A Meta-Analysis of Community Response Predictability to Anthropogenic Disturbances

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abstract: Disturbances often lead to changes in average values of community properties; however, disturbances can also affect the predictability of a community's response. We performed a meta-analysis to determine how response predictability, defined as among-replicate variance in diversity and community abundance, is affected by species removals, species invasions, nutrient addition, temperature increase, and habitat loss/fragmentation, and we further determined whether response predictability differed according to habitat and trophic role. Species removals and nutrient addition decreased response predictability, while species invasions increased response predictability. In aquatic habitats, disturbances generally led to a decrease in response predictability, whereas terrestrial habitats showed no overall change in response predictability, suggesting that differences in food web and ecosystem structure affect how communities respond to disturbance. Producers were also more likely to show decreases in response predictability, particularly following species removals, highlighting widespread destabilizing effects of species loss at the producer level. Overall, our results show that whether disturbances cause changes in response predictability is highly contingent on disturbance type, habitat, and trophic role. The nature of changes in response predictability—for example, strong decreases following species invasions and increases following species removals—will likely play a major role in how communities recover from disturbance.

Keywords: disturbance, invasive species, predictability, nutrient addition, species loss.

Introduction

The structural properties of communities subjected to disturbances often differ from those of undisturbed communities. This includes differences in diversity and abundance as well as in the dynamic nature of population and community fluctuations (Syms and Jones 2000; Keitt 2008). The changes that occur following disturbances can have major impacts on community functioning (Ives and Carpenter 2007). Most studies that have examined how

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disturbance affects community structure have focused on how average values of community properties, such as diversity or abundance, change with disturbance. However, disturbance can also affect the consistency, or predictability, of a response (Fraterrigo and Rusak 2008). Response predictability, which measures the extent of divergence in community structure, is defined as the variation among replicates of the same experimental treatment (McGrady-Steed et al. 1997; Carpenter and Brock 2006) and is most often represented as the standard error (Forrest and Arnott 2007).

The recent emphasis in ecology on the relationship between biodiversity and ecosystem functioning has highlighted the importance of determining how disturbances affect stability or predictability in structure and function over time (Loreau 2000; Cottingham et al. 2001; Cardinale et al. 2006; Jiang and Pu 2009; Campbell et al. 2011). Disturbance also affects the predictability of communities in space, such that structural and functional features of disturbed communities can become more or less predictable relative to communities that have not been subjected to disturbance (Naeem and Li 1997; Morin and McGrady-Steed 2004).

A change in variability among replicates is a relatively unexplored consequence of disturbance but is an important outcome both ecologically and in terms of interpreting the results of experiments. Response predictability can be thought of as a form of ecosystem reliability, such that changes in response predictability will affect the consistency of the level of ecosystem performance (Naeem 1998). Response predictability can therefore be used as an indicator of the resistance of ecosystems to disturbance (Naeem and Li 1997; Morin and McGrady-Steed 2004; Carpenter and Brock 2006), where a change in response predictability following disturbance indicates low resistance to disturbance. Response predictability may also be an important metric for assessing potential for recovery following disturbance. For example, disturbances such as species invasions that result in reductions in beta diversity

or biotic homogenization (Olden et al. 2004) may reduce opportunities for recolonization of native species.

We conducted a meta-analysis to determine how response predictability is affected by species extinction and by four additional anthropogenic disturbances (species invasions, nutrient addition, temperature increase, and habitat loss/fragmentation). These disturbances have all been identified as major drivers of biodiversity decline. We further determined whether response predictability differed in aquatic versus terrestrial habitats and between producers and consumers.

We developed three major predictions for how response predictability would be affected by the specific type of disturbance and across different habitat types and trophic roles. First, biotic disturbances, which directly affect species interactions, will lead to higher magnitude changes in response predictability than abiotic disturbances (Van Cleve et al. 1991; Chapin et al. 2000). Second, potentially stronger species interactions and shorter turnover times in aquatic systems compared with terrestrial systems will lead to higher magnitude change in response predictability in aquatic systems (Shurin et al. 2002). Third, disturbances that involve species at the base of food webs will lead to higher magnitude changes in response predictability than disturbances that involve higher trophic levels (Brett and Goldman 1997; Marczak et al. 2007). The five disturbances included here may also result in differences in the direction of the response. Species-poor communities are more temporally variable than species-rich communities (Jiang and Pu 2009). Because spatial and temporal variability are typically highly correlated (Wiens 1989), it is likely that species removals will lead to decreases in response predictability. Species invasions have been shown to lead to widespread biotic homogenization (Rahel 2002), suggesting that species invasions might increase response predictability. Nutrient addition is often associated with temporal destabilization of both population and community properties; thus, it is likely to lead to decreases in response predictability. Habitat loss/fragmentation is a primary cause of species loss; thus, it may lead to decreases in response predictability through its negative effect on diversity. Habitat loss/fragmentation may also lead to increases in response predictability, since smaller patches are more likely to be similar to each other in composition than larger patches. Finally, increases in temperature could lead to either increases or decreases in response predictability. Increased response predictability could result as species respond more similarly under stressful conditions due to weaker inter- and intraspecies interactions (Van der Putten et al. 2010). However, higher temperatures might also lead to decreases in response predictability, particularly if local extinctions occur and species ranges change (Pounds et al. 1999; Wake and Vredenburg 2008).

Methods

We performed a literature search for studies that experimentally manipulated abiotic or biotic disturbances. We focused specifically on manipulations of common anthropogenic disturbances. We found articles by both using the ISI Web of Knowledge database and reviewing the references of appropriate articles. A total of 91 articles that included 345 experimental manipulations were included in the final analysis. All articles reported a mean measure of abundance, biomass, density, species diversity, or species richness in both a control and a disturbance treatment. No significant difference was found between responses for species richness and diversity or between abundance, density, or biomass (see fig. A1, available online). As a result, we grouped these measures into two main response variables to assess response predictability (RP). The diversity group ($RP_{diversity}$) included responses for species richness, number of species, as well as various measures of abundance weighted diversity (e.g., H'). The abundance group ($RP_{abundance}$) included numerical counts (abundance, density) and biomass.

The studies chosen reported experimental manipulations spanning five abiotic and biotic disturbance types: temperature increase, nutrient addition, habitat loss/fragmentation, species removals, or species invasions. We categorized habitat loss/fragmentation, temperature increase, and nutrient addition as abiotic disturbances and species invasions and removals as biotic disturbances. All experimental manipulations had either two or more replicates per treatment, and the standard error of the response variable for each treatment either was reported in the article (33 articles) or could be easily measured from the figures (58 articles). Articles where the standard error bar values displayed in the figures were too difficult to extrapolate were not included in our analysis. For studies that manipulated disturbance over a range of disturbance intensities, we used the average value across all treatments rather than including each intensity's response value (complete data set available in Dryad; http://dx.doi.org/10.5061/dryad.2js47).

