

IDEA AND
PERSPECTIVE

Separating the influence of resource ‘availability’ from resource ‘imbalance’ on productivity–diversity relationships

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Abstract

One of the oldest and richest questions in biology is that of how species diversity is related to the availability of resources that limit the productivity of ecosystems. Researchers from a variety of disciplines have pursued this question from at least three different theoretical perspectives. *Species energy theory* has argued that the summed quantities of all resources influence species richness by controlling population sizes and the probability of stochastic extinction. *Resource ratio theory* has argued that the imbalance in the supply of two or more resources, relative to the stoichiometric needs of the competitors, can dictate the strength of competition and, in turn, the diversity of coexisting species. In contrast to these, the field of *Biodiversity and Ecosystem Functioning* has argued that species diversity acts as an independent variable that controls how efficiently limited resources are utilized and converted into new tissue. Here we propose that all three of these fields give necessary, but not sufficient, conditions to explain productivity–diversity relationships (PDR) in nature. However, when taken collectively, these three paradigms suggest that PDR can be explained by interactions among four distinct, non-interchangeable variables: (i) the overall quantity of limiting resources, (ii) the stoichiometric ratios of different limiting resources, (iii) the summed biomass produced by a group of potential competitors and (iv) the richness of co-occurring species in a local competitive community. We detail a new multivariate hypothesis that outlines one way in which these four variables are directly and indirectly related to one another. We show how the predictions of this model can be fit to patterns of covariation relating the richness and biomass of lake phytoplankton to three biologically essential resources (N, P and light) in a large number of Norwegian lakes.

Keywords

Biodiversity and ecosystem functioning, resource ratio theory, species energy theory.

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INTRODUCTION

The relationship between species diversity and the productivity of ecosystems is one of the most fundamentally important and widely studied relationships in biology. Evolutionary biologists have shown that mass extinction and radiation events have often been associated with changes in the productivity of biological communities and ecosystems (Retallack *et al.* 1996; Ward *et al.* 2001). Paleontologists have found that the diversification of life throughout the geological record has been coupled with increases in the fraction of global carbon sequestered in biological tissue (Rothman 2001; Kiessling 2005).

Biogeographers have shown that latitudinal, altitudinal and other spatial gradients in species diversity are correlated with the production of biomass (Currie 1991; Rosenzweig & Abramsky 1993; Abrams 1995; Waide *et al.* 1999; Mittelbach *et al.* 2001). Within any single ecosystem, ecologists have shown that the number of species comprising a food web is often related to the productivity of that ecosystem (Naeem *et al.* 1994; Duffy *et al.* 2005; Cardinale *et al.* 2006). There are, in fact, so many associations between biodiversity and the production of living tissue that researchers dating back to at least Darwin (1859) have argued that there must be a direct causal relationship linking these variables.

Despite more than a century of research into productivity–diversity relationships (PDR), our understanding of the mechanisms that generate PDR remains limited. At least three problems have hampered our progress towards understanding mechanisms. First, the form and magnitude of PDR are known to differ among groups of organisms and between scales of observation; yet, we currently have no mechanism to explain how or why PDR might qualitatively shift at different scales or levels of biological organization. Two recent reviews have argued that for most natural gradients, diversity is either a monotonically increasing or a concave-down function of productivity (Waide *et al.* 1999; Mittelbach *et al.* 2001). Concave-down PDR tend to be more common for plants, whereas animals more often exhibit positive PDR (Mittelbach *et al.* 2001). In addition to differences among groups of organisms, PDR are thought to switch from being concave-down at ‘local’ scales where assemblages of species compete, to monotonically increasing at regional scales where species disperse across different types of habitats (Chase & Leibold 2002). If this variation was not confusing enough, recent summaries have also shown that PDR along natural gradients are often markedly different from PDR that result when productivity is manipulated experimentally, such as when nutrient additions lead to declines in diversity with increasing productivity (Gough *et al.* 2000; Suding *et al.* 2005).

A second problem that has hampered our ability to understand the mechanisms that give rise to PDR is that studies have tended to use a plethora of different variables to represent ‘diversity’ and ‘productivity’. Consider, for example, just a subset of variables that have been used to characterize productivity. These range from direct estimates of the rate of carbon flux through plants or animals (meaning production of new biomass per unit area or volume per time), to standing stock biomass or density (per area or volume), to standing stock resource availability (per area or volume), to rates of resource supply (amount per area or volume per time), to derived covariates such as latitude, depth or elevation (Mittelbach *et al.* 2001). Researchers often assume that these variables are all mechanistically equal, and thus can be used as surrogates for one another. However, many studies have argued that these variables are not interchangeable, nor do they even show the same qualitative relationship to species diversity (Mittelbach *et al.* 2001; Groner & Novoplansky 2003; Gillman & Wright 2006). By using non-causally related variables as surrogates, it is possible that some of the widely cited patterns of PDR stem from spurious correlations among variables (see fig. 5 of Gross & Cardinale 2007).

One final problem that limits our ability to understand PDR is that there are two seemingly different perspectives on the direction of causality in these relationships. Historically, species richness has been viewed as the dependent

variable. From this perspective, variation in the number of species among communities or ecoregions is thought to result from variation in productivity – or, more precisely, the supply rate of essential resources (nutrients, water, light, etc.) that are presumed to limit production (Currie 1991; Rosenzweig & Abramsky 1993; Abrams 1995; Waide *et al.* 1999; Mittelbach *et al.* 2001). Ecologists have recently viewed PDR from a fundamentally different angle, asking how diversity controls, rather than responds to, the production of biomass (Chapin *et al.* 2000; Tilman 2000; Fridley 2001; Loreau *et al.* 2002; Naeem 2002; Hooper *et al.* 2005). This has led to much debate about whether diversity is the cause or the consequence of ecosystem productivity (Grime 1997; Huston 1997; Fridley 2002; Worm & Duffy 2003; Gross & Cardinale 2007).

