

POLISH JOURNAL OF ECOLOGY (Pol. J. Ecol.)	61	2	345–354	2013
--	----	---	---------	------

Regular research paper

Werner ULRICH<sup>1\*</sup>, Marcin ZALEWSKI<sup>2</sup>, Izabela HAJDAMOWICZ<sup>3</sup>,  
Marzena STAŃSKA<sup>3</sup>, Wojciech CIURZYCKII<sup>4</sup>, Piotr TYKARSKI<sup>5</sup>

<sup>1</sup>Department of Animal Ecology, Nicolaus Copernicus University in Toruń, Lwowska 1, 87–100 Toruń; Poland, \*e-mail: ulrichw@umk.pl (correspondence author)

<sup>2</sup>Centre for Ecological Research, Polish Academy of Sciences, M. Konopnickiej 1, Dziekanów Leśny, Poland, e-mail: zlewek@yahoo.com

<sup>3</sup>Department of Zoology, Siedlce University of Natural Sciences and Humanities, Prusa 12, 08–110 Siedlce, Poland

<sup>4</sup>Warsaw University of Life Sciences SGGW, Faculty of Forestry, Department of Forest Botany, Nowoursynowska 159, 02–776 Warsaw, Poland

<sup>5</sup>Department of Ecology, Faculty of Biology, University of Warsaw, Banacha 2, Warsaw 02–097, Poland

## TOWARDS A GENERAL SPECIES – TIME – AREA – SAMPLING EFFORT RELATIONSHIP

**ABSTRACT:** Species – area (SAR) and species time (STR) relationships describe the increase of species richness with study area and study time and have received much attention among ecologists and are used in different branches of biodiversity research. Unknown sample size effects often hinder a direct comparison of SAR and STR shapes of different taxa and regions. Further, space and time interact during the accumulation of species due to the common sample universe. Here we develop a simple power function scaling model of species richness that integrates space, time, sample size and their interactions. We show that this model is able to precisely describe average species densities and the increase of species richness in a regional meta-community of a large sample of spiders on Mazurian lake islands (Northern Poland). The model predicts strong area – sample size and time – sample size interactions. Judged from the SAR ( $z = 0.08$ ) and STR ( $y = 0.64$ ) slopes it points to only moderate spatial  $\beta$ -diversities but high local temporal species turnover. We suspect that the parameters of many published SARs are strongly influenced by unknown sampling time and sample size effects that make direct comparison difficult.

**KEY WORDS:** Araneae, spiders, species richness, species accumulation, power function, SAR, Mazurian lakes, island

### 1. INTRODUCTION

Species numbers increase with the area surveyed. This well known species – area relationship (SAR) has received considerable interest among ecologists (reviews in Rosenzweig 1995, Scheiner 2003, Tjørve 2003, 2009) and is used for biodiversity estimates (Myers *et al.* 2000), species loss forecasting (Brooks *et al.* 1997, Ulrich and Buszko 2003, 2004), and the identification of ecological hot spots (Ulrich and Buszko 2005).

Most SARs are fitted by power functions (Drakare *et al.* 2006, Dengler 2009). In 1960, Preston proposed that the accumulation of species with sampling time follows a similar power function relationship. He also predicted that the slope of this species – time relationship (STR) has a similar slope to that found in SARs. Preston's first prediction is strongly supported by the available data (Preston 1960, Adler and Lauenroth 2003, Adler 2004, Maurer and McGill 2004, Adler *et al.* 2005, Fridley *et al.* 2006, Ulrich 2006, White *et al.* 2006). The second prediction, though, has less corroboration. Adler and Lauenroth (2003) found

at least for grasslands higher slope values of STRs in comparison to respective SAR slopes and Ulrich (2006) reported STR slopes of forest Hymenoptera to be four times lower than the respective SAR slopes. In a meta-analytical study White *et al.* (2006) compared STRs across taxonomic groups and found the slopes of power function fits typically to a range between 0.2 and 0.4. While this at least in part overlaps with the typical range of SAR slopes, it does not mean that both slopes are similar within a taxonomic group.

A third aspect of species accumulation is sampling effort (for instance numbers of observations or traps). A large body of work dealt with such species accumulation or collector's curves (SACs) (reviewed in Dove and Cribb 2006 and Thompson and Thompson 2007). Asymptotic SACs were mainly fitted to Michaelis Menten or negative exponential models (Coleman 1981, Williams 1995, Keating 1998) while for non-asymptotic SACs power or logarithmic functions have been applied (Connor and McCoy 1979, Azovsky 2011). Because the term SAC has been referred to different aspects of species accumulation (Colwell *et al.* 2004) below we use the species – sampling effort relationship (SER) for the pure increase of species richness with sample size.

