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Sampling design and the shape of species–area curves on the regional scale

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ABSTRACT

Species–area relationships (SARs) are one of the fundamental patterns in ecology. However, how the way they were constructed influences resulting SAR shapes has gained astonishingly little attention. We use data of the distribution atlas of Polish butterflies to compare SARs constructed from four different designs: adding up species numbers of independent areas (species accumulation curves using contiguous and non-contiguous areas), using a nested design, and comparing species numbers of independent areas of different sizes. It appeared that the way of constructing SARs influences the outcome. We attribute this influence to the pronounced faunal dissimilarities of more distant areas (spatial species turnover). The nested design resulted in significantly higher slopes and lower intercepts of power function SARs than the other designs. SARs from all four sampling designs showed a pronounced downward curvature on small spatial scales. Only the nested design predicted species densities correctly. The implications of these results for the use of SARs in bioconservation are discussed.

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1. Introduction

That the number of species increases as the area under study increases has been called one of the few laws in ecology (Scheiner, 2003). The study of these species–area relationships (SARs) has a long tradition in ecology (MacArthur and Wilson, 1967; Connor and McCoy, 1979; MacIntosh, 1983; Rosenzweig, 1995). Nevertheless, SARs are still a matter of intensive research and scientific discussion (Lomolino, 2000; Lomolino and Weiser, 2001; Williamson et al., 2001; Lennon et al., 2002; Scheiner, 2003, 2004; Storch et al., 2003; Tjørve, 2003; Gray et al., 2004; Šizling and Storch, 2004; Ulrich and Buszko, 2004; Turner and Tjørve, 2005; Fridley et al., 2005).

Recently Scheiner (2003, 2004) reviewed SAR shapes and the way SARs can be constructed. He identified four major types of SARs. Mainland SARs above the local scale are traditionally constructed in a nested manner (in the following

termed ND) (Rosenzweig, 1995). For islands a nested design is often impossible and SARs are constructed by comparing species numbers of islands of different size (island design, ID). On the local scale SARs (also termed species accumulation or collector's curves) frequently stem from replicated plots and are constructed by a sequential accumulation of these plots (sequential accumulation design, SD). Scheiner (2003) divided this SAR type into two, one using contiguous (SC) and one using non-contiguous (SN) plots. Surely, the first subtype is of minor importance because the plots of a contiguous array are prone to pseudoreplication (Hurlbert, 1984).

The question whether and how the sampling design influences SAR patterns above the local scale has gained astonishingly little interest (Scheiner, 2003, 2004). Rosenzweig (1995), following Gleason (1922) and Goodall (1952), already noticed that the SD design must not be applied on larger scales with significant regional species turnover. There, SARs constructed

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by SD will have a curvature even in log-log plots due to a sampling effect: the immediate combination of more distant areas adds too many species at the beginning of the process. This process leads to SARs that are curved downward in their lower part. Gleason (1922), Goodall (1952) and Kobayashi (1974, 1976) argued that on smaller scales ND slopes should be lower than those derived from the sequential accumulation design (SD). Pielou (1977) following Goodall (1952) briefly discussed SD and ND and advised that local SARs have to be constructed from SD and 'must not be nested'.

A critical comparison of SAR construction methods on the local scale was provided by Palmer and White (1994), who argued that the grain, the largeness of the unit of area, is the most important determinant of SAR shapes. However, critical field tests of whether and how the sampling designs SD, ND, and ID influence the shape of SARs are scarce and concentrate on local plant species accumulation curves (Braun-Blanquet, 1932; Cain, 1938; Palmer and White, 1994; Fridley et al., 2005). This little interest surely stems on one side from the tacit assumption that at least ID and ND give similar results and on the other side from the methodological difficulties involved in a sound comparison.

Ecologists most often fitted the power function model of Arrhenius (1921) to SARs. This model is defined by

$$S = S_0 A^z \quad (1)$$

where S denotes the species number in area A and z is the slope. S_0 , the intercept in a log-log plot, is the expected mean number of species per unit of area (the species density).