We followed strict guidelines in choosing the types of disturbance manipulation studies to be included in the analysis. For the temperature increase category, we included only studies that increased temperature per se (e.g., Chapin et al. 1995). Studies that combined other climate change effects, such as altered light and precipitation, with increases in temperature were not included (e.g., Zhou et al. 2006). Additionally, observational studies that compared natural communities growing in areas that differ in ambient temperature (e.g., Kennedy 1996) were not included. For nutrient addition, we included studies that enriched the experimental community with nitrogen (e.g.,
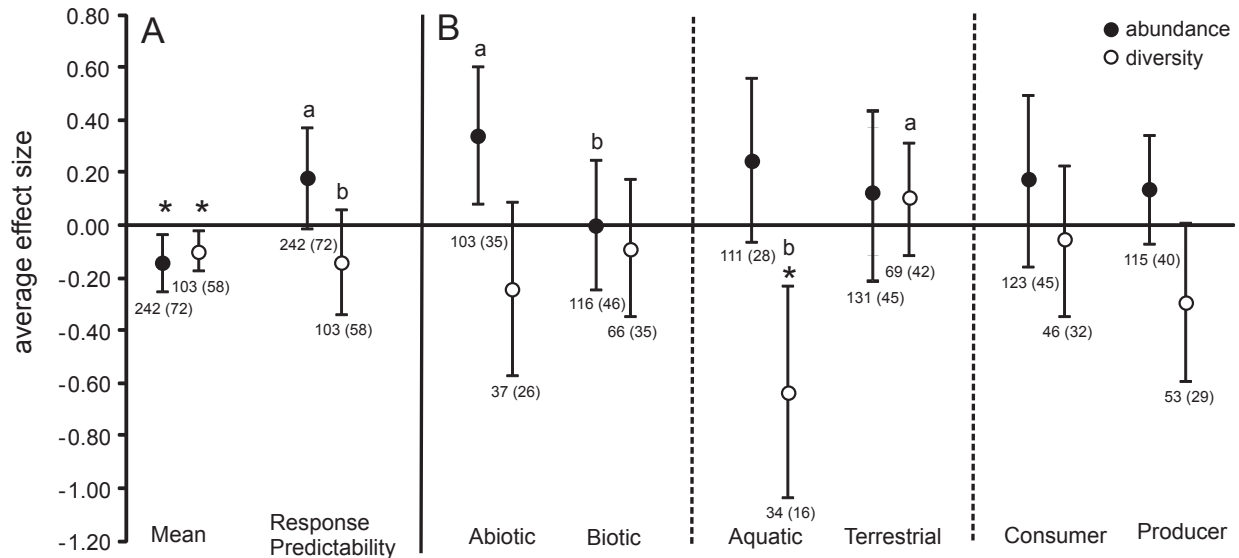
Figure 1: Average response ratios (ln[disturbance/control treatment]) and 95% confidence intervals of abundance and diversity responses to experimental disturbance manipulations across all disturbance types. The values below each point represent the number of results included in the analysis and, in parentheses, the number of articles from which those results were taken. Values that significantly differ from 0 ($P = .05$) are indicated with an asterisk, and different letters indicate significant differences between two values ($P = .05$). *A*, Average response ratios for the mean and response predictability across all disturbances *B*, Average response ratios for response predictability for abiotic versus biotic disturbance, habitat type, and trophic role of affected species.

Bonanomi et al. 2009), phosphorus (e.g., Cherwin et al. 2008), or a fertilizer solution containing one or both of these nutrients (e.g., Lindberg and Persson 2004). For habitat loss and fragmentation, we included studies that fragmented experimental plots (e.g., Gonzalez and Chaneton 2002) or those that compared communities present in control sites with those that had been clear cut or logged (e.g., Dumbrell et al. 2008; Biswas and Mallik 2010). We did not include studies that examined abundance and diversity in different-sized patches without actually fragmenting the patches experimentally, nor did we include studies that combined corridor effects with fragmentation (e.g., Rantalainen et al. 2004). The only studies included in the species removal category were those in which a single species or group of species was removed from the experimental community. We did not include studies that created communities based on biodiversity gradients (e.g., Symstad et al. 1998) or those that decreased the abundances of species without completely removing them. Finally, for species invasions, we included only studies in which a nonnative species or group of nonnative species was added to an established community. We did not include studies that examined the effects of removing nonnative species from previously invaded communities (e.g., Ostertag et al. 2009).

We converted standard errors to variance and calculated

response ratios (RR = ln disturbance/control). The response ratio is a common effect size measure in ecological meta-analyses (Hedges et al. 1999). Response ratios that are significantly greater than or less than 0 indicate a larger change in the response between the control and disturbance treatments. The direction of change indicates whether the disturbance treatment had a positive (decreased response predictability) or negative (increased response predictability) response relative to the control treatment. Response ratios were calculated for the mean response in diversity and abundance for both the control and the disturbed groups across all studies (see fig. 1) and for a standardized measure of the variance: the ratio of the lnRR variance and the mean lnRR (the variance-mean ratio).

We calculated the effect sizes using average values of the response ratios. We determined significant differences from 0 using *t*-tests and significant differences between categories using one-way ANOVA. A common practice in meta-analyses is to weigh the effect sizes based on standard error, so that studies with less variance have a higher weighting in the analysis. Since our study uses variance : mean ratios as the measure of effect size and we did not want variance to be a factor in how the effect sizes were weighted, we did not weight effect sizes.

Studies were grouped on the basis of the response var-

iable, either abundance or diversity, for all factors. Five factors were used in the meta-analysis. (1) Mean versus variance: (*a*) the total mean effect size, (*b*) the total variance : mean effect size (RP). (2) Disturbance type: disturbance types were grouped into abiotic disturbances (habitat loss/fragmentation, temperature increases, nutrient addition) or biotic disturbances (invasive species, species removal) and further grouped into one of the five specific disturbance types: habitat loss/fragmentation, nutrient addition, temperature increase, invasion by a nonnative species, and removal of a species. (3) Habitat: whether the disturbance manipulation was conducted in an aquatic or terrestrial system. Habitat was further separated into the different disturbance types. (4) Response trophic role: whether the species or group of species being measured in the study was a producer or consumer. Response trophic role was further separated into the different disturbance types. (5) Effect trophic role: whether the species invading or being removed from the system was a producer or consumer.