At constant area and sampling time, sampling effort should be proportional to the number of individuals. Empirical studies pointed to the power function as the best description of such species – individuals relationships (Palmer and White 1994, Azovsky 2011). Indeed, sampling effort can be seen as another form of the increase of individuals and therefore species in space or time. Thus species richness should increase with sample size (sampling intensity) in a similar manner as with area and time, hence according to an unbounded power function (but see McGlenn and Palmer 2009). In the present paper we evaluate how area, time

and sampling effort work together to form a general species – time – area – sampling effort relationship (STAER). The starting point is the assumption that species richness  $S$  is allometrically proportional to area  $A$ , time  $t$ , and sampling effort  $n$ :

$$S = S_0 A^z t^y n^x \quad (1)$$

where:  $A$  denotes the area and  $S$  the associated number of species.  $S_0$  is then an estimator of the average number of species per sampling unit (species density) and  $z$  an estimator of spatial species turnover. The parameter  $y$  of eq. 1 can be interpreted as temporal species turnover within a given area  $A$  under fixed sampling effort and describes the number of new species in a sequence of surveys. For completely surveyed habitats this equals the rate of immigration (Ulrich 2006). The last term describes the increase of richness with sample size  $n$  (the SER) and should in a homogeneous habitat only depend on the underlying abundance distribution and the pattern of aggregation of the individuals of each species (Green and Plotkin 2006).

Eq. 1 assumes independence of area, time, and sample size. There is a discussion whether species accumulation curves need to be extended for interactions between predictors. For instance, smaller areas might have higher rates of temporal species turnover than larger areas. Repeated sampling might then increase the species numbers of smaller areas faster than of larger areas and decrease the SAR slopes depending on sampling time because STRs and SARs refer to the same sample universe. This is not to say that the SAR becomes asymptotic to a maximum number of species (Williamson *et al.* 2001).

Several correction terms for deviation of SARs from the power function model have been used (Ulrich and Buszko 2005, Tjørve 2009) although only the multiplicative interaction term of Schoereder *et al.* (2004) referred explicitly to sampling effort.

**Table 1.** Slopes and coefficients of determination of fits of the power, logarithmic, and linear function to simple species – time (STR) relationships ( $n = 8$ ), SARs ( $n = 30$ ), and SERs ( $n = 22$ ).

Accumulation curve	Power function		Logarithmic function		Linear function	
	Slope	R <sup>2</sup>	Slope	R <sup>2</sup>	Slope	R <sup>2</sup>
STR	0.24	0.85	30.1	0.75	8.8	0.75
SAR	0.41	0.98	30.3	0.97	0.9	0.92
SER	0.55	0.92	62.4	0.90	1.4	0.91

Adler and Lauenroth (2003) and Adler *et al.* (2005) introduced an additive interaction term to the log transformed species – time – area relationship (STAR) to describe the reciprocal relationship of area and time:

$$\ln S = \ln S_0 + z \ln A + y \ln t + u \ln A \ln t \quad (2)$$

The interaction term  $u$  describes the deviation of the SAR depending on sampling time. Adler and Lauenroth (2003) reported decreasing SAR and STR slopes with time and area, respectively, and Adler *et al.* (2005) reported a better fit to plant and bird STARs than the non-interactive model. However, in a previous paper one of us (Ulrich 2006) found the area – time interaction as being insignificant in six superfamilies of forest Hymenoptera.

Only a few papers explicitly included sampling effort in SAR and STR models (Palmer and White 1994, Goldberg and Estabrook 1998). More recently, Schoereder *et al.* (2004) used general linear model regression to disentangle the effect of sampling effort  $n$ , area  $A$  and the interaction of  $A$  and  $n$  on species richness  $S$  and found the interaction term as being significant. Most work, however, tried to control for different sampling effort and either used ‘uniform sampling’ (Hill *et al.* 1994), rarefaction (Hurlbert 1971), or a top-down approach to estimate species richness from sampling models (Pielou 1975, Coleman 1981, Cam *et al.* 2002). A general model of species richness that includes area, sampling time, and sampling effort was hitherto missing.

It is also unknown whether the reported interaction of area and time might be due to the influence of differential sample sizes at larger areas and longer study times. The aim of the present study is to disentangle the effects of area, time and sample size on the process of species accumulation at the regional scale. Following the logic of Schoereder *et al.* (2004) and Adler and Lauenroth (2003) eq. 2 has to be extended by interaction terms that describe the covariance of area, time and sampling effort:

$$\ln(S_{pred}) = \ln S_0 + z \ln A + y \ln t + x \ln n + u \ln A \ln t + v \ln A \ln n + w \ln t \ln n + s \ln A \ln t \ln n \quad (3)$$

where:  $u$ ,  $v$ ,  $w$ , and  $s$  are the interaction parameters of the model. The interaction pa-

rameters  $v$  and  $w$  describe the deviation of the SAR and the STR depending on time and area, respectively. Negative values of  $v$  and  $w$  can be interpreted as the saturation in species richness with increasing sampling effort.

