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Relationship between species richness and productivity in plants: the role of sampling effect, heterogeneity and species pool

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Summary

1. The relationship between environmental productivity and the number of species [species richness–productivity relationship (SRPR)] has been thoroughly studied, but the mechanisms responsible for its form are still largely unknown, possibly because the majority of studies have focused on evaluating the sole effect of a single hypothesis.

2. We tested whether variation in species richness along a productivity gradient is due to variation in (i) the number of individuals, (ii) the number of species in the species pool or (iii) habitat heterogeneity.

3. We measured species richness (S), individual abundance (N) and productivity (P) estimated as standing biomass in different herbaceous communities in the Czech Republic at two spatial scales. Species pool (S_{pool}) was obtained from a database concerning individual habitats, and habitat heterogeneity (H) was measured using the community dissimilarity index.

4. The SRPR was scale-dependent: at the smaller spatial scale of individual plots, there was a significant curvilinearly negative relationship between S and P, whereas at the larger site scale it turned into a non-significant relationship.

5. Species richness was significantly affected by a combined effect of N and S_{pool} at the plot scale and by a combined effect of S_{pool} and H at the site scale. None of these variables was sufficient to explain the SRPR by itself.

6. *Synthesis*. Our findings indicate that there is no universal form of the species–productivity relationship, and the SRPR is driven by multiple scale-dependent mechanisms. It is important to consider the joint effect of different factors in explaining species richness patterns rather than to focus on the sole effect of productivity.

Key-words: abundances, determinants of plant community diversity and structure, Heterogeneity Hypothesis, local scale, species diversity, Species Pool Hypothesis, species–productivity relationship

Introduction

For many decades, ecologists have been trying to explain the observed relationship between the number of species and productivity or available energy (Waide *et al.* 1999; Mittelbach *et al.* 2001; Currie *et al.* 2004). Dozens of hypotheses have accumulated, but mechanisms behind the species richness–productivity relationship (SRPR) remain controversial. This is possibly partly because the SRPR is scale-dependent. At the continental to global scale, a positive relationship prevails (Currie *et al.* 2004), and most hypotheses focus on explaining why the number of species increases with available energy. At small spatial scales, however, observed trends in the SRPR differ. A unimodal (hump-shaped) form of this relationship has long been considered to be typical at the local to regional scale (Rosenzweig 1992; Rosenzweig & Abramsky 1993). A hump-shaped SRPR is often explained by competitive exclusion (Grime 1973; Tilman & Pacala 1993). According to this explanation, the number of species decreases towards low productivity levels due to an increase in environmental stress, which puts stress-tolerant species at an advantage. By

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contrast, a decrease in species richness towards high productivity levels may be caused by increasing competition for light, which becomes a limiting resource at these levels of productivity. This leads to the exclusion of poor competitors. At sites of intermediate productivity, both stress and competition are of intermediate intensity. Both stress-tolerant species and species able to compete for resources can therefore coexist in such places.

The competitive exclusion hypothesis has several problems. First, it is based on the assumption that intensified competition following higher productivity necessarily leads to a higher rate of competitive exclusion. It has been suggested, however, that lower resource availability has indeed an indirect positive effect on lower competition intensity, but a direct negative effect on species' tolerance to competition (Chesson & Huntly 1997). As a result, lower resource availability may in fact hasten competitive exclusion (Chesson & Huntly 1997). Second, competitive exclusion cannot explain other forms of observed SRPRs. Recent studies show that at the local to regional scale, a positive SRPR is more common than has been thought. Also, U-shaped, negative or non-significant relationships have been reported (Mittelbach *et al.* 2001; Gillman & Wright 2006; Adler *et al.* 2011). Competitive exclusion hypothesis fails to explain this variability.

Three other main classes of hypotheses address the SRPR at the local scale: (i) hypotheses concerning an effect of sampling [More Individuals Hypothesis (MIH) and Self-Thinning Hypothesis (STH)], (ii) the Heterogeneity Hypothesis (HH) and (iii) the Species Pool Hypothesis (SPH). These hypotheses differ not only in the mechanism they propose but also in the form of the relationship they predict. The first group of hypotheses is based on the sampling effect (i.e. the increased probability of obtaining a new species with an increasing number of individuals in each sample), which can be related to productivity in two possible ways. The first one is represented by the MIH (Wright 1983; Srivastava & Lawton 1998), which predicts a positive SRPR due to the positive effect of productivity on the total number of individuals. The increase in the number of species with productivity should therefore be mediated by an increase in total abundance. Although there is some empirical support for a positive relationship between productivity and total abundance, as well as between abundance and the number of species (Kaspari, O'Donnell & Kercher 2000; Hurlbert 2004; Yee & Juliano 2007), the number of species often increases with productivity more tightly than with the number of individuals (Currie *et al.* 2004; Šímová *et al.* 2011; Storch 2012; but see Chiarucci, Alongi & Wilson 2004). The second option concerning the sampling effect is represented by the STH (Oksanen 1996), which assumes that plant individuals increase in their size with productivity, leading to the reduction in their abundance and consequently to the reduction in the total number of species. Abundance and species richness are allowed to increase with productivity at unproductive sites because densities are not high enough to deplete all the available space. This self-thinning mechanism results in a hump-shaped species–productivity relationship, but in contrast to the competitive exclusion hypothesis, species loss is predicted to be random. Empirical work nevertheless suggests that a decrease in abundance alone is often insufficient to explain the decreasing phase of the unimodal SRPR (Zobel & Liira 1997; Goldberg & Estabrook 1998).

