REVIEW AND SYNTHESIS

Disturbance-driven changes in the variability of ecological patterns and processes

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Abstract

Understanding how disturbance shapes the dynamics of ecological systems is of fundamental importance in ecology. One emerging approach to revealing and appreciating disturbance effects involves examining disturbance-driven changes in the variability of ecological responses. Variability is rarely employed as a response variable to assess the influence of disturbance, but recent studies indicate that it can be an extremely sensitive metric, capturing differences obscured by averaging and conveying important ecological information about underlying causal processes. In this paper, we present a conceptual model to understand and predict the effects of disturbance on variability. The model estimates qualitative changes in variability by considering disturbance extent, frequency and intensity, as well as ecosystem recovery, and thereby captures not only the immediate effects of disturbance but also those that arise over time due to the biotic response to an event. We evaluate how well the model performs by comparing predictions with empirical results from studies examining a wide variety of disturbances and ecosystems, and discuss factors that may modify or even confound predictions. We include a concise guide to characterizing and detecting changes in variability, highlighting the most common and easily applied methods and conclude by describing several future directions for research. By considering variability as a response to disturbance, we gain another metric of fundamental system behaviour, an improved ability to identify organizing features of ecosystems and a better understanding of the predictability of disturbance-driven change – all critical aspects of assessing ecosystem response to disturbance.

Keywords

Aquatic and terrestrial ecosystems, Beyond-Before-After-Control-Impact, heterogeneity, mean–variance scaling, scale.

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INTRODUCTION

Disturbance is a key component of all ecosystems. It affects every level of biological organization and spans a broad range of spatial and temporal scales. With origins that can be either natural or anthropogenic, and either endogenous or exogenous, disturbances are inherently diverse (White 1979; White & Jentsch 2001). Not surprisingly, ecosystem response to disturbance is also enormously diverse. Within ecosystems, disturbance may have non-uniform effects due to the fact that ecosystems are themselves heterogeneous with respect to their abiotic characteristics and history.

Among ecosystems, differences in the physical environment and the biota determining the processes that control ecosystem dynamics may result in wide variation in ecosystem response (White & Jentsch 2001). These factors make discerning generality in disturbance effects difficult. Examining changes in the *variability* of ecological responses following disturbance may provide additional insights about disturbance effects and their causal processes.

That disturbance can alter the variability of ecological systems has been suggested for some time. More than 30 years ago, Rosenzweig (1971) showed that nutrient enrichment could have a destabilizing effect on the

dynamics of a simple predator–prey model. In the same decade, Beddington & May (1977) demonstrated that the variability of fishery yields in a stochastic environment would consistently increase when populations were harvested under particular regimes. A more general treatise was later published by Odum et al. (1979), who argued that ecosystems perturbed beyond a threshold value would experience increased variability (Odum 1985). Research on the topic then waned, despite the steady emergence of concepts fostering appreciation for the spatial and temporal variability of ecological systems and the role of disturbance in generating patterns. These included concepts such as stability, resistance and resilience (Holling 1973; May 1973; Harrison 1979; Pimm 1984), as well as the concept of historical or natural variability (Sprugel 1991; Swanson et al. 1994; Landres et al. 1999). In the early 1990s, however, interest in variability as a response to disturbance resurfaced when Underwood et al. began designing studies to detect environmental disturbances by focussing on variability (Underwood 1991, 1992; Chapman et al. 1995).

Since then, recognition that variability per se contains important ecological information has broadened tremendously. Whereas variability was once considered a meaningful attribute of ecological systems only in association with the mean, ecologists increasingly cite a need for independent examinations of variability (Collins 1992; Palmer et al. 1997; Micheli et al. 1999; Benedetti-Cecchi 2003), where variability describes a deviation from some measure of central tendency for a given variable. One reason for this enhanced interest is that variability can be a highly sensitive metric independent of the mean, capturing effects that are, in some cases, not detected or obscured by averaging (Underwood 1991; Callaghan & Holloway 1999; Piazzi et al. 2004). For example, increasing temporal variability in the abundance of exploited fish populations can signal negative impacts of fishing, even in the absence of declining fish abundance (Hsieh et al. 2006). Similarly, altered spatial variability in soil resources can indicate legacies of historical agriculture, despite averaged values remaining comparable with undisturbed areas (Fraterrigo et al. 2005; Flinn & Marks 2007). As a response, variability can also provide insights on the processes that structure ecosystems when assessed over multiple spatial and/or temporal scales. For instance, Palmer et al. (1997) showed that variance in the abundance of stream biota mapped onto the spatial heterogeneity of nearbed stream velocity, and thus generated several hypotheses about the factors driving species distributions. Altered variability may have a predictive capacity as well. Recent work has demonstrated linkages between increased variability and impending state transitions in both aquatic and terrestrial systems (Schlesinger et al. 1996; van Nes & Scheffer 2003; Oborny et al. 2005; Carpenter & Brock 2006; Su et al. 2006). Investigating changes in variability in

response to disturbance will generate an increased understanding of pattern and process across a broad spectrum of ecological systems, scales and applications.

Given mounting evidence for disturbance effects on variability, we need a means of identifying the conditions that produce changes in variability, and an appreciation for why they emerge. Here, we present a conceptual model that addresses how and why disturbance can alter variability. The model is an extension of a previous effort by Turner et al. (1993) to describe changes in landscape dynamics due to the immediate effects of disturbance frequency, extent and intensity in a successional ecosystem. We incorporate indirect effects of disturbance due to biotic response to address changes in temporal variability and spatial variability over time. We evaluate the accuracy of model predictions using empirical results from an extensive literature search. We also address how disturbance intensity and biological organization can affect response variability.

