

## THE EFFECTS OF PRODUCTIVITY, HERBIVORY, AND PLANT SPECIES TURNOVER IN GRASSLAND FOOD WEBS

JONATHAN M. CHASE,<sup>1</sup> MATHEW A. LEIBOLD, AMY L. DOWNING, AND JONATHAN B. SHURIN

Department of Ecology and Evolution, 1101 East 57th Street, University of Chicago, Chicago, Illinois 60637 USA

**Abstract.** In order to evaluate the patterns and processes of food web structure in grasslands, we compiled data from published studies on the relationship between precipitation (which is a predictor of primary productivity in grasslands), plant and herbivore standing crop biomass, and the results of large-herbivore exclosure experiments on plant abundance and composition. Three informative patterns emerged: (1) both producer and herbivore biomass increase across a natural precipitation gradient; (2) the relative effect of large herbivores on plant biomass, inferred from exclosure studies, decreases with increasing precipitation; and (3) the effect of herbivores on changes in plant species composition increases with precipitation. Simple resource-controlled and consumer-controlled food chain models can explain different subsets of these patterns. However, models of heterogeneous food webs that incorporate differences among species within trophic levels, and compositional turnover within such trophic levels, are consistent with all of the reviewed patterns. We suggest that this compositional turnover of plant species, combined with the interactive controlling effects of consumers and resources, may help to explain why studies performed in different areas, and with different methodologies, often draw different conclusions about the patterns and structuring processes in grassland ecosystems.

**Key words:** *compositional turnover; consumer control; food web; grasslands; herbivore exclosure; herbivory; heterogeneous food web models; plant defense; primary productivity; resource control.*

### INTRODUCTION

Despite considerable empirical evidence for the importance of both resources and consumers for determining trophic structure, the relative roles of these two processes in generating patterns in communities are still unclear. Early proponents of the importance of consumers and cascading effects in food webs, referred to as top-down control, suggested that top consumers are critical in shaping species abundance and distribution (Hairston et al. 1960, Paine 1966, 1980, Slobodkin et al. 1967, Fretwell 1977). An alternative view is that resources at the base of the food web are of primary importance and that consumers are controlled by their resources from the bottom up (Lindeman 1942, Odum 1971, White 1978, 1993).

The current consensus recognizes that top-down and bottom-up forces interact in complicated ways to structure ecological communities (Oksanen et al. 1981, Carpenter et al. 1985, McQueen et al. 1986, Leibold 1989, 1996, Hunter and Price 1992, Power 1992, Holt et al. 1994, Polis 1994, Chase 1996, Persson et al. 1996, Brett and Goldman 1997, Leibold et al. 1997). However, considerable debate endures concerning the relative importance of these processes and the nature of their interaction. In this paper, we focus on the trophic structure of communities (i.e., the distribution of biomass

among trophic levels) and on the role of food web interactions and compositional change along gradients of potential ecosystem productivity. We adopt Osenberg and Mittelbach's (1996) definitions of food web regulation, control, and limitation. Specifically, we are interested in the relative and interactive effects of resource and consumer *control* in food webs. Control is defined as the extent to which the mean density (ignoring transient responses) of a given population or trophic level is affected by consumers or resources (Osenberg and Mittelbach 1996). Following Osenberg and Mittelbach (1996), we focus on the relative, rather than the absolute, degree to which a given population or trophic level is controlled by its resources or consumers, because relative effects are more diagnostic in discriminating among conceptual models.

In this paper, we review patterns in natural grasslands, a well-studied ecosystem in which the relative roles of consumers and resources remain subject to debate. Recent reviews and experiments in grassland food webs have found contrasting evidence supporting emphasis on resources (Arditi and Ginzburg 1989, McNaughton et al. 1989, 1991, White 1993), consumers (Moen and Oksanen 1991, Hairston and Hairston 1993), or complex interactions between the two (Bowers 1993, Schmitz 1993, 1994, 1997, Ritchie and Tilman 1995, Chase 1996, Ritchie et al. 1998). These studies vary considerably in the types of evidence used to justify their conclusions. For example, White (1993) and Hairston and Hairston (1993) discussed patterns in individual systems, whereas McNaughton et al. (1989,

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<sup>1</sup> Present address: Department of Biological Sciences, University of Pittsburgh, Pennsylvania 15260 USA.  
E-mail: jchase+@pitt.edu

1991) and Moen and Oksanen (1991) discussed broad-scale gradients across several natural systems. Finally, Schmitz (1993, 1994, 1997) and Ritchie and colleagues (Ritchie and Tilman 1995, Ritchie et al. 1998) used controlled experimentation at single sites. This diversity of approaches may be a primary factor that leads to contrasting conclusions about the control of trophic structure in grasslands. Here, we use a more synthetic approach by comparing much of the available evidence from different sorts of studies (i.e., observational and experimental) to explicitly compare among three of the more commonly invoked conceptual models of consumer vs. resource regulation of grassland ecosystems (see also Leibold et al. [1997] for a similar analysis of evidence from lake ecosystems).

We begin by describing three generalized conceptual models of food web interactions and describe contrasting predictions derived from each. Each model makes similar predictions about some patterns, but anticipates significant divergence in others. Next, we compare predictions of the models with observational data and a meta-analysis of experimental data from grasslands across large gradients in primary productivity. We use this correlational evidence to attempt to discriminate between the observed patterns and the predictions of the three broad classes of conceptual models. Each model captured some elements of the variability observed in grasslands. However, we conclude that “heterogeneous food web” models that combine resource and consumer effects, as well as species compositional turnover within trophic levels, were more consistent with all of the results than simpler “consumer-controlled” or “resource-controlled” food chain alternatives.

#### MODELS: CONCEPTUAL FRAMEWORKS FOR EXPLORING TROPHIC STRUCTURE

To lay a conceptual foundation for the patterns we will present, we explicitly consider three general modeling frameworks upon which much of the current theoretical discussions of trophic structure are based (see Power [1992], Persson et al. [1996], Leibold et al. [1997] for a summary). These groups of models are as follows: (1) resource-based or “donor-controlled” food chains, in which resources supply food to consumers, but consumers have negligible effects on their resource; (2) consumer-controlled food chains, where each trophic level is either controlled by its resources or consumers but not both; (3) heterogeneous food web models, where heterogeneity among species and compositional change within a trophic level modifies the effects of resources and predators on a given trophic level.

We are interested in identifying empirical support as well as any major shortcomings of each of the models. We recognize that the first two approaches require a much simpler modeling framework than the third. The question then becomes whether there are compelling

reasons to adopt the additional complexities of the third approach, or whether either of the first two approaches adequately predicts patterns in trophic structure. For each of these modeling frameworks, we consider how trophic structure responds to gradients of primary productivity and how herbivores control plant biomass and composition. Here, we present an overview of the predictions of these different modeling frameworks. (See the Appendix, and cited work for more detail.)

