The Diversity–Disturbance Relationship: Is It Generally Strong and Peaked?

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THE DIVERSITY–DISTURBANCE RELATIONSHIP: IS IT GENERALLY STRONG AND PEAKED?

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Abstract. The contemporary literature accepts that disturbance strongly influences patterns of species diversity, and that the relationship is peaked, with a maximum at intermediate levels of disturbance. We tested this hypothesis using a compilation of published species diversity–disturbance relationships that were gleaned from a literature search of papers published from 1985 through 1996 and from references therein. We identified 116 species richness–, 53 diversity–, and 28 evenness–disturbance relationships in the literature, which we grouped according to shape of relationship (nonsignificant, peaked, negative monotonic, positive monotonic, or U-shaped). We tested the relationships between the strength and shapes of these relationships and attributes of the community, disturbance, and sampling and study design. Nonsignificant relationships were the most common, comprising 35% of richness, 28% of diversity, and 50% of evenness studies. Peaked responses were reported in only 16% of richness, 19% of diversity, and 11% of evenness cases. Explained variation in the three measures of diversity was variable among studies but averaged ∼50%. It was higher when few samples and few disturbance levels were examined and when organisms within the samples were not exhaustively censused, suggesting that procedural artifact contributes to these relationships. Explained variation was also higher in studies in which disturbance was measured as a gradient of time passed since the last disturbance (mean $r^2 = 61\%$), vs. studies of spatial variation in richness (mean $r^2 = 42\%$). Peaked richness relationships had the greatest odds of being observed when sampled area and actual evapotranspiration were small, when disturbances were natural rather than anthropogenic in origin, and when few disturbance levels were examined. Thus, on average, diversity–disturbance relationships do not have consistently high r^2 and are not as consistently peaked as the contemporary consensus would suggest.

Key words: disturbance; diversity–disturbance relationship; diversity, temporal and spatial patterns; intermediate-disturbance hypothesis; meta-analyses; sampling artifacts; sampling intensity; species diversity; species richness.

INTRODUCTION

Species diversity varies greatly through space and time. Many factors have been hypothesized to influence richness and other measures of species diversity (Palmer 1994); however, the evidence for many of these hypotheses is anecdotal and/or restricted to specific circumstances. Most authors postulate that only a small number of factors are responsible for the majority of the variation in richness in nature.

Disturbance is widely believed to be one of the main factors influencing variations in species diversity (e.g., Connell 1978, Huston 1979, 1994, Noss 1996). The ecological literature is virtually unanimous in postulating that species diversity is a peaked function of disturbance. The ''intermediate-disturbance hypothesis'' (IDH; Grime 1973*a, b*, Horn 1975, Connell 1978, Huston 1979, 1994) postulates that physical disturbance prevents competitively dominant species from excluding other species from the community, and that there is a trade-off between species' ability to compete

and their ability to tolerate disturbance. At low levels of disturbance, diversity is low because only the best competitors persist. When disturbances are very intense or frequent, few species can persist or repeatedly colonize after every disturbance. At intermediate intensities or frequencies of disturbance, there is a balance between competitive exclusion and loss of competitive dominants by disturbance; conditions favor the coexistence of competitive species and disturbance-tolerant species. Thus, a peak in diversity should occur at intermediate intensities and frequencies of disturbance, as well as at intermediate times since the last disturbance.

A cursory examination of the disturbance literature reveals that diversity–disturbance relationships do not consistently show the peaked pattern predicted by the IDH. Positive monotonic, negative monotonic, and unimodal relationships all appear. Most surprising is the large number of nonsignificant diversity–disturbance relationships in the literature.

Equivocal published evidence regarding IDH indicates a need to determine why there is so much variation in the observed shape of species diversity–disturbance relationships and percentage variance ex-

plained. Some authors suggest that peaked diversity–disturbance relationships may not be the rule (Huston 1979, Reice 1985, Reice et al. 1990, Huston 1994, Chesson and Huntly 1997, Wootton 1998, Mackey and Currie 2000). It has been hypothesized that in communities where post-disturbance succession is not driven by competitive hierarchies, disturbance intensity and frequency may have little effect on species richness (Reice 1985, Chesson and Huntly 1997). Huston (1979, 1994) suggests productivity may influence the shape of the diversity–disturbance relationship. Unpredictable, severe, episodic disturbances may have greater effects on richness than do predictable, moderate events to which communities may adapt (Reice et al. 1990). Wootton's (1998) models predict that, in multitrophic systems, IDH should hold for species competing for nondynamic basal resources (e.g., sessile organisms competing for space), but not for mobile organisms at higher trophic levels. Finally, Mackey and Currie (2000) suggest that significant and/or peaked richness–disturbance relationships are most likely to be observed when sampling intensity is low because rare species will be missed.

This paper addresses the following questions about the importance of disturbance as a regulator of species diversity. (1) Is species diversity consistently related to measures of disturbance? How strong are the relationships (i.e., how much variation in species diversity is explained by disturbance)? (2) Does the amount of explained variation in species diversity depend upon the conditions under which the relationship was observed? (3) How frequently are diversity–disturbance relationships peaked? (4) Under what conditions are peaked diversity–disturbance relationships most likely to occur?

To answer these questions, we searched the published literature for studies examining effects of disturbance on species diversity. We considered several measures including richness (the number of different species that co-occur), evenness (how evenly distributed the individuals of a community are among the different species present; e.g., Pielou's J), and measures that combined richness and evenness (e.g., Shannon-Wiener's H', Simpson's D). We will use the term ''species diversity'' when referring to the general concept of species diversity, and ''diversity'' for the specific statistic that combines measures of richness and evenness. We tested the extent to which the strength (explained variation) and shape of observed relationships were related to characteristics of the community, the habitat, the disturbance, and the sampling design (Table 1). For this study, we defined ''disturbance'' as a temporally discrete event that abruptly kills or displaces individuals or that directly results in the loss of biomass. By directly or indirectly changing the availability of substrate and/or other resources, disturbance creates an opportunity for new individuals to become established (Sousa 1984, White and Pickett 1985). Dis-

TABLE 1. A list of the predictor variables used in the diversity–disturbance relationship analyses, by category. These variables encompass traits of the biological system, the disturbance, and the sampling design of the study.

Predictor variables
Organism and system attributes
Animal vs. Plant
Terrestrial vs. Aquatic
Sessile vs. Motile
Sessile producers vs. Motile consumers
Actual evapotranspiration (mm)†
Disturbance attributes
Abiotic vs. Biotic‡
Gradient of frequency vs. Intensity vs. Time passed since last disturbance
Spatial vs. Temporal gradients
Anthropogenic vs. Natural
Chronic vs. Episodic
Habitat damaged vs. Only biomass removed/damaged
Sampling and study design attributes
Exhaustive or subsampled species counts within samples
Quadrat area (m^2)
Number of disturbance levels
Number of samples
Total area of disturbance sampled (m^2)
Single patch vs. Mosaic of patches
Time span (yr)§
Observation vs. Experimental

† Used as a surrogate for terrestrial primary productivity. Actual evapotranspiration values were estimated from USSR Committee for the International Hydrological Decade (1977) for terrestrial studies providing adequate site location information.

‡ Two variations of this predictor were examined in analyses: (1) include both natural and anthropogenic disturbances, with anthropogenic disturbances assigned to the category they best represent or were stated to simulate, and (2) include only natural disturbances.

