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Beyond description: the active and effective way to infer processes from spatial patterns

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Abstract. The ecological processes that create spatial patterns have been examined by direct measurement and through measurement of patterns resulting from experimental manipulations. But in many situations, creating experiments and direct measurement of spatial processes can be difficult or impossible. Here, we identify and define a rapidly emerging alternative approach, which we formalize as "space as a surrogate" for unmeasured processes, that is used to maximize inference about ecological processes through the analysis of spatial patterns or spatial residuals alone. This approach requires three elements to be successful: a priori hypotheses, ecological theory and/or knowledge, and precise spatial analysis. We offer new insights into a long-standing debate about process–pattern links in ecology and highlight six recent studies that have successfully examined spatial patterns to understand a diverse array of processes: competition in forest-stand dynamics, dispersal of freshwater fish, movement of American marten, invasion mechanisms of exotic trees, dynamics of natural disturbances, and tropical-plant diversity. Key benefits of using space as a surrogate can be found where experimental manipulation or direct measurements are difficult or expensive to obtain or not possible. We note that, even where experiments can be performed, this procedure may aid in measuring the in situ importance of the processes uncovered through experiments.

Key words: a priori inference; competition; dispersal; diversity; ecological processes; invasion; space as a surrogate; spatial pattern; spatial residuals.

> *[W]e must find ways to quantify patterns of variability in space and time, to understand how patterns change with scale . . . , and to understand the causes and consequences of pattern . . . .*
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> —Simon A. Levin (1992:1961)

INTRODUCTION

A major objective of ecological research has been quantifying and determining the underlying processes responsible for spatial patterns of ecological phenomena (Tilman and Kareiva 1997, Liebhold and Gurevitch 2002, Tuda 2007). To date, the link between spatial pattern and process has been addressed using: (1) experimentation (e.g., Fonteyn and Mahall 1981, Stoll and Prati 2001, Kikvidze et al. 2005, McIntire and Hik 2005); (2) direct parameterization of spatial models from data (e.g., Turchin 1998, Schultz and Crone 2001, Clark et al. 2004); (3) simulation of processes within a spatial domain (e.g., Pacala et al. 1996, He and Mladenoff 1999, Fall and Fall 2001, Fortin and Dale 2005, McIntire et al. 2007); and (4) through analysis of the spatial pattern itself with the goal of uncovering the process (e.g., Olden et al. 2001, Tuomisto et al. 2003, McIntire 2004, Fang 2005, Broquet et al. 2006, Fajardo and McIntire 2007). Authors that have attempted the fourth approach have often indicated difficulty when measuring the process directly or building experiments (e.g., Jolles et al. 2002, Fajardo and McIntire 2007) because they are not practical (Schurr et al. 2004, Clark 2007), prohibitively expensive, unethical, or overly time consuming, leaving them with this pattern–process approach as a sole option. The aim of this paper is to propose a framework for using space as a surrogate for uncovering ecological processes from the study and analysis of spatial patterns or spatial residuals.

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According to Keitt and Urban (2005), the lack of a clear link between process and spatial pattern is the Rosetta Stone of ecology, i.e., if we can unlock this difficulty, we will gain other insights into ecological functioning. Unfortunately, numerous studies have concluded that analyses of spatial patterns per se are insufficient to explain the processes responsible for the observed ecological patterns (Cale et al. 1989, Silvertown and Wilson 1994, Moravie and Robert 2003, Borcard et al. 2004), leaving the biological significance of the pattern largely unknown if subsequent manipulations are not pursued (Murrell et al. 2001). This perspective has prevailed because of several known *biological* phenomena: (1) various processes may create the same pattern (Cale et al. 1989, Perry et al. 2006); (2) causality may not be straightforward (Rees et al. 1996, Turner et al. 2001) (e.g., well-defined nonrandom processes can produce patterns indistinguishable from apparent random assembly; Cale et al. 1989, Molofsky et al. 2002); and (3) processes may also be the result of specific patterns (Stoll and Prati 2001)—a dominant paradigm of landscape ecology (Turner 1989). While these phenomena have elements of truth, their inverses are not necessarily false. In other words, a single process *can* create a single precise pattern (e.g., Schurr et al. 2004, Fajardo and McIntire 2007), nonrandom processes *can* create highly structured patterns (e.g., Molofsky et al. 2002, Broquet et al. 2006), and the impact of pattern on process may not act at the same scales as the impact of process on pattern and so will be discernible. Though the bridge between process and pattern is imperfect and can be confounded by other processes acting at diverse scales (Real and McElhany 1996, Jolles et al. 2002), biological organization exists, and so the link between process and pattern remains to be uncovered and utilized for understanding and prediction (e.g., Barot et al. 1999, Schurr et al. 2004).