The HH states that higher productivity is associated with a broader range of environmental conditions. The increase in the number of species at more productive sites then results from a higher species spatial turnover (Chase & Leibold 2002) and/or higher habitat specialization (MacArthur 1965). Since the degree of heterogeneity can vary with scale, this hypothesis can explain the scale dependence of the SRPR (Stevens & Carson 2002; Chalcraft *et al.* 2004; Zhang *et al.* 2011). It is possible that other processes (e.g. competitive exclusion or sampling effect) prevail at small scale and that the positive effect of heterogeneity on species richness becomes more important at larger (coarser) scales by accumulating the effect of environmental variation from smaller areas (Chesson 1998). So far, many studies have attempted to show the effect of environmental heterogeneity on species richness with mixed results (e.g. Stevens & Carson 2002; Lundholm & Larson 2003). Most of these studies measured heterogeneity as variation in only a few environmental variables. Nonetheless, species may have adapted to local environmental conditions in a different way than reflected by these environmental parameters, so it might be more appropriate to use some measure of spatial change in species composition (Araya *et al.* 2010; see also Harrison, Vellend & Damschen 2011) as a surrogate of relevant habitat heterogeneity.

The SPH (Taylor, Aarssen & Loehle 1990; Pärtel *et al.* 1996; Zobel 1997) assumes that the number of species at a given site simply results from the total number of species able to tolerate local conditions. At larger scales (e.g. continental scales), this hypothesis is equivalent to the Niche Conservatism Hypothesis (Wiens & Donoghue 2004) or the Climatic Tolerance Hypothesis (Terborgh 1973; Brown 1988; Šímová *et al.* 2011), which tries to explain why there are more species in warm and humid (and therefore more productive) habitats at low latitudes. At regional scales, the factors shaping the size of the species pool may vary depending on the history of a particular region. For instance, during ice ages, very productive habitats were rare in Europe (Hodgson 1987), which may have caused a reduction in the number of species inhabiting them. The decrease of the number of species with productivity in Europe is therefore supposed to be caused by a decrease in the size of the respective species pool. Mounting evidence supports the SPH (Pärtel, Laanisto & Zobel 2007; Xiao *et al.* 2010; Zobel *et al.* 2011). However, defining a species pool can be problematic (Grace 2001; Hillebrand & Blenckner 2002). Moreover, the effect of the species pool on species richness at low productivity levels is often being overlooked (but see Xiao *et al.* 2010).

None of the abovementioned hypotheses alone can explain the SRPR sufficiently. The MIH, the STH and the HH ignore the fact that the number of species is also influenced by processes acting at the regional scale, whereas the SPH does not account for small-scale biotic interactions (see also Zobel & Pärtel 2008). The mechanisms behind the SRPR can be thus better understood by simultaneous testing of multiple hypotheses across multiple scales (Grace *et al.* 2007). Unfortunately, most studies have been focused only on one particular hypothesis, ignoring the fact that multiple mechanisms can drive the SRPR (but see Rajaniemi *et al.* 2006). Here, we aim to test the hypotheses described above using herbaceous communities differing in species richness and productivity located in the Czech Republic. We ask which factors are responsible for the observed relationship between the number of species and productivity by evaluating following predictions:

1 If the MIH holds, there should be a positive relationship between the number of individuals (*N*) and productivity (*P*) as well as between the number of species (*S*) and *N*.

2 If STH holds, there should be a positive relationship between *S* and *N*, but *N* should be a unimodal function of *P*.

3 If the increase in *S* is caused only by the increase in *N*, there should be no relationship between *P* and the number of species standardized by rarefaction (S_{rar}) (Gotelli & Colwell 2001).

4 If the SPH holds, species richness *S* should increase with the number of species in a species pool (S_{pool}). Additionally, since evolutionary processes primarily influence species richness at larger spatial scales, the role of the species pool should be stronger at larger spatial scales.

5 If the HH holds, there should be a positive relationship between *S* and environmental heterogeneity (*H*), as well as between *H* and *P*.

6 Since the relationship between *S* and *P* can be driven by multiple mechanisms, we also tested for the effect of the combination of mechanisms proposed by all hypotheses.

Materials and Methods

DATA COLLECTION

Field observation data were obtained using a hierarchical spatial design. First, we selected three regions: Polabi, Milovice and Doksy (Fig. 1), in order to capture a relatively continuous gradient in precipitation and soil nutrients. The Polabi region is characterized by a mild climate with mean annual temperatures around 8–9 °C and annual precipitation of 500–600 mm (www.chmu.cz). Soil reaction here is neutral or slightly acidic, and its overall character is rather eutrophic (http://eusoils.jrc.ec.europa.eu/library/data/250000/Czech.htm). The Milovice region is climatically similar to the Polabi region, but the soil reaction is neutral or slightly calcareous. The Doksy region is cooler and wetter (mean annual temperatures are 7–8 °C, annual precipitation 600–700 mm) with oligotrophic and acidic soils. Without any human impact, the dominant vegetation of the study area would be oak forests with a mixture of hornbeams, ashes or pines (Neuhäuslová & Moravec 1998). Due to intensive land use, this area is presently covered with fields, meadows, pastures and fragmented forests, typical of the cultural, central-European landscape.

