

Compensation: an alternative method for analyzing diversity-productivity experiments

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Although recent experimental results demonstrate a positive effect of diversity on primary productivity, the interpretation of these experiments has been controversial, creating a need for new methods of analysis. The methods developed in response to this need all use the production of individual species grown in monocultures to calculate the expected production of each species mixture, then analyze departures from these expectations as a function of species richness. We propose an alternative method that treats the same assembly experiments as species removals, and calculates the expected production of each mixture based on the production of individual species when grown together in the full community (the experimental mixture containing all species in the pool). Using the observed production of the full community, and the observed and expected productions of less diverse mixtures, we calculate an index of compensation that measures the degree of functional recovery following species loss. To explore whether losses of dominant versus subordinate species have different ecosystem effects, we suggest a multiple regression approach that tests the influence of both species richness and expected production on compensation. If compensation varies with species richness or expected production consistently in many experimental systems, then we may be able to predict the ecosystem effect of different types of extinctions.

While existing monoculture approaches more directly test hypotheses about complementary resource use, the compensation approach offers two advantages: 1) it is more appropriate for testing how extinctions will affect ecosystem function, and 2) it may provide an important link between assembly experiments in artificial communities and removal experiments in natural systems.

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Recent experiments using artificial communities appear to show that primary productivity increases with increasing species richness (Naaem et al. 1994, 1996, Tilman et al. 1996, Hector et al. 1999, Spehn et al. 2000, Bullock et al. 2001, Engelhardt and Ritchie 2001, Mulder et al. 2001). However, the interpretation of these results has been extremely controversial. The strongest criticisms assert that hidden treatments or statistical artifacts produced the observed, positive diversity-productivity relationship (Aarssen 1997, Huston 1997, Wardle 1999). For example, as the number of species in a mixture increases, the probability of the

mixture including a highly productive species increases as well. This “sampling effect” implies that the positive diversity-productivity relationship is driven by the presence or absence of key species, rather than by species richness. Loreau (1998a, 2000) showed that for a positive sampling effect to occur not only must a highly productive species be present in a mixture, it also must establish some degree of dominance through shifts in abundance. By contrast, the sampling effect, termed the “selection effect” by Loreau, can be negative when unproductive species, rather than productive ones, increase in relative abundance. Diversity may also influ-

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ence productivity through a second set of mechanisms that involve facilitation or niche differentiation, and improve the collective performance of a community (Tilman 1997, Loreau 1998a). Separating selection effects from these “complementarity effects” has become an important focus in biodiversity research (Hector 1998, Loreau 1998b, Loreau and Hector 2001).

The objective of diversity-productivity experiments is to test the null hypothesis that species richness has no effect on productivity. While the original, controversial analyses directly tested the response of production to variation in richness, subsequent methods (Garnier et al. 1997, Wardle et al. 1997, Hector 1998, Hooper 1998, Loreau 1998b, Loreau and Hector 2001) adopt a variety of null hypotheses in order to calculate the expected production each mixture, and then analyze how deviations from the expectations vary with species richness. For example, the “overyielding” index (Garnier et al. 1997, Hector et al. 1999) uses the maximum single monoculture performance of all component species in a mixture as the expectation, while an index of Relative Yield Totals (Hooper 1998) is based on the mean of the monoculture performances of component species. Only the most recent method (Loreau and Hector 2001) clearly partitions and quantifies selection and complementarity effects. All of these methods calculate the expected production of each mixture based on the monoculture performance of its component species. While this approach effectively tests hypotheses about complementary resource use, and thus improves our understanding of the potential impacts of decreases in biodiversity, it does not directly test the implicit question: how will species loss affect ecosystems?

Species removal experiments offer a more appropriate test of the effects of species loss on ecosystem function. However, separating the effects of species loss from the inevitable disturbance required to remove or artificially kill plants can be problematic. We propose analyzing the same assembly experiments previously discussed as if they were species removals by using the mixtures that contain all species, rather than monocultures, as the basis for calculating the expected production of less diverse mixtures. Our approach has two advantages: first, because it focuses on species deletions rather than additions, it directly tests the effects of extirpation on ecosystem function. Second, by attacking the problem from a species removal point of view (McNaughton 1983, Sala et al. 1996), we have produced a method that is appropriate for analyzing data from both species addition experiments in artificial systems and species removal experiments in natural ecosystems, where growing every species in monoculture is essentially impossible. The availability of comparable results from both types of experiments will increase our confidence in any emerging trends.