#### *Resource-controlled food chains*

Several models assume that resources are of overriding importance in the regulation of trophic structure. They include the “donor-controlled” models of DeAngelis (1975, 1992) and Pimm (1982), the “food-limited” models of Schmitz (1992, 1993), and the “ratio-dependent” models of Arditi and Ginzburg (1989). Although these approaches differ in their specific formulations (and underlying mechanisms), they share common assumptions that consumer effects are weak relative to resource effects, leading to the following predictions: (1) consumer and resource biomass will both increase along a productivity gradient, and (2) relative consumer control of resource biomass does not vary with productivity (see the Appendix for more detail). The former prediction results because of the assumed importance of resource control vs. consumer control, and the latter prediction results because the models generally assume that consumers take a constant proportion of resources, regardless of resource availability or consumer abundance.

#### *Consumer-controlled food chains*

These are generally based on a linear approximation of the Lotka-Volterra predator-prey model (Oksanen et al. 1981). In these models, while resources control overall system productivity (Power 1992), top consumers strongly regulate their prey populations, often leading to indirect effects (i.e., trophic cascades) on the rest of the community. These models predict (1) decoupled or “stepwise” increases in consumer or resource abundance (but not both) along a productivity gradient or with nutrient additions, and (2) strong proportional control by top consumers that increases with productivity (see the Appendix). Consequently, relative differences in resource abundance with and without top consumers increase as environmental productivity increases (Sarnelle 1992). Nonequilibrium and nonlinear versions of these models (Abrams and Roth 1994), as well as the addition of strong interference in the consumer trophic level (Oksanen et al. 1995), add complexities to these simple predictions. Specifically, the addition of both of these types of complexities predict that average densities of both herbivores and plants can increase concurrently with productivity (contrary to the first prediction), but these models also predict that herbivore control of plant biomass will increase with productivity (as in the second prediction). That is, while

the linear and more complex models disagree on the patterns of consumer resources along a productivity gradient, both sets of models predict increasing herbivore control with productivity.

#### *Heterogeneous food web models*

These more complex models (Armstrong 1979, Jaeger et al. 1984, Holt et al. 1994, Leibold 1989, 1996, Grover and Holt 1998) incorporate heterogeneity among species within a trophic level. That is, while the above conceptual models assume that species with similar trophic relationships (e.g., producers or herbivores) can be reasonably lumped into a single trophic level, these food web models suggest that differences among species within a trophic level, such as their ability to compete and their susceptibility to consumers, are important enough to explicitly consider. Specifically, Leibold (1996) focuses on the way that compositional turnover within a trophic level regulates trophic structure when species exhibit a trade-off between an ability to exploit resources and susceptibility to predation. Although somewhat more complicated depending on a variety of specific assumptions made, heterogeneous food web models predict: (1) concurrent increases of all trophic levels with increasing productivity, and (2) a declining strength of consumer control of the resource trophic level with increasing productivity. These predicted patterns hinge upon the prediction that at low productivity resource communities should be dominated by species that are vulnerable to consumption, but do not incur the assumed costs associated with adaptations to herbivory, whereas well defended species are predicted to be favored at higher productivity (Holt et al. 1994, Leibold 1996, Grover and Holt 1998). Similar predictions also arise in evolutionary models of plant-herbivore interactions and optimal plant defense strategies (Coley et al. 1985). (3) A final prediction of the heterogeneous food web models that we will consider is the composition of resource species along a productivity gradient. Because of the assumed trade-offs and predicted responses to resources along a productivity gradient, we predict that the relative effect of consumers on resource species composition should increase with increasing productivity. That is, at low productivity, vulnerable resource species are expected to dominate both with and without consumers, such that consumer effects on composition are small; whereas, at high productivity, resource species that are less susceptible to consumers become favored in the presence, but not the absence, of consumers, leading to a greater effect of consumers on resource composition. (See Appendix and Leibold [1996] for more detail.)

#### PRODUCER AND CONSUMER BIOMASS ALONG GRADIENTS OF RAINFALL IN GRASSLANDS

Several authors describe patterns of positive covariation in grasslands between rainfall (a measure of

resource supply rate) and plant (Rosenzweig 1968, Leith 1975, Whittaker 1975, McNaughton et al. 1989, 1991), herbivore (Sinclair 1975, Coe et al. 1976, East 1984, McNaughton 1985, McNaughton et al. 1989, 1991), and, in at least one case, carnivore (East 1984) abundance. Two reviews of patterns of producer and herbivore productivity in terrestrial systems (McNaughton et al. 1989, 1991, Moen and Oksanen 1991) found positive correlations among herbivore (secondary) productivity and net primary productivity. However, the three main classes of conceptual models (see *Models* and the Appendix) make predictions about standing crop biomass (i.e., the equilibrium abundance) of plants and herbivores in relation to productivity or resource supply rates, and not about how plant (primary) productivity and herbivore (secondary) productivity correlate. Thus, while these previous reviews are suggestive of the fact that increasing primary productivity increases herbivore abundance, they do not provide conclusive evidence about which model(s) (that are based on standing crops) best predict natural observations. To explicitly test the model predictions, we reviewed the literature so that we could correlate patterns of resource supply (precipitation) with standing crop biomass of plants and herbivores in grasslands.

In grasslands, the rate of plant primary productivity (measured in grams per square meter per year) is tightly correlated with the amount of precipitation a given site receives (see Rosenzweig 1968, Leith 1975, Whittaker 1975, Milchunas and Lauenroth 1993). We therefore used precipitation (i.e., resource supply) as an independent predictor of primary productivity. We compiled data from 21 relatively natural grassland sites from which comparable data were available. These 21 sites occurred throughout the world, but data were collected in similar ways in order to facilitate comparisons among sites as part of the International Biosphere Program, Grassland Biome Project. Data on precipitation, plant standing crops, and herbivore standing crops for each grassland site were gathered from several different tables throughout the compilation books from these projects (Coupland 1979, Breymer and Van Dyne 1980).