Particularly we ask:

- what functions describe observed SARs, STRs, and SERs best,
- whether area, time and sampling effort act independently or whether interaction terms have to be considered,
- whether slopes of SARs, STRs, and SERs are similar according to Preston’s (1960) second hypothesis,
- whether the STR can be used to assess temporal species turnover, and
- whether the constant of eq. 3 can be used to estimate species density.

We use an extensive data set of spider species richness on two complexes of Mazurian lake islands (northern Poland) obtained for 26 lake islands and four surrounding mainland sites during a two-year study (Ulrich *et al.* 2010a, b). Apart from the direct fitting of eq. 2 and 3 to the whole data set the data allow for the construction of SARs for identical sampling times and numbers of traps, the construction of STRs for identical areas and numbers of traps, and the construction of SERs for identical areas and sampling times. This data structure gives therefore a unique opportunity to decompose different aspects of species accumulation into important parts and their interactions and allows for the construction and study of a general STAER model.

## 2. MATERIALS AND METHODS

### 2.1. Study sites and sampling

We sampled spiders from two large complexes of lake islands in Northern Poland: the Lake Wigry islands (54°00′ – 54°05′N, 22°01′ – 22°09′ E) and the Lake Nidzkie, Beldany and Mikołajskie islands (54°37′ – 53°46′ N, 21°31′ – 21°37′E, hereafter NBM) (Ulrich *et al.* 2010a, b). Lake Wigry is part of the Wigierski National Park and its protected forested islands have a primeval character. NBM form a complex of three connected lakes and are part of the Mazurian Lake District. They are the centre of aquatic tourism in Poland.

On 13 islands on Wigry, 13 islands on NBM (hence all islands except of a few very distant and inaccessible ones) and four floristically similar sites on the surrounding mainland, we placed 3 to 15 roof covered Barber traps ( $\varnothing$  12 cm opening) in dependence on island area. Placement was done to cover representative parts of the floral composition per site. The distance between the traps was always 25 m (Zalewski and Ulrich 2006). They were monthly controlled from May to October 2004 and 2005. Spiders were classified into species according to Platnick (2009). Island sizes span a range from 0.0003 to 38.82 ha (for detailed information on island characteristics cf. Ulrich *et al.* 2010a).

We constructed SARs, STRs, and SERs from the species richness in all combinations of traps ( $n = 1080$ ) with constant sampling time and number of traps (SAR), area and number of traps (STR), and area and time (SER). In the following we call them pure accumulation curves. We fitted power function, logarithmic and linear models to SARs, STRs and SERs. Because the ordering of islands, sampling times and traps might have an influence on the resulting species accumulation curves (Ulrich and Buszko 2007) we reshuffled this order for each new curve. The STRs refer therefore to the completely nested type of Carey *et al.* (2007). Area refers always to island area. We used ordinary least square regression (after log linearization) for model fit to pure SARs, STRs, and SERs. Models with and without interaction terms were fitted by multiple regression after log-transformation. We used the consistent Akaike information criterion (CAIC) for model choice. Errors refer to standard errors.

Due to our nested design the data points used to construct regressions and parameter errors were not independent. This might influence estimates of standard errors and probability levels. Therefore we do not compare parameter values of different models but concentrate on the qualitative aspect of model fit.

### 3. RESULTS

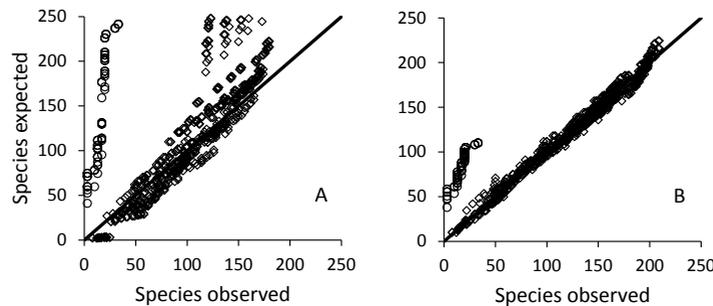
#### 3.1. Basic Model choice

In the first step we compared the fit of the linear, the logarithmic and the power function models of the pure SARs, STRs, and SERs. In all three cases we found the power function models to fit best (Tab. 1) although the differences are small. The average number of species per trap  $S_0$  ranged between 1 and 38 with an arithmetic mean of 5.53.  $S_0$  was independent of the area sampled (Spearman's  $r = 0.03$ , n.s.). In the case of the SER the logarithmic model predicted in all cases negative values of  $S_0$  while the linear model constantly overestimated  $S_0$  by a factor of more than ten (not shown).

