



Habitat reduction and patterns of species loss

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Summary

This paper uses data of The Distribution Atlas of Polish Butterflies to simulate the effect of four different types of area loss (aggregated, fractal, random, and nested) on species diversity and species–area relationships (SARs). We found that power function and logarithmic SAR models overestimated species loss in the case of aggregated, fractal, and random patterns of area reduction. Instead, the modification of the power function by Plotkin et al. (Proc. Natl. Acad. Sci. USA 97 (2000b) 10850) ($S = S_0 A^z e^{-kA}$) with k being a shape-adjusting parameter worked better and gave sufficient predictions of species loss. The net effects of the aggregated, fractal, and random types of area loss on species diversity were very similar with an aggregated pattern of area loss leading to slightly higher rates of species loss than both other processes. We conclude that SARs might be useful tools for biodiversity forecasting if they are constructed in a case-specific manner. The use of standard models instead might be misleading.

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Zusammenfassung

Die Auswirkungen verschiedener Typen von Habitatreduktionen (aggregiert, fraktal, geschachtelt und zufällig) auf regionale Diversitätsmuster und Arten-Arealbeziehungen (SARs) werden anhand der Daten des Verbreitungsatlasses der polnischen Tagsschmetterlinge untersucht. Allometrische und logarithmische SAR Modelle tendierten bei aggregierten, fraktalen und zufälligen Reduktionsmustern dazu, den Verlust an Arten zu überschätzen. Das neu entwickelte SAR Model von Plotkin et al. (Proc. Natl. Acad. Sci. USA 97 (2000b) 10850) ($S = S_0 A^z e^{-kA}$), in dem k ein zusätzlicher Gestaltjustierungsparameter ist, erwies sich hingegen als tauglicher und schätzte den Artenverlust hinreichend genau. Die Nettoeffekte geklumpter, fraktaler und zufälliger Reduktionsmuster waren sehr ähnlich, wobei ein aggregiertes Muster zu einem leicht höheren Artenverlust führte. Wir schließen daraus, dass SARs ein hilfreiches Werkzeug zur Vorhersage von Artenzahlen sein können, wenn sie fallspezifisch angewendet werden. Die reine Verwendung von Standardmodellen kann jedoch irreführend sein.

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Introduction

The species–area relationship (SAR) is one of the best documented patterns in macroecology (Rosenzweig, 1995; Lomolino, 2000; Blackburn & Gaston, 2003; Peintinger, Bergamini, & Schmid, 2003). It is also one of the few ecological patterns that have practical application. SARs are applied to estimate species loss after habitat destruction (Harte, Kinzig, & Green, 1999a; Harte, McCarthy, Kinzig, & Fischer, 1999b; Pimm & Lawton, 1998; Kinzig & Harte, 2000; Ney-Nifle & Mangel, 2000; Panzer & Schwartz, 2000; Brook, Sodi, & Ng, 2003), to identify biodiversity hotspots (Veech, 2000), to infer consequences of species introductions and faunal homogenization (McKinney, 1998; Rosenzweig, 2001; Collins, Vazquez, & Sanders, 2002), to estimate β -diversities (Ricotta, Carranza, & Avena, 2002), or to estimate global biodiversity patterns (Gaston & Hudson, 1994; Ulrich, 1999).

Continental SARs are typically triphasic with a lower (local) concave and an upper (continental) convex shape (Rosenzweig, 1995; Hubbell, 2001; Allen & White, 2003). At intermediate (regional) scales, species numbers S most often scale to area A by a power function of the type

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

where S_0 is the expected number of species per unit area and z a scaling coefficient that ranges frequently between 0.1 and 0.3 (Rosenzweig, 1995; Lomolino, 2000; Williamson, Gaston, & Lonsdale, 2001).

From this model it is possible to estimate the fraction of species f_{lost} that will be lost after some amount of area A_{lost} is destroyed. Simple rearrangement of Eq. (1) results in

$$f_{\text{lost}} = 1 - \left(1 - \frac{A_{\text{lost}}}{A_0}\right)^z \quad (2)$$

with A_0 being the original area. Conservationists apply this model in biodiversity forecasting studies (May, Lawton, & Stork, 1995; Pimm & Askins, 1995; Brooks, Pimm, & Collar, 1997; Pimm & Lawton, 1998; Kinzig & Harte, 2000; Veech, 2000; Seabloom, Dobson, & Stoms, 2002; Brook, Sodhi, & Ng, 2003; Ulrich & Buszko, 2003a).

