LETTER

Species' traits predict the effects of disturbance and productivity on diversity

Nick M. Haddad,[1]* Marcel
Holyoak,[2] Tawny M. Mata,[2] Kendi
F. Davies,[2]† Brett A. Melbourne[2]†
and Kim Preston[2]

[1]Department of Zoology, North
Carolina State University, PO
Box 7617, Raleigh, NC 27695-
7617, USA

[2]Environmental Science and
Policy, 1 Shields Ave, University
of California, Davis, Davis, CA
95616, USA

*Correspondence: E-mail:
nick_haddad@ncsu.edu

†Present address: Department
of Ecology and Evolutionary
Biology, University of Colorado,
UCB 334, Boulder CO 80309,
USA.

Abstract

Disturbance is an important factor influencing diversity patterns. Ecological theory predicts that diversity peaks at intermediate levels of disturbance, but this pattern is not present in a majority of empirical tests and can be influenced by the level of ecosystem productivity. We experimentally tested the effects of disturbance on diversity and show that species' autecological traits and community relations predicted species loss. We found that – alone or in concert – increasing disturbance intensity or frequency, or decreasing productivity, reduced diversity. Our species did not exhibit a clear competition-colonization trade-off, and intrinsic growth rate was a more important predictor of response to disturbance and productivity than measures of competitive ability. Furthermore, competitive ability was more important in predicting responses when, in addition to killing individuals, disturbance returned nutrients to the ecosystem. Our results demonstrate that species' traits can help resolve conflicting patterns in the response of diversity to disturbance and productivity.

INTRODUCTION

The relationship between disturbance and diversity is often described as unimodal, with the highest diversity at intermediate levels of disturbance. Such a relationship is predicted by the Intermediate Disturbance Hypothesis (Grime 1973; Connell 1978). However, recent synthesis of the empirical literature shows responses that are more variable (Mackey & Currie 2001). The Intermediate Disturbance Hypothesis does not explain a majority or even a plurality of cases. The poor performance of the Intermediate Disturbance Hypothesis has provoked a call for greater attention to mechanisms that might explain when diversity does and does not peak at intermediate levels of disturbance (Shea *et al.* 2004).

One reason a general response has been elusive is that the pattern often depends on the level of another important determinant of diversity – productivity. The Dynamic Equilibrium Model (Huston 1979) and empirical observations supporting it show that disturbance and productivity can interact to determine their effects on diversity (Kondoh 2001; Wilson & Tilman 2002; Worm *et al.* 2002; Scholes *et al.* 2005; Cardinale *et al.* 2006). One explanation for this interaction is that if species coexist through trade-offs

between competitive ability and growth rate, increased productivity favours good competitors, and increased disturbance favours poor competitors (Kondoh 2001). It follows that at higher levels of productivity, more intense or frequent disturbances are needed to prevent competitive dominance and maximize species diversity. This interaction is complicated by the fact that disturbance can influence productivity, as disturbance may free nutrients that were stored in sediments or organisms. Such interactive effects have rarely been tested.

All theories of the effects of disturbance on diversity assume a trade-off in traits (Huston 1994; Kondoh 2001; Ostman *et al.* 2006; Cadotte 2007), generating predictions that we test in our study. Under low levels of disturbance, strong competitors eliminate inferior ones. Under high levels of disturbance, only species that can withstand disturbance or can quickly grow to reach densities sufficient to avoid stochastic extinction after disturbance can persist. Trade-offs lead to the highest level of diversity where competitors and disturbance tolerators are able to coexist. Trade-offs that enable species coexistence may involve spatial mechanisms like colonization or non-spatial mechanisms like a temporal storage effect (e.g. plants that withstand disturbance in the seedbank). Coexistence may

also be explained by niche differentiation, such as species differences in relative nonlinearities in growth rates when competition varies in competitive environments (Chesson 2000; Roxburgh *et al.* 2004; Shea *et al.* 2004).