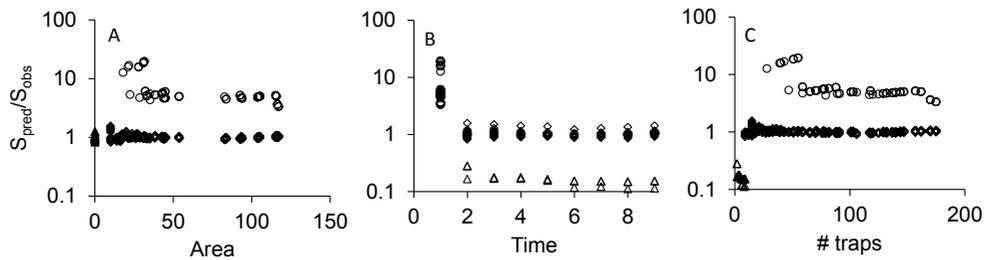
If area, time and sampling effort acted independently the non-interaction model (eq. 2) with observed SAR, SER, and STR slopes should correctly predict the observed species richness. Using the observed species density and the average slopes (Tab. 1) gives for the 1080 single data points

$$\ln(S_{pred}) = \ln(5.53) + 0.41 \ln A + 0.24 \ln t + 0.55 \ln n \quad (4)$$

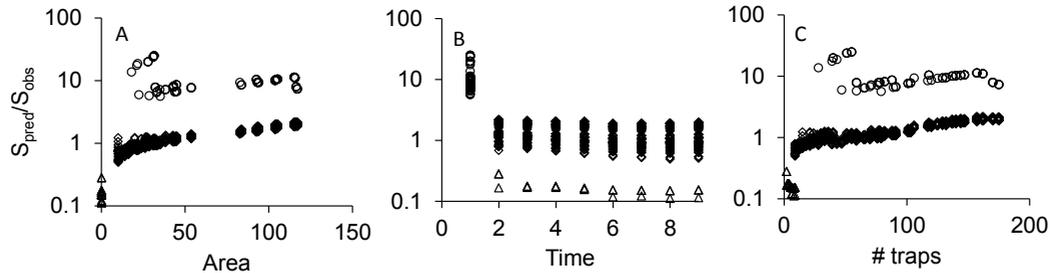
This model explains 63% of the variance in  $S$  (Fig. 1A). However, it overestimates ob-



**Fig. 1.** Observed and expected species richness of the regression models obtained from the model without interaction terms (eq. 1: A) and the interaction model (eq. 3: B). Open circles refer to data obtained from only one sampling date. The bold line gives in both cases the 1:1 relationship.



**Fig. 2.** Dependence of the quotient of predicted and observed species richness ( $S_{\text{pred}}/S_{\text{obs}}$ ) on area (A), sampling times (B), and sampling effort (C, numbers of traps).  $S_{\text{pred}}$  refers to non–interaction model (eq. 4). Open circles refer to data obtained from only one sampling date, open triangles denote the data from the smallest island. Cumulative island area in ha.



**Fig. 3.** Dependence of the quotient of predicted and observed species richness ( $S_{\text{pred}}/S_{\text{obs}}$ ) (A), sampling times (B), and sampling effort (C, numbers of traps).  $S_{\text{pred}}$  refers to the prediction of the best Akaike model with interaction terms (Tab. 2, eq. 5). Open circles refer to data obtained from only one sampling time, open triangles denote the data from the smallest island. Cumulative island area in ha.

served richness  $S_{\text{obs}}$  at single sampling dates and underestimates  $S_{\text{obs}}$  in the smallest areas below 0.2 ha, but not at low numbers of traps (Fig. 2). Further, the relation  $S_{\text{pred}}/S_{\text{obs}}$  increases with area and sampling effort (Fig. 1A) due to an overestimation of  $S_{\text{obs}}$  in large areas (Fig. 2A) and at high numbers of traps (Fig. 2C). The latter deviation implies some degree saturation of species richness at these scales.

