

CONTRASTING PLANT PRODUCTIVITY–DIVERSITY RELATIONSHIPS ACROSS LATITUDE: THE ROLE OF EVOLUTIONARY HISTORY

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Abstract. The relationship between net primary productivity and biological diversity has been a central topic in ecology for several decades. The unimodal (“hump-back”) relationship has been the most widely accepted for plants with the decrease in diversity at high productivity usually attributed to competitive exclusion. However, the relatively small species pool size under high productivity conditions may account for this pattern as well. Small species pool sizes for highly productive habitats are characteristic of temperate regions, where productive habitats for speciation and species migration have historically been rare. In contrast, productive habitats in the tropics have been relatively common during evolutionary history, resulting in large species pools. We hypothesize that evolutionary history contributes to the observed productivity–diversity relationship of plants, and that the productivity–diversity relationship differs between temperate and tropical regions. We investigated the productivity–diversity relationship patterns from 163 case studies throughout the world. Latitude described ~80% of the variation in the shape of the relationships. The unimodal relationship was found to dominate in the temperate zone, whereas the positive relationship was significantly more common in the tropics. We detected no influence due to methods of productivity measurement, but unimodal or positive productivity–diversity relationships were more likely within larger ranges of productivity. The length of the productivity gradient did not affect the latitudinal influence. In summary, the shape of the productivity–diversity relationship differs between temperate and tropical regions and the different evolutionary history of the local species pools is a probable cause for the difference.

Key words: biodiversity conservation; generality of ecological rules; global diversity patterns; latitudinal gradient; macroecology; meta-study; plant biomass; plant species richness; primary productivity; productivity–diversity relationship; species pool; tropical ecology.

INTRODUCTION

The productivity gradient has very often been related to plant diversity. In most cases there emerges a unimodal relationship, showing the highest diversity at intermediate productivity (Grace 1999, Keddy 2005). The unimodal (also called hump-back or “humped-backed”) productivity–diversity relationship was first described by J. P. Grime for British herbaceous vegetation (Grime 1973, Al Mufti et al. 1977). This approach rapidly gained great popularity among ecologists, and was soon widely recognized as a general empirical relationship (e.g., Begon et al. 1996). Although later studies also reported positive, negative, or U-shaped response patterns, the unimodal relationship remains the most commonly reported one for plants (Waide et al. 1999, Mittelbach et al. 2001; but see Gillman and Wright 2006). Huston (1994), however, warned that this pattern is most likely found in communities with intermediate to high frequencies of disturbance, such as herbaceous plant communities.

At extremely low productivities, only a few organisms are expected to survive. One may consequently expect a simultaneous increase in both the number of individuals and species with increasing productivity. Why, however, does diversity decrease at high productivity? The dozens of explanations can be classified into two groups: those that focus on the changing intensity of biotic interactions (mainly competition) along the productivity gradient, and those that emphasize the different evolutionary history of productive and unproductive habitats within a given region (reviewed in Rosenzweig and Abramsky 1993, Scheiner and Willig 2005).

The original explanation by J. P. Grime focused on biotic interactions and claimed that at high productivity, intense competition results in the competitive exclusion of many species (Grime 1979). In contrast, Goldberg et al. (1999) performed a meta-analysis of competition–facilitation studies with plants, and found that the intensity of competition often declines significantly, instead of increasing with productivity. Since facilitative interactions are more common in unproductive and competitive interactions in productive environments (Kikvidze et al. 2005), Michalet et al. (2006) recently combined both facilitation and competition to explain the unimodal productivity–diversity relationship. Hus-

Manuscript received 13 June 2006; revised 4 December 2006; accepted 15 December 2006. Corresponding Editor: J. A. Jones.

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ton (1979, 1994) showed that competitive exclusion can influence the productivity–diversity relationship by interacting with a local disturbance regime. Seed addition experiments have confirmed the hypothesis of Huston (1994, 1999) and shown that competition may suppress plant establishment in productive habitats—seed sowing only increases richness at high productivity in combination with local disturbance (Foster 2001, Foster et al. 2004). Subsequent research has involved the impact of competition on the number of coexisting species in combination with the effect of habitat heterogeneity and the relative role of aboveground and belowground competition (Rajaniemi 2003).

