factor in a bivariate regression.

Temporal predictors of persistent spatial variation

The superiority of temporal properties for predicting PSV was evident in both lake and rock pool systems. The strong association of PSV with stability from just one site (R^2 = 0.59-0.80; Fig. 4.3c,d) suggests that a time series from a single, well-monitored location (e.g., a culturally-important or resource-rich site) may be sufficient for inferring which variables will display PSV. This should be true as long as two criteria are satisfied: First, stability measured at a single site must be representative of other sites to ensure it is a good proxy for the multi-site stability component of PSV ($CV_{t.var}^{-1}$). Second, species or variables should differ meaningfully in intrinsic stability so that the differences in $CV_{t.var}^{-1}$ translate into clear differences in PSV. Species have indeed been suggested to differ in intrinsic stability (Taylor and Woiwod 1980, Galloway and Lamb 2014) and there is evidence that environmental variables may also (e.g., Kling et al. 2000). However, these criteria remain to be tested explicitly. Also to be assessed is whether any predictive power is lost when stability is estimated from shorter time series (ours were 13-29 years) or applied to larger or smaller landscapes. Ongoing research into the patterns, causes and consequences of stability will no doubt help to answer these questions.

The above may be a new application in the underused method of *time-for-space substitution* (see Blois et al. 2013) wherein spatial variation is inferred from temporal variation. This is the inverse of the established practice of space-for-time substitution (Pickett 1989) but with some important differences. First, Fig. 4.3 implies that stability is substitutable for PSV, but PSV is not strictly the same as spatial variation because it includes a temporal component. Second, the relationship between spatial and temporal measures is quantitative (as in Eqs. 4.1, 4.4) whereas most space-for-time substitution is qualitative (but see Hammond and Kolasa 2014).

Correlates of stability were less important predictors of PSV than stability itself, but had the advantage of not necessarily relying on long time series. Published values of chemical hardness, for example, predicted PSV quite well in lake ions (Fig. U.2, Appendix U) because conservative ions (e.g., Ca, Mg) had higher stability which led to higher PSV. PSV also correlated negatively with time series skewness like that typical of outbreak populations (low abundance punctuated by infrequent population explosions; e.g., agricultural pests). While we measured skewness from time series, it would perhaps be possible to glean evidence of such abundance cycles from anecdotal sources (e.g., citizen science surveys, fishing records).

A final determinant of PSV appeared to be whether a variable was an aggregate of other variables. Theory suggests that the stability of an aggregate, as measured by the inverse CV, will tend to be higher than its components because uncorrelated fluctuations of components cancel out at the aggregate level (Lehman and Tilman 2000). This stabilization will tend to increase $CV_{t.var}^{-1}$ in Eq. 4.1 and, all else equal, F. Thus, PSV should generally be high in aggregate variables like species richness (Σspecies occurrences) and community abundance (Σspecies abundances). Furthermore, resource managers should expect PSV to be higher for an aggregate (e.g., total nitrogen) than for its components (e.g., nitrogen species). These data-efficient predictors may be important given that data collection in ecology is often hampered by expense and site accessibility.

Spatial predictors of persistent spatial variation

Factors driving spatial variation were weaker predictors of PSV than those driving stability. Nonetheless, they offered some insight into mechanisms underlying the pattern. For instance, species with high niche marginality exhibited considerable spatial variation that appeared to arise from differences in population sizes among occupied sites (Fig.4.5). This is consistent with patterns reported for habitat specialists (e.g., Holbrook et al. 2000).

Species traits were among the poorest predictors of PSV. Yet it seems likely that traits could explain patterns of at least some species. High stability and PSV of rock bass (*Ambloplites rupestris*) populations (Fig. 4.2c), for instance, might be explained by the species' high resistance and resilience (Ryan and Harvey 1977). On the whole, however, results cast doubt on trait-based prediction (Williams et al. 2010) of which species will display PSV. This limitation could arise if traits used are not directly involved in pattern-generating mechanisms or if they are appropriate but, as indicators, are highly dependent on biotic or environmental context. Using multiple traits may address such shortcomings but would likely be data-intensive. The greater success of pattern-based measures, like stability, may reflect the fact that they are generic and integrate many of the context-dependent effects of community and environment. When multiple spatial and temporal mechanisms drive PSV, it may be best predicted by a combination of factors as with niche marginality and stability in rock pool species (Table T.1, Appendix T).

Factors influencing spatial and temporal components

In some cases a single factor may affect both the spatial and temporal components of PSV, as did species abundance. Abundance is of great interest to ecologists because of its potential influence on population dynamics and we found it to weakly increase PSV. Theoretically, abundance will increase PSV most when it inflates spatial variance (mean-variance scaling $b > 2$) and dampens temporal variances of sites ($b < 2$). Such a pattern might be expected in landscapes of “local opportunity” in which spatially-restricted habitat specialists are rewarded with large, stable populations. Conversely, the pattern would be weakest where widespread generalist species are abundant but face the tradeoff of being unusually unstable. In lakes and rock pools, the pattern was intermediate to these scenarios. This was because abundance had, at times, opposing effects on the spatial and temporal components of PSV.

The stabilizing effect of abundance on rock pool and lake population dynamics in both rock pools, shown by mean-variance scaling, had two likely causes: First, as well as occupying more sites, abundant species generally occur more often over time because they less often go extinct or drop below the limits of detection (Guo et al. 2000). Consequently, there are fewer zero counts in time series which may lead to lower temporal variance. Second, mean-variance slopes slightly less than two (mean b = 1.76) suggest that population dynamics are mostly driven by environmental forcing (b approaches 2) but that large populations are less destabilized by chance demographic events (b approaches 1; Ballantyne and Kerkhoff 2007, Linnerud et al. 2013). We note that similar slopes can be generated if sampling misses clusters of organisms (Kalyuzhny et al. 2014). However, we used high quality data and the stabilizing role of abundance is widely reported in other systems (e.g.,Taylor and Woiwod 1980, Linnerud et al. 2013). Based on this evidence, it seems that abundance should generally increase the stability component of PSV ($CV_{t.var}^{-1}$).

The effect of abundance on the spatial components of PSV was less consistent, decreasing spatial variance and CV_s^2 in one system but not the other. This inconsistency may be due to differences in dispersal limitation between the two systems. Rock pools species, for instance, disperse regularly among pools (Sciullo and Kolasa 2012) which would let abundant species redistribute and reduce spatial variation, resulting in the observed scaling slope ($b < 2$). Meanwhile, lake fish and macroinvertebrate species are unlikely to disperse sufficiently among lakes to dampen spatial variation, which would explain a scaling slope equal to the null value ($b = 2$; see Hanski 1982).

In general, abundance appears to slightly enhance spatial variation, at least in a broad sample of terrestrial taxa (Taylor et al. 1983). But we found one component of spatial variation – variance from site absences – that consistently declined with abundance. This effect arises because abundance tends to increase occupancy, and should be widespread given that positive abundance-occupancy relationships are almost inevitable (Hartley 1998). The abundance-occupancy effect thus dampens PSV and opposes the temporal tendency of abundance to strengthen PSV. If the magnitudes of these countervailing effects were known for other systems, it would be possible to predict the effect of abundance on PSV. However, it is not currently known whether the various scaling slopes and their combinations are system- or taxon-specific.

CONCLUSION

Findings demonstrate that generic property- and pattern-based measures can serve as indicators of whether an ecosystem variable will display PSV in the form of consistent “hotspots”. We conclude that variable type (e.g., environmental) and temporal properties like stability and temporal scale have promise as data-efficient predictors. Potential benefits of this predictive capability range from forecasting the strength and permanence of spatial resource gradients to predicting species distributions. Furthermore, our general framework for decomposing PSV into its spatial and temporal components may prove a useful platform for future work on PSV. We also note that it can be applied to the temporal analog of PSV, inter-patch synchrony, which may yield insights into the drivers, correlates and predictors of this important landscape pattern.

ACKNOWLEDGEMENTS

We thank the North Temperate Lakes LTER for data use, Discovery Bay Marine Lab for field support, Ermias Azeria for assistance with OMI analysis, April Hayward for rock pool body size data, and numerous workers and volunteers for data collection. We also thank Madhur Anand, Clive Jones, Kevin McCann, David Rollo and Jim Quinn for helpful manuscript comments.

REFERENCES

Ballantyne, F., and A. J. Kerkhoff. 2007. The observed range for temporal mean-variance scaling exponents can be explained by reproductive correlation. Oikos 116:174–180.

Beisner, B., P. Peres-Neto, E. Lindstrom, A. Barnett, and M. Longhi. 2006. The role of environmental and spatial processes in structuring lake communities from bacteria to fish. Ecology 87:2985–2991.

Blois, J. L., J. W. Williams, M. C. Fitzpatrick, S. T. Jackson, and S. Ferrier. 2013. Space can substitute for time in predicting climate-change effects on biodiversity. Proceedings of the National Academy of Science 110:9374–9379.

Brown, J. H., D. W. Mehlman, and G. C. Stevens. 1995. Spatial variation in abundance. Ecology 76:2028–2043.

Cohen, J. E., M. Xu, and W. S. F. Schuster. 2012. Allometric scaling of population variance with mean body size is predicted from Taylor's law and density-mass allometry. Proceedings of the National Academy of Sciences of the United States of America 109:15829–34.

Curnutt, J. L., S. L. Pimm, and B. A. Maurer. 1996. Population variability of sparrows in space and time. Oikos 76:131–144.

Dai, L., D. Vorselen, K. S. Korolev, and J. Gore. 2012. Generic indicators for loss of resilience before a tipping points leading to population collapse. Science 336:1175–1177.

Doledec, S., D. Chessel, and C. Gimaret-Carpentier. 2000. Niche separation in community analysis: A new method. Ecology 81:2914–2927.

Flom, P. L., and D. L. Cassel. 2007. Stopping stepwise: Why stepwise and similar selection methods are bad, and what you should use. North East SAS Users Group:1–7.

Froese, R., and D. Pauly. 2014. FishBase. www.fishbase.org.

Galloway, T. D., and R. J. Lamb. 2014. Abundance and stability are species traits for four chewing lice (Phthiraptera: Menoponidae, Philopteridae) on feral pigeons, Columba livia (Aves: Columbiformes: Columbidae). The Canadian Entomologist 146:444–456.

Guisan, A., and W. Thuiller. 2005. Predicting species distribution: Offering more than simple habitat models. Ecology Letters 8:993–1009.

Guo, Q., J. Brown, and T. Valone. 2000. Abundance and distribution of desert annuals: Are spatial and temporal patterns related? Journal of Ecology 88:551–560.

Hammond, M. P., and J. Kolasa. 2014. Spatial variation as a tool for inferring temporal variation and diagnosing types of mechanisms in ecosystems. PloS one 9:e89245.

Hanski, I. 1982. On patterns of temporal and spatial variation in animal populations. Annals Zoology Fennici 19:21–37.

Hartley, S. 1998. A postive relationship between local abundance and regional occupancy is almost inevitable (but not all positive relationships are the same). Journal of Animal Ecology 67:992–994.

Hastings, A. 2004. Transients: The key to long-term ecological understanding? Trends in Ecology & Evolution 19:39–45.

He, F., and K. J. Gaston. 2003. Occupancy, spatial variance, and the abundance of species. The American Naturalist 162:366–75.

Holbrook, S. J., G. E. Forrester, and R. J. Schmitt. 2000. Spatial patterns in abundance of a damselfish reflect availability of suitable habitat. Oecologia 122:109–120.

Hsieh, C., S. M. Glaser, A. J. Lucas, and G. Sugihara. 2005. Distinguishing random environmental fluctuations from ecological catastrophes for the North Pacific Ocean. Nature 435:336–340.

Hurlbert, A. H., and E. P. White. 2007. Ecological correlates of geographical range occupancy in North American birds. Global Ecology and Biogeography 16:764–773.

Ives, A. R., and E. D. Klopfer. 1997. Spatial variation in abundance created by stochastic temporal variation. Ecology 78:1907–1913.

Jackson, D., D. Allen, I. Perfecto, and J. Vandermeer. 2014. Self-organization of background habitat determines the nature of population spatial structure. Oikos 123:751–761.

Kalyuzhny, M., Y. Schreiber, R. Chocron, C. H. Flather, R. Kadmon, D. A. Kessler, and N. Shnerb. 2014. Temporal fluctuation scaling in populations and communities. Ecology 95:1701–1709.

Kling, G. W., G. W. Kipphut, M. M. Miller, and W. J. O'Brien. 2000. Integration of lakes and streams in a landscape perspective: The importance of material processing on spatial patterns and temporal coherence. Freshwater Biology 43:477–497.

Lecomte, J., K. Boudjemadi, F. Sarrazin, K. Cally, and J. Clobert. 2004. Connectivity and homogenisation of population sizes: An experimental approach in Lacerta vivipara. Journal of Animal Ecology 73:179–189.

Lees, A. C., and C. a. Peres. 2009. Gap-crossing movements predict species occupancy in Amazonian forest fragments. Oikos 118:280–290.

Lehman, C. L., and D. Tilman. 2000. Biodiversity, stability, and productivity in competitive communities. The American Naturalist 156:534–552.

Lewis, W. M. 1978. Comparison of temporal and spatial variation in the zooplankton of a lake by means of variance components. Ecology 59:666–671.

Linnerud, M., B.-E. Saether, V. Grøtan, S. Engen, D. G. Noble, and R. P. Freckleton. 2013. Interspecific differences in stochastic population dynamics explains variation in Taylor's temporal power law. Oikos 122:1207–1216.

Martin, T. G., B. A. Wintle, J. R. Rhodes, P. M. Kuhnert, S. A. Field, S. J. Low-Choy, A. J. Tyre, and H. P. Possingham. 2005. Zero tolerance ecology: Improving ecological inference by modelling the source of zero observations. Ecology letters 8:1235–46.

Orland, M. C. 2003. Scale-dependent interactions between intrinsic and extrinsic processes reduce variability in protist populations. Ecology Letters 6:716–720.

Parr, R. G., and R. G. Pearson. 1983. Absolute hardness: companion parameter to absolute electronegativity. Journal of the American Chemical Society 105:7512–7516.

Pickett, S. T. A. 1989. Space-for-time substitution as an alternative to long-term studies. Pages 110–135 Long-term studies in ecology: Approaches and alternatives.

Proulx, R., C. Wirth, W. Voigt, A. Weigelt, C. Roscher, S. Attinger, J. Baade, R. Barnard, N. Buchmann, F. Buscot, N. Eisenhauer, M. Lange, A. Milcu, P. A. Niklaus, Y. Oelmann, S. Rosenkranz, and M. Vicky. 2010. Diversity promotes temporal stability across levels of ecosystem organization in experimental grasslands. PLoS One 5:1–8.

Ryan, P., and H. Harvey. 1977. Growth of Rock Bass, Ambloplites rupestris, in relation to the morphoedaphic index as an indicator of an environmental stress. Journal of the Fisheries Research Board of Canada 34:2079–2088.

Sagarin, R. D., and S. D. Gaines. 2002a. The “abundant centre” distribution: To what extent is it a biogeographical rule ? Ecology Letters 5:137–147.

Sagarin, R. D., and S. D. Gaines. 2002b. Geographical abundance distributions of coastal invertebrates: Using one-dimensional ranges to test biogeographic hypotheses. Journal of Biogeography 29:985–997.

Santora, J. A., and R. R. Veit. 2013. Spatio-temporal persistence of top predator hotspots near the Antarctic Peninsula. Marine Ecology Progress Series 487:287–304.

Sciullo, L., and J. Kolasa. 2012. Linking local community structure to the dispersal of aquatic invertebrate species in a rock pool metacommunity. Community Ecology 13:203–212.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. Page 859. Second edition. W. H. Freeman and Co., New York.

Tamburello, L., F. Bulleri, I. Bertocci, E. Maggi, and L. Benedetti-Cecchi. 2013. Reddened seascapes: Experimentally induced shifts in 1/f spectra of spatial variability in rocky intertidal assemblages. Ecology 94:1102–11.

Taylor, L. R., R. A. J. Taylor, I. P. Woiwod, and J. N. Perry. 1983. Behavioural dynamics. Nature 303:801–804.

Taylor, L. R., and I. P. Woiwod. 1980. Temporal stability as a density-dependent species characteristic. Journal of Animal Ecology 49:209–224.

Timilsina, N., F. J. Escobedo, W. P. Cropper, A. Abd-Elrahman, T. J. Brandeis, S. Delphin, and S. Lambert. 2013. A framework for identifying carbon hotspots and forest management drivers. Journal of Environmental Management 114:293–302.

Vandergast, A. G., A. J. Bohonak, S. a. Hathaway, J. Boys, and R. N. Fisher. 2008. Are hotspots of evolutionary potential adequately protected in southern California? Biological Conservation 141:1648–1664.

Vogt, R. J., J. A. Rusak, A. Patoine, and P. R. Leavitt. 2011. Differential effects of energy and mass influx on the landscape synchrony of lake ecosystems. Ecology 92:1104–1114.

Voigt, W., J. Perner, A. Davis, T. Eggers, J. Schumacher, R. Bahrmann, B. Fabian, W. Heinrich, G. Kohler, D. Lichter, R. Marstaller, and F. Sander. 2003. Trophic levels are differentially sensitive to climate ¨. Ecology 84:2444–2453.

Wetzel, R. G. 2001. Limnology: Lake and River Ecosystems. Page 1006. Third edition. Academic Press, San Diego.

Williams, N. M., E. E. Crone, T. H. Roulston, R. L. Minckley, L. Packer, and S. G. Potts. 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. Biological Conservation 143:2280–2291

CHAPTER 5.

NEW APPROACHES TO ECOSYSTEM DYNAMICS USING SPATIOTEMPORAL PATTERNS

This chapter and Chapter 1 *are*
adapted from a manuscript to be submitted to Oecologia *as a* Review and Synthesis
article

The tight connection between space, time and ecological dynamics implies that they must be considered together for new insight into ecological problems like human disturbance (Guichard and Gouhier 2014). This view resonates with a new paradigm in ecology. Ecologists no longer view natural systems as closed to external shocks and subsidies and tending towards a climax state. Rather ecosystems are seen as nonequilibrial and strongly influenced by chance events and flows from outside the system (O'Neill 2001, Perry 2002, Cushman 2010). Antarctic community change, for example, is a product of different site histories and environments as well as temporal shocks of climate and species invasions (Chown and Convey 2007). But even though ecologists have made significant progress in finding rule and order in spatiotemporal dynamics (reviewed in Perry 2002; Cushman 2010), the ability to predict change in ecosystems remains limited (Guichard and Gouhier 2014).

Chapter 1 identified research gaps in the ability to make ecological inferences from readily-available data. This general discussion evaluates the strengths and weaknesses of new applications that fill these gaps, and suggests future work to extend and synthesize spatiotemporal research. Overall, findings support new uses of spatiotemporal patterns for predicting dynamics in ecosystems. Results generally agreed with hypotheses and met many of the criteria for useful ecological applications from Chapter 1 (Table 5.1). Namely and with few exceptions, they were data-efficient and applicable across ecosystems and ecological processes (see Chapter 1 for criteria).

Table 5.1. Study hypotheses, findings and usefulness of applications

Hypothesis	Findings and conclusions	Data efficient?	Applies across systems?	Applies across variables?
Spatial variation can be a quantitative substitute for temporal variation	Spatial variability can be a quantitatively or qualitatively substituted for temporal variability	Yes	Yes	Yes
Patterns of spatiotemporal variation can be used to predict responses to connecting ecosystem fragments	Spatiotemporal patterns strongly predict responses to connecting aquatic microcosms	No	Maybe	Yes
Measurable properties of ecosystem variables help to predict the occurrence of persistent spatial variation	Temporal properties (e.g., stability) predict persistent spatial variation best, followed by species attributes (e.g., niche position)	Yes	Yes	Yes

The quantitative space-for-time substitution in Chapter 2 is, to my knowledge, the first of its kind. The framework and approach comes at a time of renewed interest in substituting temporal for spatial information (Blois et al. 2013, Carpenter 2013, Banet and Trexler 2013), and so may join a wave of new inferences that overcome the problem of time series scarcity. The procedure of swapping spatial and temporal CV's seems to have high potential for use in a range of systems, having worked in all three study ecosystems and across a range of ecosystem variables. Its analytical form will no doubt help in its application.

A weakness of the approach is that it works best when dynamics are uncorrelated among sites and among times and, if not, needs a correction factor. For this reason, optimal use will be either; in ecosystems with rather ephemeral or stochastic dynamics, like intermittent water bodies and small islands or; when correction factors (based on a variable's spatiotemporal pattern) can be accurately estimated from indirect, proxy or historical measures. Even when this is possible, estimating temporal from spatial variability assumes a certain stationarity: That temporal patterns will not be seriously perturbed by some future event. Future studies should work within these limitations or discover means to overcome them. Meanwhile, the framework may provide an exciting platform for exploring the substitutability of other spatial and temporal concepts (e.g., resilience, resistance) and measures (e.g., scale, skew, kurtosis, and autocorrelation).

Another problem involving spatiotemporal dynamics is landscape modification and its effects, which can include changes in mean, variability, spatial synchrony and extinction rate (Gonzalez et al. 1998, Liebhold et al. 2004, Staddon et al. 2010). Predicting the responses of ecosystem variables to spatial connection (Chapter 3) answers the call for general rules (Ellis et al. 2010), and seems promising. The principle for prediction – that spatiotemporal patterns indicate the potential for and constraint on change from connection – is general and not based on variable-specific mechanisms. It should thus apply to other systems and both biotic and physicochemical variables. Yet, because microcosms lack some of the complexity and large-scale attributes of many ecosystems

(Carpenter 1996), findings should be confirmed in natural systems. Another drawback is that the approach is data-intensive, requiring estimates of spatiotemporal pattern from a less-connected system. The application is thus not ready for broad deployment in landscapes facing fragmentation or wildlife corridor installation. Rather, results can be seen as providing a close-up view of connection-induced reorganization; proof of concept for predicting the resulting changes in dynamics; and clues for how different variable types (e.g., energetic variables) are impacted by landscape modification.

A final problem is the reliability of finding ecological resources in the same locations, which is reflected in the pattern of persistent spatial variation (PSV). Splitting this pattern into its spatial and temporal components adds a new dimension to the search for causes and correlates of spatial variation (Brown et al. 1995, Ives and Klopfer 1997, He and Gaston 2003). The superior ability of temporal properties like stability to predict PSV suggests the potential of time-for-space substitution – an apparently unexplored approach (but see Blois et al. 2013). It is data-efficient by requiring only a single time series to predict the landscape pattern of PSV, though even these may be scarce. Furthermore, the predictive relationship held in two disparate ecosystems and across many ecological processes. It will likely face similar limitations to its analog, space-for-time substitution (e.g., Fukami and Wardle 2005, Walker et al. 2010; also see above). Nonetheless, predicting the spatial distribution and reliability of resources from few highly-resolved time series could be valuable in helping managers forecast beyond the measured range. For this reason, the approach should be studied in more systems and in direct comparison with space-for-time substitution.

Applications show potential for making inferences about the dynamics of a broad range of ecosystem variables. But it must be noted that, in all studies, considerable noise existed around the dynamics of species populations and biotic variables like NPP. These limitations exist because of the inherent complexity of biota that includes transient responses (Hastings 2004) and high contingency on local conditions and interactions (Beckage et al. 2011). General rules like those presented here are unlikely to provide highly-resolved predictions but they may offer firm guidance about what patterns of variability to expect in multi-variable landscapes.

Future directions: A synthesis for spatiotemporal research

The research presented here adds to broader ecology by adding new conceptual and statistical tools (e.g., variability indices, statistical frameworks) that can be further refined and applied. More generally, it adds to a growing understanding of spatiotemporal dynamics and provides fodder for synthesis. Synthesis is the combining of information to create general and applicable knowledge (Carpenter et al. 2009) and is needed to answer the ‘big questions’ of how small details of community and environment add up to the ecosystem level or larger scales of space and time (Baskin 1997). The big questions considered by this thesis include: What do spatial patterns reveal about temporal dynamics? How do patterns of spatiotemporal variation differ for energy, material and organisms? And, how can spatiotemporal information be most profitably used for understanding and prediction?