§ Range of temporal gradient.

turbance, by this definition, includes abiotic processes such as fire, landslides, wave exposure, and floods, as well as the biotic processes of predation and grazing. It does not include prolonged stresses such as contamination by pollutants, invasion by exotics, or climate change.

METHODS

Data Collection

Our literature search was as broad as possible, including all studies we could locate that related richness, diversity, or evenness to gradients of disturbance, whether or not those studies specifically tested the intermediate–disturbance hypothesis (IDH). We began by searching Biological Abstracts on CD-ROM (1990–1996, inclusive), using the following search strings with some minor variations: intermediate disturbance, disturbance, disturbance gradients, species richness, species diversity, species evenness, patterns in species richness (or diversity or evenness), community dynamics, and community structure. Bibliographies of publications retrieved from the electronic search were searched for additional studies of diversity and distur-

bance. We then searched Biological Abstracts 1985 through 1990 in hard-copy format. Because "disturbance" is not a key word in hard-copy volumes, the search was limited to the following strings: species composition, species diversity, species evenness, species richness, and succession. To prevent bias towards studies of particular types of disturbance, we did not use key words such as fire, grazing, mining, logging, etc. We are confident that our search identified the majority of the disturbance literature published over at least 12 years and also many of the studies published prior to 1985.

Species diversity–disturbance relationships were retained in our analyses provided that: (1) Three or more disturbance levels were examined (at least three are required to detect a peaked relationship). Papers examining disturbance presence/absence are very abundant and frequently make conclusions about the IDH, but these could not be included in our analyses because such studies cannot identify the shape of the species diversity–disturbance relationship. (2) The disturbance gradient consisted of different levels of a single disturbance type (e.g., forest fire frequency, time since flooding, or intensity of sheep grazing) and was measured on either a continuous or an ordinal scale. Studies that used composite disturbance measures (combinations of disturbance types) were included only if their estimates of disturbance level could be confidently quantified or ranked. (3) The disturbance gradient was calculated from the actual disturbance frequency or intensity, or time passed since the last disturbance event, or some other physical environmental attribute that was shown to be an indicator of disturbance. When gradients were inferred from a biological response to a supposed disturbance, we did not include them in our analyses. (4) The study examined species/taxonomic richness, evenness, and/or diversity. (5) Statistical results were reported, or sufficient data were included in the paper for us to perform statistical analyses. Studies reporting only qualitative relationships were excluded. (6) Potential explanatory variables could be determined (see below). Not all explanatory variables could be obtained from each study; therefore the sample sizes of our analyses varied. Studies failing to report methodology and descriptions of the community and/or disturbance were excluded.

A total of 1962 abstracts and papers were consulted. From these, 85 papers satisfying our criteria were found, providing a total of 116 richness–disturbance relationships, 53 diversity–disturbance relationships, and 28 evenness–disturbance relationships (see Appendix).

We used two forms of meta-analysis to evaluate the form of the relationships between species diversity and disturbance and to summarize how much of the observed variation in species diversity can be related to disturbance. First, to determine the form of the species diversity–disturbance relationships, we used a vote-

counting procedure based, in part, on statistical significance. Vote-counting and other forms of meta-analysis based on statistical significance have been criticized (Gurevitch et al. 1992, Osenberg et al. 1997). While a measure of effect strength would have been preferable (Osenberg et al. 1999), the diversity of studies in our data set made this impossible. Vote-counting provided an effective way to examine the conditions under which peaked relationships are detected in empirical studies. Second, we also extracted from each study the proportion of the variation in species diversity explained by disturbance (i.e., r^2) using a quadratic polynomial regression model or an analysis of variance. We then performed unweighted meta-analyses using r^2 from each study as the effect size. The three measures of species diversity (richness, diversity, and evenness) were analyzed separately because papers that contained relationships for two or three of these measures indicated that the form of the relationship for the three measures are frequently different.

Some of the relationships included in our data set are composed of data pooled from two or more relationships in a primary study. To avoid non-independence of multiple relationships retrieved from a single paper, we pooled data from studies in a single paper sharing a common sampling regime and examining the same taxa, disturbance, and measure of species diversity. Studies within a single paper that examined different taxa, different habitats, or different disturbances, or applied different sampling methods were all included in our data set because of our objective to determine whether any of these attributes are related to the form of species diversity–disturbance relationship observed in a study.

Each relationship was categorized as having one of five observed shapes: flat, positive monotonic, peaked, negative monotonic, or U shaped. We performed the pattern analyses described below for 80 richness, 27 evenness, and 39 diversity relationships. In further cases (36, 1, and 14 cases, for richness, evenness, and diversity, respectively), we could not analyze the data ourselves, but the original authors had performed the analyses that we describe below. We accepted these analyses. Cases where we could not re-analyze the data were almost always studies of categorical disturbance gradients, and the authors provided only the mean species-diversity values per category.

To characterize the shape of a relationship when the measure of disturbance was continuous, we used second-degree polynomial regressions. Statistically nonsignificant relationships ($P > 0.05$) were categorized as "flat." When the linear regression term in a relationship was significant ($P \leq 0.05$) but the quadratic term was not, we categorized the relationship as "monotonic positive or negative," according to the sign on the linear term. A relationship was categorized as "peaked" or "U-shaped" if: (a) the quadratic term in the regression was significant, and (b) the maximum

or minimum of the curve fell within the observed range of disturbance values, as determined by an MOS test (Mitchell-Olds and Shaw 1987). If the maximum fell outside the range of the data, the relationship was categorized as monotonic positive or negative. In a few cases where the distribution of the residuals violated the assumptions of least-squares regression, we used nonparametric correlation analysis to test the significance of monotonic relationships, after examining scatterplots of these few relationships for peaks.

When measures of disturbance were ordinal, we used ANOVA to test for significance. Multiple-comparison tests were then done to determine which categorical levels of disturbance differed significantly. Relationships were classified as peaked if species-diversity measures at both extremes of the disturbance gradient were significantly lower than at some intermediate level of disturbance.

The proportion of the variation in species diversity explained by disturbance in each relationship was obtained only from parametric analyses. When regressions were performed, explained variation was always obtained from models including both linear and quadratic terms. Parametric ANOVAs also yielded r^2 values, which we included in our analyses.

Variables that could potentially account for differences in total explained variation (i.e., strength) and shape of relationships are listed in Table 1. These variables are grouped into three categories: (1) organism and system attributes, (2) disturbance attributes, and (3) sampling and study design. Organism and system attributes include whether study organisms were animals or plants, terrestrial or aquatic/marine, and sessile or motile. Also, sessile producers were differentiated from motile consumers, based on Wootton's (1998) hypothesis that IDH should hold for species competing for non-dynamic basal resources, but not for mobile species at higher trophic levels.

Measures of productivity were not provided in the original papers. However, Rosenzweig (1968) and Lieth (1975) showed that terrestrial productivity strongly correlates with actual evapotranspiration (AET). Therefore, by using the geographic locations provided in the papers, we estimated AET for terrestrial systems from the Atlas of World Water Balance (USSR National Committee for the International Hydrological Decade 1977), and used this as a surrogate for productivity. Productivity could not be estimated for aquatic systems because such studies rarely provided productivity or related data (e.g., chlorophyll, total phosphorus).