We demonstrate that a combination of species' traits and community properties predict species' abundance and persistence in response to disturbance and associated changes in productivity. Across the community, these traits then determine the effects of disturbance on diversity and composition. We analysed traits related to species' autecology that are intrinsic to the species, such as intrinsic growth rate, dispersal ability and body mass, as well as properties related to species' interactions with both the environment (carrying capacity) and competitors (competitive rank). As we expected and demonstrate, many of these traits were correlated. We predicted that species that were better able to recover from disturbance (with higher intrinsic growth and dispersal rates) would persist at higher rates of disturbance. We also expected traits related to disturbance tolerance would be negatively related to competitive ability (Cadotte *et al.* 2006). However, because traits related to disturbance tolerance and competitive ability were not correlated for our species, we tested how individual traits predict species' responses to disturbance, and if these depended on whether disturbance killed organisms and/or altered productivity.

METHODS

We conducted our experiments in aquatic microcosms with protozoans and bacteria, a simple biological system with a manageable number of species for which many traits are readily measured (Cadotte *et al.* 2006). We recognize that these microcosms are less complex than natural systems, yet they offer a useful bridge between theory and other empirical tests in nature. The protozoans we studied coexist in a pond where many were originally collected (McGrady-Steed *et al.* 1997). Our lab has described a larger, related community of species in experiments addressing other hypotheses (K. D., M. H., unpublished data), and others have used these communities in research examining effects of disturbance (McGrady-Steed *et al.* 1997; Ostman *et al.* 2006; Cadotte 2007). We began each replicate with a standard group of eight species (Table 1). All species were bacterivores, although three species could both photosynthesize and eat bacteria.

Treatments

We conducted a factorial experiment in which we varied disturbance intensity and frequency, and the effects of disturbance on productivity. Our experimental design was motivated by two impacts disturbance could have on ecosystems. Many disturbances, such as fire and flooding, initially reduce population densities (Sousa 1984). Additionally, disturbance may cause the regeneration or loss of nutrients. For example, fire returns nutrients sequestered in biomass to the soil, where they become available to other individuals (Christensen 1977), and high amounts of precipitation can transport terrestrial nutrients to flooded aquatic systems or vice versa (Bayley 1995). Alternatively, nutrients can be volatilized, carried away in streams during flooding, or removed through extraction by humans (Pickett & White 1985).

Disturbance *intensity* was related to density reduction and was accomplished by replacing bottle contents with media containing no protozoans. Disturbance intensities included 0%, 50%, 89% and 98% density reduction. Although we did not know the level of disturbance intensity that would constitute 'intermediate', we disturbed over a wide range of values that would presumably span intermediate levels. We

Table 1 Species' traits. Parameter details are reported in the methods and Supplementary Material

Species	Cell mass (g)	High nutrient r (per day)	Low nutrient r (per day)	K (per mL)	Dispersal rank	Competitive rank
Coleps sp.	2.02×10^{-8}*	0.40	0.37	84	3.704	2.53
Colpidium sp.	1.52×10^{-8}*	1.95	0.67	467	11.343	−4.25
Cyclidium sp.	4.73×10^{-10}†	1.51	1.03	4038	7.300	3.42
Euglena gracilis‡	1.28×10^{-10}§	0.87	1.31	84578	7.571	4.14
Euplotes aediculatus‡	8.05×10^{-8}*	0.43	0.46	359	3.750	4.73
Paramecium aurelia	4.30×10^{-8}*	1.48	0.84	296	9.429	6.49
Paramecium bursaria‡	1.96×10^{-7}§	0.23	0.30	1639	2.300	8.09
Spirostomum ambiguum	3.76×10^{-6}*	0.57	0.51	17	3.300	4.82

*Fukami (2004).
†Calculated from volumes after measuring length and width of 30 individuals using methods in Wetzel & Likens (1991).
‡Mixotroph that can eat bacteria or photosynthesize.
§McGrady-Steed & Morin (2000).

disturbed microcosms at two *frequencies*, every 3.5 days or every 14 days. We also varied the effect of disturbance on *productivity*, accomplished by manipulating nutrient levels. In high-nutrient treatments, we replaced all nutrients lost to disturbance with a standard soil–water medium that is described below (organisms lost to disturbance were not replaced, and 'nutrients' here refers to those added in the form of liquid medium). These treatments had high-nutrient levels comparable with eutrophic ponds, and supported protozoan densities higher than in a typical pond (Pace 1982). In low-nutrient treatments, the medium was removed and initially replaced with sterile spring water. In subsequent disturbances, nutrient levels were fixed at the soil–water concentration following the first disturbance. Hence, in low-nutrient treatments disturbance caused an initial loss of nutrients, whereas in high-nutrient disturbances the total amount of nutrients did not change and per-capita nutrients increased. Nutrient manipulations affected protozoan productivity, resulting in average protozoan biomass being over an order of magnitude higher in high-nutrient treatments. The experiment lasted for 31 days, or 30–120 generations depending on species.