As with the previous analyses, we show that both plant biomass (regression:  $y = 409x - 1474$ ;  $N = 21$ ,  $df = 1, 19$ ,  $R^2 = 0.79$ ,  $P < 0.0001$ ) and herbivore biomass (regression:  $y = 320x + 367$ ;  $N = 21$ ,  $df = 1, 19$ ,  $R^2 = 0.49$ ,  $P < 0.0001$ ) increase with precipitation, and that plant and herbivore biomass are also positively correlated (regression:  $y = 4.6x + 0.7$ ;  $N = 21$ ,  $df = 1, 19$ ,  $R^2 = 0.50$ ,  $P < 0.0001$ ) (Fig. 1). These positive relationships among the standing biomass of adjacent trophic levels support predictions from the models that emphasize resource control (category 1; Arditi and Ginzburg 1989, Schmitz 1992), certain nonlinear models of consumer control (category 2; Abrams and Roth 1994), or heterogeneous food webs (category 3; Holt et al. 1994, Leibold 1996), but not the linear

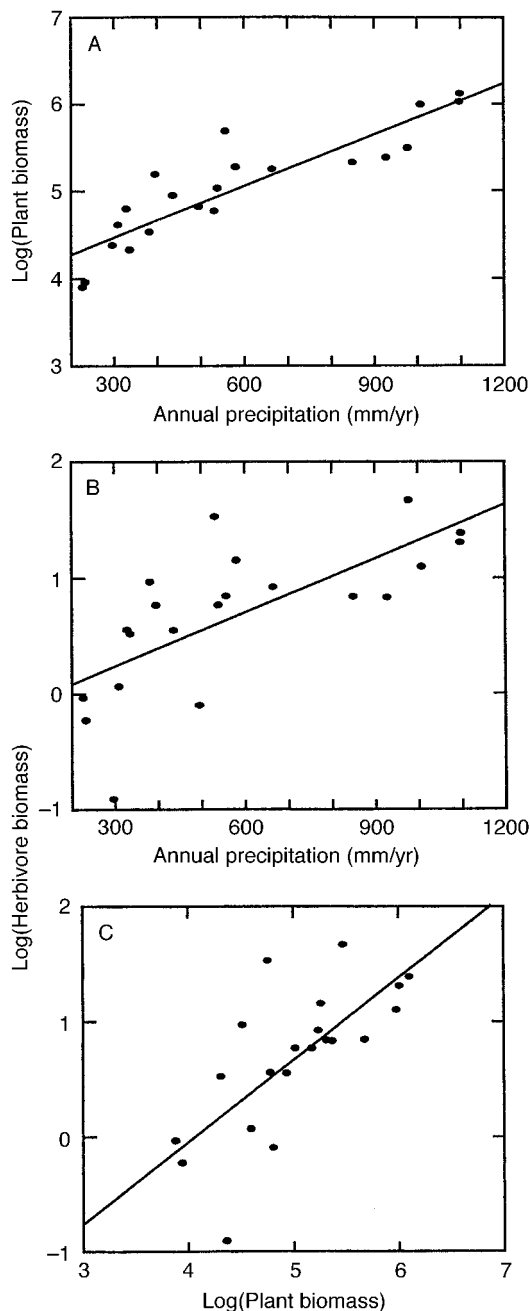


FIG. 1. Relationships of (A) plant and (B) herbivore standing crops ( $\text{g}/\text{m}^2$ ) with rainfall from 21 grassland sites throughout the world (data from Coupland 1979, Breymeyer and Van Dyne 1980). (C) Relationship between plant and herbivore standing crops. Plant  $\times$  precipitation regression:  $y = 0.36x - 24.12$ ;  $N = 21$ ,  $df = 1, 19$ ,  $R^2 = 0.78$ ,  $P < 0.0001$ . Herbivore  $\times$  precipitation regression:  $y = 0.003x + 0.53$ ;  $N = 21$ ,  $df = 1, 19$ ,  $R^2 = 0.48$ ,  $P < 0.0001$ . Plant  $\times$  herbivore regression:  $y = 4.6x + 0.7$ ;  $N = 21$ ,  $df = 1, 19$ ,  $R^2 = 0.50$ ,  $P < 0.0001$ .

consumer-control (category 2; Oksanen et al. 1981) models that predict no positive covariation between adjacent trophic levels.

Moen and Oksanen (1991) suggest that stepwise patterns of consumer and resource biomass in their review indicate a decoupled pattern consistent with consumer-controlled models. These "breakpoints" may be viewed as critical productivities, where there are changes in the number of trophic levels present as predicted by Oksanen et al. (1981). Data in Fig. 1 possibly suggest similar breakpoints (although not statistically significant) in both herbivore and plant biomass when precipitation is 500–1000 mm/yr. However, in striking contrast to the predictions of the consumer-control models, this effect occurs in parallel for herbivores and plants, instead of alternately. The presence of simultaneous transitions (if significant) does not support the hypothesis for an increase in the number of trophic levels between those precipitation values. Furthermore, if the "breaks" observed in Fig. 1 in plant and herbivore biomass are slightly offset in accord with the hypotheses that increasing productivity increases the number of trophic levels, this would indicate that there are two additional trophic levels at precipitation levels  $>1000$  mm/yr compared to the levels  $<500$  mm/yr. Given current knowledge about the distributions of large carnivores (East 1984, Messier 1994, Crete and Manseau 1996), it seems highly unlikely that a system could go from two to four trophic levels across this small range in the precipitation gradient.

The patterns we observed in Fig. 1 are in qualitative support for all of the conceptual frameworks we have discussed, except the linear version of the consumer-control food chain model. Thus, we conclude that this line of evidence alone can not be sufficient to discern which conceptual framework provides the most accurate caricature of the structure of these grassland food webs. Next, we review two other lines of evidence, the experimental effects of herbivores on plant abundance and plant species composition, to further elucidate patterns that are consistent and inconsistent with the hypotheses we have discussed.

#### HERBIVORES' EFFECTS ON PLANT BIOMASS ALONG A PRECIPITATION GRADIENT

In their reviews of grassland community structure, McNaughton et al. (1989, 1991) and Cyr and Pace (1993) also found a positive relationship between primary productivity and the amount of that productivity that was consumed by herbivores in grasslands. From this result, Cyr and Pace (1993) inferred that the magnitude of control by herbivores on plants should also increase with primary productivity, as predicted by consumer-controlled food chain models (see also Oksanen et al. 1981). However, the rate at which plant biomass is consumed by herbivores does not necessarily indicate control of plant standing crops by herbivores (Mitchell and Wass 1996). All three of the con-

ceptual models that we present (see *Models*) make predictions about how standing crops will vary with environmental variables (see Appendix), not about rates of consumption. In particular, if plants are able to compensate for losses to herbivores by regrowing tissues, the amount of plant biomass consumed by herbivores may have little to do with the controlling effects of herbivores on plants.