As empirical knowledge accumulates, there is an apparent need for complementary explanations in addition to those based solely on ecological processes such as competitive exclusion (Abrams 1995, Aarssen 2004). An alternative explanation for the unimodal productivity–diversity relationship is related to the species pool concept, which claims that local diversity is defined largely by the size of the species pool for particular habitat conditions (Taylor et al. 1990, Pärtel et al. 1996, Zobel 1997). The species pool is the set of available species that are potentially capable of living in given ecological conditions (Eriksson 1993). Areas that are widespread and stable over time will feature more species that evolve to suit the local conditions, forming a species pool for a particular region and community, or acting as a diaspora source for other regions (Zobel 1992, Pärtel 2002, Pärtel and Zobel 2007). In particular, Hodgson (1987) has related the low diversity of productive plant communities in central England to the scarcity of this habitat type in the evolutionary scale and thus to the reduced chance for speciation.

In addition to the interaction-based and species pool-based explanations, sampling bias may also affect the shape of the emerging productivity–diversity relationship. A specific method of productivity measurement (e.g., by annual precipitation or standing biomass) may be spuriously related to the shape of a particular productivity–diversity relationship. Nonlinear gradients may also confound ecologists if the observations are made within a limited set of environmental conditions (Huston 2002). For example, no unimodal pattern can be detected if the productivity gradient is too short (Grace 1999, Mittelbach et al. 2001). Similarly, the unimodal relationship is more likely to be found if different community types are analyzed collectively, probably also representing a larger range of productivity (Waide et al. 1999). Spurious results may also arise if the gradient range differs systematically between regions. Consequently, the method and range of productivity measurement should also be considered when comparing the results of different studies.

An increasing amount of evidence has emerged that ecological patterns may differ between climatic and biogeographical regions (Pärtel 2006). For example, several authors have documented a positive relationship

between plant diversity and soil pH in the temperate and boreal zones (e.g., Gough et al. 2000, Gilbert and Lechowicz 2005). However, the opposite relationship has typically been detected in the tropics (Pärtel 2002). These contrasting patterns may reflect the different evolutionary history of the respective species pools. More speciation has occurred in those conditions more common throughout evolutionary history. In the temperate regions, high pH soils have been common in evolutionary centers and glacial refugia, whereas tropical regions have featured low pH soils because abundant rain and high temperatures have efficiently leached carbonates from the soil (Pärtel 2002).

We were interested whether the relationship between plant diversity and productivity may also depend on the evolutionary history of particular species pools. In particular, we focused on a comparison of the relationship between productivity and plant diversity in temperate and tropical regions, which obviously differ in their evolutionary history. The temperate zone is relatively unproductive, and productive habitats are uncommon. Some of the existing productive habitats are associated with agricultural activities and are too young to have provided for evolution and the historical migration of many species (Hodgson 1987). In contrast, in areas with sufficient precipitation tropical habitats usually feature high productivity (Lieth 1975, Cramer et al. 1999, Saugier et al. 2001). Productivity in tropical regions has also been more stable than in temperate areas affected by glacial–interglacial cycles (Beerling 1999, Birks and Birks 2004). Nutrient release from rapid plant decomposition and rapid uptake of nutrients by plants from the top layers of the soil compensates for the relatively low soil fertility in the tropics (Thorp and Baldwin 1940, Grubb 1995, Hartemink 2002). In addition, high temperatures and rainfall (often year around) promoted high plant productivity. Therefore, one can expect larger species pools in highly productive tropical habitats than in temperate regions. Consequently, the unimodal productivity–diversity relationship with decreasing diversity in highly productive habitats is expected to be common to the temperate zone, but not to the tropics, where a positive productivity–diversity relationship is likely to be found (see also Cornwell and Grubb 2003).

We examined the productivity–diversity relationship for plants across climatic and geographical gradients at the global scale. We hypothesize that the unimodal productivity–diversity relationship is more likely to be found in temperate climates, whereas the positive relationship is more common to the tropics. We also proposed to test the possible effects of the method and range of productivity measurement on the productivity–diversity relationship.

METHODS

We compiled published data on the habitat productivity–plant diversity relationship into a literature meta-

study (see Pärtel 2006). We used the earlier local and regional plant data from Mittelbach et al. (2001), but included additional studies (Appendix). Mittelbach et al. (2001) divided local studies into five groups according to the relationship found: unimodal, positive, negative, U-shaped, or no relationship. We reclassified these studies into three groups: unimodal, positive, and no relationship. The negative productivity–diversity relationship was merged with the unimodal relationship because most studies reporting a negative correlation focused on intermediate and high productivities. Because the U-shaped relationship has been reported so infrequently, and no viable biological explanation for it has been proposed, it was merged with the group with no relationship.

