FORUM

INTERMEDIATE DISTURBANCE AND ITS RELATIONSHIP TO WITHIN- AND BETWEEN-PATCH DYNAMICS

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The intermediate disturbance hypothesis has been the focus of considerable analysis in terrestrial and aquatic systems. This model predicts that species diversity will be highest at intermediate frequencies of disturbance. Despite numerous theoretical and empirical analyses, the utility of the model is still the subject of intense debate. Rather than developing restrictive time and space constraints on application, we suggest that the model may best be used as a generalizable framework for testing hypotheses in both aquatic and terrestrial systems. In addition, we believe that the model may be applied to both within- and between-patch scales. Finally, we propose an empirical model in which disturbance is an extinction causing event, and post-disturbance succession is modeled based on the dynamics of immigration and extinction. Such a model can incorporate a variety of patterns in species diversity in response to disturbance.

Introduction

Factors controlling patterns of species diversity at a range of spatial and temporal scales, and the mechanisms creating those patterns, have long been of interest to community ecologists (Huston, 1994; Rosenzweig, 1995). Many equilibrium and non-equilibrium hypotheses (Wilson, 1990) have been examined to explain the variety of patterns of diversity observed in terrestrial and aquatic systems. Historically, equilibrium models dominated ecological thinking, but patterns of diversity observed in the field were not compatible with these models (Hutchinson, 1961). More recently, with the recognition that disturbances are common in most communities, ecological sentiment has shifted in favor of non-equilibrium explanations of species coexistence and community structure (e.g., Connell, 1978; Huston, 1994; Rosenzweig, 1995; Wu and Loucks, 1995).

Understanding the role of disturbances and the relevance of equilibrium and non-equilibrium models has implications for sustainable management of our renewable resources. Increasing emphasis on mimicking natural disturbance regimes in human managed systems (e.g., Steuter *et al.*, 1990) relies on a fundamental understanding of the effects of disturbances on community processes.

This forum was initiated by Wilson's (1990) excellent attempt to determine the relative importance of a number of mechanisms in maintaining Hutchinson's (1961) paradox of "indefinite species coexistence" as it applies to New Zealand plant communities. In our contribution, we choose to focus more on the generality of the Intermediate Disturbance Hypothesis (IDH), one of the models that Wilson (1990) assessed and rejected in his analysis. Although the notion of indefinite species coexistence is intellectually intriguing, it is, in our opinion, to a large extent purely theoretical because there are many ecological and non-ecological mechanisms that can affect species coexistence in communities. Our goal, therefore, is to direct the discussion toward the IDH and its utility as a source of ecological hypotheses regarding species diversity as discussed by Padisák (1994), Wilson (1994), and Reynolds (1995).

The intermediate disturbance hypothesis is one model of species diversity that has contributed to the widely accepted doctrine that communities rarely reach equilibrium. This model was formalized by Connell (1978), but the roots of the model extend back to Watt (1947), Hutchinson (1953; 1961), Loucks (1970), and Grime (1973), among others. The intermediate disturbance hypothesis predicts that diversity will be highest in communities with intermediate levels of disturbance. If disturbances are too rare, the competitive dominants will eliminate other species and reduce diversity as equilibrium conditions develop. If disturbances are too frequent, most species will go locally extinct, which lowers diversity, because they can not tolerate repeated disturbances. Under intermediate levels of disturbance, diversity is maximized because disturbance-tolerant species and competitively dominant species coexist.

The intermediate disturbance hypothesis is one of several alternative models to explain patterns of species diversity in communities (Connell, 1978; Wilson, 1990). As noted by Juhász-Nagy (1993), this model is difficult to falsify because it makes only qualitative predictions regarding changes in species diversity in response to disturbance frequency. Because it is qualitative, we view the intermediate disturbance hypothesis not so much as a specific hypothesis to be tested within a set of rigidly defined spatial and temporal criteria, but more as a general conceptual framework, based on a series of assumptions, from which system-specific questions can and should be asked.

Specifically, for the intermediate disturbance hypothesis to work, the following assumptions must be met: (1) species diversity is reduced by competition, (2) a trade-off exists between ability to tolerate disturbance and competitive ability, (3) a trade-off exists between colonizing ability and competitive ability, (4) successional seres have at least two seral stages, and (5) the regional species pool is much larger than the number of species that can occur in a small patch.