However, despite its popularity the model has theoretical and practical shortcomings. Recent investigations revealed small deviations from the power function at various scales (Plotkin et al., 2000a, b; Crawley & Harral, 2001; Lennon, Kunin, & Hartley, 2002; Ulrich & Buszko, 2003a). This led to some modifications of the model of which the extension by Plotkin et al. (2000a, b) seems to be

the most promising

$$S = S_0 A^z e^{-kA}, \quad (3)$$

where k is a new parameter that corrects for deviations from the power function at smaller scales. It describes changes in species spatial distribution patterns at these scales. These changes are closely connected with accompanying changes in patterns of relative abundance (Hanski & Gyllenberg, 1997). k might therefore be interpreted as a parameter that describes the relation between abundance and spatial distribution patterns (Ulrich & Buszko, 2003a).

There are many ways to construct SARs (Rosenzweig, 1995). Regional mainland SARs are most often constructed from a nested design where beginning from a large area smaller and smaller subareas are taken in a fully nested manner (Rosenzweig, 1995). Although there is no formal argument to reject other methods (sequential accumulation of samples, using disjoint areas of different sizes, or using transects), this procedure has become a de facto standard. The reason is that theoretical derivations of the power function SAR model (May, 1975; Durrett & Levin, 1996; Harte, Kinzig, & Green, 1999a; Harte, McCarthy, Kinzig, & Fischer, 1999b; Ney-Nifle & Mangel, 1999; Hubbell, 2001; Allen & White, 2003) relied on nested SARs. Additionally, Palmer and White (1994) and Rosenzweig (1995) argued that SARs constructed by a sequential accumulation of samples might deviate from power functions in the case of pronounced spatial autocorrelation.

However, habitat destruction does not proceed in a nested manner. Applying standard SAR models to biodiversity forecasting after area loss might therefore give false impressions about species loss. Additionally, the way of constructing SARs might influence the parameter values of the model (Rosenzweig, 1995). We might therefore also expect deviating estimates of species loss.

The question of how patterns of area loss affect species loss and shapes of SARs has already been addressed. Ney-Nifle and Mangel (2000) applied a range size model to show that habitat reduction causes changes in SAR slopes. From this they inferred that the pattern of habitat reduction might influence the number of species lost. Seabloom et al. (2002) used various existing stages of habitat fragmentation to infer patterns of species loss in California vascular plant communities. They concluded that aggregated patterns of habitat loss might lead to higher extinction rates than those predicted by SARs. In a previous paper (Ulrich & Buszko, 2003a), we showed that power function SARs are able to predict species loss if

habitat reduction proceeds in a nested manner. However, neither study compared the effects of different patterns of habitat loss. Additionally, none of these studies dealt with anything other than the power function SAR model. It remains therefore largely unknown whether and how more realistic ways of habitat reduction influence patterns of species loss and whether different SAR models are able to track this. It seems therefore worthwhile to study patterns of species loss in more detail and to infer the predictive power of SARs.

Materials and methods

As in Ulrich and Buszko (2003a), we use the quantitative distributional atlas of Polish butterflies that relies on 15 years of observation (1986–2001). It is based on a UTM matrix of $10 \times 10 \text{ km}^2$ cells (Buszko, 1997; Buszko & Kartanas, 1998; Buszko, unpubl.). The atlas deals with all species of the families HesperIIDae, Papilionidae, Pieridae, Lycaenidae, and Nymphalidae (Karsholt & Razowski, 1996; van Swaay & Warren, 1999). In total, it contains distribution data of 162 Polish butterfly species.

We simulated habitat destruction in four different ways. First, we randomly eliminated cells of the matrix and counted the remaining number of species. Second, we applied the Metropolis Monte Carlo simulation algorithm of particle kinetics (Metropolis, Rosenbluth, Rosenbluth, Teller, & Teller, 1953) to simulate the process of aggregated area loss. The Metropolis algorithm starts from a small number of randomly chosen cells that are eliminated. These cells are the core for further aggregated elimination with the cell elimination probability being an exponential function of the form

$$p = e^{-k/T}, \quad (4)$$

where k is the distance of the target cell from the nearest eliminated cell and T a shape generating parameter, the matrix temperature. We used a strong ($T = 0.1^\circ$) and a medium pattern of aggregation ($T = 1^\circ$) (Fig. 1a–c).