We determined geographical coordinates, mean annual temperature, and annual precipitation for each case study with CLIMATE database version 2.1 (W. Cramer, *personal communication; available online*).² We also recorded four indirect measures of productivity in addition to direct measurement of net primary productivity as plant biomass growth per unit area over time: measurement of standing biomass, amount of different soil nutrients, annual precipitation, or other (e.g., altitude, vegetation height, trophic indexes, evapotranspiration). We calculated the productivity range $\log(\max) - \log(\min)$ for data subsets where productivity was measured as standing biomass or annual precipitation, given that these parameters are comparable between studies (see Mittelbach et al. 2001).

We used multinomial logit regressions to test whether the shape of the productivity–diversity relationship was related to latitude, temperature, precipitation, or the method of productivity measurement. Latitude, temperature, and precipitation all differ when temperate and tropical regions are compared. Therefore, it is reasonable to start regression modeling with several climatic and geographic parameters simultaneously and to select the best model according to the Akaike Information Criterion. In order to test the effect of the productivity range on the shape of the productivity–plant diversity relationship, we calculated the range for comparable data subsets where productivity was measured either as standing biomass or annual precipitation, and added the range into the model. Multinomial regressions were performed using Statistica 6.1. (StatSoft 2004).

In addition, we studied how proportions of unimodal and positive relationships vary across latitudes. We divided the latitudinal gradient into 10°-wide zones from the equator to the poles until latitude of 70°, and looked for proportions of different productivity–diversity relationships within each zone. Each latitudinal zone represented at least 11 case studies (we added a study from latitude 82° into the 60–70° zone). Log-ratios were used for statistics in order to derive independent and

normal distributions from the compositional data (Aitchison 1986). For this purpose we applied \log_{10} -transformation to ratios of the proportions of unimodal or positive relationships to the proportion of cases with no relationships. Because zero proportions cannot be used in log-ratios, we replaced a zero proportion by 0.001 (which is much less than our minimal observed proportion 0.08). Polynomial regressions were used to relate log-ratios to latitudinal zones.

RESULTS

We used data from a total of 163 case studies, which represented all climatic zones and all continents except Antarctica (Fig. 1). Of these case studies, 57 featured a unimodal relationship (including 20 that reported a negative relationship), 46 found a positive relationship, and 60 found no relationship (including six U-shaped relationships). Methods of productivity measurement were as follows: standing biomass was used in 54 cases, precipitation in 48 cases, the amount of different soil resources in 21 cases, biomass growth in 24 cases, and 16 studies featured other measures.

The shape of the productivity–plant diversity relationship was significantly different between tropical and temperate regions, inasmuch as it was identically well-related to mean annual temperature ($\chi^2 = 23.1$, $df = 2$, $P < 0.0001$), and latitude ($\chi^2 = 22.7$, $df = 2$, $P < 0.0001$). Latitude and mean annual temperature were indeed strongly related across case studies ($r = -0.9$, $P < 0.0001$). According to the Akaike Information Criterion, annual precipitation and the method of productivity measurement were not included in the best model.

Subsequently, we studied whether the relationship with latitude continues when the productivity range is included in the model. Standing biomass was the most common method of productivity measurement; in the multinomial regression with the subset in which standing biomass was used as a productivity measure, both latitude ($\chi^2 = 13.3$, $df = 2$, $P = 0.0013$, Fig. 2) and biomass range ($\chi^2 = 6.7$, $df = 2$, $P = 0.0342$) were significant. Annual precipitation was the second common measure of productivity; the multinomial regression with this subset also had significant relationships with both latitude ($\chi^2 = 6.8$, $df = 2$, $P = 0.0327$, Fig. 2) and precipitation range ($\chi^2 = 15.5$, $df = 2$, $P = 0.0004$). Thus, the productivity–diversity relationship depends on the range of productivity because a significant relationship (be it unimodal or positive) is more likely to be found within a larger range of productivity, but the productivity range does not affect the relationship with latitude.

The proportions of different productivity–diversity relationships were nonlinearly related to latitude (Fig. 3). From the equator to the poles, the proportion of the unimodal productivity–diversity relationship increases significantly ($R^2 = 0.72$, $P = 0.0337$), and the proportion of the positive productivity–diversity relationship decreases significantly ($R^2 = 0.93$, $P = 0.0019$).