We highlight numerous published studies throughout, both for illustration and to identify deficiencies in our understanding of the relationship between disturbance and variability. The latter discussion focusses mainly on how scale can confound efforts to relate disturbance and variability within a predictive framework, and includes suggestions that should stimulate progress in light of these obstacles. Papers were located through electronic searches using the keywords: disturbance, heterogeneity, variance and variability, and by examining the references in these citations. A number of the studies focus on marine communities and soil resources, reflecting topics on which many early papers were published (e.g. Robertson et al. 1988; Underwood 1991; Warwick & Clarke 1993). Although these search methods may have missed studies, those included here represent a wide range of disturbances, ecosystems and scales, and thus allow for broad inference and testing of our model.

To encourage research on disturbance–variability relationships, we also review methods for quantifying and detecting changes in variability. Our goal is to offer guidance in choosing appropriate measures and tests for a variety of applications and levels of biological organization. Thus, we focus on approaches that, in our judgement, have the most potential for being applied to a wide range of responses, rather than provide an exhaustive review of available methods. We conclude by suggesting future research directions that will expand our ability to understand and predict disturbance-driven changes in variability. We describe four topical areas that are ripe for investigation: regime shifts, multiple disturbances, duration of effects and isolation of effects due to different disturbance characteristics. We close by identifying potential candidate analyses and perspectives that may yield further insight into

predicting and understanding variability as response to disturbance.

A CONCEPTUAL MODEL FOR UNDERSTANDING DISTURBANCE EFFECTS ON VARIABILITY

Disturbance is usually defined as 'any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resource pools, substrate availability, or the physical environment' (White & Pickett 1985). In this review, we examine events that fall under the conventional definition, as well as events that might be thought of as chronic (e.g. loss of predators, eutrophication, pollution). Evaluating disturbance effects on variability across this frequency gradient allows for a more complete test of our conceptual model and increases the generality of our understanding of the relationship between disturbance and variability.

It is widely recognized that disturbance frequency, defined as the mean number of events per time period (Pickett & White 1985), affects ecosystem response. As frequency increases, the recovery potential of disturbance-intolerant organisms declines (Collins et al. 2001). This in turn can destabilize community dynamics and increase the variability of a system (Collins 2000; Collins et al. 2001). Under extremely high frequency or chronic conditions, species sorting may occur over time due to the selection of individuals adapted to the disturbance. Thus, we might expect post-disturbance variability, relative to pre-disturbance conditions, to be elevated for a longer period of time compared with systems that have experienced a discrete event. Variability in these systems may also stabilize more gradually, and only after the disturbed state has become the baseline condition (Collins 2000). Discrete events, in contrast, would be expected to produce more transient changes in variability.

Other attributes of disturbance that may influence resultant patterns of variability include the extent and intensity of an event (Sousa 1984; Petraitis et al. 1989; Moloney & Levin 1996). Similar to Pickett & White (1985), we define disturbance extent as the size of the area affected by the event, and intensity as the physical force of the event per unit area per unit time. Spatially extensive disturbances may initially reduce variability by homogenizing pre-existing differences within patches, whereas smaller disturbances may create heterogeneity and thus enhance within-patch variability. Disturbance intensity can influence patterns of variability by altering the biological template of source populations (Turner et al. 1998), even though intensity per se is defined independently of its effects on the biota. More intense disturbances are likely to cause greater reduction in species' abundances, which may translate to higher community variability as poorer competitors vie for newly available resources (Collins et al. 2001; Bertocci et al. 2005). It is the outcome of the interaction among frequency, extent and intensity that will ultimately determine how variability changes following disturbance (Moloney & Levin 1996); thus, any model predicting the impact of disturbance on variability needs to consider these characteristics simultaneously.

The landscape equilibrium model developed by Turner et al. (1993) generates predictions about the effects of disturbance on variability for events that vary in several attributes. To allow comparison among disturbances and ecosystems, extent is scaled to ecosystem size (S), and disturbance return time (1/frequency) is scaled to the recovery interval of the response variable (T). This approach not only describes the spatial and temporal characteristics of an event, but also provides a mechanism for incorporating differences in disturbance intensity by adjusting the recovery interval of the response. The resultant state space shows that qualitatively different landscape dynamics are achieved under various combinations of S and T (Turner et al. 1993).

The Turner et al. model focusses on the physical changes in ecosystem properties caused by disturbance itself, exploring how fires with different spatial and temporal characteristics might alter the spatial patterns of eight vegetation classes representing various seral stages. The potential for biotic responses, due to changes in species abundances and distributions, to further affect ecosystem variability was not investigated in the original study. For example, the model assumes that a seed source for each vegetation class is available instantaneously in the landscape following fire (Turner et al. 1993), despite the fact that fires, particularly those of high intensity, can reduce propagule availability and species may vary in dispersal capacity (Turner et al. 1998). Such indirect effects of disturbance are likely to alter variability in unique ways, and it is vital to consider them when predicting changes in variability following disturbance.

Our review of the literature indicated that recruitment strategy and trophic status are key factors influencing variability over time, and thus among the primary determinants of indirect effects. Recruitment strategy directly affects how species recolonize space following disturbance. In a spatial context, the ability to regenerate in situ tends to favour a return to pre-disturbance patterns of heterogeneity, whereas regeneration strategies that require the dispersal of propagules or organisms may increase or decrease population variability over time (Mou et al. 2005). Increases in spatial variability tend to arise when species have limited dispersal capacity, reflecting the patchy distribution of remnant populations. Decreases in spatial variability occur when species have the capacity for widespread dispersal because this promotes an even distribution of individuals (Ranta et al. 1998; Reed et al. 2000; Liebhold et al. 2004;

Forrest & Arnott 2007). In time, patterns of spatial variability are likely to converge as species with limited dispersal recover (Reed *et al.* 2000). There are, however, instances in which patterns can become entrenched for several decades. Dominance by a single life-history type may reduce colonization opportunities for other species, fixing an established pattern of low variability until competitive hierarchies develop or mortality occurs (Armesto *et al.* 1991). The isolation of uncolonized habitat from source populations can also increase the likelihood that colonization by dispersal-limited species will be slow and that widely dispersed species, or species whose recruitment is stimulated by disturbance (e.g. serotinous species, species that persist in resting stages or can spread vegetatively or parthenogenically), will initially dominate an area (Turner *et al.* 1998). In a temporal context, these circumstances may contribute to enhanced community variability, as less diverse communities may show greater fluctuation in time compared with more diverse communities (Cottingham *et al.* 2001).