We wish to emphasize that these two approaches are, appropriately, complementary. The monoculture ap-

proach, which treats the problem from a species addition perspective, has the advantage of information on the intrinsic productivity of each species in the absence of interspecific competition, allows testing hypotheses about complementary resource use and niche partitioning, and may have important applications in restoration and invasion ecology. The full community approach, by contrast, lacks any information on the intrinsic productivity of each species. Instead, it contains information on the dominance hierarchy among species, the end result of competitive interactions. This information allows us to compare the ecosystem effects of removing dominant versus subordinate species, and perhaps identify the mechanisms maintaining dominance in the community.

Our first objective is to define and interpret an index of “compensation”, illustrated using hypothetical numerical examples. Our second objective is to propose a multiple regression analysis of this compensation index to explore how the loss of dominant or subordinate species may influence the ability of a community to replace lost function. In addition, we suggest a method to explore the relative contributions of dominant and subordinate species to total compensation. We conclude by discussing the potential for using the compensation index to compare results from experiments in artificial and natural systems.

Compensation

In order to use diversity-productivity experiments to study the functional impacts of extinction events, we need an index of production based on species removals, rather than species additions. To this end, we define compensation as the degree to which a community recovers productivity lost through species removals. The first step in calculating compensation is describing the dominance-diversity curve of the experimental community. Natural plant communities typically display extremely skewed dominance-diversity curves (Grime 1998). A few productive species account for the vast majority of production while many species, scattered across the tail of the curve, contribute very little to production, typically measured in terrestrial communities as annual biomass increment (Fig. 1A). We assume that dominance-diversity curves are meaningful descriptors of experimental communities as well. For this to be true, the dominance hierarchy must remain relatively constant across experimental replicates containing all species in the pool. Our assumption seems safer for experimental terrestrial plant assemblages, where a few fast growing species should consistently dominate most plots, than for aquatic systems where trophic cascades can produce dramatically different communities (Polis 1999).

Once the dominance-diversity curve for the whole community is constructed, we can calculate the expected production following species loss. Our expectation, or null hypothesis, is based on the Sala et al. (1996) model that assumes no replacement in function following the loss of a species, at least in the short term. In other words, the production of each remaining species remains constant following the removal of a species. The expected total community production, therefore, is simply the production of the original, full community, minus the contributions (in the full community) of the species we have omitted (Fig. 1B). For example, if Species A produces 10 g m^{-2} and Species B produces 5 g m^{-2} in the full community, the expected production of a community containing only Species B will be 5 g m^{-2} . This is not a prediction of how communities will actually respond, but simply a null hypothesis. We are not interested in rejecting this null

hypothesis, but in quantifying how departures from it vary with the number of species removed.

The next step is to compare the expected production of the “depleted” community with its observed production. The remaining species may take advantage of resources formerly used by the now missing species, resulting in increases in the production of individual species relative to their performance in the full community. The sum of all individual species responses determines compensation. We can define an index of compensation, C , as the difference between the observed and expected biomass divided by the expected loss of biomass following extinction, or more formally:

$$C = \frac{\sum_i^n (O_i - E_i)}{\sum_i^N E_i - \sum_i^n E_i}$$

where O_i is the observed yield of species i in the depleted community, E_i is the expected yield of species i in the depleted community (equal to the yield of species i in the full community), n is the set of species in the depleted community, and N is the set of all species in the full community.

Compensation can range from less than zero to greater than one. Partial compensation occurs for values of C between zero and one, and indicates a net loss of production relative to the full community, but some recovery of function (Fig. 2A). Compensation equals one when no change in community production follows species loss (Fig. 2B). Overcompensation, or values of C greater than one, indicates the removal of negative interactions or interference following extinction and a resulting increase in net production (not illustrated). Negative values of C , occurring when the community's observed production is less than expected (Fig. 2C), would indicate the loss of a positive interaction or facilitation that existed in the full community, such as the extinction of a nitrogen fixing species.

Our method does not separate the distinct but simultaneous mechanisms that determine net compensation (Fig. 3). The selection effect could have either a positive or negative effect on compensation, depending on whether high or low productivity species establish dominance. Niche differentiation should push compensation towards zero: the more complementary that species are in their resource use, meaning the less their niches overlap, the more difficult it will be to compensate for species loss. In contrast, increases in redundancy cause increases in compensation (Walker 1992). The loss of facilitation will have a negative effect on C , while the loss of interference will have a positive effect. Changes in resource use efficiency (Nijs and Impens 2000) can influence C in either direction.