Third, we used a fractal landscape for simulation. We constructed fractal landscapes superimposed upon the UTM matrix using the random midpoint displacement algorithm (Peitgen & Saupe, 1988) (Fig. 1d). We divided the height axis of these fractal landscapes into 100 height classes and determined for each class the species numbers remaining after eliminating the more elevated cells.

We repeated each of these three area reduction algorithms 20 times and determined for each reduction stage mean species numbers and the respective variance. Twenty replicates appeared to be enough to produce stable patterns.

For comparison, we also used the data of Ulrich & Buszko (2003a) who studied the pattern of species loss during a nested habitat reduction design. These data are mean values of 40 replicates of the elimination process.

The outcomes of these simulations were compared with the predictions of five different SAR models. We first used the power function (Eq. (1)) and the Plotkin model (Eq. (3)) based on random combinations of disjoint areas as reported in Ulrich and Buszko (2003a). The power function had the form

$$S = (16 \pm 15)A^{0.2 \pm 0.07}, \quad R^2 = 0.91; \quad (5)$$

the Plotkin model

$$S = (45 \pm 3)A^{0.11 \pm 0.01}e^{-132 \pm 34/A}, \quad R^2 = 0.99. \quad (6)$$

Errors are always one standard deviation.

Additionally, we constructed SARs from 12 replicates of a fully nested design (Fig. 2). The SAR is fitted by a power function of the form

$$S = (13 \pm 1)A^{0.21 \pm 0.01}, \quad R^2 = 0.92. \quad (7)$$

For completeness, we also fitted a logarithmic SAR model (Gleason, 1922) to the data of Fig. 2. This model is often appropriate to local patterns of species accumulation (Palmer & White, 1994)

$$S = (18 \pm 1)\ln(A) - (67 \pm 5), \quad R^2 = 0.89. \quad (8)$$

Although it explained a high proportion of variance (89%), this model failed to predict S_0 , the expected number of species per unit area.

Finally, we compared simulated and predicted species loss using the SAR of the European butterflies north of the Alps (non-Mediterranean butterflies; for the countries included in the computation, see Ulrich & Buszko, 2003b). Ulrich and Buszko (2003b) found that the SAR closely follows a power function SAR of the form

$$S = (43 \pm 20)A^{0.10 \pm 0.04}, \quad R^2 = 0.23. \quad (9)$$

At each stage of the area loss process, we fitted a power function (Eq. (1)) to the resulting SAR (Eq. (3)) and tracked the change in z and S_0 in dependence of the area remaining. All regressions used here are ordinary least-square regressions calculated with the non-linear regression module of STATISTICA 5 (Statsoft, 1997).