Another way that recruitment strategy can indirectly alter patterns of variability is by influencing the buffering capacity of a population to future environmental stochasticity. Populations in which recruitment is size-, age- or stage-dependent are the most likely to experience altered buffering capacity because, in such populations, disturbance could lead to the selective removal of a class with high reproductive effort. This in turn could drastically reduce overall population growth and impair a population's ability to rebound from other events that decrease abundance. Fisheries offer a prime example of these dynamics: in some cases, they have elevated the temporal variability of fish populations by truncating the size–age structure of exploited populations, which in turn reduced their capacity to buffer environmental events (Hutchings & Reynolds 2004; Hsieh *et al.* 2006). There are potentially many other systems in which these dynamics could occur (e.g. silviculture, game), but have not been investigated.

Trophic status can also differentially affect variability by influencing how fluctuations in driving variables are transmitted along the food chain. For example, while there is ample evidence suggesting that longer food chains that include predators can enhance the temporal variability of herbivores due to over-compensation (Pimm & Lawton 1977; He *et al.* 1994; Halpern *et al.* 2005), a recent study concludes that the effects of predators on the variability of autotrophs are idiosyncratic and vary by ecosystem (Halpern *et al.* 2005). Because many studies document top–down control of systems, it is surprising that the effect of changes in predator abundance on autotrophs would not be consistently large. However, previous work indicates that the magnitude of a trophic cascade attenuates down the food chain, thus buffering lower trophic levels from both mean and variance effects of changing trophic diversity

(Shurin *et al.* 2002). Thus, an autotroph may be more sensitive to environmental fluctuations that affect a limiting resource (e.g. nutrient and light availability) than to food-web interactions (Halpern *et al.* 2005). An herbivore, on the other hand, may be sensitive to both variance in its prey base and variance in the abundance and distribution of its predators. The potential for such hierarchical scaling within food webs to impact patterns of temporal variability has been documented in a variety of systems (Carpenter *et al.* 1987; Ives *et al.* 2000; Rusak *et al.* 2001; Schmitz 2003); as have similar effects on the temporal correlation of spatial patterns (i.e. spatial synchrony; Liebhold *et al.* 2004).

Because indirect effects primarily influence the recovery of an ecosystem, we incorporated them into the model when estimating the recovery interval of the response variable. For example, we increased the recovery interval for species that are dispersal limited compared with those that disperse widely. Similarly, the food-web context of a particular species or assemblage, relative to the type of disturbance affecting it, might also alter the estimation of recovery. While this approach will not capture all indirect effects, it provides a useful starting point for integrating these processes into our proposed framework for understanding how disturbance alters variability.

MODEL PREDICTIONS VS. EMPIRICAL RESULTS

We examined how well empirical results reported in the literature (see above for search criteria) corresponded with the model's predictions to assess the utility of this framework (Appendix S1). We calculated the parameters S and T as defined above using information provided by individual studies. In cases where the information was not sufficient to calculate these parameters, we contacted the study's author(s) or experts in the field to obtain additional information about the disturbance and/or the focal organisms/processes. We then determined expected changes in variability according to the state space the parameters occupied (Fig. 1) and evaluated the consistency of the observed and predicted results (Appendix S1). When more than one response was examined in a study, we evaluated them separately, with the exception of responses that had identical values for S and T and showed qualitatively equivalent changes in variability. We did not estimate an overall effect size or perform a formal meta-analysis because of the qualitative nature of the model predictions and our interpretation of empirical results. We did, however, examine the potential for disturbance intensity or biological organization to affect the agreement between predicted and observed outcomes.

We found strong agreement between observed and predicted results when increases in variability were noted (Table 1). A spatial increase in variability was accurately
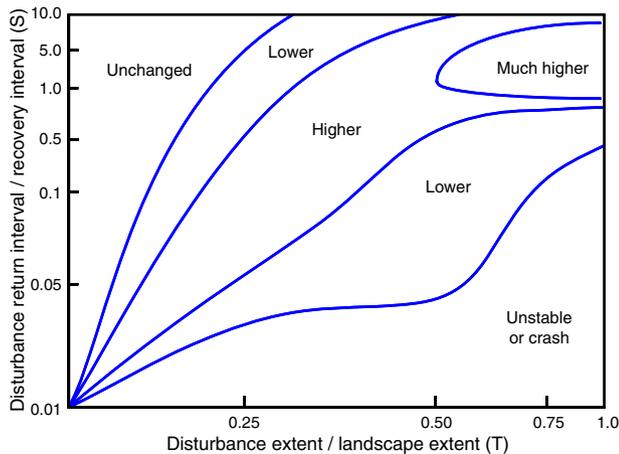
Figure 1 State-space diagram showing predicted changes in variability resulting from different combinations of S and T, where S describes the spatial characteristics and T describes the temporal characteristics of an event (adapted from Turner *et al.* 1993; see Appendix S2 for model parameters and assumptions). Differences in disturbance intensity can be incorporated by adjusting the recovery parameter. Likewise, indirect effects of disturbance can be integrated into the model by increasing or decreasing the recovery interval.