Results

Effects on Response Predictability (RP)

Disturbance had a strong negative effect on mean diversity ($P = .016$) and mean abundance ($P = .013$), showing significantly lower diversity and abundance in disturbed treatments relative to the control across all disturbance types. In contrast to these consistent changes in community structure for average values, response predictability for both $RP_{abundance}$ and $RP_{diversity}$ did not differ significantly between control and disturbed treatments (fig. 1; table 1). This lack of an overall change in response predictability with disturbance was due to the presence of a strong bimodal pattern, with 42 negative and 56 positive $RP_{abundance}$ effect sizes and 16 negative and 13 positive $RP_{diversity}$ effect sizes. Despite these directionally different responses within $RP_{abundance}$ and $RP_{diversity}$, $RP_{abundance}$ showed a trend toward a decrease in response predictability in disturbed treatments, and $RP_{diversity}$ showed a trend toward an increase in response predictability in disturbed treatments (fig. 1; table 1). The mean effect size for $RP_{abundance}$ and $RP_{diversity}$ differed significantly ($P = .049$), with $RP_{abundance}$ showing reductions and $RP_{diversity}$ showing increases in RP with disturbance.

Across all disturbances, $RP_{diversity}$ was significantly greater in aquatic systems than in terrestrial systems ($P = .001$), while $RP_{abundance}$ did not differ significantly between the two habitat types ($P = .534$; table 2). Both $RP_{abundance}$ and $RP_{diversity}$ did not significantly differ between producer and consumer species across all disturbances ($RP_{abundance}$: $P = .88$; $RP_{diversity}$: $P = .36$; table 2).

Disturbance Type

Due to strong habitat differences (fig. 3), $RP_{abundance}$ and $RP_{diversity}$ did not show significant changes for any of the disturbance types (fig. 2); however, two trends are of significant interest. Species invasions led to a marginally significant increase in $RP_{diversity}$ ($P = .055$), and species removals led to a marginally significant decrease in $RP_{diversity}$ ($P = .069$). Neither of these disturbances led to changes in $RP_{abundance}$. $RP_{abundance}$ and $RP_{diversity}$ both did not differ between each of the five disturbances ($RP_{abundance}$: $P = .63$; $RP_{diversity}$: $P = .08$). $RP_{abundance}$ was significantly lower following abiotic disturbances than biotic disturbances ($P = .03$), while $RP_{diversity}$ did not significantly differ between abiotic and biotic disturbances ($P = .4$).

Disturbance × Habitat Type

When disturbance was separated according to habitat, a number of significant changes in RP were observed. In aquatic habitats, nutrient addition decreased $RP_{abundance}$ ($P = .005$), and invasive species increased $RP_{diversity}$ ($P = .036$; fig. 3). In terrestrial habitats, species removal decreased both $RP_{abundance}$ ($P = .021$) and $RP_{diversity}$ ($P = .02$). $RP_{abundance}$ differed significantly between disturbances when separated by habitat ($P = .0006$). Post hoc analysis showed that this difference was driven by a significant difference in temperature increase between aquatic and terrestrial systems. However, this difference was likely due to low sample sizes within all the terrestrial study comparisons. $RP_{diversity}$ did not differ between disturbances when separated according to habitat ($P = .69$).

Disturbance × Trophic Role

When separated according to the trophic role of the species for which the response was measured, the only significant change in RP was for producers, which showed an increase in $RP_{diversity}$ with species invasions ($P = .029$; fig. 4). When separated according to the trophic role of the invading or removed species, disturbances involving producers had stronger effects than disturbances involving consumers (fig. 5). There was a significant decrease in $RP_{abundance}$ ($P = .007$) and $RP_{diversity}$ ($P = .01$) for producer removals. Invasions by producers led to marginal increases in $RP_{abundance}$ ($P = .099$) and $RP_{diversity}$ ($P = .08$). None of the five disturbances differed significantly from one another for either $RP_{abundance}$ or $RP_{diversity}$ when disturbances were separated according to trophic role ($RP_{abundance}$: $P = .34$; $RP_{diversity}$: $P = .52$).

Table 1: Sample sizes, effect sizes, and t-test P values for each of the comparisons included in the meta-analysis for response predictability in abundance and diversity

	Abundance			Diversity		
	n	Mean effect size	P	n	Mean effect size	P
Across all disturbances (fig. 1):						
Overall mean response ratio	242	.14	.004	103	.096	.009
Overall response predictability	242	.183	.17	103	−.141	.24
Abiotic	103	.342	.01	37	.239	.147
Biotic	116	.002	.99	66	−.086	.513
Aquatic	111	.249	.115	34	−.632	.003
Terrestrial	131	.127	.304	69	.101	.348
Consumer	123	.169	.305	46	−.058	.688
Producer	115	.139	.184	53	−.291	.056
Disturbance types (fig. 2):						
Habitat loss	24	.45	.328	20	−.034	.871
Nutrient addition	74	−.031	.869	36	−.393	.055
Invasive species	54	.286	.127	19	−.211	.335
Species removal	52	.225	.179	15	.306	.069
Temperature increase	36	.241	.326	4	−.755	.329
Habitat with disturbance type (fig. 3):						
Aquatic:						
Habitat loss	1	−1.372	...	1	−2.086	...
Invasive species	69	.071	.718	23	.595	.036
Nutrient addition	14	1.252	.005	4	.767	.231
Species removal	24	−.077	.775	5	.268	.322
Temperature increase	3	2.82	.211	1	−1.3	...
Terrestrial:						
Habitat loss	23	.529	.265	19	.074	.693
Invasive species	7	−1.038	.066	13	−.036	.894
Nutrient addition	40	−.051	.785	15	−.063	.785
Species removal	28	.484	.021	19	.456	.02
Temperature increase	33	.006	.973	3	−.572	.582
Trophic role of response species with disturbance type (fig. 4):						
Consumer:						
Habitat loss	20	.606	.258	17	.002	.995
Invasive species	45	−.24	.337	12	−.046	.891
Nutrient addition	22	.364	.365	10	.245	.416
Species removal	27	.229	.347	7	.047	.899
Temperature increase	9	.582	.519	0	...	...
Producer:						
Habitat loss	4	−.334	.668	3	−.235	.651
Invasive species	31	.273	.336	24	−.567	.029
Nutrient addition	32	.233	.159	9	−.174	.618
Species removal	21	−.096	.633	13	.267	.228
Temperature increase	27	.127	.443	4	−.755	.329
Trophic role of invasive or removed species (fig. 5):						
Consumer:						
Invasive species	62	.092	.671	7	.099	.477
Species removal	36	−.015	.943	9	.007	.803
Producer:						
Invasive species	14	−.573	.099	14	−.392	.008
Species removal	16	.764	.007	7	.531	.01

Table 2: ANOVA results for each of the main effects and interaction effects included in the meta-analysis for response predictability in abundance and diversity

	SS	df	MS	*F*	*P*
Abundance:					
Disturbance type	5.97	4	1.49	.64	.63
Abiotic vs. biotic	10.75	1	10.75	4.7	.03
Aquatic vs. terrestrial	.904	1	.905	.389	.534
Consumer vs. producer	.05	1	.05	.02	.88
Diversity:					
Disturbance type	8.9	4	2.23	2.18	.08
Abiotic vs. biotic	.78	1	.78	.71	.4
Aquatic vs. terrestrial	11.34	1	11.34	11.45	.001
Consumer vs. producer	.94	1	.94	.85	.36
Abundance:					
Habitat × disturbance	43.66	4	10.92	5.08	.0006
Trophic × disturbance	10.53	4	2.63	1.14	.34
Diversity:					
Habitat × disturbance	2.2	4	.55	.57	.69
Trophic × disturbance	2.42	4	.81	.75	.52

Discussion

Response predictability is an important ecological response to disturbance and has major implications for understanding how disturbances affect ecological communities. It can also be used as a metric when assessing the potential for recovery following disturbance and for interpreting the results of experiments.