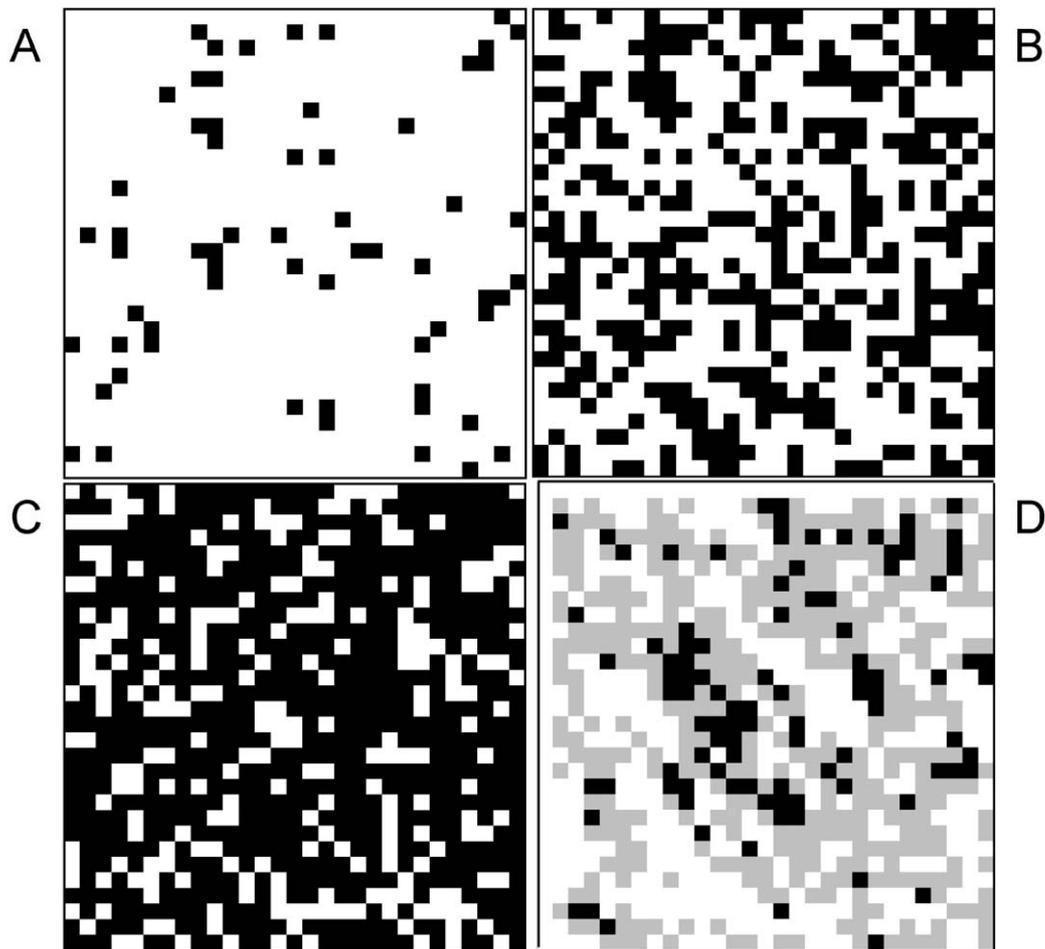


Figure 1. Examples of how the simulation processes of area elimination by the Metropolis (A–C) and the random midpoint displacement algorithm (D) proceed. Matrix temperature 1° ; (A) 1% area loss; (B) 50% area loss; (C) 90% area loss. (D) Fractal dimension = 2.5, three different levels of area loss (99%, 50%, 10%) are shown (white, grey, black, respectively).

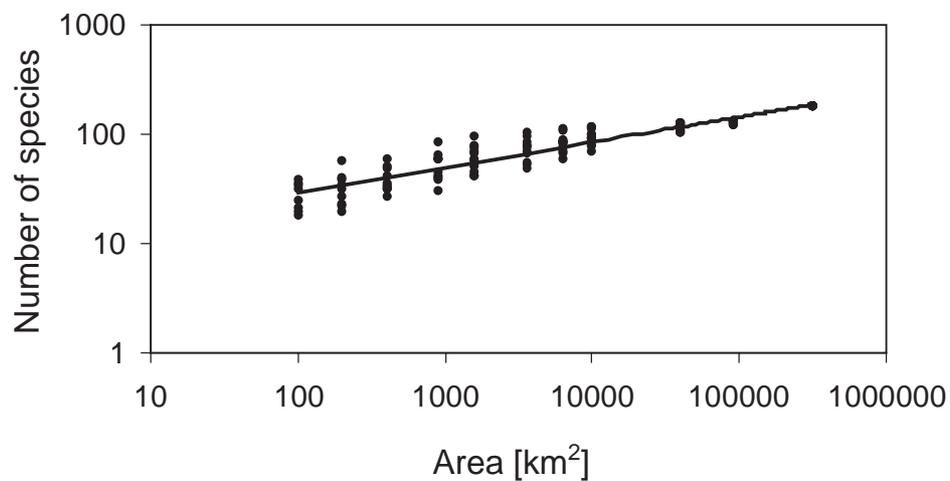


Figure 2. The SAR of Polish butterflies as inferred from 12 replicates of a nested design. Least-squares regression: $Y = (13 \pm 1)X^{(0.21 \pm 0.1)}$, $R^2 = 0.92$.

