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Composition: Decoupling Cause and Effect**

Scott L. Collins, Susan M. Glenn, David J. Gibson

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EXPERIMENTAL ANALYSIS OF INTERMEDIATE DISTURBANCE AND INITIAL FLORISTIC COMPOSITION: DECOUPLING CAUSE AND EFFECT¹

SCOTT L. COLLINS

*Ecological Studies Program, Room 635, National Science Foundation,
4201 Wilson Boulevard, Arlington, Virginia 22230 USA*

SUSAN M. GLENN

Department of Forest Sciences, University of British Columbia, Vancouver, British Columbia, Canada V6T 1W5

DAVID J. GIBSON

Department of Plant Biology, Southern Illinois University, Carbondale, Illinois 62901 USA

Abstract. The intermediate disturbance hypothesis predicts that richness will be highest in communities with moderate levels of disturbance and at intermediate time spans following disturbance. This model was proposed as a nonequilibrium explanation of species richness in tropical forests and coral reefs. A second model of succession, initial floristic composition, states that nearly all species, including late seral species, are present at the start of succession. This leads to the prediction that richness should be highest immediately following disturbance. We tested these predictions using plant species composition data from two long-term field experiments in North American tallgrass prairie vegetation. In contrast to one prediction of the intermediate disturbance hypothesis, there was a significant monotonic decline in species richness with increasing disturbance frequency, with no evidence of an optimum, in both field experiments. Species composition on an annually burned site was a subset of that of infrequently burned sites. The average number of species per quadrat and the number of grass, forb, and annual species were lowest on annually burned sites compared to unburned sites and sites burned once every 4 yr. The second prediction of the intermediate disturbance hypothesis, however, was supported. Richness reached a maximum at an intermediate time interval since the last disturbance. This contradicts the prediction from the initial floristic composition model of succession. These results also suggest that the two predictions of the intermediate disturbance hypothesis are independent and unrelated. We propose that this may be explained by uncoupling the effects of disturbance as a single, relatively discrete event from system response to disturbance. From this perspective, disturbance becomes an extinction-causing event in these grasslands, whereas recovery following disturbance is a balance between immigration and extinction.

Key words: fire frequency; initial floristic composition; intermediate disturbance hypothesis; species diversity; tallgrass prairie.

INTRODUCTION

The hypothesis that species richness is maximized at intermediate levels of disturbance (Connell 1978) has gained support from empirical field studies and mathematical modeling (e.g., Huston 1979, Abugov 1982, Tilman 1982). One fundamental assumption of the intermediate disturbance hypothesis is that a trade-off exists between the ability of a species to tolerate disturbance and its ability to compete. Superior competitors are assumed to be most susceptible to disturbance. As a consequence, if disturbance occurs frequently, richness decreases because species intolerant to disturbance become locally extinct. If disturbances are too infrequent, richness decreases because dominant species occupy resources and eliminate weak competitors. Richness should be highest at intermediate

frequencies of disturbance when conditions favor competitive species and those that tolerate disturbance. As a result, the relationship between disturbance and species richness has important implications for community structure, composition, and dynamics.

A second and related prediction of the intermediate disturbance hypothesis is that species richness will be highest at intermediate time spans during postdisturbance (secondary) succession (Connell 1978, Peet et al. 1983). As with the former prediction, this prediction is based on the assumption that late successional species will competitively displace early successional species, thus lowering richness later in succession. This pattern of change in species richness following disturbance differs from that predicted by the initial floristic composition model of succession (Egler 1954, Finegan 1984, Wilson et al. 1992). As presented by Egler (1954: Fig. 1), the initial floristic composition model predicts that early and late seral species in a successional se-

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quence are present at the beginning of succession. Succession is then a function of differential growth rates and survivorship among early and late successional species (Pickett et al. 1987). Although Egler (1954) did not specifically address species richness, the initial floristic composition model clearly predicts that species richness should be highest during early successional stages, and that richness decreases during succession.