Within each region, we selected one or two transects. We set up the position and length of each transect in a way that maximized the diversity of habitats therein. Habitats were defined according to the Natura 2000 habitat classification (AOPK ČR 2009; see also Guth & Kučera 2005), and we used the digital map of all habitats mapped during the years 2000–2004. The width of each transect was fixed to 200 m. Within each transect, we considered every patch of non-cultivated herbaceous vegetation (annual or perennial) whose minimum length was 100 m and minimum width was 10 m as a site (Fig. 1). We excluded sites under intensive disturbance regimes and sites with a coverage of woody species exceeding 5%. Patches larger than 200 × 200 m^2 were divided into two sites and those larger than 200 × 400 m^2 into three sites. Each site contained one or multiple habitats. Elevations of sites varied between 160 and 190 metres above sea level (m.a.s.l.) in the Polabi region, between 250 and 350 m.a.s.l. in the Doksy region and between 180 and 240 m.a.s.l. in the Milovice region. The habitats of the sites varied from reeds to sandy grasslands, with dominating mesic *Arrhenatherum* meadows; for the list of

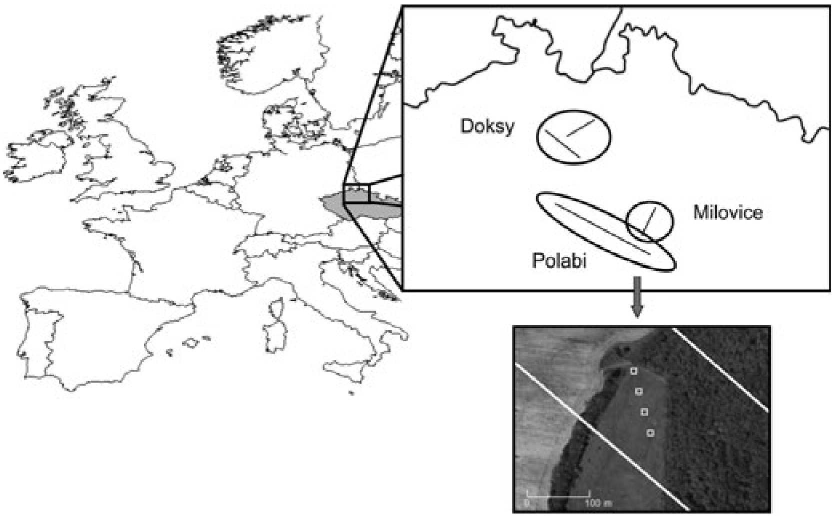

Fig. 1. Location of our study sites in the Czech Republic. Four transects were located within three regions. Sites were defined as patches of non-cultivated herbaceous vegetation located along each transect. Within each site, we sampled four 5 × 5 m vegetation plots, 15 m apart.

all habitats present, see Appendix S1 in the Supporting Information. Most of the sites are old meadows or (less often) abandoned fields and pastures (http://oldmaps.geolab.cz). Mowing is still practised at some of the sites, but the rest is unmanaged. At each site, we sampled four 5 × 5 m study plots (Fig. 1). These four plots were 15 m apart and were located along a line that was randomly positioned within the site and was parallel to the longest edge of the site. In our analyses, we focused on variation among sites (site scale) and among plots (plot scale).

DATA USED

Table 1 lists a detailed description of variables used in the study. To determine plot-level S, we sampled all plant species and estimated their coverage within each plot according to the Braun-Blanquet method (Braun-Blanquet 1932). S was determined as the total number of herbaceous plant species in each plot. We used dry above-ground biomass as a surrogate of P. To obtain plot-level above-ground biomass, we used Rising Plate Meter (RPM) measurements (ten measurements per sample; Earle & McGowan 1979). A RPM consists of a disc (plate) and a pole with a scale bar in the middle of the disc. The disc is allowed to fall freely into the vegetation. The height of the disc is then read off the scale bar. This method is commonly used as non-destructive above-ground biomass estimation in agriculture (Michell & Large 1983; Murphy, Silman & Barreto 1995; Benkobi *et al.* 2000). To calibrate the RPM method with the real biomass at the study sites, we randomly chose one plot per site where we harvested the above-ground biomass in four 0.07 m^2 areas in which we had previously made RPM measurements. The 0.07 m^2 area corresponded to the size of the RPM disc. The biomass was dried at 60 °C to a constant weight. We found a strong linear relationship between mean plot biomass and mean RPM measurement ($r^2 = 0.73$, and after excluding three outliers, r^2 increased to 0.85; see Appendix S2). We estimated total biomass per plot by averaging the ten RPM measurements using the linear regression function between RPM and biomass dry weight (see Appendix S2). For vegetation that was taller than the pole of the plate meter, we used solely the harvesting method. Similarly, in cases of a few plots dominated with *Calluna*, we harvested only the biomass from the current year. We harvested the biomass and carried out the RPM measurements at the peak biomass season.