Other than the generalized prediction of a hump-shaped species diversity curve, the IDH only yields a mechanistic understanding of species diversity through an analysis of its assumptions. If a sufficient disturbance frequency gradient is analyzed, and a hump-shaped curve is not evident, then a formal analysis of the assumptions of the IDH is warranted. For this reason, we suggest that the IDH is not necessarily an explicit hypothesis. Rather, we believe that it provides a conceptual framework for ecological hypotheses relating disturbance and diversity. If we consider the IDH to be a general framework, the assumptions of the intermediate disturbance hypothesis can be defined explicitly and applied to specific empirical and experimental tests. When this is done carefully, hypotheses associated with the assumptions of the model are falsifiable with respect to the particular system of interest (Pickett *et al.*, 1994).

It is the generality of the intermediate disturbance hypothesis that appears to have spawned an interesting controversy between terrestrial plant ecologists (Wilson, 1990; 1994) and lake phytoplankton ecologists (Padisák, 1994; Reynolds, 1995) over the relevance of the hypothesis to explain the maintenance of species diversity in aquatic and terrestrial systems. Although the role of disturbance-generated patch dynamics has been clearly defined in many terrestrial systems, patch structure and dynamics are less obvious in lakes. Specifically, the controversy seems to revolve around the particular issues of whether or not lakes are patchy, and whether or not there are mechanisms in lakes that can create patches at appropriate spatial and temporal scales. In addition, Wilson (1994) poses the more general question of whether or not the intermediate disturbance hypothesis applies to within- or between-patch scales.

The first two issues reflect the difficulty of separating intermediate disturbance from a competing model, gradual climate change (Connell, 1978) in lake ecosystems (Padisák, 1994; Wilson, 1994; Reynolds, 1995). In the gradual climate change model, changes in environmental conditions such as those due to seasonality prevent any species from achieving dominance in a community. As conditions change gradually over some period of time, they favor different species such that competitive exclusion does not occur and diversity remains high. A clear distinction between the intermediate disturbance hypothesis and gradual climate change can be made, however (Connell, 1978). In the former, a disturbance is a relatively discrete event (e.g., Pickett and White, 1985), so changes associated with disturbances are abrupt, whereas changes are gradual in the gradual climate change model. Confusion arises between terrestrial and aquatic systems because seasonality in lakes occurs over time scales that are much longer than the life cycles of most phytoplankton species. Seasonality is often distinctly bounded by lake turnover, and equilibrium conditions can develop between turnover events. In terrestrial systems, complete turnover of species within a season typically does not occur and seasonal boundaries are more nebulous. Thus, species in terrestrial and aquatic systems differ in their rate of response to seasonality relative to the average length of a life cycle (Padisák, 1994; Wilson, 1994; Reynolds, 1995).

More generally, however, we propose that the intermediate disturbance hypothesis and gradual climate change are not competing models, but are, instead, hierarchically related in space and time. Given that gradual climate change is, in fact, *gradual* change over some period of time, and that a disturbance is an *abrupt* change, these models are not mutually exclusive. Both mechanisms can operate in communities. Within one growing season, for instance, gradual climate change has been demonstrated to influence species phenology producing seasonal turnover in dominance in terrestrial and aquatic systems (Wetzel, 1983; Lieth, 1975). Gradual climate change generally occurs at regional or whole system scales. At any time while gradual change is occurring, an abrupt disturbance can impact community structure at a range of scales. In North American tallgrass prairie, phenological change in community composition and structure is well documented (Parrish and Bazzaz, 1979; Anderson and Adams, 1981). Within a growing season, a number of small- and large-scale disturbances (fire, grazing, animal diggings, etc.) occur as well (Collins and Barber, 1985; Collins and Glenn, 1988). Both gradual climate change and disturbances simultaneously affect community structure in these grasslands and the impact of disturbance depends on the stage of gradual climate change. That is, disturbances early in the growing season have a different impact on community structure than those that occur later in the season, or during dormant periods (Peet *et al.*, 1983; Howe, 1994; Benning and Bragg, 1993).

If the primary mechanism leading to species coexistence in lakes is simply seasonal turnover rather than abrupt disturbances we would agree with Wilson's (1994) concerns. We argue, however, that there are numerous relatively discrete disturbances in lakes that create patchiness at a variety of spatial and temporal scales. These patches may not seem as discrete as a tree-fall in a forest, but even forest canopy gaps may create environmental gradients rather than distinctly defined patches in terrestrial systems (Lieberman *et al.*, 1989). Also, these disturbances may not fit the rigidly defined spatial and temporal constraints on patchiness proposed by Padisák (1994) and Wilson (1994).

