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ON SPECIES–AREA RELATIONSHIPS III: THE INTERCEPT OF THE POWER FUNCTION AND THE EXPONENTIAL MODEL

ABSTRACT: Using model assemblages the dependence of the intercept of the power function and the exponential model of species–area relationships on slope and factor value were studied. It is shown that the quotient of intercept and total species number in the assemblage (S_{unit}/S_a) can be interpreted as a relation between local and regional diversity and linked with species–area relations. Two general relations are derived and tested combining both concepts: $z=\frac{a}{\ln(area)}\ln\frac{S_{unit}}{S_a}$, and $\frac{S_{unit/1}}{e^{\frac{\beta_1 H_{a/1}}{\beta}}}=\frac{S_{unit/2}}{e^{\frac{\beta_2 H_{a/2}}{\beta}}}$ with z being the slope of the power function model, H the Shannon diversity, β, β_1 and β_2 constants, and a the constant of the relation between S_{unit}/S_a and z. It is concluded that with the above functions species–area relationships can be used to infer the relation between local and regional species numbers and to compute regional diversities.

KEY WORDS: species–area relationship, model species assemblages, diversity, evenness, relative abundance distributions, random sampling, local and regional diversity

1. INTRODUCTION

The intercept of the power function and the exponential model of species–area relationships (SPAR) has gained the least interest of all model parameters (Preston 1962, White and Gould 1965, Connor and McCoy 1979, Gould 1979, Rosenzweig 1995). This surely because the intercept is not independent of units of measurement and because of lack of theoretical underpinning. Many authors considered the intercept only as a fitted constant, the scaling coefficient (MacArthur and Wilson 1967, Connor and McCoy 1979, LaBarbera 1985). The few examples trying to relate the intercept with other variables contain Johnson and Raven's (1970) hypothesis that the intercept will decrease with increasing latitude and Heatwole's (1975) suggestion, that negative intercept values indicate a minimal area [not to confuse with the minimal area concept of plant ecologists (Hopkins 1955, Moravec 1973)], necessary to sustain species of the studied community, and Gould's (1979) interpretation as a size independent invariant for curves with similar slopes. The simplest interpretation of the intercept is of course the view that it gives the mean number of species per unit of area.

It had long been noticed that in the power function model of SPAR intercept and slope are not independent. White and Gould (1965) deduced that in allometric relations there may be either a positive or a negative relation between slope and intercept depending on the units of measurement and concluded that simple relations between slope and inter-

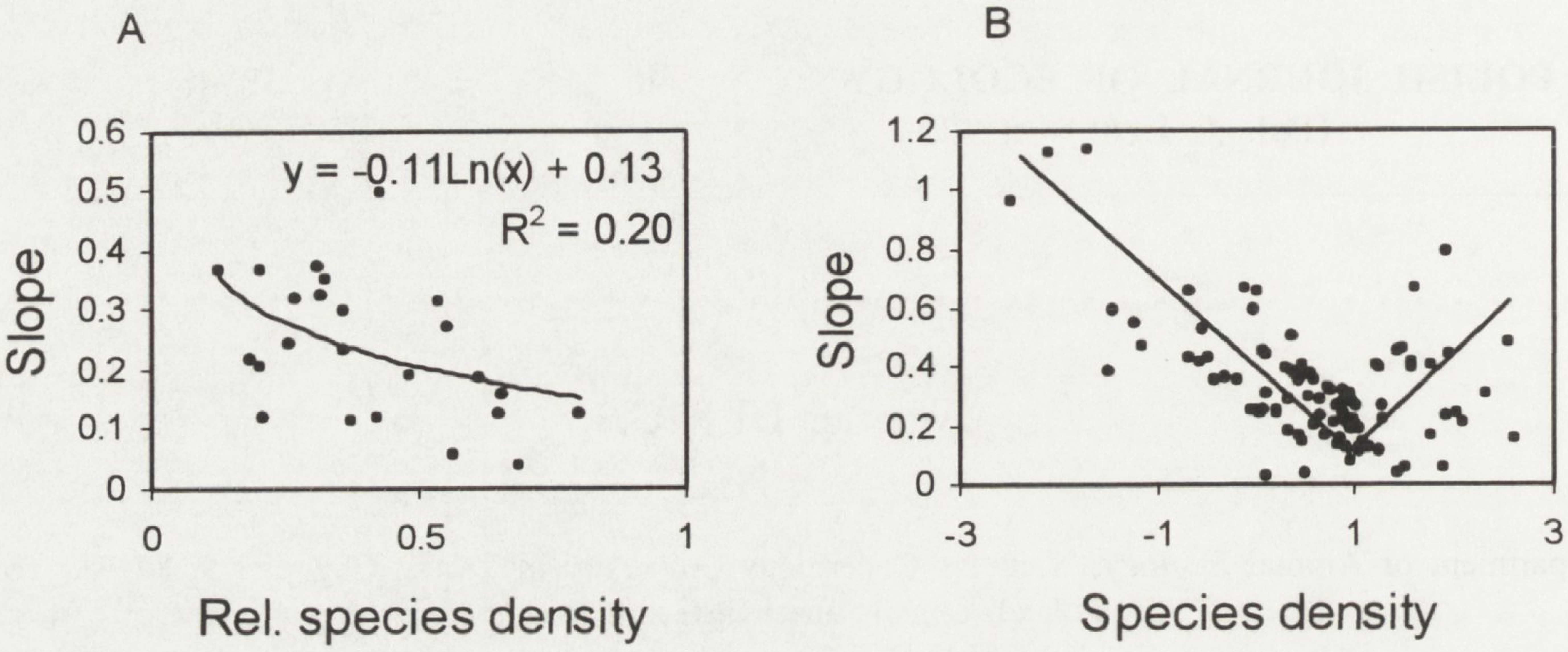

Fig. 1. Slope of the power function model of species–area relationships in dependence on relative species density (A) and species density (= number of species per unit area) (B) of 28 (A) and 100 species–area relationships from Connor and McCoy (1979). The species densities are log-transformed. R^2: variance explanation, p(t) < 0.05)

cept have no biological significance. A similar switch can also be seen in species–area curves (Fig. 1B). Plotted are intercept and slope of 100 species–area relationships given by Connor and McCoy (1979). At ln (intercept) < 1, there is an inverse relation, at values above 1 a direct relation. Therefore, changing the unit of measurement also changed the relation between intercept and slope. This phenomenon may also be a cause why the intercept has gained so few attention. (Note that the relation of the Connor and McCoy (1979) data is exactly the inverse of the Gould and White (1965) pattern. The reason is that the data are given as logarithms of intercept).

However, in part II of this paper (Ulrich 2000a) I argued that the slope of the power function model is more dependent on relative measures. In this case we may express the relation between intercept and slope in terms of the relative species density, the quotient between species number per unit area (the species density S_{unit}) and the total number of species in the assemblage (S_a). After such a transformation the intercept becomes dimensionless, the above ambiguity vanishes, and a clear inverse relationship comes up (Figs 1A and 3). Such a relation can then be interpreted ecologically.

As far as I know the relationship between intercept and factor value of the exponential SPAR model has not been studied. The aim of the present study will therefore be to clarify the relations between intercept and parameter values and to clarify what environmental factors influence the intercept. In doing so I will largely use the same model assemblages as in part I and II (Ulrich 2000a, b).

2. MATERIAL AND METHODS

The assemblages used in this study are the same as in part I (Ulrich 2000a), the generation procedure, the properties of these assemblages, and the generating variables are listed in Tab. 1 of part I (Assemblages 1 to 10). For each of these 768 assemblages species area curves of the exponential and the power function type were computed and the slope value *z* (power function) and the factor *b* (exponential function) recorded (Formulas 1 and 2 in part I). Again three different sampling regimes (sequential adding, nested, non-nested) will be studied. Additionally (to study the behavior of the intercept at similar relative abundance distributions but different species numbers) 180 further assemblages were generated. The properties of these as-

Table 1. Parameter design of Community Model to generate 120 assemblages used in this study. Max. Density: upper density boundary of the smallest species; min. density: minimum allowed density per cell; type of density fluctuation: densities set randomly between the max. and min. allowed density either using untransformed densities (normal), or log-transformed densities (log-normal), or a random mixture of both (mixed). The random assessment of densities was done with a normal random number generator producing random numbers with a mean = Flucmean and a variance = Flucvariance, or with linear random numbers (non). DWD: type of density-weight relationship with a slope of the upper density boundary = DWDslope; SWD: species-weight relationship with maximum 16 binary size classes, a mean = SWDmy, and a variance = SWDvar; The degree of aggregation of the species (Aggr) was set to 0 (resulting in a value of Lloyd's index around 1) The heterogeneity was either fixed for all species (Hetfix = yes) or different for each species (Hetfix = no).