Recent changes in our understanding of causality (Pearl 2000, Shipley 2000), the continued development of analytical tools for spatial data (Perry et al. 2002, Borcard et al. 2004, Wiegand and Moloney 2004, Fortin and Dale 2005, Keitt and Urban 2005, Ives and Zhu 2006), and our awareness that a priori multiple hypothesis testing is inferentially strong (Burnham and Anderson 2002), have started to minimize the perceived biological limitations of the process–pattern link. This has allowed studies across a broad range of topics and using a wide variety of spatial analytical tools to successfully infer process from pattern (e.g., Barot et al. 1999, Jolles et al. 2002, Schurr et al. 2004). With this novel understanding, the numerous prior studies stating that focal processes cannot be determined by the observed patterns may, in part, reflect a limitation of the precision of the analytical approach used, rather than an insurmountable biological phenomena limiting process–pattern linkages. We propose that the perception of biological limitations may be heavily rooted in analytical issues (which we address and elaborate on below) that, once detected and solved, can help us enhance the link between process and spatial pattern.

Here, we demonstrate the rapidly emerging use of spatial patterns to help elucidate the underlying ecological processes and formalize this procedure with the title "space as a surrogate" for unmeasured or unmeasurable processes. This is not just a statistical technique per se, rather, it is a merging of three components that *must* act together: precise implementation of ecological theory and/or knowledge, a priori inference, and precise application of spatial analytical tools. In essence, this is related to the inverse modeling approach that examines the outcomes of ecological processes and infers the cause via direct parameterization of process models (Ogle et al. 2004). We also contextualize this procedure within the broader literature of model inference (Burnham and Anderson 2002), spatial analysis (Fortin and Dale 2005), and strong inference (Platt 1964), while demonstrating its importance and utility. Our presentation of the concept of space as a surrogate is organized in three sections. In the first section, we examine why the process–pattern link (in the absence of experimentation) has been often rejected in the past. Second, we present a framework for utilizing space as a surrogate for underlying processes. In the third section, we present six case studies from a diverse set of fields showing the success of this approach.

PREVIOUS ATTEMPTS

In many cases, efforts to deduce process from spatial pattern have been rejected or deemed insufficient due to the aforementioned biological limitations, leaving the interpretation of spatial patterns in the realm of suggestion or impossibility rather than inferential determination (Phillips and MacMahon 1981, Lepš 1990, Real and McElhany 1996, Jeltsch et al. 1999, Jolles et al. 2002, Molofsky et al. 2002, Fortin and Dale 2005). We propose that these apparent biological limitations are in part due to two analytical issues: (1) the spatial statistical hypotheses used had limited model precision, i.e., use of the spatial-statistics toolbox that was limited to relatively vague pattern description (Grieg-Smith 1961, Pielou 1962, Kershaw 1973, Phillips and MacMahon 1981, Real and McElhany 1996); and (2) studies used spatial analysis in an inductive description mode and not in a deductive model comparison mode (e.g., Haase et al. 1997, Jeltsch and Moloney 2002, Borcard et al. 2004; numerous examples in Dale [1999] and Fortin and Dale [2005]) (Fig. 1: left oval). Since the aim of our paper is to demonstrate the idea that process *can* be at least partly understood by pattern, we do not spend time reviewing spatial-pattern analysis (see Cressie [1993], Dale [1999], and Fortin and Dale [2005] for this purpose) nor do we critique the spatial-pattern analysis literature in the past. Instead, we elaborate on previous inference limitations perceived by authors in light of the two analytical issues identified above.

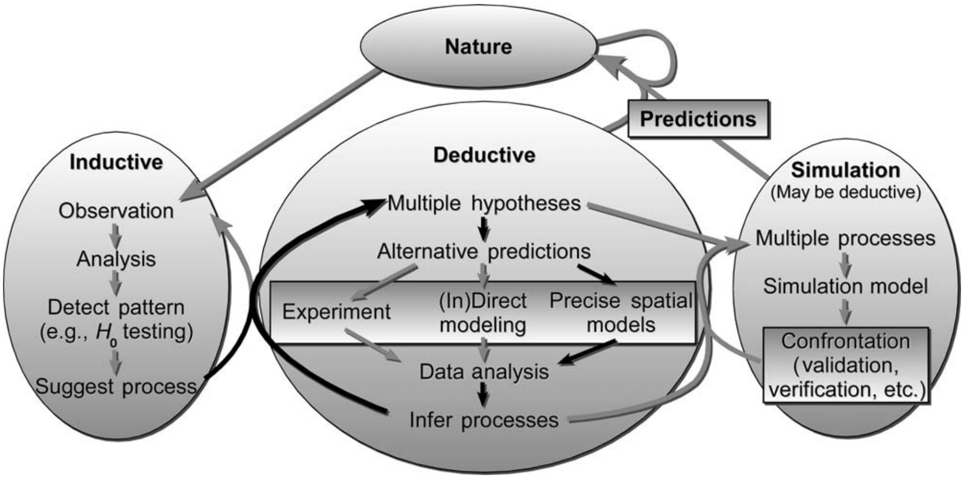

FIG. 1. Our proposed framework within the contexts of inductive, deductive, and simulation approaches to description and prediction for spatial phenomena and ecology in general. The black arrows show our space-as-a-surrogate framework within the deductive approach, alongside experimentation and modeling by parameterization of processes. The black arrows outside of the central oval indicate sources of ecological knowledge. Rectangular boxes indicate where we confront our predictions with data. The arrow from Nature to Nature reflects strict empiricism.