Our control treatment could not be part of the factorial design, because any variation in one attribute of disturbance induced variation in another. For example, it was impossible to vary disturbance intensity without creating a positive disturbance frequency. In our control, and starting during the third week, we replaced 10 mL of media with soil water weekly. We did this because our previous experiments showed that some nutrient replacement was needed to prevent population collapse.

Microcosm description and setup

Each of 10 replicates per treatment consisted of a 240-ml bottle filled with 100 mL of medium. Each bottle was initiated with a population of *c*. 50 individuals, with starting numbers set to avoid extinction caused by demographic stochasticity before the first disturbance. This was true for all species but *Spirostomum ambiguum*, which normally grows at lower densities and which we started with *c*. 20 individuals per bottle. All species were capable of persisting at these starting densities, as demonstrated by their persistence in controls. The initial medium was a standard soil–water solution that was prepared by mixing 2.4 g of sterilized and sifted soil and 0.6875 g of Protozoan Pellet (Carolina Biological Supply Company, Burlington, NC, USA) in 1.5 L of spring water and then sterilized. Twelve hours before adding protozoa, this solution was inoculated with 2 mL of a mixed bacterial culture to provide resources for protozoans. The culture consisted of *Bacillus cereus*, *B. subtilus*, and *Serratia marcescens*. All communities were allowed to grow for 1 week before disturbance treatments were implemented.

Sampling

After 31 days, we counted the eight study species in 10 mL of each treatment. Before removing a sample, we thoroughly mixed contents of each bottle. We then used a pipette to transfer samples to a Petri dish for counting. We first tried to estimate density in 10 drops (*c*. 0.25 mL) that we weighed to measure volume. If densities were too high to count accurately in small drops, we diluted samples. We then sampled 1.0-mL drops and counted until either we had observed at least eight individuals per species or until we had scanned 10 mL. Subsampling was a necessary constraint to increase our ability to sample replicates, and we recognize that subsampling may affect the observed relationship between disturbance and diversity (Mackey & Currie 2001). However, we believe this sampling issue is less important for the conclusions of our study because (1) species' persistence was consistent across many replicates (Fig. S5), increasing our confidence that observed loss was real, (2) even if species were not extinct, extreme rarity represents an important compositional difference imposed by disturbance and (3) the crux of our results was not the relationship between disturbance and diversity, but rather the ability of species' traits to predict persistence.

Analyses

To test for the effects of disturbance on species richness and on the abundance of individual species, we conducted factorial three-way ANOVAs with disturbance intensity, frequency and effects on productivity as factors. We did not include controls that were not part of the factorial design. Exclusion of controls was justified by Dunnett's test that showed that species richness in controls was not significantly different from the next lowest levels of disturbance.

To test the ability of species' traits to predict the effects of disturbance on persistence, we conducted multiple regression analyses. We considered inclusion of intrinsic growth rate, carrying capacity, competitive rank and dispersal rank as independent variables, but excluded collinear variables (see Supplementary Material). For each type of disturbance, we created one dependent variable for each species as follows. We measured the effect of disturbance intensity on persistence as the slope of a regression for each species between disturbance intensity and the proportion of replicates occupied, averaged across all levels of disturbance frequency and effects on nutrient loss. We measured the effect of disturbance frequency on persistence as the difference between proportion of replicates occupied under low- and high-disturbance frequency, averaged across all levels of disturbance intensity and effects on nutrient loss. For disturbance effects on

nutrient loss, we measured the effect of disturbance on persistence as the difference between proportion of replicates occupied under high and low nutrients following disturbance, averaged across all disturbance intensities and frequencies. We then conducted three separate multiple regression analyses, testing the ability of species' traits to predict species' persistence in the face of each type of disturbance. Because our sample size was low ($n = 8$ species), we could not conduct analyses with interactions.