Disturbances were characterized as biotic (e.g., grazing) vs. abiotic (e.g., fire), natural (e.g., windthrow) vs. anthropogenic (e.g., cultivation), and chronic (e.g., grazing) vs. episodic (e.g., landslides). To eliminate the anthropogenic factor from the abiotic vs. biotic variable, we also examined abiotic vs. biotic for natural disturbances only. Each disturbance was classified as

a gradient of either disturbance frequency or disturbance intensity at multiple sites (spatial gradient), or a gradient of time passed since the last disturbance occurred at single sites sampled several times (temporal gradients). Disturbances were also categorized as removing or damaging only the biomass of the community being examined, vs. damaging the habitat of the community in question (or both). Although other aspects of disturbance might be associated with the strength and shape of species diversity–disturbance relationships (e.g., species-specific vs. non-specific disturbance, the size of the disturbance in relation to the area sampled, duration of disturbance events, etc.), data were not available for us to test these.

Other variables in our analyses describe sampling design (Table 1). We estimated sampling intensity with three variables: exhaustive sampling of the community vs. incomplete or subsampling (e.g., point counts), the number of disturbance levels examined, and the total number of samples taken. We defined a "sample" as yielding one datum; if authors pooled several samples to obtain a single estimate of species diversity, then we classified the sum of those pooled samples as one sample. Two measures of sampling area were also examined: quadrat area and the total area sampled per level of disturbance. "Quadrat area" is the area sampled to obtain a single data point. If a datum resulted from pooling sampled areas, then quadrat area is the sum of those areas. "Total area of a disturbance level sampled" is defined as the sum of all areas sampled for each level of disturbance in the study (i.e., area per sample multiplied by number of samples per disturbance level). Another variable, single patch vs. mosaic, differentiates studies that measured species diversity within individual disturbed patches (e.g., recolonization of a gap created by a windthrow) vs. studies that measured species diversity in areas that contained small patches of disturbance (cf. Wilson 1994). In "mosaic" studies (e.g., a forest stand containing uprooted trees) the disturbance level assigned to an area was the overall intensity or frequency of disturbed patches in the whole area (e.g., the frequency of tree uprooting within the stand). The duration of temporal gradients of studies examining patterns of species diversity over time was also included in our set of potential predictor variables. Finally, observational studies were compared with experimental or manipulative studies.

We located 119 species diversity–disturbance relationships examined along spatial gradients, and 78 examined on temporal gradients, either at replicate sites following a given disturbance, or at a series of sites differing in the time since the last disturbance (and assumed to be otherwise identical). Only four studies (Reice 1984, Armesto and Pickett 1985, Lake et al. 1989, Ambrose 1993; for a total of nine species diversity–disturbance relationships) examined temporal and spatial gradients simultaneously: a set of sites differing in disturbance intensity or frequency, followed

TABLE 2. The proportion of variation in species richness, diversity, or evenness statistically related to disturbance in a compilation of 85 published studies. Results are shown separately for relationships that are nonsignificant (—), positive monotonic (/), peaked (∩), negative monotonic (\), U-shaped (∪), and for all studies combined.

Diversity measure	—	/	∩	\	∪	All studies
Species richness						
No. studies	25 (16)	25 (4)	16 (3)	18 (6)	3 (0)	87 (29)
Median	0.179[a]	0.665[b]	0.524[a,b]	5.14[a,b]	0.710[b]	0.534
Skewness	+0.590	−0.206	−0.025	−0.239	+0.243	−0.156
Range	0.001–0.855	0.250–0.994	0.080–0.973	0.096–0.900	0.538–0.970	0.001–0.994
Species diversity						
No. studies	11 (4)	12 (0)	6 (4)	12 (3)	1 (0)	42 (11)
Median	0.707[a]	0.516[a]	0.678[a]	0.594[a]	0.611[a]	0.605
Skewness	−0.561	−0.354	+0.350	−0.179	⋯	−0.392
Range	0.036–0.952	0.113–0.769	0.501–0.978	0.171–0.940	0.611	0.036–0.978
Species evenness						
No. studies	11 (3)	2 (0)	3 (0)	7 (2)	0 (0)	23 (5)
Median	0.266[a]	0.723[a]	0.993[a]	0.794[a]	⋯	0.601
Skewness	+0.381	⋯	−0.707	−0.463	⋯	−0.137
Range	0.025–0.855	0.663–0.782	0.423–1.000	0.147–0.999	⋯	0.025–1.000

Notes: The diversity measure includes the studies that provided either r^2 values or sufficient data to calculate r^2. Numbers in parentheses are the number of additional studies found that observed the same shape of relationship but did not provide a value for r^2. The very high, but nonsignificant r^2 values came from studies with very small sample sizes (generally $n = 3$). In the Median rows, entries with the same lowercase superscript letter are not statistically different from one another at $P > 0.05$ (Kruskal-Wallis).

through time (sometimes at just two times). Three of these four studies indicated that the observed relationship between species diversity and disturbance among sites changed temporally. Although timescale can be an important consideration in meta-analyses (Downing et al. 1999, Osenberg et al. 1999), there are insufficient data and few theoretical considerations to guide the selection of appropriate timescales for these studies. Therefore, we restricted our analyses to the longest timescale available from each study that presented a time series.

Details of the 197 relationships examined in this study are provided in the Appendix.

Analyses

We used r^2 as the measure of the strength of species diversity–disturbance relationships. Some authors use regression slope as the measure of the strength of a relationship. Note that these two metrics are equivalent in our present study. The standardized regression coefficient (i.e., the regression slope calculated on standardized data) is equal to r for bivariate linear relationships. It is practical in this study to use r (or rather, r^2) because it can also be used to describe bivariate nonlinear relationships, which do not have a unique slope.

Logistic regressions were used to determine under what conditions the odds of observing the different shapes of disturbance–species relationship (flat, positive monotonic, negative monotonic, and unimodal) is greatest. The resulting statistical models take the form:

$$\log \hat{O} = \alpha + \beta_1(E_1) + \beta_2(E_2) + \ldots$$

where $\hat{O}$ is the estimated conditional odds of the relationship shape of interest, given the explanatory variables (E_i). Each β represents the change in log odds due to a unit increase in the value of the explanatory variable, controlling for all other predictors in the model. For binary explanatory variables, β is the change in log odds between group $= 1$ and group $= 0$. For continuous variables, β is the change in log odds per one-unit increment in the predictor. The interpretation of logistic regression results is more intuitive when expressed as the percentage change in odds (PCO) for a unit increment in the predictor:

$$\text{PCO} = 100[\exp(b_i) - 1]$$

where b_i is the sample estimate of β_i, and $\exp(b_i)$ is the estimated multiplicative change in the odds of observing the relationship shape of interest for a one-unit increment in the ith explanatory variable (DeMaris 1992).

Predictive efficacy of logistic models was measured with McFadden's rho^2, which is analogous to r^2 and ranges between 0 and 1. This measure of efficacy generally underestimates the total variation explained by the model; therefore, the predictive efficacies we provide are conservative.

All statistical analyses were performed with SYSTAT 9.0 (Wilkinson 1998).

RESULTS

Does species diversity have a consistent and significant relationship with disturbance?

1. *Total Explained Variation in Species Diversity.*— The amount of variation in richness, diversity, and evenness statistically related to disturbance, using quadratic polynomial regression or ANOVA, varied enormously among studies, from 0.1% to 100% (Table 2).

Not surprisingly, nonsignificant (i.e., flat) richness and evenness relationships generally explained less variation than significant relationships; however, this difference was not statistically significant for evenness relationships. Note that polynomial regressions always have r^2 values > 0, even when both variables are generated randomly. When the number of disturbance levels and samples is three, the r^2 for a random data set will equal 1.0. As the number of levels (or samples taken per level) increases, r^2 will decrease towards 0. Thus, our analysis overestimates the fraction of the variation in diversity that can be statistically explained by disturbance gradients, particularly when sample sizes are small. We return to this point below (see *Discussion*).