Examples of the first issue, that pattern analysis may have been insufficiently precise to gain strong inference on process, are those that examine relationships between inter-plant distance and plant size (Pielou 1962, Fowler 1986, Biging and Dobbertin 1995, Briones et al. 1996, Kikvidze et al. 2005) or those asking whether individuals are clustered or random using a spatial-point pattern analysis (e.g., Barbour 1969, Ripley 1976, Phillips and MacMahon 1981). The limitations with pattern analysis were often attributed to the imprecision of the biological process (Phillips and MacMahon 1981), or to the possibility that multiple processes may be the cause of a single spatial pattern (Real and McElhany 1996). The longstanding question about whether competition drives desert shrub occurrence, for example (Fonteyn and Mahall 1981, Phillips and MacMahon 1981), has been recently revisited using a sequence of alternative models that were more sophisticated than simple clustering or complete spatial randomness (for some specific scale), thereby quantifying the relative support for competition and dispersal processes (Schurr et al. 2004). In the case of multiple processes creating single patterns, we cannot reexamine the particular data set as used by Real and McElhany (1996), but dispersal of disease has been approached successfully in an aquatic system (Jolles et al. 2002), demonstrating that it is possible. We note also that a spatial pattern has *numerous* features, including scale, intensity, autocorrelation, clustering, and variability, that can each be addressed with precision. If a study only examines general notions of scale (e.g., larger, small, fine), the inference will be weaker than if precise notions of scale are used (e.g., the pattern resulting from the process of interest must be 1–4.5 m). Thus, the spatial pattern of a phenomenon can be simultaneously characterized by multiple features, such as a combination of a precise scale and spatial correlation structure (e.g., Fajardo and McIntire 2007).

There are numerous examples of the second analytical issue where the links between pattern and process were deemed insufficient to gain good inference because of the inductive approach to spatial analysis used (Anderson 1971, Borcard et al. 2004, Kikvidze et al. 2005). In these and other cases there were implicit or explicit statements (e.g., Borcard et al. 2004, Paoli et al. 2006) that correlation does not imply causation and that processes can only be deduced via experimental manipulation (Levin 1992, Silvertown and Wilson 1994). We now know such formulations are at best incomplete, and the recent emphasis on a priori model comparisons partly addresses this problem (Burnham and Anderson 2002). Furthermore, numerous statistical tools can aid in revealing this correct specification, including using biologically inspired neutral models (e.g., see Olden et al. 2001, Broquet et al. 2006) and structural-equation models (e.g., McIntire [2004]).

In a previous attempt to link spatial patterns and ecological processes in a general framework, Jeltsch et al. (1999) explicitly proposed three steps to detect underlying processes in nature from a spatial pattern: (1) characterization of the spatial pattern; (2) development of hypotheses about the underlying processes generating the observed pattern; and (3) evaluation of the hypotheses (experimental or modeling mediated). A similar a posteriori mode is presented in Fortin and Dale (2005: Fig. 1.1).

APPROACH

Our framework constitutes an enhanced version of these previous attempts and we place it within the context of scientific inference alongside other deductive methodologies (Fig. 1). Thus, we diverge from Jeltsch et al.'s (1999) approach and propose that process and pattern can be explicitly linked with precise statistical analysis and rigorous ecological knowledge using a priori reasoning. We present here the whole approach as follows: (1) collect ecological understanding of spatial structures, both conceptual and empirical, about the system of interest (Fig. 1: black arrows outside of central oval); (2) develop precise ecological, multiple a priori hypotheses (or single hypothesis if the model structure is known, but the intensity of pattern is not; Clark et al. 2004) that cover all reasonable relevant processes affecting the system under study, and the development of resulting spatial patterns these hypothesized processes would create for such a system (including any neutral hypotheses) (Fig. 1: upper part of central oval); and (3) evaluate and select the best hypotheses using advanced spatial-analysis techniques, parameter-precision (constrained parameters to biologically meaningful values), and model-selection approaches (Fig. 1: lower part of central oval). We next explain these three elements in detail.

