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LETTER

Predator effects on herbivore and plant stability

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Abstract

Humans are rapidly altering the diversity and composition of ecological communities by accelerating rates of species extinctions and introductions. These changes in diversity are not random and disproportionately involve the addition or extinction of predators. Theoretical and microcosm studies suggest predator removal may either increase or decrease ecosystem stability. Here we test whether the addition or removal of predators affects aggregate biomass stability in 40 experiments carried out in six different ecosystems. Predators did not alter the temporal variability of autotroph biomass, but significantly destabilized herbivore biomass. The effects of predators on herbivore biomass stability varied significantly among ecosystems, with benthic and pelagic lake systems showing the greatest shifts. Consequently, the addition of predators to communities, as occurs in many conservation efforts, biological control programmes and species introductions, may lead to more variable system dynamics.

Keywords

Biomass stability, cross-system comparison, ecosystem stability, predators, trophic cascades.

INTRODUCTION

One of the primary ways humans affect biological communities is through the intentional or accidental addition or removal of predators (Kaufman 1992; Pauly *et al.* 1997; Fritts & Rodda 1998; Thirgood *et al.* 2000; Alroy 2001; Jackson *et al.* 2001; Infante *et al.* 2003; Ruzycki *et al.* 2003). Conservation efforts often have reviving or reintroducing predators as a primary goal. Stocking of lakes and streams for recreational fishing often adds predators (Ruzycki *et al.* 2003), as does the introduction of biological control agents for agricultural pests. A single database lists 4769 introductions of predators and parasitoids for biological control, of which 1445 have become established (Infante *et al.* 2003). Furthermore, some of the most dramatic and influential species invasions have been top carnivores, such as the Nile Perch in Lake Victoria (Kaufman 1992) and the Brown Tree Snake in Guam (Fritts & Rodda 1998). In contrast, most marine extractive activities target predators (Pauly *et al.* 1997; Jackson *et al.* 2001), while on land, many predators were removed long ago (Alroy 2001). Thus, humans are dramatically altering trophic structure in different habitats by changing the diversity and composition of predators, and

in more dramatic cases either increasing or truncating food chain length.

Recent work has shown that higher predator diversity can dampen the magnitude of trophic cascades (Finke & Denno 2004), but the impact of predator diversity or composition on ecosystem stability remains unresolved and poorly addressed (Loreau *et al.* 2001). For those cases where predator additions or removals result either in longer or shorter food chains, early theory predicted that longer food chains should be dynamically less stable (Pimm & Lawton 1977), a prediction that has found support in empirical tests in experimental microcosms where longer food chains led to more variable populations (Lawler & Morin 1993). In contrast, more recent modelling suggests that longer food chains may be more stable depending on the degree and prevalence of 'self-damping' (i.e. density-dependent response rates) within and among trophic levels (Sterner *et al.* 1997). However, few empirical tests of these predictions have been performed in more natural food webs with complex habitat structure, omnivory and multiple species within trophic levels. Consequently, the effect of predators, via changes in diversity or food chain length, on community stability remains unknown. As

population and ecosystem instability (variability) increases rates of extinction (Lande 1993) and decreases the economic value of ecosystem services (Armsworth & Roughgarden 2003), it is critical from both a conservation and management perspective to gain a more general understanding of the ways in which predators can affect system stability.

METHODS

From a database of 114 empirical studies of trophic cascades (Borer *et al.* 2005), a subset of 40 experiments from 29 studies were selected that reported data on temporal fluctuations in autotroph (hereafter, plant) and herbivore aggregate biomass (or herbivore density in 29% of the experiments) in the presence and absence of predators (see Table S1). From these studies we calculated the variability of aggregate biomass over time and recorded values for methodological and biological factors thought to influence how consumers affect prey biomass (reviewed in Borer *et al.* 2005). These 10 factors included sample size (number of temporal measurements), predator and herbivore type (vertebrate or invertebrate and endothermic or ectothermic), species richness (plant, herbivore and predator), spatial scale of the study (the size of experimental plots or enclosures), and plant generation time for each study. Plant generation time was classified categorically as short (*c.* 1 day), medium (*c.* 10 days), or long (*c.* 365 days), as in Borer *et al.* (2005).