Table 1 Summary of results from an analysis evaluating the correspondence between empirical results reported in the literature and model predictions

Observed response	% of responses in agreement (observed/predicted)	% of studies in agreement (observed/predicted)*
Increase		
Spatial	72.2 (13/18)	93.8 (15/16)
Temporal	93.3 (14/15)	100 (7/7)
Decrease		
Spatial	50 (3/6)	50 (3/6)
Temporal	25 (1/4)	0 (0/2)
No change	33 (1/3)	33 (1/3)

*A study reporting more than one response was counted in agreement if the majority (> 50%) of responses were yes.

predicted by the model in 13 of 18 responses (72%). A temporal increase in variability was accurately predicted by the model in 14 of 15 responses. These patterns were consistent when we accounted for studies that reported multiple responses (Table 1). We did not detect any patterns that would suggest the model was biased towards certain types of disturbances or ecological attributes. Accurate predictions were made for studies focussing on the effects of natural and anthropogenic disturbances, as well as population-, community- and process-based responses. For example, observed increases in the spatial variability

of soil nutrient concentrations were correctly predicted following cultivation (Bennett 2004; Fraterrigo *et al.* 2005; Diekmann *et al.* 2007), timber harvest (Guo *et al.* 2004) and grazing (Schlesinger *et al.* 1996; Su *et al.* 2006). The model also accurately predicted an increase in the spatial variability of kelp forest communities following an El Niño disturbance (Reed *et al.* 2000), and tree density and plant cover and structure following fire (Kashian *et al.* 2005), and fire and grazing combined (Fuhlendorf *et al.* 2006). Accurate predictions about increases in temporal variability arose from studies concerning population or community response to fishing (Hsieh *et al.* 2006), predator manipulations (Micheli *et al.* 1999; Rusak *et al.* 2001), eutrophication (Cottingham *et al.* 2000) and simulated storm events (Bertocci *et al.* 2005). The model also correctly predicted that grassland invasion by a non-native species would result in an increase in the temporal variability of productivity (Bradley & Mustard 2005), and that fire would lead to an increase in the temporal variability of plant community composition (Collins 2000).

The model performed poorly, however, when decreases in variability were observed. The model accurately predicted a spatial decrease in variability in only three of six studies (50%), and a temporal decrease in variability was never predicted by the model, although we reviewed two studies that observed this response.

In these cases, we noted several factors that might have contributed to the inconsistencies. First, the disturbances in several of these examples were chronic rather than discrete. For instance, sewage discharge (Chapman *et al.* 1995; Balestri *et al.* 2004; Piazzi *et al.* 2004), release from grazing (Coleman *et al.* 2006), thermal pollution (Lardicci *et al.* 1999) and a variety of disturbances including organic enrichment, drilling, mining and an El Niño event (Warwick & Clarke 1993) all occurred essentially continuously in the cited studies. We assumed a disturbance return interval for these studies that was high (i.e. rapid return) relative to response recovery time and that was reasonable given the disturbance type (Appendix S1), but it is possible that these values still did not accurately characterize disturbance frequency. The fact that there was no recovery phase between when the disturbances occurred and when the systems were sampled may also present a problem because recovery is implicit in the model and factors into the temporal parameter. Consequently, our model generally may not be appropriate for predicting how chronic events affect variability.

In contrast, when the model was adjusted for differences in disturbance intensity, predicted and observed responses showed agreement. In the two studies we reviewed in which disturbance intensity was manipulated explicitly (Guo *et al.* 2004; Bertocci *et al.* 2005), the model accurately predicted an increase in variability (Appendix S1). In the study in which disturbance intensity was manipulated in a rocky intertidal

community, the temporal variability of community structure increased with disturbance intensity, whereas the temporal variability of individual taxa both increased and decreased (Bertocci *et al.* 2005). These patterns resulted because the disturbance reduced the abundance of some taxa by direct removal, and space became available for utilization by other taxa (Bertocci *et al.* 2005). These findings emphasize the importance of adjusting the recovery interval of the focal response to reflect differences in disturbance intensity. The results also beg the more general question of whether one can expect similar patterns of variability to emerge at different levels of biological organization.

Previous research has shown that populations tend to be more sensitive to perturbations than aggregate community properties such as total biomass, productivity and nutrient cycling (Cottingham & Carpenter 1998; Gonzalez & Descamps-Julien 2004). This pattern may arise for two reasons. First, complementarity among functionally similar species may exist within a community, which could buffer aggregate community properties from change (Cottingham & Carpenter 1998). Second, the component species of a community rarely, if ever, fluctuate in perfect synchrony (Doak *et al.* 1998). The more species in a community, the greater the chance that species fluctuations will overlap due to an increase in the range of responses to environmental variation (Gonzalez & Descamps-Julien 2004). We found several studies in which aggregate community variability tended to decrease while population or compositional variability tended to increase following disturbance (Cottingham & Carpenter 1998; Micheli *et al.* 1999; Bertocci *et al.* 2005). Yet there were also instances where the opposite was true. For example, both Terlizzi *et al.* (2005) and Stark *et al.* (2003) observed an increase in the variability of aggregate properties (total abundance) and a decrease in the variability of community composition in a marine system subjected to pollution by sewage discharge. In these examples, however, conclusions have to be tempered by the fact that there was no recovery period (discussed above).

Issues of scale

In our review of the literature, we found several studies in which the effects of disturbance on variability varied with spatial and/or temporal scale. For instance, the homogenization of plant communities following agricultural abandonment reduced the spatial variability of soil nutrients at fine spatial scales (Robertson *et al.* 1993; Lane & BassiriRad 2005), whereas diverse land management decisions enhanced broad-scale resource variability (Bennett 2004; Fraterrigo *et al.* 2005). Similarly, lake flushing due to typhoon activity decreased temporal variability in aquatic bacterial community composition over the short term, while community assembly and succession increased composi-

tional variability over the long term (Jones *et al.* in press). Scale-dependency emerges because different ecological processes drive distributions of resources and organisms, and the temporal and spatial extents of these processes vary (Greig-Smith 1979; Wiens 1989). In addition to shifts in the directions of the response, scale-dependency can lead to patterns of variability that converge over time as the relative influence of one process overtakes another (Kashian *et al.* 2005; Lane & BassiriRad 2005).

