COMMUNITY ECOLOGY 5(1): x-xx, 2004
1585-8553/$20.00 © Akadémiai Kiadó, Budapest

The species richness-productivity relationship: time to stop searching for a "true" pattern?

Y. Ziv[1] and A. Tsairi

Department of Life Sciences, Ben-Gurion University, Beer-Sheva, 84105 Israel
[1] *Corresponding author. E-mail: yziv@bgumail.bgu.ac.il*

Keywords: Conceptual model, Monotonic-increase relationship, Species diversity, Unimodal pattern.

Abstract: Contrary to the past belief that the species richness-productivity relationship (SRPR) is characterized by a single "true" pattern, several analyses have shown that a heterogeneous distribution of SRPRs exist and that the patterns' distribution of a SRPR is sensitive to the directness of the estimates of productivity. A simple conceptual model demonstrates that taking into account underlying relationships connecting productivity with species richness produces heterogeneous distribution of relationships. We suggest that the search for a single pattern for SRPR has reached a dead end, and that we should direct our research focus to exploring the mechanisms responsible for the various SRPRs.

Abbreviation: SRPR- species richness-productivity relationship

Introduction

The relationship between species richness and productivity (SRPR) has attracted much attention in the last decade with an increasing interest in the last few years. In particular, several ecologists have looked for a single "true pattern" (Rosenzweig and Abramsky 1993) and its underlying mechanism. While a few ecologists have demonstrated both theoretically (Abrams 1995) and empirically (Waide et al. 1999) that a diversity of patterns might be possible, many others argued that the unimodal pattern is the most dominant (Rosenzweig and Abramsky 1993) and even ubiquitous (Huston and DeAngelis 1994). However, ecologists in a working group at the US National Center for Ecological Analysis and Synthesis (NCEAS; Santa Barbara, CA) who attempted to analyze and synthesize a large number of datasets with respect to the SRPR (Waide et al. 1999, Gross et al. 2000, Mittelbach et al. 2001) concluded that "*categorization of studies with respect to geographic extent, ecological extent, taxonomic hierarchy, or energetic basis of productivity similarly yielded a heterogeneous distribution of relationships*" (Waide et al. 1999).

In a recent article, Groner and Novoplansky (2003) found that in animal studies the distribution of SRPR patterns was sensitive to the directness of productivity estimates (i.e., whether species richness corresponded to its own productivity or to the productivity of the next lower trophic level). In plant studies, however, a more consistent pattern occurred as plant diversity was always correlated to its own productivity. They suggested that while SRPRs based on direct productivity estimates involve the apportionment of biomass and energy production among certain number of species (see for example Grace 1999), SRPRs based on the productivity estimates of a lower trophic level depend on compound and often complex effects. Such effects may include interactions between primary productivity and trophic interactions, top-down niche specialization, and feedback interactions. As a result, they concluded: *"... 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*".

New conceptual model to suggest that diverse patterns and processes of SRPR may exist

Support for Groner and Novoplansky's conclusion is given by a simple conceptual model that relies on the understanding that productivity does not affect species diversity directly, but rather through intermediate effects.

For simplicity, we suggest that, among others, several factors (variables) are likely to vary with productivity. Three such important factors may be: i) resource quantity; ii) resource diversity; and iii) habitat structure (i.e., the physical environmental heterogeneity that may affect physiological conditions and predation risk). Figure 1A visualizes the relationship between productivity and each of the factors.

Resource quantity (or biomass), in general, increases with productivity (Whittaker 1970), because more energy is available for growth and reproduction (Wright et al. 1993), and hence biomass. Resource diversity may increase monotonically (Wright et al. 1993), increase until reaching a maximum value and then decreases (Abramsky 1989), or remain constant as productivity increases (in the latter case, because resources must have zero diversity at zero productivity, we started line '3' in Figure 1A with a sharp increase from zero to the constant level of diversity). Habitat structure may also increase monotonically (Whittaker 1970), increase until reaching a maximum value and then decrease (Tilman and Pacala 1993), or remain constant (or alternatively, show no effect) as productivity increases.

The ecological literature clearly shows that resource quantity, resource quality, and habitat structure affect species diversity (Figure 1B). Empirical and theoretical studies suggest that an increase of each of these factors can form, among others, both a monotonic-increasing and unimodal relationship with species diversity. As resource quantity increases, more species may persist because more resources support more individuals, which consequently, increase the probability of attracting or sampling more species, especially the rare ones (Preston 1962). However, from a certain point on, the addition of more individuals of a particular species may cause the exclusion of other species (the competition hypotheses; Rosenzweig and Abramsky 1993). Similarly, as resource diversity increases, more species may persist through habitat selection and partitioning mechanisms (Tilman and Pacala 1993). However, as with resource quantity, the addition of more individuals of a particular species beyond a certain point may cause the exclusion of other species. Habitat structure has an enormous effect on species diversity. Species diversity may increase with habitat structure when the latter provides more ecological opportunities, which consequently, promote greater niche separation as well as increased specialization (MacArthur 1972). However, if habitat structure peaks at intermediate levels of productivity (e.g., Rajaniemi 2003), then a unimodal relationship between habitat structure and productivity is possible.