Here we use the temporal variability (magnitude of variance) in aggregate biomass as a measure of ecosystem stability. This is a common approach to measuring ecosystem stability (e.g. Tilman 1996; reviewed in Cottingham *et al.* 2001). Between-experiment comparisons of temporal variability must account for mean-variance scaling. Two common metrics that scale variance to the mean are the coefficient of variation (CV) and the standard deviation of the log-transformed values (SDlogX). The former assumes a linear relationship between the mean and variance, while the latter assumes an exponential relationship. To select an appropriate metric for these analyses, we regressed the standard deviation (SD) and the log of the standard deviation (lnSD) against the mean from all experiments, for plants and herbivores with and without predators present. In all four comparisons, the R^2 for the linear fit was substantially larger than the R^2 for the exponential fit, and so we chose to use the CV. The CV has the added advantage of providing a dimensionless measure for comparing diverse data types collected across multiple studies and systems that is easy to interpret (Ives *et al.* 2000) and commonly used (McGrady-Steed *et al.* 1997; Naeem & Li 1997), although it is relatively sensitive to sample size and potential biases from sampling error (McArdle & Gaston

1995). We account for sample size in our multiple-regression models (see below).

We then calculated the difference in the variability of herbivore and plant biomass without (CV−) compared with with (CV+) predators. Differences >0 indicate greater variability without predators present; differences <0 indicate the opposite. We also analysed the data using another common meta-analysis metric, the log of the response ratio [Hedges *et al.* 1999, i.e. ln(CV−) − ln(CV+)], which has the added advantages that it is not susceptible to amount of replication (Englund *et al.* 1999) and meets the assumptions of parametric analyses (Hedges *et al.* 1999). Results were qualitatively the same, and so we used the difference rather than the log ratio as it is a more intuitive metric of differences in CVs. Values were not weighted by their accuracy because no work to date has thoroughly evaluated the statistical properties of different potential methods for conducting weighted meta-analyses of temporal data (L. Hedges, personal communication). Furthermore, larger-scale studies tend to have fewer replicates, such that weighting by replication would create a bias towards small-scale, well-replicated studies and increase the probability of type I estimation errors (Englund *et al.* 1999). We opted to maximize sample size and simultaneously place equal weight on large (although potentially poorly or unreplicated) studies because these large manipulations likely provide the best information on whole-system responses.

To test for predator effects on ecosystem stability, we first used paired *t*-tests to compare average CVs for plants or herbivores with and without predators present. We then used a multiple-regression model of the full data set that included all 10 predictor variables and that used the difference in CV of plant or herbivore biomass with predators present vs. without as the response variable. The variable with the smallest chi-square value was removed by a backwards sequential procedure and remained out of the model if the change in the model AIC was <2.0. This parameter-selection criterion is derived from the AIC model, which discounts any given model by 2 times the number of explanatory parameters (i.e. each parameter must change the AIC value by more than 2 for it to have a significant effect on the regression model). In our analyses, parameter removal either improved the fit of the AIC model (positive change) or had a large negative effect (change >−9.0), and so this criterion was rigorously met. Paired *t*-tests were also conducted on only those studies that were longer than five plant generations (which removed all terrestrial studies but preserved all others) and for all studies but with CVs recalculated without temporal data prior to experimental treatment in order to determine if variance in system biomass was simply a response to the experimental disturbance (i.e. addition or removal of the predator). Furthermore, only a subset of the studies recorded species

richness at the herbivore (73%) and plant (35%) levels. To avoid limiting the full regression model to only the six studies that reported both plant and herbivore richness (see Table S1), we tested the effect of herbivore and plant species richness on system stability using a separate multiple regression model with only the response metric and plant or herbivore species richness included.