Another consequence of scale-dependency is that disturbance effects on variability may go undetected if there is a mismatch between the scale of observation and the scale at which dominant processes are operating (Duarte 1991). For example, in a study of the response of a Mediterranean seagrass (*Posidonia oceanica*) and its associated epiphyte community to urban and industrial effluent, differences in variability between disturbed and reference areas were most pronounced at fine scales, with intermediate scales often showing no difference and the response at broad scales varying depending on the taxa being considered (Balestri *et al.* 2004; Piazzi *et al.* 2004). This type of scale-dependency suggests that patterns of variability conditional upon disturbance extent may change depending on the tolerance and life-history attributes of individual taxa.

Given the potential for scale-dependency, what is the appropriate scale at which to investigate disturbance-driven changes in variability? Species-specific time scales, such as generation time, have been found to be appropriate for sampling the variability of animal and plant populations (Connell & Sousa 1983). The most appropriate temporal scale at which to sample abiotic attributes will vary, however, depending on their rate of turnover as well as the mechanisms that control turnover rate. Controlling processes will also dictate the scale at which to measure spatial variability because they define the domain at which the phenomenon of interest operates. In general, hierarchy theory (Allen & Starr 1982; O'Neill *et al.* 1986) offers a useful framework for evaluating the temporal and spatial scales of sampling. By decomposing a phenomenon into its functional components, and defining the lower-level mechanisms that determine pattern and the higher-level context that constrains it (O'Neill *et al.* 1986), there is the potential to predict how external factors will influence variability. Although few studies are implemented with this framework in mind, there are a growing number of examples that suggest *post hoc* applications can provide new insights about the scaling of ecological phenomena (Bennett 2004; Fraterrigo *et al.* 2005; Brown 2007). For example, in explaining patterns of carbon and nitrogen mineralization in black spruce forests following fire, Smithwick *et al.* (2005) implicitly invoked a hierarchical framework to tease apart governing factors at multiple spatial scales and evaluate their effects post-fire. Considered *a priori*, a hierarchical model

can be an effective tool for identifying the temporal and spatial domains of factors that could potentially alter response variability. These domains of scale could then be used to develop a sampling strategy appropriate for capturing the most interesting dynamics of the response (Horne & Schneider 1995; Palmer *et al.* 1997).

METHODOLOGICAL CHALLENGES TO CHARACTERIZING AND DETECTING CHANGES IN VARIABILITY

Our ability to understand how disturbance influences variability and manage the implications of disturbance-generated shifts in variability rests largely on how effectively we can characterize this response and distinguish between random and non-random fluctuations in its pattern. Characterizing and detecting changes in variability pose several non-trivial challenges; we discuss two critical problems here. First, there are numerous ways to measure variability, and the choice of measure can influence the result. Second, although statistical changes in variability can

be evaluated using standard linear models (e.g. regression, ANOVA, GLM), this approach may not always be sufficient to detect ecologically meaningful changes in variability. Several exhaustive reviews on the measurement and comparison of spatial and temporal variability have been published (Hurlbert 1990; McArdle *et al.* 1990; McArdle & Gaston 1992; Lepš 1993; Gaston & McArdle 1994), including one that focusses exclusively on spatial synchrony (Buonaccorsi *et al.* 2001); we point interested readers to these sources. Instead, we focus on the chief obstacles to furthering our understanding of disturbance-driven changes in univariate and multivariate variability and attempt to provide guidance on potential solutions (Table 2).

How do we measure variability?

Most ecologists are familiar with absolute and relative measures to characterize the spread of univariate data with respect to a frequency distribution. Absolute measures provide an index of dispersion in the same units as the data, have desirable statistical properties and are thus widely used

Table 2 Approaches to quantifying and comparing ecological variability

	Suitability	Advantages	Disadvantages	References and/or examples
Metrics for characterizing variability of response (Y)				
Standard deviation (SD)	U	Straightforward	No mean-variance scaling	McArdle *et al.* (1990), Gaston & McArdle (1994)
Coefficient of variation	U	Mean–variance scaling	Sensitive to skewed data	see above
SD of log-transformed Y	U	Mean–variance scaling, robust to skewed data	A constant must be added to zero values	see above
Population variability	U, T	Robust to non-Gaussian behaviour, suitable for short time series	Less straightforward	Heath (2006)
Multivariate dispersion	M	Measure compositional variability	Transformations may be needed to achieve mean–variance scaling	Anderson *et al.* (2006)
Time-lag analysis	M, T	Suitable for short time series, can reveal temporal patterns and rates of change	Transformations may be needed to achieve mean–variance scaling	Collins *et al.* (2000)
Semivariogram analysis	U, S	Can reveal scale-dependent patterns in spatial structure	Need many samples to estimate semi-variance at each lag	Burrows *et al.* (2002)
Variance components	U, S, T	Can reveal scale-dependency	No mean–variance scaling	Bennett (2004)
Approaches to comparing metrics				
Linear models	U	Straightforward	Sensitive to non-normality	Kashian *et al.* (2005)
Levene's test with median	U	Robust to non-normality		Brown & Forsythe (1974), Schultz (1985)
Euclidean-based analogue to Levene's test	M	Robust to non-normality		Rusak *et al.* (2001), Brown (2003), Piazzi *et al.* (2004)
Non-Euclidean-based analogue to Levene's test	M	Robust to non-normality		Anderson (2006)

Suitability refers to the type of data for which the metric or method is best suited: U, univariate, M, multivariate, T, time series, S, spatial.