No.	No. of Assem-blages	No. cells sampled	Method of sampling	No. of samples	Unit of area	No of species	Max. density	Min. density	Type of density fluctuation	FlucMean	Fluc Variance
1	20	100	seq. adding	100	1	15 to 400	10	0.001	normal	0.5	0.4
2	20	100	seq. adding	100	1	15 to 400	10	0.001	log-normal	0.5	0.4
3	20	100	seq. adding	100	1	15 to 400	10	0.001	mixed	0.5	0.4
4	20	100	seq. adding	100	1	15 to 400	10	0.001	mixed	0.5	0.4
5	20	100	seq. adding	100	1	15 to 400	10	0.001	mixed	0.5	0.4
6	20	100	seq. adding	100	1; 4; 9;...100	15 to 400	10	0.001	mixed	0.5	0.4
7	20	100	seq. adding	100	1; 4; 9;...100	50	10	0.001	mixed	0.5	0.4
8	20	100	seq. adding	100	1; 4; 9;...100	200	10	0.001	mixed	0.5	0.4
9	20	100	seq. adding	100	1	15 to 400	10	0.001	normal	0.5	0.4

No.	DWD	SWD	Classes	SWDmy	SWDvar	DWDmy	Aggr	Het	Hetfix
1	power	normal	16	8	2	1	0	0	no
2	power	normal	16	8	2	1	0	0	no
3	power	normal	16	8	2	1	0	0	no
4	power	normal	16	8	2	0.5	0	0	no
5	power	normal	16	8	2	0	0	0	no
6	power	normal	16	8	2	1	0	0	no
7	power	normal	16	8	2	1	0	0	no
8	power	normal	16	8	2	1	0	0	no
9	power	normal	16	8	2	1.5	0	0	no

semblages are given in Table 1. For all assemblages the total number of species (S_a), the species density (S_{unit}), the rel. species density (S_a/S_{unit}), the number of singletons in the assemblage, the number of species found (S_s), the standard deviation of $\log_2$ (densities), and Shannon diversity and evenness (in the latter three cases separately for the total assemblage and the sample) were computed.

3. RESULTS

3.1. INTERCEPT AND LOCAL AND REGIONAL SPECIES NUMBERS

If one sets the area in the power function and the exponential model to 1, the intercept should give the mean number of species per unit area because of

$$S_{unit} = b \ ln(1) + s \quad \text{and} \tag{1}$$

$$S_{unit} = s \ (1)^z \tag{2}$$

where *b*, *s*, and *z* are constants by conventional notation.

Fig. 2 shows that there is indeed in both models a very good linear correlation between S_{unit} (the number of species per unit area) and the fitted intercept. But least square regression yields in a systematic bias in the estimation of the intercept (LaBarbera 1985). And indeed the regression in Figure 2 has not a factor of one. The fitting process of both models constantly overestimated S_{unit} by a factor of about 1.5. This result cannot be explained by the variance in S_{unit}. Their values are means of 20 sampled units (cells, see Methods in part I, Ulrich 2000b). When interpreting the intercept value the fitting process has therefore to be taken into account and appropriate correction factors have to be used (Sprugel 1983).

Westoby (1993) and Srivastava (1999) were the first to combine slope of SPARs and comparisons of local and regional species numbers. This is possible because for any given assemblage structure S_s will depend in a specific way on the total number of species in the assemblage (S_a) and therefore in the power function model a relation between S_{unit}/S_a (the relative species density) and the slope z can be derived by rearranging the power function. Slope and relative species density can be expressed by a logarithmic function (Fig. 3 A, B):

$$z = -\frac{a}{\ln(area)} \ln \frac{S_{unit}}{S_a} \tag{3}$$

with *a* being a constant and *z* the slope of the power function SPAR. This relation proofed to be independent of assemblage structure and sampling method. The constant however proofed to be slightly dependent on

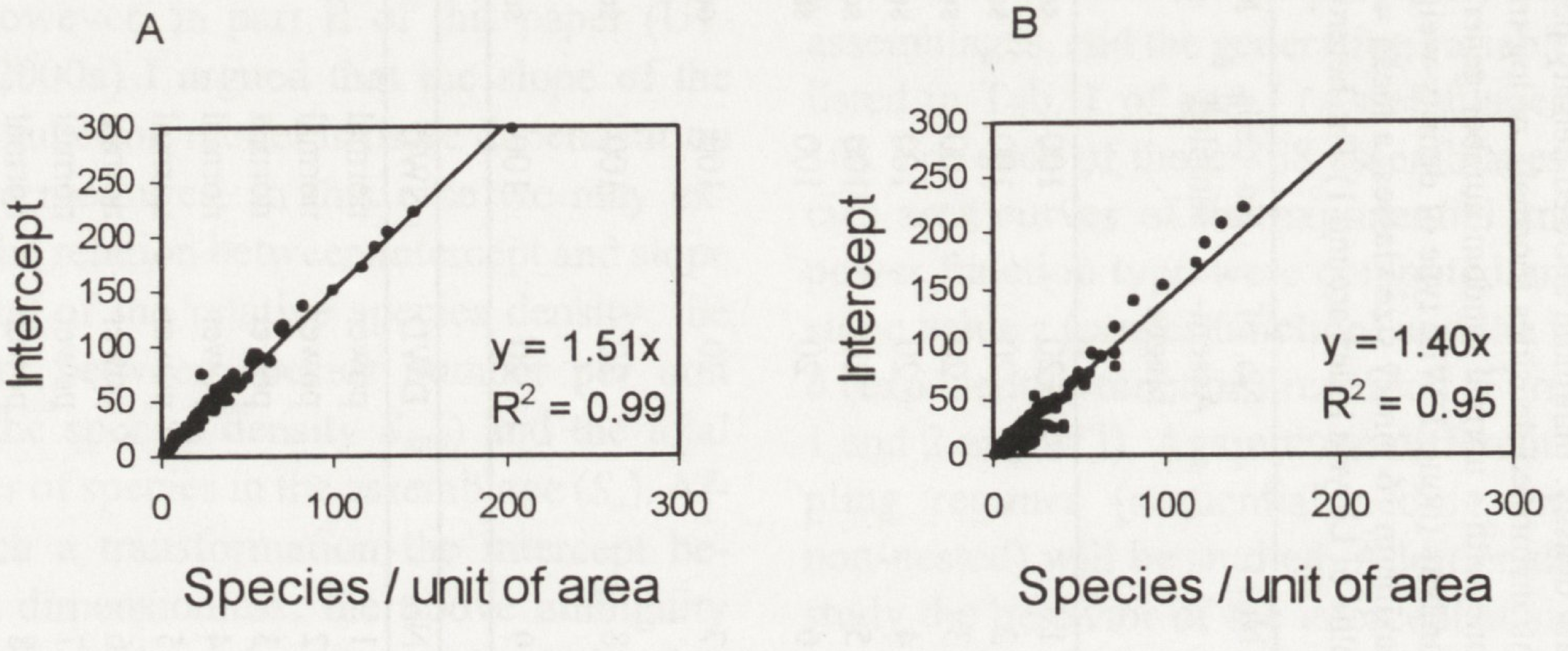

Fig. 2. Relationship between intercept of the power function (A) and exponential (B) model of species–area relationships and real number of species per unit area of 120 model assemblages (assemblages 1 to 6 of Table 1). R^2: variance explanation