Over the past several years, ecologists have begun to re-evaluate the mechanistic bases of PDR, and a number of conceptual and mathematical models have helped clarify how the different variables that have been the focus of past research might be related to one another. One advance was made by Loreau *et al.* (2001) and Schmid (2002), who separately used graphical models to distinguish between the ‘potential’ productivity of an ecosystem, which is determined by the availability of resources that limit the growth of a particular trophic group of organisms (say plants), and the ‘actual’ productivity of an ecosystem, which is determined by how efficiently that group of organisms captures limited resources (say nutrients or light) and converts them into biomass. They argued that variation in the availability of limiting resources (potential production) across ecosystems constrains the diversity of competing species, whereas the number of competing species within any given ecosystem determines how efficiently the available resources are converted into new tissue (actual production). Gross & Cardinale (2007) formalized key elements of this idea by linking a widely used model of competition that describes how resource supply can limit species richness (resource-ratio theory, Tilman 1982) to a meta-community model (Holyoak *et al.* 2005) that distinguishes between the richness of species in a ‘regional’ colonist pool from the richness of species that compete for resources within a ‘local’ community. Their model argued that three causal pathways operate concurrently to influence the production of biomass by a local community: (i) resource availability directly affects the standing stock biomass and/or rate of new production by primary producers, (ii) resource availability affects the fraction of species from a colonist pool that can locally coexist in a community and (iii) richness of a colonist pool influences how efficiently limited resources are captured by a local community and converted into new biomass. Their model was later called the ‘Multivariate Productivity-Diversity’ hypothesis by Cardinale *et al.* (2009) who showed that the proposed set of three causal pathways could

reproduce PDR observed in numerous streams in the western United States.

In this paper, we add to the renewed discussion of PDR by outlining a potential improvement to recent multivariate models. We argue that when we consider how resources affect the richness of competing species, it is important to distinguish between the total ‘availability’ of resources that ultimately affects the absolute population sizes of species, and resource ratios that dictate the ‘imbalance’ in supply rates that can influence local coexistence (Braakhekke & Hooftman 1999). Resource availability and imbalance have been the focus of two different bodies of ecological theory about PDR, but it is not widely appreciated that each can have a qualitatively different impact on species richness. Our paper is organized as follows. First, we briefly review three bodies of literature that are relevant to our ideas, and outline what each has contributed to our understanding of PDR. We argue that species energy theory (SET) was primarily developed to predict how the total availability of all limiting resources can influence richness by reducing rates of stochastic extinction. In contrast, resource ratio theory (RRT) was developed to describe how the imbalance of different types of limiting resources can moderate interactions among competitors and, in turn, the number of locally coexisting species. In contrast to both of these, which focus on how resources influence diversity, the field of *Biodiversity–ecosystem functioning* has focused on how the richness of competing species controls the fraction of available resources that are captured and converted into biomass. We argue that each field has unique information that can be fit together into a multivariate hypothesis outlining how species richness, biomass production, and both the availability and ratios of limiting resources might be causally related. We then use a large, observational data set on the diversity of phytoplankton in Norwegian lakes to illustrate how our hypothesis can be tested, and conclude by discussing the limitations and future development of our ideas.

THEORETICAL BACKGROUND

In this section we briefly review three bodies of research that have contributed to our understanding of PDR. Our goal is to show that these three bodies of research have focused on different variables that all contribute to PDR, but which do so in mechanistically distinct ways.

Species-energy theory

Species-energy theory (SET) is a body of research that was formalized in the 1980s, and was stimulated by a seminal paper by Wright (1983). The goal of SET is to predict how species richness in a local community is influenced by

‘available energy’, which as we show below, was originally conceived to be the summed availability of all resources that might limit species population sizes. SET is perhaps the most widely cited explanation of why species richness tends to increase with increasing ‘productivity’ of an ecosystem (Fig. 1a). It has been used to explain both monotonically increasing PDR, as well as the increasing portion of the unimodal PDR (see Rosenzweig & Abramsky 1993). According to SET, as the productivity of an ecosystem goes up, so do the population sizes of the resident species. For rare species, an increase in population size leads to a reduced risk of stochastic extinction, which increases the total number of species that co-occur in any given location (Wright *et al.* 1993). Srivastava & Lawton (1998) referred to this as the ‘more-individuals’ hypothesis in their review of mechanisms that generate PDR.

There are at least three things that are important to point out about SET. First, and importantly, SET only predicts monotonically increasing PDR; it fails to predict decreasing PDR. Second, SET assumes no direct causal relationship between productivity and species diversity. Productivity, which is usually represented as the summed abundance or biomass of species in a local community, is only related to diversity because each is independently controlled by a third variable that Wright (1983) called ‘available energy’. As available energy goes up, this leads to both greater population sizes (and thus, total biomass production) and more species. Third, SET provides only a vague notion about what ‘available energy’ represents mechanistically. Wright (1983) originally defined available energy as ‘the rate at which resources available to the species of interest are produced’, and went on to say:

‘available energy should be estimated by considering what amount of energy production in general is available to a given group of species, due to the unique requirements and constraints of that group. For example, a measurement of energy available to plants might recognize solar energy as the ultimate source of plant energy, and then also take into account constraints on the usability of raw solar energy due to factors such as lack of water or nutrients.’

In a later attempt to provide a more rigorous definition, Wright *et al.* (1993) developed a simplistic binomial model that showed how the probability of observing any single species in a community is influenced by the number of ‘packages’ of energy, which in this model represented an amalgam of every possible resource on which a species might depend. The model assumed that a certain number of packets were required to maintain at least one individual of a given species; therefore, as the number of packets increases (i.e. ‘productivity’ increased), more rare species could maintain viable population sizes in a community.

