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LETTER

Reconsidering diversity–productivity relationships: directness of productivity estimates matters

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Abstract

Despite extensive research efforts, the controversy over diversity–productivity (D–P) patterns in natural communities still looms large. Recent meta-analyses suggest that unimodal D–P relationships tend to pre-dominate in plant studies, while positively linear relationships are more common in animal studies. These patterns, however, are based on studies in which productivity is estimated either directly, based on the biomass or energy of the studied organisms, or indirectly, according to the productivity of lower trophic levels, and various surrogates. Our analysis shows that the distribution of D–P patterns is sensitive to the directness of productivity estimates in animal studies but not in plant studies. Analysis of D–P patterns should be based on direct productivity estimates of the studied organisms, especially in comparative meta-analyses of communities from multiple trophic levels, where productivity is often affected nonlinearly by indirect factors or when complex feedback interactions are expected between productivity and diversity.

Keywords

Apportionments, complex interactions, diversity, diversity–productivity patterns, productivity, trophic levels.

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INTRODUCTION

A major area of debate in the study of biodiversity concerns the relationship between diversity and productivity (Rosenzweig & Abramsky 1993; Waide *et al.* 1999). In spite of over three decades of continuous attention, diversity–productivity (D–P) relationships and their underlying mechanisms remain a controversial topic (Waide *et al.* 1999; Mittelbach *et al.* 2001a,b). While some suggest that unimodal D–P relationships are more prevalent in natural communities (Tilman & Pacala 1993; Leibold 1999), others propose that monotonic and especially positively linear D–P relationships are more common (e.g. Brown & Davidson 1977; Abrams 1995). Recent meta-analyses suggest that unimodal D–P relationships are dominant in plant studies and at relatively small spatial scales (Waide *et al.* 1999; Mittelbach *et al.* 2001a). Conversely, animal studies are dominated by positively linear relationships, regardless of spatial scale (Waide *et al.* 1999).

Unlike diversity and species richness, which are measured in similar ways in D–P studies (but see Gotelli & Colwell 2001), the estimation of productivity is largely inconsistent (Abrams 1995; Mittelbach *et al.* 2001a). Some studies use direct productivity values of the studied organisms, measured by production of mass (g m^{-2} $year^{-1}$), energy (J m^{-2} $year^{-1}$), or the community standing biomass (g m^{-2}). Others use various indirect estimates of available energy and corollary surrogates such as latitude, altitude, actual evapotranspiration and average annual temperatures of the studied ecosystems (Mittelbach *et al.* 2001a,b; Bengtsson *et al.* 2002). Furthermore, in many of the animal studies, primary productivity and its surrogates are used as indexes of secondary productivity (e.g. Dodson 1992).

Here, we test the hypothesis that some of the differences found in D–P patterns between plant and animal studies result from differences in the *directness* of the estimates of productivity. In particular, we suggest that while both direct and indirect estimates of productivity can serve equally well for studying D–P patterns in plants and other primary producers, they should be interpreted differently when studying higher trophic levels. Analysing D–P relationships in higher trophic levels based on primary productivity or

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productivity of lower trophic levels may shed light on the structure and functioning of specific ecosystems (e.g. Horner-Devine *et al.* 2003), but only the direct productivity of the studied organisms can be used in comparative meta-analyses where communities from multiple trophic levels are studied and productivity is potentially affected nonlinearly by multiple indirect factors.

METHODS

We studied the distribution of D–P patterns based on the results of a meta-analysis of 254 individual D–P studies summarized in Mittelbach *et al.* (2001b). Studies were included in the analysis if they were based on samples of 10 or more individuals in natural communities that were subjected to no major anthropogenic disturbances (Mittelbach *et al.* 2001b).

The studies were sorted according to kingdom (plants, animals), and productivity estimates (direct, indirect). Animal studies related to species from various trophic levels. Productivity was considered direct if its estimates corresponded to the relevant studied group. indirect productivity referred to cases in which productivity was estimated based on available resources, energy or biomass of lower trophic levels, or abiotic surrogates such as rainfall, soil moisture etc. The D–P patterns were determined according to categories used by Mittelbach *et al.* (2001b): unimodal, positive, negative, *U*-shaped and none. The original meta-analysis (Mittelbach *et al.* 2001b) was based on both ordinary least square (OLS) and generalized linear model analyses. Here, only the results of the OLS analyses were used as these were based on a larger set of studies. We calculated the frequencies of studies belonging to each of the five possible D–P pattern groups within each of the following main categories: plants-direct, plants-indirect, animals-direct and animals-indirect. The frequencies were transformed to proportions by dividing them by the total number of studies within each category. Within each kingdom the difference between the proportion of indirect and direct studies for each of the five D–P patterns was then calculated. The larger the difference, the more important the directness of productivity measures for the D–P pattern. In particular, we tested the hypothesis that the difference between direct and indirect proportions was different in plants and animals by comparing the standard deviations of the differences between direct and indirect studies in each of the five D–P categories in plants and animals, using the Ansari–Bradley test (Daniel 1990).