Based primarily on wind-driven circulation patterns, Reynolds (1995) demonstrates that patches can indeed be defined quantitatively in lakes, but it does appear from his definition that most lakes represent a single large patch. Abiotic factors that create patch structure within lakes include periodic, intensive storm runoff, ground water recharge zones, and complex interactions along lake shores. Turbular and laminar flow, eddy diffusion and conductivity, surface waves and currents, langmuir circulation, and metalimnetic entrainment all create patches in lakes at large spatial scales, especially when considered relative to the size of most aquatic organisms (Wetzel, 1983). Additional biotic mechanisms include predator-prey interactions and trophic cascades which can impose structure at small spatial scales (<1cm) and short time intervals (hours to days)(Power, 1992; Carpenter and Kitchell, 1993). Fish move in patch-like 'schools.' At very small scales elemental stoichiometric relationships associated with foraging behavior and food web dynamics lead to nutrient fluxes that impact plankton community structure over very short time intervals (minutes) (Elser and Hassett, 1994; Sterner *et al.*, 1992; Vanni, 1996). These complex processes produce heterogeneity at various spatial and temporal scales creating a 'contemporaneous disequilibrium' in lakes (Richerson *et al.*, 1970). Thus, many processes may create patches in lakes at scales appropriate to the general assumptions of the intermediate disturbance hypothesis.

The other questions driving the controversy between the lake and terrestrial ecologists focus on the relationship between patch structure and the intermediate disturbance hypothesis. The lack of apparent patchiness in aquatic systems led Wilson (1994) to conclude that the intermediate disturbance hypothesis does not have "_any applicability to the plankton." We doubt that ecologists studying plankton in other systems would agree with such a sweeping assertion (Ward and Stanford 1983; Resh *et al.*, 1988; Poff, 1992; Reice, 1994). As noted above, we are confident that lakes are indeed patchy at a variety of spatial and temporal scales, but we will leave the details of that argument to limnologists.

The role of patch structure in the intermediate disturbance hypothesis is a separate and more general issue raised by Wilson (1994). Wilson (1994) states that, "_only between-patch diversity can be the basis of the intermediate disturbance hypothesis." He attributes this assertion to Hutchinson (1953) who explicitly described a between-patch mechanism. We concur with Wilson (1994) that Hutchinson (1953) does indeed imply that a community is composed of a set of patches in different stages of community development. Therefore, at some larger spatial scale, the diversity of species among patches is highest if patches are created at some intermediate frequency. Abugov (1982) demonstrates just such a phenomenon based on co-occurrence of patch formation. As long as patch creation is asynchronous, meaning that the system is composed of patches of different age, then diversity at the larger scale is maximized at some intermediate frequency of patch formation (Abugov, 1982).

Based on Hutchinson's (1953) notion of patch structure Wilson (1994: 178) states, "We can not apply the concept of intermediate frequency of disturbance to one patch. A single patch does not have a frequency of disturbance, only a time since last disturbance." The literature on this topic is itself heterogeneous. For example, Rosenzweig (1995) seems to adopt a fairly explicit between-patch perspective. On the other hand, Connell (1978) did not explicitly distinguish among the within- vs between-patch perspectives. Fuentes and Jaksic (1988) state that the intermediate disturbance hypothesis is explicitly a within-patch phenomenon. Confusion abounds.

The intermediate disturbance hypothesis has been the subject of experimental analyses in marine (e.g., Sousa, 1979a,b; McGuinness, 1987; Sommer, 1995), freshwater (e.g., Reice, 1985; Gaedeke and Sommer, 1986; Ward and Stanford, 1988; Robinson and Sandgren, 1983; Robinson and Minshall, 1986; Power and Stewart, 1987) and terrestrial (e.g., Armesto and Pickett, 1985; Collins *et al.*, 1995) systems. In many of these studies, the experimental unit has been the patch, such as an area of grassland or an intertidal boulder. The experimental protocol has been to experimentally disturb replicated patches (turning over boulders, burning grassland) at different frequencies and then determining which patch has the highest species diversity (e.g., Sousa, 1979a,b; 1980; Armesto and Pickett, 1985; Robinson and Marshall, 1986; Collins *et al.*, 1995). Indeed, Sousa (1979a,b) followed this protocol in his experimental analysis of IDH while he was a student of Connell's at the time Connell developed his paper (Connell, 1978). Therefore, it seems clear that Connell, among many others, considers the hypothesis as relevant to within-patch dynamics. For intermediate disturbance to work within patches, the disturbance must not be so intense as to eliminate all species, which Wilson (1994) notes, as well. Rather, the implication is that disturbances negatively affect the competitive dominants, freeing space and resources for weaker competitors. This generates coexistence and high species diversity within a patch.