Synthesis may be especially productive in spatiotemporal research, where all fields grapple with the same generic problem: The emergence of complex dynamics when variables act and interact at various scales. Elements of a synthetic solution to this problem may already exist. Consensus exists, for instance, on the need for an organism- or process-based view to understand the dynamics of any single variable (Turner et al. 1995, Manning et al. 2004) and on the importance of considering the full spectrum of interacting ecosystem processes (Loreau et al. 2003, Leavitt et al. 2009). Moreover, more insight into scaling issues and patterns of variability is considered essential for dealing with ecological complexity (Fraterrigo and Rusak 2008, Hastings 2010, Wang and Loreau 2014). Findings in this thesis reinforce these ideas and suggest that the key to synthesis may lie in linking spatiotemporal patterns to the concept of scale.

Scale has long permeated ecological thought and practice. As a concept, it has proven indispensable for studying; (i) dynamics that occur over multiple domains of time and space (e.g., Fahrig 1992, Anand and Kadmon 2000), (ii) interactions between differently-scaled variables (e.g., Raffa et al. 2008), and (iii) cause-and-effect relationships that change with observation scale (e.g., Paradis et al. 1999). The term ‘scale’ has various meanings. It can refer to a level of ecological organization, the grain or size of observation window, the lag between related events, or the spatial or temporal extent of an ecological process (Anand and Kadmon 2000). I use the term in the latter sense – that is, the area or timespan over which a process varies significantly (Denman and Powell 2003). This definition has a clear affinity to patterns of variation, which emerge where the scales of observation meet the scales of dynamics (Levin 1992). Yet spatiotemporal patterns of applied importance, like spatial synchrony of populations and others studied in this thesis, are rarely viewed as scaling problems. Approaches are thus needed that apply the insights of scale-based theory to real-world spatiotemporal patterns.

Below I offer three (tentative) guiding principles, supported by my and others' research, that use the scale concept to more clearly link spatiotemporal patterns to their underlying dynamics and consequences for communities and ecosystems.

(1) Spatiotemporal patterns reflect the interaction between scales of ecological processes and scales of observation

While it is commonly noted that pattern depends on observation scale (e.g., Levin 1992), this idea can be sharpened for better interpretation of spatiotemporal patterns. As an illustration, the average human can directly observe patterns over a 75 year timescale and perhaps a 10^5 km^2 spatial scale, extents that scientific instruments and methods expand considerably. If ecological processes act at scales that exceed or fall short of these observation scales, they are perceived to have spatiotemporal pattern. A Stommel diagram (Stommel 1963, Vance and Doel 2010), which plots the spatial and temporal scales of processes, illustrates four such patterns (Fig. 5.1a). Fast processes occurring at small spatial scales relative to the observer appear as ephemeral (e.g., fire regimes); slow processes occurring at small spatial scales are seen as persistent spatial variation (e.g., bedrock composition); slow processes occurring at large spatial scales are seen as uniform or unchanging (e.g., tectonics); and fast processes occurring at large spatial scales appear as spatially-synchronous (e.g., weather). Scaling is thus the bridge connecting the main forms of spatiotemporal pattern.

The tangle of spatiotemporal patterns seen in ecosystems, and Chapters 2-4, may be simplified if seen as the result of an observer viewing differently-scaled processes (Fig. 5.1b). Furthermore, this view could serve as a means to integrate fields of study working at different spatial and temporal scales, like population and landscape ecology (Fig. 5.1c). Progress on these fronts will likely require making Stommel or other scaling diagrams both quantitative (Vance and Doel 2010; see Blöschl and Sivapalan 1995 for a start) and explicit with respect to important spatiotemporal patterns like synchrony.

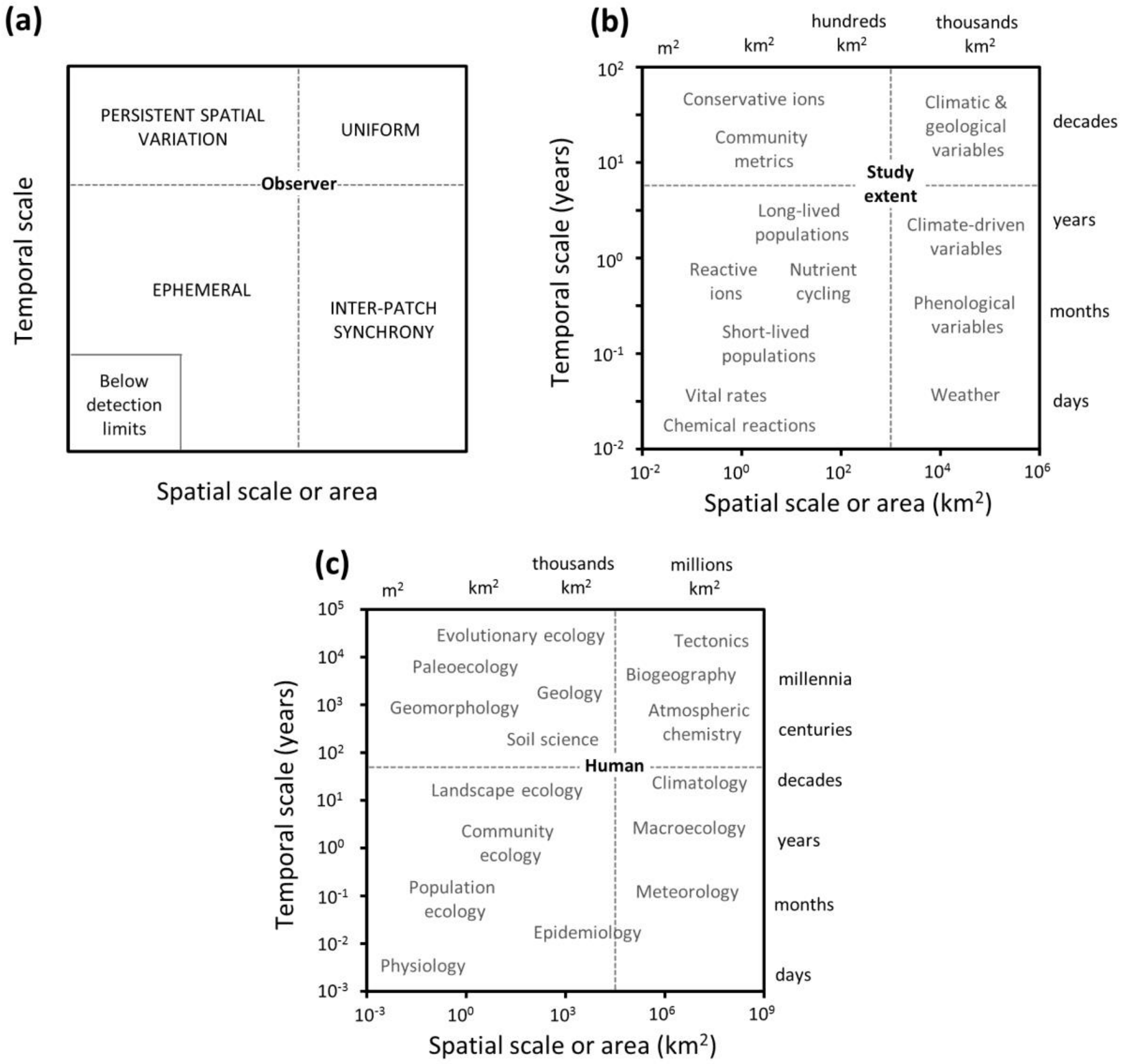


Figure 5.1. Two-dimensional Stommel diagram illustrating the origins of different spatiotemporal patterns. (a) The interaction between the scaling of a process and the scale of observation produce four regions of spatiotemporal pattern. But variation at spatial or scales temporal scales finer than the grain or detection limits of the observer goes undetected. **(b)** Hypothetical scaling and patterns of ecosystem variables in a multi-annual landscape study. **(c)** Different fields study processes of different spatial and temporal scales, and thus focus on different spatiotemporal patterns as seen from the human perspective of lifespan and geographic range.

(2) Spatiotemporal patterns reflect the relationship between spatial and temporal patterns, and so govern their interchangeability

Spatiotemporal patterns are important indicators of how spatial and temporal patterns are related and whether one can be used as a surrogate for the other (e.g., Pickett 1989, McIntire and Fajardo 2009). Spatial and temporal variation are fully substitutable when they are equal or ergodic (Paine 1985), which occurs in the ephemeral region of Fig. 5.1a. But substitutability is low for other spatiotemporal patterns and regions of Fig. 5.1a. This was a major finding of Chapter 2. Persistent spatial variation, for instance, means that spatial variation is high relative to temporal variation at each site. This may occur if contrasting site histories or slow rates of change confound substitution (Pickett 1989, Walker et al. 2010). Space and time are also not interchangeable when inter-patch synchrony aligns the peaks and troughs of fluctuations and makes spatial variation low relative to temporal variation. This may occur from a regional disturbance (e.g., drought) that forces all sites to share the same trajectory (e.g., Jongejans and De Kroon 2005).

The same spatiotemporal patterns that prevent substitution of spatial and temporal variation arise from a mismatch of spatial and temporal scales (Fig. 5.1a). Accurate substitution thus appears to hinge on the equivalence or proportionality of spatial and temporal scales (Fig. 5.2a). This condition is often satisfied as spatial and temporal scales of variables tend to scale linearly (Marquet et al. 1993, Wu 1999, Wu and Li 2006). Linear scaling is expected when: Variables are hierarchical such that smaller subunits change faster than large aggregates (Urban et al. 1987, Delcourt and Delcourt 1988), variables are correlated with hierarchical structure like nested habitat (e.g., Holling 1992, Steele et al. 1994, Blöschl and Sivapalan 1995) or particles or organisms with longer "lifetimes" can spread further in space (e.g., gas molecules; Seinfeld and Pandis 2006 p. 18). Substitution should be particularly effective in these cases. But correcting factors, models or expanded observation scales will be needed for outliers that do not follow linear scaling, as in Fig. 5.2a (Chapter 2; Walker et al. 2010, Buyantuyev et al. 2012). Space-for-time research will benefit from explicit consideration of these scaling issues.

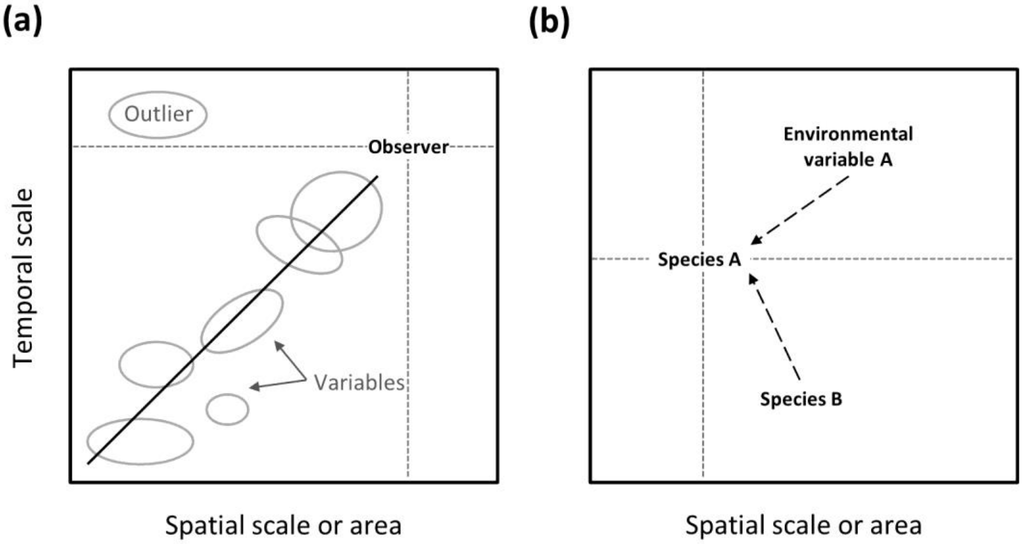


Figure 5.2. Novel perspectives on spatiotemporal dynamics from a Stommel diagram. (a) The linear increase in temporal scale with spatial scale necessary for space-for-time substitution, plus an outlier to that relationship. **(b)** Interaction of a hypothetical species with differently-scaled variables.

(3) Spatiotemporal patterns reflect the scales of processes, and thus their possibilities for interaction

Ecological interactions occur over many scales of time and space, and because of the link between scale and pattern (Fig. 5.1a), over a range of spatiotemporal patterns. This view can be useful for evaluating the possibilities for interaction. For example, taking the viewpoint of Species A in Fig. 5.2b, we notice that competing Species B lies in the synchrony region of the plot. Species B will thus be perceived by Species A, and interacted with, as an occasionally widespread competitor. Meanwhile, Species A will experience Environmental variable A as a uniform background, changing over broader spatial and temporal scales. A scaling view thus constrains the universe of possible interactions to those matching a variable’s perspective.

A scaling approach to visualizing ecological interactions has been advocated before (e.g., Steele 1989, Holling 1992), but remains underdeveloped. The conceptual framework in Chapter 3 adds to this topic by showing how differently-scaled processes respond to regional spatial connection. Future work must develop the problem further in at least two ways. First, we need better understanding of the effects of cross-scale interactions, as in the coupling of; fast and slow processes (Carpenter and Turner 2001, Walker et al. 2012), broadscale and finescale processes (Peters et al. 2007), and their various combinations (Fraterrigo and Rusak 2008). This understanding will also need to address the phenomenon of ecological resonance which occurs when driver and response variables operate at similar scales (Denman and Powell 2003, Orland 2003). Second is an empirical issue. Because ecological processes vary over multiple spatial and temporal scales and may lack a single "characteristic" scale (Marquet et al. 1993), a more scale-based ecology will need to estimate these scale distributions from limited information (e.g., Horne and Schneider 1994). Progress in these areas may yet produce simple and scale-accurate representations of spatiotemporal dynamics.

CONCLUSION

New insights into the functioning and management of ecosystems are possible when research approaches match the dynamism of nature. This thesis demonstrates three cases of improved inference and prediction in ecosystems from conceptual advances at the interface of spatial and temporal variation. Continued work at this interface promises innovation within specific fields but also, given the ubiquity of spatiotemporal dynamics, the potential for synthesis from populations to landscapes.

REFERENCES (CHAPTERS 1 & 5)

Anand, M., and R. Kadmon. 2000. Community-level analysis of spatiotemporal plant dynamics. Ecoscience 7:101–110.

Adler, P. B., and W. K. Lauenroth. 2003. The power of time: Spatiotemporal scaling of species diversity. Ecology Letters 6:749–756.

Adrian, R., C. M. O'Reilly, H. Zagarese, S. B. Baines, D. O. Hessen, W. Keller, D. M. Livingstone, R. Sommaruga, D. Straile, E. Van Donk, G. a Weyhenmeyer, and M. Winder. 2009. Lakes as sentinels of climate change. Limnology and Oceanography 54:2283–2297.

Aukema, B. H., A. L. Carroll, Y. Zheng, J. Zhu, K. F. Raffa, R. D. Moore, K. Stahl, and S. W. Taylor. 2008. Movement of outbreak populations of mountain pine beetle: Influences of spatiotemporal patterns and climate. Ecography 31:348–358.

Banet, A. I., and J. C. Trexler. 2013. Space-for-time substitution works in everglades ecological forecasting models. PloS one 8:1–10.

Barnes, J. B., T. A. Ehlers, N. Insel, N. Mcquarrie, and C. J. Poulsen. 2012. Linking orography, climate, and exhumation across the central Andes. Geology 40:1135–1138.

Bascompte, J. 1998. Spatiotemporal patterns in nature. Trends in Ecology and Evolution 13:173–174.

Baskin, Y. 1997. Center seeks synthesis to make ecology more useful. Science 275:310–311.

Beckage, B., L. J. Gross, and S. Kauffman. 2011. The limits to prediction in ecological systems. Ecosphere 2:1–12.

Becks, L., and H. Arndt. 2013. Different types of synchrony in chaotic and cyclic communities. Nature communications 4:1359.

Berkes, F., J. Colding, and C. Folke. 2000. Rediscovery of traditional ecological knowledge as adaptive management. Ecography 10:1251–1262.

Bjørnstad, O. N., R. A. Ims, and X. Lambin. 1999. Spatial population dynamics: Analyzing patterns and processes of population synchrony. Trends in Ecology and Evolution 14:427–432.

Blois, J. L., J. W. Williams, M. C. Fitzpatrick, S. T. Jackson, and S. Ferrier. 2013. Space can substitute for time in predicting climate-change effects on biodiversity. Proceedings of the National Academy of Science 110:9374–9379.

Blöschl, G., and M. Sivapalan. 1995. Scale issues in hydrological modelling: A review. Hydrological Processes 9:251–290.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: Effect of immigration on extinction. Ecology 58:445–449.

Brown, J. H., D. W. Mehlman, and G. C. Stevens. 1995. Spatial variation in abundance. Ecology 76:2028–2043.

Bull, J. C., and M. B. Bonsall. 2010. Predators reduce extinction risk in noisy metapopulations. PLoS One 5:1–8.

Bull, J. W., K. B. Suttle, N. J. Singh, and E. Milner-Gulland. 2013. Conservation when nothing stands still: Moving targets and biodiversity offsets. Frontiers in Ecology and the Environment 11:203–210.

Buyantuyev, A., P. Xu, J. Wu, S. Piao, and D. Wang. 2012. A space-for-time (SFT) substitution approach to studying historical phenological changes in urban environment. PloS one 7:e51260.

Carpenter, S. R. 1996. Microcosm experiments have limited relevance for community and ecosystem ecology. Ecology 77:677–680.

Carpenter, S. R. 2013. Spatial signatures of resilience. Nature 496:308–309.

Carpenter, S. R., E. V. Armbrust, P. W. Arzberger, F. S. Chapin, J. J. Elser, E. J. Hackett, A. R. Ives, P. M. Kareiva, M. a. Leibold, P. Lundberg, M. Mangel, N. Merchant, W. W. Murdoch, M. a. Palmer, D. P. C. Peters, S. T. a. Pickett, K. K. Smith, D. H. Wall, and A. S. Zimmerman. 2009. Accelerate synthesis in ecology and environmental sciences. BioScience 59:699–701.

Carpenter, S. R., J. J. Cole, M. L. Pace, R. Batt, W. A. Brock, T. Cline, J. Coloso, J. R. Hodgson, J. F. Kitchell, D. A. Seekell, L. Smith, and B. Weidel. 2011. Early warnings of regime shifts: A whole-ecosystem experiment. Science 332:1079–1082.

Carpenter, S. R., and M. G. Turner. 2001. Hares and tortoises: Interactions of fast and slow variables in ecosystems. Ecosystems 3:495–497.

Carr, M. H., E. Saarman, and M. Caldwell. 2010. The role of “rules of thumb” in science-based environmental policy: California’s Marine Life Protection Act as a case study. Stanford Journal of Law, Science and Policy 2:1–17.

Chown, S. L., and P. Convey. 2007. Spatial and temporal variability across life’s hierarchies in the terrestrial Antarctic. Philosophical transactions of the Royal Society of London. Series B, Biological sciences 362:2307–31.

Clark, J. S., S. R. Carpenter, M. Barber, S. Collins, A. Dobson, J. A. Foley, D. M. Lodge, M. Pascual, R. P. Jr, W. Pizer, C. Pringle, and W. V Reid. 2001. Ecological forecasts: An emerging imperative. Science 293:657–659.

Cloern, J. E. 2007. Habitat connectivity and ecosystem productivity: Implications from a simple model. The American naturalist 169:E21–33.

Coffman, C. J., J. D. Nichols, and K. H. Pollock. 2001. Population dynamics of Microtus pennsylvanicus in corridor-linked patches. Oikos 93:3–21.

Cottenie, K., and L. De Meester. 2004. Metacommunity structure: Synergy of biotic interactions as selective agents and dispersal as fuel. Ecology 85:114–119.

Cowles, H. C. 1899. The ecological relations of vegetation on the sand dunes of Lake Michigan. Botanical Gazette 27:167–202.

Cushman, S. A. 2010. Spatial complexity, informatics, and wildlife conservation. Pages 19–41 *in* S. A. Cushman and F. Huettmann, editors. Spatial Complexity, Informatics and Wildlife Conservation. Springer Japan, Tokyo.

Dai, L., K. S. Korolev, and J. Gore. 2012a. Slower recovery in space before collapse of connected populations. Nature 496:355–358.

Dai, L., D. Vorselen, K. S. Korolev, and J. Gore. 2012b. Generic indicators for loss of resilience before a tipping points leading to population collapse. Science 336:1175–1177.

Delcourt, H. R., and P. A. Delcourt. 1983. Dynamics plant ecology: The spectrum of vegetational change in space and time. Quaternary Science Reviews 1:153–175.

Delcourt, H. R., and P. A. Delcourt. 1988. Quaternary landscape ecology: Relevant scales in space and time. Landscape Ecology 2:23–44.

Denman, K. L., and T. Powell. 2003. Effects of physical processes on planktonic ecosystems in the coastal ocean. Page 350 Oceanography and Marine Biology, An Annual Review 22. Aberdeen University Press.

Doak, D. F., J. A. Estes, B. S. Halpern, U. Jacob, D. R. Lindberg, J. Lovvorn, D. H. Monson, M. T. Tinker, T. M. Williams, J. T. Wootton, I. Carroll, M. Emmerson, F. Micheli, and M. Novak. 2008. Understanding and predicting ecological dynamics: Are major surprises inevitable? Ecology 89:952–961.

Elith, J., and J. R. Leathwick. 2009. Species distribution models: Ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics 40:677–697.

Ellis, A. M., T. Václavík, and R. K. Meentemeyer. 2010. When is connectivity important? A case study of the spatial pattern of sudden oak death. Oikos 119:485–493.

Eppinga, M. B., C. A. Pucko, M. Baudena, B. Beckage, and J. Molofsky. 2013. A new method to infer vegetation boundary movement from "snapshot" data. Ecography 36:622–635.

Estay, S. A., A. A. Albornoz, M. Lima, M. S. Boyce, and N. C. Stenseth. 2011. A simultaneous test of synchrony causal factors in muskrat and mink fur returns at different scales across Canada. PloS one 6:e27766.

Ettema, C. H., S. L. Rathbun, and D. C. Coleman. 2000. On spatiotemporal patchiness and the coexistence of five species of Chronogaster (Nematoda: Chronogasteridae) in a riparian wetland. Oecologia 125:444–452.

Fahrig, L. 1992. Relative importance of spatial and temporal scales in a patchy environment. Theoretical Population Biology 41:300–314.

Floyd, M. L., W. H. Romme, and D. D. Hanna. 2000. Fire history and vegetation pattern in Mesa Verde National Park, Colorado, USA. Ecological Applications 10:1666–1680.

Fox, J. W., D. A. Vasseur, S. Hausch, and J. Roberts. 2011. Phase locking, the Moran effect and distance decay of synchrony: Experimental tests in a model system. Ecology Letters 14:163–168.

Fraterrigo, J. M., and J. a Rusak. 2008. Disturbance-driven changes in the variability of ecological patterns and processes. Ecology Letters 11:756–70.

Fukami, T., and D. A. Wardle. 2005. Long-term ecological dynamics: Reciprocal insights from natural and anthropogenic gradients. Proceedings of the Royal Society B 272:2105–2115.

Garibaldi, L. a, I. Steffan-Dewenter, C. Kremen, J. M. Morales, R. Bommarco, S. a Cunningham, L. G. Carvalheiro, N. P. Chacoff, J. H. Dudenhöffer, S. S. Greenleaf, A. Holzschuh, R. Isaacs, K. Krewenka, Y. Mandelik, M. M. Mayfield, L. a Morandin, S. G. Potts, T. H. Ricketts, H. Szentgyörgyi, B. F. Viana, C. Westphal, R. Winfree, and A. M.

Klein. 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. Ecology letters 14:1062–72.