Among significant relationships, the different shapes of relationships (positive, peaked, negative, and U shaped, as determined by quadratic polynomial regression, ANOVA, or nonparametric correlation) accounted for indistinguishable amounts of explained variation for any of the three measures of species diversity (Table 2).

2. *Frequency of Different Shapes of Relationship.*—

Richness.—Flat (i.e., nonsignificant) relationships were observed more frequently than any other shape (H_0: uniform distribution; $\chi^2 = 33.5$, df = 4, $P < 0.001$) (Table 2, Fig. 1). Among significant relationships, positive, negative, and peaked relationships were observed equally frequently ($\chi^2 = 2.1$, df = 2, $P > 0.25$), but U-shaped relationships were observed much less frequently than any other shape ($\chi^2 = 20.3$, df = 3, $P < 0.001$).

Diversity.—There were no significant differences in the observed frequencies of nonsignificant, positive, peaked, and negative relationships ($\chi^2 = 3.9$, df = 3, $P > 0.25$). As with richness, U-shaped relationships were observed much less frequently than any other shape of relationship ($\chi^2 = 12.6$, df = 4, $P < 0.025$) (Table 2, Fig. 1).

Evenness.—Flat relationships were again observed more frequently than any other shape ($\chi^2 = 23.8$, df = 4, $P < 0.001$) (Table 2, Fig. 1). Among significant relationships, negative ones were observed most frequently ($\chi^2 = 6.1$, df = 2, $P < 0.05$).

In sum, there is no evidence that a particular shape of species diversity–disturbance relationship is consistently detected.

Under what conditions are significant species diversity–disturbance relationships most likely to be observed?

Richness.—Only one of our predictors was significantly associated with the probability that a richness–disturbance relationship would be significant or nonsignificant. Odds of observing a significant relationship were 133% greater when the examined disturbance was natural rather than anthropogenic in origin (Mc-
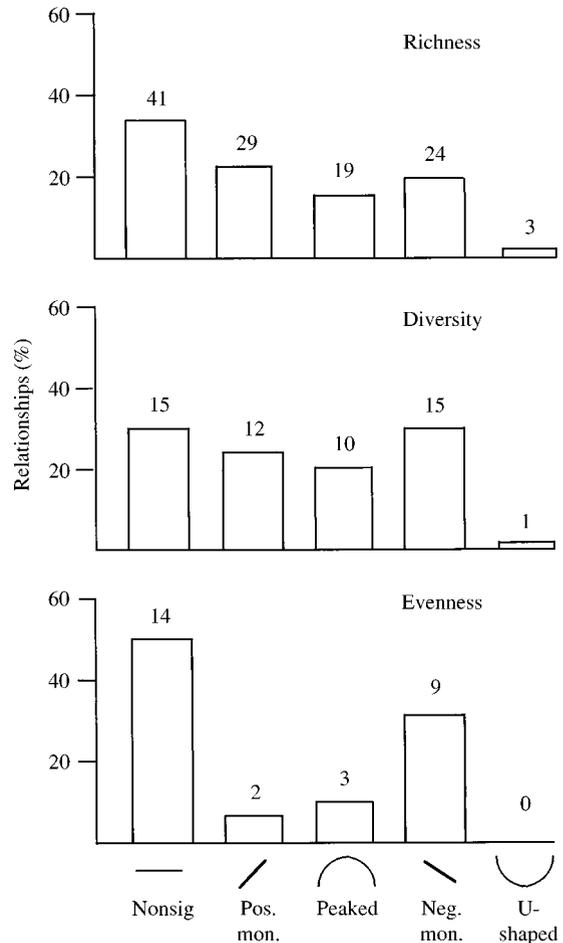

Fig. 1. The percentage of species richness–, diversity–, and evenness–disturbance relationships exhibiting each of the five observed patterns (nonsignificant [nonsig.], positive monotonic [pos. mon.], peaked, negative monotonic [neg. mon.], and U-shaped). The number of observations in each category is indicated above each bar.

Fadden's rho^2 = 0.031, $n = 116$ relationships, $P = 0.032$; Fig. 2).

Diversity.—Odds of observing a significant diversity–disturbance relationship were significantly related to three attributes of the disturbance and two attributes of the sampling design (Table 3). Studies examining chronic disturbances had odds 1209% greater than studies of episodic disturbance events. Odds of a significant relationship were 268% greater for studies of spatial gradients of disturbance vs. temporal gradients, and, more specifically, 653% greater when gradients of disturbance intensity vs. any other gradients were examined. The number of samples examined in a study had a great effect on the odds of observing a significant relationship: odds increased 6422% for each 10-fold increase in sample size. Finally, odds were 550% greater in studies examining communities in mosaics of patches, rather than in single patches. Many of these
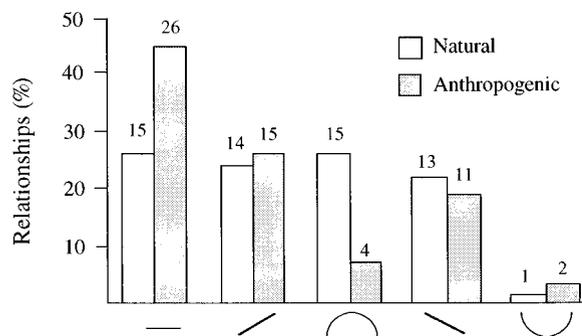
Fig. 2. Natural ($n = 58$ relationships) vs. anthropogenic ($n = 58$ relationships) causes of disturbance. The percentage of richness–disturbance relationships exhibiting each of the five observed patterns (nonsignificant, positive monotonic, peaked, negative monotonic, and U-shaped; symbols are as in Fig. 1). The number of observations is indicated above each bar.

predictor variables were collinear: studies examining mosaics of patches, compared to single patches, more frequently involved chronic disturbances ($\chi^2 = 14.2$, df $= 1$, $P = 0.0002$) and spatial gradients ($\chi^2 = 11.8$, df $= 1$, $P = 0.0006$). Studies of both chronic disturbances vs. episodic disturbances and spatial gradients vs. temporal gradients were also more likely to have greater samples sizes (chronic: $U = 402$, $\chi^2 = 5.1$, df $= 1$, $P = 0.02$; spatial gradients: $U = 461$, $\chi^2 = 7.1$, df $= 1$, $P = 0.008$). The best multiple-regression model for predicting whether a significant diversity–disturbance relationship will be observed included the number of samples examined and whether studies examined individual patches or mosaics of patches.

Evenness.—None of our predictor variables were significantly associated with the odds of observing a significant evenness–disturbance relationship. This may be a result of the small number of studies in this group ($n = 28$).

Does the amount of explained variation in species diversity depend upon the conditions under which the relationship was observed?

Richness.—The amount of variation in richness explained by disturbance was significantly related to two attributes of the disturbances studied (Table 4). More variation in richness was related to disturbance when disturbances were biotic rather than abiotic, and when richness was measured along a gradient of time passed since the last disturbance rather than along spatial gradients of disturbance frequency or intensity.

Five attributes of sampling design were also related to the total explained variation. Relationships were stronger when sample sizes were small (Fig. 3a) and when the organisms within the samples were not enumerated exhaustively. Explained variation was also greater when low to moderate numbers of levels of disturbance were examined (i.e., a peak occurs at ~7 levels), and when the duration of temporal gradients was moderate (~7 yr) (Fig. 3).