There have been few field experiments designed to test these models (Sousa 1979, McGuinness 1987), and no study has explicitly tested either the intermediate disturbance hypothesis or initial floristics using long-term field experiments in native perennial plant communities subjected to different frequencies of natural disturbance. Here, we report the results of two long-term field experiments on fire frequency and species diversity at different spatial scales in native North American tallgrass prairie. Fire is considered to be a common and important component of the natural disturbance regime in these grasslands (Evans et al. 1989, Collins 1990). Although repeated fire is an essential component of grassland ecosystems, each individual event is considered to be a disturbance because each fire has a clear impact on species composition and ecosystem function (Evans et al. 1989, Collins 1990). Given that repeated spring burning has been shown to increase productivity (Rice and Parenti 1978, Hulbert 1988), and reduce species richness and heterogeneity (Collins 1987, 1992), the intermediate disturbance hypothesis may not be a valid model for understanding the fire–richness relationship in grasslands, yet this idea needs to be tested.

In this report, we test two hypotheses. First, we test the intermediate disturbance hypothesis that species richness will peak at intermediate frequencies of burning and/or intermediate time after burning. As an alternative, based partly on initial floristic composition model and previous research (Collins 1987, 1992), we test the hypothesis that richness will decrease with increasing burning frequency and/or time following burning.

METHODS

The study was conducted at Konza Prairie Research Natural Area (KPRNA) in northeastern Kansas. In 1972, KPRNA was divided into a series of experimental management units subjected to burning frequencies of 1-, 2-, 4-, and 20-yr intervals. Grazing by cattle was excluded at this time. Prior to 1972, these sites were burned every 2 or 3 yr, a common land management practice in the region (Aldous 1934, Hulbert 1985). Management units in this study range from 12 to 20 ha. This experimental design imposes fixed intervals between burns on the different treatments. Because the burning treatments were initiated at different times after 1972, some sites had variable intervals of burning prior to the establishment of the fixed burning regime.

Beginning in 1981, plant species composition has

been measured in May, July, and September in 20 permanently located 10-m² circular quadrats at 19 sites within 12 management units at KPRNA. At each sampling period, aerial cover was visually estimated using a modified Daubenmire scale: 1 = 0.1–1% cover (e.g., present), 2 = 2–5, 3 = 6–25, 4 = 26–50, 5 = 51–75, 6 = 76–95, and 7 = 96–100%. Annual species richness is the cumulative number of species recorded in the 20 quadrats at a site over the three sample periods.

In a second field experiment, a series of 10 × 25 m plots (0.025 ha), known as the Hulbert plots, was arrayed in four rows on a gentle west-facing slope, with about a 5-m vertical displacement between top and bottom rows. There is a 5-m buffer between plots. The lower two rows were established in 1980, and the upper two rows were established in 1982. Each row contains one replicate of the same fire frequency treatments as on the KPRNA management units; that is, burning at fixed intervals of every 1, 2, 4, and 20 yr. The 20-yr burn plots have not yet been burned since the beginning of this experiment. Treatments were randomly assigned among plots in each row. In 1990, plant species composition was sampled in each replicate plot using 12 randomly located 50 × 50 cm quadrats during May, July, and September. Aerial cover of each species in each quadrat was visually estimated in 5% increments. Following quantitative sampling, the plots were visually surveyed for species that did not occur in the quadrats. Annual species richness was the cumulative number of species observed in the entire treatment plot.

Connell (1978) considered species richness (defined here as the total number of species on a treatment) to be the most direct measurement of species diversity. In this paper, we follow that convention. Our statistical analyses are based on species richness values measured in 1990 because this was the last year in which all 19 sites were sampled. The number of times a site was burned between 1972 and 1990, inclusive, was used as a measure of disturbance frequency for the KPRNA management unit data. This value is expressed as a proportion of the total number of years in which a burn occurred divided by 19 (sites are burned only once a year). The number of times a plot was burned between 1980 and 1990, inclusive (also expressed as a percentage), was used as a measure of disturbance frequency on the Hulbert plots. A second variable relevant to testing these hypotheses is the number of years since the last fire. A third potentially confounding variable is the longest interval without fire (Johnson and Gutsell 1994). During long fire-free intervals many species may become established and they may not be adversely affected by a single, recent fire (Adams et al. 1982). Thus, the hypotheses were tested for the KPRNA management unit data using multiple regression, partial regression, and polynomial regression in which species richness was the dependent variable and the independent variables were burning frequency, number of years since burning, and longest interval without burning. In