A more straightforward way to explore the effects of herbivores across a productivity gradient is to quantify the relative impact of herbivores on plant biomass from experimental studies. We used data compiled by Milchunas and Lauenroth (1993) from a number of experiments that excluded large mammalian herbivores. We searched all studies cited in this compilation, and included studies in our analysis that compared (1) the standing crops of plants in herbivore exclusion and control treatments, and (2) plant composition in these same treatments. All of the studies we included were performed in primarily grassland communities that contained <10% woody species biomass. Small mammal and insect herbivores were not manipulated in these studies. This provided a total of 54 studies from those listed in the appendix of Milchunas and Lauenroth (1993). We performed a meta-analysis (see Sarnelle 1992, Arnquist and Wooster 1995, Osenberg et al. 1997) to compare the relative impact of herbivores on plant biomass in each experiment using the unitless metric, "effect size."

$$\text{effect size} = \frac{[(\text{Plant Biomass without herbivores}) - (\text{Plant Biomass with herbivores})]}{(\text{Plant Biomass without herbivores})}$$

Results from the 54 studies measuring plant biomass with and without herbivores show that the effect size of herbivores significantly declined with increasing precipitation, although there was considerable scatter around this relationship (regression:  $y = -591x + 640$ ;  $N = 54$ ,  $df = 1, 52$ ,  $R^2 = 0.19$ ,  $P < 0.001$ ) (Fig. 2).

Small herbivores, such as insects and rodents, were not controlled in any of the experiments we reviewed here. Compensation by these small herbivores might have contributed to this pattern if consumption by small herbivores becomes more important, relative to herbivory by large mammals, at high productivity. The authors in all of the 54 studies included in this analysis subjectively considered the large-herbivore exclusions to be effective at eliminating a large proportion of total herbivore biomass. Nevertheless, small mammals and insects can sometimes have important effects on plant dynamics, even in the presence of large herbivores (Huntly 1991). Although there is no a priori reason to suspect that the importance of these smaller herbivores (relative to large herbivores) should vary systematically with precipitation, they may nevertheless have had higher than negligible effects on plant biomass in these experimental studies. It is not clear just how ro-

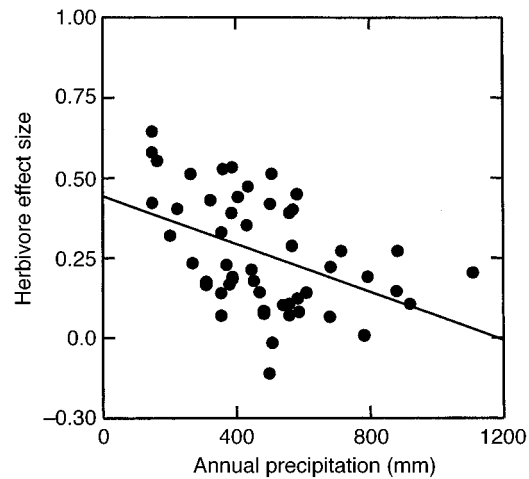


FIG. 2. The effect of herbivores on plant biomass (effect size) in relation to annual precipitation. Data are from 54 large-herbivore exclusion experiments listed in Milchunas and Lauenroth (1993) that measured plant biomass in the presence and absence of large herbivores. Regression:  $y = -591x + 640$ ;  $N = 54$ ,  $df = 1, 52$ ,  $R^2 = 0.19$ ,  $P < 0.003$ .

bust the relationship we observed would have been if such small herbivores had also been removed. However, Schmitz (1994, 1997) has shown similar patterns of the effects of insect herbivores with primary productivity, suggesting that the effects of small herbivores are likely to be similar to those of large herbivores.

As discussed above (see *Models*) and in the Appendix, the pattern of herbivore control along productivity gradients can also be used to discriminate among the conceptual models of food web structure. Resource-controlled models predict no relationships between the strength of consumer control and primary productivity, and thus are not likely to explain the results in Fig. 2. Similarly, consumer-controlled models predict that the effect size of the top consumer should increase with productivity, not decrease as in Fig. 2. However, if the importance of the herbivores' own predators increases with productivity, then the impact of herbivores might be expected to decrease in consumer-controlled models. Most of the studies in the review by Milchunas and Lauenroth (1993), and discussed here, were in areas where large predators capable of killing the large herbivores in these studies (e.g., deer, bison, buffalo, hippopotami) were rare or absent, either artificially or naturally. Thus, predators were unlikely to have caused the observed variations in the interactions among large herbivores and plants. Furthermore, the pattern of increasing herbivore biomass with increasing precipitation observed in Fig. 1 does not support the hypothesis that decreasing herbivory is due to unseen changes in predation pressure by carnivores. Nevertheless, predation by large carnivores has been shown in some instances to affect large vertebrate herbivore abundance (Sinclair and Norton-Griffiths 1982, McLaren

and Peterson 1994), and thus may have influenced the relationship between herbivores and plants. Finally, heterogeneous food web models can directly predict the result of decreasing consumer control of plants with increasing productivity. Specifically, heterogeneous food web models suggest that proportional herbivore effects on total plant biomass become smaller as the plant community shifts in favor of less susceptible species at high levels of primary productivity. Nevertheless, because the patterns observed in Fig. 2 (as with the patterns in Fig. 1) can result from more than one of the conceptual frameworks discussed thus far, we next use a final piece of evidence to further differentiate among the models.

#### HERBIVORE EFFECTS ON PLANT COMPOSITION ALONG A PRECIPITATION GRADIENT

A final pattern that we examined to differentiate among the conceptual models of food web structure in these grasslands was how plant species composition responded to herbivory along a productivity gradient. We used the same experimental herbivore exclusion experiments used in Fig. 2 and explored how plant species composition changed in the presence (controls) vs. the absence (exlosures) of large mammal herbivory. To examine how the effects of herbivory on plant species composition varied with environmental productivity, we used the same 54 large-herbivore exclusion studies in grasslands from the review by Milchunas and Lauenroth (1993) and discussed in *Herbivores' effects on plant biomass along a precipitation gradient*. In addition to measuring plant biomass with and without large herbivores, the studies included in this analysis also measured plant species composition in the controls and herbivore exlosures. Dissimilarity between treatments was calculated as 1-Whittaker's (1952) similarity index, which indicates the proportion of species not shared between the exclusion and control treatments. Results from the published studies indicate a significantly positive relationship between precipitation and plant species dissimilarity between exlosures and controls (regression:  $y = 461x + 282$ ;  $N = 54$ ,  $df = 1, 52$ ,  $R^2 = 0.21$ ,  $P < 0.0001$ ) (Fig. 3) (see also Milchunas and Lauenroth 1993).