So crudely, when SET has referred to ‘available energy’, it is presumed to represent an aggregate measure of the

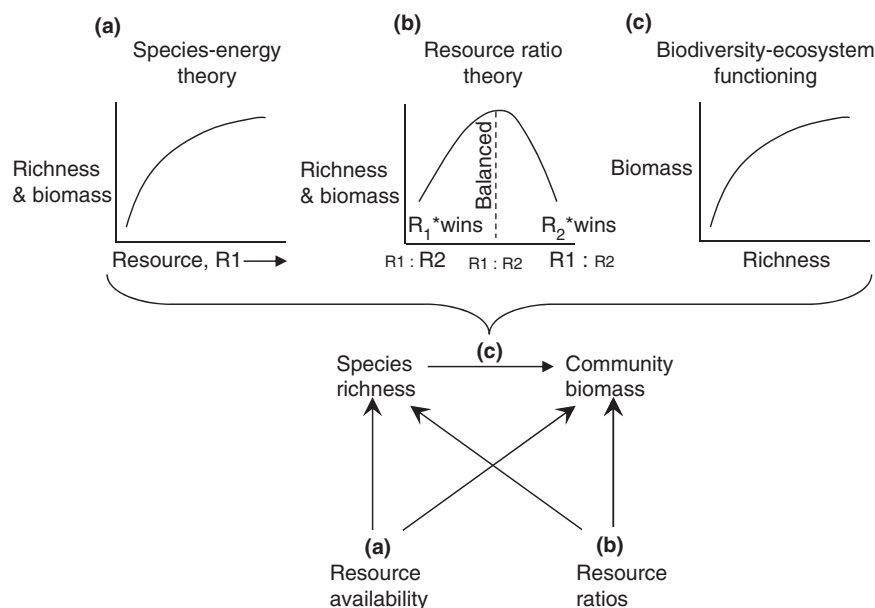


Figure 1 Three theories that make differing predictions about productivity–diversity relationships (PDR). (a) *Species energy theory* argues that the richness and biomass of species in a local community should increase monotonically with the availability of energy or other limiting resource. This is because species population sizes increase as a function of resource availability, which decreases stochastic rates of extinction of rare taxa. (b) *Resource ratio theory* argues that as the availability of any one resource increases, R1, some other resource is likely to become limiting, R2. Because different species are superior competitors for different resources, a balanced resource supply between R1 and R2 can help maintain species coexistence. When species coexist by niche partitioning, community biomass is also higher. (c) The field of *Biodiversity and Ecosystem Functioning* predicts that the efficiency by which communities capture resources and convert those into new biomass is determined by the richness of the community. In the bottom figure, we outline how the focal variables of these different bodies of research might be integrated.

summed availability of all resources that might limit the production of an assemblage of organisms. When talking about plants, Wright specifically referred to available sunlight, water and inorganic nutrients. While there can be little doubt that the availability of all these resources influences species population sizes and, in turn, has some influence over species richness, it also seems clear that we cannot simply lump all potentially limiting resources together into a single qualitative measure and have any hope of emerging with a clear understanding of what limits species diversity. We must consider not only the total availability of resources in a system, but also the fact that resources are not necessarily equally required by all of the different species in a community, nor are resources equally available within a system relative to the needs of the organisms. This point is one that has been made independently by several different fields of research, including studies of ‘ecological stoichiometry’ (Sterner & Elser 2002) and ‘geometric frameworks’ used to understand animal nutrition (Raubenheimer & Simpson 2004). Resource ratio theory was developed, in part, to account for the possibility that species coexistence may depend on the ratios at which different resources are supplied relative to the resource requirements of competing organisms.

Resource ratio theory

Resource ratio theory (RRT) is a well-established and widely used explanation of competition and coexistence (Fig. 1b). This theory is frequently used to explain the concave-down relationship between species richness and productivity, which occurs as a result of two key assumptions. First, RRT assumes that monotonically increasing PDR (as in Fig. 1a) are theoretically impossible because high levels of any one resource (e.g. nutrients) will ultimately cause some other resource (e.g. light) to become limiting. A corollary is that greater numbers of limiting resources in balanced supply allow greater numbers of coexisting species (Interlandi & Kilham 2001), and therefore, combined changes in supply and ratio of multiple limiting resources drive the joint response of productivity and diversity (Harpole & Tilman 2007). Second, this theory also assumes that no single species can simultaneously be the ‘best’ competitor for all potential resources that might limit the growth of species in a community. Instead, species inherently have trade-offs in the efficiency by which they capture and/or utilize different resources (Tilman 1977, 1980, 1982). For example, a plant may allocate growth to roots such that it is a good competitor for below-ground nutrients, or it may allocate growth to aboveground shoots to be a

superior competitor for light. But because a plant faces an inherent trade-off between allocation to roots or shoots, it cannot be the best competitors for all resources simultaneously (or so the theory goes).

When the two aforementioned assumptions are met, RRT predicts that multiple species can coexist when the supply of two or more resources are ‘in balance’ – meaning the different resources are supplied at rates that are intermediate relative to the needs of the organisms. Intermediate supply rates can ensure that different species are limited by different resources such that they can coexist by exhibiting trade-offs in their competitive abilities (Tilman 1980, 1982; Grover 1997). However, whenever one resource becomes more abundant than others (i.e. the ratio of supply is imbalanced), the single best competitor for the most limiting resource comes to dominate the biomass of a community to the exclusion of other species (i.e. the species with the lowest R^* for resource λ).

As is true of SET, RRT makes a number of simplifying assumptions about the nature of species interactions, and it ignores many aspects of spatial and temporal heterogeneity, as well as a variety of trophic interactions, that are thought to influence species coexistence. As such, some have questioned the relevance of RRT to natural systems, and summaries of existing data have emphasized that RRT has yet to receive adequate empirical testing and support (for a summary, see Braakhekke & Hooftman 1999). In spite of these limitations, RRT ranks among the best developed theories of competition, and it is one of the most widely used explanations of PDR (Miller *et al.* 2005). One important point to keep in mind about RRT is that, like SET, the production of biomass is not the proximate cause of species richness. Rather, it is the ratio of supply of different resources – or more precisely, the imbalance in the supply of two or more resources relative to the needs of the competitors – that limits how many species can locally coexist via resource partitioning. By regulating the number of species that can coexist through resource partitioning, resource ratios simultaneously impact community biomass.