Comparing compensation to indices derived using the monoculture approach is difficult because of the

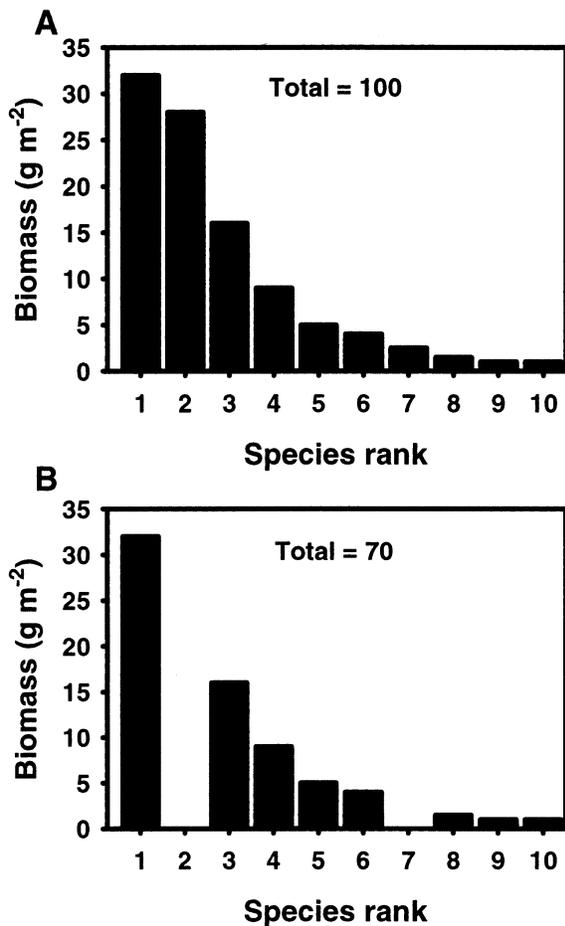


Fig. 1. A) Hypothetical dominance-diversity curve for an experimental community. Total biomass production of the community is the sum of each individual species' biomass. B) Expected biomass, based on the null hypothesis of perfect complementarity, following the loss of species 2 and 7. The biomass of each remaining species is the same as in A.