The categories of models that emphasize resource control (category 1) or consumer control (category 2) assume that species can be reasonably lumped into homogeneous trophic levels within a food chain, and thus make no systematic predictions about how species composition should vary with environmental conditions. Similarly, the alternative hypothesis that the patterns shown in Fig. 2 are driven by unseen variation in carnivore effects on herbivore populations also makes no prediction as to how plant species composition should vary between controls and herbivore exlosures. However, heterogeneous food web models (category 3), inherently assume heterogeneity among species within trophic levels. More specifically, these

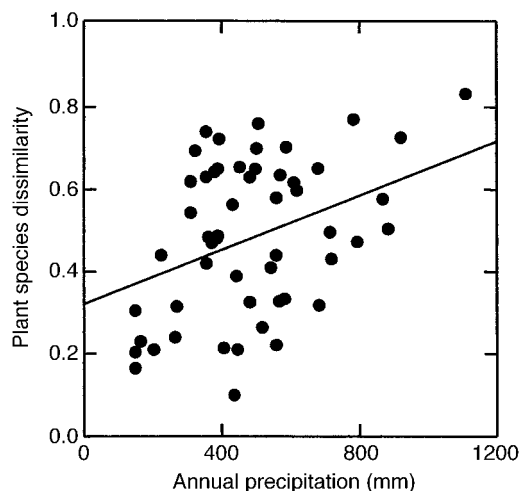


FIG. 3. The effect of herbivores on plant species composition, measured as plant species dissimilarity between plots exposed and free from herbivory, relative to annual precipitation. Data are from the same 54 exclusion experiments from Milchunas and Lauenroth (1993) used in Fig. 2. Regression:  $y = 461x + 282$ ;  $N = 54$ ,  $df = 1, 52$ ,  $R^2 = 0.21$ ,  $P < 0.0001$ .

models predict that species composition between herbivore removal and control treatments should be relatively similar at low productivity. However, as productivity increases, plant species composition should be highly divergent in the presence and absence of herbivores. At high productivity, in the presence of herbivores, plants that are more able to deal with herbivory (through some defense or tolerance) should predominate, but in herbivore exlosures superior competitive plant species should dominate. Heterogeneous food web models predict this pattern where species dissimilarity (i.e., the relative difference in species composition) between large-herbivore exclusion and control treatments increases with increasing productivity. Although other models explain changes in plant composition with productivity (Tilman and Pacala 1993), these models do not predict that herbivory will drive such compositional change.

An alternative explanation for the pattern in Fig. 3 is that as the effect size (on biomass) of herbivores increases, so should the effect on plant species composition (dissimilarity), because as more biomass is eaten by herbivores, the likelihood of a plant species being eliminated by herbivory should increase. However, because effect size decreases with increasing precipitation (Fig. 2), this explanation can not explain the pattern observed in Fig. 3. Furthermore, there was a negative relationship between herbivore effect size and plant species dissimilarity among treatments (regression:  $y = -0.56x + 0.61$ ;  $N = 54$ ,  $df = 1, 52$ ,  $R^2 = 0.24$ ,  $P < 0.001$ ) (Fig. 4), showing a pattern opposite to this alternative hypothesis; as herbivore effects on plant composition (dissimilarity) increased, their effects on plant biomass (effect size) decreased.

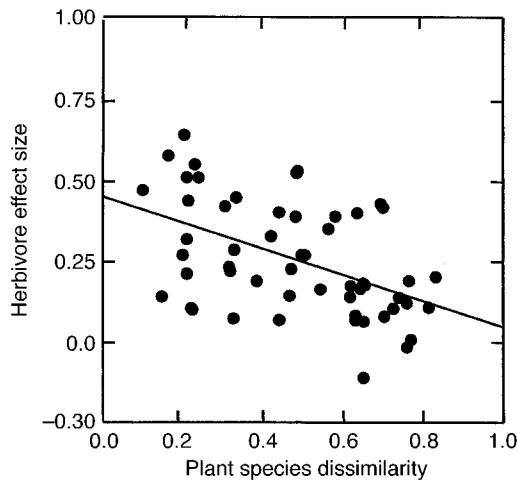


FIG. 4. The relationship between herbivore effects size (Fig. 2) and plant species dissimilarity (Fig. 3) from the 54 large-herbivore enclosure experiments reviewed in Milchunas and Lauenroth (1993). Regression:  $y = -0.56x + 0.61$ ;  $N = 54$ ,  $df = 1, 52$ ,  $R^2 = 0.24$   $P < 0.001$ .

#### DISCUSSION

Thus far, we have reviewed how plant and herbivore abundance, composition, and food web interactions vary along gradients of primary productivity. We have explicitly used this gradient analysis as a means to attempt to discern among three major classes of concepts that are currently the center of debate and controversy about the basic framework in which ecosystem variation and food web interactions should be placed. Specifically, we are interested in whether models of (1) resource-controlled food chains, (2) consumer-controlled food chains, or (3) heterogeneous food webs, are best able to explain the reviewed patterns.

The pattern in Fig. 1 shows that the biomass of all trophic levels increases with productivity, and is supported by the predictions of at least a subset of all of the conceptual frameworks. The pattern in Fig. 2 shows a decline in the effect size of herbivory with increasing productivity. This pattern can possibly be explained by either increasing levels of carnivory on herbivores, or a decrease in the susceptibility of plants to herbivores with productivity. We suggest that the former scenario is unlikely, given that the abundance of herbivores increases with productivity (Fig. 1) and that carnivores were typically rare in the ecosystems reviewed here. Thus, the pattern in Fig. 2 is most likely to be explained by heterogeneous food web models that consider variation in the susceptibility of plants to herbivores. Finally, the pattern in Fig. 3 shows that the change in plant species composition resulting from herbivory increases with productivity. Of the conceptual models discussed, this pattern is only predicted by heterogeneous food web models.

From our observations, we conclude that of the three conceptual frameworks—resource-controlled food

chains, consumer-controlled food chains, and heterogeneous food webs—the latter, more complex model, which allows heterogeneity within trophic levels and a strong interaction between resource control and consumer control as well as species compositional change, is most consistent with all of the patterns reviewed here. However, as with any correlational study, ours can only suggest evidence for and against the various hypotheses, and can not provide definitive proof. Thus, while we conclude that heterogeneous food web models appear to be best (of the three models) at describing all of the available evidence, we can not conclude that these grasslands are necessarily structured by models of this form.