The logarithmic function, first proposed by Gleason (1922), fits local plant species-accumulation curves sometimes better. This model is defined by

$$S = S_0 + z \log(A) \quad (2)$$

where S_0 is again an estimate of the species density.

The prevalence of the power function stems on one side from the many real world SARs that are best fitted by power functions (Connor and McCoy, 1979; Williamson, 1988; Rosenzweig, 1995; Williamson et al., 2001) and on the other side by theoretical considerations. Harte et al. (1999) and Ostling and Harte (2003) argued that the process of species accumulation is self-similar and driven by the underlying geometry of species spatial distribution (but see Lennon et al. (2002) and Šizling and Storch (2004)). Ney-Nifle and Mangel (1999) derived power function SARs from passive sampling in heterogeneous model landscapes, and Carlson and Doyle (1999, 2000) predicted power functions from optimization theory. Neutral community models (Bell, 2000; Hubbell, 2001) also point to power function SARs.

However, if the method of constructing SARs influences its shape we have to include the way of constructing them in our SAR models (Tjørve, 2003; Scheiner, 2003, 2004). Further, systematic deviations from the power function and all other models proposed so far (Tjørve, 2003) should occur depending on the construction method. There is actually no formal test available to detect such deviations for single SARs (Lennon et al., 2002). However, the extension to the power function of Plotkin et al. (2000a,b) might give the basis for such a test. To get a better fit to real small to medium scale data Plotkin

et al. (2000a) extended the classical power function SAR by a shape correcting term and got

$$S = S_A A^z e^{-k/A} \quad (3)$$

where k is a second shape generating parameter that forces the power function into a curvature in larger areas. To get a curvature in small areas Eq. (3) has to be modified (Ulrich and Buszko, 2003a, 2004)

$$S = S_A A^z e^{-k/A} \quad (4)$$

After fitting a SAR by non-linear regression a positive value of k points to a downward curvature and a negative k to an upward curvature in small areas. If multiple replicates exist high frequencies of non-zero k -values point to systematic deviations from a simple power function. It should be noticed that S_A in Eqs. (3) and (4) is no longer an unequivocal estimate of the species density. It is an estimate of the intercept derived from the upper part of the SAR where $A \gg k$ (Fig. 1). Larger values of k ($k > A$) asymptotically force S to go through the origin. This feature and the undesired decrease of species numbers in very large areas (for $A > k$ the exponential term of Eq. (3) becomes less than 1) make the Plotkin model and our modification not ideal candidates for a general SAR model. The model is mainly a tool to infer curvatures of SARs on intermediate scales.

The present study intends to compare the four designs SC, SN, ND, and ID with respect to the resulting SAR shape on the regional scale. On this scale, the majority of studies reported power function SARs (Rosenzweig, 1995; Michalak and Ulrich, 2005). We use the Distribution Atlas of Polish Butterflies (Buszko, 1997; Ulrich and Buszko, 2003a, 2004) to take samples from the Polish butterfly fauna according to these four designs. We will show that the sampling design indeed influences the resulting SAR and that systematic deviations from the power function occur due to regional species turnover.

2. Materials and methods

Butterflies in the sense of the Distribution Atlas of Polish Butterflies (Buszko, 1997; Buszko and Kartanas, 1998) are all species of the families Hesperidae, Papilionidae, Pieridae,

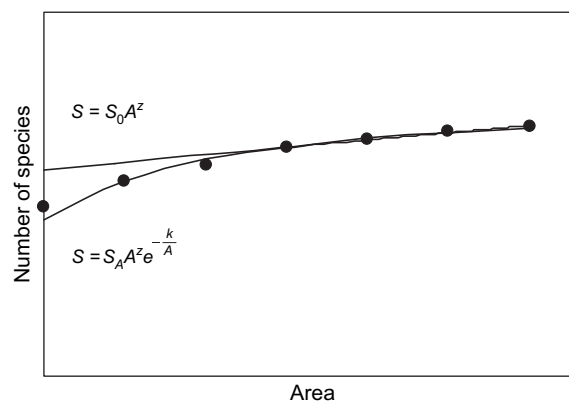


Fig. 1 – A: a positive value of the parameter k , in Eq. (3), forces a power function SAR towards a lower downward curvature.