Results

The influence of the type of area reduction on species loss

The random, aggregated and fractal types of area reduction resulted in very similar patterns of species loss (Figs. 3 and 4). Pairwise comparisons between species numbers at each reduction stage revealed significant differences only between the fractal and the highly aggregated type. In this case 79 of 460 pairwise comparisons were significant at $p(t) < 0.05$. If more than 80% of area was eliminated, the highly aggregated pattern ($T = 0.1^\circ$) caused a slightly higher species loss than the fractal pattern.

However, although statistically significant, the mean absolute differences between these elimination types were comparably low (in the mean 1 ± 1 species; Fig. 5). The medium aggregated and the random types of area elimination caused patterns of species loss that were intermediate between the highly aggregated and the fractal (data not shown).

However, we observed marked differences in species loss between these ways of area elimination and the nested way of Ulrich and Buszko (2003a). The latter caused during nearly the whole process of area reduction a higher species loss (Figs. 3 and 4). The absolute differences between the nested and the non-nested designs were around 15–25 species. Hence, the more realistic non-nested

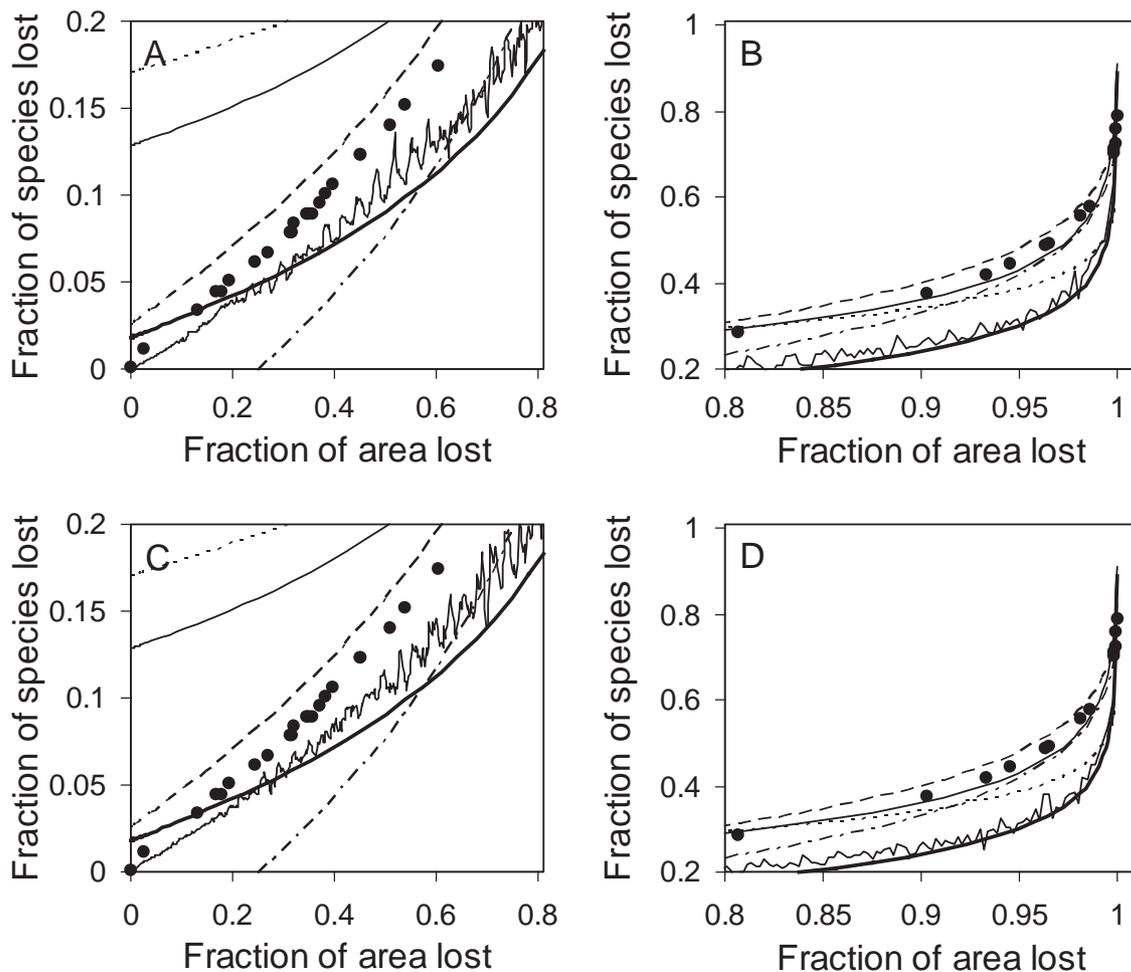


Figure 3. Simulated species loss after area loss (full light data lines; mean values of 20 replicates). Left sides: less than 80% of area eliminated; right sides, more than 80% of area eliminated. (A,B) random area loss; (C,D) rmd simulation fractal dimension = 2.5. Data points: Simulated species loss after area loss as inferred from a nested design (data from Ulrich & Buszko, 2003a; means of 40 replicates each). Regression lines: Dotted lines: Expectation from a power function SAR of European butterflies ($S = 43A^{0.10}$). Broken lines: Expectation from the nested power function SAR of Polish butterflies of Fig. 2 ($S = 13A^{0.21}$). Broken/dotted lines: Expectation from a power function SAR of Polish butterflies in Ulrich and Buszko (2003a) ($S = 16A^{0.20}$). Full bold lines: Expectation from the Plotkin approach to Polish butterflies ($S = 45A^{0.11}e^{-132/A}$). Full light line: Expectation from the fit of a logarithmic model to the data of Fig. 2 ($S = 18 \ln(A) - 67$).