to characterize variability (Sokal & Rohlf 1995; Zar 1999). Unfortunately, these measures are not appropriate for examining changes in variability of relative properties (e.g. abundance) because of the tendency for variance to increase with the mean [Taylor's power law (Taylor 1961; Duarte 1991]. Relative measures of variability, such as the coefficient of variation (CV) and the SD of log-transformed observations [SDL: (SD[log($C + X$)])], can accommodate variance–mean scaling and thus are more useful for comparing variability among biological properties (Williamson 1984; McArdle et al. 1990; Heath 2006). While the CV is the most common, the SDL is actually a more robust measure because it is less sensitive than the CV to highly skewed distributions and not subject to calculation bias if zero values are excluded (McArdle et al. 1990). Both metrics will be biased when the scaling coefficient between the mean and variance is not equal to 2 (McArdle et al. 1990). Given that the scaling coefficient generally falls between 1 and 2 (Murdoch & Stewart-Oaten 1989), some uncontrollable bias will likely be present in either measure for many ecological variables. Explicit recognition of biases in studies where the mean differs among the variables being compared is thus essential for ensuring the validity of comparisons based on these measures (Cottingham et al. 2001).

Other issues related to quantifying variability involve the corruption of estimates of response variability by other sources of variation. Sampling error is one such source that can potentially affect any metric. McArdle & Gaston (1995) describe an approach to separating variability due to sampling from an estimate of variability of underlying density. Compromised estimates of temporal variability can arise when measurements are collected in more than one site due to spatial variance (Stewart-Oaten et al. 1995). Because spatial replication is necessary for inferring general patterns, however, such confounding can be difficult to avoid. Stewart-Oaten et al. (1995) suggest an alternative estimator, which uses an estimate of spatial variance to correct this problem. Finally, Heath (2006) has proposed a new metric for measuring temporal variability when populations are subject to non-Guassian behaviour. Population variability (PV) quantifies variability as the average percent difference between all combinations of observed abundances. In addition to being robust to non-Gaussian behaviour, zero counts can be included in the data without biasing the calculation. Because variability is measured on a proportional scale, the metric is also useful for comparative applications (Heath 2006).

Measures of multivariate dispersion are needed to characterize the variability of most multivariate data sets. Multivariate dispersion is quantified by computing the average distance from an individual unit to the group centroid using an appropriate distance or dissimilarity measure (Anderson et al. 2006). Numerous dissimilarity measures are available, each placing a different level of emphasis on the importance of abundance (Clarke 1993; McCune & Grace 2002; Chao et al. 2005). Thus in choosing an appropriate dissimilarity measure to estimate multivariate dispersion, the first step is to determine the degree to which abundance should be emphasized. If measures use relative abundance data (e.g. Bray–Curtis), dispersion results may be biased due to mean–variance scaling (Anderson et al. 2006). Most relative dissimilarity measures also incorporate data transformations that alter collinearity in the system and make multivariate dispersion difficult to interpret with regard to the original species data (Anderson et al. 2006). For these reasons, the most valuable dissimilarity measures may be those that allow the relative weight placed on changes in composition vs. abundance to be explicitly specified and interpreted with reference to original species abundances (Anderson et al. 2006). One method, proposed by Collins et al. (2000), quantifies rates and patterns of variability in communities over time using abundance data in an approach similar to autocorrelation analysis. A conservative strategy to estimating multivariate dispersion will use a range of dissimilarity measures that span the continuum from emphasizing compositional change to changes in abundance (Anderson et al. 2006).

As above, 'compositional variability' can be characterized using multivariate dispersion measures, or with summary statistics from ordination and cluster analyses (Micheli et al. 1999). Whereas compositional variability expresses fluctuations in the abundance of component species, aggregate variability is concerned with changes in variables created by additively combining multiple species, such as total abundance, biomass or production (Micheli et al. 1999). Aggregate variability can be characterized using univariate measures of variability (e.g. SD, CV, SDL), although care is required when comparing aggregate communities that differ in diversity because of the potential for statistical averaging (Doak et al. 1998). Armed with these two expressions of community variability, ecologist can investigate different, but complementary, aspects of community dynamics (Micheli et al. 1999) and their response to disturbance.

Detecting meaningful changes in variability

There are a variety of approaches available for detecting ecologically meaningful changes in variability that may arise following disturbance. Perhaps the simplest of these is to use relative measures of variability as the response variables in standard linear models. If means are equivalent, absolute measures of variation can be used, but if distributions are skewed, log-transformation may be necessary to normalize the data prior to analysis. Both ANOVA designs and regression approaches (e.g. Cottingham et al. 2005) offer a rich architecture for delineating simple or complex

approaches to detecting changes in metrics such as the CV or SDL.

Absolute and relative measures of variability can also be used as responses in homogeneity of variance tests to investigate changes in variability. Homogeneity of variance tests were designed and are conventionally used to determine whether data meet equal variance assumptions, with the null hypothesis being equal variances. Evidence in favour of the alternative hypothesis thus implies significantly different variances. One of the most common of such tests, Bartlett's test, is extremely powerful if the data are normally distributed; however, because the test is highly sensitive to departures from normality, it is not recommended when data are non-normal (Sokal & Rohlf 1995). An alternative is Levene's test (Levene 1960), which, in its simplest form, consists of applying a one-way analysis of variance F-test on the absolute deviations of the observations from their means. Levene's test performs best when data have symmetric, moderate-tailed distributions (Brown & Forsythe 1974). For skewed distributions, Brown & Forsythe (1974) found that extending Levene's test to use either the median or the trimmed mean created a more robust test. In general, Levene's test based on the median provides robustness against non-normal data while retaining good power and is therefore often recommended (Brown & Forsythe 1974; Schultz 1985; Manly & Francis 2002) and increasingly used to detect univariate changes in variability (e.g. Cottingham *et al.* 2000; Fraterrigo *et al.* 2006). Similarly, Euclidean-based tests can be applied to evaluate changes in multivariate dispersion in a Levene's context (Rusak *et al.* 2001; Brown 2003). When non-Euclidean dissimilarity is more appropriate, Anderson (2006) advocates using an extension of Levene's test to test for differences in multivariate variability.