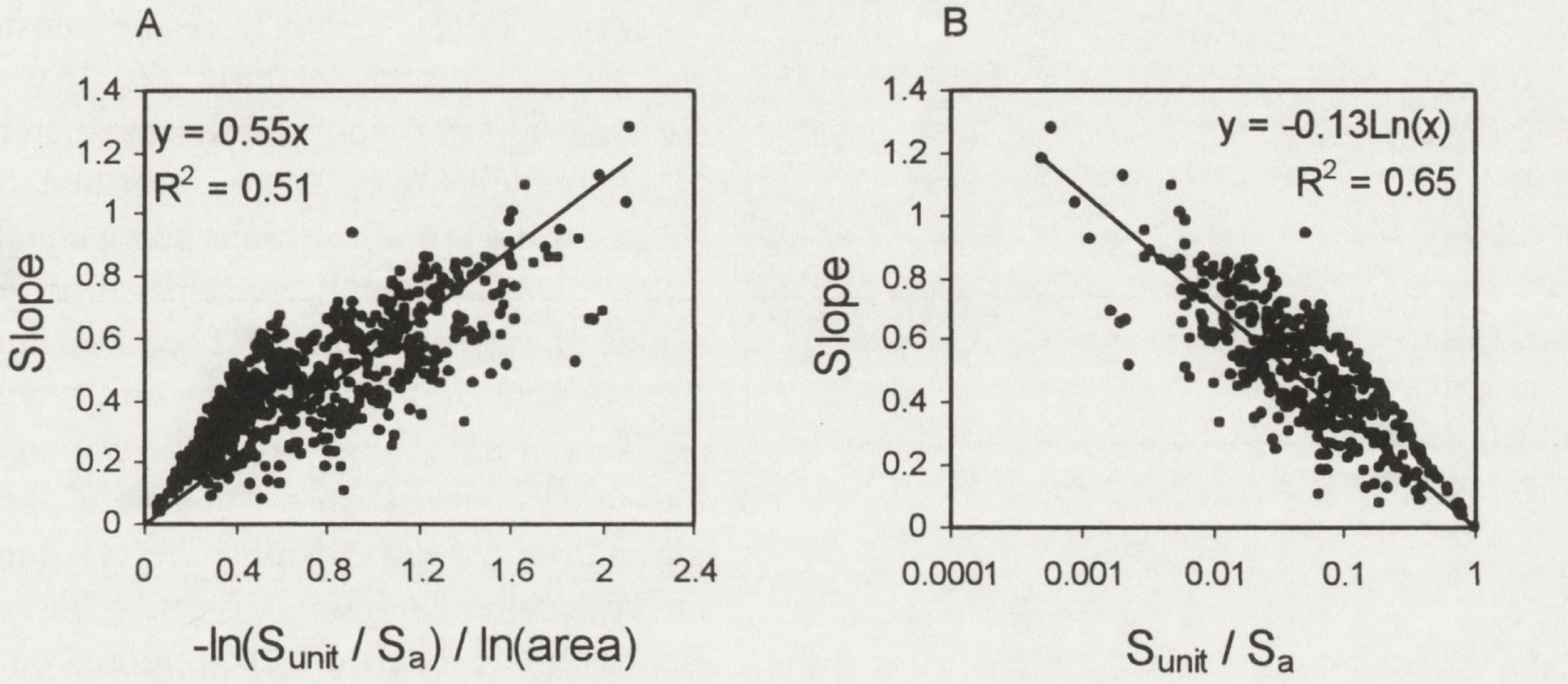

Fig. 3. A: Relationship between slope and $-\ln(S_{unit}/S_a)/\ln(\text{area})$ (assemblages 1 to 8 of Table 1 in part I, Ulrich 2000b); B: Relationship between slope and (S_{unit}/S_a) (assemblages 1 and 4 to 6). R^2: variance explanation, all regressions are significant at $p(t) < 0.0001$

the unit of area (Fig. 4). The larger the unit of area (given as a fraction of the total area), the larger the absolute value of a. The regression has the function $a = 76.7$ (*unit area*) $+ 0.5$. As expected, if the unit of area equals the total area then a becomes the value of 1. From the outer boundary lines of Figure 1A and the regression in Figure 4 it is concluded that a will generally range between 0.3 and 1. From the regression we derive a lower limit of a of 0.5.

In the case of the exponential SPAR model no simple relationship between relative species density and factor exist, but because the factor is closely related to regional diversity (see part II, Ulrich 2000a), S_{unit} and factor are correlated ($r = 0.58$, $p(t) < 0.001$).

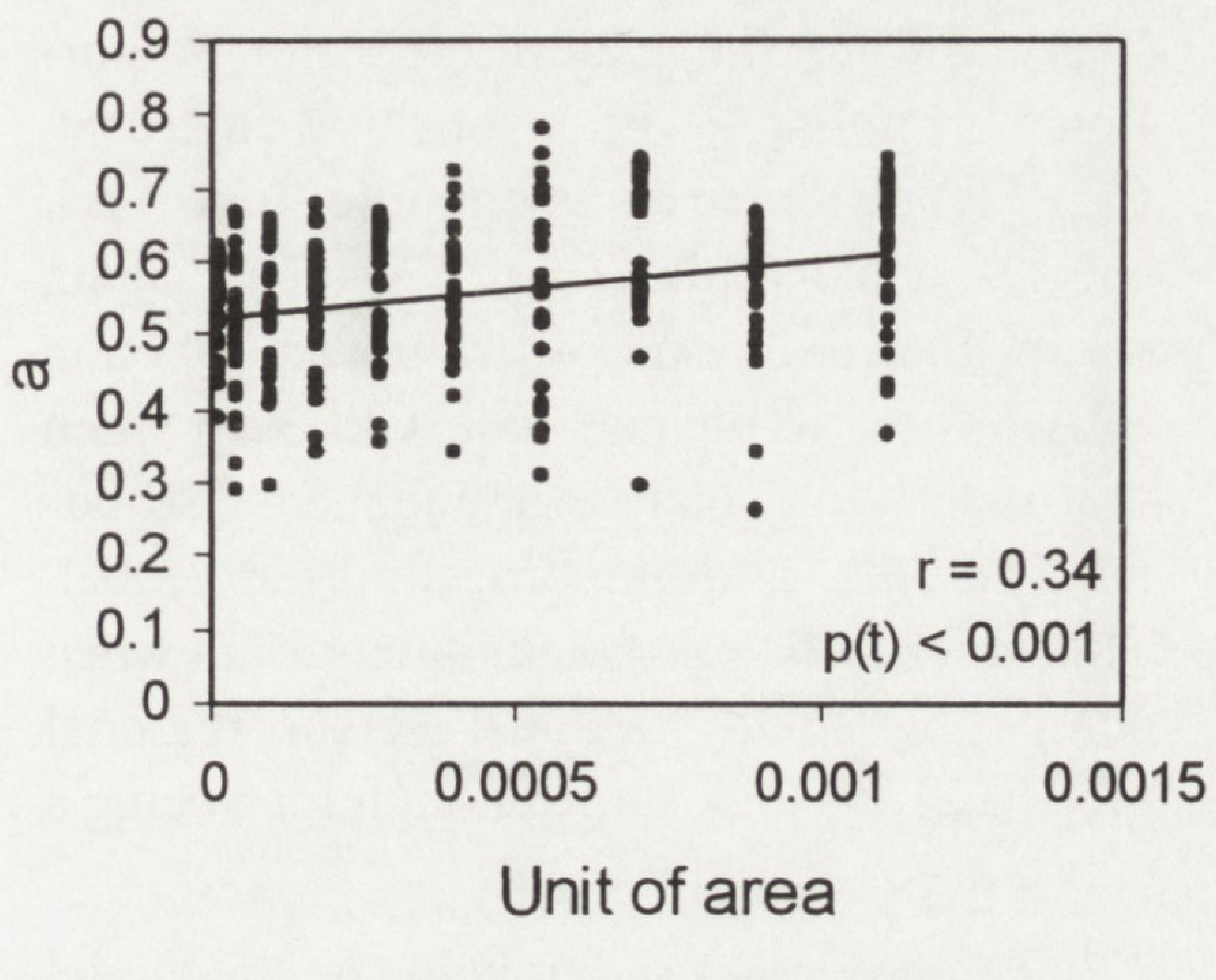

Fig. 4. Dependence of the constant a of formulas 3 and 4 on unit of sampling area. Assemblages 7 and 8 of Table 1. R^2: variance explanation, $p(t) < 0.01$

Of course, the above relation (3) depends on the fit of the power function model. But Figure 5A shows that formula 3 even at low degrees of variance explanation results in good approximations of the slope value. At R^2-levels below 0.95 formula 3 generally underestimates the real slope value. If the variance explanation exceeds 95% no bias could be detected. The fit of formula 3 depends slightly on the evenness of the assemblage (Fig. 5B), the higher the evenness the better the model fit.