To estimate plot-level N, we counted the number of individuals (N_s; number of all ramets) in the four 0.07 m^2 subplots of each plot, in which RPM measurements were made. For each subplot, we estimated the percentage of vegetation cover (C_s). The total number of individuals per plot (N) was then calculated as $(N_s/C_s)*C_T$, where C_T is the percentage vegetation cover of the whole plot.

We used the database of regional species pools of vascular plants for Czech habitats (Sádlo, Chytrý & Pyšek 2007) to obtain S_{pool} for each plot. This database contains all species and all habitats found in the Czech Republic. Habitat delimitation is based on phytosociological syntaxa (mainly at the level of alliance; see Sádlo, Chytrý & Pyšek 2007 for details). Each habitat is associated with a list of species that can potentially grow there, based on the Czech National Phytocenological Database (Chytrý & Rafajová 2003) and expert knowledge. We first classified all plots into different groups according to their species' composition using the TWINSPAN classification method (TWINSPAN for Windows, version 2.3; Hill & Šmilauer 2005). Subsequently, we linked our species' groups with habitats in the database according to the dominant and diagnostic species (Sádlo, Chytrý & Pyšek 2007) and used the number of listed species in particular habitats as plot-level $S_{pool.}$

We then took the total S and N from all plots and the average of P per plot to obtain the site-level S, P and N. We calculated the site-level S_{pool} as the number of species associated with all habitats found within a site.

As an indicator of site-level heterogeneity (H), we calculated Chao's multiple community similarity index C_{qN} (application SPADE; Chao *et al.* 2008) using species' relative abundances in all four plots at each site (i.e. $N = 4$). This index is independent of alpha (i.e. plot-scale) diversity. Since it is also independent of gamma-diversity for equally weighted sites (Chao *et al.* 2008), spatial heterogeneity represented by this index does not necessarily correlate with site-scale diversity. This index therefore allows us to examine the influence of site-scale spatial heterogeneity on species richness. C_{qN} is mainly affected by the variation of relative abundances of most abundant species in the community and is largely insensitive to the variation in rare species, thus avoiding the problem of under-sampling of rare species. C_{qN} varies between 0 and 1, with 0 representing communities sharing no species. Our site-scale community dissimilarity (H) was expressed as $1 - C_{qN}$, with its increasing value representing increasing H.

DATA ANALYSIS

First, we analysed the relationship between P and S at both the plot and the site scale using linear mixed effect models (function

Table 1. Overview of the variables used in the analyses

Variable abbreviation	Full name	Scale	Estimation
S	Number of species	Plot	Total number of species per plot
		Site	Total number of species per site
S_{pool}	Number of species in the species pool	Plot	Number of all species that can be present in the particular habitat of each plot
		Site	Sum of all potential species estimated for each plot
S_{rar}	Number of species estimated from rarefaction	Plot	Number of species estimated from individual-based rarefaction, using minimum sample size (1600)
		Site	Number of species estimated from individual-based rarefaction, using minimum sample size (20000)
P	Productivity	Plot	Dry above-ground biomass calculated from regression on the average of 10 Rising Plate Meter measurements (see Methods and Appendix S2)
		Site	Mean plot productivity
H	Heterogeneity	Site	1-Chao's index (Chao *et al.* 2008)

'lme' in 'nlme' library; Pinheiro *et al.* 2011) in R (version R 2.14) (R Development Core Team 2011). We considered site (only for the plot scale) and region (for both scales) as random factors that affect the intercept of the tested relationships. We did not transform the values of S, but P and N were square-root transformed to obtain normal distributions.

We examined both plot- and site-scale N–P and S–N relationships to distinguish the MIH from the STH. Using multiple regression, we then tested whether P remained significant in explaining S even after accounting for the effect of N. Because it is very likely that the number of species increases nonlinearly with the number of individuals, accounting for N as a covariable might not be sufficient (Gotelli & Colwell 2001). For this reason, we accounted for the sampling effect using the method of individual-based rarefaction (Gotelli & Colwell 2001). For each sample, we calculated the number of species predicted by the rarefaction for minimum observed number of individuals (S_{rar}). To calculate S_{rar}, we need information on the abundance of each species in each sample. We estimated these abundances using data on the total number of individuals within whole plots (N) and the relative percentage coverage of each species within plots. We examined whether there was a significant relationship between P and S_{rar} to evaluate the effect of productivity which is independent of the number of individuals. Nevertheless, the presence of clonal, clumped species can cause overestimation of S_{rar}. Also, estimating abundances based on the relative cover of each species may bias the results due to the difference in average individual size among species. For these reasons, we kept both rarefaction and the simple N as two alternative methods of how to account for the sampling effect.

To test the SPH, we first examined both the plot- and site-scale relationship between S_{pool} and P, as well as between S and S_{pool}. Then we used multiple regression to see whether P remained significant in explaining S even after accounting for the effect of S_{pool}. To test the HH, we examined the relationship between H and site-scale P as well as between H and site-scale S. Additionally, we performed multiple regression using both H and P to see whether the effect of P can be fully substituted by the effect of spatial heterogeneity. SRPR can be driven by multiple mechanisms acting simultaneously. For this reason, (i) we tested the combined effect of P, S_{pool} and H on S when the effect of N was removed in the multiple regressions and (ii) performed path models (i.e. structural equation models with observed variables, Grace 2006).