Multiple regression using the interaction model (eq. 3) returned the area – sampling effort and the time – sampling effort interaction terms as being statistically significant at the 5% error benchmark (Tab. 2). A stepwise parameter reduction and Akaike model choice retained these interaction terms (Tab. 2). The model predicts 98% of the observed variance in  $S$ .

$$\ln(S_{\text{pred}}) = 1.09 + 0.08 \ln A + 0.64 \ln t + 0.80 \ln n - 0.04 \ln A \ln n - 0.06 \ln t \ln n \quad (5)$$

This model still overestimates species richness for only one sampling date and the smallest island (0.0003 ha (Figs. 1B, 3), while otherwise the ratios of predicted to observed species numbers became independent of area (Fig. 3A), time (Fig. 3B), and the number of traps (Fig. 3C). The intercept of eq. 5 ( $S_0 = \text{Exp}(1.09) = 2.97$ ) ranges well within the 95% confidence limit (lower CL = 0.5; upper CL = 8.0) of the observed species density.

Coefficients and beta values of multiple regression do not directly indicate the relative importance of the predictor variables. Using partial correlation coefficients we found the  $\log S - \log n$  partial correlation to be strongest ( $r = 0.91$ ) followed by  $\log S - \log t$  ( $r = 0.75$ ) and  $\log S - \log A$  ( $r = 0.51$ ). The  $\log S - \log A \log n$  interaction ( $r = -0.64$ ) appeared to be stronger than the  $\log S - \log t \log n$  interaction ( $r = -0.42$ ). All partial correlations were significant at the 0.001% error benchmark.

## 4. DISCUSSION

The present paper shows that a simple additive interaction STAER model is able to predict species richness of spiders at the regional scale. Previous attempts to include sample size in SARs involved predefined sample theoretical models to normalize sample size (Pielou 1975, Coleman 1981, Cam *et al.* 2002). In a homogeneous environment and equal species detection probabilities species richness will increase with area according to a Poisson model (He and Legendre 1996). However, in heterogeneous landscapes SARs are forced towards an allometric shape (Harte *et al.* 1999, Pueyo 2006). Accordingly, in heterogeneous landscapes and under unequal detection probabilities species richness should scale to sample size according to a power function (Schoereder *et al.* 2004). The present paper confirms this assumption (Tab. 1). Pure SERs, controlled for the effect of area and time were best fitted by power functions.

We did not fit asymptotic functions like the Michaelis-Menten or the negative exponential model. These are always more curved than the logarithmic function and predict lower species richness above certain thresholds. Hence if the logarithmic function fits worse than the lesser curved power function the asymptotic models would do even worse. These results justify the inclusion of the SER into power function STAER models as done in eq. 3.

Our study also confirms and extends previous work (Adler and Lauenroth 2003, Adler *et al.* 2005) that showed that area, time and sampling effort do not act independently. SARs have often been found to deviate from a power function shape (Connor and McCoy 1979, Rosenzweig 1995, Plotkin *et al.* 2000, Ulrich and Buszko 2005, Tjørve 2009) and several authors included correction terms to account for deviations at small (Ulrich and Buszko 2005, Tjørve 2009) and large areas (Plotkin *et al.* 2000). Our results extend those of Schoereder *et al.* (2004) that much of the deviation from the power function might be explained by the interaction of area with sampling effort (Tab. 2).

Adler and Lauenroth (2003) and Adler *et al.* (2005) favoured a time – area in-

teraction to describe the increase of species richness with area and time. However, one of us (Ulrich 2006) did not corroborate this hypothesis in an eight year study on forest Hymenoptera. Our model also does not contain the time – area interaction and a model that contained area, time, and the time – area interaction identified this interaction term as being insignificant ( $P(t) = 0.36$ ; not shown). Our model implies also the possibility that the significant interaction term of Adler and Lauenroth (2003) and Adler *et al.* (2005) might be due to the unknown interaction of area and time with sampling effort.

An intriguing aspect of our model is that SAR slopes decrease and STR and SER slopes increase after correcting for variable interactions (eqs. 4 and 5). Most mainland SARs have slopes between 0.1 and 0.20 while island SAR slope frequently range between 0.2 and 0.4 (Rosenzweig 1995, Drakare *et al.* 2006). Many of the SAR slopes reported in the literature stem from repeated sampling during many seasons and contain therefore unknown time and sampling effort covariates. Drakare's *et al.* (2006) recent meta-analysis on SAR slopes across various environmental gradients used raw literature data. We suspect that at least part of the variability in slope values might result from unknown sample size effects.