Biodiversity and ecosystem functioning

Biodiversity and ecosystem functioning (BEF) is a paradigm in which ecologists have viewed the relationship between species diversity and productivity from a fundamentally different angle, asking how diversity controls, rather than responds to, the production of biomass (Chapin *et al.* 2000; Tilman 2000; Fridley 2001; Loreau *et al.* 2002; Naeem 2002; Hooper *et al.* 2005). This view became prominent in the 1990s after seminal experiments showed that reducing the number of herbaceous plant species leads to less efficient use of soil nutrients and lower plant biomass (Tilman *et al.* 1996; Hector *et al.* 1999). Since that time, more than 200

experiments have manipulated the richness of bacteria, fungi, plants and animals to examine how the number of species impacts productivity in terrestrial, freshwater and marine ecosystems (Schlapfer & Schmid 1999; Covich *et al.* 2004; Hooper *et al.* 2005; Stachowicz *et al.* 2007). At least five recently published meta-analyses have summarized the findings of experiments performed to date (Balvanera *et al.* 2006; Cardinale *et al.* 2006, 2007; Worm *et al.* 2006; Stachowicz *et al.* 2007). These analyses have shown that experimental reductions in species richness can reduce the efficiency by which communities capture resources and convert those into new biomass by as much as 50%. This generally occurs due to two types of mechanisms: (i) Complementarity stems from multi-species effects whereby species in diverse communities use resources in ways that are either different from one another in space or time, or that facilitate each other's efficiency and production of biomass, and (ii) Selection stems from single-species effects whereby diverse communities are more likely to contain and become dominated by a species that is highly productive. The key point here is that BEF argues that species richness is the proximate cause of community biomass because the number of species in a community dictates how efficiently resources are captured and converted into new tissue.

A MULTIVARIATE HYPOTHESIS

We believe that SET and RRT both outline necessary, but not sufficient, conditions for species coexistence in local communities based on the availability of resources. At local scales where species in a focal trophic group compete for shared resources, RRT predicts that the right balance of resources is needed for local coexistence to maintain diversity. At the same time, SET argues that each resource must be abundant enough so that populations of different species can persist above a minimum viable size. While RRT and SET both predict how species richness should vary with different aspects of resources, BEF predicts how diversity should influence the efficiency of resource use and production of new tissue. Taken collectively, these three paradigms suggest that PDR involve at least four distinct, non-interchangeable variables: (i) the overall availability of limiting resources, (ii) the stoichiometric ratios of different limiting resources, (iii) the summed biomass produced by a group of potential competitors and (iv) the richness of co-occurring species in a local competitive community.

Here we outline a multivariate hypothesis that proposes one way in which the aforementioned variables might be related to one another (Fig. 1). We argue that richness in any local community of interacting species is simultaneously influenced by the availability of limiting resources that regulate population sizes, and by the stoichiometric ratios of different limiting resources that impact the potential for

coexistence of competing species. Increases in the absolute magnitude of a limiting resource in an ecosystem will generally increase species richness by increasing population sizes until the point that the availability of resources becomes imbalanced. When the availability of resources becomes imbalanced, we predict that diversity will generally decline as the availability of one resource (say nutrients) increases disproportionate to the availability of another resource (say light). We might, therefore, expect the highest levels of species richness to occur when all resources are available in large quantities and, at the same time, the ratio in the supply of different resources are in balance with respect to the needs of the competitors. In contrast, we would expect diversity to decrease along an axis of lower total resource availability as well as along an axis of imbalanced resource supply.

At the same time that species richness is a function of the availability and imbalance of different resources, we propose that the production of biomass in a community is a function of species richness, as well as the direct impact of resource availability and imbalance. As resource availability and imbalance determine the number of co-occurring species, the number of co-occurring species dictates how efficiently those resources are utilized and converted into new biomass (as in Ptacnik *et al.* 2008; Cardinale *et al.* 2009). As species richness increases, so too does the amount of community biomass. We also expect biomass to increase as a function of overall resource availability, and to be higher when resource ratios are more aligned with the needs of the focal group of organisms. Importantly, this conceptual model assumes no reciprocal causal effect of productivity (*per se*) on diversity, as has been assumed by some (Grace *et al.* 2007). Indeed, none of the theory discussed in this paper provides any mechanism by which production can directly control species diversity (though it may indirectly influence richness by altering the availability or imbalance of resources).

Figure 1 predicts that any relationship between species diversity and the production of community biomass is the product of several direct and indirect causal pathways linking biomass to the availability and imbalance of different resources. If this multivariate hypothesis is a viable explanation of PDR, then three predictions must all simultaneously hold true.

- (1) Ecosystems characterized by a greater total availability of resources should also have a greater number of species and summed biomass of those species.
- (2) Ecosystems characterized by a greater imbalance in the supply of different resources should show lower levels of species richness and summed biomass.
- (3) When resource availability and imbalance are held constant, summed biomass should increase as a function of species richness.

EMPIRICAL EXAMPLE

In this section we illustrate how our multivariate hypothesis might be tested by examining patterns of covariation between algal species richness, algal biomass, and both the availability and imbalance of three potentially limiting resources (light, nitrogen and phosphorus) in an extensive data set for Norwegian lakes. By including resource ratios, our analysis is an extension of a previous analysis, which has shown that algal biomass is a function of both the amount of limiting resources and species richness of the phytoplankton community (Ptacnik *et al.* 2008). Before going further, we should point out that this data set was not specifically collected for purposes of testing our multivariate hypothesis. As such, there are a number of limitations that make the data set less than ideal for scrutinizing our ideas, and we discuss these limitations at length at the end of our paper. However, we should also point out that despite considerable effort, we have found few studies with the data needed to evaluate our hypothesis. In the absence of having studies that were specifically designed to test our hypothesis, we present our analysis of the Norwegian lakes data primarily as an example of how one might go about testing our ideas.