RESULTS

The number of temporal observations ranged from 3–19 sampling dates among studies (mean $\pm$ SE = 6.83 $\pm$ 0.70). Seventy per cent of predators were vertebrates and 5% ($n = 2$) were endothermic; 5% of herbivores were vertebrates ($n = 2$) and 2.4% ($n = 1$) were endothermic. Plant species richness ranged from 3 to 26 (mean $\pm$ SE = 10.33 $\pm$ 1.67), herbivore species richness from 2 to 14 (mean $\pm$ SE = 7.89 $\pm$ 1.02), and predator species richness from 1 to 12 (mean $\pm$ SE = 2.17 $\pm$ 0.40). For studies that reported species richness for all three trophic levels ($n = 6$), species richness ranged from 7 to 41 (mean $\pm$ SE = 16.17 $\pm$ 5.19).

Across all experiments, the temporal variability of plant biomass was not affected by the presence of predators (paired t-test comparing CV− and CV+, d.f. = 38, $t = 0.90$, $P = 0.38$; Fig. 1). In contrast, there was a significant destabilizing effect of predators on herbivore biomass (CV− > CV+, d.f. = 33, $t = -3.52$, $P = 0.001$; Fig. 1). For plants, the backwards selected multiple-regression model yielded a final model that included ecosystem type
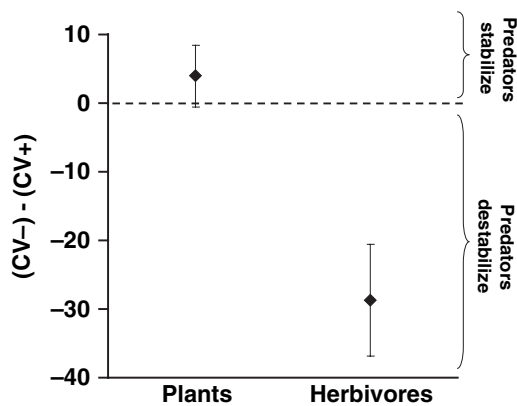
($\chi^2 = 14.00$, $P = 0.007$), number of temporal measurements ($\chi^2 = 6.55$, $P = 0.01$), experimental plot size ($\chi^2 = 5.48$, $P = 0.02$), and number of plant generations within the study ($\chi^2 = 7.96$, $P = 0.005$) as variables explaining model variance. For herbivores, the only significant explanatory variable was ecosystem type ($\chi^2 = 17.17$, $P = 0.004$). The overall destabilizing effect of predators on herbivore biomass was primarily driven by studies from lake systems (Fig. 2a), although there was a trend of destabilized herbivore biomass for three of the other four ecosystems (Fig. 2a). In contrast, there was an inconsistent effect of predators on plants across ecosystem type (Fig. 2b). Plant biomass was more variable with longer food chains in marine and terrestrial systems, and less variable in lake plankton and benthos. Comparisons between the magnitude of change in plant or herbivore biomass (Shurin *et al.* 2002) and the variability in that biomass over the duration of the experiment (results presented here) show that the strength of a trophic cascade does not affect the resulting variability in either plant or herbivore biomass (Fig. 3).

Results were equivalent when data were reanalysed including only studies with more than five plant generations (plants: $n = 35$, d.f. = 34, $t = 1.09$, $P = 0.28$; herbivores: $n = 30$, d.f. = 29, $t = -3.38$, $P = 0.002$) and when CVs were calculated without data collected before the experimental treatment (plants: $n = 39$, d.f. = 38, $t = 1.01$, $P = 0.32$: herbivores: $n = 34$, d.f. = 33, $t = -2.60$, $P = 0.01$).
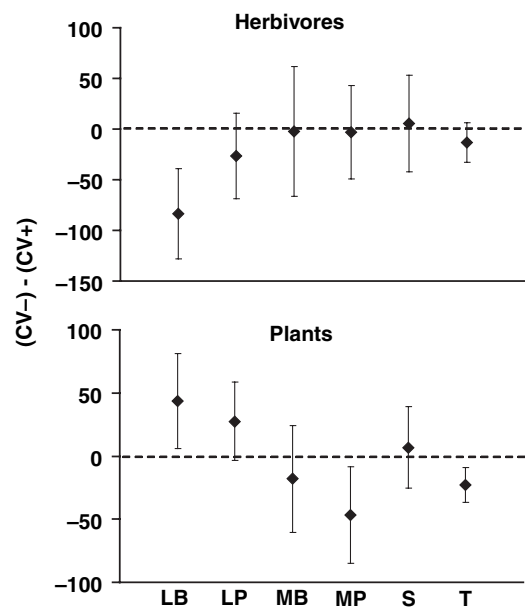