Formula 3 is independent of unit of measurement and combines in a simple way two basic ecological concepts: the species–area curve and the relation between local and regional diversity. S_{unit}/S_a is the expression for the latter and is generally used to infer local species saturation by plotting S_{unit}/S_a at various scales (Fig. 6) (Cornell 1985, Lawton 1990, Cornell 1993, Caley 1997, Caley and Schluter 1997, Leibold 1998, Srivastava 1999). If S_{unit} equals S_a (local and regional diversity are equal, Case A in Fig. 6) z becomes zero, in the case of unsaturated local assemblages (Cornell and

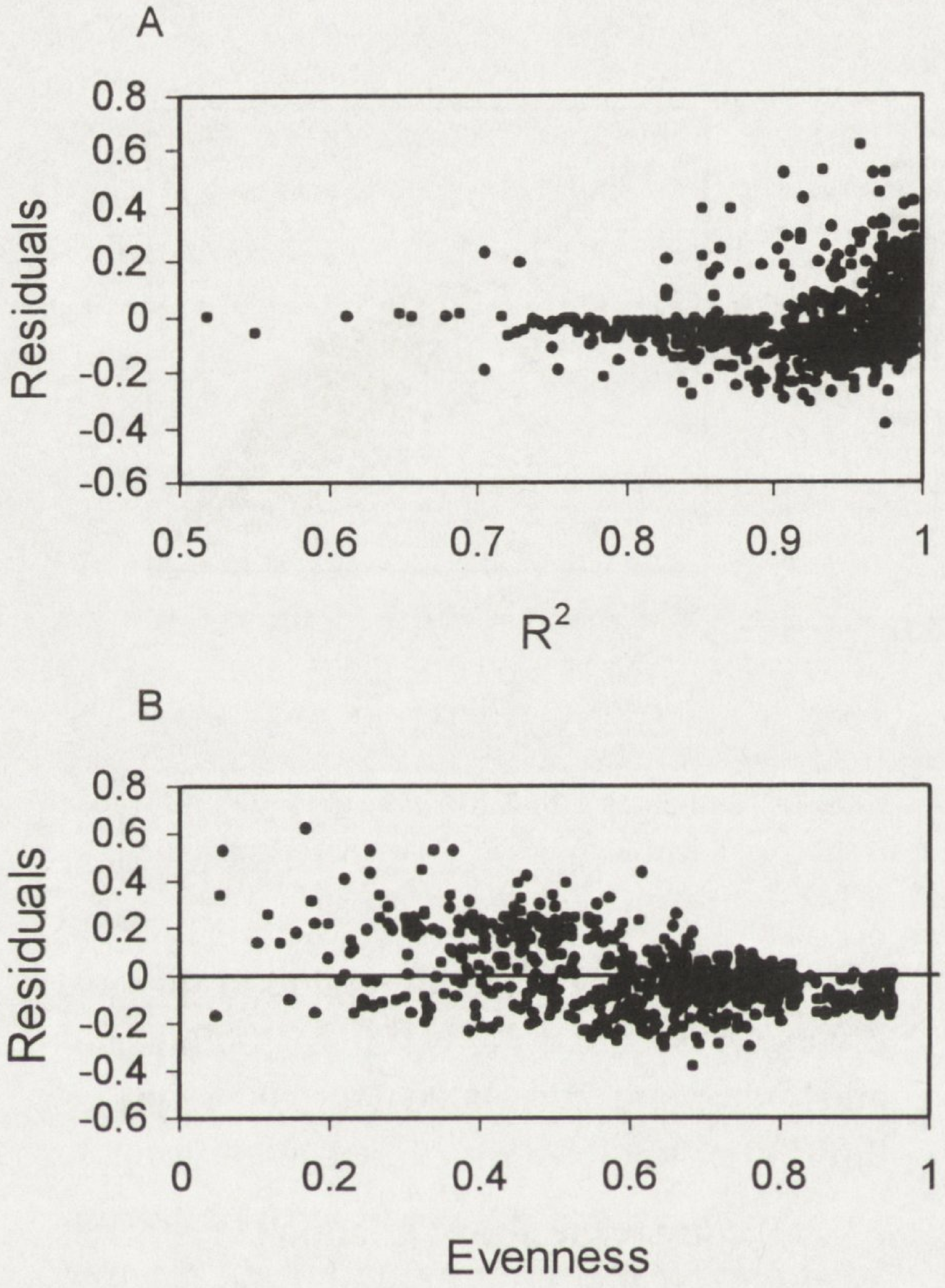

Fig. 5. Residuals (observed – predicted slopes) of formula 3 in dependence of the variance explanation of the power function model of SPAR (A) and the evenness (B). Assemblages 1 to 8 of Tab. 1 in part I, Ulrich (2000b)

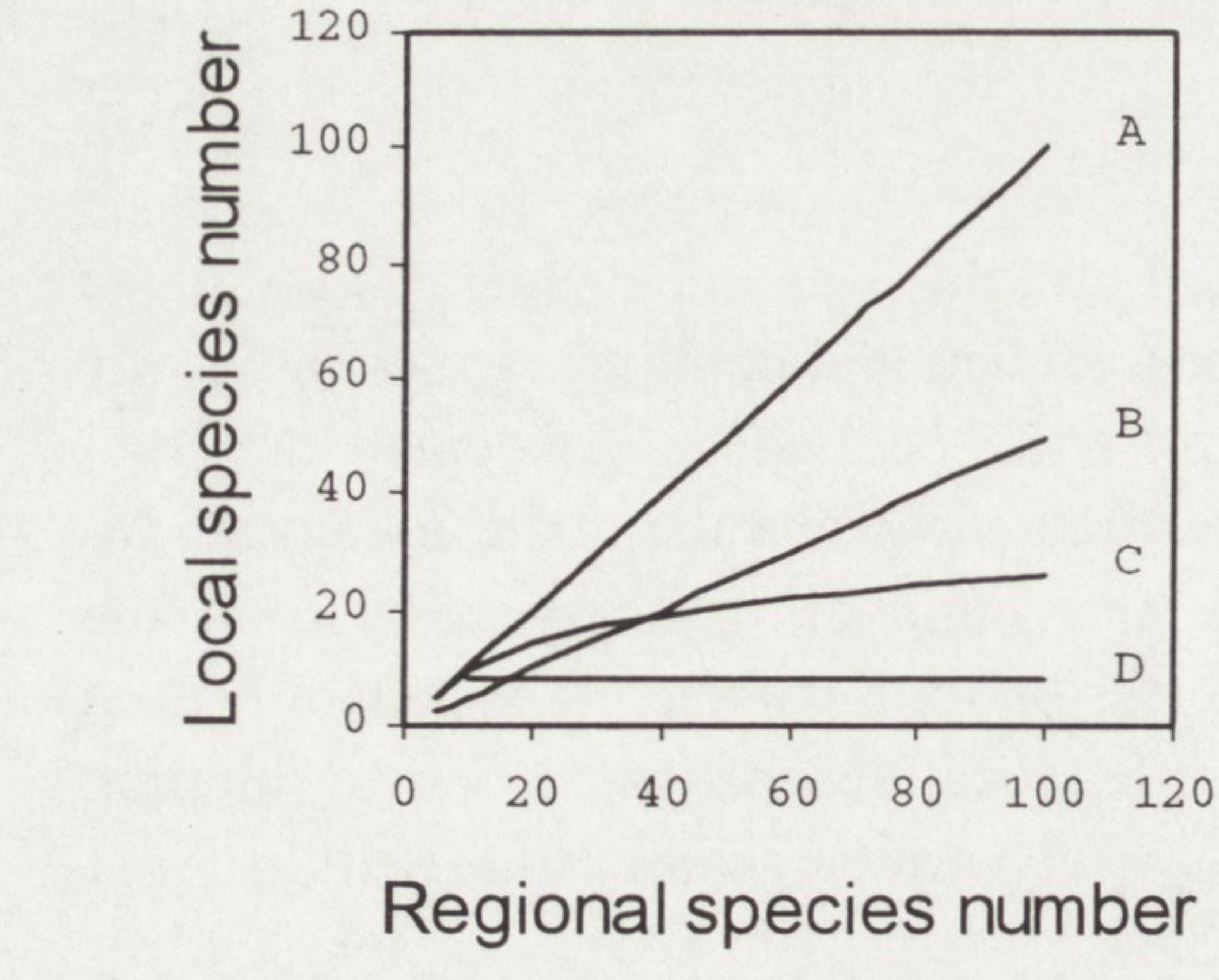

Fig. 6. Four models describing the relationship between local and regional number of species. A: all species of the regional species pool are found in the local scale; B: proportional sampling, there is a fixed ration between S_{unit} and S_a; C and D: local communities are saturated with species

Lawton 1992) – which is the most frequently observed pattern (Caley and Schluter 1997 and references therein) – S_{unit} is smaller than S_a at a constant factor (Case B) and (all other things being equal) the slope *z* will remain constant at different scales. If local assemblages become saturated the quotient S_{unit}/S_a decreases and *z* will increase (cases` C and D). The use of species–area curves may therefore be an alternative for establishing the relation between local and regional diversity where it is impossible to determine the regional number of species (Westoby 1993, Srivastava 1999).