Ecological understanding of spatial structures

Both physical and biological variables in nature display spatial patterns (Levin 1992, Legendre 1993, Dale 1999, Legendre et al. 2002, Tuda 2007). One explanation of this is that endogenous ecological processes operate between neighboring individuals, thus creating autocorrelation (Tilman and Kareiva 1997, Lennon 2000, Stoll and Bergius 2005). The traditional way of describing spatial pattern is based on the premise that samples taken from nearby locations may be more similar to each other than samples taken far apart, due to some unmeasured factor that varies spatially (i.e., spatial autocorrelation) (Rossi et al. 1992, Cressie 1993, Legendre 1993, Fortin and Dale 2005, Ives and Zhu 2006). This is a non-process-based description that leaves spatial analysis in the inductive domain, and may be overly static for numerous applications. Using a more active mode of description, patterns of individuals' distributions may be spatially autocorrelated because of contagious biotic processes (e.g., dispersal, competition), historical factors (e.g., disturbance; Leduc et al. 1992), or spatially structured environmental predictors (e.g., soil carbon; Haining 1993, Legendre et al. 2004, Bellier et al. 2007; MacKenzie et al. 2008). If we are unable to easily measure these processes directly, a spatial pattern will be evident in the raw data or in the model residuals. These spatial structures can be used in our favor if we conceive of them as active results of (or contributions to) biological processes. Spatial autocorrelation, while often seen as a data nuisance (i.e., observations' dependency), can become a great aid in our understanding of natural systems (e.g., Dale 1999, Liebhold and Gurevitch 2002, Keitt and Urban 2005).

A good knowledge of the system becomes crucial when developing and stating hypotheses about the ecological processes responsible for the phenomenon under study. These hypothesized processes must be translated into observable spatial patterns that need to be identified and characterized quantitatively in an accurate way. Translating these processes or underlying causes of spatial dependence into spatial pattern is not always straightforward. Below (see *Examples*) we present six different examples where this translation was achieved successfully and with great inferential gain.

Multiple a priori hypotheses

We have known for a long time that studies that contain a single working hypothesis (including a single null statistical hypothesis) are flawed for several reasons (Chamberlin 1890, Hilborn and Stearns 1982, Anderson et al. 2000). For example, we may only look at ecosystems or subsystems where we know we can find support for the hypothesis of interest, regardless of how important it is to ecological systems in general (Johnson 1999). Furthermore, it is well known, though not universally appreciated, that rejecting a hypothesis does not confirm any particular alternative hypothesis (Popper 1979) because innumerable unstated alternative hypotheses might also be correct. Third, when data do support a single hypothesis, we still do not know how important that hypothesis is, compared to alternative processes. Thus, we may find support for the phenomenon of interest without being aware of its importance in the system.

In contrast, proposing several alternative hypotheses that could explain an ecological phenomenon before a project gets underway (hypothetico-deductive reasoning) can promote inference by reducing spurious model fits (Burnham and Anderson 2002). To illustrate, predicting an ecological outcome based on hypothesized functioning of the system (i.e., a priori hypothesis) is akin to betting on the horse race before it starts. Success is unlikely due to fortuitous idiosyncrasies. In contrast, explaining why a horse won after the race is over (i.e., a posteriori explanation) will always be correct, but may be prone to idiosyncrasies of that particular race (e.g., the faster horse fell). Good predictions of the next similar situation are much less likely due to this hindsight bias. Furthermore, it is best to generate several plausible and reasonable hypotheses (Chamberlin 1890, Burnham and Anderson 2002) because in an unmanipulated system, correlations between predictor variables may cause a hypothesis to appear good, when in reality it is a second, correlated hypothesis that is actually driving the support for the first hypothesis. If these hypotheses include biological processes (i.e., not only empirical relationships), then the inference about the functioning of the system is maximized because causality in unmanipulated systems is contained within the hypotheses, not within the data analysis (Borcard et al. 2004).

Spatial analytical techniques

The objective of this section is not to provide a comprehensive guide to spatial analyses in ecology (for this see Cressie [1993], Dale [1999], Fortin and Dale [2005], and the 2002 special issue in *Ecography* [Volume 25, Issue 5]), but to highlight some key points about spatial analyses in the context of using space as a surrogate for unmeasured or unmeasureable processes. Notably, the modern tools for spatial analysis allow precise descriptions of the patterns (e.g., not just "clustered" or "not clustered"). When field studies use only a portion (e.g., point pattern) of the information available in the spatial patterns, they are less likely to discern the process–pattern link than if a more complete analysis of the spatial pattern is performed (see *Examples*, below). This occurs because, statistically speaking, any residual variance from a model implies model misspecification (Fotheringham et al. 2002). From a biological perspective, this misspecification may have structure and therefore information, if it is anticipated. The portion of this residual variance that can be identified as having spatial structure (Borcard et al. 1992, 2004, Legendre 1993, Wagner and Fortin 2005) (i.e., spatial dependence) is more useful than unstructured residual error (McIntire 2004). Since it may not be physically, biologically, or logistically possible to specify or even measure the perfect model for any particular ecological system, it is reasonable to utilize this spatial variance as part of the study (Keitt et al. 2002), rather than attempting to eliminate it through a variety of statistical tools.