Figure 1 Changes in stability (measured as the CV) for plants and herbivores in the presence (CV+) and absence (CV−) of predators. Data are given as mean $\pm$ SE. The dashed line [(CV−) − (CV+) = 0] is where predators had no effect on stability. Values above this line indicate that biomass was more stable with predators present; values below the line indicate that biomass was less stable with predators present.

Figure 2 Changes in stability (mean $\pm$ SE) of herbivores and plants in the six different ecosystems. See Fig. 1 legend for details. MP, marine pelagic; MB, marine benthic; S, stream; T, terrestrial; LB, lake benthic; LP, lake pelagic.
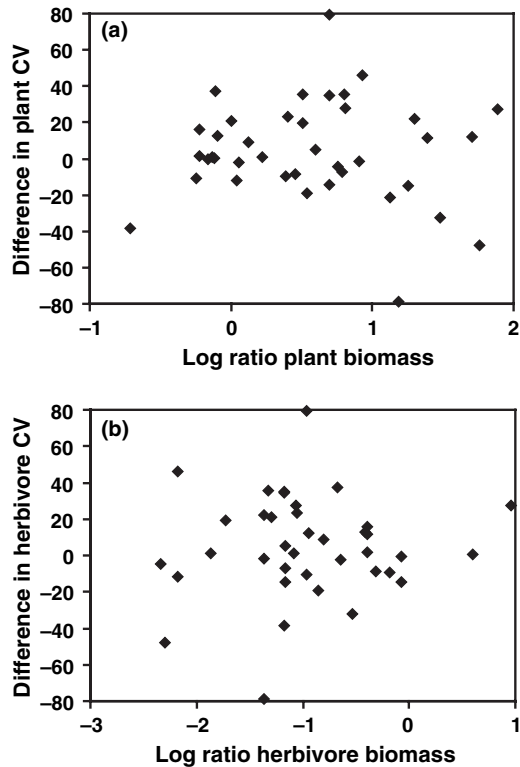
Figure 3 Relationship between changes in mean biomass and the concordant variability (CV) in that biomass over time for plants (a) and herbivores (b). Y-axes in both plots are the difference in CV of aggregate biomass with vs. without predators (see Methods). X-axes are the log-ratio of mean biomass with over without predators (see Shurin *et al.* 2002 for details). Each datum represents results from a single study.

Furthermore, neither plant ($n = 15$) nor herbivore ($n = 29$) richness had any effect on the stability of plant and herbivore biomass in the presence or absence of predators (multiple regression models of plant and herbivore biomass stability accounting for plant and herbivore species richness; $P > 0.40$ for all four comparisons).

DISCUSSION

The addition of higher trophic levels to communities consistently destabilized aggregate herbivore biomass in spite of the variety of biological and methodological differences between ecosystems and studies. More variable herbivore density did not translate into changes in plant stability, indicating that predator effects on temporal dynamics became attenuated at lower trophic levels. The magnitude of trophic cascades also attenuates down the food chain (Shurin *et al.* 2002), indicating that lower trophic levels are buffered from both mean and variance effects of changing trophic diversity. Furthermore, our results suggest

that greater vertical species diversity (i.e. longer food chains) in natural systems does not necessarily enhance system stability, although few studies included all species within a community when calculating changes in community biomass.

It is also interesting to note that there is no obvious relationship between susceptibility to strong trophic cascades (i.e. changes in mean biomass; Shurin *et al.* 2002) and strong effects of predators on plant and herbivore stability (i.e. changes in biomass variance; Fig. 3), suggesting that the mean and variance of biomass are constrained by different factors and that the stability results are not simply an artefact of focusing on communities prone to cascades. Furthermore, the stability results were consistent when accounting for possible short-term responses to experimental disturbance (i.e. analyses with studies that spanned multiple plant generations, and using post-treatment CV), suggesting that results reflect actual stability differences at temporal scales relevant to ecological processes. Results were also robust to the type of meta-analytic metric used for the analyses. Finally, as few of the studies synthesized here were intended to test questions of system stability, it is unlikely that any experimental bias exists.