On first sight, our model predicts higher STR slopes than previously reported in the literature. White *et al.* (2006) reported slopes between 0.2 and 0.4 for a variety of taxa. Our uncorrected slope ( $y = 0.24$ ; eq. 4) fits into this expectation while the corrected slope

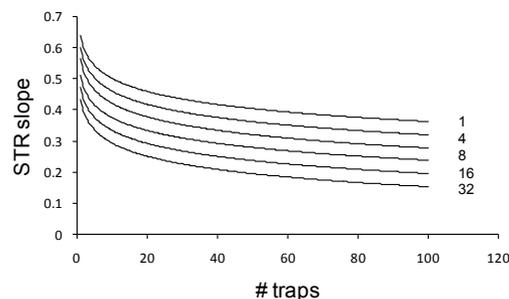


Fig. 4. STR slopes obtained from eq. 5 at different numbers of traps per unit area and areas between 1 and 32 ha. Slope  $y_{A,n}$  decreases logarithmically with the number of traps  $n$  and area  $A$  by  $y_{A,n} = y - 0.06 (\ln A + \ln n)$

**Table 2.** Model parameters of eq. 6 and the best model after Akaike model choice (eq. 7). Full model: Adj.  $R^2 = 0.99$ ; CAIC: 67.60; Best model: Adj.  $R^2 = 0.98$ ; CAIC: 47.74.  $n = 1080$ .

Variable	Full model			Best CAIC model		
	Coefficient	StdError	P(t)	Coefficient	StdError	P(t)
ln A	0.08	0.060	<0.00001	0.08	0.004	<0.00001
ln t	0.67	0.020	<0.00001	0.64	0.020	<0.00001
ln n	0.82	0.040	<0.00001	0.80	0.010	<0.00001
ln A ln t	0.00	0.001	0.99	–	–	–
ln A ln n	–0.04	0.004	<0.001	–0.04	0.001	<0.00001
ln t ln n	–0.08	0.020	<0.001	–0.06	0.004	<0.00001
ln A ln t ln n	0.002	0.002	0.42	–	–	–
Constant	1.04	0.060	<0.00001	1.09	0.040	<0.00001

$y = 0.64$  (eq. 5) is much higher. The latter refers to the temporal increase in species richness at a unit of area and one trap. However, species turnover rates generally refer to whole habitats and sufficiently precise estimates of species richness (high sampling effort). To study the effects of area and sample size we recalculated eq. 5 for different island areas and sample sizes and plotted the resulting STR slopes against sampling effort and island area (Fig. 4). The Figure shows that for larger areas and higher sampling effort STR slopes quickly reach the values within the range of 0.2 to 0.4 that White *et al.* (2006) reported. This area and sampling effort dependence of our model is of course a desired feature because it nicely reflects the common notion that temporal species turnover decreases with habitat area. Further our model predicts how the results of the meta-analysis of White *et al.* (2006) might be influenced by habitat area and sample size effects. Nevertheless, neither the study of White *et al.* (2006) nor our results confirm the ‘ergodic’ conjecture of Preston (1960) that area and time are equivalent with respect to  $\beta$ -diversity and that STR and SAR slopes are similar.

Our model predicts similar temporal species turnover rates to those previously observed in the field. Temporal species turnover can be calculated from the STR using two consecutive sampling dates:  $\frac{S_2}{S_1} = 2^y$ . Slope values between 0.2 and 0.4 as predicted from Fig. 3 B result then in turnover rates  $S_2/S_1$  between  $1.07 = 7\%$  and  $1.32 = 32\%$ . Available data for local terrestrial communities of arthropods (Den Boer 1985, Harrison 1991, Ulrich 2006) and plants (Carey *et al.* 2007) pointed to turnover rates between 3% and more than 30%. These values are well

within the range predicted by our model and obtained by White *et al.* (2006).

Our study used the number of traps as the measure of sampling effort. Of course the natural way to assess sampling effort is to use the number of individuals trapped. However, this needs quantitative trapping and roughly equal catch probabilities for all species across the landscape. In spiders and in many other animal taxa such an assumption is unjustified. In the present case log-transformed spider individual and traps numbers were only moderately correlated ( $r = 0.58$ ). Further, the use of individuals instead of traps does not allow for the construction of SARs and STRs under equal sampling intensity.

An undesired feature of any STAER model with interaction terms is that negative parameters of these terms force the function inevitably towards decreasing species richness far beyond the observed values. Such an extrapolation reaches beyond the local scaling region covered by the model and needs additional variables and variable interactions to be considered. This demands again not to extrapolate too far to estimate total species richness in space and time (Colwell and Coddington 1994). Our study cannot precisely answer the question about the upper boundary of this local scaling region; however the model reaches its maximum not before an area of 7000 ha and 100 sampling years. These values are far beyond the observed scales. Hence the model allows precise estimation of species richness and spatial and temporal  $\beta$ -diversity within the lower part of the scaling region.

In contrast, Figs. 2 and 3 identify a lower boundary of this region. Both models failed

at areas below 0.1 ha and one sampling date. The respective data points refer to the smallest island (0.003 ha) where in total only six species occurred while the second largest island (0.14 ha) already contained 31 species. The individual numbers per trap on the smallest island were only 1/5 (12 individuals trap<sup>-1</sup>) of the average number for all sites. Apparently, this island was too small to harbour a normal spider population.