To determine intrinsic growth rates and carrying capacities of individual species, we separately conducted single species growth experiments. Cultures were prepared as in the main experiment. For each species, we prepared 10 bottles, five with soil–water solution (high nutrient) and five with diluted 1 : 9 soil–water : sterilized spring water (low nutrient). Treatments were started with *c.* 10 individuals per millilitre in 100-mL replicates when possible; for *S. ambiguum* we used 3.8 individuals per millilitre and for *Coleps* sp., 7.9 individuals per millilitre. We measured densities in cultures of ages 0.5, 1, 2, 3, 4, 7, 14, 21 and 28 days, and then approximately weekly until each species appeared to reach or surpass carrying capacity, estimated as the long-term equilibrium density. We counted densities as in the main experiment, but searched up to 3.0 mL per sampling interval. We did not replace medium that we had removed to sample. We used PROC NLIN in SAS (SAS Inc., Cary, NC, USA) to test for exponential, logistic, or theta-logistic growth. In all cases, logistic growth was supported, and we report r and K from those analyses (Table 1, see Supplementary Material, Fig. S1).

Many trait variables initially considered were strongly correlated, and were removed from analysis (Supplementary Material, Table S1). Because the natural logs of cell mass and K were highly correlated (Pearson's correlation coefficient, $\rho = 0.85$), we used $\ln(K)$ in analysis as it was most ecologically relevant to our study. Consistent with suites of traits associated with *r*- and *K*-selected species (MacArthur & Wilson 1967), intrinsic growth rate was strongly, positively correlated with dispersal rank (Table S1). This correlation was supported using a measure of dispersal rank

we developed ($\rho = 0.95$), a measure of colonization used by Cadotte *et al.* (2006) that included six of our eight species ($\rho = 0.80$), and a measure of spreading speed that combined dispersal and intrinsic growth rate that is more similar to the colonization rank used by Cadotte *et al.* (2006) ($\rho = 0.87$, see Supplementary Material). To rank dispersal ability among species, we conducted 10–14 replicate trials by inoculating one bottle connected to another sterile bottle by a 10-cm tube. Dispersal was then measured by the average density in the sterile bottle after 5–9 h (within approximately one generation), and the dispersal rank of a species was determined by its average rank over all trials (see Supplementary Material). Because our disturbance experiment was not spatial, we used only intrinsic growth rate in high nutrients, and not dispersal rank, in our analyses.

Competitive rank was determined in our study and in Cadotte *et al.* (2006). Between the two studies, all species in our study were analysed (Table 1, Supplementary Material, S2–3). In our study, we measured the competitive ability of each species in replicated trials for all possible pairs of species. Species were ranked by their competitive ability, which was derived from species' competitive effects and responses (Mouquet *et al.* 2004). We created a single competitive rank for each species by rescaling ranks from Cadotte *et al.* (2006) and averaging ranks for species that were included in both studies (Supplementary Material, Fig. S2). We did not find a significant negative relationship between intrinsic growth rate or dispersal rank and competitive rank with our species [$\rho = -0.61$; but see Cadotte *et al.* (2006), Table S1], and thus were able to use both variables in regression analyses.

RESULTS

Species richness was always reduced by disturbance, including disturbance intensity, frequency and disturbance-induced reduction in productivity (Fig. 1, Table 2). Consistent with the Dynamic Equilibrium Model, there were interactions among disturbance attributes. Disturbance intensity (but not frequency) caused a larger reduction in
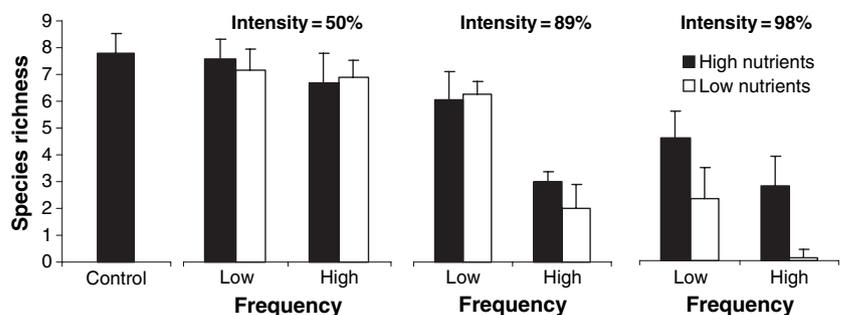

Figure 1 Mean (± 1 SD) protozoan species richness in response to disturbance intensity, frequency and effects of disturbance on productivity.