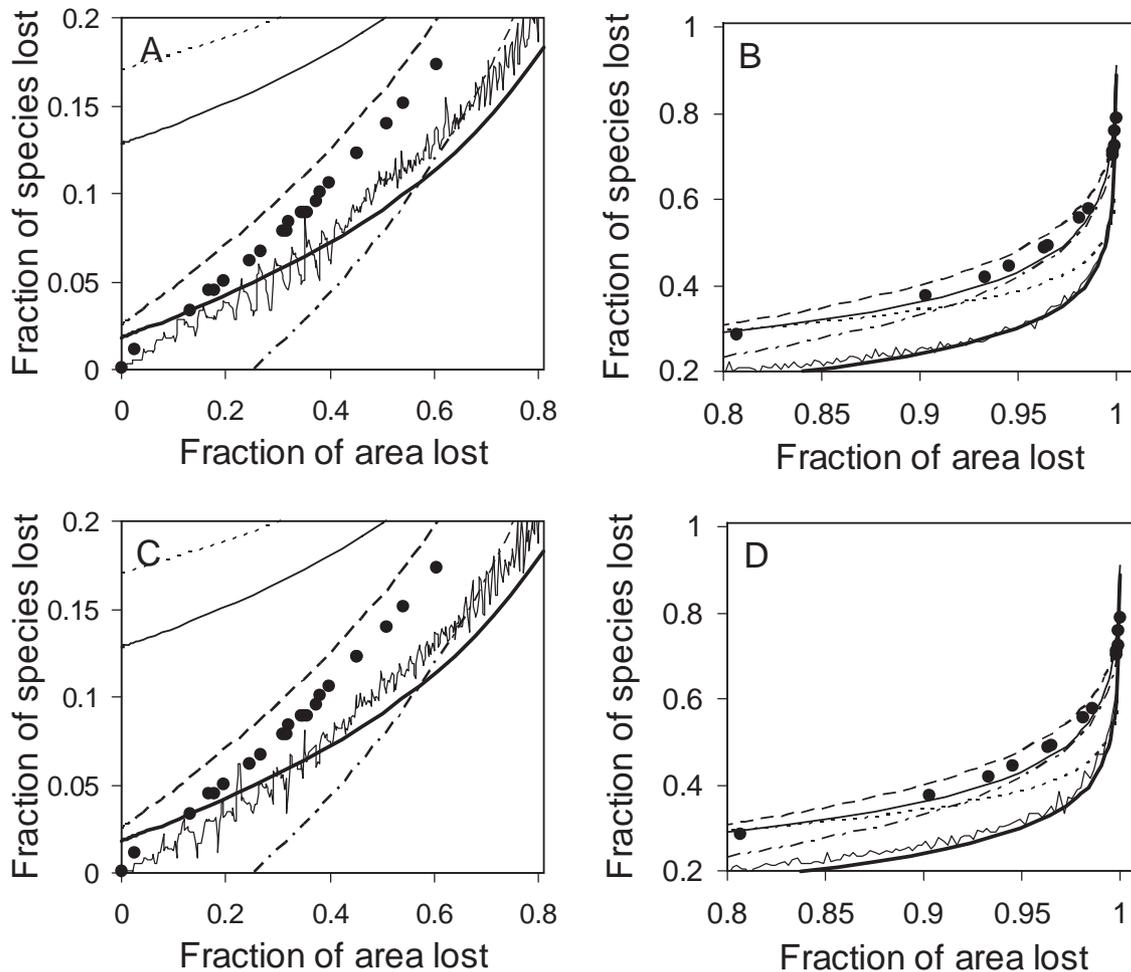


Figure 4. Simulated species loss after area loss (full light data lines; mean values of 20 replicates). Left sides: less than 80% of area lost; right sides: more than 80% of area lost. (A,B) Metropolis simulation $T = 1^\circ$; (C,D) metropolis simulation $T = 0.1^\circ$. Data points and regression lines as in Fig. 3.

patterns of area elimination caused a significantly smaller species loss than the nested pattern until only a small proportion of area remained (about 1‰).

Neither the fractal nor the aggregated types of area elimination resulted in a constant pattern of species loss. This is best seen when fitting a power function SAR to the data at each stage of area elimination (Fig. 6). Below 100,000 km² (44% of total Poland) the scaling exponents z constantly rose to values of about 0.4 when only small areas remained.

The ability of SARs to predict species loss

Mainland SARs are commonly constructed from nested subsets of area (Rosenzweig, 1995; Lomolino, 2000). Such a SAR (Eq. (7); Fig. 2; the broken lines in Figs. 3 and 4) was indeed able to track the nested pattern of area reduction as had already

been reported by Ulrich and Buszko (2003a). During the whole process of area elimination it overestimated species loss by about 1–3 species.