However, formula 3 is strictly valid only if the relation between S_{unit} and S_a is of the form $S_{unit} = facS_a$ with intercept zero. In reality this is seldom met and the intercept (*icpt*) will be either positive or negative (normally there is a lower limit in local species density that means *b* is less than zero). In this case formula 3 changes into

$$z = \frac{a}{\ln(area)} \ln \frac{facS_a + icpt}{S_a} \qquad (4)$$

Now the slope *z* is not a constant but will asymptotically reach a constant value at higher regional species numbers. If *icpt* is less than zero the initial slope values will be higher than the asymptotic value, if *b* is greater than zero this pattern reverses. Figure 7 exemplifies the pattern. A strict proportional sampling (with a positive intercept, Fig. 7 B) results in an asymptotic slope – rel. species density plot (Fig. 7A). This again shows that the slope of the power function SPAR is by no means a constant even when the underlying relative abundance distributions and the sampling procedures are equal. This fact has also be taken into account when comparing slopes in local versus regional plots. S_{unit} has to be large enough for *z* being a constant.

The program used to generate the model assemblages of this study and to sample uses a random placement algorithm without an up-

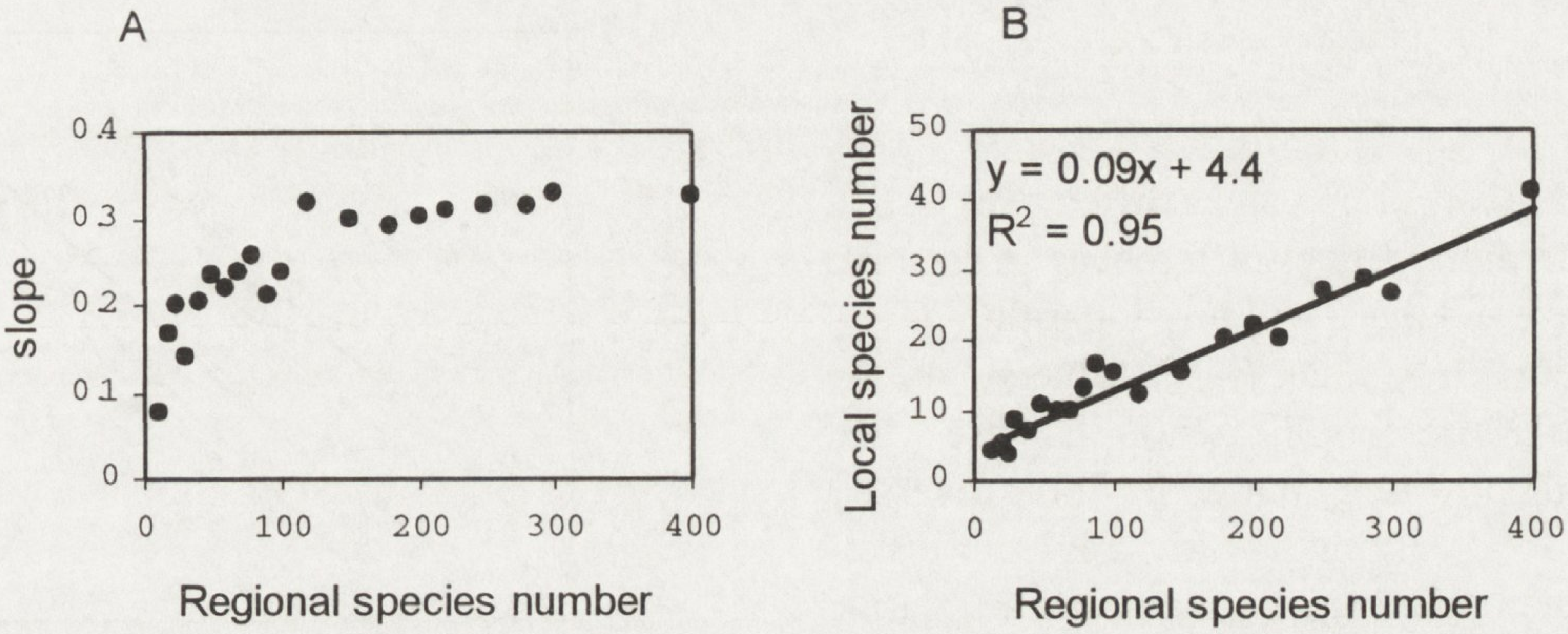

Fig. 7. Relation between slopes of the power function SPARs (A) and local species numbers (B) and regional species number. Assemblages 2 of Table 1. R^2: variance explanation

per limit of species or individuals per unit of area (a cell). In this case proportional sampling is expected when comparing assemblages of different species numbers but the same underlying relative abundance distributions. Figure 8 shows that this was indeed the case. This is not a trivial result as it may seem at first glance. Enhancing the number of species changes in some relative abundance distribution the fraction of rare species and Caley and Schluter (1997) predicted from model assemblages that log-normal distributed assemblages will generally be curvilinear at lower sample sizes (less than 200 times the regional species number). The plots in Figure 8 do not conform this prediction. Even at sample sizes around 4 times the regional species number (Fig. 8C) no curvilinearity could be detected. However, local and regional relative abundance distributions are not necessary of the same type. There may be changes at higher or very low species numbers. In this case even under the conditions of random placement and sampling the relative species density is not a constant and the slope may also vary.