Gonzalez, A., and R. D. Holt. 2002. The inflationary effects of environmental fluctuations in source-sink systems. Proceedings of the National Academy of Science 99:14872–14877.

Gonzalez, A., J. H. Lawton, F. S. Gilbert, T. M. Blackburn, and I. Evans-Freke. 1998. Metapopulation dynamics, abundance, and distribution in a microecosystem. Science 281:2045–2047.

Grenfell, B. T., O. N. Bjornstad, and J. Kappey. 2001. Travelling waves and spatial hierarchies in measles epidemics. Nature 414:716–723.

Guichard, F., and T. C. Gouhier. 2014. Non-equilibrium spatial dynamics of ecosystems. Mathematical Biosciences 255:1–10.

Hammond, M. P., and J. Kolasa. 2014. Spatial variation as a tool for inferring temporal variation and diagnosing types of mechanisms in ecosystems. PloS one 9:e89245.

Hanski, I. 1991. Metapopulation dynamics: Brief history and conceptual domain. Biological Journal of the Linnean Society 42:3–16.

Hassell, M. P., H. N. Comins, and R. M. May. 1994. Species coexistence and self-organizing spatial dynamics. Nature 370:290–292.

Hastings, A. 2004. Transients: The key to long-term ecological understanding? Trends in Ecology & Evolution 19:39–45.

Hastings, A. 2010. Timescales, dynamics and ecological understanding. Ecology 91:3471–3480.

He, F., and K. J. Gaston. 2003. Occupancy, spatial variance, and the abundance of species. The American Naturalist 162:366–75.

Heino, M., V. Kaitala, E. Ranta, and J. Linstrom. 1997. Synchronous dynamics and rates of extinction in spatially structured populations. Proceedings of the Royal Society B 264:481–486.

Helfield, J. T., and R. J. Naiman. 2001. Effects of salmon-derived nitrogen on riparian forest growth and implications for stream productivity. Ecology 82:2403–2409.

Hilderbrand, R. 2003. The roles of carrying capacity, immigration, and population synchrony on persistence of stream-resident cutthroat trout. Biological Conservation 110:257–266.

Holling, C. S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. Ecological Monographs 62:447–502.

Horne, J. K., and D. C. Schneider. 1994. Analysis of scale-dependent processes with dimensionless ratios. Oikos 70:201–211.

Howeth, J., and M. Leibold. 2010. Species dispersal rates alter diversity and ecosystem stability in pond metacommunities. Ecology 91:2727–2741.

Huffaker, C. B. 1958. Experimental studies on predation: Dispersion factors and predator-prety oscillations. Hilgardia 27:795–835.

Ives, A. R., and E. D. Klopfer. 1997. Spatial variation in abundance created by stochastic temporal variation. Ecology 78:1907–1913.

Jackson, D. A., P. R. Peres-Neto, and J. D. Olden. 2001. What controls who is where in freshwater fish communities – the roles of biotic, abiotic, and spatial factors. Canadian Journal of Fisheries and Aquatic Sciences 58:157–170.

Jongejans, E., and H. De Kroon. 2005. Space versus time variation in the population dynamics of three co-occurring perennial herbs. Journal of Ecology 93:681–692.

Kareiva, P., and U. Wennergren. 1995. Connecting landscape patterns to ecosystem and population processes. Nature 373:299–302.

Kumar, P., and E. Foufoula-Georgiou. 1993. A multicomponent decomposition of spatial rainfall fields. 1. Segregation of large- and small-scale features using wavelet transforms. Water Resources Research 29:2515–2532.

Landres, P. B., P. Morgan, and F. J. Swanson. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecological Applications 9:1179–1188.

Larsen, D. P., T. M. Kincaid, S. E. Jacobs, and N. S. Urquhart. 2001. Designs for evaluating local and regional scale trends. BioScience 51:1069–1078.

Leavitt, P. R., S. C. Fritz, N. J. Anderson, P. A. Baker, T. Blenckner, L. Bunting, J. Catalan, D. J. Conley, W. O. Hobbs, E. Jeppesen, A. Korhola, S. McGowan, K. Ruhland, J. A. Rusak, G. L. Simpson, N. Solovieva, and J. Werne. 2009. Paleolimnological evidence of the effects on lakes of energy and mass transfer from climate and humans. Limnology and Oceanography 54:2330–2348.

Legendre, P., M. De Caceres, and D. Borcard. 2010. Community surveys through space and time: Testing the space-time interaction in the absence of replication. Ecology 91:262–272.

Legendre, P., and O. Gauthier. 2014. Statistical methods for temporal and space−time analysis of community composition data. Proceedings of the Royal Society B 281:1–9.

Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. M. Chase, M. F. Hoopes, R. D. Holt, J. B. Shurin, R. Law, D. Tilman, M. Loreau, and A. Gonzalez. 2004. The metacommunity concept: A framework for multi-scale community ecology. Ecology Letters 7:601–613.

Leroux, S. J., and M. Loreau. 2011. Dynamics of reciprocal pulsed subsidies in local and meta-ecosystems. Ecosystems 15:48–59.

Levin, S. A. 1992. The problem of pattern and scale in ecology: The Robert H. MacArthur Award lecture. Ecology 73:1943–1967.

Lewis, W. M. 1978. Comparison of temporal and spatial variation in the zooplankton of a lake by means of variance components. Ecology 59:666–671.

Liebhold, A., W. D. Koenig, and O. N. Bjørnstad. 2004. Spatial synchrony in population dynamics. Annual Review of Ecology, Evolution and Systematics 35:467–490.

Limberger, R., and S. A. Wickham. 2012. Transitory versus persistent effects of connectivity in environmentally homogeneous metacommunities. PloS one 7:e44555.

Litzow, M. A., J. D. Urban, and B. J. Laurel. 2008. Spatial variance accompanies reorganization of two continental shelf ecosystems. Ecological Applications 18:1331–1337.

Long, J. N. 2009. Emulating natural disturbance regimes as a basis for forest management: A North American view. Forest Ecology and Management 257:1868–1873.

Loreau, M., N. Mouquet, and R. D. Holt. 2003. Meta-ecosystems: A theoretical framework for a spatial ecosystem ecology. Ecology Letters 6:673–679.

Lucifora, L., V. Garcia, and B. Worm. 2011. Global diversity hotspots and conservation priorities for sharks. PLoS one 6.

Magnuson, J. J., B. J. Benson, and T. K. Kratz. 1990. Temporal coherence in the limnology of a suite of lakes. Freshwater Biology 23:145–159.

Mann, M. E., R. S. Bradley, and M. K. Hughes. 1998. Global-scale temperature patterns and climate forcing over the past six centuries. Nature 392:779–788.

Manning, A. D., D. B. Lindenmayer, H. A. Nix, C. Resource, and T. Australian. 2004. Continua and Umwelt: novel perspectives on viewing landscapes. Oikos 104:621–628.

Marquet, P. A., M. Fortin, J. Pineda, D. O. Wallin, J. Clark, Y. Wu, S. Bollens, C. M. Jacobi, and R. D. Holt. 1993. Ecological and evolutionary consequences of patchiness: A marine-terrestrial perspective. Pages 277–304 *in* S. A. Levin, T. M. Powell, and J. W. Steele, editors. Patch Dynamics. Springer, Berlin.

Massol, F., D. Gravel, N. Mouquet, M. Cadotte, T. Fukami, and M. Leibold. 2011. Linking community and ecosystem dynamics through spatial ecology. Ecology Letters:1–11.

Matamala, R., J. D. Jastrow, R. M. Miller, and C. T. Garten. 2008. Temporal changes in C and N stocks of restored prairie: Implications for C sequestration strategies. Ecological Applications 18:1470–1488.

McCauley, D. J., P. A. Desalles, H. S. Young, R. B. Dunbar, R. Dirzo, M. M. Mills, and F. Micheli. 2012. From wing to wing: the persistence of long ecological interaction chains in less-disturbed ecosystems. Scientific Reports 2:1–5.

McIntire, E. J. B., and A. Fajardo. 2009. Beyond description: The active and effective way to infer processes from spatial patterns. Ecology 90:46–56.

Mitchell, M. G. E., E. M. Bennett, and A. Gonzalez. 2013. Linking landscape connectivity and ecosystem service provision: Current knowledge and research gaps. Ecosystems 16:894–908.

Morfin, M., J.-M. Fromentin, A. Jadaud, and N. Bez. 2012. Spatio-temporal patterns of key exploited marine species in the Northwestern Mediterranean Sea. PloS one 7:1–14.

Morrison, C. A., R. A. Robinson, J. A. Clark, and J. A. Gill. 2010. Spatial and temporal variation in population trends in a long-distance migratory bird. Diversity and Distributions 16:620–627.

Olff, H., R. G. M. de Goede, W. H. van det Putten, B. Hoorens, and M. Gleichman. 2000. Small-scale shifting mosaics of two dominant grassland species: The possible role of soil-borne pathogens. Oecologia 125:45–54.

O'Neill, R. 2001. Is it time to bury the ecosystem concept? Ecology 82:3275–3284.

Orland, M. C. 2003. Scale-dependent interactions between intrinsic and extrinsic processes reduce variability in protist populations. Ecology Letters 6:716–720.

Paine, A. D. M. 1985. "Ergodic" reasoning in geomorphology: Time for a review of the term? Progress in Physical Geography 9:1–15.

Paradis, E., R. Baillie, W. J. Sutherland, and R. D. Gregory. 1999. Dispersal and spatial scale affect synchrony in spatial population dynamics. Ecology Letters 2:114–120.

Perry, G. L. W. 2002. Landscapes, space and equilibrium: Shifting viewpoints. Progress in Physical Geography 26:339–359.

Peters, D. P. C., B. T. Bestelmeyer, and M. G. Turner. 2007. Cross-scale interactions and changing pattern-process relationships: Consequences for system dynamics. Ecosystems 10:790–796.

Pickett, S. T. A. 1989. Space-for-time substitution as an alternative to long-term studies. Pages 110–135 Long-term studies in ecology: Approaches and alternatives.

Plato, and B. Jowett. (n.d.). Cratylus. Champaigne III: Project Gutenberg.

Post, E., and M. C. Forchhammer. 2002. Synchronization of animal population dynamics by large-scale climate. Nature 420:168–71.

Prange, S., S. D. Gehrt, and E. P. Wiggers. 2004. Influences of anthropogenic resources on Raccoon (Procyon lotor) movements and spatial distribution. Journal of Mammalogy 85:483–490.

Pysek, P., and P. E. Hulme. 2005. Spatio-temporal dynamics of plant invasions: Linking pattern to process 1. Ecoscience 12:302–315.

Raffa, K. F., B. H. Aukema, B. J. Bentz, A. L. Carroll, J. A. Hicke, M. G. Turner, and W. H. Romme. 2008. Cross-scale drivers of natural disturbances prone to anthropogenic amplification: The dynamics of Bark Beetle eruptions. BioScience 58:501–517.

Ranta, E., and V. Kaitala. 1997. Travelling waves in vole population dynamics. Nature 390:1997.

Rietkerk, M., and J. van de Koppel. 2008. Regular pattern formation in real ecosystems. Trends in Ecology and Evolution 23:169–75.

Ringsby, T. H., B.-E. Saether, J. Tufto, H. Jensen, and E. J. Solberg. 2002. Asynchronous spatiotemporal demography of a House Sparrow metapopulation in a correlated environment. Ecology 83:561–569.

Roff, A. D. A. 1974. The analysis of a population model demonstrating the importance of dispersal in a heterogeneous environment. Oecologia 15:259–275.

Saether, B.-E., V. Grøtan, S. Engen, D. G. Noble, and R. P. Freckleton. 2011. Rarity, life history and scaling of the dynamics in time and space of British birds. The Journal of animal ecology 80:215–24.

Saether, B.-E., T. H. Ringsby, O. Bakke, and E. J. Solberg. 1999. Spatial and temporal variation in demography of a house sparrow metapopulation. Journal of Animal Ecology 68:628–637.

Salomon, Y., S. R. Connolly, and L. Bode. 2010. Effects of asymmetric dispersal on the coexistence of competing species. Ecology Letters:1–10.

Santora, J. A., and R. R. Veit. 2013. Spatio-temporal persistence of top predator hotspots near the Antarctic Peninsula. Marine Ecology Progress Series 487:287–304.

Seinfeld, J. H., and S. N. Pandis. 2006. Atmospheric chemistry and physics: From air pollution to climate change. Page 1232. Second edition. Wiley.

Sluyter, A. 1994. Intensive wetland agriculture in Mesoamerica: Space, time, and form. Annals of the Association of American Geographers 84:557–584.

Sole, R. V, and J. Bascompte. 1995. Measuring chaos from spatial information. Journal of Theoretical Biology 175:139–147.

Spatiotemporal. 2007. Spatiotemporal mechanisms of life. Nature Chemical Biology 3:593.

Staddon, P., Z. Lindo, P. D. Crittenden, F. Gilbert, and A. Gonzalez. 2010. Connectivity, non-random extinction and ecosystem function in experimental metacommunities. Ecology Letters:1–10.

Steele, J. H. 1989. The ocean "landscape". Landscape Ecology 3:185–192.

Steele, J. H., E. W. Henderson, M. Mangel, and C. Clark. 1994. Coupling between physical and biological scales [and discussion]. Philosophical Transactions of the Royal Society of London B 343:5–9.

Stommel, H. 1963. Varieties of oceanographic experience. Science 139:572–576.

Tansley, A. G. 1935. The use and abuse of vegetational concepts and terms. Ecology 16:284–307.

Tirado, R., and F. I. Pugnaire. 2003. Shrub spatial aggregation and consequences for reproductive success. Oecologia 136:296–301.

Tobin, P. C., and O. N. Bjørnstad. 2003. Spatial dynamics and cross-correlation in a transient predator–prey system. Journal of Animal Ecology 72:460–467.

Townsend, C. R., S. Doledec, and M. R. Scarsbrook. 1997. Species traits in relation to temporal and spatial heterogeneity in streams: A test of habitat templet. Freshwater Biology 37:367–387.

Turner, M. G., and F. S. Chapin III. 2005. Causes and consequences of spatial heterogeneity in ecosystem function. Pages 9–30 *in* G. M. Lovett, M. G. Turner, C. G. Jones, and K. C. Weathers, editors. Ecosystem function in heterogeneous landscapes. Springer.

Turner, M. G., R. H. Gardner, and R. V. O. Neill. 1995. Ecological dynamics at broad scales. Bioscience 45:S29–S35.

Uezu, A., J. P. Metzger, and J. M. E. Vielliard. 2005. Effects of structural and functional connectivity and patch size on the abundance of seven Atlantic Forest bird species. Biological Conservation 123:507–519.

Urban, D. L., R. V O'Neill, and H. H. Shugart. 1987. Landscape ecology: A hierarchical perspective can help scientists understand spatial patterns. BioScience 37:119–127.

Urquhart, N. S., S. G. Paulsen, and D. P. Larsen. 1998. Monitoring for policy-relevant regional trends over time. Ecological Applications 8:246–257.

Valett, H. M., F. R. Hauer, and J. a. Stanford. 2014. Landscape influences on ecosystem function: Local and routing control of oxygen dynamics in a floodplain aquifer. Ecosystems 17:195–211.

Vance, T. C., and R. E. Doel. 2010. Graphical methods and Cold War scientific practice: The Stommel Diagram's intriguing journey from the physical to the biological environmental sciences. Historical Studies in the Natural Sciences 40:1–47.

Vogt, R. J., J. A. Rusak, A. Patoine, and P. R. Leavitt. 2011. Differential effects of energy and mass influx on the landscape synchrony of lake ecosystems. Ecology 92:1104–1114.

Walker, B. H., S. R. Carpenter, J. Rockstrom, A. Crépin, and G. D. Peterson. 2012. Drivers, "slow" variables , "fast " variables, shocks, and resilience. Ecology and Society 17:30.

Walker, L. R., D. A. Wardle, R. D. Bardgett, and B. D. Clarkson. 2010. The use of chronosequences in studies of ecological succession and soil development. Journal of Ecology 98:725–736.

Wang, S., and M. Loreau. 2014. Ecosystem stability in space: α, β and γ variability. Ecology letters.

Watt, A. S. 1947. Pattern and process in the plant community. Journal of Ecology 35:1–22.

Wetzel, P. R., A. G. Van Der Valk, S. Newman, D. E. Gawlik, T. T. Gann, C. A. Coronado-molina, D. L. Childers, and F. H. Sklar. 2005. Maintaining tree islands in the Florida Everglades: Nutrient redistribution is the key. Frontiers in Ecology and the Environment 3:370–376.

White, E. P., S. K. M. Ernest, A. J. Kerkhoff, and B. J. Enquist. 2007. Relationships between body size and abundance in ecology. Trends in ecology & evolution 22:323–30.

Williams, C. K., A. R. Ives, and R. D. Applegate. 2003. Population dynamics across geographical ranges: Time-series analysis of three small game species. Ecology 84:2654–2667.

Williams, N. M., E. E. Crone, T. H. Roulston, R. L. Minckley, L. Packer, and S. G. Potts. 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. Biological Conservation 143:2280–2291.

Wilson, D. S. 1992. Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. Ecology 73:1984–2000.

Wu, J. 1999. Hierarchy and scaling: Extrapolating information along a scaling ladder. Canadian Journal of Remote Sensing 25:367–380.

Wu, J., and H. Li. 2006. Concepts of scale and scaling. Pages 3–15 *in* J. Wu, H. Li, and O. L. Loucks, editors. Scaling and Uncertainty Analysis in Ecology: Methods and Applications. Springer, Netherlands.

APPENDIX A. ANALYTICAL EXPRESSION OF TEMPORAL VARIANCE IN SPATIAL TERMS

X_{ik} denotes the value of an ecosystem variable at patch *i* and time *k.* Each patch *i* has a temporal variance var(X_i) from a time series of n_k time points. Each time point *k* has an associated spatial variance var(X_k) from a spatial series of n_i patches. Regional variance is the variance of the spatially-aggregated time series (i.e., Var(Y) where $Y_k = \sum_{i=1}^{n} X_{ik}$), and reflects variation at the aggregate (i.e., landscape) scale. Here we analytically express this variance in terms of spatial variance var(X_k).

Temporal variation can also be expressed as a portion of the data matrix's total variation (SS_{Tot}), using sums of squares (SS) in ANOVA definitional formulas (Sokal and Rohlf 1981):

$$\mathrm{SS_{Tot}} = \mathrm{SS_K} + \mathrm{SS_{within\ K}} \qquad \text{Eq. A.1}$$

where SS_K is the variation *between* time points *k* and *l*, and $SS_{within\ K}$ is the variation *within* time point *k* (i.e., of values across space).

Note that total variation of the data matrix can equivalently be partitioned with space as a factor instead of time. This casts SS_{Tot} in terms of variation *between* patches *i* and *j* (SS_I) and variation *within* patch *i* ($SS_{within\ I}$; i.e., variation of values over time):

$$\mathrm{SS_{Tot}} = \mathrm{SS_I} + \mathrm{SS_{within\ I}} \qquad \text{Eq. A.2}$$

Substituting SS_{Tot} in Eq. A.2 for the same in Eq. A.1, we equate components of spatial and temporal variation:

$$\mathrm{SS_K} + \mathrm{SS_{within\ K}} = \mathrm{SS_I} + \mathrm{SS_{within\ I}} \qquad \text{Eq. A.3}$$

SS terms can also be expressed as spatial and temporal variances. For instance, the variance analogue of variation between time points (SS_K) is regional temporal variance Var(Y). Meanwhile, the equivalent of variation between patches (SS_I) is an aggregate variance Var(Z), which is the variance of the temporally-aggregated series (i.e., $\mathrm{Z_i} = \sum_{\mathrm{k=1}}^{\mathrm{n}} \mathrm{X_{ik}}$). We converted all SS terms into temporal and spatial variances according the identities in Eqs. A.4-A.7. These identities were obtained by first converting SS to mean sums of squares, and then adjusting for computational differences arising from using sums (as for aggregate variances, Var(Y) and Var(Z)) as opposed to using means (as for SS).

$$\mathrm{SS_K} = \frac{\mathrm{n_k} - 1}{\mathrm{n_i}} \mathrm{Var(Y)} \qquad \text{Eq. A.4}$$

$$\mathrm{SS_I} = \frac{\mathrm{n_i} - 1}{\mathrm{n_k}} \mathrm{Var(Z)} \qquad \text{Eq. A.5}$$

$$\mathrm{SS}_{\mathrm{within\ K}} = (\mathrm{n_i} - 1)\sum_{\mathrm{k=1}}^{\mathrm{n}} \mathrm{var}(\mathrm{X_k}) \qquad \text{Eq. A.6}$$

$$\mathrm{SS}_{\mathrm{within\ I}} = (\mathrm{n_k} - 1)\sum_{\mathrm{i=1}}^{\mathrm{n}} \mathrm{var}(\mathrm{X_i}) \qquad \text{Eq. A.7}$$

Substituting the identities (Eq. A.4-A.7) into Eq. A.3 and rearranging, we obtain:

$$\frac{\mathrm{n_k} - 1}{\mathrm{n_i}} \mathrm{Var(Y)} = (\mathrm{n_k} - 1)\sum_{\mathrm{i=1}}^{\mathrm{n}} \mathrm{var}(\mathrm{X_i}) - (\mathrm{n_i} - 1)\sum_{\mathrm{k=1}}^{\mathrm{n}} \mathrm{var}(\mathrm{X_k}) + \frac{\mathrm{n_i} - 1}{\mathrm{n_k}} \mathrm{Var(Z)} \qquad \text{Eq. A.8}$$

We may simplify by decomposing the temporal and spatial aggregate variances, Var(Y) and Var(Z), into yet more components of variation. It has long been recognized that any aggregate variance is a sum of the variances of its components and their covariances (Feller 1950), as follows for the case of regional temporal variance, Var(Y):

$$\mathrm{Var(Y)} = \sum_{\mathrm{i=1}}^{\mathrm{n}} \mathrm{var}(\mathrm{X_i}) + 2\sum_{\mathrm{i=1}}^{\mathrm{n}}\sum_{\mathrm{j=1}}^{\mathrm{i-1}} \mathrm{cov}(\mathrm{X_i}, \mathrm{X_j}) \qquad \text{Eq. A.9}$$

where var(X_i) is the temporal variance of patch *i* and cov(X_i, X_j) is the covariance of patch *i* with patch *j*.

An analogous decomposition applies to aggregate spatial variance Var(Z):

$$\mathrm{Var(Z)} = \sum_{\mathrm{k=1}}^{\mathrm{n}} \mathrm{var}(\mathrm{X_k}) + 2\sum_{\mathrm{k=1}}^{\mathrm{n}}\sum_{\mathrm{l=1}}^{\mathrm{k-1}} \mathrm{cov}(\mathrm{X_k}, \mathrm{X_l}) \qquad \text{Eq. A.10}$$

where var(X_k) is the spatial variance observed at time *k*, and cov(X_k, X_l) is the covariance between spatial series at times *k* and *l*.