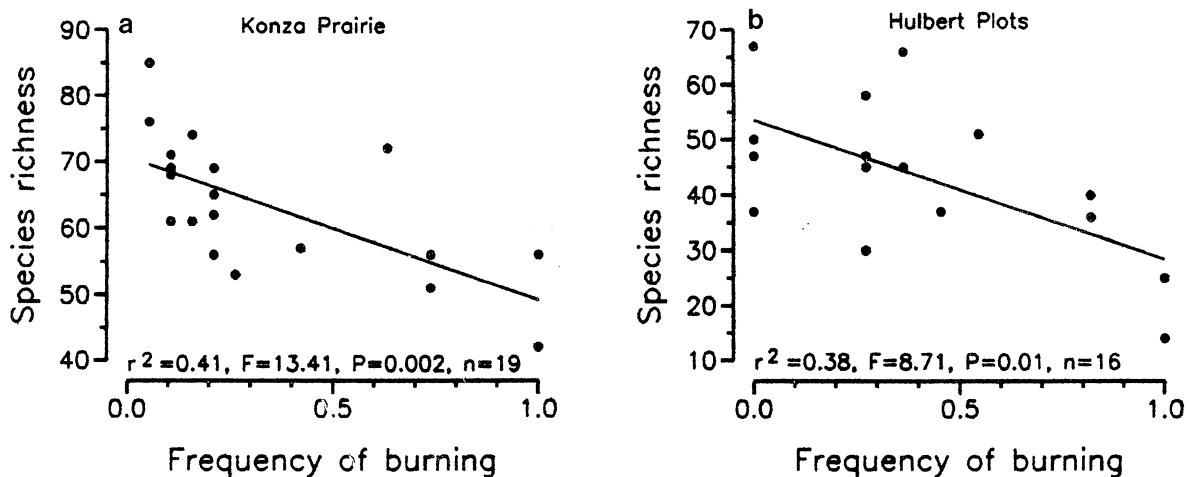


FIG. 1. Relationship between species richness and frequency of disturbance in two long-term field experiments, (a) Management units on Konza Prairie, Kansas, USA, and (b) Hulbert plots at Konza Prairie. Disturbance frequency was measured as the number of times a site was burned from 1972 to 1990. Species richness was measured in 1990.

addition, we plotted species richness data from all upland sites on Konza sampled from 1981 to 1990 vs. years since burning. Regression analyses are not appropriate on these data because the samples within a site over time are not independent. Nevertheless, this larger data set can be used to assess the overall pattern of changes in species richness with time since burning. This analysis was conducted only on the KPRNA management units because there were not enough data from intermediate time periods in the more recently established Hulbert plot experiment, nor were there temporal data from these plots. In the latter case, we used simple linear and curvilinear regression to determine the relationship, if any, between fire frequency and species richness in these plots.

RESULTS

In the first experiment using the Konza Prairie management units, species richness ranged from 42 species on an annually burned site to 85 species on a site burned once every 20 yr (Fig. 1a). Based on multiple regression analysis, species richness on KPRNA management units had a significant negative and linear relationship to burning frequency (adjusted $r^2 = 0.41$, richness = $70.7 - 1.13[\text{burn frequency}]$, $F = 13.41$, $df = 1, 17$, $P = 0.002$). Neither years since burning nor longest unburned interval entered the equation (standardized partial regression coefficients $P > 0.20$ for each additional variable). When number of burns was controlled statistically, neither burning nor years since burning were linearly related to species richness. When years since burning was controlled statistically, the partial regression of fire frequency and species richness was still significant (partial $r = -0.54$, $P < 0.05$, $n = 19$). If longest interval without fire was controlled, the partial regression between fire frequency and species richness was again significant (partial $r = -0.66$, $P <$

0.05 , $n = 19$). Thus, the only variable that is significantly and linearly related to species richness is fire frequency.