RESULTS

Out of the studies that fulfilled the selection criteria, 121 dealt with plants and 133 with animals. Only 32% of the animal studies and 48% of the plant studies were based on direct measures of productivity. Fig. 1a shows the internal distribution of the studies according to the five D–P patterns within each one of the four main (directness X kingdom) categories. The proportions of indirect and direct studies were similar in plant studies but tended to differ in animal studies in all the D–P categories (Fig. 1). The statistical power was too low to test each D–P pattern separately but it was clear that the differences between the proportions of direct and indirect were much greater (differences more different from zero) in animals than in plants (Fig. 1b).

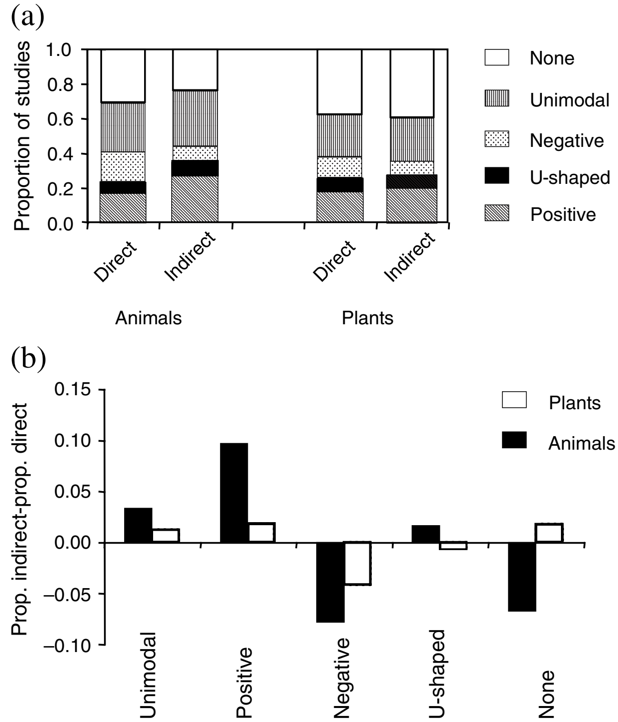

Figure 1 Proportions of diversity–productivity (D–P) patterns in animal and plant studies in which productivity was estimated directly or indirectly (a). The difference between proportions of studies in which productivity was estimated indirectly and directly in each D–P category in animal and plant studies (b). Data were extracted from Mittelbach *et al.* (2001b).

The sum of squares of the differences between the proportions of indirect and direct studies was over eight times greater in animals than in plants ($n_1 = n_2 = 4$, $t = 7$, $P = 0.0143$ in an Ansari–Bradley test).

As the controversy over D–P relationships is mainly related to diversity at high productivity levels, it was interesting to note that the proportion of D–P studies demonstrating increasing diversity at high productivity (*U-shaped* and *positive*) was almost the same in plant-direct and plant-indirect studies (0.26 and 0.27, respectively) but differed in animal studies (0.35 and 0.24 in indirect and direct studies, respectively; Fig. 1a).

DISCUSSION

Our analysis shows that the directness of productivity estimates might be important for the analysis of D–P patterns in animal studies. Furthermore, it is possible that apparent differences in D–P relationships between plant and animal studies (Waide *et al.* 1999; Mittelbach *et al.* 2001a,b) are the result of the way productivity is accounted for in some animal studies. Here, we briefly review a few mechanisms that might underlie these patterns.

Diversity–productivity patterns can be studied in two distinctly different ways based on the measurement of productivity. Studying D–P based on *direct* productivity measurements of the studied organisms involves the apportionment of a zero-sum game biomass or energy production among a certain number of species (Fig. 2; *sensu* Tokeshi 1999; Hubbell 2001). The statistical properties of such apportionments have been extensively studied in ecology (Tokeshi 1999) and other fields in order to describe the distribution of a given amount of resource among a number of equivalent entities of variable sizes. Examples include the size distribution of cars in a parking lot (Renyi 1958) or of DNA fragments in the genome (Lobrich *et al.* 1996). In contrast, analysing D–P relationships of a given trophic level based on the productivity estimates of a lower trophic level is no longer related to productivity apportionment. Instead, it deals with the compound and often-complex effects of the following factors on species diversity:

1 Interactions between primary productivity and intra- and inter-trophic interactions (e.g. Loreau *et al.* 2001; Schmitz 2003).
2 Top–down niche specialization of animals on plants (Price 1997; Fig. 2).
3 Feedback interactions between productivity and diversity (Loreau *et al.* 2001; Mouquet *et al.* 2002; Schmid 2002; Fig. 2).