Average values of diversity and abundance decreased across all disturbance types, showing a significant widespread reduction in the complexity of communities following disturbance (fig. 1). In contrast to this clear negative effect of disturbance on average values, which we do not consider here further, we did not detect a significant difference in response predictability for either abundance or diversity across all disturbance types (fig. 1). This lack of an overall effect of disturbance on response predictability was due to the highly dichotomous nature of the response ratios, which included 169 negative and 175 positive response ratios, showing that disturbances can both increase and decrease response predictability. This strong dichotomy arose as a result of the opposite effects of species invasions, which led to increased response predictability, versus nutrient addition and species removal, which led to decreases in response predictability.

Whether community structure converges (response predictability increases) or diverges (response predictability decreases) following a disturbance may be partly due to the role that deterministic versus stochastic processes play in restructuring communities following disturbance (Houseman et al. 2008; Chase and Myers 2011; Myers and Harms 2011). For example, Chase (2007) showed that var-

iance in species composition between replicate ponds decreased (became more predictable) in ponds exposed to drought compared with ponds not exposed to drought. Chase (2007) attributed this increase in similarity to an increase in deterministic processes structuring the drought-affected communities. While both deterministic and stochastic processes interact to structure communities (Chase 2007), the importance and strength of each process may differ on the basis of different environmental stresses. Deterministic—or niche assembly—processes, where community structure results from the niche requirements of species, may be associated with increases in response predictability. On the other hand, stochastic—or dispersal assembly—processes, which structure communities through variations in dispersal and demographic stochasticity, may be associated with decreases in response predictability (Myers and Harms 2011).

The decrease in diversity response predictability caused by removals and increase caused by invasions that we found suggest that during community restructuring, species invasions may lead to a stronger role for deterministic processes, while species loss may lead to stronger roles for stochastic processes. For example, the increase in response predictability we observed for species invasions is suggestive of the reductions in beta diversity or biotic homogenization that is considered a major consequence of nonnative species invasions (McKinney and Lockwood 1999; Rahel 2002; Olden et al. 2004). In contrast, the decrease in diversity response predictability, and thus divergence in composition, following species removals suggests that removing species may increase the importance of stochastic processes. That species loss can increase variability within ecosystems has been widely documented (Loreau 2000; Ives and Carpenter 2007; Campbell et al. 2011); however, the majority of studies have focused on temporal variability. Those studies that have focused on variability among replicates have found a trend of decreased variability (increased response predictability) in more species-rich treatments (Naeem and Li 1997), suggesting that response predictability is correlated with species richness. While species richness may be an important determinant of response predictability within experiments, we found no correlation between species richness and response predictability overall or within any of the disturbance types (see fig. A2, available online).

The potential for a stronger role for deterministic processes following species invasions and stochastic processes following species removals could lead to differences in how communities restructure following a disturbance. Invasions appear to lead to greater similarity in diversity among replicates, whereas species loss leads to divergence in community structure. Whether an invading species will be successful depends on the niche requirements of the species
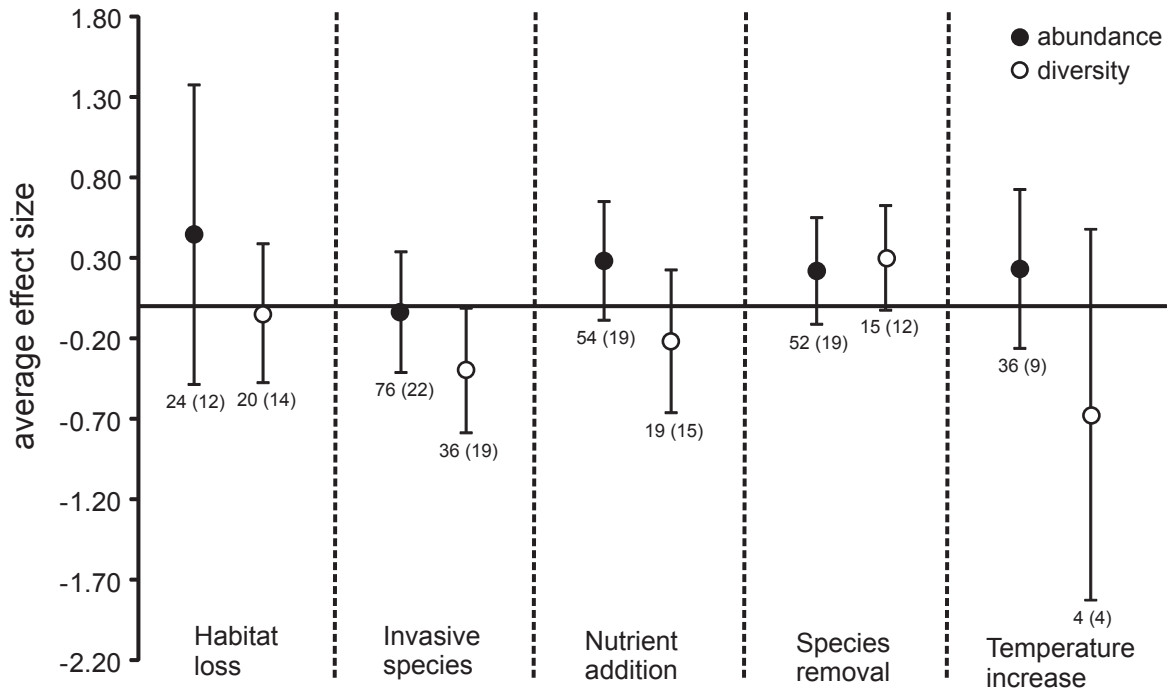
Figure 2: Average response ratios (ln[disturbance/control treatment]) and 95% confidence intervals of abundance and diversity response predictability to experimental disturbance manipulations for groups of studies differing with regard to type of disturbance. The values below each point represent the number of results included in the analysis and, in parentheses, the number of articles from which those results were taken.