Indeed, many recent studies in diverse fields (see examples elaborated below) have utilized specific spatial structures tied strongly with pertinent biological hypotheses to achieve a better understanding of their systems (Desrochers and Fortin 2000, Lugon-Moulin and Hausser 2002, Fang 2005, Fajardo and McIntire 2007). Furthermore, we can add precision to our analysis of spatial scale; rather than simply discussing "scale" we can discuss "particular scales" (Wiegand et al. 2007). For instance, if we were to look at the spatial pattern of forest-tree growth using semivariograms, we could quantify the spatial scale of the spatial pattern. But this would not necessarily help us in understanding which processes were driving the patterns at this scale. If, on the other hand, we proposed that tree competition acts between trees, and trees are growing at approximately 1–4.5 m spacing, then we would expect that there should be a spatial pattern occurring at 1–4.5 m, if competition is happening. We develop this further as an example below. To enhance many analyses, using marked analyses (Fortin and Dale 2005) (i.e., analysis of the spatial pattern of a variable of interest, not just its mere location in space) to assess continuous processes (e.g., competition) even when there are only discrete entities that experience it (i.e., plants) can be very advantageous. Thus, we can examine continuous processes (e.g., growth increment, xylem pressure, dispersal distance, bird song, mortality rate) sampled at the individual's spatial location, with much greater precision than if we analyze it as a discrete process.

EXAMPLES

Here we describe six examples from recent literature where several alternative, a priori spatial pattern models were merged with biological understanding of the processes to gain insight into how the system under study works. With these six examples, we attempt to show the diverse array of topics for which this approach is useful, but we note that these are just a sample; there are other studies, produced over a span of decades, that have had similar success using this approach (e.g., Bachacou and Decourt 1976, Franklin et al. 1985, Barot et al. 1999, Wiegand et al. 2000, Jolles et al. 2002, Schurr et al. 2004).

Example 1: forest-stand dynamics

Inter-tree competition is often thought of as the primary driver of forest-stand dynamics (Hara 1984, Bullock and Burkhart 2005). It is clear, however, that microsite will have an important impact on stand dynamics as well. Empirical studies have repeatedly shown that spatial and size distributions of trees in a community bear the fingerprint of these factors (Bachacou and Decourt 1976, Bullock and Burkhart 2005). It is difficult to directly measure these two processes simultaneously, as they dynamically affect individual growth and development of a forest stand. In a recent study conducted in *Pinus ponderosa* plantations in Patagonia, Chile, we detected and separated these two confounded factors using semivariograms and a priori hypotheses about the functional form of the process linked with precise a priori parameter ranges of these semivariogram models (Fig. 2) (Fajardo and McIntire 2007). We used the following knowledge of the biological system to develop our analysis. Competition in early developing forests will be predominantly asymmetrical, with taller trees shading adjacent shorter trees (Weiner 1990). As a result of this asymmetric relationship, immediate tree neighbors will have a greater difference in growth rates than between any given tree and the average tree of the site. Also, two trees that are separated by a third tree will have more similar growth rates to each other than the intermediate neighbor. Thus, the proposed spatial structure to represent this pattern would be a dampening wave of growth rates through space from all trees, but limited to a tight range of spatial scale for the sill parameter in the semivariogram (i.e., the scale of tree–tree neighbor distance, 1–4.5 m, in this example). The dampening effect will be due to overlapping competitive signals from all trees. As an alternative hypothesis, microsite variability will create the more generally observed positive spatial autocorrelation, represented by an increasing semivariogram model. A third hypothesis is that growth is random, represented by a nugget semivariogram model. We added a nested function combining the competitive and microsite processes to allow for the possibility that both would be acting simultaneously (see Fig. 2). Using tree cores collected at the base of the trees, we evaluated the support for these alternative hypothesized processes, solely by the spatial pattern of growth through the forest stands.

We found that the processes affecting forest growth through the first 20 years is dynamic through time. Our general observed pattern began with early random growth, followed by microsite-mediated growth, followed by competition-mediated growth. There were variations on this sequence, where more dense sites showed competitive interactions earlier and less productive sites showed later competition as trees did not fill space as fast. We were able to test the approach by successfully identifying several events in which, independent of our work, some of the trees were removed from the forest with the goal of removing competitive interactions; we detected this in our analysis through a corresponding reduction in the importance of the competitive effect.

Example 2: invasion of exotic trees

Site-level mechanisms for invasion of *Acer platanoides* into native forests of the northeastern United States are not known. In general, invasion mechanisms can act either directly (competition) or indirectly (altering ecosystem processes) on the invaded community (Levine et al. 2003). In an attempt to uncover the mechanisms for this invasion, Fang (2005) presented graphs of population size structure vs. distance from a forest edge with a priori hypotheses linking spatial patterns to particular combinations of data (Fig. 3). For active invasion, the size–distance graph of the invader should have a negative upper slope, and the native species should have a flat upper slope and either a negative slope (i.e., invader preventing native-species understory recruitment) or flat lower slope (i.e., invader cutting off edge-related native-species recruitment).