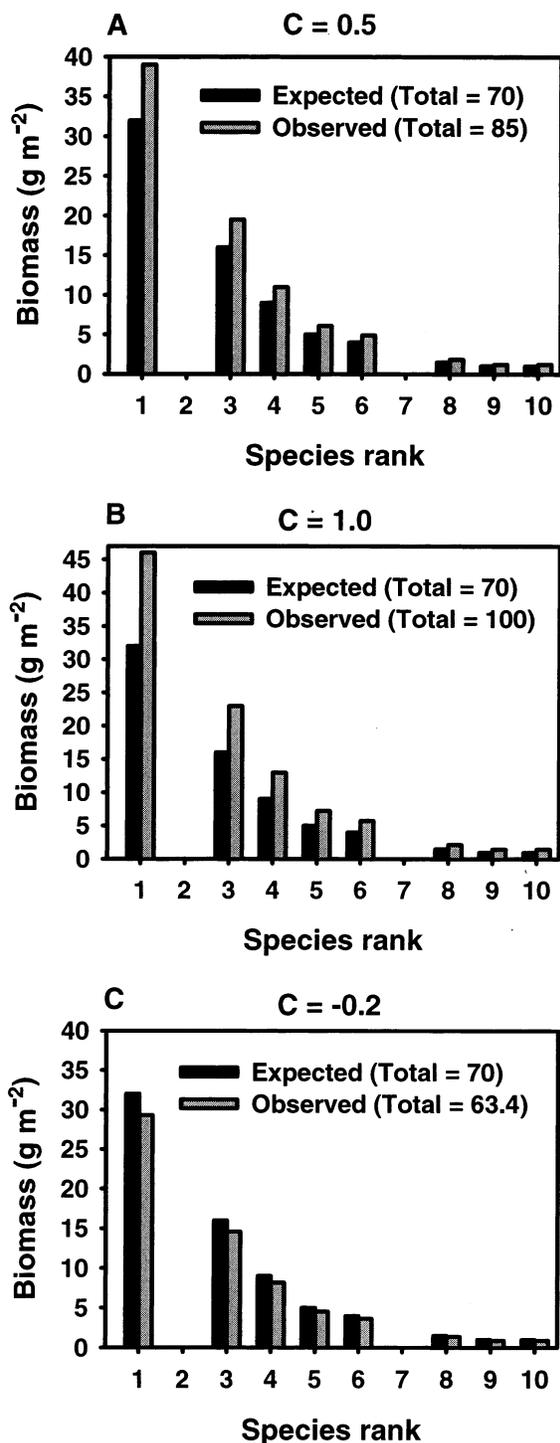


Fig. 2. Compensation is calculated by comparing observed and expected biomass, demonstrated with the assemblage shown in Fig. 1B. Hypothetical illustrations of A) partial compensation ($0 < C < 1$), B) full compensation ($C = 1$), and C) undercompensation ($C < 0$). In all cases shown, the proportional changes in each species' biomass, relative to expected, are equal.

methods' contrasting null hypotheses. Monoculture approaches assume zero complementarity in resource use, whereas the compensation index uses a null hypothesis of perfect complementarity. Thus, the two approaches always generate different values of expected production for a given assemblage (see Appendix). Whether one approach is more appropriate than the other depends on the objectives of the study. Hypotheses about complementarity should be tested using an index based on monocultures; questions about extinction impacts in complex communities should be tested using compensation.

Multiple regression analysis of compensation

Diversity-productivity experiments have used univariate regression analysis to evaluate diversity effects. In the original analyses, production was modeled as a function of species richness. The subsequent monoculture methods model deviations from null hypotheses as a function of species richness. Our index of compensation could be analyzed the same way. This univariate approach, however, ignores important information contained in the dominance-diversity curve that we constructed for the full community. Specifically, we can ask whether the loss of a dominant species has a different effect on compensation than loss of a subordinate, or whether the loss of three species composing 30% of full community biomass is equivalent to losing one species that represents the same biomass. To explore these questions, we need to model compensation as a function of both species richness and expected production.

How can we consider species richness and expected production as independent variables when they are positively correlated? After all, if no species are lost, we expect 100% of full community production, and if all

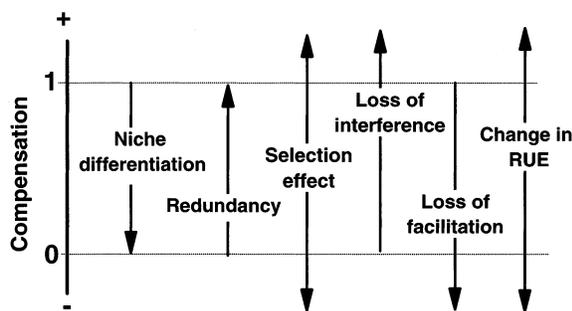
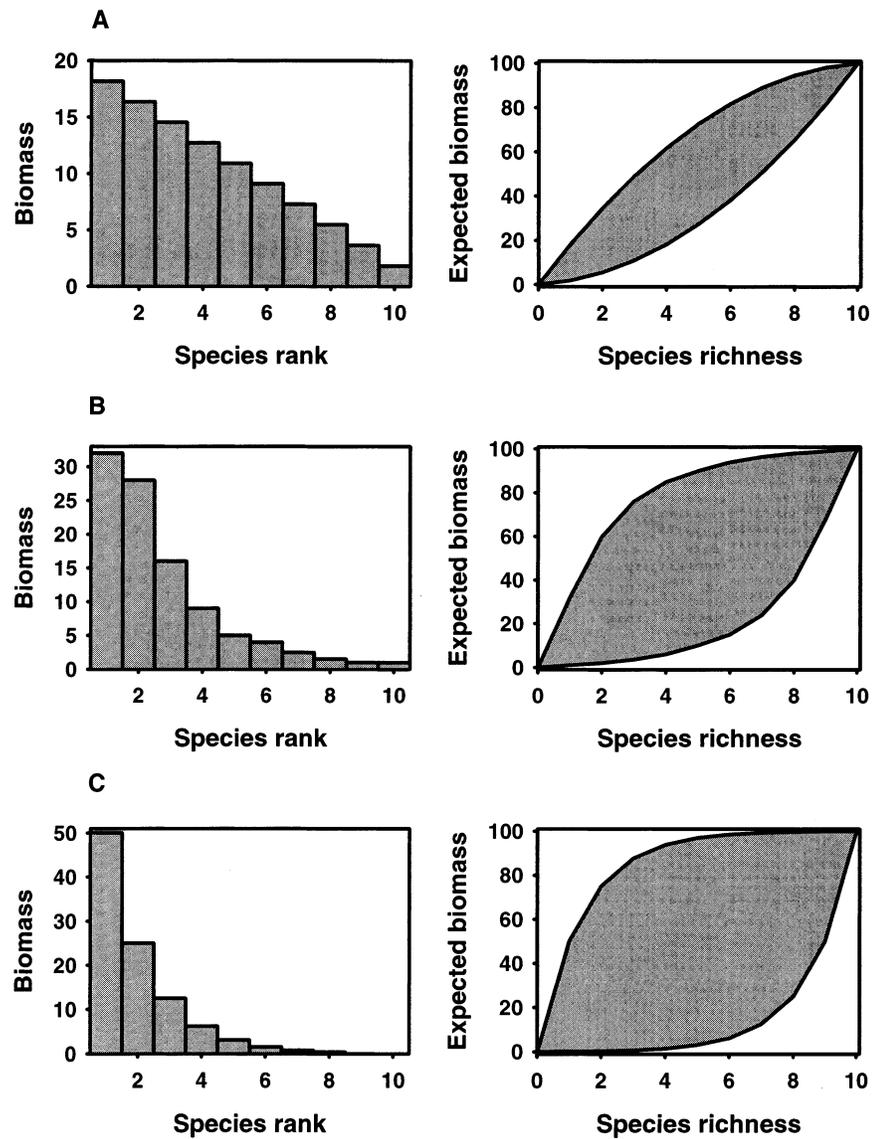