Table 2 Results of a three-way ANOVA testing for effects of disturbance on species richness ($n = 120$, $R^2 = 0.90$)

Source	d.f.	Sum of squares	F	P
Model	11	666.2	88.63	0.001
Error	108	73.8		
Corrected total	119	740.00		
Intensity	2	439.80	321.80	0.001
Nutrient loss	1	28.03	41.02	0.001
Frequency	1	120.00	175.61	0.001
Nutrient loss*intensity	2	31.27	22.88	0.001
Intensity*frequency	2	42.20	30.88	0.001
Nutrient loss*frequency	1	0.83	1.22	0.272
Nut. loss*freq*intensity	2	4.07	2.98	0.055

species richness when disturbance also reduced productivity. As disturbance intensity increased, species richness was also reduced more when disturbance frequency was higher.

In statistical tests of the effects of each factor on the abundance of each species individually, higher disturbance intensity reduced abundance of all eight species, higher disturbance frequency reduced abundance of six of eight species, and disturbance-induced loss of productivity reduced abundance of three of eight species (Table 3). The same main effects were significant in logistic regression models predicting presence. However, because of the consistency of extinction in some treatments, we could not fit logistic regression models that included all interac-

tions. Although the remainder of our results concern effects of disturbance on persistence, persistence was positively correlated with abundance for all species (Table 3; Fig. S5). Because of this correlation, we report only the results for effects of species' traits on their persistence.

Species' traits predicted the effects of disturbance on extinction. The intrinsic growth rate was consistently the most important predictor of how severely a species was affected by disturbance, and was a significant factor predicting persistence in response to each attribute of disturbance (Fig. 2, Tables S3–S5). The only other trait that was significant in predicting the extinction of a species was competitive rank; species with higher competitive ranks in high-nutrient conditions were less likely to persist when disturbance reduced productivity.

DISCUSSION

Autecological traits and community properties predicted effects of disturbance on species' persistence. Regardless of whether disturbance varied in intensity, frequency, or impact in reducing productivity, the trait that predicted persistence best was a measure of species' ability to recover from disturbance, the intrinsic growth rate. We were surprised that competitive rank was much less important in predicting a species' response to disturbance. Whether or not competitive rank was an important predictor of persistence depended on the extent to which disturbance reduced population sizes directly or reduced productivity.

Table 3 Results of three-way ANOVAs testing the effects of disturbance on density of each species. Model R^2 is for the relationship between all independent variables and the density transformed by $\ln(x + 0.001)$ of each species. Abundance vs. persistence R^2 is for the relationship between persistence and abundance by species. All *P*-values are reported after a Bonferroni correction for multiple comparisons

Species	Model R^2	Abundance vs. persistence R^2	Intensity	Nutrient loss	Frequency	Intensity* nutrient loss	Intensity* frequency	Frequency* nutrient loss
Coleps sp.	0.73	0.77	< 0.001 0.50 > 0.89 > 0.98	n.s.	< 0.002 Low > high	< 0.05	n.s.	n.s.
Colpidium sp.	0.72	0.78	< 0.001 0.50 = 0.89 > 0.98	< 0.001 High > low	n.s.	< 0.001	n.s.	< 0.05
Cyclidium sp.	0.77	0.72	< 0.001 0.50 > 0.89 > 0.98	< 0.001 High > low	< 0.001 Low > high	< 0.001	< 0.001	n.s.
Euglena gracilis	0.61	0.24	< 0.001 0.50 > 0.89 = 0.98	n.s.	< 0.01 Low > high	n.s.	n.s.	n.s.
Euplotes aediculatus	0.70	0.58	< 0.001 0.50 > 0.89 > 0.98	n.s.	< 0.001 Low > high	n.s.	< 0.001	n.s.
Paramecium aurelia	0.88	0.65	< 0.001 0.50 > 0.89 > 0.98	< 0.001 High > low	n.s.	< 0.001	< 0.05	< 0.001
Paramecium bursaria	0.95	0.41	< 0.001 0.50 > 0.89 > 0.98	n.s.	< 0.001 Low > high	< 0.001	< 0.001	< 0.001
Spirostomum ambiguum	0.42	0.68	< 0.001 0.50 > 0.89 = 0.98	n.s.	< 0.01 Low > high	n.s.	< 0.01	n.s.

