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MINI-REVIEW

Minireviews provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

Explaining productivity-diversity relationships in plants

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Relationships between productivity and diversity in plant communities have been widely documented. Unimodal productivity-diversity relationships are most common along natural productivity gradients, and fertilization generally reduces diversity. Five distinct hypotheses invoke changes in competition to explain why diversity should decline from intermediate to high productivity. Because experiments measuring the effects of competition on diversity are rare, four of the five hypotheses have not been directly tested, but each hypothesis makes unique predictions that allow for indirect tests. The indirect evidence is often conflicting, and while none of the hypotheses can be rejected, only the dynamic equilibrium hypothesis is consistently supported. A new hypothesis, however, is supported by indirect evidence and may help to explain the variation in the shape of productivity-diversity relationships, as well as the most common patterns. Diversity may be high in environments that promote size symmetric competition, where soil resources limit growth and are homogeneously distributed within the soil volume explored by individual plants. Conversely, diversity may be low in environments that promote size asymmetric competition, where light is limiting, or where soil resources are limiting and are patchily distributed within rooting zones.

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Plant ecologists' efforts to explain patterns in species diversity have recently been concentrated on explaining the relationship between diversity and community productivity. Numerous studies have reported diversity patterns along natural productivity gradients and artificial fertilization gradients. Other authors have suggested mechanisms that might produce these diversity patterns. However, the observed patterns vary greatly, and the proposed mechanisms have not explained the patterns or their variation satisfactorily. Here, I review the observed relationships between plant productivity and diversity and the mechanisms proposed to explain the patterns, and suggest a new explanation of the productivity-diversity relationship.

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The observed patterns

Diversity patterns on natural productivity gradients vary, from increasing to unimodal to decreasing. (I will use the word "diversity" in the broad sense, to encompass both species richness and diversity indices that include relative abundance of species.) These patterns have been reviewed in three recent papers, all of which stress the importance of the scale at which the pattern is observed. At the largest scale, among biomes, the pattern is most consistent, and diversity often increases with productivity (Waide et al. 1999, Mittelbach et al. 2001). Within biomes but across communities, the pattern is more variable. Waide et al. (1999) find 14 studies supporting a unimodal curve, with diversity peaking at intermediate productivity, 13 studies reporting no pattern, and fewer studies reporting increasing (four studies) or decreasing (five studies) relationships. Mittelbach et al. (2001) similarly find that unimodal curves are most common, with positive, negative, and even U-shaped curves also reported. Gross et al. (2000), combining results from 6 LTER sites in the United States, find a unimodal curve within the grassland biome. Results vary even more at the smallest scale, within communities, with about 45% of studies showing no pattern, 20% showing unimodal productivity-diversity relationships, and 20% showing increasing relationships (Waide et al. 1999, Gross et al. 2000). Despite this variation in reported relationships, the "true" relationship between productivity and diversity has often been assumed to be unimodal (Rosenzweig and Abramsky 1993, Tilman and Pacala 1993, Abrams 1995).

On experimental fertilization gradients, the pattern is more consistent: diversity decreases with increasing productivity. DiTommaso and Aarssen (1989) review seven experiments in which fertilization decreased diversity, and find none in which diversity increased or remained unchanged after fertilization. Subsequent fertilization experiments have mostly supported this pattern (Pratt 1984, Carson and Barrett 1988, Goldberg and Miller 1990, Gough et al. 2000), but exceptions do exist. For example, Carson and Pickett (1990) found that fertilizer addition did not change species diversity in a productive old field, Gibson (1988) found no diversity response to fertilizer in a dune grassland, and among LTER sites Gough et al. (2000) found that four of 17 communities had no diversity response to fertilization and diversity increased in one community. In the LTER sites, the direction of the response was unrelated to initial productivity, so the differing fertilization responses could not be interpreted as different portions of an overall unimodal productivity-diversity relationship. Despite these exceptions, the reduction in diversity following fertilization appears to be far more general than the unimodal productivity-diversity relationship for natural gradients.