One of the largest holes in the logic that grasslands follow the predictions of heterogeneous food web models is the fact that we have not been able to quantify the basic assumption of this model that plant species vary in their susceptibility to herbivores, and that this varies systematically along a primary productivity gradient. Specifically, heterogeneous food web models predict that plant composition will, under some conditions, shift from species that are more vulnerable to herbivory to less susceptible species. Ideally, we would like to quantify the defensive traits of the plant species involved in the compositional shifts observed in Figs. 3 and 4. However, this is a practical impossibility as plants can “defend” themselves from herbivores in a variety of different ways, such as chemical or structural defense, crypsis, or tolerance of herbivory. Furthermore, quantifying the defenses of plants is ambiguous when dealing with the global-scale patterns involving multiple herbivore and plant species under consideration. Because of these complexities, we can make no attempts to present evidence that the compositional shifts we have observed over this broad range of studies result directly from shifts in plant defenses. On local scale, however, studies have shown changes in plant composition resulting from defenses against herbivores in a manner similar to that predicted here (Bowers 1993, Schmitz 1994, 1997, Ritchie and Tilman 1995, Chase 1998, Ritchie et al. 1998). We believe our hypothesis that the plant species’ compositional shifts observed in Figs. 3 and 4 resulted from shifts from more to less susceptible plant species is a reasonable explanation on both empirical and theoretical grounds. Nevertheless, considerable evidence on the mechanisms leading to the decline in herbivore effects in Fig. 2 and the nature of the compositional change in Figs. 3 and 4 is necessary before more definitive conclusions can be reached.

Resources and consumers both play important roles in controlling plant biomass in grasslands. The results of this study suggest that plant compositional turnover in response to herbivory is also likely to influence grassland plants and trophic structure. We believe that much of the controversy surrounding the predominance of top-down or bottom-up forces in structuring grass-

lands might arise due to the different interpretations of different sorts of data. Experimental manipulations of herbivores in grasslands often support the top-down view of important consumer effects (Bowers 1993, Milchunas and Lauenroth 1993, Ritchie and Tilman 1995, Chase 1996, 1998, Ritchie et al. 1998, Carson and Root 2000). In contrast, natural patterns of standing crops and productivity typically support the resource-control view of concurrent increases of all trophic levels with productivity (Whittaker 1975, McNaughton et al. 1989, 1991). Here, we attempt to identify general patterns by synthesizing evidence from both types of studies in a global-scale review of many different grassland ecosystems.

From our analyses, it seems that the simple resource control models are insufficient in explaining patterns of herbivore control, especially the importance of herbivore control of plant biomass at low productivity (Fig. 2). Alternatively, the consumer control models do not satisfactorily explain joint herbivore and plant biomass responses to productivity (Fig. 1), nor do they explain the decline in herbivore control with increasing productivity (Fig. 2). We argue that these shortcomings in the simple models can be understood when the role of plant compositional turnover is considered, as in Figs. 3 and 4, and in conceptual models like the heterogeneous food web model (Holt et al. 1994, Leibold 1996).

The simpler resource-controlled and consumer-controlled models do not address such compositional change among the plant community, and therefore do not capture the important ways that compositional change alters patterns of control of plants along productivity gradients. Other models that include compositional change, besides the heterogeneous food web models described by us, might also explain some of these patterns. However, the variable effects of herbivores on overall plant biomass (Fig. 2) and composition (Fig. 3) along the productivity gradient seems difficult to explain without mechanisms closely related to those assumed by the heterogeneous food web hypothesis. Consequently, we argue that heterogeneous models of food webs better explain the qualitative patterns of abundance, interactions, and species composition in grassland ecosystems than do simpler models.

Real food webs, including those in grassland ecosystems, are much more complex than any of the models described here, including the more complex food web models that are supported by our data. Specifically, these food web models (see e.g., Holt et al. 1994, Leibold 1996, Grover and Holt 1998) emphasize only resource consumption and antiherbivory strategies, and an explicit trade-off between these processes. Heterogeneous food web models predict that vulnerable plants will dominate in low-productivity areas, whereas plants adapted to herbivory should predominate in highly productive areas. In addition, the models assume that adaptations against herbivores are general and equally

effective against all consumer species. It is not currently understood how adaptations against specific herbivores might modify the predictions of these models; particularly if there are trade-offs involved so that adaptations against one type of herbivory involve increased vulnerability to other types. Thus, these food web models can only be viewed as a caricature of a diversity of processes that structure ecosystems.

As with any generalized model, there are examples that do not conform to the assumptions or predictions of these models. For example, any naturalist can point to specific examples of species that are well defended against predators, but occur in low productivity habitats (e.g., spiny plants that live in arid, low productivity areas) or examples of highly susceptible prey that live in high productivity areas (e.g., highly susceptible understory plants in forests). Also, there are many examples of consumers that specialize on presumed "well-defended" prey, but do not appear to be inhibited by such "defenses." In addition, the heterogeneous food web models that we discuss make an explicit assumption that prey species incur a cost by having adaptations against predators. There are many reasons to expect that costs do exist; however, studies designed to explicitly examine costs have been equivocal (Bergelson and Purrington 1996).

We do not intend to downplay these very important observations that on the outset seem to violate the assumptions and predictions of simple analytical models, such as the simple food web model discussed here. However, we wish to emphasize the differences in scale on which these observations are based. Our review deals with patterns on a global scale, in which hundreds to thousands of species, interactions, and other complexities are imbedded. With all of these complexities, the assumptions and predictions of the very simplistic modeling frameworks discussed here can not hold under all (or even many) conditions. Instead, significant patterns do emerge from our large-scale review. These patterns suggest that general patterns may exist despite all of the local-scale complexities. Exceptions to the assumptions and predictions of food web models are likely due other ecologically important processes (such as colonization limitation, nutrient ratios, and so forth), which contribute to the dynamics of the component species. We believe that the utility of simplified conceptual frameworks, such as models of heterogeneous food webs with simple trade-offs, lies in their ability to make broad predictions about the overriding patterns along large-scale gradients such as the productivity gradient described here. Thus, even though the relationships between experimental herbivore effects and precipitation were significant (Figs. 2–4), there was considerable variation around these relationships ( $R^2 = 0.18\text{--}0.21$ ). The models we examined make predictions about qualitative patterns (i.e., significant slopes), and not on the quantitative variation around the relationships (i.e., proportion of variance explained by the

$R^2$  statistic). This sort of generalized modeling framework can not predict the exact locations or responses of every species and interaction. Rather, we hope that these generalized models can elucidate some large-scale patterns upon which we can begin to search for mechanisms that are more specific and reasons for deviations in the patterns. Such deviations suggest that processes other than the simplified trade-off scenario described in the heterogeneous food web models are also important in structuring grassland ecosystems and that much further study to elucidate these complexities is warranted.