Fig. 3. Compensation represents the net effect of a number of different mechanisms. In the absence of any other effects, complete niche differentiation would suppress compensation to zero, while redundancy in the use of space would push compensation towards a value of 1. At least one of the other mechanisms would be required to explain values of compensation less than zero or greater than one. "RUE" is resource use efficiency.

Fig. 4. With increasing skewness in the dominance diversity curve, the degree of correlation between species richness and expected biomass decreases, and the area of testable parameter space increases. A) A community with a linear dominance-diversity curve on the left, and on the right, all its possible combinations of species richness and expected biomass shown in the shaded area between the two curves. B) The community used in the previous examples on the left, and its corresponding parameter space (shaded) on the right. C) A community with an exponential dominance-diversity curve and its corresponding parameter space.



species are lost, we expect zero production. But the degree of correlation depends on the skewness of the dominance diversity curve. Sala et al. (1996) hypothesized that ecosystem response to species loss depends on whether species are lost in descending or ascending order with respect to the dominance-diversity curve. Under our null hypothesis of perfect complementarity, maximum expected production (minimum loss) for a given level of species richness occurs when species are deleted in ascending order, from least to most productive. The minimum expected production is obtained when species are deleted in descending order, beginning with the most productive species. These two curves mark the boundary for all possible combinations of species richness and expected production. Each unique species mixture corresponds to a point in the parameter

space defined by the boundary curves. A linear dominance-diversity curve produces a stronger correlation between species richness and expected production, and a narrower parameter space (Fig. 4A); more skewed distributions create a wider parameter space, and more independence between richness and expected production (Fig. 4B, C).

Once we have calculated compensation for each species mixture, we can search for systematic variation in compensation with variation in both species richness and expected production. We can combine a moderate loss of species richness with little change in expected production by deleting subordinate species. The remaining dominant species need only increase production marginally relative to their full community performance to compensate for the loss of the subordi-

nates (Fig. 5A). To combine little loss of richness with a large loss in expected production, we delete a few dominant species. The remaining species must increase production dramatically to compensate for the loss of dominants (Fig. 5B). When large loss in richness combines with a large loss in expected production, even greater increases in production are required of the remaining species to reach the same level of compensation (Fig. 5C). The responses we illustrate in Fig. 5 represent only a sample of many possible outcomes. Because of the potentially significant correlation between species richness and expected production, caution should be used when regressing compensation on both these variables simultaneously. Regression results may be sensitive to the order in which the independent variables are entered or the procedure used for calculating sums of squares.