Substituting the definition of aggregate spatial variance from Eq. A.10 into Eq. A.8, we express Var(Y) in part as spatial variances and covariances. Then, we rearrange Eq. A.9 to isolate ∑var(X_i) - the summed temporal variances of patches - and substitute this into the result of the preceding step to yield:

$$\begin{aligned}\frac{\mathrm{n_k} - 1}{\mathrm{n_i}} \mathrm{Var(Y)} = {} & (\mathrm{n_k} - 1)\mathrm{Var(Y)} - (\mathrm{n_i} - 1)\sum \mathrm{var}(\mathrm{X_k}) + \left(\frac{\mathrm{n_i} - 1}{\mathrm{n_k}}\right)\sum \mathrm{var}(\mathrm{X_k}) - (2\mathrm{n_k} - 1)\sum \mathrm{cov}(\mathrm{X_i}, \mathrm{X_j}) \\ & + \left(\frac{2\mathrm{n_i} - 1}{\mathrm{n_k}}\right)\sum \mathrm{cov}(\mathrm{X_k}, \mathrm{X_l})\end{aligned} \qquad \text{Eq. A.11}$$

Rearranging and simplifying, we define aggregate temporal variance exactly in terms of spatial variances, covariances among patches, and covariances among time points:

$$\mathrm{Var}(\mathrm{Y}) = \frac{\mathrm{n_i}}{\mathrm{n_k}}\sum_{\mathrm{k}=1}^{\mathrm{n}} \mathrm{var}(\mathrm{X_k}) + \frac{2\mathrm{n_i}}{\mathrm{n_i} - 1}\sum_{\mathrm{i}=1}^{\mathrm{n}}\sum_{\mathrm{j}=1}^{\mathrm{i}-1} \mathrm{cov}(\mathrm{X_i}, \mathrm{X_j}) - \frac{2\mathrm{n_i}}{\mathrm{n_k^2} - \mathrm{n_k}}\sum_{\mathrm{k}=1}^{\mathrm{n}}\sum_{\mathrm{l}=1}^{\mathrm{k}-1} \mathrm{cov}(\mathrm{X_k}, \mathrm{X_l}) \qquad \text{Eq. A.12}$$

As in Eq. A.9, aggregate variance increases when patches covary in time ($\sum \mathrm{cov}(X_i, X_j)$). Here, however, two spatial terms replace the term corresponding to the temporal variances of patches ($\sum \mathrm{var}(X_i)$). These two terms depict the spatial signature left behind when local patches vary ($\mathrm{var}(X_k)$), and a stabilizing effect when spatial variation persists over time ($\sum \mathrm{cov}(X_k, X_l)$).

REFERENCES

Feller, W. 1950. An introduction to probability theory and its applications. Page 461. Wiley, New York.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. Page 859. Second edition. W. H. Freeman and Co., New York.

APPENDIX B. ANALYTICAL EXPRESSION OF REGIONAL TEMPORAL CV IN TERMS OF SPATIAL CV

Eq. A.12 may be re-expressed in dimensionless terms from which the effect of the mean is removed. Below we derive an exact expression that incorporates commonly-used Coefficients of Variation (CV) as well as φ indices of patch synchrony or persistence of spatial variation.

We first divide Eq. A.12 by the square of the mean of the regional temporal series, $\overline{X_Y}$ to get:

$$\frac{\mathrm{Var(Y)}}{(\overline{X_Y})^2} = \frac{\mathrm{SD_Y}}{\overline{X_Y}} \cdot \frac{\mathrm{SD_Y}}{\overline{X_Y}} = \mathrm{CV}^2$$
$$= \frac{n_i}{n_k}\frac{\sum \mathrm{var}(X_k)}{(\overline{X_Y})^2} + \frac{2n_i}{n_i - 1}\frac{\sum \mathrm{cov}(X_i, X_j)}{(\overline{X_Y})^2} - \frac{2n_i}{n_k^2 - n_k}\frac{\sum \mathrm{cov}(X_k, X_l)}{(\overline{X_Y})^2} \qquad \text{Eq. B.1}$$

where *n*n_i and n_k are numbers of patches and time points, respectively, and $\mathrm{SD_Y}$ is the regional standard deviation. We then substitute variance and covariance terms for dimensionless coefficients.

(1) Converting spatial variance term (∑var(X_k)) into spatial CV's

From Loreau and de Mazancourt (2008) it is known that maximum aggregate variance occurs when covariance among components is highest and is equivalent to the square of their summed standard deviations. The maximum variance of a temporally-aggregated series is thus:

$$\mathrm{Var(Z)_{max}} = \left(\sum_{k=1}^{n} \mathrm{SD}\,(X_k)\right)^2 \qquad \text{Eq. B.2}$$

where SD(X_k) is the spatial standard deviation at time *k*. Dividing by ∑SD(X_k) and expressing $\mathrm{Var(Z)_{max}}$ as summed spatial variances and covariances (Eq. A.10), we get:

$$\sum \mathrm{SD}\,(X_k) = \frac{\mathrm{Var(Z)_{max}}}{\sum \mathrm{SD}\,(X_k)} = \frac{\sum \mathrm{var}(X_k) + 2\sum \mathrm{cov}(X_k, X_l)_{\max}}{\sum \mathrm{SD}\,(X_k)} \qquad \text{Eq. B.3}$$

Rearranging for ∑var(X_k), we find:

$$\sum \mathrm{var}\,(X_k) = \left(\sum \mathrm{SD}\,(X_k)\right)^2 - 2\sum \mathrm{cov}(X_k, X_l)_{\max} \qquad \text{Eq. B.4}$$

Plugging this into the ∑var(X_k) term of Eq. B.1 yields:

$$\frac{\mathrm{n_i}}{\mathrm{n_k}}\frac{\sum \mathrm{var}(\mathrm{X_k})}{(\overline{\mathrm{X_Y}})^2} = \frac{\mathrm{n_i}}{\mathrm{n_k}}\left(\frac{\sum \mathrm{SD}\,(\mathrm{X_k})}{\overline{\mathrm{X_Y}}}\cdot\frac{\sum \mathrm{SD}\,(\mathrm{X_k})}{\overline{\mathrm{X_Y}}} - \frac{2\sum \mathrm{cov}(\mathrm{X_k},\mathrm{X_l})_{\mathrm{max}}}{(\overline{\mathrm{X_Y}})^2}\right) \qquad \text{Eq. B.5}$$

Re-writing the temporal mean $\overline{\mathrm{X_Y}}$ as the sum of spatial means at time *k*, $\sum \overline{\mathrm{X_k}}$, we get:

$$\frac{\mathrm{n_i}}{\mathrm{n_k}}\frac{\sum \mathrm{var}(\mathrm{X_k})}{(\overline{\mathrm{X_Y}})^2} = \frac{\mathrm{n_i}}{\mathrm{n_k}}\left(\frac{\sum \mathrm{SD}\,(\mathrm{X_k})}{\frac{\mathrm{n_i}}{\mathrm{n_k}}\sum \overline{\mathrm{X_k}}}\cdot\frac{\sum \mathrm{SD}\,(\mathrm{X_k})}{\frac{\mathrm{n_i}}{\mathrm{n_k}}\sum \overline{\mathrm{X_k}}} - \frac{2\sum \mathrm{cov}(\mathrm{X_k},\mathrm{X_l})_{\mathrm{max}}}{(\overline{\mathrm{X_Y}})^2}\right) \qquad \text{Eq. B.6}$$

The first term within brackets divides summed spatial standard deviations by summed spatial means. Thibaut and Connolly (2013) point out that this quantity is equivalent to a weighted-mean CV, $\widetilde{\mathrm{CV}}_k$, where each spatial CV at time *k* is weighted by its relative mean:

$$\widetilde{\mathrm{CV}}_{\mathrm{k}} = \sum_{k=1}^{n}\frac{\overline{\mathrm{X}}_{\mathrm{k}}}{\sum_{\mathrm{l}}\overline{\mathrm{X}}_{\mathrm{l}}}\mathrm{CV_k} \qquad \text{Eq. B.7}$$

Therefore:

$$\frac{\mathrm{n_i}}{\mathrm{n_k}}\frac{\sum \mathrm{var}(\mathrm{X_k})}{(\overline{\mathrm{X_Y}})^2} = \frac{\mathrm{n_k}}{\mathrm{n_i}}\widetilde{\mathrm{CV}}_{\mathrm{k}}^2 - \frac{\mathrm{n_i}}{\mathrm{n_k}}\cdot\frac{2\sum \mathrm{cov}(\mathrm{X_k},\mathrm{X_l})_{\mathrm{max}}}{(\overline{\mathrm{X_Y}})^2} \qquad \text{Eq. B.8}$$

(2) Converting inter-patch synchrony term (∑cov($X_{i,}$ X_j)) into φ_T index

The φ_T index is a dimensionless statistic of synchrony between patches *i* and *j*. It works by comparing observed aggregate-level variance to the theoretical maximum when patches are perfectly synchronized and is defined as:

$$\varphi_{\mathrm{T}} = \frac{\mathrm{Var(Y)}}{\left(\sum \mathrm{SD}\,(\mathrm{X_i})\right)^2} = \frac{\mathrm{Var(Y)}}{\mathrm{Var(Y)_{max}}} = \frac{\sum \mathrm{var}(\mathrm{X_i}) + 2\sum \mathrm{cov}\left(\mathrm{X_i},\mathrm{X_j}\right)}{\sum \mathrm{var}(\mathrm{X_i}) + 2\sum \mathrm{cov}\left(\mathrm{X_i},\mathrm{X_j}\right)_{\mathrm{max}}} \qquad \text{Eq. B.9}$$

where SD(X_i) is the temporal standard deviation of patch *i*. We can rearrange this expression to isolate ∑cov($X_{i,}$ Xj) and simplify to:

$$\sum \mathrm{cov}\left(\mathrm{X_i},\mathrm{X_j}\right) = \frac{1}{2}\left(\varphi_{\mathrm{T}}\left(\sum \mathrm{var}(\mathrm{X_i}) + 2\sum \mathrm{cov}\left(\mathrm{X_i},\mathrm{X_j}\right)_{\mathrm{max}}\right) - \sum \mathrm{var}(\mathrm{X_i})\right) \qquad \text{Eq. B.10}$$

Substituting this for the covariances in the second term of Equation B.1 and simplifying, we link our variance-based formula to φ_T:

$$\frac{2\mathrm{n_i}}{\mathrm{n_i}-1}\cdot\frac{\sum \mathrm{cov}(\mathrm{X_i},\mathrm{X_j})}{(\overline{\mathrm{X_Y}})^2}=\frac{\mathrm{n_i}}{\mathrm{n_i}-1}\cdot\frac{\varphi_\mathrm{T}\mathrm{Var(Y)_{max}}-\sum \mathrm{var}(\mathrm{X_i})}{(\overline{\mathrm{X_Y}})^2} \qquad \text{Eq. B.11}$$

(3) Converting persistence term (∑cov($X_{k,}$ X_l)) into φ_S index

To eliminate the extra covariance term from Eq. B.8, we combine it with the third term of Eq. B.1 to yield:

$$\frac{2\mathrm{n_i}}{\mathrm{n_k^2}-\mathrm{n_k}}\cdot\frac{\left((\mathrm{n_k}-1)\sum \mathrm{cov}(\mathrm{X_k},\mathrm{X_l})_{\mathrm{max}}+\sum \mathrm{cov}(\mathrm{X_k},\mathrm{X_l})\right)}{(\overline{\mathrm{X_Y}})^2} \qquad \text{Eq. B.12}$$

To introduce φ_S into the equation, we define it in terms of covariance of time point *k* with *l* (persistence). φ_S is the exact analogue of φ_T, and so contrasts the variance of the temporally-aggregated series *Z* with the maximum possible aggregate variance when covariances of spatial series are highest:

$$\varphi_\mathrm{S}=\frac{\mathrm{Var(Z)}}{\left(\sum \mathrm{SD}\ (\mathrm{X_k})\right)^2}=\frac{\mathrm{Var(Z)}}{\mathrm{Var(Z)_{max}}}=\frac{\sum \mathrm{var}(\mathrm{X_k})+2\sum \mathrm{cov}(\mathrm{X_k},\mathrm{X_l})}{\sum \mathrm{var}(\mathrm{X_k})+2\sum \mathrm{cov}(\mathrm{X_k},\mathrm{X_l})_{\mathrm{max}}} \qquad \text{Eq. B.13}$$

Rearranging for ∑cov($X_{k,}$ X_l), we find:

$$\sum \mathrm{cov}(\mathrm{X_k},\mathrm{X_l})=\frac{1}{2}\left(\varphi_\mathrm{S}\left(\sum \mathrm{var}(\mathrm{X_k})+2\sum \mathrm{cov}(\mathrm{X_k},\mathrm{X_l})_{\mathrm{max}}\right)-\sum \mathrm{var}(\mathrm{X_k})\right) \qquad \text{Eq. B.14}$$

Substituting this for ∑cov($X_{k,}$ X_l) in Eq. B.12 and simplifying, we link φ_S to our final term from Eq. B.1:

$$\frac{2\mathrm{n_i}}{\mathrm{n_k^2}-\mathrm{n_k}}\frac{\sum \mathrm{cov}(\mathrm{X_i},\mathrm{X_j})}{(\overline{\mathrm{X_Y}})^2}= \qquad \text{Eq. B.15}$$
$$\frac{\mathrm{n_i}}{\mathrm{n_k^2}-\mathrm{n_k}}\cdot\frac{\varphi_\mathrm{S}\mathrm{Var(Z)_{max}}-\sum \mathrm{var}(\mathrm{X_k})+2\left((\mathrm{n_k}-1)\sum \mathrm{cov}(\mathrm{X_k},\mathrm{X_l})_{\mathrm{max}}\right)}{(\overline{\mathrm{X_Y}})^2}$$

Writing out all converted terms from Eq. B.1 and taking the square root, we find the dimensionless relationship between CV_Y, spatial CV and the modifying effects of synchrony and persistence:

$$\mathrm{CV_Y}=\left(\frac{\mathrm{n_k}}{\mathrm{n_i}}\widetilde{\mathrm{CV}}_\mathrm{k}^2+\frac{\mathrm{n_i}}{\mathrm{n_i}-1}\cdot\frac{\varphi_\mathrm{T}\mathrm{Var(Y)_{max}}-\sum \mathrm{var}(\mathrm{X_i})}{(\overline{\mathrm{X_Y}})^2}-\frac{\mathrm{n_i}}{\mathrm{n_k^2}-\mathrm{n_k}}\right. \qquad \text{Eq. B.16}$$
$$\left.\cdot\frac{\varphi_\mathrm{S}\mathrm{Var(Z)_{max}}-\sum \mathrm{var}(\mathrm{X_k})+2\left((\mathrm{n_k}-1)\sum \mathrm{cov}(\mathrm{X_k},\mathrm{X_l})_{\mathrm{max}}\right)}{(\overline{\mathrm{X_Y}})^2}\right)^{1/2}$$

While φ_T and φ_S do not contribute in a simple way to CV_Y, these indices of synchrony and persistence have the same effect on temporal variability as expected from Eq. B.1: All else equal, an increase in φ_T increases CV_Y, while increasing φ_S decreases CV_Y.

REFERENCES

Loreau, M., and C. de Mazancourt. 2008. Species synchrony and its drivers: Neutral and nonneutral community dynamics in fluctuating environments. The American Naturalist 172:E48–E66.

Thibaut, L. M., and S. R. Connolly. 2013. Understanding diversity-stability relationships: Towards a unified model of portfolio effects. Ecology Letters 16:140–50.

APPENDIX C. ANALYTICAL APPROXIMATION OF REGIONAL TEMPORAL CV VALUE FOR "INDEPENDENT DYNAMICS"

Eq. B.16 presents regional (aggregate) temporal CV in terms of a weighted-mean spatial CV and indices of synchrony (φ_T) and persistence (φ_S). But when φ_T and φ_S are zero, their terms do not drop out fully, making it difficult to derive a null expectation. Furthermore, φ_T and φ_S values of zero actually reflect negative covariance among patches and among time points, respectively. In contrast, we are interested in the case of independent dynamics, where inter-patch and inter-time covariances are zero. We therefore derive a simpler approximation of regional temporal CV values that applies to zero covariances, and will be more useful for generating expected CV's.

From (Tilman et al. 1998), we note that when patches are uncorrelated in time, regional temporal CV is proportional to the mean temporal CV of patch *i* as a function of patch number n_i:

$$\mathrm{CV_Y} = \frac{1}{\sqrt{\mathrm{n_i}}}\overline{\mathrm{CV_i}} \qquad \text{Eq. C.1}$$

When values are uncorrelated among time points (i.e., low persistence) as well as among patches, ergodicity applies. This means that, on average, the temporal CV of patch *i* will be roughly equivalent to the spatial CV at time *k*:

$$\overline{\mathrm{CV_i}} \cong \overline{\mathrm{CV_k}} \qquad \text{Eq. C.2}$$

Substituting Eq. C.2 into C.1, we find it possible to estimate regional CV values ($\mathrm{CV_Y}$) from spatial CV's ($\mathrm{CV_k}$) when dynamics are independent in time and space:

$$\mathrm{CV_Y} \cong \frac{1}{\sqrt{\mathrm{n_i}}}\overline{\mathrm{CV_k}} \qquad \text{Eq. C.3}$$

The $\mathrm{CV_Y}$ approximation compared well with values drawn from random datasets designed to simulate independent dynamics (see Appendix D). Values from the two methods were 94 and 98% correlated when using arithmetic and logged values, respectively. Regressions had slopes near one and y-intercepts near zero.

REFERENCES

Tilman, D., C. L. Lehman, and C. E. Bristow. 1998. Diversity-stability relationships: Statistical inevitability or ecological consequence? The American Naturalist 151:277–282.

APPENDIX D. ROBUSTNESS AND BEHAVIOR OF THE SPATIAL-TEMPORAL VARIABILITY RELATIONSHIP IN A NULL MODEL

We verified the observed relationship between spatial and temporal variability, and explored the conditions of its emergence, using a stochastic null model. Random numbers, corresponding to the range of microcosm experiment values, were drawn from a uniform distribution in Excel 14.0 (Microsoft Corporation 2010) and were assigned to arrays of three patches over 20 time steps. Spatial CV and regional temporal CV were estimated in replicate arrays of patches for 20 null "variables" representing processes with the same statistical properties. These variables were allowed to randomly vary within the same bounds (i.e., 0.001-28.000).

No regressions of mean spatial CV and temporal CV were significant (Fig. 2.3B; $r^2 = 0.06$, $p = 0.28$, $n = 20$), demonstrating that intrinsic properties of variables, and not statistical happenstance, generate empirical patterns. This result also suggests that relationships will be undetectable in real variables when they share similar variation around the mean in space and/or in time. Cases of similar variability that might obscure relationships include; measurement error, measurements of the same variable in replicate systems, species that vary over similar spatiotemporal scales (see scatter around biotic variables in Fig. 2.4B) or any other variables with similar rates of spatial and temporal change (e.g., chlorophyll a, phytoplankton biomass and primary productivity; Rocha et al. 2011). In contrast, significant regressions emerged when some variables differed meaningfully from others in their spatial and temporal CV's. Variability of a variable was manipulated by constraining patch values to a randomly chosen range, and assigning a different range (i.e., level of constraint) to each variable. The result was variables which span a range of spatial and temporal CV's to form a (positive) near-unity relationship on a log-log plot (Fig. 2.3C-D).

Our null model also illustrated how the positions of points on a spatial-temporal CV plot change with the degree of synchrony or persistence experienced by a variable. Moreover, these responses agreed entirely with expectations from Fig. 2.1 and Eqs. A.12 and B.16. For a single variable (point), increasing synchrony among patches caused data points to migrate above the regression line, while increasing persistence moved the point below the line. This pattern held for the collective of variables too: When synchrony was induced among patches systematically for all variables, the regression slope remained the same, but all points shifted upwards on the plot, increasing the y-intercept (Fig. 2.3C). Enhancing persistence, in contrast, displaced all data points downwards, decreasing the y-intercept (Fig. 2.3C). When a variable's spatiotemporal pattern was a function of its variability, slopes deviated from 1 as shown by Fig. 2.3D.

Extreme behaviors occur in spatial-temporal CV plots when (i) patches have identical means and are perfectly synchronized or (ii) patches have different means and show perfect persistence. In these cases, data points of the slope approach: (i) a vertical line for perfect synchrony because temporal variability exists but spatial variability is zero for all variables, and (ii) a horizontal line for perfect persistence because spatial variability exists but temporal variability is zero in all variables. It is important to note, however, that natural systems do not experience these extremes of order.

REFERENCES

Rocha, M. R., D. A. Vasseur, M. Hayn, M. Holschneider, and U. Gaedke. 2011. Variability patterns differ between standing stock and process rates. Oikos 120:17–25.

APPENDIX E. SUPPLEMENTARY MATERIALS AND METHODS

Variables in the aquatic microcosm experiment were measured using the protocols listed in Table E.1. Table E.2 lists variables from the three datasets included in analyses.

Table E.1. Community and ecosystem variables measured over the 20-week microcosm connectivity experiment

Variable	Measurement / method
Total ecosystem respiration	Rate of dissolved oxygen loss in a 'dark' bottle of microcosm water. A homogeneous sample of the community within a microcosm was incubated *in situ* in a sealed, lightproof, 25 mL glass vial for three hours, always at the same time of day (Wetzel and Likens 1991). Precision: ±3%
Net primary productivity	Rate of dissolved oxygen gain in a 25 mL 'light' bottle of microcosm water. The remaining procedures followed those applied to 'dark' bottles (Wetzel and Likens 1991). Precision: ±3%
Gross primary productivity	Combined absolute magnitudes of the above two measurements (Wetzel and Likens 1991). Precision: ±6%
Phytoplankton (>1um) density	Spectral absorption of chlorophyll-a on a BioTek Synergy 2 microplate reader (Winooski, Vermont, USA). A 12 mL sample of homogenized microcosm water was concentrated on a 1.1 µm glass micro-fiber filter, boiled in 2.5 mL of 95% ethanol for 20 minutes and extracted for 24 hours (Ritchie 2006, Warren 2008). Precision: ±3%
Picoplankton / particulate (<1um) density	Spectral absorption at 550 nm of 2 mL of microcosm water after being passed through a 1.1 µm glass micro-fiber filter. Precision: ±22%
Dissolved oxygen	Microcosm dissolved oxygen concentration, as measured by an ExStik® DO600 probe (Waltham, Massachusetts, USA). Precision: ±0.4%
Temperature	Microcosm water temperature. Precision: ±0.3%

Table E.2. Variables from lake, rock pool and microcosm data sets used in analyses. An additional 36 rock pool species (not shown), known from fewer occurrences, were included for calculating spatiotemporal signatures (Fig. 2.6).

Lakes LTER		**Rock pools**	**Microcosms**
Magnesium	*Chaoborus* larvae	Temperature	NPP
Sodium	*Chaoborus* pupae	Salinity	GPP
Sulfate	Leptodora	Dissolved oxygen	Ecosystem respiration
Calcium	Mysis	pH	Chlorophyll-a
Chloride	Rainbow smelt	Oxygen saturation	Picoplankton/particulate
Potassium	Black bullhead	Chlorophyll a	Dissolved oxygen
Iron	Blackchin shiner	Total invert. abundance	Temperature
Manganese	Black crappie	*Culex* sp.	
Specific conductance	Blacknose shiner	*Paracyclops* sp.	
pH	Bluegill	*Orthocyclops* sp.	
Alkalinity	Bluntnosed minnow	*Gyratrix hermaphroditus*	
Dissolved inorganic carbon	Burbot	*Sesarma miersi* larvae	
Total inorganic carbon	Common shiner	Ceratopogonid sp.	
Dissolved organic carbon	Fathead	*Candona* sp.	
Total organic carbon	Golden shiner	Oligochaeta sp.	
Nitrate	Iowa darter	*Cyrpicercus* sp.	
Ammonia	Johnny darter	*Cytheromorpha* sp.	
Total nitrogen (filtered)	Largemouth bass	*Cyrprinotus heterocypris*	
Total nitrogen (unfiltered)	Log perch	*Nitocra* sp.	
Total phosphorus (filtered)	Mimic shiner	*Alona davidii*	
Total phosphorus (unfiltered)	Mottled sculpin	Nematoda sp.	
	Mud minnow	*Cerodaphnia regaudi*	
Dissolved reactive silica	Pumpkinseed	*Potamocyrpis* sp.	
Bicarbonate reactive silica	Smallmouth bass	*Orthocyclops modestus*	
Total organic matter	Walleye	*Cypridopsis mariae*	
Temperature	White sucker	*Nitocra spinipes*	
Dissolved oxygen	Yellow bullhead	*Leydigia leydigi*	
O_2 saturation	Yellow perch	*Metis* sp.	
Surface light	Northern pike	*Cyprideis* sp.	
Light at depth	Rockbass	Chronomid sp.	
Light attenuation		*Cytheromorpha* sp.	
		Dorvelleidae sp. 1	
		Dorvelleidae sp. 2	

REFERENCES

Ritchie, R. J. 2006. Consistent sets of spectrophotometric chlorophyll equations for acetone, methanol and ethanol solvents. Photosynthesis Research 89:27–41.