However, the power function SAR models tested here were unable to predict species loss of non-nested patterns of area elimination. The power function SARs of the non-Mediterranean butterflies (Eq. (9); dotted lines in Figs. 3 and 4) and the nested SAR (Eq. (7); broken lines in Figs. 3 and 4) highly overestimated the observed species loss. The difference between simulated and predicted species loss was between 6 and more than 20 species. The SAR of Eq. (5) instead underestimated species loss if less than 60% of area had been eliminated and then also overestimated it (broken/dotted lines in Figs. 3 and 4). It predicted no species loss below 25% of area elimination whereas the real process of species loss set on immediately.

The logarithmic SAR model behaved even worse (Eq. (8); full light lines in Figs. 3 and 4). Below 80% habitat reduction, the model highly overestimated

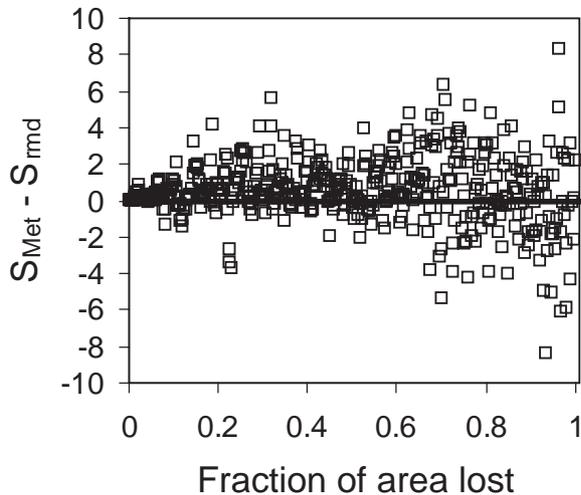


Figure 5. Below 80% area loss an aggregated pattern of area loss ($T = 0.1^\circ$) caused on average a higher species loss (S_{Met}) than a fractal one (S_{rmd}). A 277 of 366 (76%) differences $S_{\text{Met}} - S_{\text{rmd}} > 0$. Above 90% area loss the fractal pattern caused a slightly, although statistically not significantly ($p(x \neq 23) = 0.08$) higher species loss (26 of 46 differences < 0).