Applying the intermediate disturbance hypothesis to within-patch phenomena does not exclude the concept from also applying at the between-patch scale. If patches resulting from disturbances have high beta diversity, then regional species diversity will be highest at some intermediate frequency of disturbance. If however, disturbance increases alpha diversity and reduces beta diversity (Peet *et al.*, 1983), then patch dynamics may have little affect on regional species richness. In such a case, the assumption that the regional species pool is much larger than the local species pool does not hold. So, application of the model is not necessarily restricted to between-patch scales.

In our own research, we used two long-term field experiments to examine the effects of fire frequency on species diversity and community heterogeneity in tallgrass prairie vegetation (Collins, 1992; Collins *et al.*, 1995). Patches of vegetation were burned at different frequencies over a 19 year period. In our system, plant species diversity did not peak at an intermediate frequency of disturbance. Instead, diversity decreased linearly as disturbance frequency increased. However, our results did support a second prediction from the intermediate disturbance hypothesis that diversity peaked at some intermediate time since disturbance (Gibson and Hulbert, 1987; Collins *et al.*, 1995). We concluded from these analyses that the mechanisms controlling species diversity in response to disturbance are not the same as those affecting post-disturbance succession.

Because our results demonstrate that different mechanisms affect diversity, we believe that the IDH can explicitly be applied to within-patch phenomena. We suggest that Wilson's (1994) viewpoint links disturbance, as an event, with processes that take place between disturbances. Following Rykiel (1985), we prefer to differentiate explicitly between these phenomena. In general, we view disturbance to be an extinction causing event (Collins *et al.*, 1995). The degree of extinction is a function of the severity of disturbance. At the risk of being tautological, one measure of severity might be the proportion of extinctions that occur in a patch following a disturbance (e.g., Schimmel and Gramström, 1996).

Because our results indicated that different mechanisms applied to disturbance and post-disturbance dynamics (Collins *et al.*, 1995), we suggest that changes in species diversity within a patch can be modeled as the dynamic interaction between rates of immigration (I) and extinction (E) (MacArthur and Wilson, 1967; Glenn and Collins, 1992; Petraitis *et al.*, 1989; Gibson and Brown, 1991). We have developed a graphical model of changes in diversity within a disturbed patch using a discrete time-step function (Yodzis, 1988), based on certain patterns of immigration and extinction (Fig 1a). The first assumption is that there is a positive correlation between the number of species at a site and the number of species that disappear from one year to the next. This assumption is based on our own analysis of immigration and extinction dynamics in mature grassland vegetation at Konza Prairie (Collins and Glenn 1991, Glenn and Collins, 1992). The second assumption is that rate of immigration increases for a period of time after disturbance, but then it decreases as the local species pool is depleted.