Compensation by dominant versus subordinate species

In the previous section we presented a method for determining whether the loss of dominant or subordinate species has different effects on a community. Of equal importance is whether the dominant and subordinate species that remain following extinction contribute proportionally to the community's ability to compensate. Since in most communities subordinate species represent the vast majority of species richness, their functional role is of great interest to ecologists (Grime

1998, Gibson et al. 1999, Murray et al. 1999). The ability of subordinate species to compensate may depend on the mechanisms maintaining dominance in the community. We suggest a continuum defined on one end by intrinsic differences among plant species and on the other end by competition. When interspecific competition is minimal and dominance is the result of differences in size, physiology, or adaptation to local conditions among species, subordinates will not be able to compensate for the loss of dominants – they simply lack the physiological capacity to dramatically increase production despite increased resource availability. At the other extreme, where differences among species are minimal (i.e. redundancy) and interspecific competition maintains dominance, we should expect greater compensation following the loss of the original dominant species (Walker 1992). Released from competition, the remaining species will be able to utilize resources previously captured by the dominants and increase production dramatically, “sliding up” the dominance-diversity curve. In natural communities, we should expect both intrinsic differences among species and interspecific competition to play a role in maintaining dominance.

While the compensation index measures the community-level response, to compare the importance of dominant and subordinate species we must analyze individual species responses. We suggest regressing the observed/expected production of each species on its expected production. This approach is analogous to Loreau and Hector's (2001) use of covariance to quantify shifts in the relative yield of species in mixtures

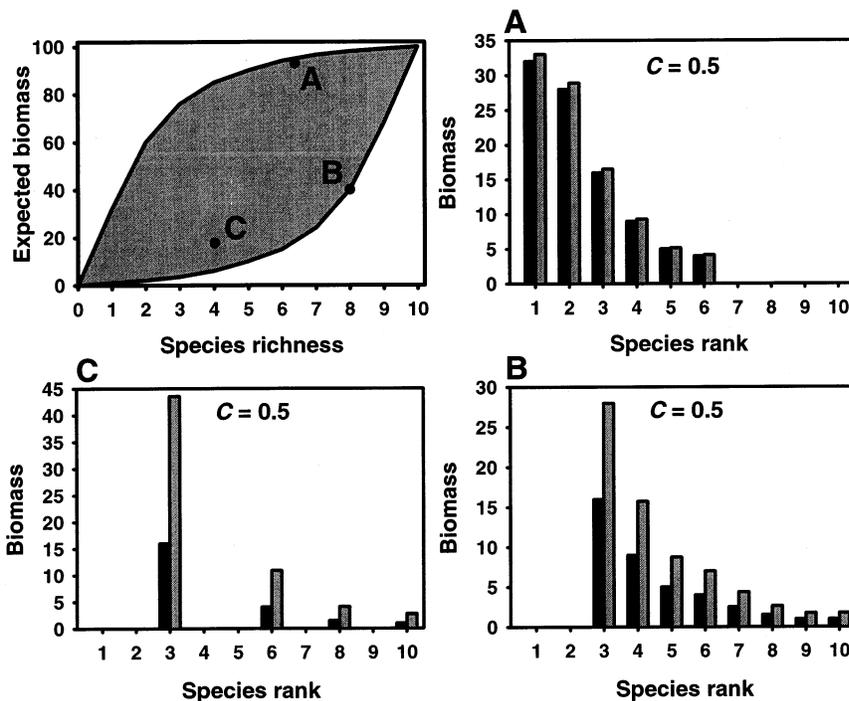
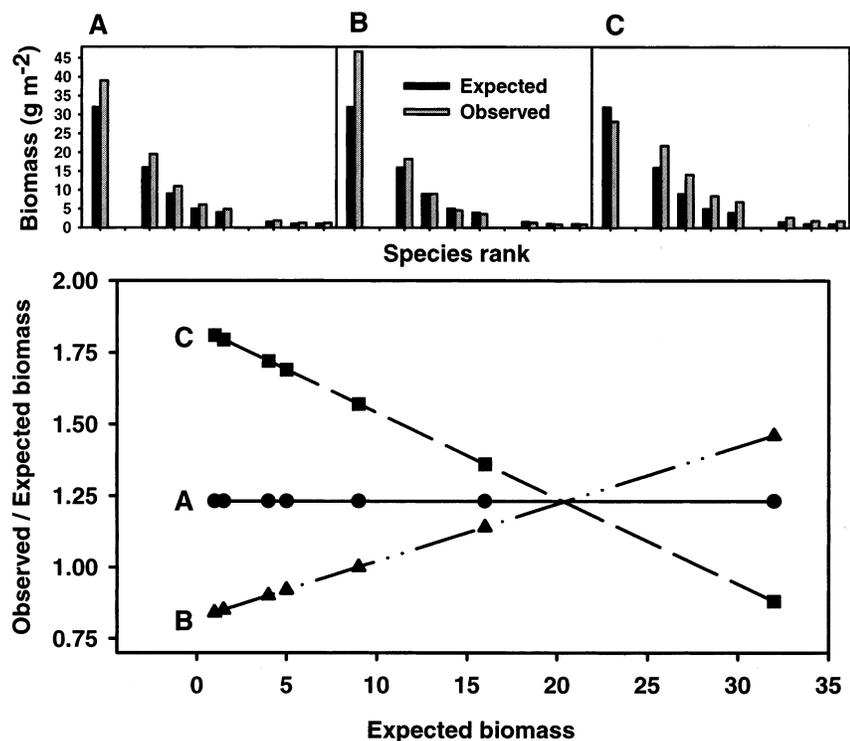


