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What Does Productivity Really Mean? Towards an Integrative Paradigm in the Search for Biodiversity-Productivity Relationships

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Abstract

How species diversity relates to productivity remains a major debate. To date, however, the underlying mechanisms that regulate the ecological processes involved are still poorly understood. Three major issues persist in early efforts at resolution. First, in the context that productivity drives species diversity, how the pathways operate is poorly-explained. Second, productivity *per se* varies with community or ecosystem maturity. If diversity indeed drives productivity, the criterion of choosing appropriate measures for productivity is not available. Third, spatial scaling suggests that sampling based on small-plots may not be suitable for formulating species richness-productivity relationships (SRPRs). Thus, the long-standing assumption simply linking diversity with productivity and pursuing a generalizing pattern may not be robust. We argue that productivity, though defined as 'the rate of biomass production', has been measured in two ways–environmental surrogates and biomass production–leading to misinterpretations and difficulty in the pursuit of generalizable SRPRs. To tackle these issues, we developed an integrative theoretical paradigm encompassing richer biological and physical contexts and clearly reconciling the major processes of the systems, using proper productivity measures and sampling units. We conclude that loose interpretation and confounding measures of productivity may be the real root of current SRPR inconsistencies and debate.

Keywords: biodiversity-ecosystem functioning, pathway, plant-plant interaction, sampling effect, scale, species richness

Introduction

The plant species richness-productivity relationship (SRPR), also known as the diversity-productivity relationship (DPR) or more widely the biodiversity-productivity relationship (BPR), is a central notion of the long-standing biodiversity-ecosystem functioning tenets that fascinate many leading ecologists. Related research includes theoretical models, empirical diversity-manipulation experiments or nature-based observations, or in combination (Cardinale *et al.*, 2009; Gillman and Wright, 2006; Gross and Cardinale, 2007; Hooper *et al.*, 2005; Mittelbach and Scheiner, 2003; Mittelbach *et al.*, 2001; Tilman, 1999; Waide, 1999; Whittaker and Heegaard, 2003; Whittaker, 2010). However, obtained results have been contentious (reviewed by: Hooper *et al.*, 2005; Mittelbach *et al.*, 2001).

First, whether plant community diversity depends on productivity, or productivity depends on diversity, or both simultaneously affect each other (Cardinale *et al.*, 2006; Tilman, 1999; Tilman *et al.*, 1996) is still a major debate. It is clear that both variables are simultaneously affected by physical factors, component species and their interactions, and even history (Fridley, 2001; Fukami and Morin, 2003; Gross and Cardinale, 2007). Additionally, many underlying mechanisms that regulate ecosystem components have

not been identified or well understood. For example, it is commonly asserted that productivity drives species diversity, yet the underlying driving pathways are still under-explained. Second, previous efforts seeking direct causal links between productivity and species diversity and to identify generalizing patterns are often based on a simple reasoning paradigm with paradoxes and dilemmas (Jiang *et al.*, 2009; Tilman, 1999). Positive, negative, hump-shaped or unimodal, U-shaped, and not-significant or no single, generalizable relationships have all been reported (Cardinale *et al.*, 2000; Gillman and Wright, 2006; Mittelbach *et al.*, 2001); the positive relationship has been regarded as a main form in manipulated communities, whereas the unimodal or negative relationships are frequently found in natural communities (Jiang *et al.*, 2009; Rajaniemi, 2003).

Past explanations for the inconsistencies and underlying mechanisms behind the SRPRs have included: (1) spatio-temporal scales, such as plot size (Oksanen, 1996), sampling area and timing (Hooper *et al.*, 2005; MacArthur and Wilson, 1967; Moore and Keddy, 1989; Scheiner and Jones, 2002; Whittaker and Heegaard, 2003); (2) sampling or selection probability effect of productive species, plant size, or other 'hidden treatments' (Aarssen, 1997; Fridley, 2001; Huston, 1997; Oksanen, 1996; Wardle, 1999); (3) spatial heterogeneity and disturbance (Car-