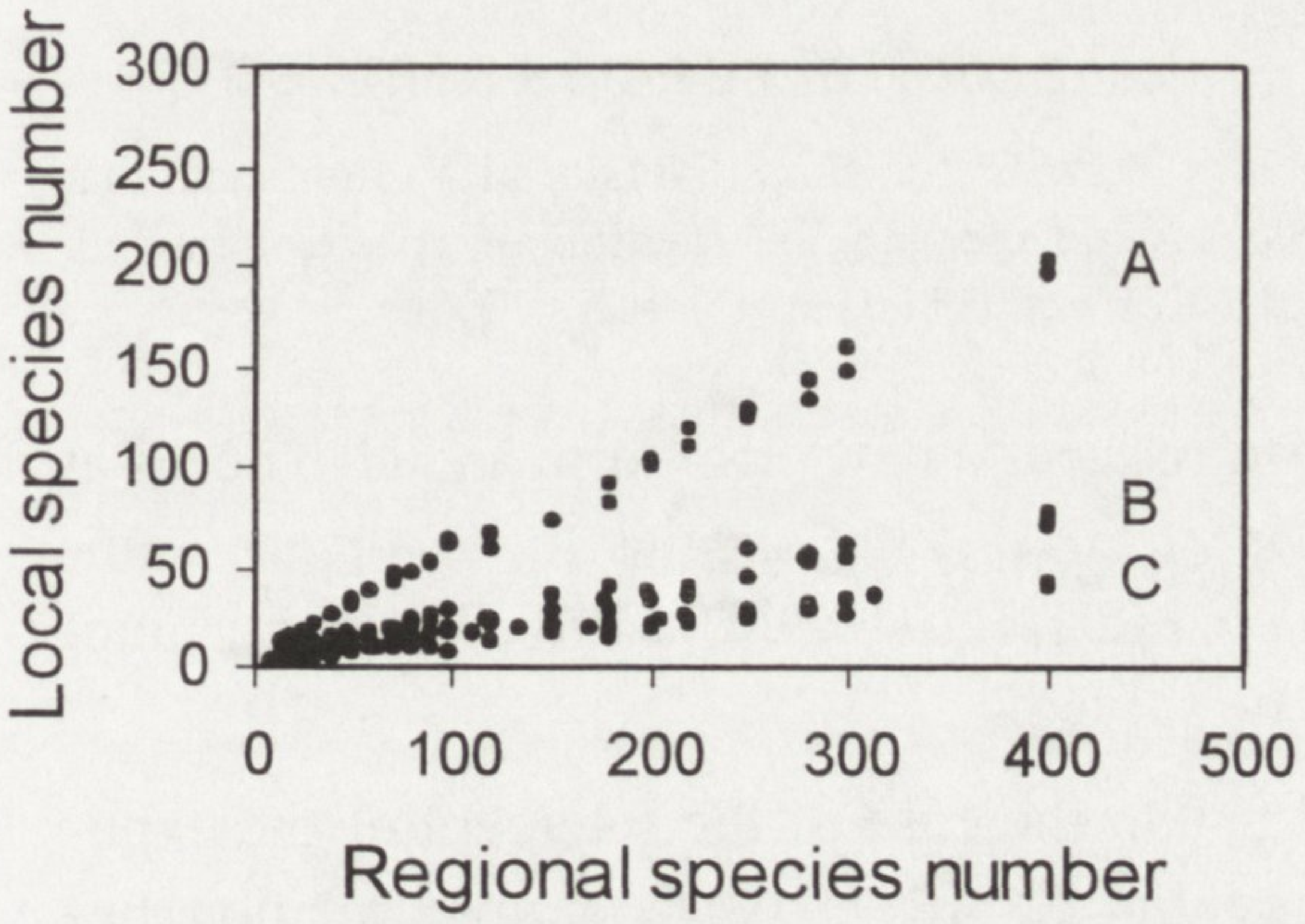

Fig. 8. Local and regional species numbers for log-normal distributed assemblages after random placement and sampling (assemblages No. 9 of Table 1). Sample size: A: 50 times max. regional species number (S_a), B: 20 times S_a, C: 4 times S_a

3.2. COMPARING DIFFERENT SPARS WITH SIMILAR SLOPES

Gould (1979) showed that in allometric studies the intercept may serve to compare curves with similar slopes (at constant unit of measurement). This simply because we can divide two power functions with equal slope an get

$$\frac{S_{unit/1}}{S_{n/1}} = \frac{S_{unit/2}}{S_{n/2}} \qquad (5)$$

with $S_{unit|1,2}$ and $S_{n|1,2}$ species number at unit of area and area *n*.

In part II of this study (Ulrich 2000a) it was derived that for any given relative abundance distribution the Shannon diversity *H* is a logarithmic function of S_n ($H = \beta\, ln(S_n)$. Therefore, we can rewrite 5 into

$$\frac{S_{unit/1}}{e^{\frac{H_{n/1}}{\beta}}} = \frac{S_{unit/2}}{e^{\frac{H_{n/2}}{\beta}}} \qquad (6)$$

At given slope values differences in S_{unit} will therefore reflect differences in regional diversity and there will be a logarithmic relation between S_{unit} and H_n, the diversity of the sample. More complicated is the case when we deal not with H_n but with H_a, the diversity of the total assemblage (the regional diversity). In this case (assuming the same relative abundance distribution) H_n is a fraction $\beta_1 H_a$ of H_a and we get

$$\frac{S_{unit/1}}{e^{\frac{\beta_1 H_{a/1}}{\beta}}} = \frac{S_{unit/2}}{e^{\frac{\beta_2 H_{a/2}}{\beta}}} \qquad (7)$$

This is exemplified in Figure 9A. Plots of Shannon diversity of the whole assemblage against $ln(S_{unit})$ resulted always in linear regressions (at constant slope of the power function SPAR). When testing SPAR slopes of 0.10, 0.15, 0.2, 0,.25. 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, and 1 the resulting regression slopes appeared to be roughly constant and ranged between 0.82 and 1.1 with a mean of 0.93. Differences in species density (S_{unit}) reflect, therefore, differences in regional diversity. When dealing with the same type of relative abundance distribution and using the same unit of area, we have to know the regional diversity of one area, the species density and the species density of a second area to compute the diversity of the latter.

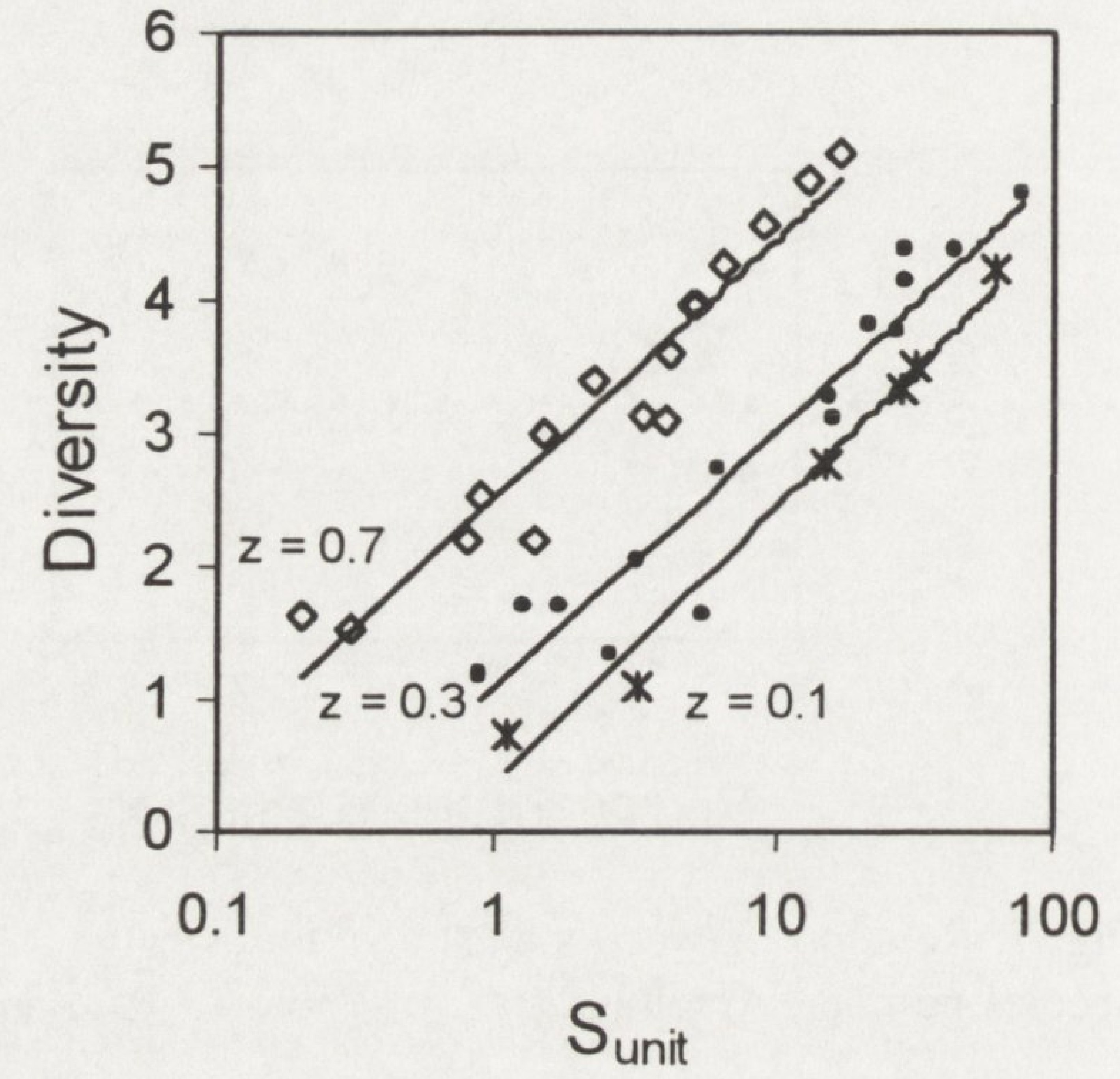

Fig. 9. Relation between species density (S_{unit}) and Shannon diversity of total assemblage for three slope values z (computed using all assemblages with z ± 0.02) of the power function SPAR. Note that the species densities are given in a logarithmic scale. Assemblages 1 and 4 to 6 of Table 1 of Ulrich (2000b)