Data set

This data set originates from various monitoring programmes carried out in Norway between 1987 and 2000 (Moe *et al.* 2008), and collectively comprises 2657 samples taken from 492 lakes (Fig. 2). The largest monitoring programme encompassed 1370 samples from 374 lakes (Hessen *et al.* 2003). All chemical and biological variables were analysed by standardized methods in the same laboratory (Hessen *et al.* 2003), which gives confidence in the comparability of measures among lakes. Phytoplankton species richness was estimated by standard limnological techniques that are widely used to count and assess algae (Utermöhl 1958). The data set also contains information on algal biomass, measured as concentration of chlorophyll-*a* L^{-1} , plus two potentially limiting resources (nitrogen, phosphorus). Total nitrogen (TN, $\mu\text{g L}^{-1}$) and total phosphorus (TP, $\mu\text{g L}^{-1}$) represent the sum total for the two nutrients that most frequently limit the production of algal biomass in freshwater ecosystems (Elser *et al.* 2007). The third potentially limiting resource, light, was not measured *in situ*, but rather, was obtained from a separate database that has geographical estimates of photosynthetically active radiation (PAR) that could be cross-referenced to the dates of sample collection (Pinker & Laszlo 1992). Ideally, all potentially limiting resources would be measured as supply rates (amounts per area or volume per time), which conform better to the assumptions of the previously

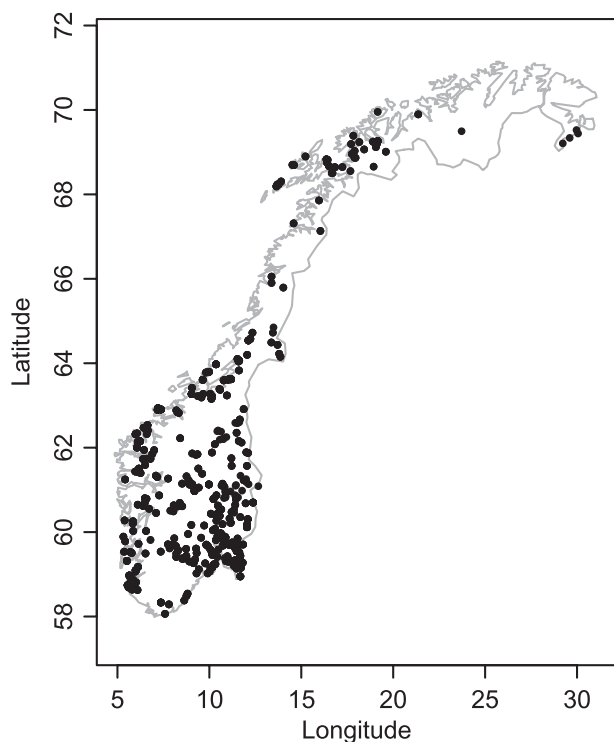


Figure 2 Map showing locations of Norwegian lakes. Data analysed in this paper originate from various monitoring programmes carried out in Norway between 1987 and 2000, and collectively comprises 2657 samples taken from 492 lakes. The data set contains information on algal biomass (chlorophyll-*a* L^{-1}), algal richness (no. species per lake) and three potentially limiting resources (nitrogen, phosphorus, and light).

discussed theories than do standing stocks measured at a single point in time. Unfortunately, empiricists seldom measure rates of resource supply in these types of studies; thus, we focus on the data available in the following analyses with the caveat that stocks may or may not be proportional to supply.

Separating resource availability from imbalance

In order to test our multivariate hypothesis, we must first come up with a means to separate the quantity of resources like N, P and PAR from the ratio in the availability of these different resources. To do so, we used Euclidean geometry. Although we did this for the three resources simultaneously, and although the method can be generalized to any number of resources, it is easier to illustrate the method in two-dimensional space (Fig. 3a). Assume that R_1 and R_2 represent resources 1 and 2, respectively, and that these resources have been measured in a consistent manner across a wide variety of lakes. When measurements are standardized to have a mean of zero and standard deviation of 1,

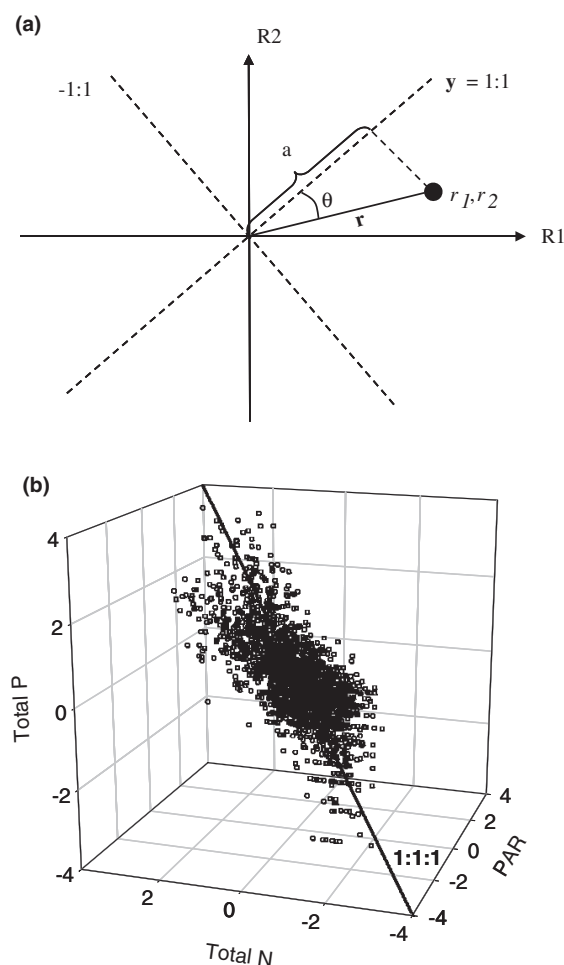


Figure 3 (a) A two-dimensional representation of the Euclidean geometry used to separate the total availability of resources from the (im)balance in the availability of individual resources. (b) A depiction of the resource vectors in three-dimensional space for the Norwegian lakes data set. Axes represent values of nitrogen, phosphorous and light (each dot represents one lake).

changes on the coordinate system $R_1 \times R_2$ are in units of standard deviations from the mean value of all lakes. The purpose of standardizing is to rescale resource measurement units to a common scale and makes no assumptions about stoichiometric requirements or constraints (e.g. Redfield ratios).