dinale *et al.*, 2000; Grime, 1973; Grubb, 1977; Maranon and Garcia, 1997; Pianka, 1966); (4) life history or successional stage or assembly maturity (Fischer, 1960; Fukami and Morin, 2003; Guo, 2005; Partel *et al.*, 2007; Thompson *et al.*, 2005; Zobel and Partel, 2008); (5) species pool (Hillebrand and Blenckner, 2002; Safford, 2001; Taylor *et al.*, 1990; Weiher, 1999; Weiher and Howe, 2003); and (6) dispersal limitation (Zobel and Partel, 2008), etc. Meanwhile, many variables such as soil resource / fertility (Baer *et al.*, 2003; Fridley, 2002), precipitation (Kay *et al.*, 1997; Rey-Banayas and Scheiner, 2002; Whittaker and Heegaard, 2003), actual evapotranspiration (AET; Rosenzweig, 1995), potential evapotranspiration (PET; Hawkins *et al.*, 2003), biomass production (Gillman and Wright, 2006) and energy (Hutchinson, 1959; Wright, 1983) have been used as surrogates of productivity. However, so far, no substantial consensus has been reached.

Using a 'standardized' field-scale plot sampling across the globe, Adler *et al.* (2011) recently claim that productivity is a poor predictor for species richness, with no exceptions within sites, within regions, or across the globe. They suggest that investigations should focus on the complex and multivariate processes that regulate both productivity and richness. However, after collectively reading over 500 published articles centred on this subject and only based on a terminological examination of *productivity* in the DPR assumption, we are doubtful whether the scientific community has asked the right questions and used appropriate methodology. For example, does habitat productivity actually drive diversity, and how? If diversity indeed drives productivity, how do we choose the time during a year and successional stage to harvest the biomass that measures productivity? What are the primary drivers for both diversity and productivity? Have we rigorously defined proper measures for productivity? Thus, in particular we suspect that there are no robust grounds for the long-standing DPR assumption that attempts to relate biodiversity directly to productivity and to search for generalizing patterns (e.g., Tilman, 1999), because it may be missing certain fundamental elements.

Here, in contrast to previous claims, we carefully re-examine the terminology and measures of *productivity*. We argue that the real root leading to current SRPR controversies may simply rest in the misinterpretation, inappropriate use of variable surrogates, and even an inherent complexity in the definition of productivity *per se*. These problems are also probably due to a flawed or unjustifiable theoretical paradigm. Therefore, the objective of this analysis is to generate an integrative paradigm that can direct future SRPR formulations. It may also help elucidate the root mechanisms underlying current SRPR debates and, eventually, draw more persuasive SRPRs (e.g., explain whether there is a generalized pattern and if the original DPR assumption is robust).

What does productivity really mean?

Productivity was originally defined as the rates of biomass production within an ecological assemblage (Fridley, 2001). However, the evidently casual use, misuse, and even abuse, of the term *productivity* have all been seen in determination of SRPR.

To date, there have been two major schools for using and interpreting the concept *productivity*. One follows the original definition of biomass production. However, this obviously produces a paradox, i.e., if productivity drives biodiversity, what are the driving pathways that link biomass production and diversity in the system? Additionally, can living biomass alone operate as an environmental context that drives species diversity or other variables? In this regard, the answer would be negative. The only biomass production that can be a direct driving resource will reside in the litter, which can in fact be included as a fertility input (Wardle *et al.*, 1997). Taking the view that productivity drives richness, productivity may have been mistakenly viewed as a dominant driver of richness, which has confounded the role of productivity and the real driver behind it. Thus, the widely used annually harvested biomass-based productivity in formulating SRPRs (e.g., Bai *et al.*, 2007; Chase and Leibold, 2002; Guo and Berry ,1998) may need to be re-considered. On the other hand, if species richness indeed drives productivity, choosing the right time during the growing season and successional stage in which to measure productivity is another challenge (Guo, 2005; Thompson *et al.*, 2005). Therefore, this inherent complexity in the definition of *productivity* may raise a need to build a criterion for selecting a proper productivity measure.