Hypotheses to explain the patterns

Plant competition theory has produced five plant-specific explanations of productivity-diversity relationships (Fig. 1). Four of the five hypotheses explain the increase phase of the curve the same way: few species can tolerate very low resource levels, and as productivity increases, more species have their minimum resource requirements met. Thus, the increasing portion of the curve is determined by evolutionary processes that have generated greater diversity at intermediate productivity than at low productivity. The hypotheses reviewed here do not attempt to explain these evolutionary processes, concentrating instead on the ecological processes that maintain greater diversity at intermediate than at high productivity. The hypotheses share a basic explanation of the decrease phase of the curve: competition has little or no effect on diversity at intermediate productivity, but a strong effect on diversity at high productivity. However, they differ in their explanations of why the effect of competition on diversity increases with productivity.

1) *Total competition intensity*. Total competition intensity increases with productivity (Grime 1977). Species tolerant of resource stress survive at low productivity. Species able to compete for resources survive at high productivity. A mixture of the two coexists at intermediate productivity, where competition is of intermediate intensity.
2) *Dynamic equilibrium*. Population dynamics are faster at high productivity (Huston 1979). All populations grow faster, and therefore poor competitors are excluded faster. A dynamic equilibrium with regular, periodic disturbance means that, given the same frequency or rate of disturbance, a more productive habitat will experience more competitive exclusion before disturbance resets the community. Under this hypothesis, productivity is expected to have the greatest impact on diversity when disturbance is of intermediate frequency; with very frequent or very rare disturbances, diversity will remain relatively low in habitats of any productivity.
3) *Habitat heterogeneity*. Very productive and very unproductive sites have low resource heterogeneity. Sites with intermediate productivity have the highest resource heterogeneity and allow many species, specialized for different resource conditions, to coexist (Tilman 1982, Tilman and Pacala 1993). In the most recent formulation of this model (Tilman and Pacala 1993), growth at low productivity is entirely limited by a soil resource such as nitrogen, and only the best nitrogen competitor can persist. At high productivity, when plants become very large and create dense shade, growth is entirely light limited, and only the best light competitor persists. In be-