Fig. 5. Each species mixture occupies a point in the richness-biomass parameter space (shaded area in top-left panel). Point A corresponds to a mixture from which only the subordinate species were lost (histogram A). Point B represents a community in which only the dominant species were deleted (histogram B). Point C represents a community from which a variety of species were lost (histogram C). For compensation to be constant in the different scenarios ($C = 0.5$ in these examples), the remaining species must respond in dramatically different ways.

Fig. 6. The relationship between the expected biomass of individual species (on the x -axis of the line graph) and their relative departure from expected (on the y -axis) indicates whether compensation is driven by dominant or subordinate species. The three histograms and corresponding lines (A–C) illustrate three hypothetical responses ($C = 0.5$ in all cases). Scenario A) occurs when all species have similar proportionate changes in biomass following species loss, or when there is no significant relationship between observed/expected and expected biomass. Scenario B), a positive slope, is caused by disproportionate increases in dominant species. A negative slope C) results from disproportionate increases by subordinate species.



relative to monocultures. The regression of observed/expected on expected will fail to show a significant relationship when both dominant and subordinate species compensate proportionally (Fig. 6A), or idiosyncratically. A positive slope will occur when dominant species show disproportionate increases in production, and thus disproportionate contributions to compensation (Fig. 6B). Negative slopes will occur when subordinate species contribute disproportionately to compensation (Fig. 6C). In general the sign of significant slopes is more important than their steepness, since the latter is likely to depend on the amount of biomass removed: when a significant portion of community biomass is removed, we should expect much larger differences between each remaining species' observed and expected production than when only a small portion of biomass is lost. Within a given range of biomass removal, however, the steepness of the slope will describe the degree to which dominants or subordinates drive compensation.

Once this "dominance-response" slope is calculated for all mixtures in an experiment, we can analyze the frequency and magnitude of positive, negative, and zero slopes. We might also ask whether the sign of the slope depends on the type of species removed from the community. For example, we could search for systematic variation in the sign of the slope over the parameter space formed by possible combinations of species richness and expected production (as in Fig. 5). Positive values of the slope over much of the parameter space

would indicate that dominant species are generally responsible for compensation, and may imply that physiological variation maintains dominance in the community. If positive values of the slope are rare, or are limited to particular regions of the parameter space, we should suspect that competition plays a strong role in maintaining the dominance hierarchy.

Linking experimental and natural communities

Although our discussion has focused on diversity-productivity studies in experimental communities, the compensation index may be most valuable for analyzing data from removal experiments in natural systems. The ability to directly compare results from natural and artificial systems would be an exciting addition to research on the diversity-productivity relationship. However, the obvious differences between seeding experimental plots and removing species from natural communities mean that any comparisons will require careful consideration.

One consideration is the amount of time necessary for compensation to occur. In seeded experimental communities, enough time must be allowed for seedlings to mature and for competitive interactions to produce shifts in abundance among species. In removal experiments in natural communities, time must be provided for demographic responses such as the coloniza-

tion of space previously occupied by the removed species, a process that may require many years in perennial plant communities (Symstad and Tilman 2001). Whether longer time scales are always required in removal experiments depends on plant functional types (annuals vs perennials), on the choice of an above or belowground focus (compared to removals, the preparation of experimental plots may have very large impacts on belowground processes), and on ecosystem productivity (abundance shifts should be more rapid in more productive systems). Ideally, in both types of experiments, plots should be approaching a steady state in the relative abundance of individual species by the time of harvest. This steady-state requirement could be problematic when inter-annual variation in environmental factors causes continual shifts in relative abundance.