The other school interprets productivity using resource supply or environmental surrogates (see reviews and meta-analyses by Gillman and Wright, 2006; Mittelbach *et al.*, 2001; Whittaker, 2010). This raises other questions, i.e., do resource supply and biomass production both play the same role, and can productivity be simply replaced by those surrogates? Since resource supply often operates as a driving force in a system, whereas biomass production is usually the resulting product, the answer may be linked to an 'indirect' effect. It is highly probable that these surrogates can impact the performance of SRPRs. However, there has rarely been any rigorous and clear terminological examination of the definition of *productivity*. Although caution on the use of biomass as a surrogate for productivity has been expressed (Gillman and Wright, 2006; Grace, 1999), little has been done to assess the likely consequences of using these diverse '*productivity*' measures on SRPRs. Researchers often use a biomass-based *productivity* measure, owing to its easy measurability, e.g., above-ground net primary production (ANPP; in some cases, maximized ANPP during the year) (Gillman and Wright, 2006) or other

environmental measures (e.g., resource supply) based on their requirements. In particular, higher *resource availability* usually means higher *productivity* (e.g., the latitudinal gradient of productivity). Therefore, *resource supply* or *environmental context* and biomass-based *productivity* have been confounded with rare exceptions (Cardinale *et al.*, 2009; Gross and Cardinale, 2007). This ill-defined use of productivity measures or surrogates may alter SRPRs. In effect, biomass only accounts for a small proportion of variation in species richness (Grace, 1999), relative to other surrogates of productivity (Gillman and Wright, 2006).

Apart from the above, the presumed DPR assumption that simply relates biodiversity to productivity may have strengthened the confounding effects. In a highly simplified paradigm, much attention may have been paid to within-system elements (e.g., diversity and productivity only), while other critical constituents are neglected. In this light, the flawed paradigm may have hidden consequences. This may be the real 'devil in the detail' that determines how the debate may be settled.

What productivity measure do we need?

However, if we are to continue an interest in the better assessment of SRPRs, it is critical to evaluate the two schools of productivity measures.

Firstly, an environmental surrogate such as resource supply indeed works well as representing productivity statistically on some occasions; however, it remains difficult to find a specified and, ideally, exclusive measure to describe the exact resource supply performance that decides the SRPR. This is mainly because the surrogates themselves should reflect the environmental resource availability that a system can provide to the organisms it contains. Other resource measures such as soil fertility, energy, precipitation, do not meet such a criterion. For instance, precipitation plays a critical role in regulating plant growth, particularly in water-limiting areas. Yet, what really takes influences on the plant is not the overall precipitation, but only the available part of it which the plant utilizes.

Secondly, environmental surrogates should reflect the pooled availability of all resource sources. Therefore, a single environmental context measure, usually with a respective definition, may not be appropriate for describing the overall supply availability within a system. In fact, this has proven to be the case in field experiments which show that nitrogen addition can cause species and/or biomass loss (Crawley *et al.*, 2005; Gough *et al.*, 2000; Suding *et al.*, 2005). In this respect, the difficulty of distilling an ideal environmental surrogate, or in other words, the use of diverse surrogates of productivity, would lead to skewed or varied SRPRs (Gillman and Wright, 2006).

Thirdly, there is significant variation in biomass production both within a growing season and across successional stages. For example, mature and immature assemblages support different plant traits, biodiversity, and ecosystem functioning (Guo, 2005; Thompson *et al.*, 2005). Given no dramatic environmental fluctuation or disturbance in early succession, both species diversity and biomass production would increase through positive interactions (Callaway, 1995), leading to a positive SRPR. In contrast, in late succession, biomass production remains at a relatively high level and species diversity declines due to competitive exclusion, leading to a negative (Thompson *et al.*, 2005) or other forms (Fridley, 2001; Huston, 1997; Jiang *et al.*, 2009) of SRPR. Since most diversity-manipulated communities are still in early assembly stages (Jiang *et al.*, 2009), a positive SRPR is common.

Since it is difficult to separate the effects of species and environmental context on biomass production during the immature stage, we suggest that the measure should be limited within the mature stage of succession (Thompson *et al.*, 2005). On the other hand, an exact sampling time point during the growth period should also be decided. Since there is asynchrony in biomass production over a year (Hector *et al.*, 2010), the widely used ANPP measure might be challenged. Here, we suggest an exact measure that takes into account a yearly summed ANPP of all plant species in the mature assemblage.