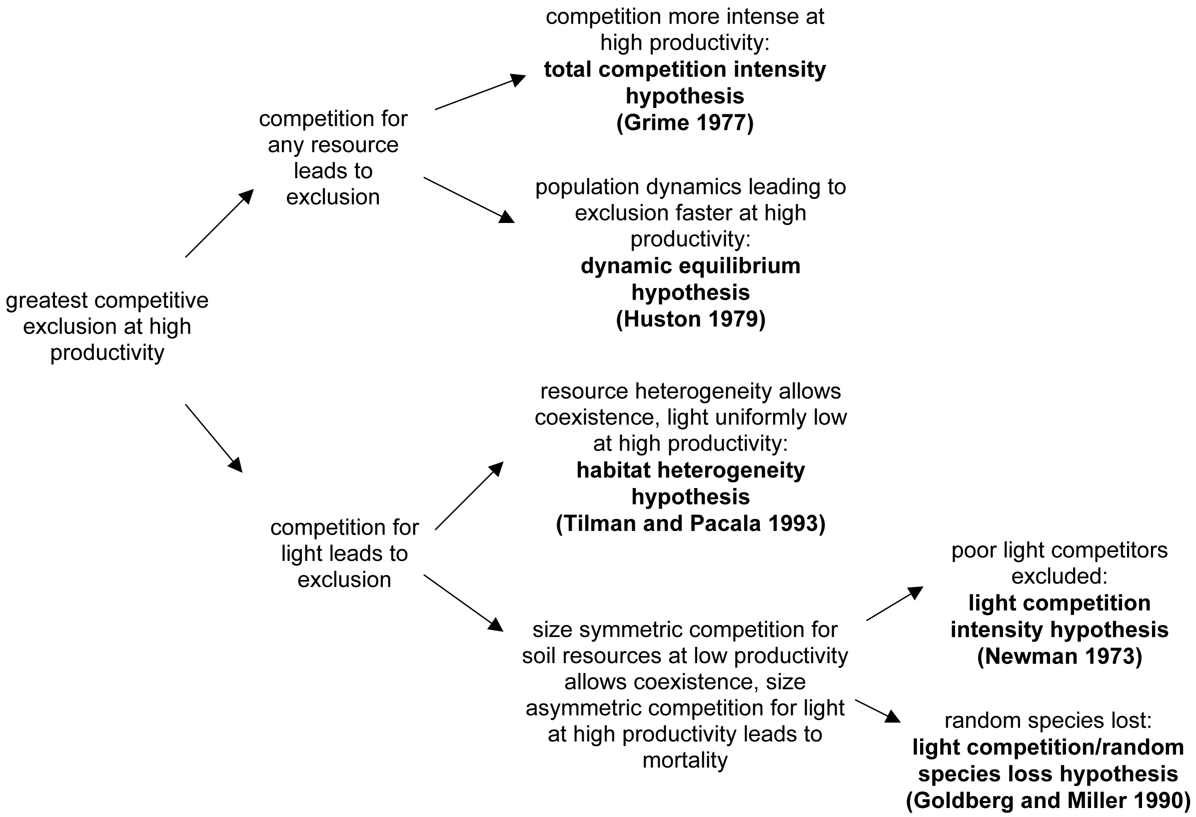

Fig. 1. Five hypotheses to explain unimodal productivity-diversity curves in plants. All the hypotheses except the habitat heterogeneity hypothesis share an explanation of the increase phase of the unimodal curve (see text), so only the explanation of the decrease phase is described here.

tween, different micro-sites have different nitrogen:light ratios, and different species are the best competitors at each type of micro-site, so many species coexist. This is the only one of the five hypotheses to explain the entire unimodal curve through ecological mechanisms.

4) *Light competition intensity*. Competition shifts from belowground at intermediate productivity to aboveground at high productivity, and aboveground competition results in more competitive exclusion (Newman 1973). Competition for light is expected to become more intense with increasing productivity because plant cover increases and creates more shade. Light competition is more likely to result in competitive exclusion because light competition is size asymmetric. A plant with a small height advantage can pre-empt light from a smaller neighbor; the larger plant uses its advantage to grow taller and pre-empt even more light, until the smaller neighbor no longer receives enough light to survive. Such pre-emption is much less likely in competition for soil resources, so species that are poor light competitors are more likely to be excluded than species that are poor belowground competitors.
5) *Light competition with random species loss*. Competition shifts from belowground at intermediate productivity to aboveground at high productivity, and aboveground competition results in random species loss (Goldberg and Miller 1990). This hypothesis is very similar to hypothesis 4, except that species that are poor light competitors are not differentially excluded. Instead, small individuals of all species die under intense light competition, leading to local extinction of initially rare species or stochastic loss of species from plots.

An additional hypothesis to explain unimodal productivity-diversity curves for plants is the “no-interactions model” (Oksanen 1996). According to this hypothesis, the productivity-diversity curve is an artifact of limited plot size. From low to intermediate productivity, individuals become less sparse and the number of individuals, and therefore the potential number of species, in a plot increases. At the same time, individual plants become larger as productivity increases. At some point, the plot becomes full, and fewer larger plants, and therefore fewer species, fit in the plot as productivity becomes very high. Unless plant size changes dramatically along the productivity gradient (for example, a gradient from grassland to forest), however, this model is not in fact a no-interactions null model: it includes density-dependent thinning, which must result from interactions. If thinning is a consequence of competition for light, as generally assumed (Yoda et al. 1963, Harper 1977, Weiner and Thomas 1986), this hypothesis becomes the same as hypothesis 5.

Evaluating the hypotheses

The hypotheses to explain productivity-diversity relationships in plants are rarely tested directly. Because all the hypotheses predict that competition has greater effects on diversity at high productivity than at intermediate productivity, direct tests would require measuring the impacts of competition on species diversity. Experiments in which the dominant species is removed often show that competition reduces species diversity (Abul-Fatih and Bazzazz 1979, Armesto and Pickett 1986, Bobbink et al. 1987, Gurevitch and Unnasch 1989, Keddy 1989, Leps 1999, Smith et al. 1999, Wardle et al. 1999; but see Pinder 1975, Allen and Forman 1976, Hils and Vankat 1982, Belsky 1992, Spackova et al. 1998). The effects of competition from all species, not just the dominant, can be measured using combined monocultures (Goldberg 1994) or low-density communities (Goldberg et al. 1995). In a community of desert annuals, competition decreased species richness and diversity at high plant densities (Goldberg and Estabrook 1998). On the other hand, competition decreased individual growth and biomass, but did not affect species diversity, in a community of bryophytes (Zamfir and Goldberg 2000) and a first-year old field (Rajaniemi and Goldberg 2000).