as well as competition for resources or space with local species. In contrast, species loss opens space in a community or increases availability of resources. Thus, the relative importance of the roles of deterministic and stochastic processes operating following species invasion and loss should shift on the basis of the type of biotic disturbance. While we observed a strong effect of direct species removal on response predictability, we did not observe a significant effect of temperature or habitat loss/fragmentation on response predictability. These disturbances affect many aspects of ecosystem functioning as well as lead to changes in species richness. Interestingly, we did not observe a significant change in response predictability for temperature increase or habitat loss. The most likely explanation for the lack of significant effects of temperature and habitat loss on response predictability is that the outcome of these disturbances differs strongly across habitats, trophic roles of the disturbed taxa, and environmental conditions. Broad ranges in effect sizes were observed for both of these disturbances (fig. 4). Furthermore, for temperature ($n = 3$) and habitat loss ($n = 1$) in aquatic systems in particular, fewer appropriate studies were included in our meta-analysis than for the other disturbances. Thus, it is likely that a finer level of categorization, such as across

biomes (e.g., Sala et al. 2000), is necessary to determine how response predictability is affected by habitat loss or temperature. However, on the basis of our results for species invasions and species loss, it is likely that if temperature increase or habitat loss affects the numbers of species in the system, by increasing rates of invasions or rates of species loss, an increase or decrease in response predictability may result on the basis of how diversity is affected.

That stochastic processes might play a stronger role in restructuring communities following nutrient addition is particularly intriguing. We observed a strong decrease in response predictability in abundance with nutrient addition in aquatic communities. That increased productivity often drives decreases in predictability has long been recognized (Warwick and Clarke 1992; Chase and Leibold 2002). Slight variations in initial species composition or stochastic priority effects that become magnified with fertilization are two primary mechanisms that have been suggested to underlie this pattern (Steiner and Leibold 2004; Soininen et al. 2005; Houseman et al. 2008). These mechanisms highlight the importance of stochastic processes in community restructuring following nutrient addition.

We predicted that biotic disturbances (species invasions and extinctions) would lead to higher magnitude changes
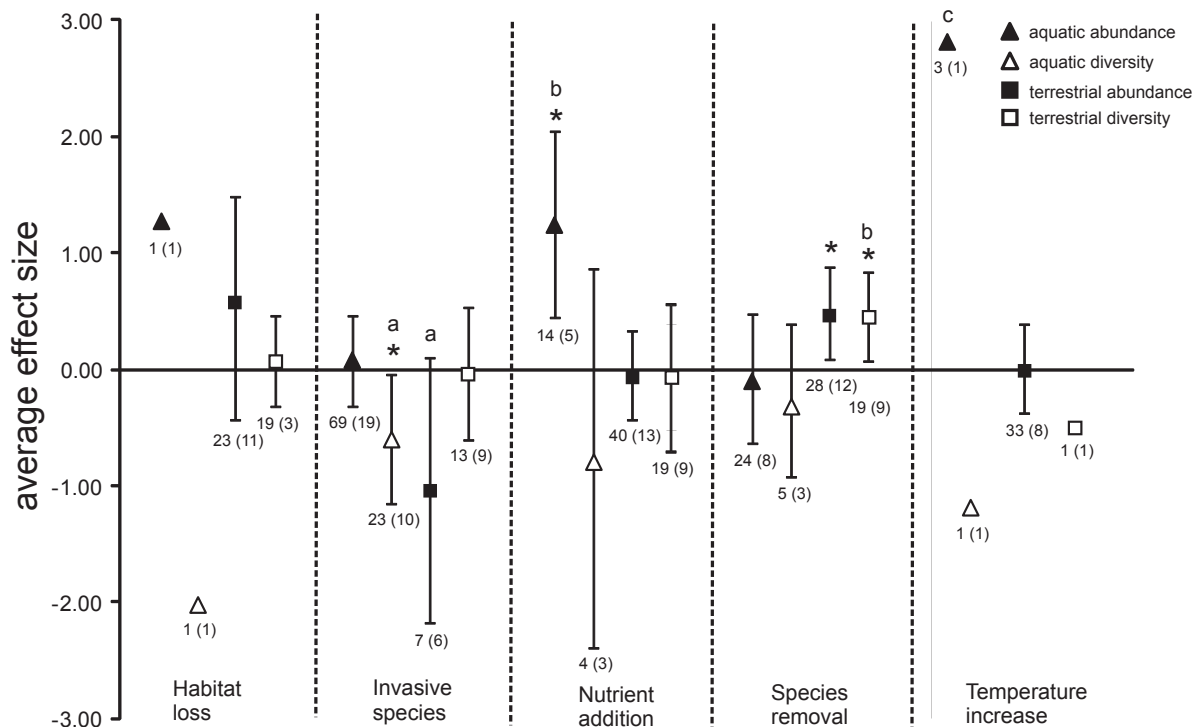
Figure 3: Average response ratios (ln[disturbance/control treatment]) and 95% confidence intervals of abundance and diversity response predictability to experimental disturbance manipulations for groups of studies differing with regard to type of disturbance combined with habitat type. The values below each point represent the number of results included in the analysis and, in parentheses, the number of articles from which those results were taken. Values that significantly differ from 0 ($P = .05$) are indicated with an asterisk, and different letters indicate significant differences between two values ($P = .05$).

in response predictability than abiotic disturbances (nutrient addition, temperature increase, habitat loss), since biotic disturbances have a more direct and potentially stronger impact on species interactions (Van Cleve et al. 1991; Chapin et al. 2000). Support for this prediction was mixed. Across habitat and trophic categories, abiotic disturbances led to significant decreases in response predictability in abundance. Abundance response predictability was also significantly lower following abiotic disturbances than following biotic disturbances (table 2). As discussed previously, this lack of effect for biotic disturbances was due to the strongly dichotomous trends in response predictability for species invasions and species removals. When separated by disturbance type, only species invasions and species removals led to changes in response predictability; however, these effects were not consistent across habitat types (figs. 2, 3). The significant decrease in response predictability for abiotic disturbances was driven by the results from the aquatic nutrient addition studies, since no significant changes in response predictability were observed for either habitat loss or temperature increase.

That changes in response predictability can differ for similar disturbances in different habitats was strongly supported by our results. Aquatic and terrestrial systems differ in terms of food web structure and ecosystem properties. Terrestrial systems are generally more productive and complex with shorter food chain lengths, while aquatic systems have shorter timescales and potentially stronger interactions between species (Shurin et al. 2002). These differences suggest that aquatic and terrestrial systems will differ in at least some aspects of their response to different disturbances. In support of this prediction, we found a significant increase in response predictability in diversity in aquatic communities across all disturbances types. This trend was not observed for terrestrial systems (fig. 1; table 1). Diversity response predictability was also significantly greater in aquatic systems than in terrestrial systems across all disturbances (table 2). Therefore, across all disturbances, aquatic systems appear to be more susceptible to changes in response predictability than terrestrial systems.