The combination of the possible effects of productivity on environmental factors (Fig. 1A) with the possible effects of environmental factors on species richness (Fig. 1B) produce diverse patterns (Fig. 1C) that characterize different mechanistic pathways connecting productivity and species richness. These patterns clearly suggest that ecologists should not expect to have a single "true" pattern for the relationship between species richness and productivity, and therefore should also not expect a single process or few processes to produce such a "true" pattern. Furthermore, given some of the revealed patterns (e.g., Fig. 1C 4xd and 1C 7xf), other patterns mentioned in the literature, such as a U-shaped pattern (Waide et al. 1999), are plausible. In addition, here, we only focused on resource quantity, resource diversity and habitat structure; however, other ecologists may offer additional or alternative effects (factors) that will be more applicable to their system. We believe that not only does it not contradict our approach, but, on the contrary, additional factors and higher complexity will only further support our argument. Interestingly, in line of the empirical evidence, our approach does predict that within the existing possibilities the unimodal pattern should be observed more frequently. We also predict that adding more complexity to the intermediate-effect hypothesis will only increase the probability of detecting unimodal patterns. However, the dominance of the expected unimodal pattern does not come from having a single or a small set of mechanisms that produce the "true" pattern, but mainly from statistical relationship between combined effects.

What should our future research focus be?

The articles reviewed as well as the conceptual model presented here, suggest that the search for a "true pattern" between species richness and productivity has reached a dead end. Furthermore, the recent conclusions on the importance of scale dependence in SRPRs (e.g., Gross et al. 2000, Chase and Leibold 2002) further direct our research focus towards understanding the underlying mechanisms. Our simple conceptual development emphasizes that ecologists have just barely begun to deal with the mechanistic explanations for how productivity, through environmental factors, may affect species diversity and composition. One line of exploration towards a mechanistic understanding of SRPRs may focus on how and what processes dominate certain systems or group of organisms. As a result, specific pathways may be more likely to characterize certain systems while other pathways may be more likely to characterize other systems. This line of exploration may allow constraining our predictions with respect to the likelihood of observing a given pattern under a particular situation.

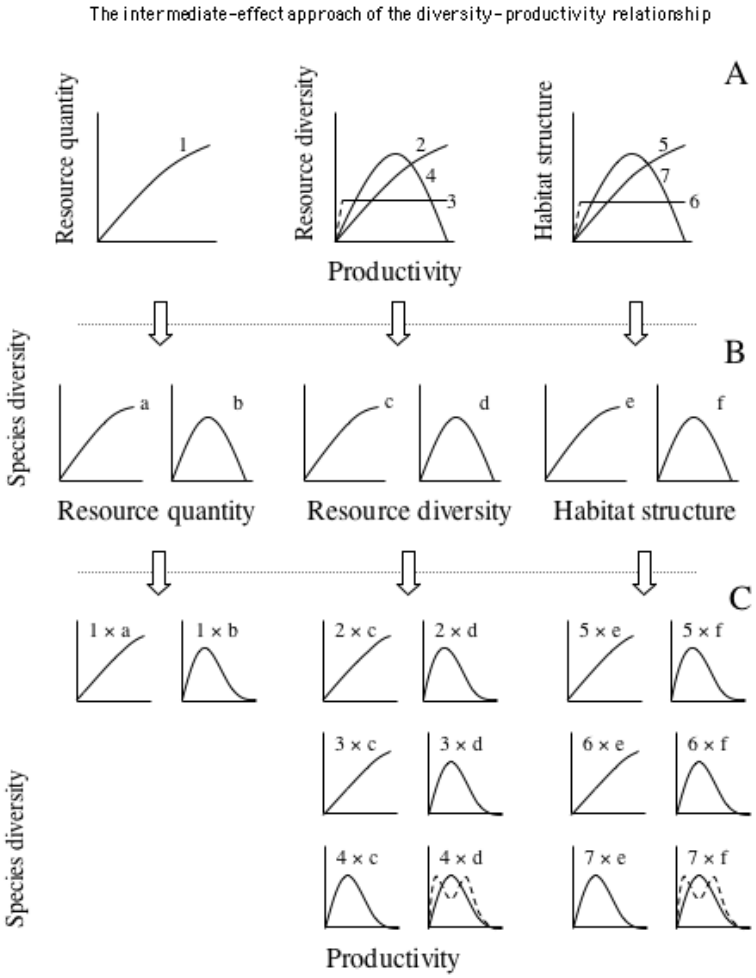

Figure 1. Sequence of mechanistic links of the SDPR. We put all figures in one frame to emphasize the indirect linkage between species diversity and productivity: Figure 1A describes how productivity may affect several environmental factors; Figure 1B describes how each of these factors may further affect species diversity; Figure 1C ties species diversity to productivity by combining Figures 1A and 1B.

Acknowledgements: We would like to thank J. Aukema, A. Ben-Natan, B. Kotler, and Z. Abramsky for their comments on different versions of this article. We would also like to thank J. Podani and two anonymous reviewers for their valuable suggestions. This research was supported by The Israel Science Foundation (grant no. 26/99) to YZ.

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