#### CONCLUSIONS

The evidence that we present suggests that the control of trophic structure in grasslands by herbivores is mediated through their effects on plant species composition (see also Olff and Ritchie 1998). Models of these effects, though simplistic, indicate that apparently contradictory lines of evidence (such as concurrent increases in biomass across trophic levels in the presence of strong consumer effects) can be synthesized. The interaction of consumers and resources in determining the distributions, abundances, and composition of species in food webs has been an area of considerable research and controversy. Lake ecosystems have historically been a major focus in studies of food web interactions, in part due to their ease of manipulation and quick response to experimental manipulations (Carpenter and Kitchell 1993, Brett and Goldman 1996, 1997, Leibold et al. 1997). Nevertheless, a number of studies have been performed in other systems, grasslands in particular, which have very different environmental properties.

The lack of consistent evidence for strong food web interactions in terrestrial systems have led some to suggest that features of terrestrial systems are fundamentally different from those of aquatic systems, and that processes structuring terrestrial communities might be very different (Strong 1992, Hairston and Hairston 1993, Polis and Strong 1996). Strong's (1992; see also Polis and Strong 1996) hypothesis is that terrestrial systems tend to be more diverse, and thus more complex, than the aquatic systems that have supported strong food web interactions and trophic cascades. He further argues that this difference in the complexities of the two systems is likely to cause the differences in the evidence for trophic cascades in these systems; more complex systems are less likely to show strong trophic cascades than less complex systems. We agree that the physical properties of disparate systems, particularly terrestrial vs. aquatic systems, can cause considerable variation in their ecological processes. We further agree that the complexity of systems has much to do with the strengths of trophic cascades that will be observed. We disagree, however, that terrestrial and aquatic systems should a priori differ in their complexity. Many aquatic communities have on the order

of hundreds of algae species, a similar order of magnitude of zooplankton species, dozens of zooplanktivorous fishes and invertebrates, and several species of top predators (Carpenter and Kitchell 1993). These systems are at least as complex as most terrestrial food webs (see Siemann [1998] for a representatively speciose grassland food web), and there do not seem to be any systematic differences in these patterns of complexity (J. M. Chase, *unpublished data*). Furthermore, a number of studies in terrestrial communities have shown strong consumer effects and trophic cascades (Kajak et al. 1968, Schoener and Spiller 1987, Spiller and Schoener 1990, 1994, Bock et al. 1992, Marquis and Whelan 1994, Dial and Roughgarden 1995, Krebs et al. 1995, Chase 1996, 1998), in addition to strong resource effects (McNaughton et al. 1989, 1991), and their interaction (Schmitz 1994, 1997, Ritchie and Tilman 1995, Ritchie et al. 1998), showing qualitative similarity to many aquatic systems.

We suggest that while there do not appear to be systematic differences in the complexity between terrestrial and aquatic systems, differences in complexity within both terrestrial and aquatic systems does lead to important variation in the relative roles of resource and consumer control in these systems. From this study, we have shown that at low productivity, the effects of consumers are quite large, while at higher productivity, herbivore effects are much weaker, and that this is likely to result from the fact that compositional turnover of plant species becomes more likely with increasing productivity (Figs. 2 and 3). Furthermore, we have used similar lines of evidence to document qualitatively similar patterns in temperate lake ecosystems (Leibold et al. 1997), suggesting that similar processes of trophic structure, as mediated by interactions between consumer and resource control, as well as species compositional turnover, may be acting in these very different types of systems.

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## APPENDIX

In this appendix, we provide a brief overview of the basic model frameworks we discussed in text, with particular reference to the effects of increasing primary productivity on the response variables of herbivore and plant standing crops, effects of herbivores on plant abundance, and effects of herbivores on plant composition.

*Resource-controlled food chains*

A variety of theoretical models have been developed that emphasize resource-limited processes, such as “donor-controlled” (DeAngelis 1975, 1992, Pimm 1982, Chase 1996), “food-limited” (Schmitz 1992, 1993), or “ratio-dependent” (Arditi and Ginzburg 1989) models. These models include varying degrees of consumer effects, but resources have overriding importance. For mathematical simplicity, we consider a three species dynamical food chain consisting of basal resources ( $R$ ), consumer-prey ( $N$ ), and top predators ( $P$ ). All three species are limited by the amount of food available to them, but species have no dynamical influence on the resources they consume. Given these properties, an appropriate caricature of this system may take the following form:

$$\begin{aligned} \frac{dR}{dt} &= bS - cR & \frac{dN}{dt} &= b'cR - c'N \\ \frac{dP}{dt} &= b''c'N - c''P \end{aligned} \quad (\text{A.1})$$

(modified from Chase [1996]).  $S$  is the total supply of  $R$ 's resource (e.g., rainfall),  $b$  refers to the conversion factor of eaten food into new consumers, and  $c$  refers to some density-independent loss of individuals that become available (donated) for consumption by their consumers. Following convention (Holt et al. 1994), parameters without primes ( $a$ ,  $b$ ,  $c$ ) are those of the resource population ( $R$ ), parameters with primes ( $a'$ ,  $b'$ ,  $c'$ ) are those of the consumer-prey population ( $N$ ), and parameters with double primes ( $a''$ ,  $b''$ ,  $c''$ ) are those of the top predator ( $P$ ) population.

To derive predictions from this model that can be compared with data from grassland patterns, we explore how the equilibrium abundance of each species will change as environmental productivity increases (i.e.,  $S$  increases). First, we set the dynamics of each species equal to zero ( $dX/dt = 0$ ), and solve for the equilibrium density of each species, which gives

$$R^* = \frac{bS}{c} \quad N^* = \frac{b'cR}{c'} \quad P^* = \frac{b''c'N}{c''}. \quad (\text{A.2})$$

From these equilibrium densities, it is easy to see that with increasing  $S$ , and thus increasing environmental productivity, the abundance of  $R^*$  increases (because  $S$  is in the numerator of  $R$ 's equation), which consequently causes increases of  $N^*$  (because  $R$  is in the numerator of  $N$ 's equation) and  $P^*$  (because the  $N$  is in the numerator of  $P$ 's equation). Thus, the abundance of all trophic levels increases with environmental productivity. Furthermore, since the abundance of each consumer does not appear in the equations for its resource, this model predicts no variation in consumer effects with variation in productivity (i.e.,  $N^*$  is the same with or without the presence of  $P$ ). Finally, this type of model assumes that there is no variation in species' traits within trophic levels, and that all species can reasonably be approximated as being identical. Given this, resource-controlled food chain models predict no relationships between environmental productivity and species composition.