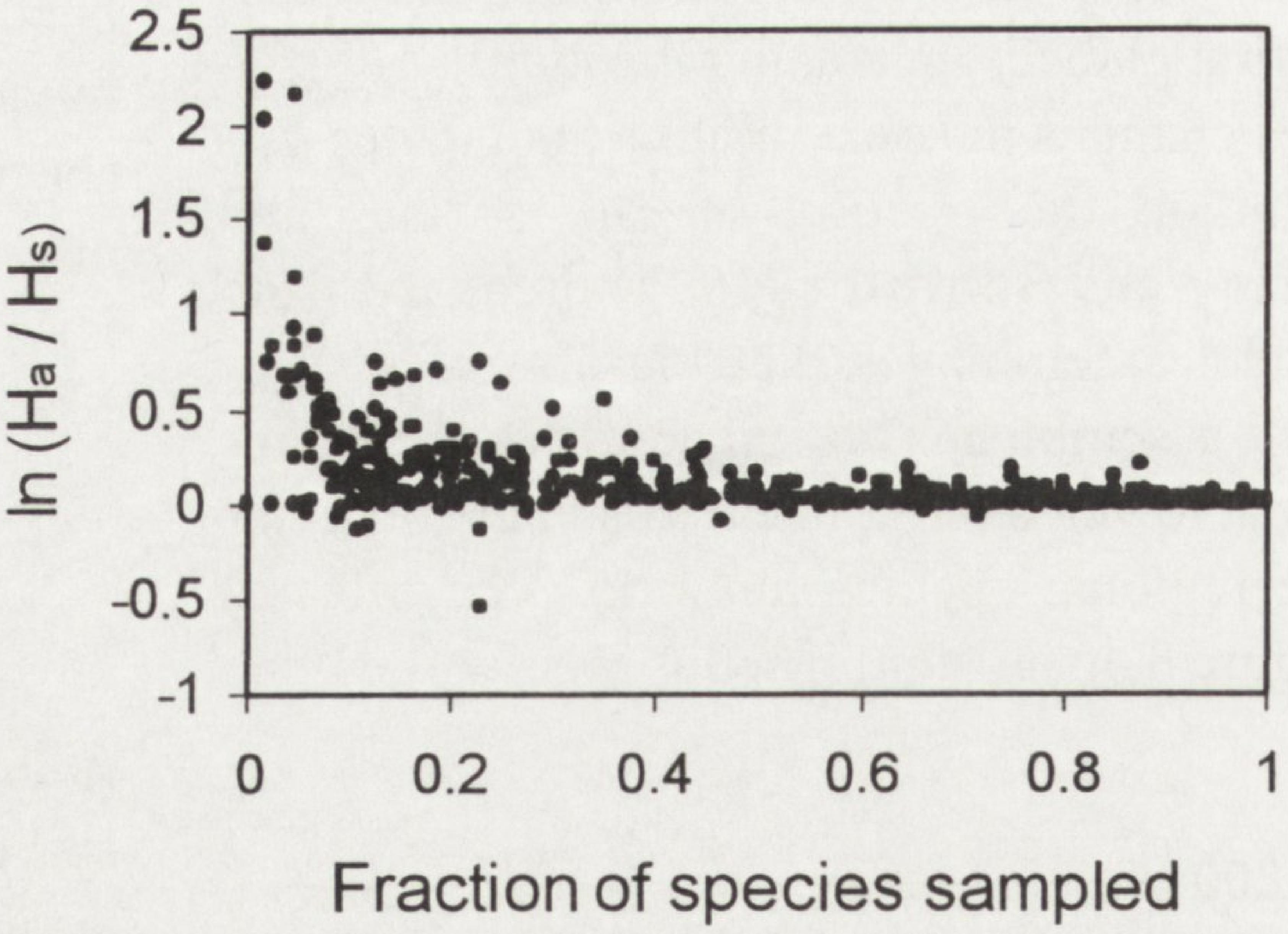

Fig. 10. Relation between Shannon diversity of a sample and that of the whole assemblage and the fraction of species sampled. Assemblages 1 to 10 of Table 1 of Ulrich (2000b)

Normally, the regional diversity is not known and has to be estimated by a sample. But Figure 10 shows that the sample diversity is a very good estimator of the regional if more than 20% of the species had been sampled. There are of course correction factors available (Pielou 1977), but these factors require knowledge of the total species numbers which are seldom known. Estimating them introduces a new error term and also needs at least 50% of the species to be already sampled (Ulrich 1999b), a circuit which cannot be solved.

In the case of the intercept of the exponential SPAR no such simple relation between S_{unit} and diversity exists, mainly because the factor b of the function is already a descriptor of regional diversity.

4. DISCUSSION

The intercept has largely been ignored by ecologists and is even often not reported in species–area studies. This surely due to the conventional wisdom that the intercept parameter is measurement dependent and gives only the mean number of species per unit of area. Only White and Gould (1965) and Gould (1979) treated the intercept of the power function in detail and found it usable to compare standardized variables used in allometric studies when the slopes are identical. However, relations between intercept and slope where not studied in detail.

The present study shows that the intercept of species–area relations deserves more attention. Not as a simple fitted constant but as a relative measure that combines the intercept and the total number of species of an assemblage under study. Such a combination (the rel. species density) is independent of units of measurement and can unambiguously be linked which the parameter z (the slope) of power function species–area relationship. For the exponential model of SPARs no such simple relations exist, a fact which favors the use of the power function.

Ulrich (1999a) studied species–area relationships in Hymenoptera and found that the published slope values grossly underestimated the species numbers at unit of area or less. This coincides with the finding in Figure 2 that the fitting process of the model assemblages used in this study results in an overestimation of S_{unit}. Ulrich (1999a) proposed to fit species area curves by a two step process, first establishing the correct intercept value by estimating or sampling S_{unit} and fitting a model which contains then only a single parameter (slope or factor). In the Hymenoptera such a process resulted in much more realistic species number estimations over the whole range of areas included in the regression. Indeed, it is known that the intercept value has frequently the highest variance (Keating 1998).The above results show that such an adjustment will inevitably change the slope value and effect the model fit.

Preston (1962) was the first to combine intercept and slope of the power function model by comparing S_{unit}/S_a and z (when sampling a fixed universe). From a canonical log-normal distribution he approximated a linear relation between the fraction of species sampled at unit area and the slope value if more than 10% of the species had been sampled. Figure 3 shows that this is not correct, the relation is logarithmic over the whole range. From Preston's plot we can deduce that a z value below 0.3 is reached if more than 50% of the species are found per unit area. In the model communities used in this study such slopes required only about 15%. Interestingly, Preston did not discuss the point in further detail.

Recently, Hanski and Gyllenberg (1997) combined the concepts of species–area curves and abundance–range size relationships. Their model predicts a nonlinear relationship between relative species density and slope over the whole range of densities and their predicted slope values are closely to the empirical ones in Figure 3B. In this respect the data presented here sustain the model of Hanski and Gyllenberg (1997). There model however does not deal with different sampling methods and the dependency of the slope on them.

The data in Connor and McCoy (1979) contain 28 assemblages of which the total number of species is given. They allow a plot similar to Figure 3B (Fig. 1A) (that means without containing the total area sampled). Indeed, in the real assemblages a similar picture than in the model communities comes up and the slope parameter a is nearly identical to the one deduced from Figure 3B. That the variance is much larger stems from the fact that the Connor and McCoy compilation contains a mix of various sampling designs and that the estimates of total species number have also some error term.

Recently, the relationship between local and regional species numbers has gained much interest (Lawton 1990, Cornell 1993, Hugueny and Paugy 1995, Shorrocks and Sevenster 1995, Caley 1997, Caley and Schluter 1997, Griffiths 1997, Hugueny *et al.* 1997, Karlson and Cornell 1998, Leibold 1998) although only a few researchers combined their results with species–area relationships (Cornell and Washburn 1979, Aho 1990, Aho and Bush 1993, Westoby 1993, Srivastava 1999). This study shows that it is possible to subsume both concepts under a general framework. Species–area relations may be expressed in terms of local and regional species numbers and patterns of the latter may be studied by analyzing species–area relations at different geographical scales.

Most of the cited studies found proportional sampling patterns and concluded that the local communities were unsaturated. Saturation had been found in some vertebrate and vertebrate parasite communities (Aho 1990, Aho and Bush 1993), although the methods used to infer a type C dependence (Fig. 6) have been criticized (Caley and Schluter 1997, Srivastava 1999). In unsaturated communities the slope of the power function at different scales should be constant or follow a logarithmic curve (Fig. 7). In saturated communities the slope will change constantly over the whole range of species numbers and the pattern of change will follow either a power function or a straight line. Species–area relationships are often more easy to construct, especially in very species rich communities and the change of slope value may also be more easy be interpreted than deviations of local versus regional species number plots from linearity (Caley and Schluter 1997, Griffiths 1997).

Of course, the above results are derived from model assemblages with random placement of individuals (see part I, Ulrich 2000b) and they have to be tested with real communities. However, the wide range of assemblage structures used in this study and the nearly identical patterns derived from the data in Connor and McCoy (1979) show that the derived relations are widely applicable. They also may serve as null models in species–area and diversity studies.