Warren, C. R. 2008. Rapid measurement of chlorophylls with a microplate reader. Journal of Plant Nutrition 31:1321–1332.

Wetzel, R. G., and G. E. Likens. 1991. Limnological analyses. Page 391. Second edition. Springer-Verlag, New York.

APPENDIX F. ALTERNATIVE ESTIMATORS OF VARIABILITY

Choices exist for indices to estimate the three components of temporal variability (Eqs. A.12, B.16). The Coefficient of Variation (CV) is a common estimator of variability in space and time. However, the CV does not always remove the effect of the mean, and may produce biased estimates of variability (Gaston and Mcardle 1994, Cottingham et al. 2001). We guarded against this possibility by reanalyzing data with a range of alternative variability indices (Table F.1). Trends were detectable using all indices, and proved insignificant in only two cases. One case used the standard deviation of the logarithms, SD[Log(x)](Lewontin 1966), and one the Population Variability (Heath 2006) index. Insignificant results, representing four percent of tests, were likely due to the low statistical power of those particular analyses. In all cases, however, semi-partial correlations between temporal variability and spatial variability, synchrony or persistence were of the same sign predicted by our analytical relationship. Results from a CV-based null model (Fig. 2.3) were also reproducible using alternative indices, further suggesting robustness of the relationship.

Fewer scale-free indices estimate synchrony or persistence. We estimated these using spatial and temporal variance ratios of the form φ_x (Loreau and de Mazancourt 2008) because their common alternative, the mean pairwise (Pearson) correlation among patch time series or spatial series (Liebhold et al. 2004), cannot accommodate rows or columns of only zeroes. This shortcoming comes about because correlation between a row/column of zeroes and another row/column is undefined. If undefined correlations are excluded, the metric is calculated from fewer *n*. This, in turn, introduces a bias towards lower synchrony estimates (Loreau and de Mazancourt 2008). Nonetheless, using the correlation-based indices yielded qualitatively similar - but not identical - results in almost all analyses.

Table F.1. Comparing CV-based results with alternative indices of variability. General Linear Models were fit between indices of aggregate temporal variability and three spatiotemporal descriptors: Spatial variability, inter-patch synchrony and persistence (see Fig. 2.1). Indices of variability included CV and four others. Asterisks denote statistical significance and p-value. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. R^2 values in parentheses.

Index	**Description**	**Significant relationship between temporal variability and:**		
		Mean spatial variability?	Spatial variability + synchrony?	Spatial variability + synchrony + persistence?
Coefficient of Variation (CV)	Standard measure of relative variation. Unaffected by zeroes. May be biased by mean.	*Microcosms****(0.93) *Rock pools**** (0.77) *Lakes****(0.73)	*Microcosms****(0.98) *Rock pools**** (0.86) *Lakes****(0.80)	*Microcosms**** (1.00) *Rock pools**** (0.94) *Lakes****(0.87)
SD [log(x)] (Lewontin 1966)	Variation of log-transformed values. Problematic for data with zeroes; not applied to most species data.	*Microcosms*** (0.81) *Rock pools*** (0.91) *Lakes*** (0.22)	*Microcosms** (0.83) *Rock pools** (0.92) *Lakes** (0.25)	*Microcosms*$^{n.s.}$ (0.85) *Rock pools** (0.99) *Lakes***(0.45)
Bray-Curtis similarity	Measures similarity of values in time or space series as ratio of value sums and differences. Robust to zeroes.	*Microcosms***(0.90) *Rock pools**** (0.58) *Lakes**** (0.76)	*Microcosms***(0.94) *Rock pools****(0.70) *Lakes****(0.77)	*Microcosms**(0.94) *Rock pools****(0.74) *Lakes****(0.84)
Population Variability (Heath 2006)	Average percent difference among values. Species and abiotic variables analyzed separately.	*Microcosms****(0.96) *Rock pools***(0.35, 0.73) *Lakes***(0.07, 0.36)	*Microcosms****(0.98) *Rock pools***(0.44, 0.91) *Lakes***(0.22, 0.37)	*Microcosms***(0.98) *Rock pools***(0.50, 0.98) *Lakes****(0.61, 0.41)
Downing's B (Downing 1991)	Empirically-derived CV variant to remove effect of mean. Applied to invertebrate data only.	*Rock pools****(0.49)	*Rock pools****(0.57)	*Rock pools****(0.76)

REFERENCES

Cottingham, K. L., B. L. Brown, and J. T. Lennon. 2001. Biodiversity may regulate the temporal variability of ecological systems. Ecology Letters 4:72–85.

Downing, J. A. 1991. Biological heterogeneity in aquatic ecosystems. Page 332 *in* J. Kolasa and S. T. A. Pickett, editors. Ecological Heterogeneity. Springer-Verlag, New York.

Gaston, K. J., and B. H. Mcardle. 1994. The temporal variability of animal abundances: Measures, methods and patterns. Philosophical Transactions of the Royal Society of London B 345:335–358.

Heath, J. P. 2006. Quantifying temporal variability in population abundances. Oikos 115:573–581.

Liebhold, A., W. D. Koenig, and O. N. Bjørnstad. 2004. Spatial synchrony in population dynamics. Annual Review of Ecology, Evolution and Systematics 35:467–490.

Loreau, M., and C. de Mazancourt. 2008. Species synchrony and its drivers: Neutral and nonneutral community dynamics in fluctuating environments. The American Naturalist 172:E48–E66.

Lewontin, R. C. 1966. On the measurement of relative variability. Systematic Zoology 15:141–142.

APPENDIX G. SPATIAL IMPRINTING OF TEMPORAL PROCESSES

A space-time correspondence has long been recognized by ecologists, for instance in the tandem increase in a process's spatial scale with its temporal scale (Holling 1992, Steele et al. 1994). We presented and tested an exact formulation of an underlying relationship between spatial and temporal variation. Below, we sketch the conceptual links between these dimensions of variation. As a starting point, regional variation over time of a population or a process, in a landscape of local patches (*i*…*n*), can be thought of as the sum of patch temporal variances and covariances among patches (Eq. A.9). Regional variation thus arises from two temporal sources; localized, patch-scale changes over time ($\sum \mathrm{var}(X_i)$) and fluctuations that are shared among those patches ($\sum \mathrm{cov}(X_i, X_j)$). Figs. 2.1 and 2.2 in the main text sketch how the variation and covariation of patches can be seen through a spatial lens; as a series of spatial snapshots, each with a distinct landscape pattern.

A spatial snapshot reflects both the variation of individual patches and covariation among them. When this covariation is minimal, the snapshot of spatial variation can be attributed solely to the temporal variation of individual patches. Spatial variation thus scales with, and becomes an index for, the typical magnitude of temporal variation (Fig. 2.2).

Many ecological mechanisms alter the temporal variation of local patches ($\sum \mathrm{var}(X_i)$), and so should affect spatial variation also. Stabilizing mechanisms (Table G.1) may be common in nature, but little consideration has been given to their influence on spatial variation. For instance, dispersal or forcing from extrinsic sources can stabilize dynamics within patches by dampening amplitudes of fluctuations. In doing so, stabilizing mechanisms should reduce the likelihood that any patch has a larger population than another and thus dampen spatial variability. It must be noted, however, that differences among patches will not be entirely erased if patches stabilize to different population sizes (e.g., have different equilibria) and stable patches may still create high spatial variation. We term this situation *persistence of spatial variation* (also known as *fixed spatial variation* (Lewis 1978)) and point out that when it occurs, spatial and temporal variation share a different relationship. Thus, the meaning of a spatial snapshot changes depending on how much persistence is displayed by a variable.

Table G.1. Mechanisms that may dampen regional variability and reduce spatial variability by stabilizing local patches

Type	Mechanism	Examples
Spatial exchange	Movement to or from patch that changes local regulation of dynamics and reduces size (amplitude) of fluctuations	Source-sink dynamics or "Rescue effects" that enhance population viability or limit overcompensation (Gonzalez et al. 1998, Amarasekare 2004, Lecomte et al. 2004, Abbott 2011)
Spatial exchange	Effluxes to or influxes from outside system equilibrate across landscape and compensate for any local decreases or increases	Diffusive environmental fluxes (Kling et al. 2000, Leavitt et al. 2009); mobile, wide-ranging organisms (With et al. 2006)
Exogenous forcing	Forcing by an exogenous variable over a large extent constrains rates of increase and variability of all patches	Demographic regulation by mobile predators (Coulson et al. 2004) or by environmental forcing (Vasseur and Fox 2007)

Because a spatial snapshot also captures inter-patch synchrony, the flows of individuals, energy or particles among patches and shared exposure to environmental factors like weather (Paradis et al. 1999) take on considerable importance. By redistributing energy and matter, these phenomena impose simultaneous changes to spatial and temporal patterns. For instance, it is well-known that dispersal or environmental forcing can synchronize patches (increase $\sum \text{cov}(X_i, X_j)$) which is destabilizing at the regional scale (Earn et al. 2000; see also Fig. 2.5). But this also minimizes spatial differences, lowering the variability of patch densities across the landscape by making fluctuations coincide. Therefore, synchrony - like persistence - modifies the interpretation of what a spatial snapshot means for the temporal variation of a process.

REFERENCES

Abbott, K. 2011. A dispersal-induced paradox: Synchrony and stability in stochastic metapopulations. Ecology Letters 14:1158–1169.

Amarasekare, P. 2004. The role of density-dependent dispersal in source-sink dynamics. Journal of Theoretical Biology 226:159–168.

Coulson, T., F. Guiness, J. Pemberton, and T. Clutton-Brock. 2004. The demographic consequences of releasing a population of Red Deer from culling. Ecology 85:411–422.

Earn, D. J. D., S. A. Levin, and P. Rohani. 2000. Coherence and conservation. Science 290:1360–1364.

Gonzalez, A., J. H. Lawton, F. S. Gilbert, T. M. Blackburn, and I. Evans-Freke. 1998. Metapopulation dynamics, abundance, and distribution in a microecosystem. Science 281:2045–2047.

Holling, C. S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. Ecological Monographs 62:447–502.

Kling, G. W., G. W. Kipphut, M. M. Miller, and W. J. O'Brien. 2000. Integration of lakes and streams in a landscape perspective: The importance of material processing on spatial patterns and temporal coherence. Freshwater Biology 43:477–497.

Leavitt, P. R., S. C. Fritz, N. J. Anderson, P. A. Baker, T. Blenckner, L. Bunting, J. Catalan, D. J. Conley, W. O. Hobbs, E. Jeppesen, A. Korhola, S. McGowan, K. Ruhland, J. A. Rusak, G. L. Simpson, N. Solovieva, and J. Werne. 2009. Paleolimnological evidence of the effects on lakes of energy and mass transfer from climate and humans. Limnology and Oceanography 54:2330–2348.

Lecomte, J., K. Boudjemadi, F. Sarrazin, K. Cally, and J. Clobert. 2004. Connectivity and homogenisation of population sizes: An experimental approach in Lacerta vivipara. Journal of Animal Ecology 73:179–189.

Lewis, W. M. 1978. Comparison of temporal and spatial variation in the zooplankton of a lake by means of variance components. Ecology 59:666–671.

Paradis, E., R. Baillie, W. J. Sutherland, and R. D. Gregory. 1999. Dispersal and spatial scale affect synchrony in spatial population dynamics. Ecology Letters 2:114–120.

Steele, J. H., E. W. Henderson, M. Mangel, and C. Clark. 1994. Coupling between physical and biological scales [and discussion]. Philosophical Transactions of the Royal Society of London B 343:5–9.

Vasseur, D. A., and J. W. Fox. 2007. Environmental fluctuations can stabilize food web dynamics by increasing synchrony. Ecology Letters 10:1066–1074.

With, K. A., G. R. Schrott, and A. W. King. 2006. The implications of metalandscape connectivity for population viability in migratory songbirds. Landscape Ecology 21:157–167.

APPENDIX H. NULL EXPECTATIONS OF SPATIOTEMPORAL CHANGE DUE TO CONNECTION

Figs. H.1 and H.2 illustrate the expected shifts in spatiotemporal pattern due to connection under the null conditions described below. These pattern shifts are the result of the closely-related processes of homogenization and synchronization, which we illustrate below and describe the necessary conditions of movement. The simplifying assumptions made are that movement of particles (e.g., organisms, molecules):

- Is bidirectional in a hypothetical, two-patch system
- Is diffusion-like i.e., from higher to lower concentration
- Redistributes particles that have no explicit growth responses to conditions in patches (e.g., density, environment)

Homogenization of site means

Homogenization is the reduction of unevenness among sites (Fig. H.1). In this scenario, movement causes the means of the two patches to equalize over a period of time. In terms of spatiotemporal pattern, this represents a transition from persistent spatial variation (Fig. H.1, left) to asynchronous fluctuations in patches with similar means (Fig. H.1, right). This transition is one of many possible changes in spatiotemporal pattern and corresponds to arrow C in Fig. 3.1.

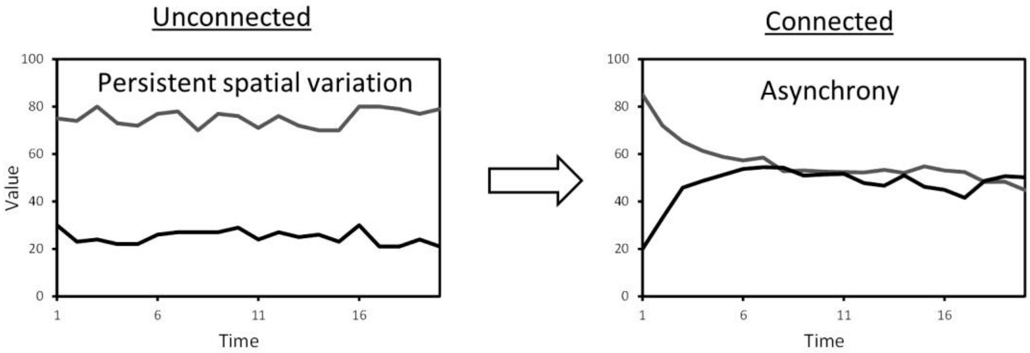


Figure H.1. Homogenization as a null expectation of structural connection. Increased movement due to connection can be homogenizing by reducing unevenness among site means, thus transforming a pattern of persistent spatial variation into asynchrony among patches.

The most direct route to homogenization requires the movement of particles from the patch of higher mean to that of lower mean. How much particle movement from patch *i* to *j*, written as $X_{i \rightarrow j}$, is needed to equalize the patch means $\bar{X}_i$and $\bar{X}_j$? To answer this question, we solve the following for $\bar{X}_{i \rightarrow j}$:

$$\mathrm{\bar{X}_i - X_{i \rightarrow j} = \bar{X}_j + X_{i \rightarrow j}} \qquad \text{Eq. H.1}$$

which yields the following total amount of movement required over *n* time steps to converge patch means on their midpoint:

$$\mathrm{X_{i \rightarrow j} = \frac{\bar{X}_i - \bar{X}_j}{2}} \qquad \text{Eq. H.2}$$

Whereas the movement required *per time step* for homogenization is given by:

$$\mathrm{X_{i \rightarrow j} = \frac{\bar{X}_i - \bar{X}_j}{2n}} \qquad \text{Eq. H.3}$$

Note from Eq. H.3 that more movement is required to equalize the spatial gradient as the difference between $\bar{X}_i$and $\bar{X}_j$ increases. Thus, homogenization depends on the balance of forces creating long-term differences among patches ($\mathrm{\bar{X}_i - \bar{X}_j}$) and movement equalizing them ($\mathrm{X_{i \rightarrow j}}$) such that:

$$\mathrm{Homogenization} = \frac{\mathrm{X_{i \rightarrow j}}}{\mathrm{\bar{X}_i - \bar{X}_j}} \qquad \text{Eq. H.4}$$

The amount of equalizing movement (numerator, Eq. H.4), and thus homogenization, is expected to increase as a function of total movement among patches or *functional connectivity* (*sensu* Taylor et al 2006). Meanwhile, differences among patches (denominator of Eq. H.4) are expected to increase with strength of response to spatial heterogeneity of the environment (e.g., different carrying capacities among sites) and to impede homogenization. Thus:

$$\mathrm{Homogenization} \propto \frac{\text{Functional connectivity}}{\text{Response to spatial heterogeneity}} \qquad \text{Eq. H.5}$$

Ecosystem variables with strong responses to the spatial environment and limited functional connectivity do not readily homogenize site differences, leading to a pattern of persistent spatial variation (Fig. H.1, left). Variables with high functional connectivity relative to response to spatial heterogeneity, on the other hand, homogenize site differences easily and present a pattern of low persistent spatial variation (Fig. H.1, right; note that, in the absence of spatial synchrony, this is the same as the 'asynchrony' region of Fig. 3.1).

Eq. H.5 implies that for structural connection to further homogenize unevenness among sites, it must either increase functional connectivity or decrease sensitivity to spatial heterogeneity beyond what it is in an unconnected system. The likelihood of the latter seems small as there is no *a priori* reason to think that connection will change the sensitivity of organisms, materials or energy to spatial heterogeneity. For the former, structural connection is likely to increase movement when functional connectivity is low. But it will not increase movement when functional connectivity is already high (movement is already unrestricted). Thus, under the null conditions described here, connection should homogenize site differences but do so least for variables with high rates of homogenization even when unconnected. Note that this situation of low potential for connective change is signaled by low persistent spatial variation.

Synchronization of patch values

The second expectation of connection is that increased movement synchronizes fluctuations across sites (Fig. H.2), and causes the shift from asynchrony to synchrony in Fig. 3.1. Like homogenization, synchronization is highly efficient when diffusive flow from high to low concentration equalizes patches. Unlike for homogenization, however, perfect synchrony requires that value differences among patches be equalized over a single time step (see below), rather than over the longer timescales of ≥ one time step for homogenization.

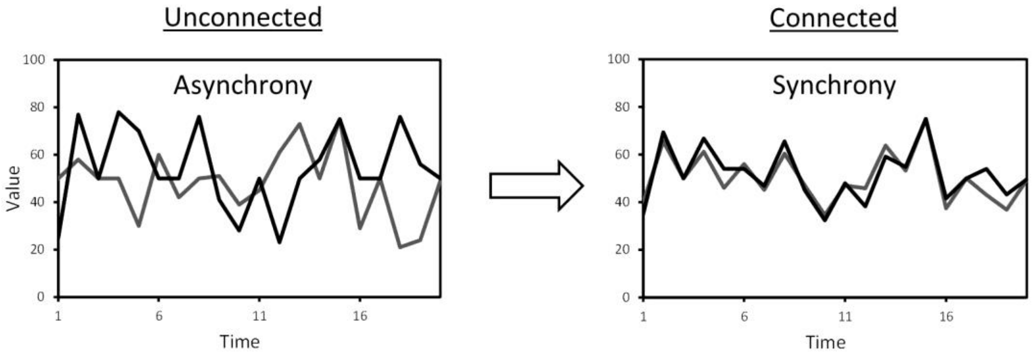


Figure H.2. Synchronization as a null expectation of structural connection. Increased movement due to connection can synchronize temporal fluctuations across sites, transforming a pattern of asynchrony into synchrony.

Similar to homogenization above, we can demonstrate the amount of movement required to maximize the temporal covariance (and thus synchrony) of patches *i* and *j.* The formula for temporal covariance is:

$$\mathrm{Cov(i,j)} = \frac{\sum(\mathrm{X_{ik}} - \overline{\mathrm{X}}_\mathrm{i})(\mathrm{X_{jk}} - \overline{\mathrm{X}}_\mathrm{j})}{\mathrm{n} - 1} \qquad \text{Eq. H.6}$$

where X_{ik} and X_{jk} are the values of patches *i* and *j* at time *k*.
We focus on the case where patch means are equal which corresponds to the particular pattern of synchrony referred to in Fig. 3.1. $\overline{\mathrm{X}}_\mathrm{i}$ and $\overline{\mathrm{X}}_\mathrm{j}$ are therefore set equal and called $\overline{\mathrm{X}}$ hereafter. Thus:

$$\mathrm{Cov(i,j)} = \frac{\sum(\mathrm{X_{ik}} - \overline{\mathrm{X}})(\mathrm{X_{jk}} - \overline{\mathrm{X}})}{\mathrm{n} - 1} \qquad \text{Eq. H.7}$$

Covariance is greatest when the deviations in the numerator of Eq. H.7 are equal. In the case of equal means, this occurs when $X_{ik} = X_{jk}$. Thus, we again solve for the movement from *i* to *j* that leads to the equivalence of values X_{ik} and X_{jk}:

$$\mathrm{X_{ik}} - \mathrm{X_{i \to j}} = \mathrm{X_{jk}} + \mathrm{X_{i \to j}} \qquad \text{Eq. H.8}$$

Yielding:

$$\mathrm{X_{i \to j}} = \frac{\mathrm{X_{ik}} - \mathrm{X_{jk}}}{2} \qquad \text{Eq. H.9}$$

which is the amount of movement required *at each time step* to make patch values equal and thus maximize temporal covariance and synchrony.

Note also from Eq. H.9 that as the difference between X_{ik} and X_{jk} grows, so too does the movement required to equalize and synchronize patches. Synchronization is thus a product of two opposing forces: One that causes value differences among patches ($X_{ik} - X_{jk}$) and the other that equalizes them by movement ($X_{i \to j}$):

$$\mathrm{Synchronization} = \frac{\mathrm{X_{i \to j}}}{\mathrm{X_{ik}} - \mathrm{X_{jk}}} \qquad \text{Eq. H.10}$$

The potential for equalizing movement (numerator, Eq. H.10), and thus synchronization, is expected to increase with total movement among patches i.e., *functional connectivity*. Meanwhile, the difference between patch values (denominator) is expected to be higher, and synchronization lower, when local responses generate fluctuations that are too large to be equalized across patches. This is most likely to occur in variables with high *reactivity* or sensitivity to local conditions (Neubert et al. 2009). Thus:

$$\text{Synchronization} \propto \frac{\text{Functional connectivity}}{\text{Reactivity}} \qquad \text{Eq. H.11}$$

Ecosystem variables with high functional connectivity relative to reactivity quickly equalize value differences among sites and present a pattern of spatial synchrony (Fig. H.2, right). But variables with high reactivity and low functional connectivity do not readily equalize value differences, leading to a pattern of asynchrony (Fig. H.2, left).

Eq. H.11 implies that for structural connection to further synchronize fluctuations, it must either increase functional connectivity or decrease reactivity beyond what it is in an unconnected system. The inherent reactivity of an ecosystem variable seems unlikely to change with connection and so further synchronization would hinge on increasing functional connectivity. Structural connection should increase movement when functional connectivity is low. But it will not when it is already high (movement is already unrestricted). Thus, connection should synchronize fluctuations under null conditions but do so least for variables with high rates of synchronization even when unconnected. This situation is reflected as a pattern of synchrony in an unconnected system.

REFERENCES

Neubert, M., H. Caswell, and A. R. Solow. 2009. Detecting reactivity. Ecology 90:2683–2688.

Taylor, P., L. Fahrig, and K. A. With. 2006. Landscape connectivity: A return to basics. Pages 29–43 *in* K. Crooks and M. Sanjayan, editors. Connectivity Conservation. Cambridge.