*Consumer-controlled food chains*

Consumer-controlled food chains are similar to those discussed above. However, in this case, consumers have an effect on their resource population dynamics determined by the resource consumption rate,  $a$ :

$$\begin{aligned} \frac{dR}{dt} &= S - R(a'N - c) \\ \frac{dN}{dt} &= N(a'b'R - a''P - c') \\ \frac{dP}{dt} &= P(a''b''N - c'') \end{aligned} \quad (\text{A.3})$$

where all of the remaining parameters are as above, except that here,  $c$ 's refer to a density independent loss rates of individuals that are not consumed by predators.

In this case, the equilibrium densities of the three species are given by

$$R^* = \frac{Sa''b''}{a'c''} \quad N^* = \frac{c''}{a''b''} \quad P^* = \frac{a'b'R - c'}{a''}. \quad (\text{A.4})$$

Here,  $R$  increases with  $S$ , and  $P$  increases with  $R$ , but  $N$  does not vary with environmental conditions. Thus, in consumer-controlled food chains, the abundance of species in adjacent trophic levels should be decoupled along a productivity gradient (Oksanen et al. 1981, Holt et al. 1994); that is, one species increases while the other remains constant. Abrams and Roth (1994) present a more limited case of this type of model, when the dynamics of the system are inherently nonlinear, that can lead to patterns of increasing mean abundance of adjacent trophic levels with increasing productivity.

A second pattern that can be evaluated from field experiments, and that can be predicted with these consumer-controlled models is how the overall effect of consumers varies with environmental productivity. Recall from above, that in resource-controlled food chains, consumer effects did not appear in the dynamics for its resources, and thus do not vary with environmental conditions. In consumer-controlled food chains, a different pattern is predicted. Here, the abundance of consumer-prey ( $N$ ) can be calculated in the presence and absence of predators to see how the effects of predators might vary with environmental conditions. In the presence of predators,  $N^*$  is given above (Eq. A.4), but in the absence of predators,

$$N^{**} = \frac{S - c}{a'}. \quad (\text{A.5})$$

The effect ( $E$ ) of predators on  $N$  is then given by calculating  $E = N^{**} - N^*/N^{**}$ , which gives

$$E = \frac{b''c'' + 2a''cS - a''c^2 - a''S^2}{aa''c - aa''S}. \quad (\text{A.6})$$

Because the  $a$ ,  $b$ , and  $c$  parameters are always comparatively small (i.e.,  $<1$ ), they are negligible relative to the  $S$  terms. The negative  $S^2$  term in the numerator will increase faster with  $S$  than will the negative  $S$  term in the denominator; thus, overall,  $E$  will increase with  $S$ . That is, as productivity increases, the overall impact of predators on prey dynamics will also increase (see also Sarnelle 1992). Furthermore, this pattern will still hold in the nonlinear version of this model presented by Abrams and Roth (1994).

Finally, as with resource-controlled food chains, consumer-controlled food chains also make a simplifying assumption that the complexity of trophic levels can be reasonably approximated as a food chain, rather than a food web. That is, species within trophic levels are similar enough to each other that they can be reasonably lumped into single species equations (Oksanen 1991). Thus, these sorts of models assume that there should be no significant variation in prey species composition along environmental or consumer gradients.

*Food webs with heterogeneous trophic levels*

For a more detailed derivation of these models, see Holt et al. (1994) and Leibold (1996). Essentially, these food web

models relax the assumption that all species within a trophic level can be approximated as identical, and instead, they assume that individual species vary in several traits related to their resource consumption and resistance to predation. In order to make the predictions of this model transparent, we assume that the consumer–resource trophic level ( $N$ ) consists of only two species that exhibit opposite ends of the trait continuum, but consume the same resources, and are consumed by the same predator. Thus, the two species trade off in their resource consumption ability (i.e., exploitative competitive ability) vs. their ability to avoid or resist predators. That is, if prey species 1 ( $N_1$ ) is a better resource consumer ( $a_1' b_1' > a_2' b_2'$ ), then prey species 2 ( $N_2$ ) is less susceptible to limitation by predators ( $a_1'' b_1'' > a_2'' b_2''$ ). These models assume that there is turnover between prey species with increasing productivity. At the lowest productivity,  $N_1$ , the better competitor/worse predator defended species, dominates the prey community, at intermediate productivity both prey species coexist, and at high productivity,  $N_2$ , the worse competitor/better predator defended species, dominates. Because of this shift in species composition, there is not a simple algebraic solution to show how prey and predator abundance and predator effect size should vary with productivity. Instead, we present a brief verbal argument; readers who want more information and detail should see Holt et al. (1994), Grover (1995), and Grover and Holt (1998), and particularly Leibold (1996) for considerable detail and proof for these claims.

As resource productivity increases, standing crops will vary such that (1) at low productivity, species 1 will dominate, with a given equilibrium biomass of both prey and predator. (2) At intermediate productivity, species 1 and 2 will coexist. Here, because of the presence of species 2, the abundance of prey will be higher than when species 1 occurred alone. Furthermore, the abundance of the predator will also increase, because of the added productivity of both prey species. Finally, (3) at high productivity, prey species 2 will exist at a higher equilibrium biomass than in (1) and (2), because it is

better defended from predators. In addition, the total abundance of predators will also be higher than in (1) and (2), despite the increased per capita defense of the prey, because of the increase in total prey abundance. Thus, with increasing productivity, the overall biomass of both prey and predator trophic levels should increase.

Consumer effect size on prey can be analyzed in a similar manner with increasing primary productivity. (1) At low primary productivity, prey species 1 dominates, but is highly susceptible to predators. Here, the relative effect of consumers will be large. (2) At intermediate productivity, if the relatively more defended prey species is consumed less than the increased effect on the less defended species (i.e., the more defended prey species is able to compensate for losses of the less defended prey species), then the overall effect size of predators on prey species  $N_1$  and  $N_2$  will be less than in (1). (3) At high productivity, the consumer effect on the more defended prey,  $N_2$  will be lower than that in (2). Thus, here, the overall pattern is that the overall effect size of consumers on prey species should decline with increasing productivity.

Looking at these results conversely, we can also make predictions about how prey species composition should vary with and without predators across a productivity gradient. (1) At low productivity, prey species 1 always dominates, but is susceptible to predators. Thus, prey composition is the same with and without predators (dissimilarity = 0). (2) At intermediate productivity, prey species 1 and 2 can coexist in the presence of predators through a mix of resource and apparent competition, but in their absence, only prey 1, the superior competitor, will exist. Thus, prey species composition shifts such that dissimilarity = 0.5 in the presence and absence of predators. (3) Finally, at high productivity, only the well-defended prey species 2 exists in the presence of predators, but the superior competitive prey species 1 exists in the absence of predators. Here, prey composition completely shifts with predator removal, and species dissimilarity = 1. Thus, from low to high productivity, the relative difference in species composition with and without predators should increase.