Figure 2 Effects of traits on species' responses to disturbance (a) intensity, (b) frequency and (c,d) effects on productivity. Each panel shows the effects of disturbance in reducing persistence, with high values representing stronger negative effects. Each point represents a single species. Disturbance responses were measured as (a) slope of regression for each species between disturbance intensity and proportion of replicates occupied, (b) the difference between proportion of replicates occupied under low- and high-disturbance frequency and (c,d) the difference between proportion of replicates occupied under high and low nutrients following disturbance. In (d), the response variable is the residual of the relationship between r and the response to productivity (multiple regression $R^2 = 0.96$).
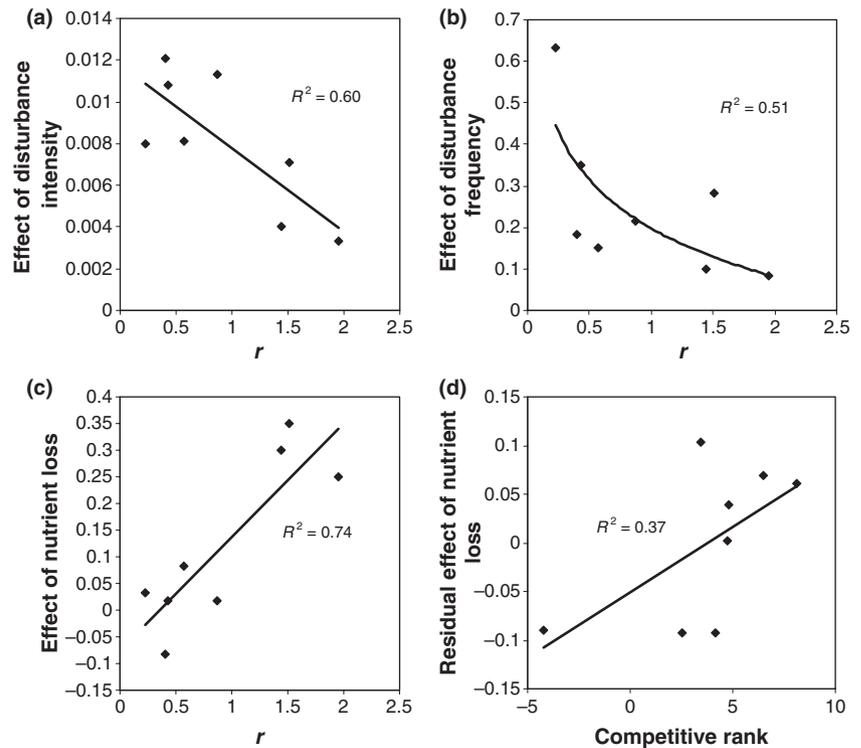
Traits and species' persistence

Intrinsic growth rate was consistently the most important factor predicting species' persistence following disturbance. A disturbance event reduced population densities of all species by proportionately equal amounts. Over the longer term, where many disturbances were experienced, species with low-intrinsic growth rates were ultimately reduced to population sizes at which extinction was likely. Here, extinction results from stochasticity (demographic and environmental), and from the disturbance itself which has a stochastic component (the probability of death for all individuals) and a deterministic component. Species with high-intrinsic growth rates were less affected by higher disturbance intensity and frequency because their populations could recover rapidly from low-population sizes. As persistence was not related to a species' ability to achieve high-carrying capacity (see Supplementary Material), it is likely that stochasticity played a strong role in driving extinctions. Our disturbances created proportionately similar effects on populations across species, allowing us to standardize the effects of disturbance in our test of the ability of traits to predict species' responses. However, our study differed from natural systems where some species are adapted to disturbance, such as plants adapted to tolerate or rapidly recover from fire (Whelan 1995). Our approach will need to be tested in such systems, where other traits may have greater predictive ability. The disturbances we created

are most consistent with disturbances to which species have not adapted, including disturbances generated by humans through land-use conversion and development.