A similar trend was also observed for species invasions, with an increase in response predictability in diversity observed for invasions in aquatic but not terrestrial habitats.
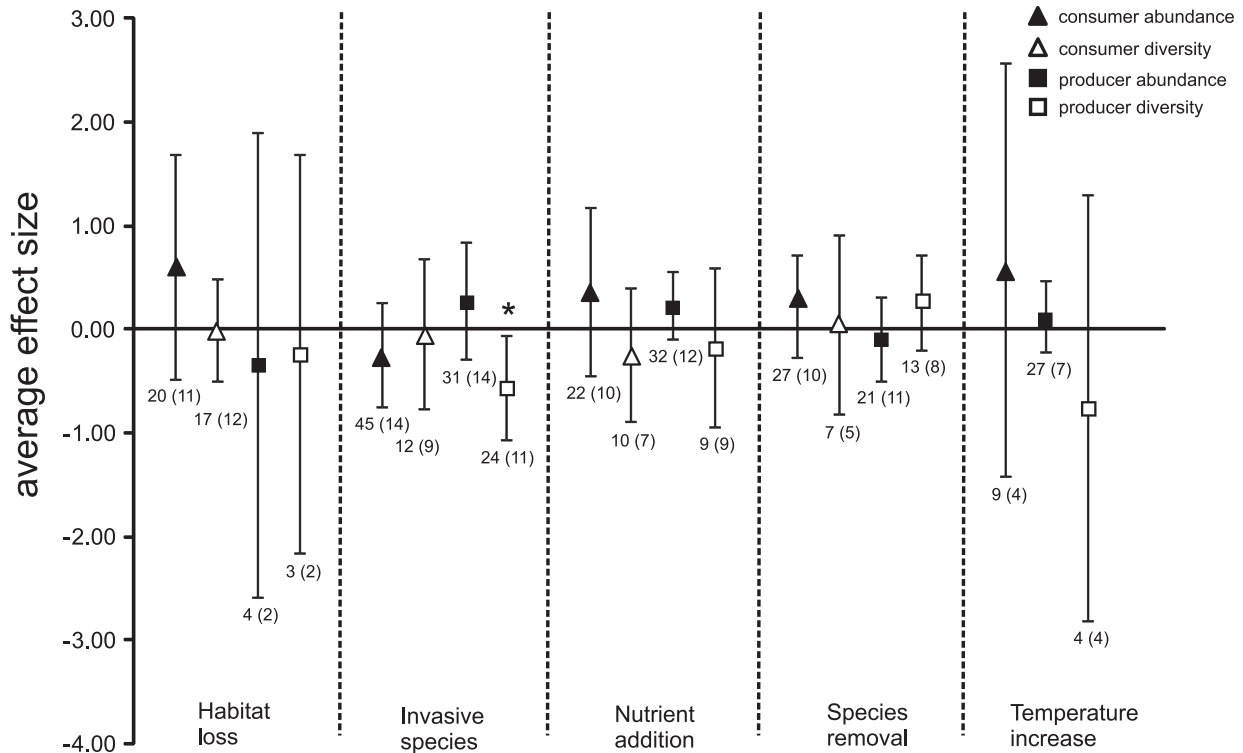
Figure 4: Average response ratios (ln[disturbance/control treatment]) and 95% confidence intervals of abundance and diversity response predictability to experimental disturbance manipulations for groups of studies differing with regard to type of disturbance combined with trophic role of the affected species. The values below each point represent the number of results included in the analysis and, in parentheses, the number of articles from which those results were taken. Values that significantly differ from 0 ($P = .05$) are indicated with an asterisk.

This suggests that biotic homogenization resulting from invasions may be more prevalent in aquatic ecosystems (Qian and Guo 2010). In contrast, in terrestrial systems, invasions increased response predictability in abundance. While this latter result could be an artifact of low sample size ($n = 7$), mechanisms underlying invasion success have been shown to differ between terrestrial and aquatic habitats. For example, positive diversity-invasibility relations are often observed at larger scales in terrestrial habitats (Levine 2000), and greater evolutionary differences between native and nonnative species have been proposed as one reason why aquatic habitats are more easily invaded than terrestrial habitats (Mooney and Cleland 2001).

Broad habitat differences were also observed for species removals. When separated by habitat, the trend of decreased predictability following a species removal was significant only for terrestrial systems. The question of why species removals would decrease response predictability in terrestrial systems but not in aquatic systems is of significant interest. It suggests that, in general, terrestrial systems may be destabilized by species loss more so than aquatic systems. It has previously been suggested that the stabi-

lizing effects of diversity may differ in terrestrial versus aquatic systems (Jiang and Pu 2009). Studies conducted in terrestrial systems typically manipulate and measure responses in plant guilds, while studies conducted in aquatic systems manipulate and measure responses in consumer guilds.

The one other disturbance for which a habitat difference was observed was for nutrient addition, which significantly decreased in response predictability in abundance only in aquatic systems. We attribute this difference in habitat response to more pronounced effects of nutrient enrichment in aquatic systems due to the shorter timescales and higher rates of herbivory, which allow nutrients to recycle faster in aquatic as compared with terrestrial systems (Shurin et al. 2002)