Results from this study supported the active-invasion model. *A. platanoides* individuals showed a strong negative upper slope in the size–distance graphs, and the dominant native species showed negative slopes of the lower slope in the size–distance graphs. In addition to the result that there was no correlation between *A. platanoides* presence and overstory mortality, these findings are inconsistent with the gap or space-filling hypothesis. This support for the a priori spatial hypothesis representing a competitive mechanism for invasion, rather than a space-filling random model, helps to elucidate the mechanisms underlying the invasion.

Example 3: landscape effects on movement

Describing connectivity in landscapes has been a key aspect of research in landscape ecology (Wiens 2001). Using biological assays allows us to understand the *effective* connectivity (McIntire et al. 2007) of a landscape, which can be more relevant than connectivity measured by various objective indices. Broquet et al. (2006) used two alternate a priori models of American marten (*Martes americana*) movements in logged and unlogged boreal forests in Ontario, Canada. To examine the effective connectivity, they built a model representing a least-cost path across the logged and unlogged landscapes, and contrasted the support of this model (reproduced here as Fig. 4) with a null Euclidean-distance model. Using known marten biology and field observations, they created these least-cost paths by assigning a high friction value to openings (e.g., from logging and roads) and a low friction value to closed forest. Least-cost paths between individuals were calculated, resulting in an estimate of the effective distance between individuals.

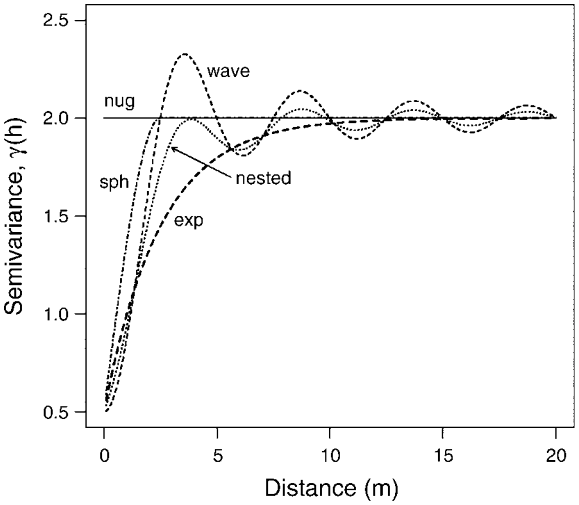

FIG. 2. The five theoretical semivariograms models [(1) nugget (nug), (2) spherical (sph), (3) exponential (exp), (4) wave, and (5) nested (a mixture of wave and exponential)], related to a corresponding set of biological processes [(1) random processes, (2 and 3) microsite processes, (4) competition among trees, and (5) a combination of competition and microsite processes] that were fitted to the spatial pattern of annual tree rings in four young, even-aged ponderosa pine plantations in Patagonia, Chile (Fajardo and McIntire 2007). These spatial signatures were tied, a priori, to competition and microsite heterogeneity, thereby acting as a surrogate for these biological processes. (Note: semivariance is half the variance of the distance h between each point and all points separated from it by the distance given on the x-axis.) (The figure is reproduced from Fajardo and McIntire [2007: Fig. 1]; used with permission.)

Results showed that in the unlogged landscape, effective distances and Euclidean distances were similar, and correlated significantly with genetic distances. In the logged landscape, genetic distance did not correlate with Euclidean distance, but it did correlate with effective distances. This indicates that the movement of individuals and gene flow through the logged landscapes was not the linear, shortest path movement. Rather, movement was along a path that is better estimated by a least-cost path that avoids openings.

Example 4: dispersal of freshwater fish

Freshwater-lake systems present various possible dispersal processes creating different levels of connec-