Fourthly, even using the selected *productivity* measure, there is still a difficulty in obtaining it in widely used diversity-manipulation experiments, e.g., the BIODEPTH (Hector *et al.*, 2007) and Cedar Creek (Tilman, 1996) experiments. This is because in experiments such as these community maturity is extremely difficult to judge, even after many years of continuing observation, not to mention that Hector *et al.* (2007) use only three years of observation in defence against critiques made by Thompson *et al.* (2005). Since any such experiment can be seen as an independent and episodic event during long-term succession, it is therefore unfortunately the case that no one can really know how long a successional stage will last, even in a relatively stable environment. Therefore, the field plot-scale experiments, especially those in early succession, are manifestly difficult to extend to vast natural and artificial assemblages, and may thus be inappropriate for drawing SRPRs. Though long-term experimentation (through permanent plots) has been considered as a solution to this problem (Bakker *et al.*, 1996), the space-for-time substitution, based on systematic succession expertise at varied scales, e.g., the climax theory, may be more useful (Pickett, 1989).

Scale justification

The issues raised above call for a new and integrated paradigm in the search for more convincing SRPRs. Apart from the afore-mentioned selection of a suitable measure for productivity, scaling is another critical factor that is required for consolidation of the theoretical foundation.

Multi-scaled research efforts have generated inconsistent SRPR patterns, which have also invoked a viewpoint that SRPRs are scale-dependent (Chalcraft *et al.*, 2004; Chase and Leibold, 2002; Gillman and Wright, 2006). However, underlying mechanisms that explain whether those inconsistencies are caused by scaling factors or by other factors, e.g., the sampling effect, are not yet clear. Here, unlike many other related issues, we argue that a fundamental question must first be asked: what scales would be proper or acceptable for drawing SRPRs? Can we draw SRPRs directly based on field plot sampling that pertains to spatial ecology (Loreau *et al.*, 2003)? Or similarly, can we work at a random scale or at spatially multiple scales? This can in fact be answered well by the research of Oksanen (1996), Aarssen (1997), Wardle (1999) and Fridley (2001), if correctly interpreted and extended.

Oksanen (1996) stressed the effects of small quadrat-plot size and plant size within the plot when interpreting an acquired unimodal pattern (Maranon and Garcia, 1997). This effect is also called the sampling effect caused by productive species (Aarssen, 1997; Wardle, 1999). In Oksanen (1996), two basic components, small quadrat-plot and diversified plant size, are required to be available at the same time in order for sampling effect to occur. However, sampling effect would be inevitable, so long as we use small field sampling plots, because plot size is always limited and spatial heterogeneity is ubiquitous, leading to 'hidden treatments' (Huston, 1997). In this respect, the sampling effect should not be viewed as a diversity effect (Naeem, 1999; Tilman *et al.*, 1997; Tilman, 1999), consistent with Wardle (1999).

We thus suggest two methodologies that use ideal 'plots' which would generate no sampling effect in determining a presumed generalizable SRPR. One is the broader scale across-ecosystem method, seeking relationships between large-scale beta or gamma diversity and macroscopic productivity over large areas, e.g., across the globe. Here, the 'plot' unit would be an individual ecosystem. In contrast, the other methodology is based on microcosm experiments (Cadotte, 2006; Fox and McGrady-Steed, 2002; Jiang and Patel, 2008). Interestingly, this has been supported by major evidence from previous large scale SRPR studies and microcosm experiments. For instance, meta-analyses by Mittelbach *et al.* (2001), Mittelbach and Scheiner (2003) and Gillman and Wright (2006) all indicate that SRPRs have an evident converging trend towards fewer patterns (positive and unimodal) or to a positive pattern when spatial scales change from landscape to local, regional, continental and up to global scales. Particularly, this convergence is enhanced when scale changes at the larger limits, e.g., from the continental to global scale, becoming more pronounced when biomass-species richness studies are excluded (Gillman and Wright, 2006). However, differently from the common interpretations of SRPRs being scale-dependent (Chalcraft *et al.*, 2004; Gillman and Wright, 2006), we argue that SRPRs may not

be linked to scale-dependency, but instead should be built on enclosed-system-based 'plots'. In other words, SRPRs cannot be addressed at randomly selected spatio-temporal scales.