Lycaenidae, and Nymphalidae (Karsholt and Razowski, 1996; Swaay and Warren, 1999). The atlas uses the $10 \times 10 \text{ km}^2$ cells of the UTM (Universal Transverse Mercator projection) coordinate system and is based on distribution data from 1986 to 2001 (Ulrich and Buszko, 2003a). It represents therefore one of the most complete large-scale data sets available. In total, the atlas contains distribution data of 162 Polish butterfly species.

Whole cells or combinations of UTM cells (areas) of the matrix are the basic sampling units used in this study. SARs were then constructed using the four designs described in Section 1. SC and SN have the drawback that the ordering of cells strongly influences the outcome. To minimize this effect the ordering was reshuffled 20 times and mean species numbers were used for constructing SARs (according to Colwell and Coddington, 1994).

In every case SARs were based on 11 data points (samples). This is the maximum number of nested areas that can be constructed using ND. We constructed ND SARs by choosing one cell of the grid and sequentially including the surrounding cells (2, 4, 9, 16, 36, 64, 100, 400, 900 cells, and all 2353 cells of the UTM grid) to get a nested pattern. In the case of ID 11 non-overlapping areas of contiguous cells (1, 2, 4, 8, 16, 32, 64, 128, 512, 1024, and all cells of the grid) were chosen at random. We constructed the SC and SN SARs by subsequently adding up 1, 2, 4, 8, 16, 32, 64, 128, 512, 1024 cells (contiguous in the SC case and non-contiguous in the NC case), and again all cells of the grid.

Incomplete cells or areas (mostly those lying at the boundary of the map) were always excluded. SARs were therefore only computed from fully censured areas. For each design the whole sampling procedure was replicated 13 times to get 13 independently constructed SARs. This is the maximum number of independent SARs (except for the last data point referring to the whole grid) that can be constructed from the nested design using different cells as a starting point of the nesting process.

We fitted the power and the logarithmic functions and the Plotkin approach to SARs (Eq. 4) using the non-linear estimation module of Statistica 7 (StatSoft, 2005). Errors refer always to standard errors.

3. Results

The Jaccard index as a measure of faunal similarity decreases with the distance of UTM cells compared (Fig. 2). This decrease follows a power function with a slope of -0.07 . There was therefore a significant spatial turnover of species.

In line with the prediction of Rosenzweig (1995) concerning the effect of species spatial turnover SARs produced by SC and SN had significantly lower downward curvatures in the log-log space and clearly deviated from power functions (Fig. 3). SC resulted in $k = 84.2 \pm 10.8$ ($p(k=0) < 0.0001$; all single k -values > 0), SN in $k = 121.5 \pm 16.1$ ($p(k=0) < 0.0001$; all single k -values > 0). However, other designs of both also produced SARs with such a curvature. ID gave $k = 46 \pm 17.3$ ($p(k=0) = 0.009$; 11 out of 13 k -values > 0). ND resulted in $k = 34.3 \pm 18.3$ (11 out of 13 k -values > 0), although this value does not deviate from 0 at the 5% error level ($p(k=0) = 0.06$). The k -values of ND

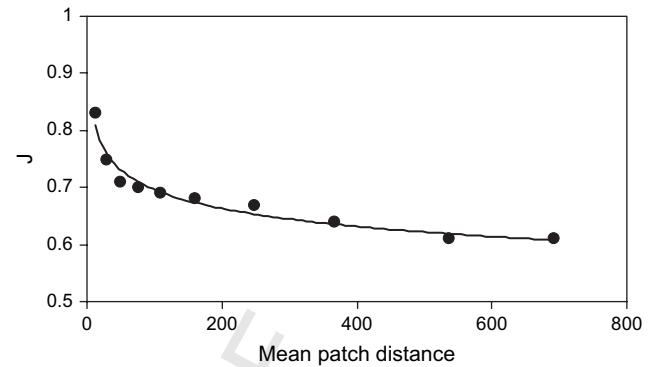


Fig. 2 – For Polish butterflies Jaccard's similarity index J decreases with increasing distances D [km] between the cells compared. Regression: $J = 0.96D^{-0.07}$.

and ID were significantly smaller than those of SC and SN ($p(t) < 0.001$). Further, slope and intercept values of ND significantly differed from ID ($p(t) < 0.001$). Slopes were higher and intercepts were lower (Fig. 3). The downward curvatures of SC and SN also caused low slope values. Both slopes ($z = 0.13$ and 0.12 , respectively) were significantly ($p(t) < 0.01$) lower than those of ID ($z = 0.16$) and ND ($z = 0.20$).