Only a few experiments have compared the effects of competition on diversity at more than one productivity level. Removing the dominant from an old field community prevented diversity from dropping when fertilizer was added (Gurevitch and Unnasch 1989). This result demonstrates the role of competition in the productivity-diversity relationship, but does not support any particular hypothesis. In a community of desert annuals, Goldberg et al. (unpubl.) found that the effect of competition on diversity actually decreased with increasing productivity, which is not consistent with any of the hypotheses. For a community of old-field perennials, I found that root competition, but not shoot competition, had a larger impact on diversity with fertilizer than without it (Rajaniemi 2001); this result is also not consistent with any of the five hypotheses.

Given the lack of direct tests at this time, indirect evidence must be used to evaluate the hypotheses. Each makes unique predictions, and if these predictions can be falsified, the associated hypotheses can be discarded. However, if the predictions are supported, the hypotheses remain in question: these predictions lay out prerequisites for the hypotheses to be upheld, but are not direct tests of the hypotheses. I will describe a key unique prediction of each of the five hypotheses, and discuss the evidence available to test those predictions. The hypotheses are summarized in Fig. 1.

1) The total competition intensity hypothesis predicts that *competition intensity increases with productivity*. The effects of competition on individual growth or survival along productivity gradients have been measured in a large number of experiments (reviewed by Gurevitch et al. 1992, Twolan-Strutt and Keddy 1996, Goldberg et al. 1999), but these experiments have been unable to resolve the question of whether total competition intensity increases with productivity. Competition intensity may increase or remain constant in individual studies (Twolan-Strutt and Keddy 1996), and a meta-analysis of studies suggests that competition intensity may even decrease with increasing productivity (Goldberg et al. 1999).

   Note that measuring the effects of competition on individuals along productivity gradients provides only a weak test of the total competition intensity hypothesis, because increasing effects on individuals do not necessarily imply increasing effects on species diversity. In fact, the two studies that have reported both individual- and community-level effects of competition have found that competition had strong effects on individuals and little or no effect on species diversity (Rajaniemi and Goldberg 2000, Zamfir and Goldberg 2000). Thus, individual-level competition experiments can test only one component of this hypothesis.
2) The dynamic equilibrium hypothesis predicts that *disturbance increases diversity more at high productivity than at intermediate productivity*. In the absence of disturbance, rates of competitive exclusion increase with productivity. At high productivity, many species are destined to be lost quickly, so many can be "rescued" by a disturbance that resets the community. If, to take the extreme example, exclusion rates are so low at low to intermediate productivity that exclusion is rarely observed, there will be no species to be rescued by disturbance, and some species intolerant to disturbance may be lost. This prediction is tested in many experiments manipulating grazers, which may be an important source of disturbance in plant communities. A review of the effects of grazers on plant communities at high and low productivity found the predicted pattern: grazing generally increased species diversity in productive sites and decreased diversity in unproductive sites (Proulx and Mazumder 1998). A meta-analysis examining a variety of communities, including phytoplankton, algae, and salt marshes,

also supported this prediction. Consumer effects on diversity shifted from negative to zero with nutrient enrichment in low-productivity sites and from zero to positive in high-productivity sites (Worm et al. 2002).