² (<http://www.pik-potsdam.de/~cramer/climate.html>)

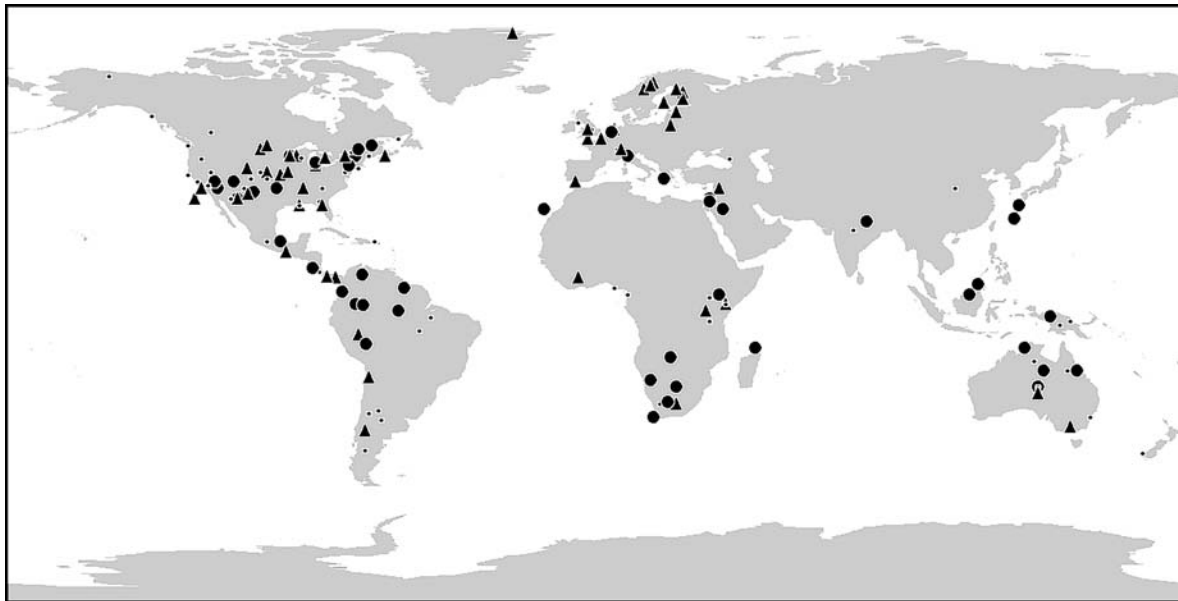


FIG. 1. Locations of plant productivity–diversity case studies throughout the world. Symbols indicate the relationship's shape (triangles, unimodal; circles, positive; points, no relationships). Some locations are slightly shifted for better visibility.

DISCUSSION

We found a significant global variation in the productivity–diversity relationship. The unimodal (hump-back) relationship was found predominantly in the temperate zone, whereas the positive relationship was significantly more common in the tropics. Latitude described $\sim 80\%$ of the variation in the shape of the relationships. This difference is attributed to the dissimilar evolutionary history of species pools in temperate and tropical zones. Productive habitats in

tropical regions have been more pervasive throughout evolutionary history (Beerling 1999), while highly productive sites in the temperate zone are less common or are fairly young (Hodgson 1987). We detected no bias with respect to methods of productivity measurement, although larger productivity ranges are more likely to reveal a unimodal or positive productivity–diversity relationship. The effect of productivity range, however, did not mask the effect of latitude.

Our results support a trend predicted by a recent theoretical model by Stevens (2006), in which a