Some of these significant relationships may reflect collinearities. Richness–disturbance relationships involving temporal gradients of disturbance were more likely to have greater numbers of disturbance levels (Mann-Whitney U test: $U = 1121$, $\chi^2 = 7.1$, df $= 1$, $P = 0.008$) and lower sample sizes ($U = 2348$, $\chi^2 = 20.5$, df $= 1$, $P = 6 \times 10^{-6}$) than were relationships for spatial gradients. More levels of disturbance were also generally examined in studies of abiotic vs. biotic disturbance ($U = 2293$, $\chi^2 = 11.7$, df $= 1$, $P = 0.006$). Relationships obtained from exhaustively searched

TABLE 3. Significant relationships observed in logistic regression analyses comparing the odds of significant (peaked, positive monotonic, and negative monotonic) vs. nonsignificant species diversity–disturbance relationships.

Explanatory variable	n	P†	McFadden's rho²	Group with highest odds	Change in odds of significant relationship‡ (%)
Simple regression					
Frequency vs. Intensity vs. Frequency $\times$ Intensity vs. Time	53	0.008	0.186	intensity	+653§
Spatial vs. Temporal	53	0.037	0.069	spatial	+268
Chronic vs. Episodic	57‖	0.002	0.143	chronic	+1209
Number of samples	52	0.0003	0.206	high number	+6422/10-fold increase
Single patch vs. Mosaic	53	0.010	0.106	mosaic	+550
Multiple regression					
Number of samples	52	0.00009	0.298	high number	+5936/10-fold increase
Single patch vs. Mosaic		···	···	mosaic	+590

Note: See Table 1 and related text for description of explanatory variables.

† Probability from likelihood ratio chi-square.

‡ For binary predictors, the percentage change in odds of a peaked relationship is reported in terms of the change predicted for the group with the highest odds vs. the group with the lowest odds. In the multiple regression, the change in odds was calculated while controlling for the other predictor in the model.

§ Percentage change in odds is given for Intensity vs. other three categories combined.

‖ Because of sparsity of cases in one cell (chronic disturbance and nonsignificant diversity–disturbance relationship), one case was added to each of the four cells for this analysis.

TABLE 4. Does the proportion of the variation in species richness that is statistically related to disturbance (r^2) in published richness–disturbance studies depend upon characteristics of the organisms, the disturbance, or the study design? Mean explained variation is reported for each category of the categorical predictors.

Predictor variable†	Mean r^2 or shape of relationship‡	n§	Statistics‖		P
			F	r^2	
Organism and system attributes					
Animal vs. Plant	0.437, 0.540	28, 58	1.64	0.019	0.204
Terrestrial vs. Aquatic	0.529, 0.466	57, 30	0.65	0.008	0.424
Sessile vs. Motile	0.539, 0.407	62, 23	2.42	0.028	0.123
Sessile producer vs. Motile consumer	0.545, 0.420	57, 24	2.12	0.026	0.149
Actual evapotranspiration		51	0.17	0.003	0.685
Disturbance attributes					
Abiotic vs. Biotic	0.427, 0.581	42, 45	4.49	0.050	0.037
Abiotic vs. Biotic (natural disturbance only)	0.474, 0.529	36, 15	0.31	0.006	0.578
Frequency vs. Intensity vs. Frequency × Intensity vs. Time	0.381, 0.466, 0.340, 0.611	11, 25, 10, 41	($H = 12.16$)		0.007
Spatial vs. Temporal	0.418, 0.611	46, 41	($U = 563, \chi^2 = 10.47$)		0.001
Anthropogenic vs. Natural	0.542, 0.482	37, 50	0.61	0.007	0.436
Chronic vs. Episodic	0.413, 0.552	28, 59	3.07	0.035	0.083
Biomass vs. Habitat vs. both	0.531, 0.380, 0.635	53, 22, 12	2.53	0.057	0.086
Sampling and study design					
Exhaustive or subsampled sampling	0.360, 0.624	30, 41	12.16	0.150	0.0009
Log_{10} quadrat area (m²)		68	0.16	0.002	0.690
Log_{10} number of disturbance levels¶	unimodal	87	7.75	0.219	0.0001
Log_{10} number of samples¶	negative monotonic	87	29.02	0.409	$<10^{-8}$
Log_{10} total area of disturbance sampled (m²)		64	0.44	0.007	0.511
Single patch vs. Mosaic	0.547, 0.426	58, 29	2.39	0.027	0.126
Log_{10} time span (yr)¶#	unimodal	39	3.80	0.174	0.032
Observed vs. Experimental	0.539, 0.432	61, 26	1.73	0.020	0.192

† Significant relationships ($P < 0.05$) are in boldface type.

‡ Mean r^2 is reported for each category of categorical variables; shape of relationship is reported for significant continuous predictor variables.

§ The number of studies in each analysis (n) is reported per category for categorical predictors and as total for continuous predictors.

‖ H refers to Kruskal-Wallis nonparametric ANOVA; U refers to Mann-Whitney nonparametric t test.

¶ Relationships are nonlinear. The statistics presented are from the following polynomial regression models: log_{10} number of disturbance levels (log_{10}NDL), $-1.34 + 6.73(log_{10}NDL) - 6.10(log_{10}NDL)^2 + 1.59(log_{10}NDL)^3$; log_{10} number of samples (log_{10}NS), $2.06 - 1.53(log_{10}NS) + 0.38(log_{10}NS)^2$; log_{10} time span (log_{10}TS), $0.95 + 0.26(log_{10}TS) - 0.15(log_{10}TS)^2$.

Includes only those studies that examined gradients of time passed since the last disturbance.

samples included greater sample sizes than did cases where organisms were sub-sampled ($U = 1664, \chi^2 = 12.7$, df $= 1$, $P = 0.004$).

Diversity.—A summary of the attributes that significantly affected the probability of observing a significant diversity–disturbance relationship is presented in Table 5. Variation in diversity explained by disturbance was greatest in studies that examined plants or, more specifically, sessile producers, as opposed to motile animals. Explained variation was also greatest when sample size was small and when low to moderate numbers ($\sim$7–8) of disturbance levels were examined. The number of disturbance levels examined was greater in studies of plants, sessile organisms (producers or consumers), and, specifically, sessile producers ($U = 361$, $\chi^2 = 6.5$, df $= 1$, $P = 0.01$) than in studies of animals, all motile organisms, and motile consumers.

Evenness.—The amount of explained variation in evenness was related to four explanatory variables (Table 6). Explained variation was greatest in studies of sessile producers (compared to motile consumers) and plants in general (includes sessile producers and nonattached phytoplankton). Relationships tended to be stronger when sample sizes were small and fewer levels of disturbance were examined. Sample size and number of disturbance levels examined were positively correlated for evenness–disturbance relationships ($r_s = 0.432$, $n = 28$ relationships, $P < 0.05$).

Under what conditions are peaked species diversity-disturbance relationships most likely to be observed?