Let us define \mathbf{y} (a vector of 1s) to be a ‘reference’ vector where a 1 standard deviation increase or decrease in R_1 corresponds to an identical 1 SD change in R_2 . In other words, \mathbf{y} defines the vector where changes in the amount of the two resources among lakes are identical to one another relative to the overall variation among lakes. Now assume that the amount of resources R_1 and R_2 available in a single lake are given by the resource vector $\mathbf{r} = (r_1, r_2)$. Define the length of \mathbf{r} as the distance from the origin (0, 0) to the point

(r_1, r_2) , which is denoted $\|\mathbf{r}\|$ and can be calculated for any n number of resources as

$$\|\mathbf{r}\| = \sqrt{\sum_{i=1}^n (r_i)^2} \quad (1)$$

For a particular resource vector \mathbf{r} we define two quantities. The first is the (signed) length of the projection of \mathbf{r} onto the reference vector \mathbf{y} , which we call a and calculate as

$$a = \frac{\mathbf{r} \cdot \mathbf{y}}{\|\mathbf{y}\|} \quad (2)$$

where $\mathbf{r} \cdot \mathbf{y}$ is the dot product of \mathbf{r} and \mathbf{y} (also known as the scalar product)

$$\mathbf{r} \cdot \mathbf{y} = \sum_{i=1}^n r_i y_i = r_1 y_1 + r_2 y_2 + \dots + r_n y_n \quad (3)$$

The value a is a measure of the total amount of resources available. It is positive whenever the sum of the r_i 's is positive (i.e. lie above the line of negative covariance in Fig. 3), and negative otherwise. Thus, highly negative values of a represent scarce resources relative to all lakes in the data set, while highly positive values represent highly abundant resources.

In addition to total resources, we also use the resource vector \mathbf{r} to measure the relative balance or imbalance among the supplies of individual resources, relative to their

variation among lakes. We measure (im)balance by the angle between \mathbf{r} and the reference vector \mathbf{y} , which we denote as θ . This angle is computed as

$$\theta = \begin{cases} \cos^{-1}\left(\frac{\mathbf{r} \cdot \mathbf{y}}{\|\mathbf{r}\| \cdot \|\mathbf{y}\|}\right) & a \geq 0 \\ 180^\circ - \cos^{-1}\left(\frac{\mathbf{r} \cdot \mathbf{y}}{\|\mathbf{r}\| \cdot \|\mathbf{y}\|}\right) & a < 0 \end{cases} \quad (4)$$

The angle θ achieves its minimum value of 0 degrees when all resources are perfectly balanced, in the sense that all resources are either equally abundant or equally scarce relative to their variation among lakes. In contrast, the angle θ achieves its maximum value of 90 degrees when all resources are maximally imbalanced, in the sense that excesses of some resources are exactly offset by deficits of others. Importantly, θ is independent of the quantity of resources represented by a , and as such, it is an unfounded measure of relative resource imbalance.

Analyses and results

To begin, we examined the bivariate relationships among variables using simple Pearson correlations, and linear or polynomial regression to illustrate the patterns of covariation (Fig. 4). Several things are worth noting. First, there is a concave-down relationship between algal biomass (measured consistently as chlorophyll-*a*) and algal species richness (no. algal species = $24 + 19 \log_{10}[\mu\text{g Chl-}a \text{ L}^{-1}] - 7 \log_{10}[\mu\text{g}$

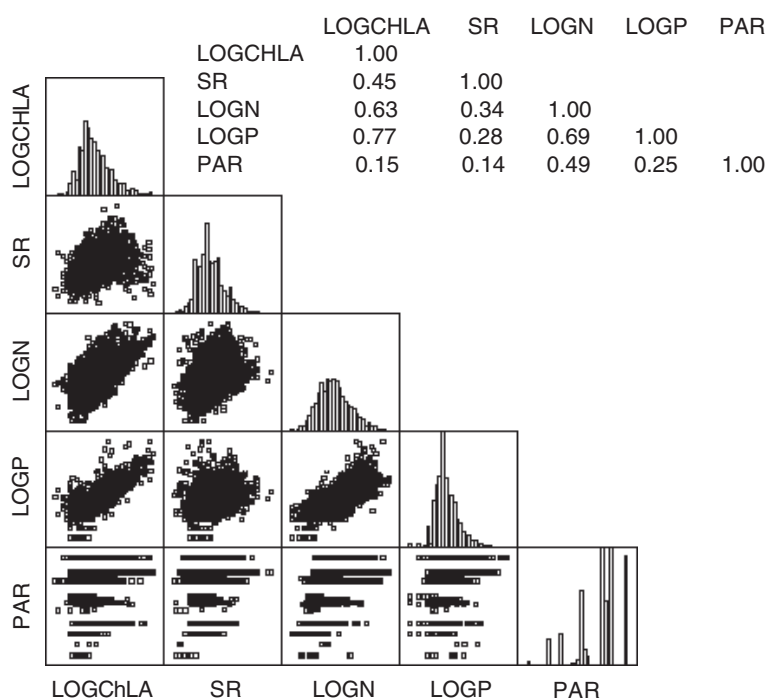


Figure 4 Bivariate relationships and Pearson correlation coefficients between algal species richness (SR), algal biomass (as Chl-*a*) and the availability of three different resources that are generally thought to limit the biomass of freshwater algae (total N, total P and PAR).

$\text{Chl-}a \text{ L}^{-1}]^2$ with chlorophyll centred to reduce correlations with the polynomial term, $P < 0.01$ for both the linear and polynomial terms). This is the typical unimodal relationship that has been observed for a variety of organisms in many different ecosystems (Waide *et al.* 1999; Mittelbach *et al.* 2001). As described in the earlier sections of our paper, this is probably not a causal relationship. Rather, all theory discussed in this paper predicts that species richness and biomass are related simply because each is influenced by the availability of resources. The univariate relationships do indeed show that algal biomass and algal species richness are both positively correlated (albeit, to differing degrees, Fig. 4) with each of the three resource variables (N, P and PAR). But all three of the resource variables are also correlated with one another – N and P are very strongly positively correlated, whereas both are weakly positively associated with changes in PAR. The fact that all of the proposed causal and response variables in this data set are highly correlated suggests that the univariate relationships (such as plots of richness vs. community biomass) have potential to give misleading, even spurious relationships. Thus, it is important to test our multivariate hypotheses through a more direct means.