In the plot-scale multiple regression, we removed the sampling effect using S_{rar} and tested the effect of S_{pool} and P on explaining S_{rar}. Similarly, at the site scale, we used multiple regressions to test the effect of H and P on S_{rar}, as well as the effect of H, S_{pool} and P on S_{rar}. Given the potential bias in the estimation of S_{rar}, we repeated these analyses using S as a response variable and N as a covariable. For all the regression models, we used P both as a linear and as a polynomial term. We then compared the AICs of these models (simple and polynomial; Burnham & Anderson 2002). If the difference in AIC was lower than 2, we used the model with the linear term, otherwise we used the model with better fit (lower AIC). Since the data were collected along transects, site-scale regression analyses were repeated using spatial models to test for the effect of autocorrelation using the spatial spherical correlation form (this form fits the data best). We did not apply the autocorrelation analyses at the plot scale because we already accounted for the nested design of four plots within each site using linear mixed effect models. As the sites (and plots) differed in their land use, we performed additional analyses that accounted for the effect of management using presence and absence of mowing as a covariable.

In our path models, we tested whether P affects S via its effect on N, S_{pool} or H. Our goal was to find the structure that provided the best fit (lowest AIC), so we added or removed the paths between particular variables while keeping P as an independent (exogenous) variable and S as a response variable. In this process, we considered only those relationships which had a justifiable ecological meaning. Similarly as in the multiple regression, we included P as a linear and a polynomial term and searched for the model with the better fit. Path models were carried out using the 'sem' library (Fox 2010) in R (version R 2.14; R Development Core Team 2011).

Results

ANALYSES AT THE PLOT SCALE

Results of the tests of each single hypothesis at the plot scale are listed in the first three columns of Table 2. The relationship between plot-scale S and P was significantly curvilinearly negative (Fig. 2a). Specifically, S increased with P when P was low, peaked at relatively low P and declined as P continuously increased, in agreement with the commonly observed form of SRPS (Grace 1999 and references in Tilman & Pacala 1993).

There was a positive relationship between plot-scale S and N and a significantly nonlinear negative relationship between plot-scale N and P. This is in contrast with the prediction of the MIH that N always increases with P but agrees with the prediction of the STH that N declines with P when P is high. The positive S–N relationship agrees with the prediction of the sampling effect (an increase in N leads to an increase in S). Still, when adding the effect of N to the S-P regression, both the linear and the polynomial term of P remained significant, indicating that variation in N cannot fully explain the variation in S. Moreover, when using S_{rar} to account for the sampling effect, there was still a significant curvilinear relationship between S_{rar} and P. This refutes the notion that the sampling effect is the sole mechanism driving the SRPR.

There was a significant positive relationship between plot-scale S_{pool} and S as well as a significantly curvilinear relationship between S_{pool} and P (Fig. 2b). These relationships agree with the prediction of the SPH. When using multiple regression, both S_{pool} and P had a significant effect on S, indicating that productivity has a significant effect on the observed number of species even after accounting for the effect of the species pool. After removing the sampling effect using S_{rar}, the effect of both S_{pool} and P remained significant (Table 3), but P was only marginally significant when we accounted for the sampling effect using N as a covariable instead of the S_{rar} (Appendix S3). All abovementioned results remained qualitatively unchanged when we accounted for the effect of management (see Appendix S4).

Path model confirmed our results from multiple regressions; P significantly affected S through its influence on both S_{pool} and N (Fig. 3). In contrast with the regression results, model with the best fit did not contain the relationship between P and S independent of both S_{pool} and N. This difference was likely due to the different statistical assumption between the method of the linear mixed-effect models (where we considered the effect of random factors) and the path models.

Table 2. Results concerning tests of individual hypotheses from mixed effect models at the plot and site scale