Richness.—Logistic regression analyses comparing peaked vs. all other shapes of richness–disturbance relationships indicated that the odds of observing a peaked relationship were significantly associated with four explanatory variables (Table 7). Odds of a peaked richness–disturbance relationship were 371% greater for natural disturbances than for disturbances with anthropogenic causes (Fig. 2). Odds of a peaked relationship decreased 31% for each 10-fold increase in quadrat area and increased 535% for each 10-fold increase in the number of disturbance levels examined. Productivity in terrestrial systems, as estimated by actual evapotranspiration (AET), also affected the odds of observing a peaked relationship: odds decreased 97% for each
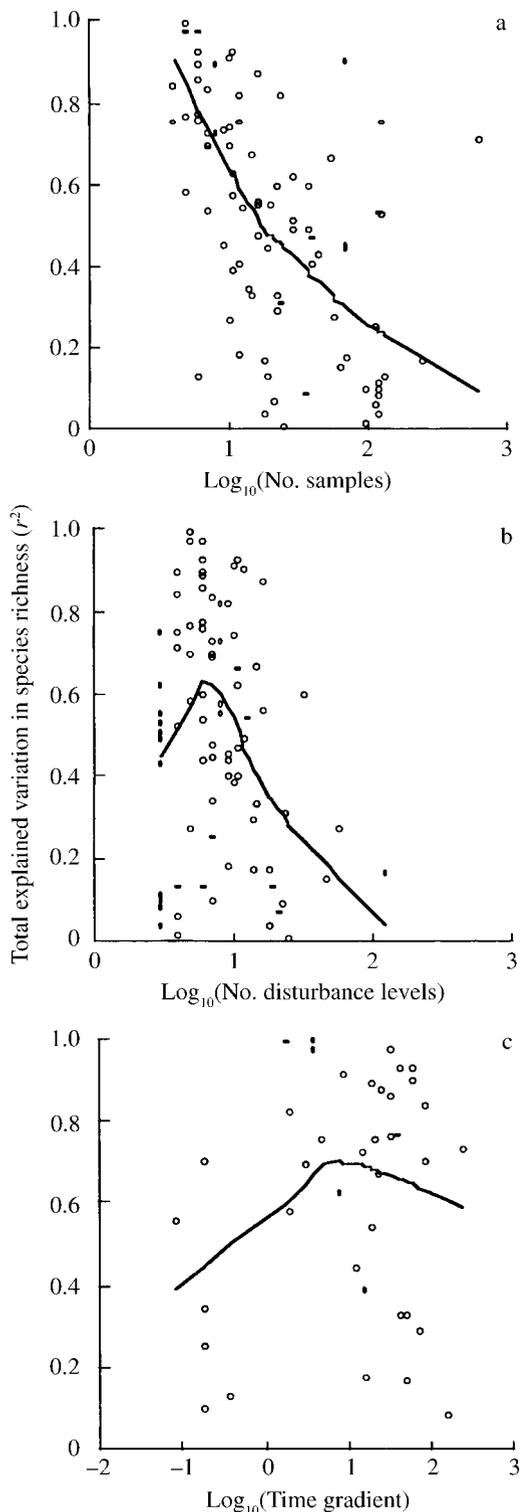
FIG. 3. The total proportion of variation in species richness explained by disturbance (r^2) is (a) negatively related to the number of samples examined, (b) a unimodal function of the number of levels of disturbance examined, and (c) a unimodal function of the duration of a temporal disturbance gradient. The solid lines represent LOWESS lines of best fit. The relationship between r^2 and number of samples is similar

10-fold increase in AET. The number of disturbance levels examined was greater in studies of natural disturbance ($U = 716$, $\chi^2 = 29$, df $= 1$, $P < 10^{-7}$).

Diversity and evenness.—Analyses provided little insight into the conditions required to observe peaked evenness– or diversity–disturbance relationships. None of the explanatory variables were significant in analyses of evenness. For diversity–disturbance relationships, the only significant predictor was whether the organisms studies were sessile producers or motile consumers: odds of a peaked relationship were 540% greater for sessile producers than for motile consumers (McFadden's $rho^2 = 0.103$, $n = 52$ relationships, $P = 0.040$; to deal with sparse data in one cell (peaked relationship, motile consumers), one case was added to each of the four cells in this analysis, increasing n from the original 48 to 52 relationships).

DISCUSSION

The general opinion in the literature is that disturbance should have a strong effect on species diversity, and that the species diversity–disturbance relationship should peak at intermediate levels of disturbance. However, upon closer examination, data are actually equivocal on the subject. In 35%, 28%, and 50% of published studies, no effect of disturbance on richness, diversity, or evenness, respectively, was observed.

The high proportion of nonsignificant relationships indicates that peaked species diversity–disturbance relationships are actually not as prevalent as commonly believed. For two reasons, our data set probably underestimates the proportion of nonsignificant relationships and overestimates the proportion of peaked relationships that are actually observed. First, nonsignificant relationships are more likely to remain unpublished than significant ones (''the file-drawer effect''; Gurevitch et al. 1992). Second, part of our search for papers involved searching bibliographies of retrieved publications for additional papers; this older literature (pre-1985) is represented by studies that first documented peaked species diversity–disturbance relationships and that continue to be cited in the recent literature, and, incidentally, contains a greater proportion of peaked relationships than does the more current literature (24% vs. 13% of relationships, respectively).

Alternatively, the abundance of statistically nonsignificant relationships in our study could be a result of low statistical power (or low sample size) in the primary studies. Gurevitch et al. (1992) state that analyses like ours contain a strong bias towards finding no effect because many ecological studies have small sample

for diversity– and evenness–disturbance relationships. Explained variation has a similar unimodal relationship with the number of disturbance levels examined in diversity–disturbance relationships, but the relationship is negative for evenness–disturbance relationships. The original units for temporal disturbance gradient are years.

TABLE 5. Does the proportion of the variation in diversity (e.g., Shannon-Wiener's index, Simpson's D) that is statistically related to disturbance (r^2) in published diversity–disturbance studies depend upon characteristics of the organisms, the disturbance, or the study design? Mean explained variation is reported for each category of the categorical predictors.

Predictor variable[†]	Mean r^2 or shape of relationship[‡]	n§	F	r^2	P
Organism and system attributes					
Animal vs. Plant	0.366, 0.665	12, 30	12.01	0.231	0.001
Terrestrial vs. Aquatic	0.589, 0.563	29, 13	0.07	0.002	0.789
Sessile vs. Motile	0.641, 0.329	33, 8	9.16	0.190	0.004
Sessile producer vs. Motile consumer	0.671, 0.339	28, 10	12.20	0.253	0.001
Actual evapotranspiration		27	0.72	0.028	0.405
Disturbance attributes					
Abiotic vs. Biotic	0.499, 0.636	17, 25	2.42	0.057	0.128
Abiotic vs. Biotic (natural disturbance only)	0.488, 0.640	14, 11	1.63	0.066	0.214
Frequency vs. Intensity vs. Frequency × Intensity vs. Time	0.412, 0.554, 0.508, 0.645	3, 13, 6, 20	0.843	0.062	0.479
Spatial vs. Temporal	0.523, 0.645	22, 20	1.99	0.047	0.166
Anthropogenic vs. Natural	0.619, 0.553	18, 24	0.56	0.014	0.461
Chronic vs. Episodic	0.555, 0.595	15, 27	0.19	0.005	0.670
Biomass vs. Habitat vs. both	0.623, 0.387, 0.641	28, 8, 6	2.46	0.112	0.098
Sampling and study design					
Exhaustive or subsampled sampling	0.561, 0.615	12, 26	0.32	0.009	0.578
$\log_{10}$ quadrat area (m²)		32	1.17	0.036	0.299
$\log_{10}$ number of disturbance levels‖	unimodal	42	5.51	0.303	0.003
$\log_{10}$ number of samples‖	negative monotonic	42	9.07	0.318	0.0006
$\log_{10}$ total area of disturbance sampled (m²)		30	0.43	0.015	0.517
Single patch vs. Mosaic	0.599, 0.553	26, 16	0.25	0.006	0.622
$\log_{10}$ time span (yr)¶		18	0.43	0.026	0.520
Observed vs. Experimental	0.558, 0.652	32, 10	0.84	0.021	0.364