APPENDIX I. REPRESENTATIVE TIME SERIES OF STUDY VARIABLES

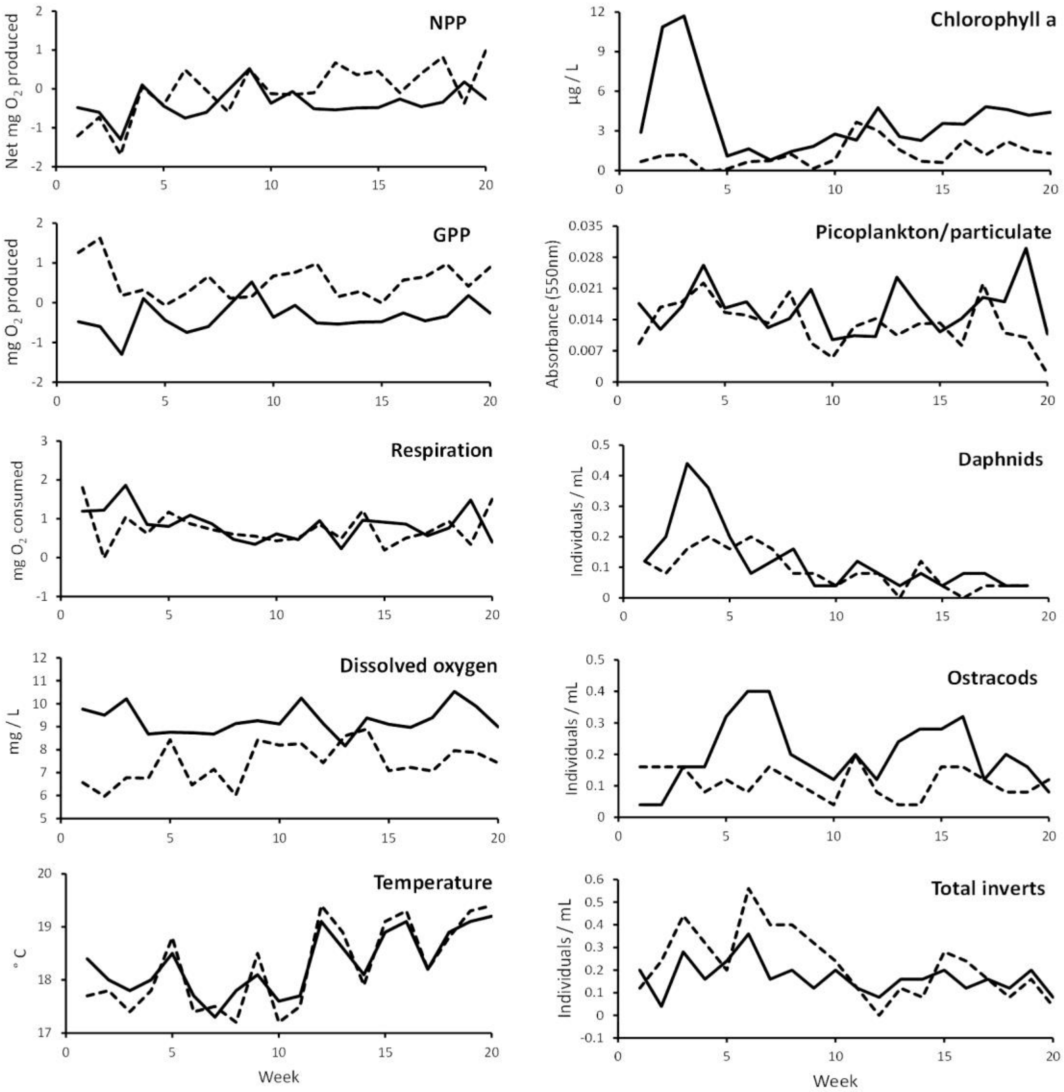


Figure I.1. Time series of a single microcosm for ten ecosystem variables. Series values have not been first-differenced as in our main analyses. Broken lines denote series from the unconnected treatment and solid lines series from the connected treatment.

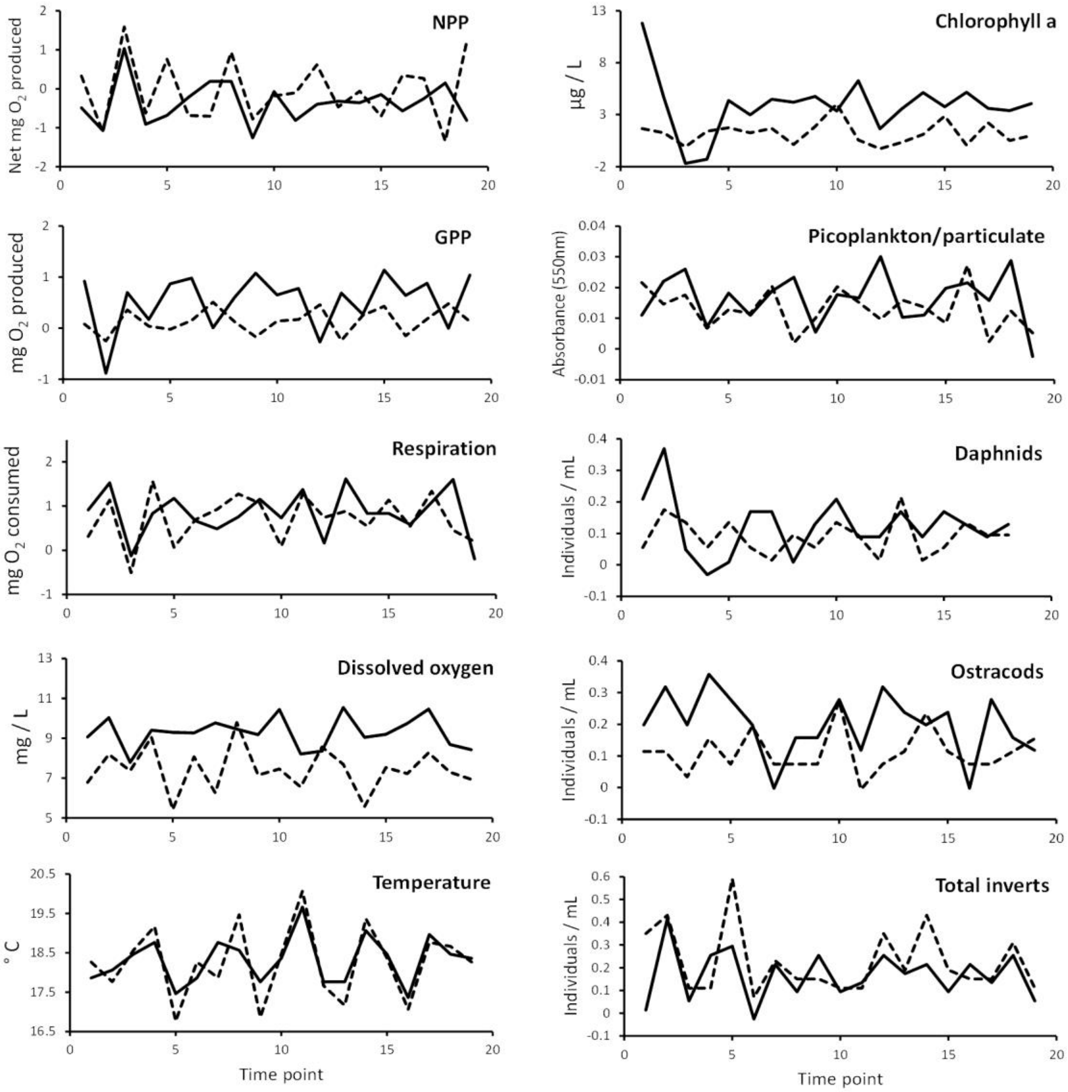


Figure I.2. Representative microcosm time series for ten ecosystem variables that have been first-differenced to remove trend and autocorrelation. Broken lines denote series from the unconnected treatment and solid lines series from the connected treatment.

APPENDIX J. DERIVATION OF COMPONENTS OF VARIANCE CHANGE

In this Appendix, we derive the components of change in temporal variance that produce the indices in Table 3.2. A system of *n* patches is measured before and after the connection of patches *i* and *j*. Regional variances estimate variation of the spatially-aggregated time series i.e., $Var(X_{i,} + X_j \ldots X_n)$, and are calculated for the unconnected system as $Var(Y)_U$ and for the connected system as $Var(Y)_C$. Any difference between $Var(Y)_C$ and $Var(Y)_U$ indicates a change has taken place in dynamics due to connection. This change is expressed in % as:

$$\%\ \text{change in regional variance} = \frac{\mathrm{Var}(Y)_C - \mathrm{Var}(Y)_U}{\mathrm{Var}(Y)_U} \cdot 100 \qquad \text{Eq. J.1}$$

Partitioning change in variability from change in mean

Because variance scales with the mean (Taylor 1961), *% change in regional variance* captures changes in variation as well as changes in mean value. We can partition these effects by estimating what the variance would be if means, *but not variation*, changed with connection. We do so using a well-known statistical rule: Scaling time series values of mean *m* and variance $Var(X)$ by constant *k* yields a new mean *km* and a new variance $k^2Var(X)$ (Tilman et al. 1998, Kilpatrick and Ives 2003). Because the new mean is *k* times the original mean, *k* can be recovered as their ratio. For connected and unconnected systems with means m_C and m_U, respectively, this ratio is m_C/m_U. We can now use this ratio as *k* in the new variance formula, and use the unconnected regional variance ($Var(Y)_U$) as $Var(X)$ to calculate the regional variance expected after connection changes the mean:

$$\mathrm{Var(Y)_{CExp}} = \left(\frac{\mathrm{m_C}}{\mathrm{m_U}}\right)^2 \cdot \mathrm{Var(Y)_U} \qquad \text{Eq. J.2}$$

We now have a benchmark with which to compare observed, connected variance $Var(Y)_C$. To use it to decompose *% change in regional variance*, we add ($Var(Y)_{CExp}$ - $Var(Y)_{CExp}$) to the numerator of Eq. J.1 and rearrange to yield:

$$\left(\frac{\mathrm{Var}(Y)_C - \mathrm{Var}(Y)_{CExp}}{\mathrm{Var}(Y)_U} + \frac{\mathrm{Var}(Y)_{CExp} - \mathrm{Var}(Y)_U}{\mathrm{Var}(Y)_U}\right) \cdot 100 \qquad \text{Eq. J.3}$$

The left term – *Δ regional variability* – is zero when connected variance equals that expected solely from changing mean ($Var(Y)_C = Var(Y)_{CExp}$). Values of this index grow as variance increases beyond that expected from the mean change ($Var(Y)_C > Var(Y)_{CExp}$). Values are negative as variance decreases below that expected from the change in mean ($Var(Y)_C < Var(Y)_{CExp}$). Meanwhile, the second term – *Δ mean* – includes variances whose values only differ because of a difference in mean. It therefore indexes that portion of *%*

change in regional variance that is attributable to an increase or decrease in mean (*Δ mean* is positive and negative, respectively).

Δ mean indexes change in mean, but is not simply the difference between two means. Its direct relationship to mean values is obtained by substituting $Var(Y)_{CExp}$ in Eq. J.2 into the second term of Eq. J.3. $Var(Y)_U$ drops out, leaving the *Δ mean* term as:

$$\Delta\ \text{mean} = \frac{\text{Var}(Y)_{CExp} - \text{Var}(Y)_U}{\text{Var}(Y)_U} \cdot 100 = \frac{m_C^2 - m_U^2}{m_U^2} \cdot 100 \qquad \text{Eq. J.4}$$

Δ mean is thus the % change in squared means.

Decomposing Δ regional variability

Δ regional variability can be further decomposed because regional variance is calculated from an aggregated time series. This stems from the well-known property that an aggregate variance is the sum of variances of patch *i* and covariances between patch *i* and *j* (Feller 1950), illustrated below for connected regional variance $Var(Y)_C$:

$$\text{Var(Y)}_C = \sum_{\text{i}=1}^{\text{n}} \text{var}(\text{X}_\text{i})_C + 2\sum_{\text{i}=1}^{\text{n}}\sum_{\text{j}=1}^{\text{i}-1} \text{cov}\left(\text{X}_\text{i}, \text{X}_\text{j}\right)_C \qquad \text{Eq. J.5}$$

An analogous decomposition applies to the expected regional variance $Var(Y)_{CExp}$, where expected summed variances and covariances are calculated from the scaling rule in Eq. J.2:

$$\text{Var(Y)}_{CExp} = \sum_{\text{i}=1}^{\text{n}} \text{var}(\text{X}_\text{i})_{CExp} + 2\sum_{\text{i}=1}^{\text{n}}\sum_{\text{j}=1}^{\text{i}-1} \text{cov}\left(\text{X}_\text{i}, \text{X}_\text{j}\right)_{CExp} \qquad \text{Eq. J.6}$$

Eq. J.5 and Eq. J.6 can now be substituted into the first term of Eq. J.3 and rearranged to get:

$$\begin{array}{l}\Delta\ \text{regional} \\ \text{variability}\end{array} = \left(\frac{\sum \text{var}(\text{X}_\text{i})_C - \sum \text{var}(\text{X}_\text{i})_{CExp}}{\text{Var}(Y)_U} + \frac{2\sum \text{cov}\left(\text{X}_\text{i}, \text{X}_\text{j}\right)_C - 2\sum \text{cov}\left(\text{X}_\text{i}, \text{X}_\text{j}\right)_{CExp}}{\text{Var}(Y)_U}\right) \cdot 100 \qquad \text{Eq. J.7}$$

Δ regional variability thus breaks down into two more terms. As with *Δ regional variability*, the left-hand term – *Δ patch variability* – is zero when the patch variances equal that expected from changing means, is positive when patch variances are greater than expected, and is negative when patch variances are less than expected.

The right-hand term – *Δ covariability* – similarly shows whether observed covariances are equal to, greater than or less than those expected if means alone changed. Because they are additive, this and other terms (above and in Table 3.2) sum to yield the *% change in regional variance*. This suite of indices thus gives a full decomposition of the types of change a variable might experience due to spatial connection.

REFERENCES

Feller, W. 1950. An introduction to probability theory and its applications. Page 461. Wiley, New York.

Kilpatrick, A. M., and A. R. Ives. 2003. Species interactions can explain Taylor's power law for ecological time series. Nature 422:65–68.

Taylor, L. R. 1961. Aggregation, variance and the mean. Nature 189:732–735.

Tilman, D., C. L. Lehman, and C. E. Bristow. 1998. Diversity-stability relationships: Statistical inevitability or ecological consequence? The American Naturalist 151:277–282.

APPENDIX K. ROBUSTNESS OF STUDY INDICES AND CV^2 AGAINST MEAN BIAS

To check for any bias arising from imperfect removal of the mean, we regressed our index values against mean values of the ten study variables. Results were not significant (Table K.1) and indicate robustness of index values to time series means. For comparison, we tested whether differences in analogous indices from the CV^2 family (CV^2, Variance CV and Covariance CV) were similarly robust to the mean. Table K.2 reports that CV^2 values showed signs of bias from the mean. Two regressions were at the threshold of statistical significance, suggesting a risk of mistaking differences in mean for differences in variability.

Table K.1. Results of linear regressions of logged variable means against indices of change between connected and unconnected systems (see Table 3.2). r^2, F and p-values are reported.

Independent variable	Index of change (dependent)	r^2	F	p-value
Log (mean)	% change in variance	0.03	0.26	0.63
Log (mean)	Δ regional variability	0.03	0.20	0.67
Log (mean)	Δ patch variability	0.03	0.25	063
Log (mean)	Δ covariability	0.00	0.00	0.99
Log (mean)	Log(abs(Δ mean))	0.10	0.91	0.37

Table K.2. Results of linear regressions of logged variable means versus indices of change from the CV^2 family. r^2, F and p values are reported.

Independent variable	Index of change (dependent)	r^2	F	p-value
Log (mean)	Difference in regional CV^2	0.40	5.24	0.05
Log (mean)	Difference in Variance CV	0.39	5.20	0.05
Log (mean)	Difference in Covariance CV	0.26	2.76	0.14

APPENDIX L. SUPPLEMENTARY RESULTS DESCRIBING CONNECTIVITY RESPONSES

Fig. L.1 shows that a variable's spatiotemporal pattern, measured in an unconnected system, strongly predicted the degree of spatiotemporal change it underwent when the system became connected. In fact, fixed spatial variation explained 97% of variance in the responses of variables (Fig. L.1a), suggesting that spatial gradients among sites were the main driver of dynamic change when sites became connected. Furthermore, change in spatiotemporal pattern was significantly and positively correlated with other metrics of change: Change in regional variance, local mean, patch variability and covariability (Table L.1). Thus, variables that underwent more reorganization in terms of spatiotemporal pattern also underwent major changes in mean value and variability.

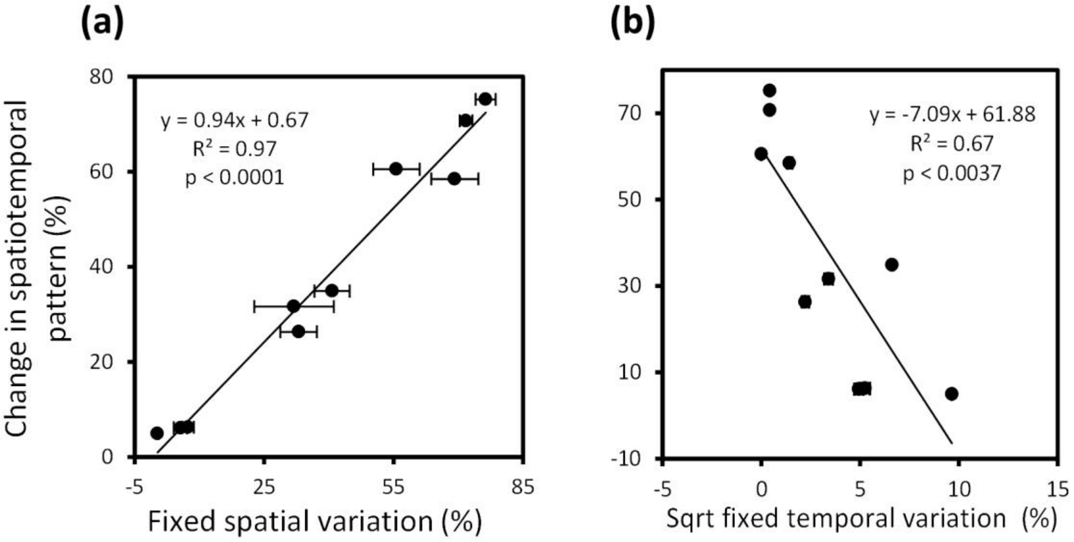


Figure L.1. Predictors of spatiotemporal change. (a) Fixed spatial variation of a variable (point) measured in an unconnected system was an exceptionally strong predictor of its response to connection, % change in spatiotemporal pattern. Change in spatiotemporal pattern is the distance by which a variable is displaced by connection on a plot like Fig. 3.1, where fixed spatial and fixed temporal variation are the x- and y-axes, respectively. **(b)** Fixed temporal variation was a weaker predictor of spatiotemporal change.

Table L.1. Correlation of % change in spatiotemporal pattern with some regional and local responses to connection. Analysis used first-differenced data and log-transformed, absolute values of responses from the ten study variables.

Response metric	Pearson correlation coefficient (ρ)	p
% change in regional variance	0.83	0.003
Δ regional variability	0.81	0.005
Δ patch variability	0.88	0.001
Δ covariability	0.70	0.024
Δ mean	0.88	0.001

APPENDIX M. TEST STATISTICS AND SCALING EXPONENTS FOR RESPONSES

Table M.1 reports differences between connected and unconnected treatments for dimensionless indices of change. Test statistics for these results are reported in Table M.2. As an alternative to our indices, which work only on differences between two variances, we employed the CV^2 of Proulx and others (2010). Defined as $Var(X)/m^2$, this metric allows decomposition of aggregate variation (CV^2) into two sub-metrics - the variance CV and the covariance CV - that capture the contributions of patch variation and covariation to total variability. We calculated the CV^2 in each replicate array and tested for differences among treatments using two-tailed t-tests. CV^2 results are most reliable when m^2 and Var(X) scale with a slope of one on a log-log plot (Proulx et al. 2010). Mean-variance scaling slopes of the ten ecosystem variables (Table M.2) approached this mark (mean = 0.70 ± 0.25 SD), but some extreme slopes (e.g., chlorophyll a) and detectable bias by the mean (Appendix K; Table K.2) may mean that differences are exaggerated or obscured for certain variables. Therefore, CV^2 results must be interpreted conservatively.

Table M.1. Responses of ten ecosystem variables to connection. Differences in regional variability (estimated as CV^2), patch variability (Variance CV) and covariability (Covariance CV), and means between connected (n = 12) and unconnected (n = 9) treatments. ↑ and ↓ indicate significant increases and decreases with increased structural connectivity, respectively. Asterisks denote significance level: *p < 0.05, **p < 0.01, ***p < 0.001. See Table M.2 for two-tailed t-test statistics.

Variable	**Regional variability (CV^2)**	**Patch variability (Variance CV)**	**Patch covariability (Covariance CV)**	**Mean**
NPP	n.s.	n.s.	n.s.	n.s.
GPP	↑*	n.s.	↑*	n.s.
Ecosystem respiration	n.s.	n.s.	n.s.	n.s.
Dissolved O_2	n.s.	n.s.	n.s.	n.s.
Temperature	↓**	↓**	↓*	n.s.
Chlorophyll a	↑***	↑**	↑**	↓*
Picoplankton /particulate	n.s.	n.s.	n.s.	↓*
Daphnia	n.s.	n.s.	↑***	↑***
Ostracods	↓**	↓**	n.s.	↓**
Total invertebrates	n.s.	↓*	n.s.	↑***

Table M.2. Two-tailed t-test results for differences in CV^2, Variance CV, Covariance CV, and means between unconnected (n = 9) and connected (n = 12) treatments. T-statistics and p-values are reported. Variability estimates are increasingly biased as scaling slopes between $mean^2$ and regional variance on a log-log plot deviate from one (Proulx et al. 2010).

Variable	**$Mean^2$-variance slope**	**CV^2 (regional variability)**	**Variance CV (patch variability)**	**Covariance CV (covariability)**	**Mean**
NPP	0.53	0.85, 0.40	1.40, 0.18	-0.18, 0.86	1.25, 0.23
GPP	0.48	**-2.66, 0.015**	-1.10, 0.29	**-2.34, 0.030**	1.65, 0.12
Ecosystem respiration	0.92	1.13, 0.27	0.30, 0.76	0.22, 0.83	1.57, 0.13
Dissolved O_2	0.43	-0.34, 0.74	-0.49, 0.63	-0.42, 0.68	-0.59, 0.56
Temperature	0.64	**4.63, <0.001**	**4.47, <0.001**	**2.23, 0.038**	-1.57, 0.13
Chlorophyll a	0.42	**-5.31, < 0.001**	**-4.01, <0.001**	**-3.31, 0.004**	**2.30, 0.033**
Picoplankton/ particulate	1.04	0.09, 0.93	0.92, 0.37	-1.25, 0.23	**2.17, 0.04**
Daphnia	1.06	-1.85, 0.080	-0.24, 0.82	**-5.47,<0.001**	**-5.70,<0.001**
Ostracods	0.66	**2.97, 0.008**	**3.85, 0.001**	-1.60, 0.13	**2.97, 0.008**
Total invertebrates	0.82	0.86, 0.40	**2.14, 0.046**	-1.95, 0.067	**-12.79, <0.001**

REFERENCES

Proulx, R., C. Wirth, W. Voigt, A. Weigelt, C. Roscher, S. Attinger, J. Baade, R. Barnard, N. Buchmann, F. Buscot, N. Eisenhauer, M. Lange, A. Milcu, P. A. Niklaus, Y. Oelmann, S. Rosenkranz, and M. Vicky. 2010. Diversity promotes temporal stability across levels of ecosystem organization in experimental grasslands. PLoS One 5:1–8.

APPENDIX N. ALTERNATIVE ANALYSIS FOR FIGURE 3.5A

Fig. 3.5a shows that variables (points) with high inter-patch synchrony experience little change in synchrony when patches are connected by corridors. However, x- and y-axes are not statistically independent because they plot fixed temporal variation in the unconnected treatment against change in inter-patch synchrony. As an alternative that prevents spurious conclusions, we plotted synchrony in connected systems against synchrony in unconnected systems (Fig. N.1). We estimated synchrony using a variance ratio of Schluter (1984) because, unlike other indices of synchrony, it can accommodate zero values from empty patches. We tested whether the slope of the resulting line differed significantly from the null slope of one, where all variables have the same synchrony in connected and unconnected treatments.