At the end of part III of this study we may ask again the question which model should be applied to study species–area relations. Surely, a simple model fit cannot answer this question because fit of a model by no means tells us whether the underlying structuring processes are really described by the applied model. The fact that frequently the power function and the exponential model give similar good fits further complicates the situation. In the past the power function model has gained by far more attention than the exponential model because of a better theoretical underpinning and ecological explanation of the slope values (Preston 1962, May 1975, Sugihara 1980, 1981, Wissel and Maier 1992, Harte and Kinzig 1997, Harte *et al.* 1999). The results of part I (Ulrich 2000b) indicated that the power function model may be better suited for random fraction and log-normal distributed communities, whereas in most other types of relative abundance distributions the exponential model may be superior.

Part II of the present study (Ulrich 2000a) gave for the first time an ecological interpretation of the factor value and showed that the exponential form of the species–area relation is closely linked to the common Shannon measure of diversity and may be used to infer regional diversity. In this respect the exponential form seems to be superior to the power function. The connection between factor value and diversity is worth to be studied in detail in real animal and plant communities. Both SPAR models can be linked to local and regional diversity patterns, although the power function may be more easy to interpret.

From the above arguments it is concluded that the exponential form of species–area relations has gained too few attention and should be studied in more detail.

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5. SUMMARY

Using model assemblages (Table 1) generated by a FORTRAN-program the dependence of the intercept of the power function and exponential model of species–area relationships were studied. It is shown that the quotient of intercept and total species number in the assemblage (S_{unit}/S_a) can be interpreted as a relation between local and regional diversity (Fig. 6) and linked with species–area relations (Figs 1, 2, 3, 4, 8).

Two general relations are derived and tested (Figs 7, 9, and 10) combining both concepts: $z=\frac{a}{\ln(area)}\ln\frac{S_{unit}}{S_a}$, and $\frac{S_{unit/1}}{e^{\frac{\beta_1 H_{a/1}}{\beta}}}=\frac{S_{unit/2}}{e^{\frac{\beta_2 H_{a/2}}{\beta}}}$ with z being the slope of the power function model, H the Shannon diversity, β, β_1 and β_2 constants, and a the constant of the relation between S_{unit}/S_a and z. It is concluded that species–area relationships can be used to infer the relation between local and regional species numbers and diversities.

6. REFERENCES

Aho J. M. 1990 – Helminth communities of amphibians and reptiles: comparative approaches to understanding patterns and processes (In: Parasite Communities: Patterns and Processes Eds G. W. Esch, S.A.. O. Bush, J. M. Aho) – Princeton Univ. Press, pp. 157–196.

Aho J. M., Bush A. O. 1993 – Community richness in parasites of some freshwater fishes from North America (In: Species Diversity in Ecological Communities, Eds R. E. Ricklefs, D. Schluter) – Chicago Univ. Press, pp. 185–193.

Caley M. J. 1997 – Local endemism and the relationship between local and regional diversity – Oikos, 79: 612–615.

Caley M. J., Schluter D. 1997 – The relationship between local and regional diversity – Ecology, 78: 70 – 80.

Connor E. F., McCoy E. D. 1979 – The statistics and biology of the species–area relationship – Am. Nat. 113: 791–833.

Cornell H. V. 1985 – Local and regional richness of cynipine gall wasps on California oaks – Ecology, 66: 1247–1260.

Cornell H. V. 1993 – Unsaturated patterns in species assemblages: the role of regional processes in setting local species richness (In: Species Diversity in Ecological Communities, Eds R. E. Ricklefs, D. Schluter) – Chicago Univ. Press, pp. 243–252.

Cornell H. V., Washburn J. O. 1979 – Evolution of the richness – area correlation for cynipid gall wasps on oak trees: a comparison of two geographic areas – Evolution, 33: 257–274.

Cornell H. V., Lawton J. H. 1992 – Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective – J. Anim. Ecol. 61: 1–12.

Gould S. J. 1979 – An allometric interpretation of species–area curves: the meaning of the coefficient.

Griffiths D. 1997 – Local and regional species richness in North American lacustrine fish – J. Anim. Ecol. 66: 49–56.

Hanski I., Gyllenberg M. 1997 – Uniting two general patterns in the distribution of species – Science, 275: 397–400.

Harte J., Kinzig A. P. 1997 – On the implications of species–area relationships for endemism, spatial turnover, and food web patterns – Oikos, 80: 417–427.

Harte J, Kinzig A. P., Green J. 1999 – Self-similarity in the distribution and abundance of species – Science, 284: 334–336.

Heatwole H. 1975 – Biogeography of reptiles on some of the islands and cays of eastern Papua – New Guinea – Atoll Res. Bull. 180.

Hopkins B. 1955 – The concept of minimal area – J. Ecol. 45: 441–449.

Hugueny B., Paugy D. 1995 – Unsaturated fish communities in African rivers – Am. Nat. 146: 162–169.

Hugueny B., de Morais L. T., Merigoux S., de Merona B., Ponton D. 1997 – The relationship between local and regional species richness: comparing biotas with different evolutionary histories – Oikos, 80: 583–587.

Johnson M. P., Raven P. H. 1970 – Natural regulation of plant species diversity – Evol. Biol. 4: 127–162.

Karlson R. H., Cornell H. V. 1998 – Scale-dependent variation in local vs. regional effects on coral species richness – Ecol. Monogr. 68: 259–274.

Keating K. A. 1998 – Estimating species richness: the Michaelis-Menten model revisited – Oikos, 81: 411–416.

LaBarbera M. 1985 – The Evolution and ecology of body size (In: Patterns and processes in the History of Life, Eds.: D. M. Raup, D. Jabłoński) – Springer (Berlin), pp. 69–98 .

Lawton J. H. 1990 – Species richness and population dynamics of animal assemblages. Patterns in body size: abundance space – Phil. Trans. R. Soc. Lond. B 330: 283–291.

Leibold M. A. 1998 – Similarity and local co-existence of species in regional biotas – Evol. Ecol. 12: 95–110.

MacArthur R. H., Wilson E. O. 1967 – The theory of island biogeography – Princeton Univ. Press, 203 pp.

May R. M. 1975 – Patterns of species abundance and diversity – (In: Ecology and evolution of communities, Eds.: M. L. Cody, J. M. Diamond) – Belknap (Cambridge), pp. 81–120.

Moravec J. 1973 – The determination of minimal area of phytocoenoses – Folia Geobot. Phytotax. 8: 23–47.

Pielou E. C. 1977 – Mathematical Ecology – John Wiley & Sons, New York, 385 pp.

Preston F. W. 1962 – The canonical distribution of commonness and rarity. Part I and II – Ecology, 43: 185–215, 410–432.

Rosenzweig M. L. 1995 – Species diversity in space and time – Cambridge, Univ. Press, 435 pp.

Shorrocks B., Sevenster J. G. 1995 – Explaining local species diversity – Proc. R. Soc. Lond. B 260: 305–309.

Sprugel D. G. 1983 – Correcting for bias in log-transformed allometric equations – Ecology, 64: 209–210.

Srivastava D. E. 1999 – Using local–regional richness plots to test for species saturation: pitfalls and potentials – J. Anim. Ecol. 68: 1–16.

Sugihara G. 1980 – Minimal community structure: an explanation of species abundance patterns – Am. Nat. 116: 770–787.

Sugihara G. 1981 – $S = CA^z$, $z \approx 1/4$; a reply to Connor and McCoy – Am. Nat. 117: 790–793.

Ulrich W. 1999a – The numbers of species of Hymenoptera in Europe and assessment of the total number of Hymenoptera in the world – Pol. J. Entomol. 68: 151–164.

Ulrich 1999b – Estimating species numbers by extrapolation I: comparing the performance of various estimators using large model communities – Pol. J. Ecol. 47: 271-291.

Ulrich W. 2000a – On species–area relationships II: slope and factor values of power function and exponential model – Pol. J. Ecol. 48: 21–35

Ulrich W. 2000b – On species–area relationships I: fit of power function and exponential model – Pol. J. Ecol. 48: 3–20

Westoby M. 1993 – Biodiversity in Australia compared with other continents (In: Species Diversity in Ecological Communities, Eds. R. E. Ricklefs, D. Schluter) – Chicago, Univ. Press, pp. 170–177.

White J. F., Gould S. J. 1965 – Interpretation of the coefficient in the allometric equation – Am. Nat. 99: 5–18.

Wissel Ch., Maier B. 1992 – A stochastic model for the species–area relationship – J. Biogeogr. 19: 355–362.

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