Intrinsic growth rate was not the only significant trait in predicting persistence, and the importance of competitive rank depended on the level of productivity. Species with high-growth rates were those that, when populations were measured in isolation, had their growth rates most severely reduced by nutrient loss (see Table 1 and Supplementary Material). Those species that were better competitors when nutrient levels were high may have been unable to exploit nutrients at lower resource levels (Tilman 1982). In our experiment, we specifically separated two consequences of disturbance, on mortality and on productivity. Our productivity treatments tested the effect of disturbance in releasing nutrients sequestered in dead organisms to the ecosystem. Our results demonstrated that competitive rank was an important predictor of persistence when disturbance affected both mortality and productivity.

Our work identifies autecological traits, rather than community interactions, as the best predictor of species' responses to disturbances. The most prominent explanation for both the Intermediate Disturbance Hypothesis and the Dynamic Equilibrium Model is that there is a trade-off between competitive ability and disturbance tolerance, often linked to colonization ability (Kondoh 2001). The species we studied did not show a significant negative relationship between disturbance tolerance and competitive rank. We

recognize that our sample size of eight species was low, and that variation in competitive rank was high (as it was in Cadotte *et al.* (2006)). Though not significant, the correlation between dispersal and competitive rank was negative, and some effects of competition may have been shared with a term for intrinsic growth rate, which was strongly correlated with dispersal rank and included in our analysis. However, because there was no negative relationship between either dispersal rank or intrinsic growth rate and competitive rank, we were able to include both intrinsic growth rate and competitive rank in statistical models. We found that intrinsic growth rate, which was highly, positively correlated with the measured dispersal rank of species, was consistently the most important predictor of a species' response to disturbance. Our work emphasizes the need to focus on a suite of traits associated with disturbance tolerance and recovery that can be used to predict disturbance effects on diversity.

In other studies that have used traits to predict species' responses to disturbance, for example habitat fragmentation (Davies *et al.* 2000), traits like body size and trophic level have been examined because they are related to the dynamics of populations. In such studies, traits are used as surrogates for information about species' population dynamics. In contrast, we examined traits that were direct measures of species' population dynamics as well as surrogate traits, allowing for stronger inference. Significantly, the most predictive trait was a population dynamic parameter, intrinsic growth rate.

Disturbance and species richness

By linking species' traits to the effects of disturbance on communities, our study suggests a general approach to resolve conflicting empirical patterns relating disturbance and diversity. Reviews that categorize studies by taxon, species' behaviour, or disturbance characteristics have not been able to predict when to expect patterns of diversity in response to disturbance, whether unimodal or other (Mackey & Currie 2001). Our results demonstrate that factors related to species' autecology (intrinsic growth rate) and community relations (competitive rank) can be used to determine the relationship between disturbance and diversity. Furthermore, we are able to reject the hypothesis generated by models in neutral theory that traits are not important in generating observed responses to disturbance and productivity (Kadmon & Benjamini 2006).

Given the diversity of patterns observed in the relationship between disturbance and diversity (Mackey & Currie 2001), our tests of the ability of species' traits to predict effects of disturbance on persistence and species richness did not hinge on any particular pattern. Nonetheless, we did not observe the unimodal pattern predicted by the Intermediate Disturbance Hypothesis. We chose our

bacterivore study species to occupy the same trophic level, and thus to be potential competitors. However, interactions between them and their mixed prey (bacteria and microflagellates) may have enabled them all to coexist through resource partitioning or indirect trophic effects, and smaller communities of protozoans have been observed to coexist for long periods (Vandermeer 1969; Fox 2002). For reduced species diversity at low levels of disturbance, it is necessary that competitive exclusion can occur. Because we did not observe competitive exclusion in controls with no disturbance, there were no conditions under which the relationship between disturbance and diversity could support the predictions of the Intermediate Disturbance Hypothesis. However, our aims were to test which species' traits and community properties predicted responses to disturbance, not to test the Intermediate Disturbance Hypothesis.