The use of non-destructive methods for estimating annual production, if used in both assembly and removal experiments, would help solve the problem of choosing one time period for analysis. While harvest methods require an arbitrary time point for termination of the experiment, non-destructive methods would allow tracking of changes in production and compensation for many years. Such data would provide great flexibility in comparing the results of assembly and removal experiments. We could compare results at fixed intervals, or only compare results once the rate of change in annual production or compensation reached zero.

A second consideration concerns spatial pattern. While the environmental homogeneity of experimental plots may limit all but biologically generated spatial patterns, virtually all natural communities contain physically generated spatial structure as well, which in turn can have important influences on ecosystem function (reviewed in Turner 1989). Thus, compensation following species removals in natural communities may be quite sensitive to the spatial pattern of remaining plant species and fine scale environmental heterogeneity. One possible solution would be to create experimental communities that include environmental heterogeneity, such as fine-scale patterns in soil texture. Including such spatial variation might also reveal the functional importance of subordinate and transient species (Grime 1998) without requiring extremely long-term studies.

Similar patterns of compensation in both artificial and natural communities would greatly strengthen our confidence in any emerging trends, perhaps allowing predictions for the ecosystem effects of different types of extinctions. Unfortunately, results from recent removal experiments do not appear to correspond well with findings from many of the experimental diversity studies (Symstad and Tilman 2001, Wardle et al. 1999). While a common form of analysis, such as our compensation index, may be one prerequisite for a valid com-

parison, monitoring experimental results over longer time periods using non-destructive measures of production may be even more important.

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Appendix

One way to understand the differences between the Relative Yield Totals approach, based on data from monocultures, and the compensation approach, based on data from the full community, is to ask, when would these approaches generate the same expected production for a given mixture? The two methods would be most likely to produce identical expectations when the performance of individual species in the full community is directly proportional to their performance in monoculture. If competitive interactions cause shifts in dominance, the two approaches will never produce similar expectations for a given mixture, with the exception of rare coincidence. We will also assume that both complementarity and selection effects are zero. The production of a species i in a mixture with n species is then

$$\frac{M_i}{n}$$

where M is the monoculture production of a species, and the total production of the mixture is

$$\sum_i^n \frac{M_i}{n} = \frac{\sum_i^n M_i}{n}$$

This formula, with the restrictive assumptions listed above, allows us to calculate the production of a full community with N species. Next we can compare the expected biomass for a mixture with $N-1$ species calculated using the relative yield and compensation approaches. Using relative yield, we expect production to equal

$$\frac{\sum_i^{N-1} M_i}{N-1} \quad (1)$$

whereas with the compensation approach, it is

$$\frac{\sum_i^N M_i}{N} - \frac{M_e}{N}$$

where M_e refers to the excluded or extinct species. By factoring out $1/N$ and summing over all species except the extinct species, the expression simplifies to

$$\frac{\sum_i^{N-1} M_i}{N} \quad (2)$$

Comparing eqs 1 and 2, we see that the expected production of the depleted assemblage calculated using the relative yield approach is greater than the expected production calculated using the compensation approach by

$$\frac{1}{N-1} - \frac{1}{N}$$

or more generally

$$\frac{1}{N-e} - \frac{1}{N}$$

where e is the number of species that have gone extinct.

The compensation approach underestimates the production of the depleted community because it assumes perfect niche partitioning in resource space and in physical space: the part of the plot formerly occupied by the extinct species will not be invaded by remaining species. In natural communities, where fine-scale environmental heterogeneity may exist, such an assumption may be reasonable, but in homogeneous experimental plots we should expect all space to be occupied. Under the restrictive conditions we have described, compensation will always be greater than zero, since the observed production will always be slightly higher than expected. As the number of species removed increases, the size of

the underestimation will increase as well. Since compensation is scaled by the expected biomass of the deleted species; however, the deviation of compensation from zero should not increase with the number of species removed. In field data, we expect that this

underestimation of expected production, which alone would result in values of compensation always greater than zero, will be overwhelmed by the competitive interactions that determine the dominance-diversity curve.