The observed slope for synchrony was significantly less than one ($t = -3.70$, $p = 0.005$), indicating that connection causes more synchrony in variables with low unconnected synchrony. Visual inspection of Fig. N.1 shows that variables with high synchrony had almost identical (close to dashed line) values whether connected or not, whereas asynchronous variables experienced jumps in synchrony when connected. Results thus validate the relationship reported in Fig. 3.5a.

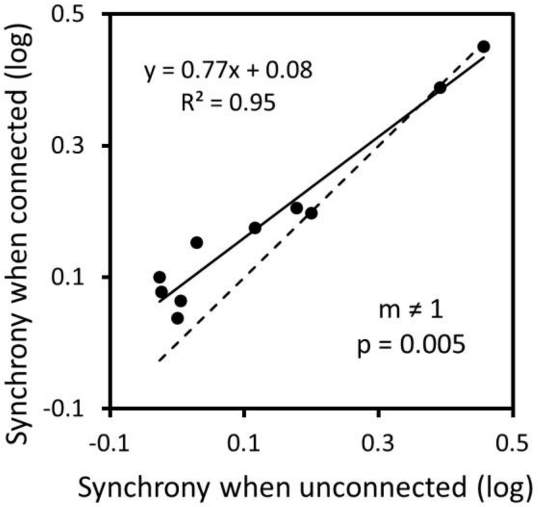


Figure N.1. Inter-patch synchrony of variables in unconnected versus connected treatments. The regression slope was significantly less than one ($t = -3.70$, $p = 0.005$) with a non-zero intercept, indicating that variables (points) with high synchrony (top right) retained it when connected. Meanwhile, variables with low synchrony (bottom left) showed a larger increase in synchrony after system connection.

REFERENCES

Schluter, D. 1984. A variance test for detecting species associations, with some example applications. Ecology 65:998–1005.

APPENDIX O. COMPARISON OF RESULTS WITH RANDOMIZED DATA

Data for each ecosystem variables were randomly shuffled between replicate microcosms, between time points and between treatments using the *Random sorter 2.2.2* add-on (Add-In Express Ltd., 2013) for Excel 14.0 (Microsoft Corporation, 2010). Repeating variance decomposition analyses on randomized data yielded no significant results, reinforcing that empirical patterns were driven by ecological mechanisms and not numerical artefacts. *% change in regional variance* (Fig. O.1) was minimal and consistent among variables (-24% to +13%) compared to the larger changes seen in unshuffled data (-77% to +460%; Fig. 3.4). Furthermore, relationships between variable spatiotemporal patterns and their responses to connection were no longer detectable in randomized data (Fig. O.2).

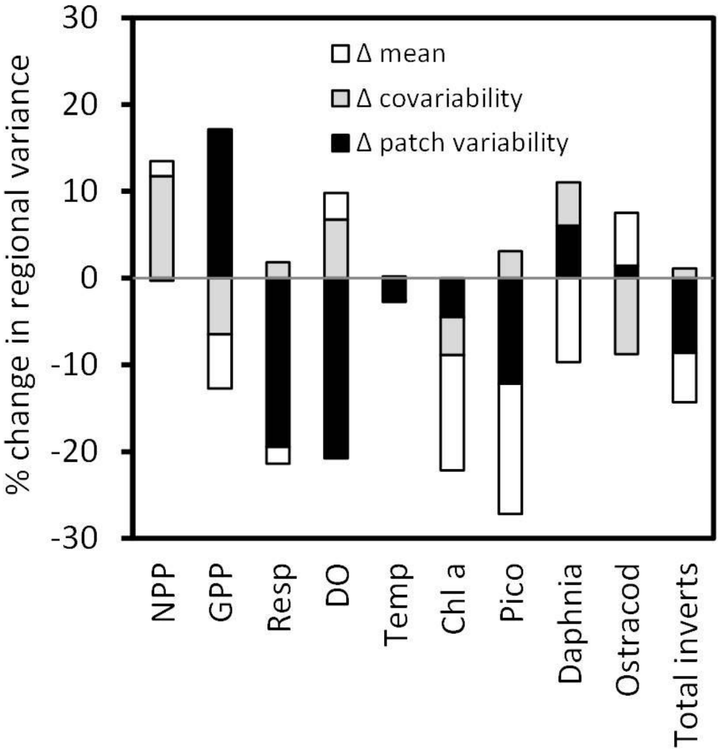


Figure O.1. Connection responses in randomly shuffled data of ten ecosystem variables. Bars show % change in mean regional variance between unconnected and connected treatments, decomposed into contributions from Δmean, Δ patch variability, and Δ covariability (Table 3.2). Positive values indicate a component that increased connected variance, negative values a component that decreased connected variance.

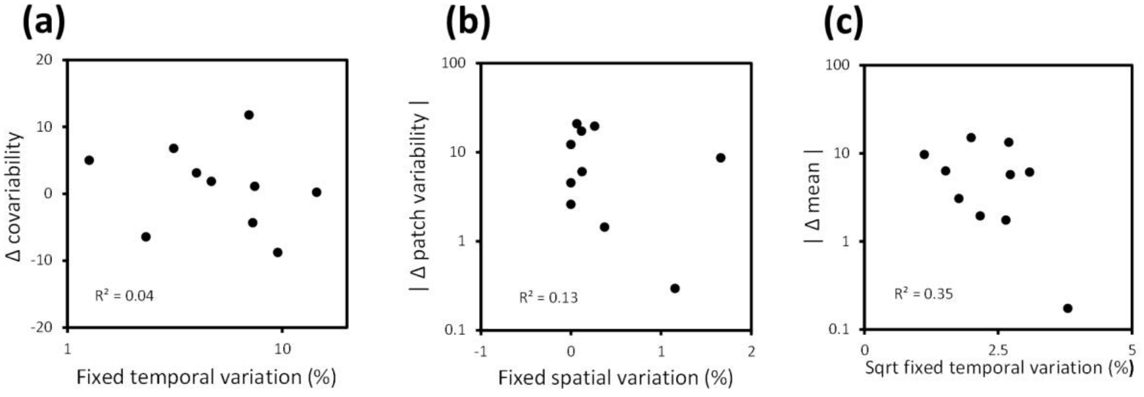


Figure O.2. Non-significant relationships between spatiotemporal patterns of variables (points) in unconnected systems and responses to spatial connection. Data randomization erased links between **(a)** change in covariability of patch i with j and fixed temporal variation, **(b)** change in patch variability and fixed spatial variation, and **(c)** change in mean and fixed temporal variation. Note log scales and absolute values.

APPENDIX P. REANALYSIS USING RAW (UNDIFFERENCED) DATA

Temporal autocorrelation can be an important aspect of ecological dynamics, for instance if structural connection led to increasing or decreasing trends in affected variables. We chose to remove short-term autocorrelation from time series for our main analysis by first-differencing the data. Fig. P.1-P.4 show the results of the same analysis repeated on raw (undifferenced) data. Results were highly similar and indicate that our choice of methods did not obscure any patterns of longer-term change. Specifically, fixed spatial variation was still a strong predictor of spatiotemporal change (Fig. P.1). As in our main analyses, this spatiotemporal change was associated with significant changes in local means, variability and covariability (Table P.1). Ecosystem variables were similarly varied in their connectivity responses (Fig. P.2), and these responses were again predictable from spatiotemporal patterns of variables in unconnected systems (Fig. P.3). Finally, a plot of spatiotemporal change corresponding to our conceptual model shows similar patterns to those seen in first-differenced data (Fig. P.4). Namely, connection displaces all variables except temperature towards the null expectation of spatiotemporal pattern – homogeneity of means and synchronized fluctuations across sites.

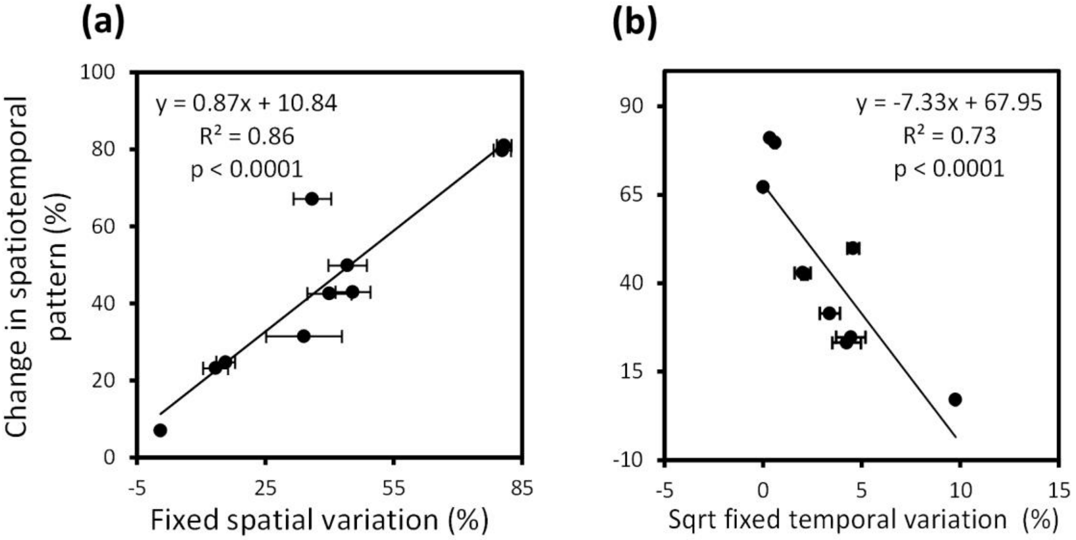


Figure P.1. Predictors of spatiotemporal change in raw (undifferenced) data. **(a)** Fixed spatial variation of a variable (point) measured in an unconnected system was the strongest predictor of its response to connection, % change in spatiotemporal pattern. This change is the distance by which a variable is displaced by connection on a plot like Fig. 3.1 where fixed spatial and fixed temporal variation are the x- and y-axes, respectively. **(b)** As in Fig. L.1, fixed temporal variation was a slightly weaker predictor of spatiotemporal change.

Table P.1. Correlation of % spatiotemporal change with some regional and local responses to connection. Analysis used raw (undifferenced) and log-transformed, absolute values of responses from the ten study variables

Response metric	Pearson correlation coefficient (ρ)	p
% change in regional variance	0.89	0.001
Δ regional variability	0.52	0.124
Δ patch variability	0.83	0.003
Δ covariability	0.81	0.005
Δ mean	0.85	0.002

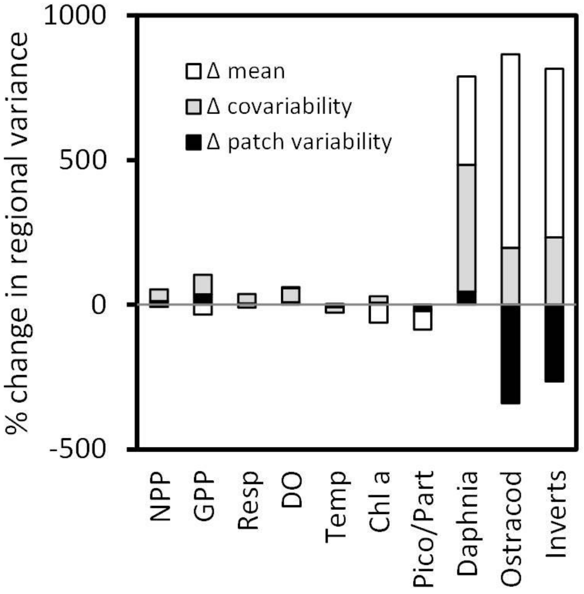


Figure P.2. Connection responses of ten ecosystem variables, calculated from raw (undifferenced) data and showing patterns similar to Fig. 3.4. Bars show % change in mean regional variance between unconnected and connected treatments, decomposed into contributions from Δmean, Δ patch variability, and Δ covariability (Table 3.2). Positive values indicate a component that increased connected variance, negative values a component that decreased connected variance.

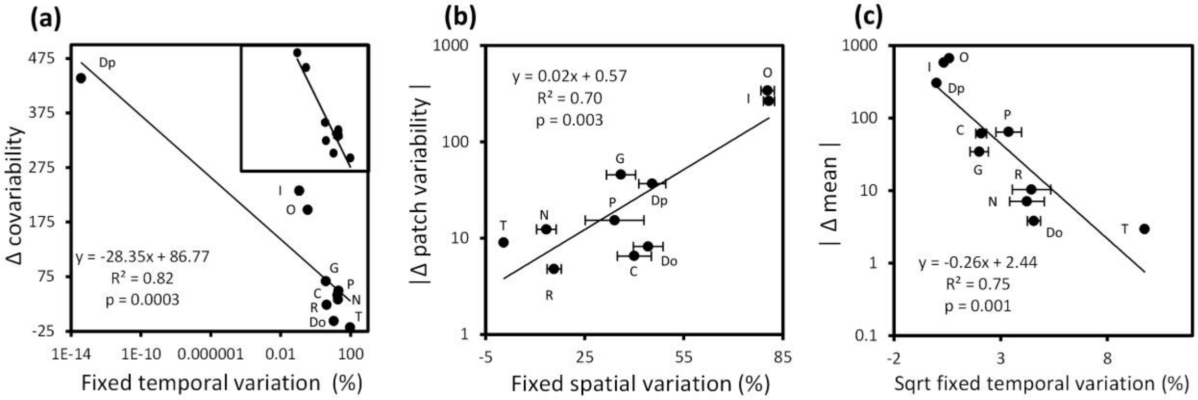


Figure P.3. Relationships between spatiotemporal patterns in unconnected systems and responses to spatial connection, calculated from raw (undifferenced) data and showing patterns similar to Fig. 3.5. Relationships show: **(a)** change in covariability of patch i with j with fixed temporal variation, **(b)** change in patch variability with fixed spatial variation (note absolute value on y-axis), and **(c)** change in mean with fixed temporal variation. Variables (points) are labelled as follows: Dp = Daphnia; I = Total invertebrates; O = Ostracods; C = Chlorophyll a; G = GPP; N = NPP; Do = Dissolved oxygen; P = picoplankton/particulate; R = Respiration; T = temperature. Note logarithmic scales.

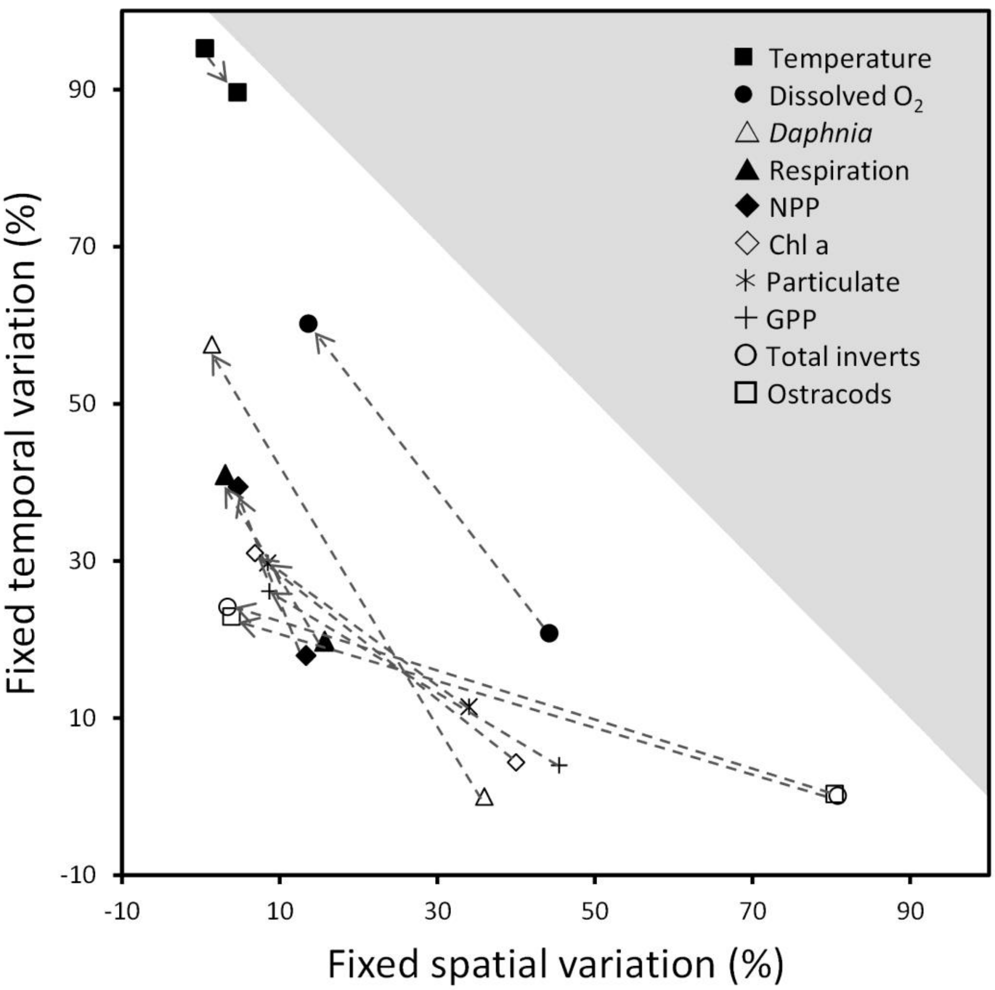


Figure P.4. Spatiotemporal change in ten ecosystem variables due to connection. Paired points represent the spatiotemporal patterns of a variable in the unconnected and connected treatment. The arrow shows the direction of change, from unconnected to connected. This plot of undifferenced data shows trends and convergence on the upper-left quadrant that is comparable to that in Fig. 3.3.

APPENDIX Q. ANALYTICAL DECOMPOSITION OF PERSISTENT SPATIAL VARIATION (PSV) INTO ITS COMPONENT PATTERNS

(1) Decomposition of *F*-value into its spatial and temporal components

Y_{ik} is the value of an ecosystem variable at site i and time k. Persistent spatial variation (PSV) occurs when value differences between sites i and j persist over times k and l (see Fig. 4.1c in main text). These spatial and temporal sources of variation are contrasted by the *F*-value of an ANOVA comparing site means. This makes F an effective index of PSV, formulated as:

$$\mathrm{F} = \frac{\mathrm{MS_{among\ sites}}}{\mathrm{MS_{within\ sites}}} \qquad \text{Eq. Q.1}$$

$\mathrm{MS_{among\ sites}}$ is the mean squares of $\overline{\mathrm{Y}}_\mathrm{i}$, the temporal mean of site i. And $\mathrm{MS_{within\ sites}}$ is the mean squares within site i (i.e., variation over times k and l). The numerator and denominator can be expressed as Coefficients of Variation (CV’s), but must first be converted into variances. $\mathrm{MS_{among\ sites}}$ is equal to the variance of site means (i.e., $\mathrm{var}\big(\overline{\mathrm{Y}}_\mathrm{i}, \overline{\mathrm{Y}}_\mathrm{j} \ldots \overline{\mathrm{Y}}_\mathrm{n}\big)$), which we term $\mathrm{Var}(\overline{\mathrm{Y}}_\mathrm{i})$, times the number of temporal observations per site n_k (Sokal and Rohlf 1981). Thus:

$$\mathrm{F} = \frac{\mathrm{n_k Var}(\overline{\mathrm{Y}}_\mathrm{i})}{\mathrm{MS_{within\ sites}}} \qquad \text{Eq. Q.2}$$

Meanwhile, $\mathrm{MS_{within\ sites}}$ is equal to the summed temporal variances of sites i and j divided by the number of sites n_i when groups are of equal size. We therefore have:

$$\mathrm{F} = \frac{\mathrm{n_k Var}(\overline{\mathrm{Y}}_\mathrm{i})}{\mathrm{n_i^{-1}} \sum_{\mathrm{i=1}}^{\mathrm{n}} \mathrm{var_i}} \qquad \text{Eq. Q.3}$$

We now express these variances in relative terms by multiplying by $\overline{\overline{\mathrm{Y}}}_\mathrm{i}^2 \big/ \overline{\overline{\mathrm{Y}}}_\mathrm{i}^2$ where $\overline{\overline{\mathrm{Y}}}_\mathrm{i}$ is the grand mean of site means. Rearranging, we get:

$$\mathrm{F} = \frac{\mathrm{Var}(\overline{\mathrm{Y}}_\mathrm{i})}{\overline{\overline{\mathrm{Y}}}_\mathrm{i}^2} \cdot \frac{\overline{\overline{\mathrm{Y}}}_\mathrm{i}^2}{\sum \mathrm{var_i}} \cdot \mathrm{n_i n_k} \qquad \text{Eq. Q.4}$$

The first term is equivalent to the squared Coefficient of Variation of the site means (i.e., $\mathrm{CV}\big(\overline{\mathrm{Y}}_\mathrm{i}, \overline{\mathrm{Y}}_\mathrm{j} \ldots \overline{\mathrm{Y}}_\mathrm{n}\big)^2$) that we term CV_s^2 with subscript *s* to emphasize that it is a relative measure of spatial variation. F thus becomes:

$$F = CV_s^2 \cdot \frac{\overline{\overline{Y}}_i^2}{\sum \mathrm{var}_i} \cdot n_i n_k \qquad \text{Eq. Q.5}$$

To turn the second term into a squared temporal Coefficient of Variation, we convert $\overline{\overline{Y}}_i^2$ - a squared spatial grand mean - into the squared regional temporal mean $\overline{Y}_K^2$. The regional temporal mean is the mean obtained by summing values across sites and averaging over time (i.e., $\overline{Y}_K$ where $K = \sum_{i=1}^{n} Y_{ik}$). $\overline{Y}_K^2$ is substituted into Eq. Q.5 using the equality $\overline{\overline{Y}}_i^2 = (1/n_i^2)\overline{Y}_K^2$. Simplifying, we obtain:

$$F = CV_s^2 \cdot \frac{\overline{Y}_K^2}{\sum \mathrm{var}_i} \cdot \frac{n_k}{n_i} \qquad \text{Eq. Q.6}$$

The new, second term of Eq. Q.6 is the quotient of the squared regional temporal mean and the summed temporal variances of each site. This term is the reciprocal of Proulx et al.'s (2010) *Variance CV.* It is thus an index of temporal stability or constancy of sites which we call $CV_{t.var}^{-1}$. Applying this term, we get:

$$F = CV_s^2 \cdot CV_{t.var}^{-1} \cdot \frac{n_k}{n_i} \qquad \text{Eq. Q.7}$$

The third term n_k/n_i changes value with the number of observations over time and across space. It is possible that this term's influence on F may complicate comparisons between data sets of different sizes. As a precaution against this, we only compared datasets of similar sizes and values of n_k/n_i.

(2) Decomposing spatial variation (CV_s^2) into its two spatial components

CV_s^2 is a dimensionless index of spatial variation among site means defined, as in Eq. Q.4, as:

$$CV_s^2 = \frac{\mathrm{Var}(\overline{Y}_i)}{\overline{\overline{Y}}_i^2} \qquad \text{Eq. Q.8}$$

The numerator $\mathrm{Var}(\overline{Y}_i)$ is the (sample) variance of site means $\overline{Y}_i$ and integrates two sources of spatial variation that are common in landscapes: First, variation arising from having unoccupied sites with densities of zero and, second, variation in population density among occupied sites (see Fig. Q.1). These sources can be partitioned from $\mathrm{Var}(\overline{Y}_i)$ using a model II (random effects), one-way ANOVA that compares two groups: Occupied sites (o) and unoccupied sites (u).