  † Significant relationships ($P < 0.05$) are in boldface type.
  ‡ Mean r^2 is reported for each category of categorical variables; shape of relationship is reported for significant continuous predictor variables.
  § The number of studies in each analysis (n) is reported per category for categorical predictors and as total for continuous predictors.
  ‖ Relationships are nonlinear. The statistics presented are from the following polynomial regression models: $\log_{10}$ number of disturbance levels ($\log_{10}$NDL), $-2.92 + 12.91(\log_{10}$NDL$) - 13.30(\log_{10}$NDL$)^2 + 4.23(\log_{10}$NDL$)^3$; $\log_{10}$ number of samples ($\log_{10}$NS), $2.05 - 1.55(\log_{10}$NS$) + 0.43(\log_{10}$NS$)^2$.
  ¶ Includes only those studies that examined gradients of time passed since the last disturbance.

sizes and relatively small effects, resulting in low statistical power. Gurevitch et al. (1992) and Osenberg et al. (1999) suggest that the number of significant, or nonsignificant, results one would expect to find in a vote-counting analysis like ours is a function of both the sample sizes of the primary studies and the actual magnitude of the effect in question. Our logistic regression analyses explicitly examined the effect of study sample size on the odds of observing a significant relationship. Sample size was not related to the odds of observing a significant richness– or evenness–disturbance relationship, but the odds did increase with sample size in the set of diversity–disturbance relationships. If low sample size were responsible for the abundant nonsignificant relationships in this study, we would have expected to find evidence of it in our analyses of richness– and evenness–disturbance relationships, but we did not.

Collinearities make it difficult to determine in which biological systems significant diversity–disturbance relationships are most likely to occur. In studies of richness, odds were higher for natural vs. anthropogenic disturbances. In the primary studies, natural disturbances more frequently caused the removal or damage

of habitat, rather than affecting only the organisms being studied. Studies of natural disturbances were also more likely to examine plant or sessile communities. Together, these collinearities could explain the observed difference between natural and anthropogenic disturbances. Motile animal colonizers from communities surrounding a disturbed patch quickly reestablish the original species assemblage of the patch with little or no change in species diversity (Fuentes and Jaksic 1988). Plant communities, especially those recovering from disturbances that affected a primary resource (e.g., space), would likely have a much slower recovery than would motile animal communities, especially those recovering from less intense losses of individuals (Fuentes and Jaksic 1988, Wootton 1998).

Explained variation in species diversity–disturbance relationships is not consistently large. The median amount of variation explained by disturbance was 53% for richness, 60% for diversity, and 60% for evenness (see Table 2). Again, because of the file-drawer effect, this is probably an overestimate. Even more importantly, these numbers are inflated because a regression always explains >0% of the variation in the dependent variable, especially when sample sizes are small. If we

TABLE 6. Does the proportion of the variation in species evenness that is statistically related to disturbance (r^2) in published evenness–disturbance studies depend upon characteristics of the organisms, the disturbance, or the study design? Mean explained variation is reported for each category of the categorical predictors.

Predictor variable[†]	Mean r^2 or shape of relationship[‡]	n[§]	Statistics		
			F	r^2	P
Organism and system attributes					
Animal vs. Plant	0.232, 0.680	5, 18	5.71	0.214	0.026
Terrestrial vs. Aquatic	0.627, 0.494	15, 8	0.52	0.024	0.479
Sessile vs. Motile	0.646, 0.170	20, 3	4.27	0.169	0.051
Sessile producer vs. Motile consumer	0.683, 0.170	17, 3	4.50	0.200	0.048
Actual evapotranspiration		13	0.54	0.047	0.479
Disturbance attributes					
Abiotic vs. Biotic	0.522, 0.636	11, 12	0.42	0.019	0.527
Abiotic vs. Biotic (natural disturbance only)	0.542, 0.441	9, 6	0.19	0.014	0.674
Frequency vs. Intensity vs. Frequency × Intensity vs. Time	0.467, 0.381, 0.423, 0.692	2, 6, 1, 14	0.87	0.121	0.474
Spatial vs. Temporal	0.404, 0.692	9, 14	2.80	0.118	0.109
Anthropogenic vs. Natural	0.724, 0.502	8, 15	1.584	0.070	0.222
Chronic vs. Episodic	0.569, 0.585	5, 18	0.01	0.000	0.943
Biomass vs. Habitat vs. both	0.578, 0.169, 0.858	18, 2, 3	2.11	0.174	0.147
Sampling and study design					
Exhaustive or subsampled sampling	0.506, 0.731	8, 12	1.62	0.082	0.220
Log_{10} quadrat area (m²)		17	2.65	0.150	0.125
Log_{10} number of disturbance levels	negative monotonic	23	12.69	0.377	0.0002
Log_{10} number of samples‖	negative monotonic	23	24.05	0.706	5×10^{-6}
Log_{10} total area of disturbance sampled (m²)		17	1.64	0.099	0.219
Single patch vs. Mosaic	0.645, 0.434	16, 7	1.23	0.055	0.280
Log_{10} time span (yr)¶		13	1.19	0.097	0.299
Observed vs. Experimental	0.593, 0.547	17, 6	0.05	0.002	0.822

† Significant relationships ($P < 0.05$) are in boldface type.

‡ Mean r^2 is reported for each category of categorical variables; shape of relationship is reported for significant continuous predictor variables.

§ The number of studies in each analysis (n) is reported per category for categorical predictors and as total for continuous predictors.

‖ Relationship is nonlinear. The statistics presented are from the following polynomial regression model: $3.22 - 3.19(log_{10}$ number of samples$) + 0.86(log_{10}$ number of samples$)^2$.

¶ Includes only those studies that examined gradients of time passed since the last disturbance.

consider only studies where $n \geq 10$, the median percentage explained variation is 44% for richness, 48% for diversity, and 27% for evenness. Thus, while disturbance sometimes explains much of the observed variation in species diversity, it does not do so consistently. In contrast, Wright et al. (1993) found that studies of energy-related factors (which generally involve large sample sizes) explained a median 70% of the spatial variation in richness.

Further, the strength of species diversity–disturbance relationships appears to reflect sampling artifacts. The proportion of variation in richness, diversity, and evenness explained by disturbance significantly decreased as the number of samples examined in a study increased. Moreover, we found that explained variation was much greater for richness–disturbance relationships inferred from partial sampling (e.g., point counts; 62%) than for those derived from exhaustive sampling (36%). Mackey and Currie (2000) argue that with less intense sampling, one is less likely to detect rarer species. As sampling intensity increases, rarer species are detected and disturbance is predicted to have less effect on richness.

Disturbance appears to have a greater role in determining temporal than spatial patterns of species di-

versity. Temporal gradients of disturbance explained more variation in all three measures of species diversity than did spatial gradients, although this difference was significant only in the studies of species richness. This might be an artifact: temporal gradients typically involved fewer samples than did spatial gradients (see discussion above). However, Collins and Glenn (1997) suggest that spatial and temporal responses of a community to disturbance are affected by different mechanisms and that the two responses may be very different. Also, data from Reice (1984), Armesto and Pickett (1985), and Lake et al. (1989) indicate that the observed relationship between diversity and spatial gradients of disturbance changes over time. The spatial variation in diversity explained by disturbance may therefore be sensitive to how soon after disturbance communities along a spatial gradient are sampled, and whether each community in a study is given the same time to recover. If this is the case, inconsistencies in sampling time along a spatial gradient may alter the apparent r^2 of the relationship.