			Plot scale			Site scale		
Hypothesis	Model	Variables	Coefficients	*F*-value	*P*-value	Coefficients	*F*-value	*P*-value
	$S \sim P + P^2$	Intercept	**25.35**	**289.6**	**< 0.001**	**64.44**	**585.66**	**< 0.001**
		P	2.38	38.94	0.079	−2.17	2.6	0.112
		P^2	**−0.39**	**11.95**	**< 0.001**	–	–	–
MIH + STH	$S \sim N$	Intercept	**16.87**	**644.26**	**< 0.001**	**37.94**	**588.74**	**< 0.001**
		N	**0.06**	**38.99**	**< 0.001**	0.05	2.93	0.093
	$N \sim P + P^2$	Intercept	**205.14**	**512.61**	**< 0.001**	**168.82**	**1281.96**	**0.007**
		P	−2.93	103.78	0.688	**71.24**	**12.89**	**0.007**
		P^2	**−1.38**	**4.92**	**0.028**	**−8.43**	**13.52**	**< 0.001**
	$S \sim N + P + P^2$	Intercept	**16.83**	**412.71**	**< 0.001**	**49.67**	**588.58**	**0.002**
		N	**0.037**	**42.22**	**0.002**	0.03	2.92	0.26
		P	**2.8**	**10.1**	**0.036**	−1.47	0.98	0.325
		P^2	**−0.36**	**10.44**	**0.002**	–	–	–
	$S_{rar} \sim P + P^2$	Intercept	**20.86**	**189.28**	**< 0.001**	**52.68**	**414.68**	**< 0.001**
		P	2.25	32.89	0.063	−1.3	1.19	0.28
		P^2	**−0.35**	**11.82**	**< 0.001**	–	–	–
SPH	$S \sim S_{pool}$	Intercept	**7.43**	**449.84**	**0.015**	**31.46**	**682.27**	**< 0.001**
		S_{pool}	**0.04**	**45.76**	**< 0.001**	**0.04**	**12.76**	**< 0.001**
	$S_{pool} \sim P + P^2$	Intercept	**453.26**	**925.45**	**< 0.001**	**373.76**	**255.04**	**< 0.001**
		P	**44.17**	**39.71**	**0.002**	101.01	<0.001	0.987
		P^2	**−5.71**	**24.87**	**< 0.001**	−9.39	1.78	0.188
	$S \sim S_{pool} + P + P^2$	Intercept	**14.07**	**235.97**	**0.043**	**43.86**	**232.38**	**< 0.001**
		S_{pool}	**0.02**	**49.53**	**< 0.001**	**0.04**	**14.4**	**< 0.001**
		P	1.28	17.77	0.335	**−2.73**	**4.28**	**0.043**
		P^2	**−0.25**	**4.73**	**0.031**	–	–	–
HH	$S \sim H$	Intercept	–	–	–	**30.89**	**239.92**	**< 0.001**
		H	–	–	–	**41.63**	**18.64**	**< 0.001**
	$H \sim P$	Intercept	–	–	–	**0.53**	**72.97**	**< 0.001**
		P	–	–	–	< 0.001	< 0.001	0.989
	$S \sim H + P$	Intercept	–	–	–	**44.37**	**203.84**	**< 0.001**
		H	–	–	–	**42.39**	**20.28**	**< 0.001**
		P	–	–	–	**−2.76**	**4.61**	**0.036**

MIH, More Individuals Hypothesis; STH, Self-Thinning Hypothesis; SPH, Species Pool Hypothesis; HH, Heterogeneity Hypothesis.
We tested the role of productivity (P) both as simple and as polynomial term and chose the model with the lower AIC value (presented here). Significant variables are highlighted in boldface.

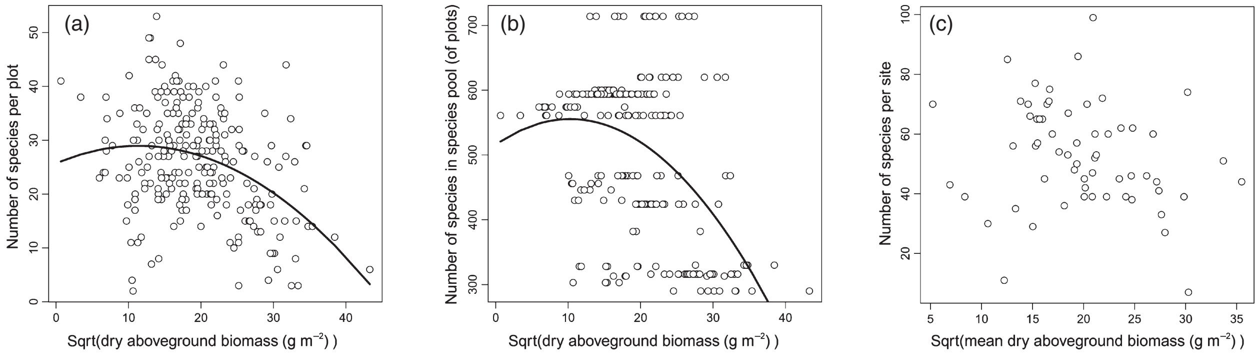

Fig. 2. (a) Relationship between the number of species (S) and productivity (P) at the plot scale, (b) relationship between the size of species pool (S_{pool}) and productivity (P) at the plot scale, (c) relationship between number of species (S) and productivity (P) at the site scale.

ANALYSES AT THE SITE SCALE

Results of the tests of each single hypothesis at the site scale are listed in the last three columns of Table 2. The site-scale N was a significant curvilinear function of P, indicating a significant effect of productivity on the number of individuals. However, there was no significant site-scale S–P relationship (Fig. 2c) and only a marginally significant positive site-scale S–N relationship. Since P affected N but not S, these results contradict the predictions of both the MIH and the STH at the site scale.

Table 3. Results of tests of combinations of multiple hypotheses from mixed effect models at both the plot and the site scale

Scale	Model	Variables	Coefficients	*F*-value	*P*-value
Plot	$S_{rar} \sim S_{pool} + P + P^2$	Intercept	**11.76**	**158.37**	**0.009**
		S_{pool}	**0.02**	**40.7**	**< 0.001**
		P	1.43	14.9	0.234
		P^2	**−0.24**	**5.37**	**0.022**
Site	$S_{rar} \sim S_{pool} + P$	Intercept	**34.17**	**168.41**	**< 0.001**
		S_{pool}	**0.04**	**14.77**	**< 0.001**
		P	−2.1	3.45	0.07
	$S_{rar} \sim H + P$	Intercept	**34.94**	**180.21**	**< 0.001**
		H	**37.07**	**21.82**	**< 0.001**
		P	−1.76	2.61	0.112
	$S_{rar} \sim H + S_{pool} + P$	Intercept	**26.31**	**151.64**	**< 0.001**
		S_{pool}	**0.02**	**18.83**	**< 0.001**
		H	**29.07**	**12.93**	**< 0.001**
		P	−1.89	3.33	0.074

We tested the role of productivity (P) both as a simple and as a polynomial term, and we chose the model with the lower AIC value (presented here). Significant variables are highlighted in boldface.