In Adler *et al.* (2011), the sampling procedure has been standardized; however, it still pertains to the field scale plot-based sampling method, which, as mentioned before, cannot eliminate sampling effects. Also, the 'standardized' sampling within sites, within regions, and across the globe (with only 48 plant communities sampled) used in the study only considers alpha diversity, not beta diversity. Therefore, although regional and global scales are referred to and no single and generalizable SRPR is found, the across-scale SRPRs still need to be re-examined. Moreover, using an unjustified productivity measure may have generated substantial 'noise' in the obtained SRPRs. Testing whether productivity is a good predictor of richness cannot rely solely on "standardized" sampling, as the terminological issue still persists.

An integrative research paradigm

To test the robustness of DPR assumptions linked to SRPRs, we need a new integrative paradigm with the following highlights.

(1) SRPRs should be fully addressed in a richer context with both elementary ecosystem components and clearly formulated linkages amongst them. At least four components, i.e., environmental context (e.g., resource supply), organism traits, biodiversity, and biomass production, and three mechanistic pathways, i.e., resource use, species interaction and litter decomposition, should be included (Baer *et al.*, 2003; Cardinale *et al.*, 2000; Cardinale *et al.*, 2009; Fridley, 2001; Gross and Cardinale, 2007).

(2) Because of the complexity inherent in the definition, productivity should be re-examined using a rigorously defined measure.

(3) An across-ecosystem examination of the relationships between beta diversity and broad scale biomass productivity over large areas, and the microcosm experimentation, should be used.

Environmental context, such as resource supply, has in fact long been found to be a major driver regulating both species diversity and biomass production (Baer *et al.*, 2003; Cardinale *et al.*, 2000; Fridley, 2002). For instance, Dovciak and Halpern (2010) state that, in natural communities, temporary increases in resource availability caused by climatic fluctuation (Frank and McNaughton, 1991; Tilman, 1996) or disturbance (Halpern, 1989; Schoennagel *et al.*, 2005) can lead to the establishment of colonizing species, rather than to simple repartitioning of resources among resident species (Belote *et al.*, 2008; Davis *et al.*, 2000; Dovciak *et al.*, 2005). While diversity effects, typically interactive mechanisms such as competitive exclusion and facilitation (Cardinale *et al.*, 2006, 2009; Hector and Schmid, 1999; Naeem *et al.*, 1994; Schwartz *et al.*, 2000;

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Srivastava and Vellend, 2005; Tilman *et al.*, 1997), it may only be secondary in regulating productivity relative to environmental context (Ives and Carpenter, 2007; McCann, 2000). Recently, the multivariate productivity-diversity hypothesis (MPD) has been proposed to reconcile the two contrasting perspectives on whether productivity drives diversity and *vice versa* (Cardinale *et al.*, 2009; Fridley, 2001; Gross and Cardinale, 2007; Loreau *et al.*, 2001; Schmid, 2002). Referring to it, we develop an integrative paradigm for the future formulation of SRPRs, as follows (Fig. 1).

In contrast to Cardinale *et al.* (2009) and other multivariate efforts for SRPR formulation, in this new paradigm a measure of productivity has been rigorously defined, justifiable research methods have been examined, and biodiversity and productivity are seen as two of many attributes of organismal assemblages (McCann, 2000). Here, *biodiversity* encompasses not only species number in the traditional sense, but also many new elements, e.g., abundance, composition, and functional roles (Cadotte, 2011; Petchey and Gaston, 2002), depending on the methodologies.

Additionally, the new paradigm encompasses environmental context as the primary driver of both biodiversity and biomass production through resource use pathways by organisms. Biodiversity, as a secondary driver, can affect biomass production through species interactions (e.g., both inter-specific and intra-specific competition and facilitation). However, biomass cannot directly influence biodiversity, but rather does so indirectly through altering the decomposition of litter and thus the resource supply (Fig. 1). This process may be relatively weak because it depends on decomposition conditions (e.g., microbial activity, soil fertility, soil moisture, temperature). However, the long-term accumulative effects may be more profound.

In addition, even under normal conditions at a single-trophic level, environmental fluctuations and diversified species interactions would complicate the shape of SRPRs. Under more complicated conditions, perturbations would affect both environmental context and assembled organisms, and stocking/predation relationships at multiple trophic levels would also influence organisms, which would reshape the performance of the SRPRs. Thus, the new paradigm strongly implies that there may not after all be a generalizable and persistent SRPR.