In the second experiment using the smaller Hulbert plots, species richness ranged from 14 species on an annually burned treatment to 67 species on a treatment burned once every 20 years (Fig. 1b). Species richness on the Hulbert plots had a significant negative and linear relationship to burning frequency ($r = -0.62$, richness = $53.5 - 2.28[\text{burn frequency}]$, $F = 8.71$, $df = 1, 14$, $P = 0.01$). The linear relationship on the Hulbert plots corresponds well with the decrease in richness during the first 10 yr on the management units. Thus, the results of both long-term field experiments directly contradict the first prediction of the intermediate disturbance hypothesis that richness is maximum at intermediate frequencies of disturbance.

Given that fire frequency decreases richness, then richness should be consistently lower on frequently burned sites over time. Patterns of average species richness over time on annually burned sites ($n = 2$), long-term unburned sites ($n = 2$), and sites burned once every 4 yr ($n = 3$) on the Konza Prairie management units provided evidence in support of this notion. Average species richness was always lower on annually burned sites compared to average richness on the long-term unburned sites (Fig. 2). Also, in 10 of 11 yr, average richness on the unburned sites was equal to or higher than average richness on the sites with intermediate burning frequencies (4-yr burn sites). Again, this directly contradicts the intermediate disturbance hypothesis, which predicts that richness would be highest on sites with intermediate disturbance frequency.

Average species composition on the annually burned sites was essentially a subset of the species assemblages on long-term unburned sites and sites burned once every 4 yr. Eighty-one percent (55/68) of the spe-

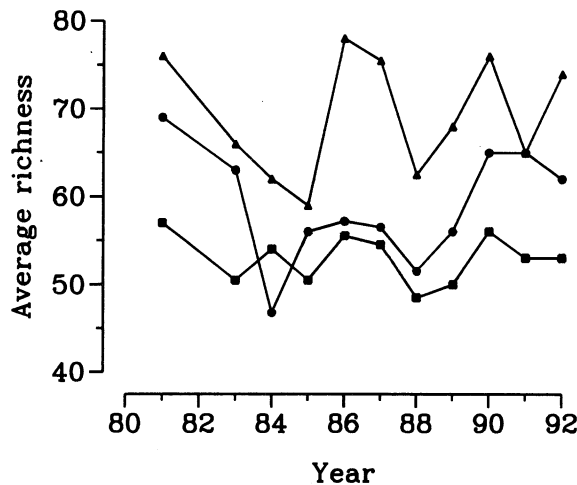


FIG. 2. Changes in average species richness over time on annually burned sites (■, $n = 2$), long-term unburned sites (▲, $n = 2$), and sites burned once every 4 yr (●, $n = 3$).

cies on the two annually burned sites were found on 4-yr burn and unburned sites. An additional 16.2% of the species on the annually burned sites occurred on either the unburned or 4-yr burn sites. Only two species, *Dicanthelium acuminatum* and *Verbena stricta* were found on the annually burned sites but not on the unburned and 4-yr burn sites. Both species, however, occur on other sites at Konza (S. L. Collins, unpublished data).

In general, sites burned once every 4 yr and unburned sites had more forb and annual species than the annually burned site (Table 1). Species density was lowest on the annually burned site. Cover of C_4 grasses was highest, and cover of forbs and C_3 grasses was lowest on the annually burned site (Table 1). Fire frequency also affected the relative importance of the different species among the sites (Table 2). Average cover of *Bouteloua gracilis* and *B. hirsuta*, species characteristic of the more arid western shortgrass prairies, and *Andropogon scoparius*, a dominant of the mixed-grass prairies, was comparatively higher on the annually burned sites compared to the other two sites. *Poa pratensis*, a non-native C_3 grass, was rare on the annually burned site and abundant on the other two sites. Cover of forbs, such as *Ambrosia psilostachya* and *Aster er-*

TABLE 2. Average cover of grass and forb species on sites subjected to different burning frequencies at Konza Prairie. Data were collected during the 1990 growing season.