None of the four sampling designs produced detectable upper curvatures in the log-log space (data not shown). Above 6000 km^2 area SARs from all four designs closely followed power functions with a slope value of 0.11 , the mean slope value of the northern European butterfly SAR (Ulrich and Buszko, 2003a,b).

The four sampling designs resulted in different slope and intercept values when fitted by simple power functions according to Eq. (1) (Fig. 4). ND produced significantly higher slope and lower intercept values than the other designs ($p(t)_{\text{intercept}}$ for all pairwise comparisons < 0.05 ; $p(t)_{\text{slope}}$ for all pairwise comparisons < 0.05). On average Poland has 25 ± 22 (mean \pm standard deviation) butterfly species per 100 km^2 and $5\text{--}10$ species per km^2 (Ulrich and Buszko, 2003a; Buszko, unpublished data). Fits of the power function model (Eq. 1) to SC and SN significantly overestimated species densities S_0 (Fig. 4). ID also overestimated S_0 although this was not significant at the 5% error level. ND instead predicted S_0 within one standard error (Fig. 4).

For comparison, we also fitted the logarithmic model (Eq. 2) to the curves of Fig. 3. This model fitted better than the simple power function (judged from the R^2 values between 0.84 (ID) and 0.96 (SC) in comparison with the respective power function values of $R^2 = 0.74$ (ID) to $R^2 = 0.84$ (SC); Fig. 4) but slightly worse than the Plotkin approach ($R^2 = 0.87$ (ID) to $R^2 = 0.97$ (SC). However, it predicted for all four sampling designs negative species densities between -47 (SN) and -87 (ND) species (data not shown). Hence, the logarithmic model did not allow for a comparison of the species densities.

4. Discussion

In a homogeneous environment where all species are randomly distributed SAR patterns are necessarily independent