The potential complications stem from the fact that primary and secondary productivities are not necessarily linearly correlated (e.g. Fretwell 1977). Additionally, trophic cascades (e.g. Cohen *et al.* 1990), differential palatability and defences of lower trophic level organisms (Leibold 1999), as well as apparent competition (Holt 1977) and predator–prey co-evolution (e.g. Thompson 1989) are expected to greatly reduce the predictability and complicate the interpretation of D–P relationships that are based on indirect estimates of productivity. These and other trophic mechanisms as well as the variability of co-existence mechanisms of species at each trophic level (Mouquet *et al.* 2002) suggest that although some D–P patterns might be more prevalent than others, at least at small spatial scales we should not expect any general D–P pattern to emerge from studies of natural communities, especially when they are based on indirect estimates of productivity.

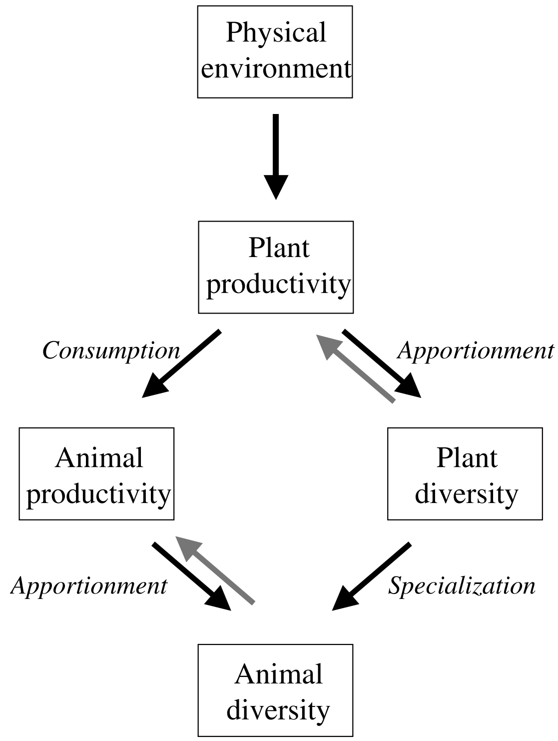

Figure 2 Some effects of productivity on species diversity in animal and plant communities. Whilst plant diversity is directly affected by apportionment of mass or energy production among plant species, animal diversity is a complex product of both the consumption of plants by animals and the apportionment of resources between animal species. Grey arrows correspond to productivity–diversity processes (Kinzig *et al.* 2001; Loreau *et al.* 2002) that are not discussed in detail in this study. For the sake of simplicity, the scheme depicts only the most essential processes that relate to the studied phenomena. Among the processes that are not presented are direct influences of the physical environment on diversity (e.g. Gough *et al.* 1994) and engineering effects (Jones *et al.* 1994).

The latest studies on the effects of biodiversity on ecosystem functioning (Kinzig *et al.* 2001; Loreau *et al.* 2002) suggest that the relationship between productivity and diversity cannot be understood by studying unidirectional causality approaches in which diversity and productivity are either the causes or the effects (Loreau *et al.* 2001). Accordingly, studying feedback between productivity and diversity must be based on integrative approaches using comparable currencies of productivity across different communities and trophic levels. We suggest that direct estimates of productivity of the studied organisms are suitable for this purpose.

In conclusion, as primary productivity is usually well correlated to climatic surrogates (Rosenzweig & Abramsky 1993) and plants are much more similar to each other than animals in their fundamental requirements (Goldberg 1990), D–P relationships are expected to demonstrate similar patterns in studies of plants and other primary producers, regardless of the directness of their productivity estimates (Fig. 1). In contrast, primary productivity and its surrogates cannot accurately represent the productivity of higher trophic levels, and D–P is expected to vary in animal studies according to the directness of the estimates of their productivity levels and the cumulative and often complex effects of productivity on a plethora of mechanisms that determine their diversity (Fig. 2). Studying D–P patterns in animal studies that are based on primary productivity or productivity of lower trophic levels, therefore, might shed light on functional relationships within specific communities and ecosystems. In comparative meta-analyses across trophic levels or where complex feedback interactions are expected between productivity and diversity (e.g. Schmid 2002), however, the study of D–P patterns should be based on direct productivity estimates of the studied organisms.

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