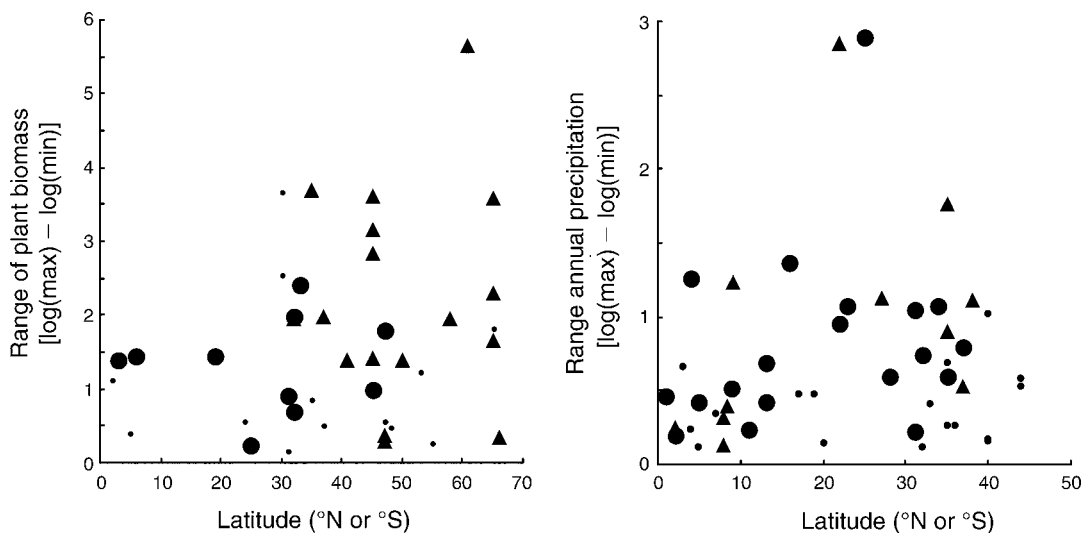


FIG. 2. Distribution of plant productivity–diversity relationships (triangles, unimodal; circles, positive; points, no relationship) across productivity range [$\log(\max) - \log(\min)$] and latitude. Only those case studies where plant biomass (g/m^2 ; left) or annual precipitation (mm; right) was used for productivity measure are included.

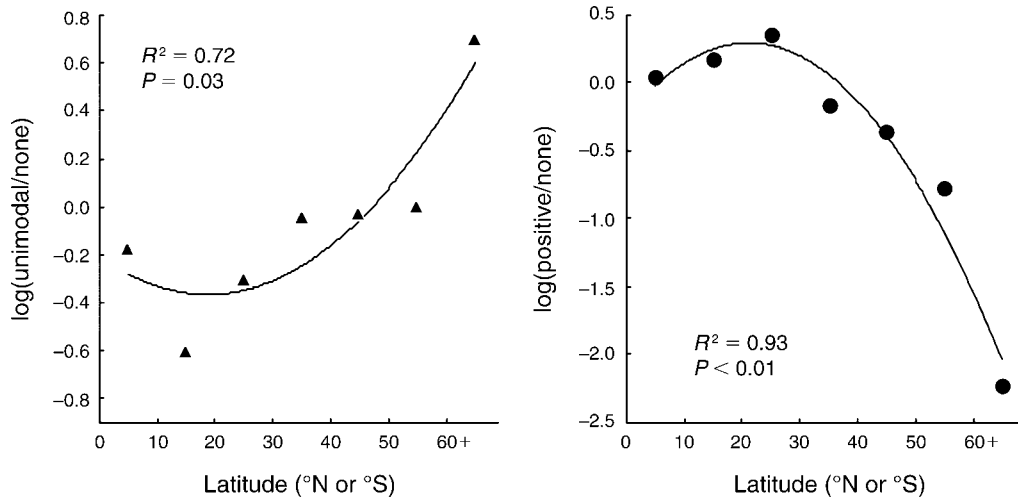


FIG. 3. Results of polynomial regression: significance of unimodal (left) and positive productivity-plant diversity relationships (right) across latitude. The log-ratios of proportions are used for the compositional data.

unimodal plant productivity-plant diversity relationship was expected when low temperature or precipitation limit diversity at low productivity, and high soil nutrients limit diversity at high productivity. The tropics feature high temperature and variable precipitation, but tropical soils are poor in nutrients (Thorp and Baldwin 1940, Grubb 1995, Hartemink 2002).

Among the initial studies on the unimodal productivity-diversity relationship, J. P. Grime (Al Mufti et al. 1977, Grime 1979) attributed the low diversity at very low productivity to evolutionary processes: very few species have managed to evolve for highly stressful conditions. The species-pool hypothesis actually began with the same idea in regard to the high end of the productivity gradient—species numbers are limited in fertile conditions due to the historical scarcity of productive habitats in the temperate zone (Hodgson 1987, Taylor et al. 1990). We provide the first support for this hypothesis on the global scale, comparing productivity-diversity relationships in temperate and tropical regions, which exhibit completely different evolutionary histories. Grime (1979) himself mainly considered the possible role of the species pool (in his terminology, species reservoir) in determining local diversity at intermediate productivity, but retained competition as the main force responsible for low diversity at high productivity. We show that in addition to the effects of ecological processes, the differential evolutionary history of species pools may also determine local diversity at high productivity. This result complements our previous study on the relationship of plant diversity to soil pH in the tropics and temperate regions (Pärtel 2002). There is increasing evidence of the important role of the evolutionary history of species pools for local biodiversity patterns.