In this scheme, $\mathrm{Var}(\overline{\mathrm{Y}}_\mathrm{i})$ is expressed as sums of squares (SS) and decomposed into among-group and within-group sources of variation, as follows:

$$\mathrm{SS_I} = \mathrm{SS_{o,u}} + \mathrm{SS_{within}} \qquad \text{Eq. Q.9}$$

where $\mathrm{SS_I}$ is the total sums of squares, $\mathrm{SS_{o,u}}$ is the sums of squares between the occupied and unoccupied group, and $\mathrm{SS_{within}}$ is the sums of squares within the groups. Among- and within-variation are converted into their corresponding variance components, as follows using formulae that can accommodate groups of unequal size (Sokal and Rohlf 1981 p.216):

$$\mathrm{s^2_{o,u}} = \frac{\mathrm{MS_{o,u}} - \mathrm{MS_{within}}}{\mathrm{n_o}} \qquad \text{Eq. Q.10}$$

$$\mathrm{s^2} = \mathrm{MS_{within}} \qquad \text{Eq. Q.11}$$

where MS are the mean squares corresponding to the above SS and $\mathrm{n_o}$ is a modified sample size for groups that differ in their respective n (see Sokal and Rohlf 1981 p.214 for details). $\mathrm{s^2_{o,u}}$ is the variance added by value differences between the occupied and unoccupied group, and so is the variance attributable to having zeros in unoccupied sites (see Fig. Q.1). Meanwhile, $\mathrm{s^2}$ is an estimate of the variance within groups. The definition of $\mathrm{s^2}$ (Eq. Q.11) can be rewritten to isolate the contributions of *SS* from the occupied ($\mathrm{SS_{within.o}}$) and unoccupied group ($\mathrm{SS_{within.u}}$):

$$\mathrm{s^2} = \frac{\mathrm{SS_{within}}}{\mathrm{n_i} - 2} = \frac{\mathrm{SS_{within.o}}}{\mathrm{n_i} - 2} + \frac{\mathrm{SS_{within.u}}}{\mathrm{n_i} - 2} \qquad \text{Eq. Q.12}$$

We note that all values within the unoccupied group are always zero, rendering $\mathrm{SS_{within.u}}$ zero also. Thus:

$$\mathrm{s^2} = \frac{\mathrm{SS_{within.o}}}{\mathrm{n_i} - 2} + 0 \qquad \text{Eq. Q.13}$$

Eq. Q.13 shows that only variation within the occupied group contributes to $\mathrm{s^2}$. Thus, in our special case, $\mathrm{s^2}$ provides an estimate of variation among populations in occupied sites.

Variance components are typically expressed in relative terms as the ratio of a single component to the total of all components. When $\mathrm{s^2_{o,u}}$ is standardized to the component total, it is called the *interclass correlation coefficient* (ICC) and measures the proportion of total variance in the sample that arises between the occupied and unoccupied group.

If we then multiply this proportion by the original spatial variance $\mathrm{Var}(\overline{\mathrm{Y}}_{\mathrm{i}})$, we obtain a new, absolute variance $\mathrm{Var}_{\mathrm{s.occ}}$ that expresses variance arising from occupancy patterns:

$$\mathrm{Var}_{\mathrm{s.occ}} = \left(\frac{\mathrm{s}_{o,u}^{2}}{\mathrm{s}^{2} + \mathrm{s}_{o,u}^{2}}\right)\mathrm{Var}(\overline{\mathrm{Y}}_{\mathrm{i}}) \qquad \text{Eq. Q.14}$$

Similarly, if we multiply $\mathrm{Var}(\overline{\mathrm{Y}}_{\mathrm{i}})$ by the proportion of variance from within-groups, we obtain $\mathrm{Var}_{\mathrm{s.pop}}$ that expresses variance arising among populations in occupied sites:

$$\mathrm{Var}_{\mathrm{s.pop}} = \left(\frac{\mathrm{s}^{2}}{\mathrm{s}^{2} + \mathrm{s}_{o,u}^{2}}\right)\mathrm{Var}(\overline{\mathrm{Y}}_{\mathrm{i}}) \qquad \text{Eq. Q.15}$$

$\mathrm{Var}_{\mathrm{s.occ}}$ and $\mathrm{Var}_{\mathrm{s.pop}}$ sum to $\mathrm{Var}(\overline{\mathrm{Y}}_{\mathrm{i}})$ and so may be substituted into Eq. Q.8 to yield:

$$\mathrm{CV}_{\mathrm{s}}^{2} = \frac{\mathrm{Var}_{\mathrm{s.occ}}}{\overline{\overline{\mathrm{Y}}}_{\mathrm{i}}^{2}} + \frac{\mathrm{Var}_{\mathrm{s.pop}}}{\overline{\overline{\mathrm{Y}}}_{\mathrm{i}}^{2}} \qquad \text{Eq. Q.16}$$

Eq. Q.16 shows that $\mathrm{CV}_{\mathrm{s}}^{2}$, an index of spatial variation among site means, decomposes into two dimensionless indices that we call *relative occupancy variance* and *relative population variance.*

We note that estimates of variance components can be biased by several factors which would, in turn, affect estimates of $\mathrm{Var}_{\mathrm{s.occ}}$ and $\mathrm{Var}_{\mathrm{s.pop}}$ and their dimensionless forms in Eq. Q.16. First, biased estimates may occur when there are few observations (sites) per group (Gray 2012), which is the case in the dataset containing only seven lakes. Second, ANOVA is not robust to unequal group variances, which is certain to occur because the unoccupied group always has zero variance. However, these biases should not affect our results because all variables within a dataset would be subjected to the same degree of bias. Thus, while the absolute magnitude of $\mathrm{Var}_{\mathrm{s.occ}}$ and $\mathrm{Var}_{\mathrm{s.pop}}$ may reflect minor bias, the relationships sought among variables (e.g., mean-variance scaling) should not be affected.

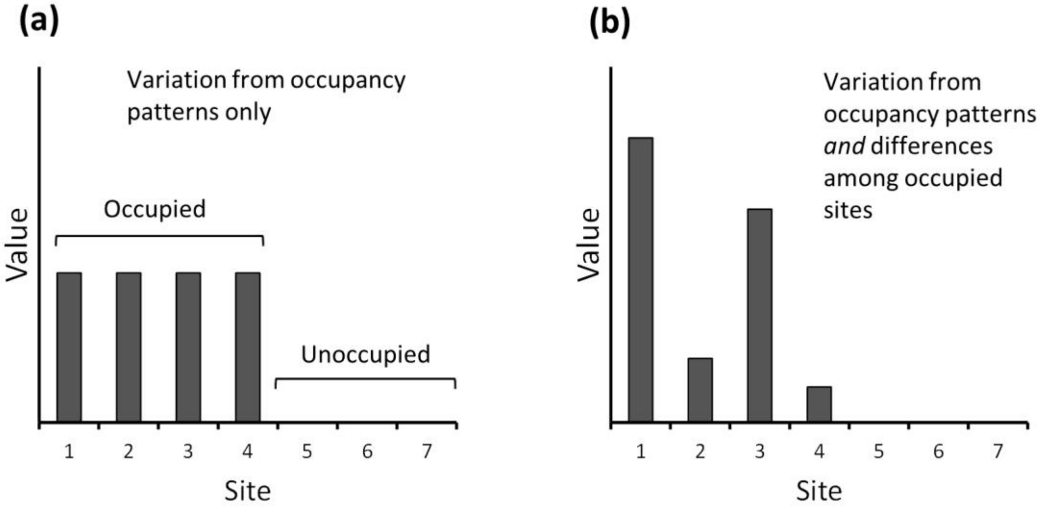


Figure Q.1. Plots showing two sources of variation among sites. (a) Spatial variation arising solely from differences between occupied and unoccupied sites i.e., no variation among populations in occupied sites (Interclass correlation coefficient = 1.0). **(b)** Spatial variation arising from both differences between occupied and unoccupied sites and variation among populations in occupied sites (ICC = 0.5).

REFERENCES

Gray, B. R. 2012. Variance components estimation for continuous and discrete data, with emphasis on cross-classified sampling designs. Pages 200–227 *in* R. A. Gitzen, J. J. Millspaugh, A. B. Cooper, and D. S. Licht, editors. Design and analysis of long-term ecological monitoring studies. Cambridge University Press.

Proulx, R., C. Wirth, W. Voigt, A. Weigelt, C. Roscher, S. Attinger, J. Baade, R. Barnard, N. Buchmann, F. Buscot, N. Eisenhauer, M. Lange, A. Milcu, P. A. Niklaus, Y. Oelmann, S. Rosenkranz, and M. Vicky. 2010. Diversity promotes temporal stability across levels of ecosystem organization in experimental grasslands. PLoS One 5:1–8.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. Page 859. Second edition. W. H. Freeman and Co., New York.

APPENDIX R. USING MEAN-VARIANCE SCALING TO QUANTIFY THE EFFECTS OF ABUNDANCE ON PSV AND ITS COMPONENTS

In this Appendix, we use a hypothetical example to illustrate how mean-variance scaling can quantify the effect of abundance on the spatial and temporal components of persistent spatial variation (PSV). From the equation for F and its components (Eq. R.1), we note that the spatial component CV_s^2 (Eq. R.2) and the temporal component ${\mathrm{CV}_{\mathrm{t.var}}}^{-1}$ (Eq. R.3) are squared CV's and thus ratios of variances and squared means.

$$\mathrm{F} = \frac{\mathrm{MS}_{\text{among sites}}}{\mathrm{MS}_{\text{within sites}}} = \mathrm{CV}_s^2 \cdot \mathrm{CV}_{\mathrm{t.var}}^{-1} \cdot \frac{\mathrm{n_k}}{\mathrm{n_i}} \qquad \text{Eq. R.1}$$

$$\mathrm{CV}_s^2 = \frac{\mathrm{Var}(\overline{\mathrm{Y}}_\mathrm{i})}{\overline{\overline{\mathrm{Y}}}_\mathrm{i}^2} \qquad \text{Eq. R.2}$$

$${\mathrm{CV}_{\mathrm{t.var}}}^{-1} = \frac{\overline{\mathrm{Y}}_\mathrm{K}^2}{\sum_{\mathrm{i}=1}^{\mathrm{n}} \mathrm{var_i}} \qquad \text{Eq. R.3}$$

Scaling of means and variances on a log-log plot is a common means of determining whether variation changes with mean abundance. The null expectation is that the scaling exponent b = 2 when variability neither increases nor decreases with mean abundance (Taylor 1961, Kilpatrick and Ives 2003). Different values of b also have specific meanings for CV's, as follows (McArdle et al. 1990, Ballantyne and Kerkhoff 2007):

1. When *b* =2, the corresponding CV does not change with mean abundance
2. When *b* >2, CV is an increasing function of mean abundance
3. When *b* < 2, CV is a decreasing function of mean abundance

Thus, scaling the variances in Eqs. R.2-R.3 and their corresponding means measures the effect of mean density on the spatial and temporal CV's; CV_s^2 and ${\mathrm{CV}_{\mathrm{t.var}}}^{-1}$. Furthermore, these CV terms combine in a known way to create PSV (Eq. R.1) and so the effects of abundance on these terms can be traced up to PSV. Note that $\mathrm{Var}(\overline{\mathrm{Y}}_\mathrm{i})$ in Eq. R.2 further decomposes into two variances, which are scaled with their means in the main text but are not part of our example here.

Fig. R.1 shows two possible ways in which abundance can affect CV_s^2 and ${\mathrm{CV}_{\mathrm{t.var}}}^{-1}$ and, in turn, PSV measured by the F-value. In Fig. R.1a, spatial variability increases with mean (b > 2) while temporal variability does not (b = 2). The net result is that F grows with abundance because abundance increases the value of CV_s^2 but does not affect ${\mathrm{CV}_{\mathrm{t.var}}}^{-1}$.

In contrast, Fig. R.1b shows the case where temporal variability increases with mean (b > 2) while spatial variability is unaffected (b = 2). In net, F decreases with abundance because abundance increases temporal variability which decreases its inverse $\mathrm{CV_{t.var}}^{-1}$ and it does not change the value of CV_s^2 . Because scaling slopes may reinforce each other (e.g., both < 2) or may act in opposition (e.g., one > 2, one <2), the net effect of abundance on F will result from their particular combination.

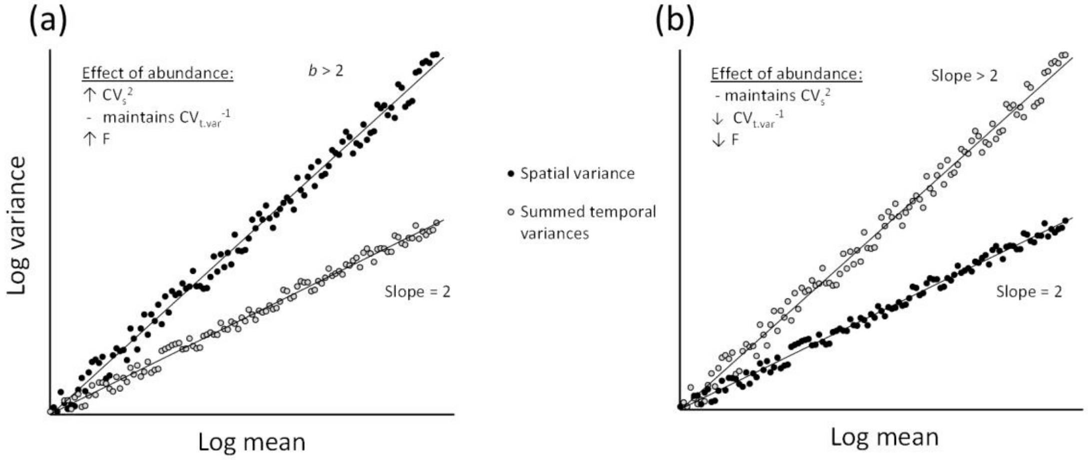


Figure R.1. Hypothetical mean-variance scaling plots illustrating possible effects of abundance on variance terms of Eq. R.1 (Eq. 4.1 in main text). Through its effects on spatial variance and summed temporal variances (corresponding to CV^2_s and $CV_{t.var}^{-1}$, respectively), abundance could: **(a)** Accentuate spatial variability (scaling slope b > 2) and not affect temporal variability (b = 2), thereby increasing F, or **(b)** not affect spatial variability (b = 2) and increase temporal variability (b > 2), thereby decreasing F.

REFERENCES

Ballantyne, F., and A. J. Kerkhoff. 2007. The observed range for temporal mean-variance scaling exponents can be explained by reproductive correlation. Oikos 116:174–180.

Kilpatrick, A. M., and A. R. Ives. 2003. Species interactions can explain Taylor's power law for ecological time series. Nature 422:65–68.

McArdle, B. H., K. J. Gaston, and J. H. Lawton. 1990. Variation in the size of animal populations: Patterns, problems and artefacts. Journal of Animal Ecology 59:439–454.

Taylor, L. R. 1961. Aggregation, variance and the mean. Nature 189:732–735.

APPENDIX S. CHEMICAL HARDNESS OF LAKE IONS

Table S.1. Sources of chemical hardness (η) estimates used in analyses. Also indicated is the related chemical species used as an alternative if an estimate could not be found.

Variable	Substitute used	Source
Mg^{2+}		Parr and Pearson 1983
Na^{+}		Parr and Pearson 1983
SO_4^{2-}		Parr and Pearson 1983
Ca^{2+}		Parr and Pearson 1983
Cl^{-}		Parr and Pearson 1983
K^{+}		Pearson 1988
Fe^{3+}		Parr and Pearson 1983
Mn^{2+}		Parr and Pearson 1983
Dissolved inorganic carbon	CO_2	Parr and Pearson 1983
Total organic carbon	Mean of six carbohydrates	Torrent-Sucarrat et al. 2010
NO_3^{-}/NO_2^{-}	NO_2^{-}	Pearson 1988
NH_4^{+}	NH_3	Parr and Pearson 1983
Dissolved oxygen	O_2	Pearson 1988
Total P	P	Parr and Pearson 1983

REFERENCES

Parr, R. G., and R. G. Pearson. 1983. Absolute hardness: companion parameter to absolute electronegativity. Journal of the American Chemical Society 105:7512–7516.

Pearson, R. G. 1988. Absolute electronegativity and hardness: Application to inorganic chemistry. Inorganic Chemistry 27:734–740.

Torrent-Sucarrat, M., F. De Proft, P. W. Ayers, and P. Geerlings. 2010. On the applicability of local softness and hardness. Physical chemistry chemical physics : PCCP 12:1072–80.

APPENDIX T. BEST PREDICTORS OF PSV: FULL AND REDUCED MULTIPLE REGRESSION MODEL RESULTS

We used multiple regression to identify the best predictors of persistent spatial variation (PSV) from those hypothesized (see Introduction and Methods). We entered all factors for which data were available into standard multiple regression models and sought terms that significantly predicted F (Table T.1). Because overfitting may occur in cases with too many factors, we repeated the analyses using the backward stepwise routine in Statistica v.8.0 to see whether the important factors were retained in reduced models (Table T.2). The two methods consistently indicated the importance of the same predictors (mainly temporal CV^{-1} and autocorrelation time) within datasets.

See following full pages for Tables T.1 and T.2.

Table T.1. Results from standard multiple regression models predicting log(F). Predictors are ranked by their semi-partial correlation coefficient. Significant predictors appear in bold. Superscripts: * = log-transformed; †= square-root transformed.

Data	Predictor	t	p	Semi-partial correlation	R^2	Df	F	p
Rock pool species	**Temporal CV^{-1}***	3.07	0.005	0.31	0.71	6,29	11.59	<0.0001
	OMI†	2.40	0.023	0.24				
	Mean density*	1.37	0.180	0.14				
	Autocorrelation time	1.26	0.217	0.13				
	Skewness	0.66	0.513	0.07				
	Tolerance	-0.25	0.805	-0.03				
Rock pool species & env. variables	**Temporal CV^{-1}***	3.25	0.003	0.35	0.60	3,34	16.67	<0.0001
	Autocorrelation time*	0.98	0.336	0.11				
	Skewness	0.84	0.407	0.092				
Lake ions	**Temporal CV^{-1}***	3.95	0.003	0.48	0.86	4,9	14.04	0.0006
	Chemical hardness†	1.86	0.096	0.23				
	Autocorrelation time*	0.47	0.652	0.06				
	Skewness	0.25	0.809	0.03				
Lake environmental variables	**Temporal CV^{-1}***	3.11	0.005	0.44	0.58	3,21	9.60	0.0003
	Autocorrelation time*	3.11	0.005	0.44				
	Skewness	-0.16	0.876	-0.02				
Lake species	Temporal CV^{-1}*	1.25	0.429	0.40	0.90	12,1	0.73	0.734
	Tolerance	0.63	0.640	0.20				
	Doubling time	0.55	0.678	0.18				
	Autocorrelation time*	0.23	0.858	0.08				
	OMI	0.18	0.887	0.06				
	Northern range limit	-0.09	0.945	-0.03				
	Trophic level	-0.14	0.911	-0.05				
	Skewness	-0.26	0.840	-0.08				
	Mean density*	-0.34	0.791	-0.11				
	Mass	-0.36	0.779	-0.12				
	Southern range limit	-0.37	0.773	-0.12				
	Fecundity*	-0.48	0.71	-0.16				
Lake species & environmental variables	**Temporal CV^{-1}***	7.22	0.000	0.44	0.83	3,48	75.69	<0.0001
	Autocorrelation time*	2.36	0.022	0.14				
	Skewness	-1.58	0.120	-0.10				

Table T.2. Results from backward stepwise regression models predicting log(F). Predictors are ranked by their semi-partial correlation coefficient. Significant predictors appear in bold. Superscripts: * = log-transformed; †= square-root transformed.

Data	Predictor	t	p	Semi-partial correlation	R^2	Df	F	p
Rock pool species	**Temporal CV^{-1*}**	6.94	0.000	0.77	0.59	1,34	48.12	<0.0001
Rock pool species & environmental variables	**Temporal CV^{-1*}**	6.88	0.000	0.56	0.57	1,36	47.28	<0.0001
Lake ions	**Temporal CV^{-1*}** **Chemical hardness†**	5.52 3.25	0.000 0.008	0.62 0.36	0.86	2,11	34.19	<0.0001
Lake environmental variables	**Temporal CV^{-1*}** **Autocorrelation time***	3.55 3.19	0.002 0.004	0.49 0.44	0.58	2,22	15.06	<0.0001
Lake species	**Temporal CV^{-1*}**	4.41	0.001	0.40	0.59	1,12	19.44	0.0009
Lake species & environmental variables	**Temporal CV^{-1*}**	13.84	0.000	0.89	0.79	1,50	191.6	<0.0001

APPENDIX U. SUPPLEMENTARY ANALYSIS OF PSV PREDICTORS

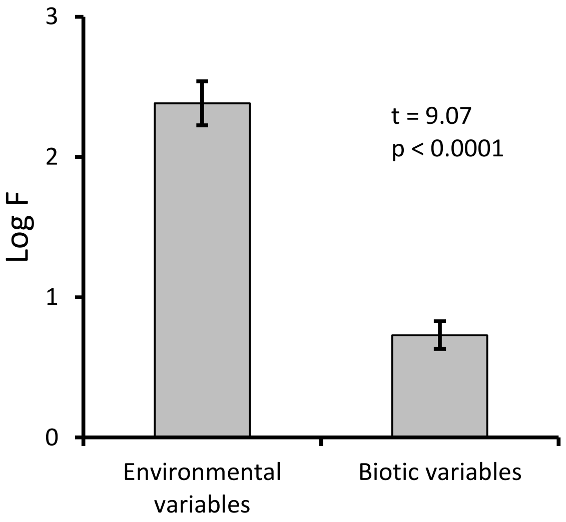


Figure U.1. Persistent spatial variation was significantly higher in lake environmental variables than biotic variables.

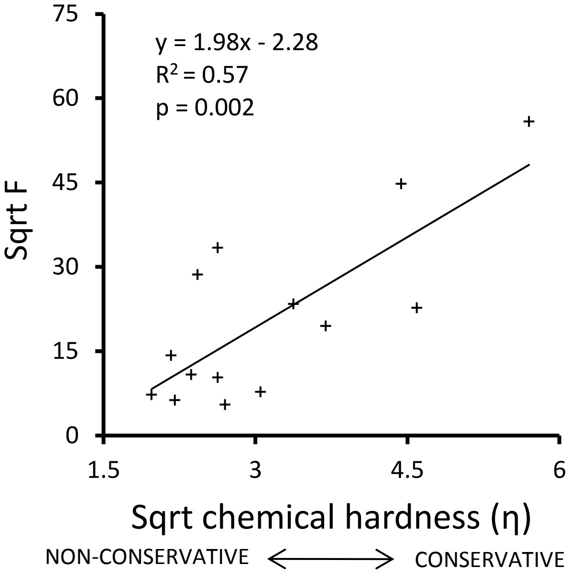


Figure U.2. In lakes, published values of hardness for a chemical species (point) was significantly related to its persistent spatial variation.

APPENDIX V. NAMES AND ABBREVIATIONS OF STUDY VARIABLES AS PLOTTED IN FIGURE 4.2

Table V.1. Abbreviation and names of study variables plotted in Figure 4.2 for Wisconsin lakes and Jamaican rock pools.

Abbreviation	**Variable**	**System**
Mg	Magnesium (Mg^{2+})	Wisconsin temperate lakes
Na	Sodium (Na^{+})	
SO_4	Sulfate (SO_4^{2-})	
Ca	Calcium (Ca^{2+})	
Cl	Chloride (Cl^{-})	
K	Potassium (K^{+})	
Fe	Iron (Fe^{3+})	
Mn	Manganese(Mn^{2+})	
SiO_2	Silica	
DIC	Dissolved inorganic carbon	
DOC	Dissolved organic carbon	
TOC	Total organic carbon	
NO_3	Nitrate (NO_3^{-})	
NH_4	Ammonium (NH_4^{+})	
DO	Dissolved oxygen	
P	Total phosphorus	
pH	pH	
Cond.	Conductivity	
Alk.	Alkalinity	
Temp.	Water temperature	
Light input	Light intensity at surface	
Light atten.	Light attenuation	
Species richness	Total species count	
Total density	Total density of organisms	
Rock bass	*Ambloplites rupestris*	
Mysis	*Mysis relicta*	
Temp.	Water temperature	Jamaican rock pools
pH	pH	
DO	Dissolved oxygen	
Chl a	Chlorophyll a	
Turbidity	Water turbidity	
Species richness	Total species count	
Total abundance	Total density of organisms	