3) The habitat heterogeneity hypothesis predicts that *resource heterogeneity decreases with productivity*. I know of only one study reporting heterogeneity of both light and soil resources over a productivity gradient. Kelly and Canham (1992) measured light at 1 cm intervals and soil moisture and nitrogen at 10 cm intervals in a series of old field communities. The coefficient of variation for all three resources decreased as their mean values increased. Thus, the most productive sites (high moisture and nitrogen but low light) had low heterogeneity of soil resources, as predicted by this hypothesis, but also high light heterogeneity, which is not predicted by this hypothesis. Two other studies have compared soil resource heterogeneity over successional gradients in which sites varied in average nutrient availability (Gross et al. 1995, Cain et al. 1999). In both cases, the sites with the highest mean nitrogen availability (the most productive sites) had the lowest coefficient of variation for nitrogen availability, as predicted by the habitat heterogeneity hypothesis. In these studies, heterogeneity was measured among samples collected 10 cm to several meters apart. A scale of one to several meters is more relevant than a scale of several centimeters (as in Kelly and Canham 1992) to testing this hypothesis, in which variation among sites occupied by individual plants, rather than within sites, allows species to coexist.
4) The light competition intensity hypothesis predicts that *size asymmetric competition leads to exclusion more easily than size symmetric competition*. This prediction has not been evaluated experimentally, but has been addressed by several models. Schwinning and Fox (1995) modeled competition between two annual plant species which were identical except in seed size. When the species competed size symmetrically, they co-existed, but when they competed size asymmetrically, the larger-seeded species excluded the smaller-seeded species, suggesting that size asymmetry does lead to competitive exclusion. Huston and DeAngelis (1994) reached a similar conclusion with a multi-species model of soil nutrient and light competition. Uptake of the nutrient by a particular individual depended only on the nutrient concentration and the size of the individual, and so was size symmetric. Light uptake, on the other hand, depended on the size of the individual relative to other plants in the model and so was size asymmetric. When soil nutrient levels were low, most plants were nutrient-limited, competition was size symmetric, and diversity was high. When nutrient levels were high, most plants were light-limited, competition was size asymmetric, and diversity was low. Neither of these models, however, included spatial effects. Rees and Bergelson (1997) demonstrated that size asymmetric competition favors founder control. Thus, the first species to reach a site is able to hold it, even against better competitors. This mechanism might lead to species coexistence over many sites with size asymmetric competition.
5) The light competition/random species loss hypothesis predicts that *higher productivity is associated with lower plant density, and reduced density accounts for reduced diversity*. This prediction has been tested in two experiments. In both, stem density decreased with fertilization, consistent with this hypothesis. In a first-year old field, this reduced density entirely accounted for the reduced diversity observed: in simulated plots in which density was reduced from control to fertilized levels by random removal of plants, diversity was equal to the observed diversity in low-density, fertilized plots (Stevens and Carson 1999). However, in an older field dominated by clonal perennials, reduced density accounted for only 20–25% of the observed decrease in species richness (Rajaniemi 2002). These two experiments are the most direct tests of any of the hypotheses, but they do not address one important aspect of the hypothesis: they do not demonstrate that light competition is responsible for the decreased density and diversity. Light levels and the intensity of light competition were not measured for the first-year old field (Stevens and Carson 1999). In the perennial community, competition for light alone appeared not to explain the observed decrease in diversity with fertilization (Rajaniemi 2002).

Finally, there is a key prediction that is common to hypotheses 3–5: *shoot competition intensity increases with productivity, while root competition intensity decreases*. These three hypotheses share the prediction that competition for light is most intense at high productivity and competition for soil resources is most intense at low to intermediate productivity. As was the case for total competition intensity, many studies have addressed this prediction for effects on individuals (reviewed by Twolan-Strutt and Keddy 1996) but no clear conclusions can be reached. Root competition intensity generally decreases with increasing productivity (Wilson and Tilman 1991, Putz and Canham 1992, Wilson and Tilman 1993, Peltzer et al. 1998, Cahill 1999), although Twolan-Strutt and Keddy (1996) found that it remained constant. Shoot competition intensity may increase (Wilson and Tilman 1991, Putz and Canham 1992, Wilson and Tilman 1993) or remain constant (Wilson 1993, Belcher et al. 1995, Cahill 1999) with increasing productivity, or remain unimportant along a fertilization gradient (Peltzer et al. 1998). These studies suffer from the same limitation as do the tests for the total competition intensity hypothesis: they only quantify effects of competition on individuals, which may not be the same as the effect on species diversity. Increasing competition intensity will only reduce diversity if species are differentially affected.

A few experiments have compared the effects of root and shoot competition on species diversity by manipulating light and soil resources separately. These have also failed to reach consistent conclusions. Gibson (1988) and Carson and Pickett (1990) found that diversity increased when shoots were tied back to increase light, but that fertilization did not affect diversity, suggesting that competition for light had a greater effect on diversity than competition for nutrients and consistent with hypotheses 3–5. On the other hand, I found that fertilization reduced diversity while adding shade had no effect in an old field, suggesting that competition for light could not explain the observed drop in diversity with fertilization (Rajaniemi 2002).

In summary, for four of the five hypotheses, the available evidence is conflicting. None of these hypotheses is strongly supported, but none can be eliminated. The available evidence does appear to uphold the predictions of the dynamic equilibrium hypothesis, however. More work is needed to test directly the mechanism invoked by this hypothesis, higher rates of population growth and competitive exclusion at high productivity.