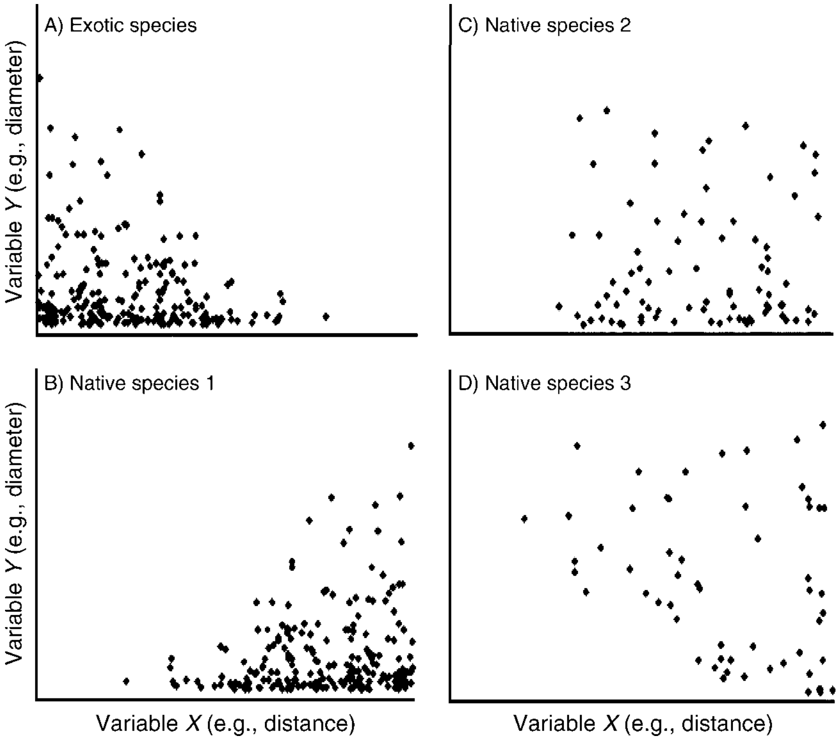

FIG. 3. A priori hypotheses (graphically depicted) relating variable X (distance from invasion origin) and variable Y (e.g., size, density) for exotic- and native-species recruitment (Fang 2005). For active invasion, the size–distance graph of the invader should have a negative upper slope, and the native species should have a flat upper slope and either a negative slope [i.e., invader preventing native-species understory recruitment: (A) and (C) co-occur] or flat lower slope [i.e., invader cutting off edge-related native-species recruitment: (A) and (D) co-occur]. (The figure is reproduced from Fang [2005: Fig. 1]; used with permission.)

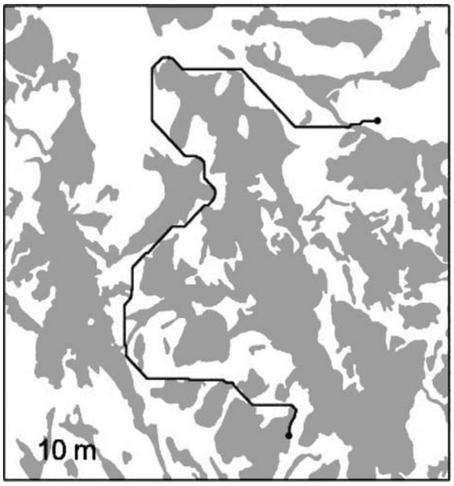

FIG. 4. Least-cost movement path connecting the location of two individuals of American marten through a heterogeneous landscape (from Broquet et al. 2006). The length of this movement path and that of a simpler Euclidean distance were compared to the genetic distance separating these individuals to understand movement. (The figure is reproduced from Broquet et al. [2006: Fig. 2a]; used with permission.)

tivity via rivers and streams (Olden et al. 2001). For example, elevation changes along water courses may modify the ability of fish to move between lakes. Furthermore, lakes may be relatively easy to cross, compared to moving along streams. Olden et al. (2001) represented these two hypotheses as part of a series of eight a priori hypotheses corresponding to different processes of dispersal for freshwater fish through a network of lakes in south central Ontario, Canada. Using a Procrustean approach, they represented these alternative movement hypotheses as alternative distance matrices to be used in the analysis. They included straight-line Euclidean-distance measures as a hypothesis representing a null model.

Results revealed a high concordance between patterns in fish community composition and lake isolation. In a few instances, community composition of a lake showed greatest concordance with straight-line distances. But in most cases, alternative isolation indices, from among the set of alternative processes proposed, demonstrated how the fish communities were established. Some lakes had a fish community that showed strongest concordance with watercourse distance, regardless of number or size of lakes, indicating that fish movement to those lakes depended upon the linear distance along the rivers and streams connecting them. Fish communities in lakes that showed greatest concordance with elevation-adjusted water-course distances indicated that elevational change created a component of lake isolation.

Example 5: natural-disturbance boundaries

Understanding why natural disturbances stop is a much-overlooked part of natural disturbance dynamics research. McIntire (2004) attempted to understand the processes responsible for stopping two types of natural disturbances, wildfires and mountain pine beetle outbreaks, using spatial signatures of disturbance effects at their boundaries in south-central British Columbia, Canada. Here, it was proposed that there could be site-level factors responsible for stopping the disturbance spread as well as non-site factors such as weather (or fire suppression efforts in the case of wildfire) or beetle dispersal limitation. Using a priori structural equations representing alternative models for disturbance stopping, estimates were made of the correspondence between site-level descriptors (e.g., aspect, tree basal area, tree species, and tree mortality). Since these boundaries would have a monotonic spatial structure in tree mortality (dead trees to live trees), it was proposed that if this spatial structure was relegated to an indirect effect through site-level factors, then exogenous factors (e.g., weather) could be removed as likely forces stopping the disturbance. Conversely, if a direct effect of spatial pattern across the boundaries remained, then the disturbance stopped at least partially due to external forcing.

Results showed that about half of the mountain pine beetle outbreaks stopped solely due to site-level factors. This indicated that insect-dispersal limitation was not a driver of the outbreak stopping. In these cases, landscape structure was responsible for stopping the disturbances. All seven fire boundaries, on the other hand, were stopped at least partially from non-site factors (most likely weather or fire suppression) in addition to site-level factors. A historical examination of the weather conditions that occurred toward the end of the fire could potentially isolate fire suppression as the primary external driver of the fire stopping (though this was not done in the study).