We would expect diversity to decline with disturbance in situations like ours, where (1) there is a wide range and even distribution of intrinsic growth rates among species; (2) there is wide range in competitive rankings within species and thus unclear competitive hierarchies; (3) the relationship between intrinsic growth rate and competitive ability is not strong and (4) intrinsic growth rate predicts species persistence. In this case, the declining relationship can be best predicted by logistic growth models. We would expect a unimodal relationship between diversity and disturbance when the relationship between intrinsic growth rate and competitive rank is stronger, and competitive hierarchies are better defined. In this case, competitive exclusion would reduce species richness at low levels of disturbance, and models of competition-colonization trade-offs would predict unimodal patterns (Kondoh 2001) (but see below regarding variation with productivity). These predictions should be tested with species sets that vary in their combinations of traits, and such studies are possible for protozoans and perhaps plants.

Competitive exclusion does occur in similar communities with larger numbers of species (K. D., T. M and M. H. unpublished data). With larger communities of species, Cadotte (2007) found a negative relationship between disturbance and diversity. They also found that species richness under 'no disturbance' was similar to the level found here (also under 'no disturbance'). In that study, even with a clear competition-colonization trade-off and competitive exclusion, spatial variation was important in generating the unimodal relationship between disturbance and diversity (Cadotte 2007).

We also showed how variation in ecosystem productivity determined how diversity was affected by disturbance. Our results confirm the predictions of the Dynamic Equilibrium Model, including a stronger, negative relationship in less productive systems (Proulx & Mazumder 1998; Kondoh 2001; Scholes *et al.* 2005; Cardinale *et al.* 2006; but see,

Svensson *et al.* 2007). The hump-shaped pattern predicted by the Intermediate Disturbance Hypothesis may be most likely when disturbances return nutrients in organisms that have died to ecosystems. When disturbance reduces density and nutrient availability, the combined impact of disturbance and productivity loss may have the strongest negative effects on diversity. Under this scenario, diversity is almost always expected to show a negative relationship with disturbance, as it did in our study.

Our results support the observation that communities of mobile species and/or predators may be less likely to exhibit the unimodal pattern than sessile and/or basal organisms (Wootton 1998). Our disturbances affected all trophic levels, and thus could not decrease the intensity of competition. Our results cannot be explained by the small scale of our microcosm relative to other studies of disturbance; the temporal scale of our study is longer in generations, which would favour competitive exclusion, and the spatial scale is comparable to other studies relative to the size and density of our study organisms (see Fig. 16.1 in Haddad & Tewksbury 2006).

We demonstrate that species' traits can be used to predict the response of diversity to both disturbance and productivity. It is a challenge for ecologists to test the ability of species' traits and community properties to predict community response to disturbance and productivity in a broader array of ecosystems. In particular, it might be instructive to test for differences in the responses of communities in which disturbances are a natural feature compared to systems subject to recent human-induced disturbance. More broadly, our results show the need to monitor and test for changes in productivity if we are going to understand community responses to disturbance.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Contains the following:
- **Table S1** Correlations among traits.
- **Table S2** Mean interaction coefficients (α_{ij}), mean competitive effects, and mean competitive responses.
- **Table S3** Mean competitive ability and mean competitive rank.
- **Table S4** ANOVA table for traits that predict species response to disturbance intensity.
- **Table S5** ANOVA table for traits that predict species response to disturbance frequency.
- **Table S6** ANOVA table for traits that predict species response to disturbance effects on nutrient loss.
- **Figure S1** Relationship between population size and growth rate for each species studied in the disturbance experiment.
- **Figure S2** Rescaled means and 95% confidence intervals of competitive ranks obtained from this and Cadotte *et al*'s (2006) studies.
- **Figure S3** Effects of disturbance intensity, frequency, and impacts on nutrients loss on the density of each species.

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