Concluding remarks

To date, much vigour in ecological research may have been devoted in vain to what has been thought to be a 'major debate', which in effect may rather be only a result of the loose definitions and improper measures for productivity, enhanced by a flawed or vague DPR assumption. In fact, to elucidate how the key components within an ecological assemblage link with each other is not a compelling challenge. This situation may be partly caused by our anxiety about ongoing species loss and extinction threat on a global scale, and by the urgency for biodiversity conservation and productivity enhancement, which is in turn linked to food security, carbon sequestration, and thus concerns about global change. However, our arguments regarding SRPRs should be based on the foundation of fact and justified reasoning. A recent trend that emphasizes the role of biodiversity in enhancing the multifunctionality of ecosystems sounds more persuasive and promising (Hector and Bagchi, 2007; Maestre *et al.*, 2012).

We thus draw the following conclusions as:
(1) Productivity has often been misinterpreted in its definition and has been inconsistently measured in draw-
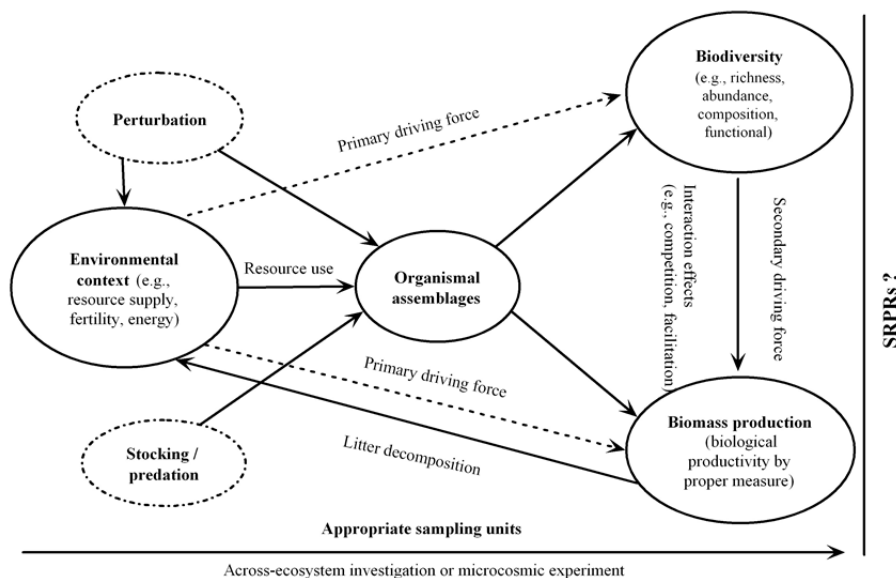

Fig. 1. An integrative single-trophic-level paradigm for SRPR formulations. Major relationships are reconciled among elementary components of ecosystems

ing SRPRs, which may have contributed much to the on-going debate. We thus reexamined productivity in order to form a proper measure.

(2) Multi-scaled studies should not suggest scale-dependent explanations; on the contrary, the implication is that the field small-plot may not be appropriate for drawing SRPRs. SRPRs should not be formulated at random scales; instead, only broader scale across-ecosystem investigation and microcosmic experimentation should be used.

(3) SRPRs should be addressed under a new integrative paradigm. In our paradigm, four key components and three mechanistic pathways have been linked with each other and reconciled; environmental context has been viewed as a primary driver of both biodiversity and productivity through resource use pathways, whereas species interactions and litter decomposition become secondary in formulating the SRPRs.

(4) SRPRs change with time, even in the same system, being complicated by the environmental context and species traits/interactions that are affected by disturbances and stocking/predation. To prompt related biodiversity-ecosystem functioning research, the old-fashioned DPR assumption may need to be revolutionized.

In short, we would like to restate that a major task for ecology is to isolate cause–effect relationships, such as, SR-PRs, in ecosystems where related variables, processes, and patterns can be appropriately identified, measured, and characterized. While identifying a common model is useful, it is time for us to admit that there may not be a single or universal SRPR, because of its highly habitat- and time-specific nature. We hope that, with additional efforts on the right track, a new generation of SRPRs can be placed on a solid foundation and soon come of age.

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