To test our multivariate hypothesis directly, we used a Structural Equations Model (SEM) to ask whether relationships between algal richness, algal biomass, resource availability (a from eqn 2), and resource ratios (θ from eqn 4) in the Norwegian lakes data set could be explained by our multivariate model in Fig. 1. SEM is an extension of general linear models in which a set of linear regressions is solved simultaneously to ask whether an entire covariance matrix is consistent with a hypothesized set of causal pathways (Shipley 2000; Grace 2006). Based on our analyses, we were unable to reject our hypothesis as a candidate explanation of the data (Fig. 5). A chi-squared test indicated that there was no significant deviation between the observed covariance matrix and that predicted by the proposed SEM ($\chi^2 = 1.18$, $P = 0.28$). Each of the individual pathways in the model was highly significant (all $P < 0.01$, see Table 1). Path coefficients indicated that algal species richness and biomass both increased as a function of the total availability of resources in any single lake. At the same time, species richness and biomass both decreased as resources became increasingly imbalanced in their availability (as indicated by θ). The model also indicated a significant direct effect of species richness on biomass that was positive, as well as significant indirect effects of a and θ on biomass that were mediated through changes in species richness.

When we constructed simplified SEM that ignored any of the proposed effects on community biomass (i.e. models that excluded effects of species richness, resource availability or resource ratios), all proved to be a significantly inferior fit to the data set (Table 1). Indeed, all three simplified models had likelihoods that approached zero, whereas a

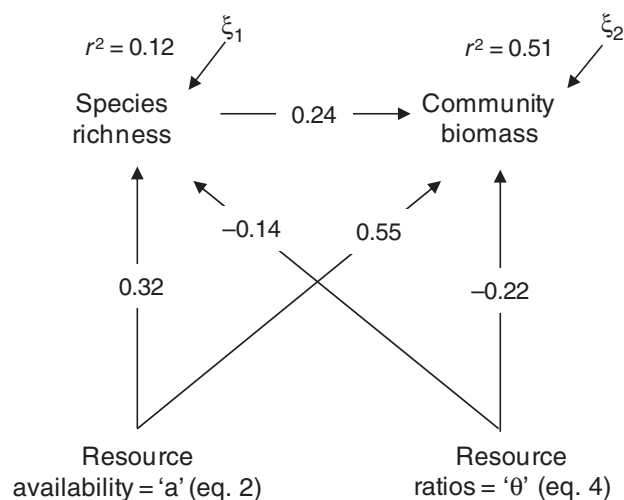


Figure 5 Results of a Structural Equations Model (SEM) used to test whether covariance among variables measured in the Norwegian lakes data set could have been produced by the covariance matrix that is predicted from the multivariate hypothesis given in Fig. 1. The coefficients for each arrow give the standard deviation change in each downstream variable Y per unit standard deviation in each upstream variable X . Epsilons represent the error term for each 'downstream' variable, with the amount of variation explained by the model given by R^2 values at top. Metrics of overall model fit suggest that the model cannot be rejected as a potential explanation of covariance in the data set ($\chi^2 = 1.18$, $P = 0.28$).

model that simultaneously accounted for effects of diversity, resource availability and resource ratios had a likelihood that approached unity. This suggests that the model in Fig. 5 was by far the most likely explanation of the data among the alternatives considered here. To the extent that this hypothetical model is correct, our analyses suggest that algal community biomass is a function of three direct (resource availability \rightarrow biomass, resource ratios \rightarrow biomass and species richness \rightarrow biomass), and two indirect causal pathways (resource availability \rightarrow richness \rightarrow biomass, resource ratios \rightarrow richness \rightarrow biomass). In total, more than 50% of all variation in algal biomass could be explained by this model. By comparison, only 12% of species richness could be explained (a limitation we discuss next).

SUMMARY AND CONCLUSIONS

Here we have added to recent discussions (Loreau *et al.* 2002; Schmid 2002; Gross & Cardinale 2007; Cardinale *et al.* 2009) that attempt to clarify how resource supply, species richness, and biomass – all distinct variables that have been the focus of past productivity–diversity research – might be causally related. Like others (e.g. Abrams 1995; Schmid

Table 1 A comparison of different Structural Equation Models (SEMs) used to explain patterns of covariance among variables measured in the Norwegian lakes data set. Beginning with the ‘base’ model presented in Fig. 5, we deleted paths to represent simplified models where effects of species richness, resource availability or resource imbalance were not considered explicitly. For each model, we report the degrees of freedom, chi-squared and *P*-value. Using the Akaike Information Criterion (AIC), we calculated the likelihood that each model m_i was the best fit to the data, $L(m_i|y)$, among the candidate models. For each model we report the unstandardized path coefficient (standardized values of the base model are given in Fig. 5), the standard errors and *P*-values