The effect of evolutionary history may also be seen on the regional scale. Cornwell and Grubb (2003) found a

unimodal productivity-plant diversity relationship for European grassland communities, but high diversity was observed in highly productive forests. This may be due to the different evolutionary history of these contrasting habitat types: forests in Europe have been commonly distributed in more productive sites and grasslands in less productive sites. Alternatively, most trees in the temperate regions actually have tropical ancestors (Ricklefs 2006), and due to niche conservatism these species may still prefer the higher productivity that prevailed in their evolutionary history.

The previous results do not rule out the ecological explanation of the relationship, since both evolutionary and ecological determinants of the response pattern act in unison (Huston 1999, Pärtel et al. 2000, Foster et al. 2004, Bruun and Ejrnæs 2006). Zobel and Liira (1997) used relative richness (the ratio of local richness to species pool size), thus eliminating the possible effect of the size of the species pool, and still found a unimodal (albeit weaker) productivity-diversity relationship. The relative role of evolutionary and ecological processes in determining the shape of the response pattern depends on specific conditions and needs further study. In addition, the disturbance regime is probably an important factor influencing the productivity-diversity relationship (Huston 1979, 1994, 1999, Pärtel et al. 2000).

The method of productivity measurement was not a significant determinant of the shape of the productivity-diversity relationship. This concurs with previous tests (Groner and Novoplansky 2003). In contrast, productivity range significantly enhanced the detection of unimodal or positive productivity-diversity relationships. In the regression models involving studies in which productivity was quantified either on the basis of plant biomass or precipitation, both productivity range and latitude remained significant. Mittelbach et al. (2001) also found that a unimodal relationship was

more likely to emerge in the case of a wide range of precipitation. A wider productivity range makes it more probable to detect a pattern of positive or unimodal response, but the shape of the relationship is still determined by evolutionary history.

In a broader sense, our results indicate that the productivity–diversity relationship is not a general ecological pattern, and significant differences in its emergence may appear between regions with different evolutionary histories (Pärtel 2002, 2006). This message is important for conservation biology because regional differences in the basic empirical relationships of diversity should be taken into account in predicting potential biodiversity, estimating the losses and planning conservation areas (Pärtel et al. 2004). Based on the unimodal relationship, it has been suggested that more conservation effort should be paid to regions with low and intermediate productivity (e.g., Wohlgemuth 1998, Hodgson et al. 2005, Wassen et al. 2005). We cannot “export” this conservation knowledge globally, since the unimodal productivity–diversity relationship is not globally dominant. We may need more high-productive areas for conservation in the tropics (e.g., Cantu et al. 2004). In contrast to previous assumptions (Huston 1993), we may also expect a conflict between agricultural land use and plant diversity conservation in highly productive areas in the tropics. Similar conflicts have already been described in regard to the conservation of animal biodiversity in Africa (Balmford et al. 2001, Chown et al. 2003).

In summary, the unimodal plant productivity–diversity relationship is not a global phenomenon, but is merely prevalent in the temperate zone. The positive productivity–diversity relationship is more common in the tropics. This difference is a reflection of differences in evolutionary history of species pools: productive habitats have been scarce in the temperate zone for purposes of speciation and historical migration, and the same concerns unproductive habitats in the tropics. Thus, the common knowledge from the well-studied temperate regions, where most of the widely publishing ecologists originate, may not be valid in the tropics. This is a clear indication of the need to test ecological relationships for their generality across biogeographic and climatic regions (Pärtel 2006).

ACKNOWLEDGMENTS

We thank Michael A. Huston, Robert Szava-Kovats, and two anonymous reviewers for valuable comments, and the Estonian Science Foundation (grant no. 6614), EU 6FP project ALARM (GOCECT-2003-506675), University of Tartu, and the World Federation of Scientists for their support.

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APPENDIX

A table providing the 163 published studies of the plant productivity–diversity relationship (including latitude, longitude, mean annual temperature, annual precipitation, method of productivity measurement, productivity range, and reference) used in this study (*Ecological Archives* E088-067-A1).