Species	Annually burned ($n = 2$)	Four-year burn ($n = 3$)	Unburned ($n = 2$)
Grass species			
<i>Andropogon gerardii</i>	57.0	54.5	56.6
<i>Andropogon scoparius</i>	23.9	6.6	0.8
<i>Bouteloua curtipendula</i>	3.1	4.9	1.6
<i>Bouteloua gracilis</i>	7.9	0.4	0.1
<i>Bouteloua hirsuta</i>	4.6	0.2	0.2
<i>Panicum virgatum</i>	2.6	0.4	0.8
<i>Poa pratensis</i>	0.1	19.8	37.3
<i>Sorghastrum nutans</i>	9.1	5.6	7.8
Forb species			
<i>Ambrosia psilostachya</i>	5.7	6.2	14.0
<i>Artemisia ludoviciana</i>	0.3	8.2	7.4
<i>Aster ericoides</i>	1.2	9.0	6.6
<i>Baptisia</i> spp.	1.4	4.3	1.2
<i>Kuhnia eupatorioides</i>	0.7	0.7	0.9
<i>Physalis pumila</i>	0.8	1.2	1.1
<i>Ruellia humilis</i>	0.2	0.4	0.6
<i>Salvia pitcheri</i>	15.4	6.8	1.9
<i>Solidago missouriensis</i>	0.8	3.8	1.4
<i>Vernonia baldwinii</i>	3.8	0.9	2.9
Woody species			
<i>Ceanothus herbaceus</i>	1.1	2.0	7.6
<i>Rosa arkansana</i>	0.1	0.1	0.4
<i>Symphoricarpos orbiculatus</i>	0.1	0.3	1.2

icoides, was higher on the infrequently burned sites compared to the annually burned sites.

Changes in species richness during succession were assessed only with the KPRNA management unit data because of a lack of samples from plots burned at intermediate frequencies on the more recent Hulbert plots. For the 1990 data, using analysis of covariance where the effects of burn frequency were removed, there was a significant quadratic relationship (Fig. 3a) between species richness and the number of years since burning ($\text{richness} = -3.66 + 3.38[\text{burn frequency}] - 0.22[\text{burn frequency}]^2$, $r^2 = 0.32$, $F = 3.73$, $df = 2$, 16 , $P < 0.047$). Both regression terms are significant ($t = 2.72$ and -2.58 , $P = 0.02$). In addition, the combined long-term data for sites over time showed that richness peaked 5–9 yr following fire, then decreased ≈ 10 yr after burning and remained relatively unchanged over the next 10-yr period (Fig. 3b). This pat-

TABLE 1. The effect of fire frequency on the average number of species, species density, and total cover of functional groups on the Konza Prairie management units ($n = 2$ for annually burned and unburned sites, and $n = 3$ for sites burned once every 4 yr).

Site	Number				Cover			Species density (no./10 m ²)
	Grasses	Forbs	Annuals	Woody	C_3 grasses	C_4 grasses	Forbs	
Annual burn	19.0	34.5	4.0	2.5	5.0	109.8	37.7	21.2
Unburned	19.3	42.7	11.3	3.0	22.6	83.7	50.1	24.6
Four-year burn	21.0	50.5	12.5	5.5	43.0	75.2	48.7	24.2