| Model, m_i | Description | Individual path | | | Entire model | | | | | |
|--------------|---|-----------------|-------|-----------------|--------------|----------|-----------------|------|-------|------------|
| | | Estimate | SE | <i>P</i> -value | d.f. | χ^2 | <i>P</i> -value | AIC | A_i | $L(m_i y)$ |
| Model I | Base model in Fig. 5 | | | | 1 | 1.18 | 0.28 | 27 | 0 | 1.000 |
| Path 1 | Richness = $f(\text{resource quantity}, a)$ | 2.250 | 0.140 | < 0.01 | | | | | | |
| Path 2 | Richness = $f(\text{resource ratios}, \theta)$ | −0.060 | 0.010 | < 0.01 | | | | | | |
| Path 3 | Community biomass = $f(\text{resource quantity}, a)$ | 0.190 | 0.010 | < 0.01 | | | | | | |
| Path 4 | Community biomass = $f(\text{resource ratios}, \theta)$ | −0.004 | 0.000 | < 0.01 | | | | | | |
| Path 5 | Community biomass = $f(\text{richness})$ | 0.010 | 0.001 | < 0.01 | | | | | | |
| Model II | Base model minus paths with species richness | | | | 2 | 227.21 | < 0.01 | 251 | 224 | 0.000 |
| Path 1 | Richness = $f(\text{resource quantity}, a)$ | 2.250 | 0.140 | < 0.01 | | | | | | |
| Path 2 | Richness = $f(\text{resource ratios}, \theta)$ | −0.057 | 0.010 | < 0.01 | | | | | | |
| Path 3 | Community biomass = $f(\text{resource quantity}, a)$ | 0.214 | 0.005 | < 0.01 | | | | | | |
| Path 4 | Community biomass = $f(\text{resource ratios}, \theta)$ | −0.005 | 0.000 | < 0.01 | | | | | | |
| Model III | Base model minus paths with resource ratios | | | | 3 | 255.80 | < 0.01 | 278 | 251 | 0.000 |
| Path 1 | Richness = $f(\text{resource quantity}, a)$ | 2.270 | 0.140 | < 0.01 | | | | | | |
| Path 3 | Community biomass = $f(\text{resource quantity}, a)$ | 0.190 | 0.010 | < 0.01 | | | | | | |
| Path 5 | Community biomass = $f(\text{richness})$ | 0.010 | 0.001 | < 0.01 | | | | | | |
| Model IV | Base model minus paths with resource quantities | | | | 3 | 1259.30 | < 0.01 | 1281 | 1254 | 0.000 |
| Path 2 | Richness = $f(\text{resource ratios}, \theta)$ | −0.060 | 0.010 | < 0.01 | | | | | | |
| Path 4 | Community biomass = $f(\text{resource ratios}, \theta)$ | −0.004 | 0.000 | < 0.01 | | | | | | |
| Path 5 | Community biomass = $f(\text{richness})$ | 0.010 | 0.001 | < 0.01 | | | | | | |

2002; Gross & Cardinale 2007; Cardinale *et al.* 2009), we have argued that (i) the availability of limiting resources, not the production of biomass *per se*, is the direct proximate cause of species richness, and (ii) biomass is dually influenced by the supply of essential resources that limit production, and the number of species that influence how efficiently limited resources are captured and converted into new biomass. We have further argued that a good deal of confusion has resulted from the fact that some theories consider resource supply to be a single dimension by which the summed quantities of all biologically essential resources influence biomass production and species richness (as in SET). In contrast, other theories have viewed resource supply as inherently multivariate whereby competing species may or may not coexist depending on the imbalance at which two or more essential resources are supplied (as in RRT). This led us to propose a multivariate hypothesis that takes a two-dimensional view of resource supply, separating how summed resource availability impacts species diversity (what Wright 1983 called ‘available energy’; or what Schmid 2002 called environmental ‘fertility’) from how the imbalance in the supply of multiple resources impact diversity.

By condensing three or more resource variables into just two dimensions (supply and imbalance), we obviously lose

potentially important information. But the question is, does a two-dimensional simplification of resource supply retain useful predictive ability? Using an extensive data set of phytoplankton diversity in Norwegian lakes, we found that patterns of covariation linking the richness and biomass of algae to three potentially limiting resources conformed to the three predictions of our multivariate model: (i) Lakes characterized by a greater total availability of resources had a greater number of species as well as greater summed biomass of those species. (ii) Lakes characterized by a greater imbalance in the availability of three different resources (N, P and PAR) had lower levels of species richness and summed biomass. (iii) For a given level of resource availability and imbalance, summed biomass among all algae in a lake increased as a function of species richness. A model that considered these three pathways simultaneously was a far more likely explanation of the data than models where any one of the paths was deleted. Thus, the multivariate hypothesis we have proposed seems, at least, to partially fit the natural patterns of variation observed in these lake ecosystems.

This is not to say that our multivariate hypothesis is correct or even a sole explanation for patterns in the data. In fact, our study suffers all of the obvious limitations of an

observational, uncontrolled study. It would have been more desirable to test our hypothesis using data from an experimentally controlled study that simultaneously manipulated (i) the quantity of resources, (ii) the ratio of resources, and (iii) the richness of species in factorial combination to examine how these factors jointly impact community biomass. To our knowledge, such studies do not exist. It is also important to note that our hypothetical model explained only a modest fraction of variation in species richness, which suggests the hypothesis is, at its best, incomplete. Our limited ability to explain variation in species richness may stem from some of the overly simplistic assumptions of different theories included in our model – all of which are intended to describe the causes and consequences of interactions among species that compete for resources in ‘local’ communities. These theories ignore many forms of heterogeneity that are known to influence the coexistence of species in a local community, such as periodic disturbances that allow for the expression of life-history trade-offs (e.g. the competition–colonization trade-off) and spatial heterogeneity among patches that allow for source–sink dynamics (Leopold 1997; Cadotte 2006). Recent theoretical and empirical studies have made progress towards the integration of meta-community dynamics into PDR (Gross & Cardinale 2007; Cardinale *et al.* 2009), but there are many more potential avenues for refinement.

There are at least two additional limitations of our multivariate hypothesis that are important to keep in mind. First, the model assumes that species competing for resources do not control their own resource availability. In other words, it assumes that resources are supplied externally to the system and/or that recycling is minimal relative to the size of the resource pool. This is an implicit assumption of the three theories that underlie our hypothesis, and this assumption is only likely to apply to ‘open’ systems with considerable donor control. Second, neither our hypothesis nor the data set analysed here have considered the well-known influence of trophic interactions on algae. We have assumed that algae are essentially regulated by bottom-up forces dictated through competition for shared resources; yet, we have ignored the roles that herbivores play in mediating algal dynamics, and ignored the higher trophic levels that might influence algae indirectly via trophic cascades. As such, our hypothesis has limited realism and, at present, we do not have data to extend these ideas to include rates of herbivory or the biomass of species at different trophic levels. But perhaps the analyses presented in this paper will serve as a template for adding the increasing complexities of top-down control as we move towards a more comprehensive model of PDR. Until that time, our analysis of the Norwegian lakes data set is best viewed as a case study and illustration of how a multivariate

PDR hypothesis might be critiqued and improved upon in future work.

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