Along with habitat differences, we also found that trophic status had a major effect on whether response predictability changed significantly following disturbance (fig. 4). While neither abundance nor diversity response predictability differed significantly between producer and consumer species across all disturbances (table 2), we found significant changes in response predictability ac-
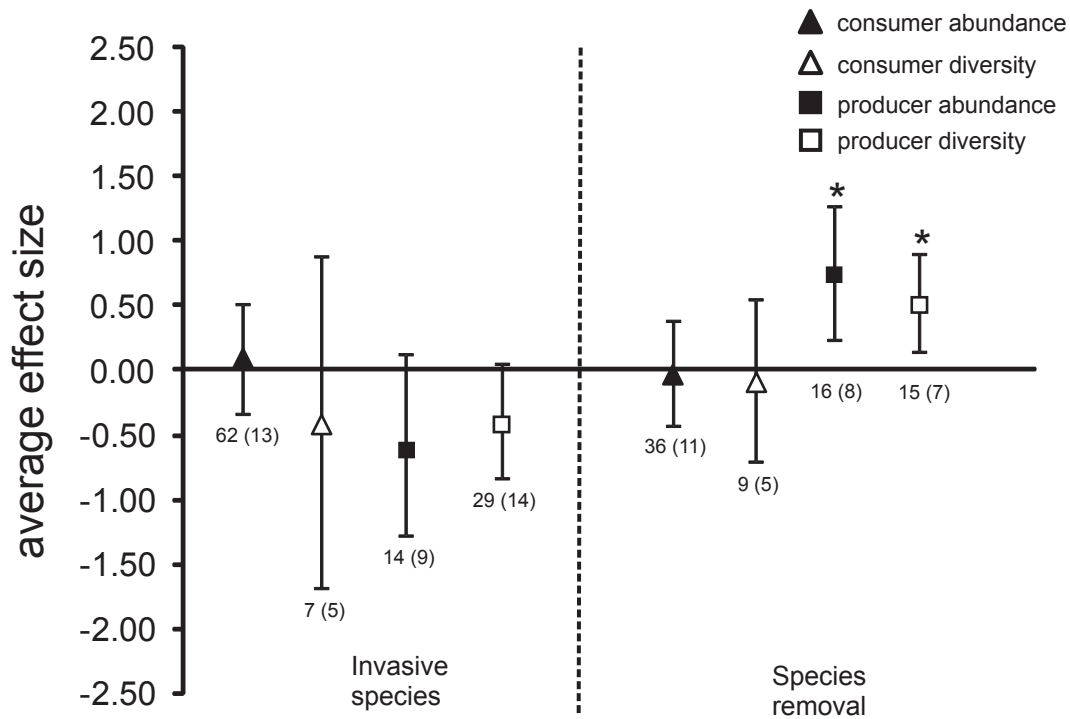
Figure 5: Average response ratios (ln[disturbance/control treatment]) and 95% confidence intervals of abundance and diversity response predictability to experimental disturbance manipulations for groups of studies differing with regard to trophic role of the invading or removed species in invasive species and species removal disturbance types. The values below each point represent the number of results included in the analysis and, in parentheses, the number of articles from which those results were taken. Values that significantly differ from 0 ($P = .05$) are indicated with an asterisk.

cording to trophic status for specific disturbances. When considering the producer-consumer distinction in terms of the response to disturbance, our results suggest that biotic homogenization following species invasions is particularly strong for producers. This is because response predictability in producer diversity was the only metric to decrease significantly following species invasions. When considering whether the invasive species or species removed was a producer or consumer, two additional trends were observed. First, only invasions or removals of producers led to significant changes in response predictability. Producer invasions led to significant increases in diversity response predictability, while producer removals led to significant decreases in both abundance and diversity response predictability. These results suggest that alterations at the base of the food web may lead to more consistent effects than disturbances involving consumers. That producer invaders have greater ecological effects than consumer invaders was recently shown by Vila et al. (2010) in a cross-taxa study in Europe. Additionally, loss of species in lower trophic levels has been hypothesized to cause

stronger changes throughout a food web than loss of higher trophic levels.

The meta-analysis presented here is the first attempt to summarize how response predictability changes following disturbance in ecological communities. Many additional patterns and trends not discussed here may be of considerable interest in understanding how disturbance affects response predictability and for assessing the implications of characteristic changes in response predictability in ecosystem management. One pattern that we did not discuss in detail is why some disturbances affect response predictability in abundance only, others diversity only, and some both. For example, species removals decreased both abundance and diversity response predictability in terrestrial systems, while the effect of species invasions was limited to diversity in aquatic systems and abundance in terrestrial systems. These types of differences provide potentially important information for predicting the consequences of a disturbance, and future studies that focus on the significance of these patterns are needed. Likewise, the implication of different directional changes in response

predictability in assessing the potential for ecosystem recovery (Benayas et al. 2009) holds considerable promise. The directional differences in response predictability observed suggest that effective methods to manage ecosystems recovering from a disturbance such as species loss may be very different from management needed following species invasions. This is due to differences in postdisturbance community assembly processes and the reduction in spatial variability in diversity that would inhibit natural recolonization. Finally, the strong effects we observed for response predictability in three out of five disturbances and the overall increase in response predictability across all disturbances in aquatic systems reinforce the importance of addressing changes in variance along with average values when interpreting the results of experiments. In conclusion, response predictability is a useful metric that can provide a wide range of information on how disturbance affects ecological communities that is overlooked when considering average values alone.

Acknowledgments

Literature Cited

Benayas, J. M. R., A. C. Newton, A. Diaz, and J. M. Bullock. 2009. Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. Science 325:1121–1125.

Biswas, S. R., and A. U. Mallik. 2010. Disturbance effects on species diversity and functional diversity in riparian and upland plant communities. Ecology 91:28–35.

Bonanomi, G., S. Caporaso, and M. Allegrezza. 2009. Effects of nitrogen enrichment, plant litter removal, and cutting on a species-rich Mediterranean calcareous grassland. Plant Biosystems 143:443–455.

Brett, M. T., and C. R. Goldman. 1997. Consumer versus resource control in freshwater pelagic food webs. Science 275:384–386.

Campbell, V., G. Murphy, and T. N. Romanuk. 2011. Experimental design and the outcome and interpretation of diversity-stability relations. Oikos 120:399–408.

Cardinale, B. J., D. S. Srivastava, J. E. Duffy, J. P. Wright, A. L. Downing, M. Sankaran, and C. Jousseau. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443:989–992.

Carpenter, S. R., and W. A. Brock. 2006. Rising variance: a leading indicator of ecological transition. Ecology Letters 9:311–318.

Chapin, F. S., G. R. Shaver, A. E. Giblin, K. J. Nadelhoffer, and J. A. Laundre. 1995. Responses of Arctic tundra to experimental and observed changes in climate. Ecology 76:694–711.

Chapin, F. S., E. S. Zaveleta, V. T. Eviner, R. L. Naylor, P. M. Vitousek, S. Lavorel, H. L. Reynolds, et al. 2000. Consequences of changing biotic diversity. Nature 405:234–242.

Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. Proceedings of the National Academy of Sciences of the USA 104:17430–17434.

Chase, J. M., and M. A. Leibold. 2002. Spatial scale dictates the productivity-biodiversity relationship. Nature 416:427–430.

Chase, J. M., and J. A. Myers. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. Philosophical Transactions of the Royal Society B: Biological Sciences 366:2351–2363.

Cherwin, K. L., T. R. Seastedt, and K. N. Suding. 2008. Effects of nutrient manipulations and grass removal on cover, species composition, and invasibility of a novel grassland in Colorado. Restoration Ecology 17:818–826.

Cottingham, K. L., J. A. Rusak, and P. R. Leavitt. 2001. Increased ecosystem variability and reduced predictability following fertilisation: evidence from paleolimnology. Ecology Letters 3:340–348.

Dumbrell, A. J., E. J. Clark, G. A. Frost, T. E. Randell, J. W. Pitchford, and J. K. Hill. 2008. Changes in species diversity following habitat disturbance and dependent on spatial scale: theoretical and empirical evidence. Journal of Applied Ecology 45:1531.

Forrest, J., and S. E. Arnott. 2007. Variability and predictability in a zooplankton community: the roles of disturbance and dispersal. Ecoscience 14:137–145.