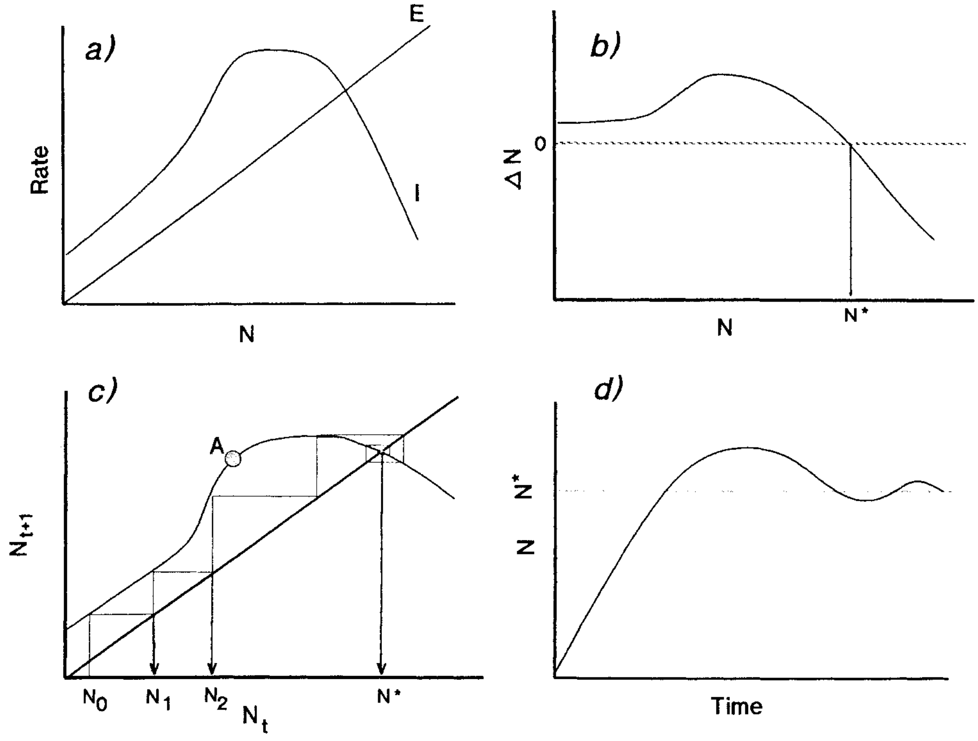

Figure 1: *A model of species diversity following disturbance based on the dynamics of immigration (I) and extinction (E). This model can explain a decrease in species diversity in response to disturbance, and a bell-shaped pattern of diversity following disturbance.* A) *Immigration rates are modeled as a quadratic function of diversity because I increases following disturbance, perhaps in response to facilitation, and then decreases as the local species pool is depleted. Extinction rates increase monotonically with N. Diversity starts above zero because of emergence of species from the soil seed bank, and because some species are resistant to disturbance.* B) *Changes in species diversity (ΔN) at a site are defined as I-E. When ΔN is positive, diversity increases; when negative, diversity decreases. The equilibrium number of species (N*) is stable.* C) *Diversity in a disturbed patch is modeled as a discrete time-step function of ΔN. The diagonal indicates where there is no change in N over time. The arrows show the hypothetical changes in N over a series of seven time steps. Point A represents a threshold in diversity. If disturbance reduces diversity below the threshold, diversity will follow a bell-shaped pattern over time. Otherwise, diversity fluctuates around N* following disturbance.* D) *The discrete time-step function in* C) *results in an increase in N over time followed by fluctuations toward N*.*

Based on these two fundamental assumptions, our model predicts that diversity will increase up to a maximum during succession, when a critical point is reached above which diversity will oscillate and then approach an equilibrium value (N*, Fig 1d). The degree of oscillation depends on the shape of the immigration curve. Oscillations will occur if immigration initially increases, perhaps through facilitation (McDonnell and Stiles, 1983), and then decreases as diversity in a patch increases. This also assumes that local extinction increases with diversity (Glenn and Collins, 1992). In this case, there is a region of instability where it is difficult to predict diversity because small changes in diversity may result in different directions of change during the next time interval.

Depending on the time interval between disturbances, a patch may or may not reach equilibrium. Disturbances that lower species diversity dramatically (N_t<A, Fig 1c) will cause diversity to increase to some peak value and resume fluctuations toward equilibrium (N*). Smaller decreases in diversity (N_t>A, Fig 1c) will yield short term fluctuations that eventually dampen out at N*. Less severe disturbances may only slightly lower diversity and allow diversity to rapidly return to N* before the next disturbance occurs. However, frequent or severe disturbances may not allow sufficient recovery time, resulting in a negative relationship between diversity and disturbance frequency. This model thus predicts that a threshold in disturbance frequency or severity may exist, beyond which diversity is lowered.

This model, which treats disturbance as an extinction causing event and treats post-disturbance dynamics as a function of the interplay between rates of immigration and extinction, is consistent with the assumptions of the intermediate disturbance hypothesis. In addition, the model can generate a variety of temporal patterns in species diversity in response to disturbance frequency and intensity, and patterns of immigration and extinction. Finally, the model provides a mechanistic explanation for our results at Konza Prairie (Collins et al. 1995) in which species diversity was negatively correlated with disturbance frequency, but showed a hump-backed response to time since disturbance.

Conclusions

The intermediate disturbance hypothesis has achieved considerable attention in community ecology because it provides a logical framework to explain patterns of diversity from a non-equilibrium standpoint. We argue that the intermediate disturbance hypothesis is a flexible conceptual framework based on a series of assumptions from which system specific predictions can be derived and tested. The intermediate disturbance hypothesis serves as a source of contention because it is not often directly tested, but rather it is inferred in a *post hoc* effort to explain differences among systems. Because the operational definition of disturbance varies among systems, investigators have battled over the relevancy of the concept within conceptually restricted disciplinary boundaries. In the current controversy, the boundary conditions are strict adherence to a between-patch perspective that is not easily translated across systems. We argue, however, that more will be gained from treating the intermediate disturbance hypothesis as a general framework, developing clearly testable hypotheses from this framework, and then investigating the mechanisms associated with patterns observed in field experiments. This approach has served to focus our own research questions on patterns and mechanisms controlling plant species diversity in the North American tallgrass prairie.

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