A common weakness of all five hypotheses is that they do not explain the great variation in observed productivity-diversity relationships. Most importantly, they predict the same pattern for natural and artificial productivity gradients, although the observed patterns are clearly different. Unimodal, increasing, and decreasing productivity-diversity relationships have been observed for natural productivity gradients, and the increases and decreases are sometimes interpreted as parts of a true unimodal relationship (Rosenzweig and Abramsky 1993). On the other hand, decreases are most common in fertilization experiments, and only one increase and no unimodal curves have been reported (DiTommaso and Aarssen 1989, Gough et al. 2000). Most fertilization experiments would not be able to detect a unimodal relationship because they include only a few fertilization levels. However, if a unimodal relationship did exist for fertilization gradients, more increases in diversity should have been observed among the many existing fertilization experiments. Also, in combining fertilization experiments in 17 sites, Gough et al. (2000) demonstrated that the differing diversity responses to fertilization could not be considered parts of a unimodal relationship, because the direction of the response was unrelated to initial productivity. None of the five hypotheses reviewed here predict that fertilization should consistently decrease diversity, and so none are sufficient to explain productivity-diversity relationships for both natural and artificial productivity gradients.

A new hypothesis

The differing diversity patterns on natural and artificial productivity gradients suggest that some aspect of the environment besides total productivity influences species diversity. I propose that small-scale resource heterogeneity, within the soil volume explored by an individual plant, is an important determinant of species diversity, because it determines size symmetry of belowground competition.

Belowground competition is generally assumed to be size symmetric, with resource uptake and competitive effect directly proportional to plant size. However, this conclusion is based mostly on indirect evidence and only a few direct tests. The indirect evidence is that skewed size distributions, which are a predicted consequence of size asymmetry, are less likely to develop when plants are very small or grown at low density (Weiner and Thomas 1986). Under these conditions, soil resources, rather than light, are expected to be limiting. Most of the experiments measuring belowground size symmetry directly have either used targets that were all smaller than their neighbors (Wilson 1994, Gerry and Wilson 1995), providing a weak test of the size-dependence of competitive ability, or have used homogenized soil (Newbery and Newman 1978, Wilson 1988, Weiner et al. 1997). Plants can potentially compete size asymmetrically for soil resources if those resources are distributed heterogeneously within the soil volumes explored by individuals (Schwinning and Weiner 1998). If larger plants are able to reach or exploit resource patches faster than small neighbors, the larger plants may be able to pre-empt soil resources, and their uptake rates and competitive effects would be disproportionate to their size. Because a small size advantage can snowball into a large competitive advantage in size asymmetric competition, size asymmetry is expected to reduce coexistence and species diversity (Newman 1973, Zobel 1992, Schwinning and Fox 1995).

If belowground competition is indeed size asymmetric when soil resources are heterogeneous, the observed relationships between productivity and diversity can be interpreted as a function of competitive size symmetry. On natural productivity gradients, nitrogen appears to become less heterogeneous as productivity increases (Kelly and Canham 1992, Gross et al. 1995, Cain et al. 1999), while average light levels become lower (Pidwirny 1990, Kelly and Canham 1992, Olff et al. 1993, Grace and Pugasek 1997). Thus, at low productivity, high nutrient heterogeneity could lead to belowground size asymmetry, keeping diversity low. With increasing productivity, decreasing nutrient heterogeneity would reduce size asymmetry and increase coexistence. At higher productivity, light would become limiting and competition would again become size asymmetric, leading to low diversity. Surveys that include only part of this productivity range might observe increasing or decreasing productivity-diversity relationships.

The heterogeneity-size asymmetry hypothesis would also explain why fertilization either reduces diversity or leaves it unchanged, but rarely increases it. If soil resources are initially limiting, fertilization should generally increase competitive size asymmetry, either by imposing light limitation or by increasing small-scale nutrient heterogeneity. Most of the fertilization experiments I have found (Gibson 1988 is one exception) used either granular fertilizer (Tilman 1987, Goldberg and Miller 1990), which would create small (centimeter-scale) resource patches, or organic fertilizer (Maly and Barrett 1984, Carson and Barrett 1988), which would create patches as organic matter decomposed. If large individuals were able to pre-empt those patches, smaller individuals would die and diversity would drop. In communities where light was initially limiting, competition would already be size asymmetric and diversity would not be expected to change with fertilization (Gibson 1988, Carson and Pickett 1990). On the other hand, granular fertilizer is often expected to homogenize soil resource availability, either because the nutrient patches created are too small to affect plant competition or because diffusion merges the patches together. More work is needed to investigate the spatial distribution of nutrients created by fertilizers and to determine whether the heterogeneity-size asymmetry hypothesis is reasonable for fertilization gradients. Along natural productivity gradients, however, heterogeneity at the relevant scale has been documented.