In conclusion our study demonstrates that a combination of the well introduced species – area and species – time relationships with a term that contains information on sampling effort improves modelling of species richness in space and time. Apparently species richness is proportional to all three factors in an allometric manner. Such an equivalence might indicate that qualitatively similar processes operate to trigger the increase in species richness. Further studies have to evaluate whether we identified a general rule or whether different taxa and ecological guilds demand additional adjustment.

**ACKNOWLEDGMENTS:** We thank Maciej Kamiński and the Wigry National Park staff for their generous help during field studies. Miss Hazel Pearson kindly improved our English. This work was supported by a grant from the Polish Science Committee (PBZ KBN 087 P04 2003 01 20).

## 5. REFERENCES

- Adler P.B. 2004 – Neutral models fail to reproduce observed species-area and species time relationships in Kansas grasslands – *Ecology*, 85: 1265–1272.
- Adler P.B., Lauenroth W.K. 2003 – The power of time, spatiotemporal scaling of species diversity – *Ecol. Lett.* 6: 749–756.
- Adler P.B., White E.P., Lauenroth W.K., Kaufman D.M., Rassweiler A., Rusak J.A. 2005 – Evidence for a general species - time area relationship – *Ecology*, 86: 2032–2039.
- Azovsky A.I. 2011 – Species-area and species-sampling effort relationships: disentangling the effects – *Ecography* 34: 18–30.
- Brooks T.M., Pimm S.L., Collar N.J. 1997 – Deforestation predicts the number of threatened birds in insular southeast Asia – *Cons. Biol.* 11: 382–394.
- Cam E., Nichols J.D., Hines J.E., Sauer J.R., Alpizar-ara R., Flather C.H. 2002 – Disentangling sampling and ecological explanations underlying species-area relationships – *Ecology*, 83: 1118–1130.
- Carey S., Ostling A., Harte J., del Moral R. 2007 – Impact of curve construction and community dynamics on the species-time relationship – *Ecology*, 88: 2145–2153.
- Coleman B.D. 1981 – On random placement and species-area relation – *Math. Biosci.* 54: 191–215.
- Colwell R.K., Coddington J.A. 1994 – Estimating terrestrial biodiversity through extrapolation – *Phil. Trans. R. Soc. Lond. B*, 345: 101–118.
- Colwell R.K., Mao C.X., Chang J. 2004 – Interpolating, extrapolating, and comparing incidence-based species accumulation curves – *Ecology*, 85: 2717–2727.
- Connor E.F., McCoy E.D. 1979 – The statistics and biology of the species - area relationship – *Am. Nat.* 113: 791–833.
- Den Boer P.J. 1985 – Fluctuations of density and survival of carabid populations – *Oecologia*, 67: 322–330.
- Dengler J. 2009 – Which function describes the species - area relationship best? A review and empirical evaluation – *J. Biogeogr.* 36: 728–744.
- Dove A.D.M., Cribb T.H. 2006 – Species accumulation curves and their applications in parasite ecology – *Trends in Parasit.* 22: 568–574.
- Drakare S., Lennon J.J., Hillebrand H. 2006 – The imprint of the geographical, evolutionary and ecological context on species-area relationships – *Ecol. Lett.* 9: 215–227.
- Fridley J.D., Peet R.K., van der Maarel E., Willems J.H. 2006 – Integration of local and regional species - area relationships from space - time species accumulation – *Am. Nat.* 168: 133–143.
- Goldberg D.E., Estabrook G.F. 1998 – Separating the effects of number of individuals sampled and competition on species diversity, an experimental and analytic approach – *J. Ecol.* 86: 983–988.
- Green J.L., Plotkin J.B. 2006 – A statistical theory for sampling species abundances – *Ecol. Lett.* 10: 1037–1045.
- Harrison S. 1991 – Local extinction in a metapopulation context, an empirical evaluation – *Biol. J. Linn. Soc.* 42: 73–88.
- Harte J., Kinzig A., Green J. 1999 – Self-similarity and the distribution of abundance of species – *Science*, 284: 334–336.
- He L., Legendre P. 1996 – On species-area relationship – *Am. Nat.* 148: 719–737.
- Hill J.L., Curran P., Foody G.M. 1994 – The effects of sampling on the species