Fraterrigo, J. M., and J. A. Rusak. 2008. Disturbance-driven changes in the variability of ecological patterns and processes. Ecology Letters 11:756–770.

Gonzalez, A., and E. J. Chaneton. 2002. Heterotroph species extinction, abundance, and biomass dynamics in an experimentally fragmented microecosystem. Journal of Animal Ecology 71:594–602.

Hedges, L. V., J. Gurevitch, and P. S. Curtis. 1999. The meta-analysis of response ratios in experimental ecology. Ecology 80:1150–1156.

Houseman, G. R., G. G. Mittelbach, H. L. Reynolds, and K. L. Gross. 2008. Perturbations alter community convergence, divergence, and formation of multiple community states. Ecology 89:2172–2180.

Ives, A. R., and S. R. Carpenter. 2007. Stability and diversity of ecosystems. Science 317:58–62.

Jiang, L., and Z. Pu. 2009. Different effects of species diversity on temporal stability in single-trophic and multi-trophic communities. American Naturalist 174:651–659.

Keitt, T. 2008. Coherent ecological dynamics induced by large-scale disturbance. Nature 454:331–334.

Kennedy, A. D. 1996. Antarctic fellfield response to climate change: a tripartite synthesis of experimental data. Oecologia (Berlin) 107:141–150.

Levine, J. M. 2000. Species diversity and biological invasions: relating local process to community pattern. Science 288:852–854.

Lindberg, N., and T. Persson. 2004. Effects of long-term nutrient fertilisation and irrigation on the microarthropod community in a boreal Norway spruce stand. Forest Ecology and Management 188:125–135.

Loreau, M. 2000. Biodiversity and ecosystem functioning: recent theoretical advances. Oikos 91:3–17.

Marczak, L. B., R. M. Thompson, and J. S. Richardson. 2007. Meta-analysis: trophic level, habitat, and productivity shape the food web effects of resource subsidies. Ecology 88:140–148.

McGrady-Steed, J., P. M. Harris, and P. J. Morin. 1997. Biodiversity regulates ecosystem predictability. Nature 390:162–164.

McKinney, M. L., and J. L. Lockwood. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends in Ecology & Evolution 14:450–453.

Mooney, H. A., and E. E. Cleland. 2001. The evolutionary impact of invasive species. Proceedings of the National Academy of Sciences of the USA 98:5446–5451.

Morin, P. J., and J. McGrady-Steed. 2004. Biodiversity and ecosystem functioning in aquatic microbial systems: a new analysis of temporal variation and diversity-predictability relations. Oikos 104: 458–466.

Myers, J. A., and K. E. Harms. 2011. Seed arrival and ecological filters interact to assemble high-diversity plant communities. Ecology 92: 676–686.

Naeem, S. 1998. Species redundancy and ecosystem reliability. Conservation Biology 12:39–45.

Naeem, S., and S. Li. 1997. Biodiversity enhances ecosystem reliability. Nature 390:507–509.

Olden, J. D., N. L. Poff, M. R. Douglas, M. E. Douglas, and K. D. Fausch. 2004. Ecological and evolutionary consequences of biotic homogenization. Trends in Ecology & Evolution 19:18–24.

Ostertag, R., S. Cordell, J. Michaud, C. T. Cole, J. R. Schulten, K. M. Publico, and J. H. Enoka. 2009. Ecosystem and restoration consequences of invasive woody species removal in Hawaiian lowland wet forest. Ecosystems 12:503–515.

Pounds, J., M. Fogen, and J. Campbell. 1999. Biological response to climate change on a tropical mountain. Nature 395:611–615.

Qian, H., and Q. Guo. 2010. Linking biotic homogenization to habitat type, invasiveness and growth form of naturalized alien plant in North America. Diversity and Distributions 16:119–125.

Rahel, F. J. 2002. Homogenization of freshwater faunas. Annual Review of Ecology and Systematics 33:291–315.

Rantalainen, M. L., J. Haimi, and H. Setala. 2004. Testing the usefulness of habitat corridors in mitigating the negative effects of fragmentations: the soil faunal community as a model system. Applied Soil Ecology 25:267–274.

Sala, O. E., F. S. Chapin III, J. J. Armesto, R. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, et al. 2000. Global biodiversity scenarios for the year 2100. Science 287:1770–1774.

Shurin, J. B., E. T. Borer, E. W. Seabloom, K. Anderson, C. A. Blanchette, B. Broitman, S. D. Cooper, and B. S. Halpern. 2002. A cross-ecosystem comparison of the strength of trophic cascades. Ecology Letters 5:785–791.

Soininen, J., P. Tallberg, and J. Horppila. 2005. Phytoplankton community assembly in a large boreal lake: deterministic pathways or chaotic fluctuations. Freshwater Biology 50:2076–2086.

Steiner, C. F., and M. A. Leibold. 2004. Cyclic assembly trajectories and scale-dependent productivity-diversity relationships. Ecology 85:107–113.

Syms, C., and G. P. Jones. 2000. Disturbance, habitat structure, and the dynamics of a coral-reef fish community. Ecology 81:2714–2729.

Symstad, A. J., D. Tilman, J. Willson, and J. M. H. Knops. 1998. Species loss and ecosystem functioning: effects of species identity and community composition. Oikos 81:389–397.

Van Cleve, K., F. S. Chapin, C. T. Dryness, and L. A. Vireck. 1991. Element cycling in taiga forest: state-factor control. BioScience 41: 78–88.

Van der Putten, W. H., M. Macel, and M. E. Visser. 2010. Predicting species distribution and abundance responses to climate change: why is it essential to include biotic interactions across trophic levels? Philosophical Transactions of the Royal Society B: Biological Sciences 365:2025–2034.

Vila, M., C. Basnou, P. Pysek, M. Josefsson, P. Genovesi, S. Gollasch, W. Nentwig, et al. 2010. How well do we understand the impacts of alien species on ecosystem services? a pan-European, cross-taxa assessment. Frontiers in Ecology and the Environment 8:135–144.

Wake, D. B., and V. T. Vredenburg. 2008. Are we in the midst of the sixth mass extinction? a view from the world of amphibians. Proceedings of the National Academy of Sciences of the USA 105: 11466–11473.

Warwick, R. M., and K. R. Clarke. 1992. Increased variability as a symptom of stress in marine communities. Journal of Experimental Marine Biology and Ecology 172:215–226.

Wiens, J. A. 1989. Spatial scaling in ecology. Functional Ecology 3: 385–397.

Zhou, X., R. A. Sherry, Y. An, L. L. Wallace, and Y. Luo. 2006. Main and interactive effects of warming, clipping, and doubled precipitation on soil CO_2 efflux in a grassland ecosystem. Global Biogeochemical Cycles 20:GB1003.

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