Our analyses used data from a particular type of study of community dynamics, i.e. trophic cascade studies, to test how predator diversity/composition and food chain length affect the stability of plant and herbivore biomass. These studies provide a unique opportunity to evaluate the role of predators in controlling community dynamics, as few if any other studies manipulate predators in a natural setting while measuring plants and herbivores, but it remains possible that the dynamics of these communities are unique. The lack of a relationship between cascade strength and system stability (Fig. 3) suggests our results may be general, but further research is needed to test this.

Although predators had a significant overall destabilizing effect on herbivores across ecosystems, the actual change in stability varied significantly between ecosystem type (Fig. 2). In fact, it was the two lake ecosystems that showed the largest change in stability (and were the primary reason the overall result was significant), while the other four ecosystems showed little difference in herbivore stability with or without predators present. This result is somewhat surprising, as herbivores and plants in pelagic lake systems are more broadly similar to those in pelagic marine systems than to plants and herbivores in benthic lake systems. Further research is necessary to determine which factors may be driving these systematic differences in the response of the temporal variability of biomass to predator manipulations.

A few of the variables included in the analyses presented here had fairly small sample sizes, and so it is not possible to draw strong conclusions about the causes of variation in

the effects of predators on stability. For example, although comparisons among other systems are valid, caution must be used when interpreting results from marine benthic systems as only two studies were available for this ecosystem. Similarly, there were only two vertebrate herbivores and one endothermic herbivore, so little can be said about the role of herbivore type in controlling the stability of aggregate biomass. Despite these limitations, we included these variables in our analyses because recent research has identified them as potentially important factors for controlling trophic cascades (reviewed in Borer *et al.* 2005). However, our results may not be applicable to systems where, for example, endothermic, vertebrate herbivores play a large role in trophic interactions. Further collection of temporal community data following predator manipulations in such communities will help determine the generality of the results we present here.

Theoretical and empirical research provides conflicting results about the effect of predators on system stability (Pimm & Lawton 1977; Lawler & Morin 1993; Sterner *et al.* 1997; Finke & Denno 2004). Pimm & Lawton (1977) concluded that the addition of predators tends to favour unstable dynamics through over-compensation, and suggested that dynamical instability may place constraints on the maximum length of food chains. Sterner *et al.* (1997) criticized this conclusion by pointing out that Pimm and Lawton's model added top predators that lacked direct self limitation (i.e. the populations were regulated by the availability of prey resources). As direct self-limitation through territoriality or other forms of direct interactions tend to stabilize predator–prey dynamics, it is expected that adding such predators should lead to dynamic instability. Thus, the question of how predators affect community stability hinges on how their numbers are controlled. Nonetheless, Lawler & Morin (1993) found in laboratory experiments that predators tended to destabilize lower trophic levels, although these experiments were performed in laboratory microcosms. Here we have shown that across diverse data from complex (species rich) communities, predator additions destabilize herbivore dynamics and have idiosyncratic effects on plant stability that depend on the ecosystem, regardless of potential biological differences among different species assemblages.

Humans are rapidly altering the trophic structure of biological communities through the addition and removal of predators, which in turn appears to decrease ecosystem stability. Such instability makes systems less predictable, which has been shown in some cases to have negative financial implications (Armsworth & Roughgarden 2003), and may also be a driving mechanism limiting the length of natural food chains. Furthermore, the ability to predict the stability of ecosystems with and without predators provides a critical tool for developing appropriate plans and expectations for resource management, conservation activities and biological control efforts.

SUPPLEMENTARY MATERIAL

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/ELE/ELE712/ELE712sm.htm

Table S1 Values for all variables included in multiple regression analyses, the plant and herbivore coefficients of variation with (CV+) and without (CV−) predators, and the references from which the data came. See Methods for details on variable chosen and analyses conducted.

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