Other potentially useful methods for detecting changes in variability are poorly represented in the ecological literature, despite their accessibility. There is an extensive history of spatial pattern analysis in plant ecology (Greig-Smith 1979; Dale 1999), and several of these methods could be applied to detect altered variability. Changes in parameters of semivariograms may provide insights into the variability of spatial structure; however, hypothesis testing with semivariogram parameters remains rare (but see Schlesinger *et al.* 1996; Fraterrigo *et al.* 2005; Smithwick *et al.* 2005). Semivariogram analysis requires that many observations be collected at fine spatial scales, which often comes at the expense of replication. Additionally, because it can be difficult to fit a model to an empirical semivariogram, the accuracy of parameter estimates can be questionable. Sampling designs developed to maximize the efficiency of data collection for semivariogram analysis may resolve some of these issues. For example, by using a cyclic sampling design, Burrows *et al.* (2002) reduced the number of plots

needed to obtain the same confidence interval width for predicting leaf-area index by 60% relative to a random sampling design.

From a sampling design and experimental perspective, Underwood (1991) recognized the need to develop an analytical protocol to test explicitly for altered variance as another way of assaying the effects of disturbance. His ANOVA-based 'Beyond BACI (Before-After-Control-Impact)' approach has since been revised and improved (e.g. Underwood 1992, 1994), most recently, by Benedetti-Cecchi (2001, 2003) who advocated the inclusion of Monte Carlo approaches (Benedetti-Cecchi 2001) and explicit manipulation of the variance of the predictor (disturbance) itself (Benedetti-Cecchi 2003) to fully unravel the relationship between mean and variance in ecological systems. Not surprisingly, a number of the studies estimating the effect of disturbance on variance have employed the 'Beyond BACI' approach, although caution must be exercised to ensure that all assumptions of this ANOVA-based design have been met to ensure interpretability and rigor (Stewart-Oaten & Bence 2001).

FUTURE DIRECTIONS

We suggest five distinct directions for future research that should advance our understanding of the relationship between disturbance and variability. The first four are prime candidates for empirical and experimental investigation. The fifth describes two promising approaches for identifying and predicting the effects of disturbance on variability that await further development.

Direction 1: regime shifts

Most ecological properties fluctuate within reasonably well-defined boundaries (Landres *et al.* 1999). Departures from those boundaries can often have unpredictable effects on community structure and function because of the tight coupling that typically occurs among physical, chemical and biological variables. Furthermore, in an increasingly human-dominated landscape, stakeholders often desire stable conditions to aid in assaying ecosystem services. Recent models suggest that increased variability can be a leading indicator of large changes arising from disturbance (e.g. van Nes & Scheffer 2003; Oborny *et al.* 2005; Carpenter & Brock 2006). Regime shifts, one such category of dramatic change, are infrequent and unusual events that can occur quickly, but typically require a considerable amount of time to reach (Carpenter 2003). Empirical examples are few, given the recent development of these models and a general absence of suitable time series, but increased variability (specifically a longer wavelength and lower frequencies of key system variables) has been noted in ocean-atmosphere

systems prior to a regime shift in the circulation of the North Atlantic Ocean (Kleinen et al. 2003), freshwater lakes undergoing eutrophication (Carpenter & Brock 2006) and semi-arid grasslands experiencing desertification (Schlesinger et al. 1990; Su et al. 2006). These examples, as well as the theory that predicts them (Carpenter & Brock 2006), deal specifically with increased variability as a precursor to large abrupt system changes. Given the ability of disturbance to both dampen as well as augment ecosystem variability, we feel that future model development might fruitfully examine both possibilities.

Direction 2: multiple disturbances

Most ecological systems are affected by multiple natural and/or anthropogenic disturbances, and there is an increased likelihood that more ecological systems will be subject to multiple disturbances in the future (Paine et al. 1998; Vinebrooke et al. 2004). Predicting the joint effects of multiple disturbances will therefore be vital for managing ecosystems in the coming decades. Disturbances may interact in unique ways that result in emergent system behaviour. For instance, Collins & Smith (2006) examined the effects of fire and grazing on the spatial and temporal variability of species composition in tallgrass prairie plant communities and found that, together, fire and grazing produced vegetation patterns that differed over time and space from the patterns generated by fire and grazing individually. Evaluating changes in variability may be useful for studying multiple disturbances that interact because variability can integrate the range of responses produced by different drivers (Fraterrigo et al. 2005). If multiple interacting disturbances alter mean response, but collectively do not alter variance, the effects of disturbance may be more difficult to interpret. Although opposing effects of disturbances that simultaneously increase and decrease variability so as to effectively cancel each other are unlikely, such outcomes may still be informative. Taylor's power law predicts that variance should scale with the mean response of a variable (Taylor 1961). An absence of covariation may thus signal that multiple factors are at play in determining the response of variability to disturbance (also see below).

Direction 3: duration of effects

Over the past decade, researches have recognized that the legacies of disturbance can be particularly enduring (reviewed by Foster et al. 2003), but the persistence of altered variability due to disturbance remains poorly understood. Examining the duration of disturbance effects on variability can provide important information about the processes governing system recovery (Kashian et al. 2005). For instance, increasing homogeneity of soil organic matter content across a chronosequence of restored prairies pointed to the primary role that plant diversity plays in re-establishing soil resource heterogeneity (Lane & BassiriRad 2005). Similarly, the spatiotemporal patterns of soil nutrient variability following contrasting timber-harvesting strategies indicated the importance of spatial discontinuities in re-initiating patterns of soil heterogeneity following disturbance (Guo et al. 2004). Understanding the duration of disturbance-induced changes in variability may help explain contemporary ecological patterns because spatial and temporal variation can influence the movement and persistence of organisms, species coexistence, the spread of future disturbance, and the redistribution of matter and nutrients (reviewed by Turner 1989).