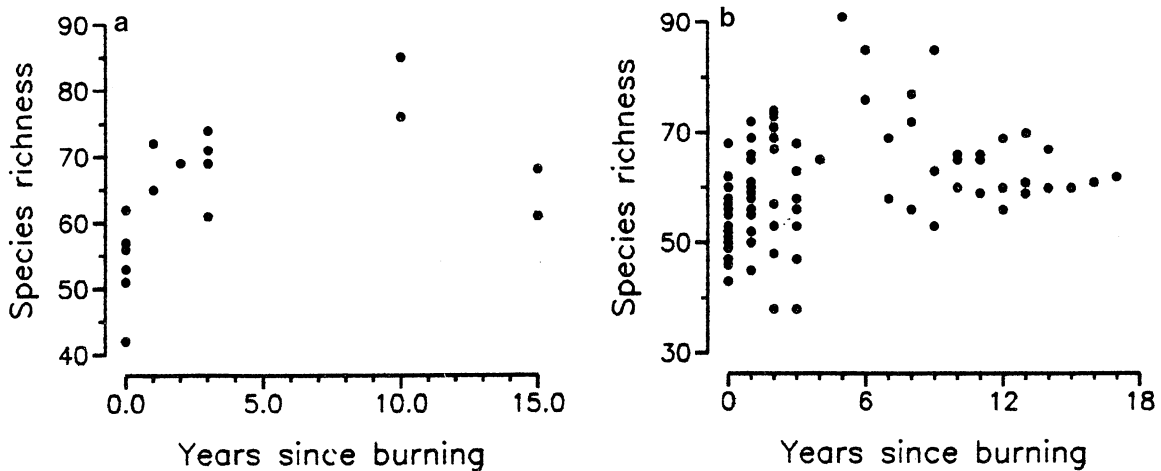


FIG. 3. Changes in species richness during postfire succession at Konza Prairie, Kansas, USA. (a) Species richness measured in 1990, and (b) species richness of all upland sites from 1981 to 1990.

tern strongly supports the second prediction of the intermediate disturbance hypothesis, and is contrary to the pattern predicted by the initial floristic composition model. Based on the 1990 data, species richness on sites 10 yr after burning was nearly doubled that on recently burned sites (Fig. 3a).

DISCUSSION

The overall results from the two fire frequency experiments are consistent and directly contradict the most commonly cited prediction of the intermediate disturbance hypothesis that richness is highest at intermediate frequencies of disturbance. In both field experiments, plant species richness decreased at low to intermediate frequencies of disturbance (Fig. 1). Compared to unburned and 4-yr burn sites, richness was lowest on annually burned sites in the longer term experiment on the KPRNA management units (Fig. 2). The concordance of results from the two experiments at different spatial scales lends further credence to the generality of these results for this tallgrass prairie plant community. Our results are consistent with other studies showing that fire decreases richness in tallgrass prairie vegetation (Collins 1987, Collins and Gibson 1990). In aquatic systems, diversity of benthic invertebrates tended to decrease with increasing disturbance frequency (Robinson and Minshall 1986). In contrast to the results of Sousa (1979), McGuinness (1987) found little relationship between disturbance and diversity in intertidal boulder communities. Luken et al. (1992) reported no relationship between disturbance frequency and diversity in vegetation of powerline corridors. Yodanis (1986) noted several examples of studies that were not consistent with the intermediate disturbance hypothesis.

Our data from the management units supported the second prediction of the intermediate disturbance hypothesis that richness is highest at an intermediate time

period following disturbance (Fig. 3). This leads to the conclusion that the two predictions of the intermediate disturbance hypothesis appear to be independent and unrelated, at least with regard to fire and plant species richness in prairies. This pattern of increasing species richness directly contradicts the prediction derived from a strict interpretation of the initial floristic composition model (Wilson et al. 1992). Indeed, data from many seres show an increase in diversity over time (e.g., Auclair and Goff 1971), but the degree of this increase may vary with site productivity (Peet et al. 1983).

By definition, disturbance is a discrete event that may initiate succession at some spatial scale (Rykiel 1985, Pickett et al. 1989). As such, a disturbance event can reduce or maintain species richness, but disturbance cannot increase richness. Of course, disturbance can create the conditions necessary for increased richness, but an increase in species richness occurs in response to mechanisms, such as seed dispersal or germination, not directly associated with a disturbance event. A single disturbance may eliminate some species, and repeated disturbances at the same location will further reduce richness by altering habitat structure and eliminating intolerant species (Connell 1978, Collins 1992). In grasslands, frequent spring fires reduce the number of grass, forb, and woody species, remove the litter layer, and expose the blackened soil to solar radiation (Hulbert 1988). Given sufficient moisture, the resultant increase in soil temperatures elevates decomposition rates, which enhances soil fertility, and hence, the productivity of the highly competitive C_4 grasses (Knapp and Seastedt 1986, Hobbs et al. 1991, Tilman and Wedin 1991). At Konza Prairie, species diversity is negatively related to productivity ($r = -0.57$, Shannon-Weiner Diversity = $92.7 - 0.11[\text{Productivity}]$, $F = 6.20$, $df = 1, 17$, $P = 0.03$) (S. L. Collins and J. M. Briggs, unpublished data). Thus, the response of the

dominant grasses to disturbance contradicts the underlying mechanistic assumptions of the intermediate disturbance hypothesis. Rather than there being a trade-off between competitive ability and tolerance to disturbance, the dominant grasses increase their competitive ability in response to disturbance.