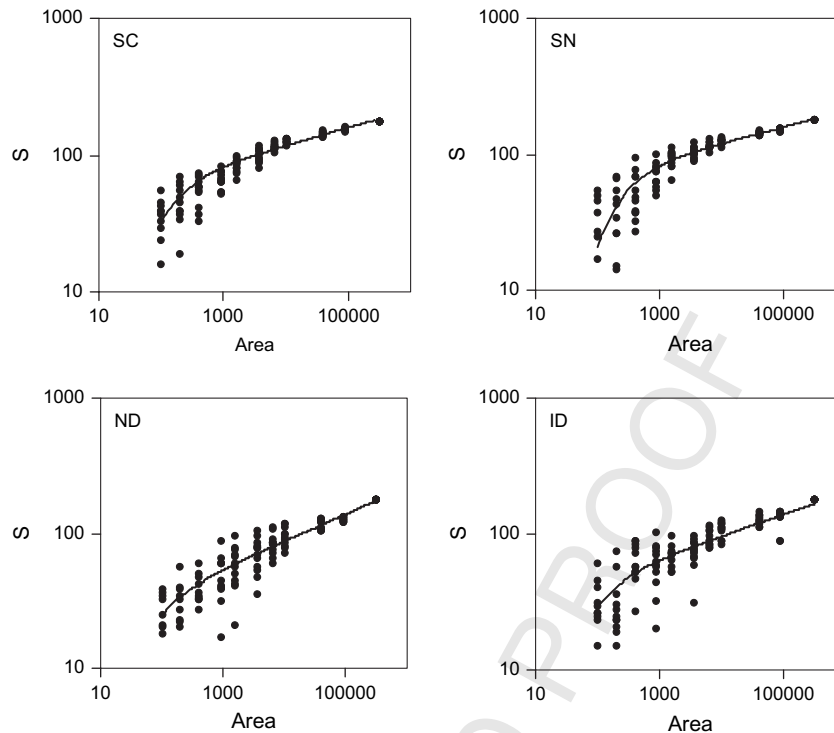


Fig. 3 – SARs of Polish butterflies produced by the four sampling designs. Regressions functions (Eq. 4): SC: $S = (35.5 \pm 1.97)A^{0.13 \pm 0.01}e^{(-84.2 \pm 10.8)/A}$; $R^2 = 0.97$. SN: $S = (40.6 \pm 2.74)A^{0.12 \pm 0.01}e^{(-121.5 \pm 16.1)/A}$; $R^2 = 0.93$. ND: $S = (14.0 \pm 1.29)A^{0.20 \pm 0.01}e^{(-34.3 \pm 18.3)/A}$; $R^2 = 0.96$. ID: $S = (22.0 \pm 2.2)A^{0.16 \pm 0.01}e^{(-46.0 \pm 17.3)/A}$; $R^2 = 0.87$.

of the sampling design. But the above results show that habitat heterogeneity that leads to aggregated species spatial distributions and spatial species turnover changes this situation. SARs constructed by SC and SN had a pronounced downward curvature and differed in this respect from ID and ND (Fig. 3). In an earlier paper Ulrich and Buszko (2003a) interpreted the fact that ND also produced a lower curvature at an area below 6000 km² with the existence of two scaling regions with different patterns of species accumulation, a lower local to regional

and an upper regional to continental. Such a pattern would be in line with the triphasic SAR model of Shmida and Wilson (1985) and Rosenzweig (1995).

SARs produced by ID and ND differed. ND produced significantly higher slope and lower intercept values than ID when fitted by the Plotkin approach and by the power function (Figs. 3, 4). This result has potential implications for the comparison of existing mainland and island SARs. Island SARs were found to have higher slope values than those of mainlands. Typical

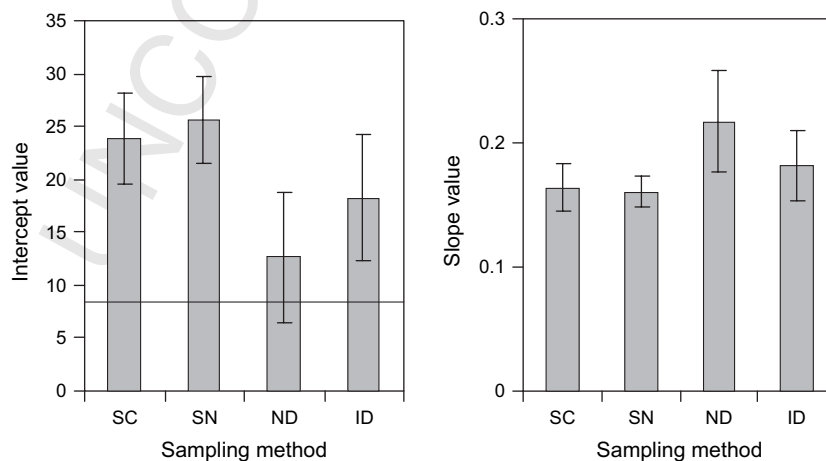


Fig. 4 – Intercept and slope values of fits of the simple power function model (Eq. 1) to the SARs produced by the four sampling designs. Errors refer to standard errors. The horizontal line of the intercept plot denotes the estimated mean species number km⁻² (eight species). Goodness of fits SC: $R^2 = 0.84$; SN: $R^2 = 0.75$; ND: $R^2 = 0.83$; ID: $R^2 = 0.74$.

mainland SARs (at least for taxa with good dispersal abilities) have slope values between 0.1 and 0.2; typical island SARs were found to have slopes between 0.2 and >0.5 (Rosenzweig, 1995; Lomolino, 2000). The SAR construction effect with its lower ID slopes enhances this difference in slope pointing to even more pronounced differences between island and mainland species–area relationships.