Direction 4: isolating the effects of different disturbance characteristics

While extent, frequency and intensity clearly influence how disturbance affects variability, other disturbance attributes may be important as well. The temporal pattern of disturbance, for example, can coincide with the timing of reproduction and recruitment, which may result in an increase in the variability of both individual taxa and assemblages due to fluctuating resources levels and competitive interactions (Benedetti-Cecchi 2000; Bertocci et al. 2005). To disentangle the relative importance of these different disturbance attributes, it is necessary to isolate their individual effects. Bertocci et al. (2005) manipulated levels of disturbance intensity, temporal variation (i.e. pattern) and spatial extent independently in a three-way factorial design and examined the temporal response of benthic species and assemblages to these treatments. Their results suggest caution when interpreting experiments where the temporal variation and intensity of disturbance cannot be separated because they can have opposite effects on variability (Bertocci et al. 2005). The extent to which these findings apply to other systems is not known, and may depend on the resilience of the system (Bertocci et al. 2005). Resolving the role that various disturbance attributes have on variability will thus require further experimentation. As disturbance regimes change, the ability to separate the effects of disturbance characteristics will be advantageous for anticipating the consequences of altered variability for ecosystem structure and function.

Direction 5: potential approaches

Although mean–variance scaling has the potential to confound the detection of altered variability, changes in power-law exponents following disturbance may be useful indicators of change in system dynamics. The mathematical expectation for the scaling exponent (b) relating log-mean

and log-variance, when scaled by a constant, is 2 (Kilpatrick & Ives 2003). Because b typically falls between 1 and 2 in nature, various biological mechanisms have been proposed to explain why b is often <2. In a temporal context, demographic stochasticity (Taylor & Woiwod 1982), negative interactions among species (Kilpatrick & Ives 2003) and uncorrelated reproductive effort (Ballantyne & Kerkhoff 2007) can all lead to reductions in b, while in a spatial context, density-dependent migration (Taylor & Taylor 1977) and random migration and variable reproductive success (Hanski 1980) can have the same effect. Monitoring the effects of disturbance on the mean–variance scaling exponent in a particular system may thus point to a set of plausible mechanisms that contribute to altered mean–variance relationships. Mean–variance relationships can also be decomposed into individual variance and covariance components to quantify the processes generating the observed scaling (e.g. Kerkhoff & Ballantyne 2003). Assuming that such scaling applies to the dynamics of ecosystem function (Kerkhoff & Enquist 2007), changes in these components may prove to be useful in diagnosing the specific effects of disturbance.

In cases where the variability of a response is a nonlinear function of disturbance, Jensen's inequality may be useful for improving qualitative model predictions. Jensen's inequality is a mathematical property stating that, for a set of x values with a mean of $\overline{x}$, the average result of a nonlinear function, $f(x)$, does not equal the result of the average x, $f(\overline{x})$. Rather, the average result depends on the shape of the function, such that for accelerating functions, $f(x)$ will be greater than $f(\overline{x})$, and for decelerating functions, $f(x)$ will be less than $f(\overline{x})$ (reviewed in Ruel & Ayres 1999). Although Jensen's inequality is typically derived for changes in the mean value of a dependent variable, when applied to variability the same properties should apply. Coupled with our conceptual model, Jensen's inequality may thus be useful for fine tuning predictions and may also help explain empirical outcomes that are not in agreement.

CONCLUSIONS

Disturbance regimes are changing and will continue to change in the future. Large fires in the western USA are occurring more frequently, in association with a warming climate (Westerling *et al.* 2006); insect outbreaks in forests are occurring over greater extents than previously observed, in geographic locations where they have not previously been documented and even in previously unaffected species or communities (Raffa *et al.* in press); climate models predict an increase in extreme meteorological events and a change in their timing (Easterling *et al.* 2000; Trapp *et al.* 2007). Employing a multitude of approaches, including evaluation of how functionally important patterns of variability will change in response to disturbance, will be essential for explaining ecosystem dynamics and anticipating future states.

Increased recognition of disturbance-driven changes in variability will also be crucial for forecasting and managing many of the ecosystem services on which humans rely. Ecological forecasting has been deemed an imperative for planning and decision-making (Clark *et al.* 2001), but uncertainty is considered a significant obstacle to progress in this area (Clark 2003; Nilsson *et al.* 2003; Peterson *et al.* 2003). Fluctuations in ecological patterns and processes due to disturbance may impede forecasting efforts by generating additional uncertainty. From a modelling and forecasting perspective, spatial and temporal variability that is not known or captured can make parameter estimates and predictions unrealistic (Clark 2003). Moreover, declines in the accuracy of forecasts from time series data will be inevitable whenever variance increases due to disturbance (Cottingham *et al.* 2000).

We have outlined the necessity, complexity and utility of investigating ecosystem variability, in addition to changes in mean response, to fully understand the effects of disturbance on ecological pattern and process. Given the potential that such investigations hold for detecting and measuring ecological responses, identifying organizing features of ecosystems and indicating state transitions, we risk overlooking key information about ecosystem response to disturbance by ignoring variability. Experimentally and empirically, without knowledge of altered variability in disturbed systems relative to undisturbed ones, it will not be possible to correctly estimate the effect size or the power of a sampling design needed to detect it (Underwood 1997). Ecologists should not shy away from explicitly evaluating variability in response to disturbance, but rather embrace this perspective for the new insights that will undoubtedly be revealed.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Studies included in the review of disturbance effects on variability.
Appendix S2 Parameterization and assumptions used to revise the Turner *et al.* (1993) model.

This material is available as part of the online article from: http://www.blackwell-synergy.com/doi/full/10.1111/j.1461-0248.2008.01191.x

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