Example 6: distribution of plant species in tropical forests

The determination of what drives tropical-plant species distributions has been a debated topic in plant ecology. Recently, Tuomisto et al. (2003) tested three alternative hypotheses about the drivers of plant species distributions in western Amazonian tropical forests. They considered inventories of plant groups with contrasting dispersal modes: pteridophytes (ferns in general) and the Melastomateceae (shrubs and small trees). These two groups provide "independent test cases" for determining the relative importance of distinct hypotheses explaining plant species distribution. They contrasted three models for floristic similarities among sites: dispersal limitation based on neutral theory (Hubbell 2001), uniform distribution (i.e., a null hypothesis), and local environmental determinism (as a contrast to neutral theory and support to the regeneration-niche theory). They tied each of these potential processes to specific predictions a priori using partial Mantel tests.

In their analysis they found no support for the uniform model but did find support for each of the other two hypotheses. Using relative measures of support allowed the authors to quantify the relative influence of each supported process. They found that environmental determinism explained more of the variation in floristic differences than dispersal limitation, where the latter process was supported mostly for the Melastomataceae, among which many species have known dispersal limitations (e.g., animal dispersed).

DISCUSSION

Cautions

It is possible that this "space as a surrogate" approach will not work in all situations. Sometimes the process–pattern link will be too diffuse. In other cases, the residual spatial structure may incorporate too many unmeasured phenomena. But it is important to distinguish imprecise spatial analysis (analysis issues) from imprecise spatial patterns (biological issues), and we believe these two types of precision have regularly been confounded. As with all a priori approaches, the success of the study will only be as good as the biologically derived a priori hypotheses. We note that many processes can act at scales much larger than they may appear. For example pollen dispersal, which is predominantly limited to relatively short distances, has been shown to have effects at scales much larger than the distance that pollen can travel (Satake and Iwasa 2002). Under certain circumstances it may be important to simulate the potential processes concurrently with confronting the hypotheses with data, as the translation between hypothesis and spatial pattern will not always be clear.

The construction of multiple hypotheses is not always straightforward or simple, i.e., there may be difficulties in making them competitive instead of compatible (Hilborn and Stearns 1982). We think, however, that this is primarily an analysis-precision problem rather than a hypothesis creation problem, as we have demonstrated here. Furthermore, the inclusion of hypotheses that correspond to process interaction should be promoted since this represents a common phenomenon in nature (see *Example 1*, above, for competition and microsite interaction).

Lastly, one argument against our approach would be that science works as an iterative process, where a priori predictions are just the result of a previous study's conclusion. Thus, the knowledge of the initial spatial patterns would be a relevant and significant first step (as recommended by Jeltsch et al. [1999] and Fortin and Dale [2005]) before the determination of any causal factor on spatial patterns. First, we note that where exploration and hypothesis creation are the objectives of the study (i.e., determination of spatial patterns), spatial approaches may be very powerful in accomplishing these objectives (see examples in Perry et al. [2002], Fortin and Dale [2005]). Second, the determination of spatial patterns constitutes an essential part of our approach, therefore this argument is not necessarily contradictory.

Conclusions and future directions

To move the analysis of spatial pattern from inductive description to deductive inference, it is important to reflect a priori about all the potential or probable underlying responsible processes behind the spatial patterns. Rather than ask "What are the spatial patterns?" we can work within an inferential mode: "What are the expected underlying processes responsible for the observed spatial structures?" Which processes can we measure directly and which ones will be impossible to measure? For those that we cannot measure, can we establish a precise and unique spatial signature? Incorporating these particular spatial signatures into a priori hypotheses and testing their support with data while utilizing precise spatial statistical analyses can thus provide us stronger inference for understanding ecological systems. From the studies presented here, we propose that spatial patterns can be usefully decomposed into underlying processes using multiple, strong a priori hypotheses linked to spatial-pattern creation. These studies could not have been done using more traditional inferential approaches because they require manipulations that were not possible. Similarly, using the intact system (rather than a manipulated system) these studies addressed the actual relevance in the system of an underlying process, instead of its potential influence or its presence/absence. Furthermore, experimental manipulations may eliminate feedback processes, thus giving the often-false appearance of a simple system with good inference (Hilborn and Stearns 1982).

The connection between space and process is in a period of rebuilding after being rejected by numerous authors over the past 50 years. With emphasis on a priori hypotheses tied to processes and more precise statistical analyses, we are dramatically enhancing the inference gained from the pervasive links between process and spatial patterns. Tying processes to other statistical analytical tools, such as wavelets, local-pattern analysis, local geostatistics, and many others, has enormous potential for enhancing our understanding of the processes underlying pattern generation and change. Finally, we have focused on spatial patterns in this paper because of the prevalence in the ecological literature; however, the identical procedure and inferential gains can be done on temporal data patterns.

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