In line with the prediction of Rosenzweig (1995) the pronounced spatial species turnover (Fig. 2) caused SC and SN to produce SARs with a steeper initial curvature (a higher increase in species number) than ID and ND. Palmer and White (1994) have already reported a similar pattern in their study of local plant SARs. These authors used semilogarithmic plots and did not fit SAR models to their data. We rescaled their data of Fig. 2A (No. 6) to double log scales and found a pattern that is very similar to ours. The local plant ND SAR is curved downward on smaller scales. This fact is expressed by the significant k -value when fitted by Eq. (4) ($k = 3.95 \pm 1.56$). The predicted slope value of 0.27 ± 0.02 is higher than the slope of our regional data, which is in line with most observations about local SARs.

An important question for the application of SARs in bioconservation is whether they are able to predict species numbers on different spatial scales (Veech, 2000; Hobohm, 2003; Ulrich and Buszko, 2005; Fattorini, 2005). The above results show that the sampling design might influence this ability. In the presence of spatial species turnover SC and SN based SARs were unable to predict mean species densities, the mean number of species per unit area. Further, residuals of SARs were used to rank prime areas for bioconservation and to identify ecological hotspots (Hobohm, 2003; Ulrich and Buszko, 2005). Apart from statistical issues (Fattorini, 2005) the present results indicate that hotspot and prime area identification might also rely on the way SARs are constructed.

One concern about this latter conclusion is connected with the question how the regional patterns of landscape heterogeneity influence species accumulation. Heterogeneity was generally found to be positively correlated with species numbers and SAR slopes (Rosenzweig, 1995; Ricklefs and Lovette, 1999). Theoretical models also favour the idea that increasing heterogeneity forces SARs and other ecological relationships towards power functions (Harte et al., 1999; Carlson and Doyle, 1999). Hence regions with a higher degree of landscape heterogeneity than Poland might have SARs with less apparent curvatures. In this case the differences between the sampling models should be less pronounced. However, we are not aware of any study that addresses this question in detail. Further studies on regional SARs are needed to clarify whether non-linear SARs (at the log-log space) are common and how the method of constructing them influences their shapes.

The present results might also have implications for the use of SARs to predict species numbers after habitat destruction (Ney-Nifle and Mangel, 2000; Ulrich and Buszko, 2004). For this task species numbers in small areas have to be estimated from extrapolations after assumed habitat loss (May et al., 1995; Kinzig and Harte, 2000). The above results (Fig. 3) indicate that ID and ND might overestimate the number of species remaining when using a simple power function to model

them. This result seems to contradict the findings of Lomolino and Weiser (2001) and Crawley and Harral (2001) who reported sigmoid SARs for islands and for British vascular plants with an upward curvature on low spatial scales. This pattern implies that power function SARs would underestimate species numbers on small spatial scales. All SARs described in this paper instead have a distinct lower downward curvature. One explanation for this different finding might be that the deviations as Lomolino and Weiser (2001) and Crawley and Harral (2001) reported occurred on spatial scales between several ha and several km². Crawley and Harral (2001) found a sigmoid SAR with a second downward curvature on scales above 100 km² where a steep regional slope becomes a more moderate continental one. This pattern agrees with the findings reported here. However, the small island effect (Lomolino and Weiser, 2001) found on scales of several to several hundred km² island size clearly deviates from the mainland pattern reported here. Further studies on mainland SARs are needed to show whether there are systematic differences between islands and mainlands on these scales.

Recent theory assumes that a random placement of species into heterogeneous (in particular fractal) landscapes should generate power function SARs (Harte et al., 1999). The lower downward curvature of all SARs studied here deviates from this prediction. Unfortunately, whether these deviations are a common phenomenon and whether existing theories about the origin of power function SARs have to be modified is a largely unsettled question (Lennon et al., 2002; Šizling and Storch, 2004). The present results point to this conclusion. Deviations from power functions on small spatial scales might be a general phenomenon. In this case the power function would have to be modified to correct for such deviations, as has been proposed by Plotkin et al. (2000a,b) and by Ulrich and Buszko (2003a, 2004).

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