- area curve – *Gl. Ecol. Biogeogr. Lett.* 4: 97–106.
- Hurlbert S.H. 1971 – The non-concept of species diversity, a critique and alternative parameters – *Ecology*, 52: 577–586.
- Keating K.A. 1998 – Estimating species richness, the Michaelis-Menten model revisited – *Oikos*, 81: 411–416.
- Maurer B.A., McGill B.J. 2004 – Neutral and non-neutral macroecology – *Basic Appl. Ecol.* 5: 413–422.
- McGlenn D.J., Palmer W.M. 2009 – Modelling the sampling effect in the species - time - area relationship – *Ecology*, 90: 836–846.
- Myers N., Mittermeier R.A., Mittermeier C.G., de Fonseca G.A.B., Kent J. 2000 – Biodiversity hotspots for conservation priorities – *Nature*, 403: 853–858.
- Palmer M.W., White P.S. 1994 – Scale dependence and the species - area relationship – *Am. Nat.* 144: 717–740.
- Platnick N.I. 2009 – The world spider catalogue, version 9.5 – American Museum of Natural History. <http://research.amnh.org/entomology/spiders/catalog/INTRO3.html>.
- Pielou E. 1975 – *Mathematical ecology* – New York, Wiley, 385 pp.
- Plotkin J.B., Potts M.D., Yu D.W., Bunyavejchewin S., Condit R., Foster R., Hubbell S., LaFrankie J., Manokaran N., Seng L.H., Sukumar R., Nowak M.A., Ashton P.S. 2000 – Predicting species diversity in tropical forests – *Proc. Natl. Acad. Sci.* 97: 10850–10854.
- Preston F.W. 1960 – Time and space and the variation of species – *Ecology*, 41: 611–627.
- Pueyo S. 2006 – Self-similarity in species-area relationship and in species abundance distribution – *Oikos*, 112: 156–162.
- Rosenzweig M.L. 1995 – *Species diversity in space and time* – Univ. Press, Cambridge, 434 pp.
- Scheiner S.M. 2003 – Six types of species – area curves – *Global Ecol. Biogeogr.* 12: 441–447.
- Schoereder J.H., Galbiati J.H., Ribas C.R., Sobrinho T.G., Sperber C.F., De Souza O., Lopes-Andrade C. 2004 – Should we use proportional sampling for species – area studies? – *J. Biogeogr.* 31: 1219–1226.
- Thompson G.G., Thompson S.A. 2007 – Using species accumulation curves to estimate trapping effort in fauna surveys and species richness – *Austral Ecol.* 32: 564–569.
- Tjørve E. 2003 – Shapes and functions of species - area curves, a review of possible models – *J. Biogeogr.* 30: 827–835.
- Tjørve E. 2009 – Shapes and functions of species-area curves (II), a review of new models and parameterizations – *J. Biogeogr.* 36: 1435–1445.
- Ulrich W. 2006 – Decomposing the process of species accumulation into area dependent and time dependent parts – *Ecol. Res.* 21: 578–585.
- Ulrich W., Buszko J. 2003 – Species - area relationships of butterflies in Europe and species richness forecasting – *Ecography*, 26: 365–374.
- Ulrich W., Buszko J. 2004 – Habitat reduction and patterns of species loss – *Basic Appl. Ecol.* 5: 231–240.
- Ulrich W., Buszko J. 2005 – Detecting biodiversity hotspots using species - area and endemics - area relationships: The case of butterflies – *Biodiv. Cons.* 14: 1977–1988.
- Ulrich W., Buszko J. 2007 – Sampling design and the shape of species - area curves at the regional scale – *Acta Oecol.* 31: 54–59.
- Ulrich W., Zalewski M., Hajdamowicz I., Stańska M., Ciużycki W., Tykarski P. 2010a – Tourism disassembles patterns of co-occurrence and weakens responses to environmental conditions of spider communities on small lake islands – *Comm. Ecol.* 11: 5–12.
- Ulrich W., Hajdamowicz I., Zalewski M., Stańska M., Ciużycki W., Tykarski P. 2010b – Species assortment or habitat filtering: a case study of spider communities on lake islands – *Ecol. Res.* 25: 375–381.
- White E.P., Adler P.D., Lauenroth W.K., Gill R.A., Greenberg D., Kaufman D.M., Rassweiler A., Rusak J.A., Smith M.D., Steinbeck J.R., Waide R.B., Yao J. 2006 – A comparison of the species - time relationship across ecosystems and taxonomic groups – *Oikos*, 112: 185–195.
- Williams M.R. 1995 – An extreme value function model of the species incidence and species - area relations – *Ecology*, 76: 2607–2616.
- Williamson M., Gaston K.J., Lonsdale W.M. 2001 – The species - area relationship does not have an asymptote! – *J. Biogeogr.* 28: 827–830.
- Zalewski M., Ulrich W. 2006 – Dispersal as a key element of community structure: The case of ground beetles on lake islands – *Div. Distr.* 12: 767–775.

*Received after revision September 2012*