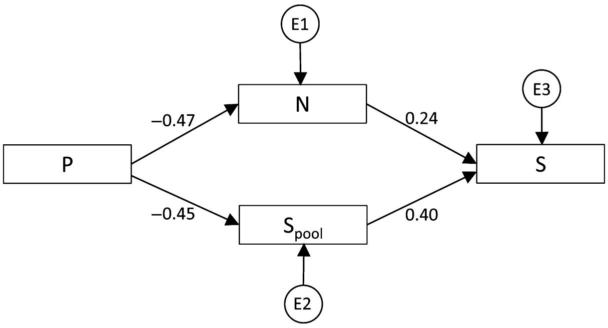

Fig. 3. Results of the path models of the relationships between productivity (P) and the number of species (S) at the plot scale. Directional arrows represent causal effects; values close to these arrows are standardized path coefficients. E1–E3 represent unique error terms. The model fit, χ^2, is 1.896, d.f. = 2, P-value = 0.3875. Root mean square error of approximation (RMSEA index) < 0.001.

There was a significantly positive relationship between S and S_{pool} at the site scale. Nevertheless, variation in S_{pool} was not significantly explained by P, contradicting the assumption in the SPH that P is related to S_{pool}, which in turn affects S. On the other hand, when we used both P and S_{pool} to explain S, they both became significant, although the significance of P became only marginal when accounting for the management (see Appendix S4) and for the sampling effect (Table 3, Appendix S3).

Although site-scale S significantly increased with H, partially supporting the HH, the relationship between H and site-scale P was not significant, contrasting the prediction of the HH. The effect of P on S became significantly negative when it was tested jointly with H in multiple regression, but this significance was again only marginal when accounting for the effect of management (see Appendix S4) and the number of individuals. When we used all three variables (S_{pool}, H and P) to explain S_{rar} in the multiple regression, the effects of S_{pool} and H were significant, but that of P was only marginally significant (see also Appendix S3 for results concerning N as a covariable).

The path model with the best fit revealed a significant effect of P on S when considering the effect of both S_{pool} and H (Fig. 4). Whereas we found support for the decrease of N with P, the effect of N on S was not significant, so we did not include it in our best path model. H affected S both directly and also indirectly via S_{pool}. Both S_{pool} and H thus play an important role in explaining the observed number of species, despite their strong correlation. Neither H nor S_{pool} depended on P. Their independence of site-scale productivity contradicts the prediction of both the SPH and the HH. In contrast with the multiple regression results, we found support for the relationship between P and S after accounting for all other explanatory variables in our path models. Nevertheless, the P-value of the P–S relationship was 0.048, indicating that this signal was rather weak.

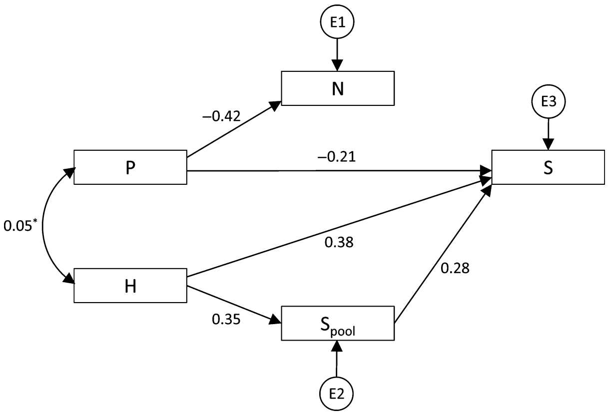

Fig. 4. Results of the path models of the relationships between productivity (P) and the number of species (S) at the site scale. Directional arrows represent causal effects; values close to these arrows are standardized path coefficients. The bidirectional arrow represents unresolved correlation, *the coefficient that was not statistically significant (α = 0.05). E1–E3 represent unique error terms. The model fit, χ^2, is 1.8523, d.f. = 4, P-value = 0.7629. Root mean square error of approximation (RMSEA index) is < 0.001.

The summary of our predictions and the evidence for each hypothesis are listed in Table 4.

Discussion

Our findings provide powerful evidence that the SRPR is driven by multiple mechanisms and that the influence of each mechanism varies with spatial scale. At the plot scale, our results are in accordance with the predictions of both the STH and the SPH. At the site scale, productivity affected the number of species only in combination with species pool or heterogeneity. At this scale, species richness increased with both species pool and habitat heterogeneity, but both factors varied independently of productivity, contrary to the assumptions of both the SPH and the HH.