Disturbance regimes are characterized by variation in frequency, size, and intensity of individual disturbances. Size of disturbance is not a factor in this study, and frequency of burning was a specific treatment. Disturbance intensity was not controlled in this study, yet it could have an impact on species richness following burning (Johnson and Gutsell 1994). Gibson et al. (1990) have shown that fires are $\approx 12^\circ\text{C}$ warmer on average in lowland vs. upland prairie at Konza. In addition, fires in infrequently burned vegetation averaged 34°C warmer than in frequently burned sites. However, our analyses indicate that species richness is consistently lowest on the frequently burned sites with lower fire intensity compared to infrequently burned sites where fires are hotter (Gibson et al. 1990). Such a pattern would suggest that fire frequency has a greater impact on species richness in this system than does fire intensity. Reynolds et al. (1993) noted that disturbance frequency was a more important variable than intensity in aquatic systems.

Both the intermediate disturbance hypothesis and the initial floristic composition model of succession are confounded by spatial scale. Given that the intermediate disturbance hypothesis is related to diversity in association with disturbance, it is not always clear if the predictions are directly related to patterns within the disturbed patch, or to patterns at larger scales that incorporate both disturbed and undisturbed patches (Collins 1992). Also, the intermediate disturbance hypothesis is confounded by interaction effects of disturbances (Collins 1987, Chaneton and Facelli 1991). The initial floristic composition model was explicitly developed to explain vegetation dynamics during old-field succession (Egler 1954, Finegan 1984). Given that abandoned fields can be quite large and variable, it is unreasonable to assume that all species will be scattered throughout the entire field at the start of succession. A more reasonable approach would incorporate multiple mechanisms and pathways (Pickett et al. 1987) in which successional rates at small spatial scales within old fields are highly variable (Czaran and Bartha 1992) as a result of environmental heterogeneity, and the vagaries of seed dispersal (e.g., Rusch 1992). Thus, a nodal model may be more appropriate, in which nodes of late successional species become locally established relatively early in succession (e.g., McDonnell and Stiles 1983). These nodes represent small-scale patches of advanced succession that expand and coalesce by providing local seed sources and facilitation during succession (Archer et al. 1988, DeBussche and Lepart 1992).

The evidence presented does not suggest that the

intermediate disturbance hypothesis has no utility as a general model to describe patterns of species diversity in relation to disturbance in communities. Indeed, cases supporting the model do exist (Sousa 1984, Pickett and White 1985, Padiasak 1993), and confirmation is an equally valid method of hypothesis testing along with the more frequently cited falsification approach (Pickett et al. 1994). Few models are likely to have global applications, thus repeated testing in different systems and at different scales is necessary to help define the spatial and temporal domains within which a model applies (Pickett et al. 1994).

As originally proposed, the intermediate disturbance hypothesis and the initial floristic composition models suffer from a simplicity that yields predictions that are confounded by spatial scale. Thus, a more pluralistic approach is needed. Indeed, in grasslands the effects of multiple interacting disturbances in grasslands (Collins 1987) yields as imprecise the notion of "intermediate" levels of disturbance. Rather, disturbance thresholds may exist beyond which frequent disturbances decrease diversity. Future models should consider the natural dynamics of ecosystems (Collins and Glenn 1991) in which disturbance is an extinction-generating mechanism, and the interaction between immigration and extinction controls diversity following disturbance (Platt 1975, Petraitis et al. 1989, Gibson and Brown 1991, Glenn and Collins 1992). Successional development within a disturbed site will reflect different rates of immigration and extinction at smaller scales, creating a nodal patchwork of successional change over time.

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