This new hypothesis to explain the relationship between productivity and diversity is supported by a set of old-field fertilization experiments. In a community dominated by perennials characteristic of unproductive sites, species diversity decreases with fertilization, and the decrease seems to be the result of belowground interactions. In one experiment, shadecloth reduced light at the soil surface by the same amount as fertilization did, but shadecloth did not affect species diversity (Rajaniemi 2002). This result suggests that competition for light was not responsible for reduced diversity. In a second experiment in the same community, monocultures of seven dominant species were grown with no competition, only belowground competition, or only aboveground competition from the surrounding community. The combined set of seven monocultures in a given treatment was considered a single null community in which species diversity was calculated and compared to diversity in a mixture of the seven species (following Goldberg 1994). Fertilization decreased diversity in the mixture and in the null community with belowground competition, but not in the null communities with no competition or only aboveground competition, again supporting the conclusion that a change in belowground, but not aboveground, interactions led to the drop in diversity (Rajaniemi 2001). This result is clearly not consistent with any of the hypotheses in Fig. 1, but is consistent with the heterogeneity-size asymmetry hypothesis.

Greenhouse experiments with three species from this community suggest that the important change in belowground interactions may have been a change in size asymmetry. I tested for size asymmetry of belowground competition using unhomogenized soil collected from the same field in which the fertilization experiments took place. *Bromus inermis*, a dominant grass, had size asymmetric effects in belowground competition (Rajaniemi 2003). There was evidence that this size asymmetric effect may have been linked to resource heterogeneity: when liquid fertilizer, which should have supplied resources homogeneously, was added, competition became less size asymmetric (Rajaniemi 2003). If the application of a granular fertilizer in the field experiments increased small-scale nutrient heterogeneity, this effect may have increased competitive size asymmetry and led to exclusion of species with small root systems.

The heterogeneity-size asymmetry hypothesis would also explain an experimental result reported by Goldberg and Miller (1990). They added water, granular nitrogen fertilizer, and granular phosphorus fertilizer to plots in a first-year old field. Water and nitrogen both increased aboveground biomass, while phosphorus had no effect. Nitrogen reduced species richness, but water did not. Under the heterogeneity-size asymmetry hypothesis, watering should not decrease diversity, because water would be supplied homogeneously and would not lead to size asymmetric competition, while addition of a granular fertilizer would create high-nitrogen patches that favored large species.

The heterogeneity-size asymmetry hypothesis is yet another explanation in a field that has made little progress in testing and distinguishing among numerous existing explanations. However, this new hypothesis has the unique strength of explaining the differing diversity patterns observed for natural and artificial productivity gradients. To further evaluate this hypothesis, many questions will need to be answered.

- What is the extent of small-scale heterogeneity, and how does it change along natural and artificial productivity gradients? Previous studies of resource heterogeneity have focused on scales of meters or larger (Robertson et al. 1988, Lechowicz and Bell 1991, Jackson and Caldwell 1993a, b, Gross et al. 1995, Ryel et al. 1996), a scale relevant to Tilman and Pacala's (1993) habitat heterogeneity hypothesis. Only a few have examined heterogeneity at the scale of a few centimeters (Ryel et al. 1996, Farley and Fitter 1999), the scale most relevant to the heterogeneity-size asymmetry hypothesis. Studies of heterogeneity along productivity gradients are also rare.

- How common is belowground size asymmetry? More experiments with unhomogenized soils, as well as field experiments using a wide range of plant sizes, are needed.
- Does size asymmetric competition reduce diversity more than size symmetric competition? Models are needed to compare the relative importance of species differences, in which size asymmetry favors larger species and leads to competitive exclusion (Schwinning and Fox 1995), and founder effects, in which size asymmetry favors the first individual to reach a site and may promote coexistence (Rees and Bergelson 1997). Experimental approaches to this question would also be helpful.

More generally, work on the productivity-diversity relationship should be shifted from trying to identify and generalize about patterns to investigating the mechanisms responsible for patterns. It is clear that relationships between productivity and diversity differ not only among scales and between artificial and natural gradients, but also within scales and gradient types. A better understanding of productivity-diversity relationships will require studying the mechanisms creating the relationships and whether differing mechanisms can explain the variation in patterns. The proposed mechanisms can best be evaluated by experiments that directly examine the effects of competition on species diversity.

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