In agreement with the STH, the number of individuals curvilinearly decreased with productivity at both scales whereas species richness significantly increased with the number of individuals only at the plot scale. This suggests that the sampling effect is more important at smaller spatial scales. However, in line with previous findings, variation in the number of individuals alone was not a sufficient explanation for the SRPR (Zobel & Liira 1997; Goldberg & Estabrook 1998; Forbes, Schauwecker & Weiher 2001; Šímová *et al.* 2011) as the role of productivity at the plot scale remained significant even after accounting for the sampling effect.

Despite a significant role of species pool in explaining species richness, our findings raise many questions concerning the SPH. Our results fully agree with the predictions of this hypothesis only at the plot scale. At the site scale, productivity and species pool become independent of each other. This is likely caused by the fact that site-scale species pool (as it is defined) is highly affected by habitat heterogeneity, since it represents the sum of the species distributed across all habitats present in all plots within a given site. At the site scale, heterogeneity thus affects species pool, which is supported by the path model. The weakened support for the SPH at a larger spatial scale contradicts the notion that this evolution-based mechanism should have a more pronounced effect at large scales. Moreover, why there is a curvilinear relationship between productivity and species pool at the plot scale is left unexplained. The SPH suggests that productive habitats largely disappeared during glaciations in Europe and that this loss of habitat caused the reduction of species pools associated with those habitats (Hodgson 1987). However, the hypothesis gives no prediction of the form of the species pool–productivity relationship when productivity is low. In fact, we cannot reject the idea that the plot-scale curvilinear species pool–productivity relationship is a consequence of the same mechanism (e.g. competitive exclusion) that generates the SRPR rather than the cause of the SRPR (Herben 2000; Lepš 2001; Akatov, Chefranov & Akatova 2005), that is, the species pool itself can be lower due to competitive exclusion of species from both the least productive and the most productive sites. Nevertheless, despite our uncertainty about the mechanism that drives the species pool–productivity relationship, we have shown that the size of the species pool is significantly related to both plot- and site-scale species richness and the plot-scale productivity, but its effect is not sufficient to explain the SRPR.

Whereas species richness increased with habitat heterogeneity, heterogeneity did not depend on productivity. This contrasts with the prediction of the HH. Heterogeneity and productivity rather affected number of species independently, in line with previous theoretical findings (Chesson & Huntly 1997). This joint effect of productivity and heterogeneity may be responsible for the scale dependence of the SRPR. The results also indicate another independent effect of productivity on species richness, which is mediated neither by the number of individuals nor by heterogeneity or the species pool. However, since this effect was only marginally significant at the site scale and was not consistently revealed when using different statistical methods at the plot scale, we cannot reject the possibility that this effect was due to some other unknown factor or due to inaccurate measurement of the variables.

Indeed, there are several caveats concerning our study. First, we limited our analyses to herbaceous vegetation communities of three regions of the Czech Republic. Despite the large variety of vegetation, all the habitats have been affected by past and present land use. Different land-use history can affect the SRPR and habitat heterogeneity. Also, the relationship between the species richness and size of the species pool can be affected by the area and the degree of isolation of particular habitats. Additionally, there might be a bias in our estimate of the number of individuals. Extrapolating the numbers of individuals from small subplots to the whole plot according to relative cover of individual species assumes small variation in average individual size between species. It

Table 4. Predictions and evidence for particular hypotheses tested in our study

Hypothesis	Predictions	Plot scale*	Site scale*
More Individuals Hypothesis (MIH)	Positive N–P	0	0
	Positive S–N	0	0
Self-Thinning Hypothesis (STH)	Unimodal N–P	1	1
	Positive S–N	1	0
Species Pool Hypothesis (SPH)	Positive S_{pool}–S	1	1
	Low S_{pool} when P is high	1	0
Heterogeneity Hypothesis (HH)	Positive S–H	–	1
	Positive H–P	–	0

*1, supported; 0, not supported.

is thus possible that part of the unexplained variation in species richness and in the SRPR is attributed to the unquantified variation in *N*. Despite these caveats, our study illustrates the influence of multiple mechanisms on SRPR using the best data that can be acquired practically.

In conclusion, we have shown that the mechanisms proposed in all three hypotheses (STH, SPH and HH) contribute to the form and scale dependence of the SRPR. At the plot scale, the number of species decreases towards high productivity due to the decrease in both the number of individuals and the size of the species pool. The role of productivity becomes weaker at larger scale, where the effects of species pool and habitat heterogeneity dominate, although neither of them was related to productivity. The fact that the SRPR results from a combination of different mechanisms is in conflict with the idea of a universal form of the SRPR. At the site scale, our findings suggest that factors independent of the resource level (e.g. environmental heterogeneity) may have a crucial influence on species coexistence. This corresponds to the recent evidence that the form of the SRPR is highly variable in nature even when compared at the same spatial scale (Adler *et al.* 2011). Our results highlight the importance of considering the joint effect of different factors in explaining species richness patterns rather than focusing on the sole effect of productivity. We propose that future studies of the SRPR should adopt similar approaches to provide a more holistic and scale-dependent view of the relationship.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. The list of all habitats present in our plots.

Appendix S2. The relationship between mean dry above-ground biomass and Rising Plate Meter measurements.

Appendix S3. Results concerning tests of combinations of multiple hypotheses from mixed effect models using *N* as a covariable.

Appendix S4. Results from linear mixed effect models when using management as a covariable and when accounting for spatial autocorrelation.