Explained variation in species diversity is also greater for studies of plants, or, more specifically, sessile producers, than for animals, or motile ones in particular. Plant ecologists have often been proponents of the

TABLE 7. Significant relationships observed in logistic regression analyses comparing the odds of peaked vs. all other shapes (nonsignificant, positive or negative monotonic) of species richness–disturbance relationships.

Explanatory variable	n†	P‡	McFadden's rho^2	Group with highest odds	Change in odds of peaked relationship§ (%)
Actual evapotranspiration, AET	69	0.030	0.078	low AET	−97/10-fold increase
Anthropogenic vs. Natural	116	0.005	0.078	natural	+371
Quadrat area	88	0.021	0.064	low quadrat area	−31/10-fold increase
Number of disturbance levels, NDL	116	0.017	0.055	high NDL	+535/10-fold increase

Notes: See Table 1 and related text for description of explanatory variables. Multiple-regression models consistently dropped all variables except the one comparing disturbances of Anthropogenic vs. Natural origin.

† The number of relationships included in each analysis.

‡ Probability from likelihood ratio chi-square.

§ For binary predictors, the percentage change in odds of a peaked relationship is reported in terms of the change predicted for the group with the highest odds vs. the group with the lowest odds.

important role of disturbance in patterns in species diversity (e.g., Grime 1973*a*, White 1979, Collins 1992, Collins et al. 1995), while ecologists studying freshwater invertebrates often fail to detect significant species diversity–disturbance relationships and are more skeptical of the role disturbance has in determining patterns in species diversity (e.g., Reice 1985, Resh et al. 1988, Lake et al. 1989). Fuentes and Jaksic (1988) discuss why peaked or strong species diversity–disturbance relationships are not frequently found among terrestrial vertebrates: their mobility and ability to diffuse into and out of disturbed patches, consumption of many different resources, and highly heterogeneous environments mean that many terrestrial animals do not meet the conditions required for disturbance to have a peaked or strong effect on species diversity. For the reasons that Fuentes and Jaksic (1988) suggest, we would expect explained variation in species diversity–disturbance relationships of plants to be greater than in most studies of motile animals.

In addition to not being consistently strong (i.e., high explained variation), species diversity–disturbance relationships are also not generally peaked. With only 16%, 19%, and 11% of richness–, diversity–, and evenness–disturbance relationships, respectively, being significantly peaked, detectable intermediate-disturbance responses are the exception rather than the rule. Even papers that are frequently cited as showing the classic peaked relationship do not consistently find peaks (e.g., Lubchenco 1978, Sousa 1979). For example, Sousa's (1979) study of intertidal boulder algal communities detected peaked richness–disturbance patterns 50% of the time. This may suggest that even when peaked relationships are the norm for a community, they may be detected in only 50% of studies. Even when this possibility is considered, our finding that 16% of richness–disturbance relationships are peaked is still low—too low for peaks to be considered the norm. Although we did identify some factors related to the probability of observing a peaked relationship, the consistently low values of McFadden's rho^2 indicate that there are no predictable circumstances (that we could identify) un-

der which species diversity–disturbance relationships are generally peaked.

Some authors have suggested that productivity influences the strength and shape of species diversity–disturbance relationships (Grime 1973*a, b*; Huston 1979, 1994). Huston (1994: 138) suggests that almost all studies supporting the intermediate-disturbance hypothesis (IDH) examined systems with high rates of population growth (or high levels of productivity), such as the intertidal zone, coral reef crests, or weedy plant communities. Yet, this evidence is anecdotal; there are no data showing that these communities are more productive than those where the species diversity–disturbance relationship was not peaked. Evidence from our study does not support Huston's conjecture that communities supporting the IDH are those with high productivity. We found that the odds of observing a peaked richness–disturbance relationship decreased by 97% for each 10-fold increase in actual evapotranspiration (AET; a surrogate of terrestrial productivity). This result may have arisen from the high proportion of tree studies in sites with high AET; trees are not the typical fast-growing organisms that Huston (1979, 1994) associates with high productivity. Among studies of field vegetation (i.e., fast-growing weeds and grasses), the odds of peaked vs. non-peaked relationships were not greater when AET was higher (McFadden's $rho^2 = 0.06$, $n = 12$ relationships, $P = 0.40$). Actual evapotranspiration is an imperfect surrogate for terrestrial productivity; a better measure might reveal a different relationship between productivity and the shape of the species diversity–disturbance relationship. However, the evidence at hand does not support the hypothesis that intermediate-disturbance relationships are associated with high-productivity systems.

The odds of observing a peaked vs. non-peaked relationship were negatively related to quadrat area (i.e., the total area sampled to collect one estimate of species diversity, or one data point). Mackey and Currie's (2000) models of richness–disturbance relationships predict that peaked relationships should be observed only when sampling intensity (number of organisms

censused) is low, as a result of rare species being overlooked when few individuals are censused. The decreasing probability of observing a peaked relationship when quadrat area is larger may indicate that peaked relationships are an artifact of restricted sampling. Alternatively, the effect of quadrat area on the odds of observing a peaked relationship may indicate that peaked richness–disturbance relationships occur mainly at small spatial scales. In apparent disagreement with Mackey and Currie (2000), the number of samples examined in a study was not a significant predictor of relationship shape, and peaked richness–disturbance relationships were more likely to be observed when higher numbers of levels of disturbance were examined. However, because neither of these variables are necessarily good indicators of the number of individuals censused, valid comparisons of these results with those of Mackey and Currie (2000) are not possible. It is apparent, though, that sampling methodology (number of individuals censused, number of disturbance levels examined, and/or quadrat area sampled) does appear to significantly influence the shape of relationship that will be observed.

There has been much confusion in the literature with respect to whether the IDH is a within-patch or among-patch phenomenon (e.g., Fuentes and Jaksic 1988, Wilson 1994, Rosenzweig 1995). Many of the studies in our data set examined community structure within individual disturbed patches (e.g., a patch of burned grassland, a forest gap resulting from a fallen tree, or an intertidal boulder). Because, as Wilson (1994: 178) states, ''A single patch does not have a frequency of disturbance, only a time since last disturbance,'' it is difficult to understand how the concept of intermediate-disturbance frequency can be applied to a single patch. We therefore hypothesized that studies examining mosaics of patches would have greater odds of observing peaked species diversity–disturbance relationships than would studies of single patches. However, whether a study utilized single patches or mosaics had no apparent effect on whether the observed relationship was peaked, indicating that the IDH may be equally applicable to both kinds of studies (cf. Collins and Glenn 1997).

The number of published diversity– and evenness–disturbance studies was relatively low. This created problems of sparse data in several of the logistic regression analyses. We did not feel that it was wise to make conclusions from either of these data sets.

In conclusion, the published literature provides evidence that disturbance plays some role in determining spatial and temporal patterns of species diversity, but species diversity–disturbance relationships are neither consistently strong nor consistently peaked. There is evidence that observed species diversity–disturbance relationships may often reflect sampling artifacts. We suggest that, of the factors that have been proposed to affect species diversity in nature, disturbance is probably not generally among the most important ones.

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APPENDIX

A list of the 85 sources of species diversity–disturbance relationships together with a table detailing the 197 species diversity–disturbance relationships used in the meta-analysis is available in ESA's Electronic Data Archive: *Ecological Archives* E082-041.