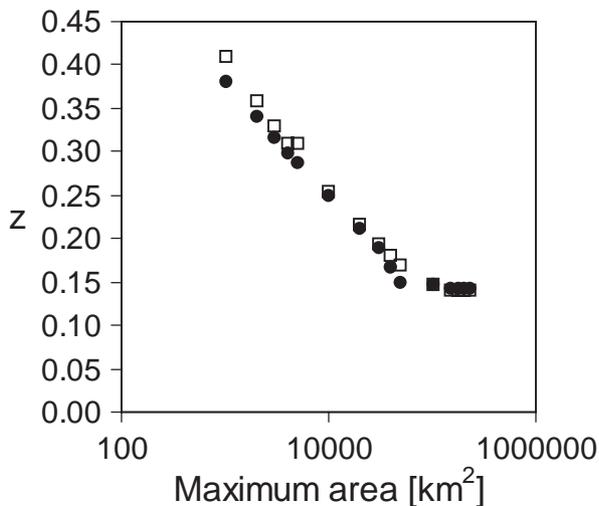


Figure 6. Scaling exponents z of the power function SAR model change during the process of area loss. Above 44% area loss (below 100000 km² remaining), the fractal rmd algorithm (fractal dimension $D = 2.5$; open squares) resulted in consistently higher exponents than the Metropolis algorithm ($T = 0.1^\circ$) although no pairwise comparison was statistically significant ($p(t) > 0.05$).

species loss. Interestingly above 80% the model closely tracked the species loss of the nested pattern of area loss.

The Plotkin approach to SARs (Eq. (6); full bold lines in Figs. 3 and 4) predicted species loss best. During the whole process of area elimination, the

model closely fitted to the species loss data. The absolute difference between simulation and prediction was always below 5 species. Above 30–40% area loss, it underestimated species loss by about 1–5 species (Figs. 3 and 4). Below 30% area loss it overestimated species loss by 1–3 species.

Discussion

The question whether SARs are able to predict species loss has recently gained much interest (May et al., 1995; Pimm & Askins, 1995; McKinney, 1998; Ney-Nifle & Mangel, 1999; Kinzig & Harte, 2000; Seabloom et al., 2002; Ulrich & Buszko, 2003a, b). However, all of these papers used simple power function SARs for estimation. Our approach is apparently the first that uses controlled simulations with real large data sets to infer how precise the predicting tool SAR can be under varying conditions of habitat loss.

The main result of the present study is that species loss is a pattern in its own right and not a simple reversal of a SAR. The nested SARs of Polish (Fig. 2) and of European (Ulrich & Buszko, 2003b) butterflies are well described by power functions indicating a self-similar process of species accumulation. Species loss instead deviated from self-similarity and could not be described by a single power function (Fig. 6). The high z -values of Fig. 6 indicate that the process of species loss was severe only at high degrees of area loss. Irrespective of the area reduction process (aggregated, fractal or random), it needed an area loss of more than 99% to reduce the number of Polish butterflies to 50%. Such a low loss rate was predicted only by the Northern European SAR (Eq. (9)), which otherwise failed (Figs. 3 and 4).

Non-random patterns of area loss (fractal or aggregated) did not differ significantly from each other and from a random pattern with respect to species loss. This result contradicts the finding of Seabloom et al. (2002) who reported for California vascular plant communities that non-random patterns of area loss caused a higher species loss than a random pattern. However, Seabloom et al. (2002) used a simple power function model (with z -values between 0.1 and 0.4) but did not control for systematic deviations from this model at different scales of resolution. In this respect their approach remains questionable.

Seabloom et al. (2002) also reported that real species loss proceeded much faster than predicted by their SAR model. We instead found that power function and logarithmic SAR models overestimated

species loss. While both studies relied on simulated area loss, it seems that the contradicting results stem either from the different ways SARs were constructed or from systematic deviations of the real species accumulation curves from power functions. This, however, only highlights the fact how sensible the tool SAR is and that we have to be careful for instance when applying 'standard' SARs from the literature to a specific problem.

In this respect, it was interesting to see that the Plotkin approach to SARs (Eq. (6)) that introduces a parameter to deal with upper or lower curvatures of species accumulation curves was also the best predictor of species loss over the whole range of area reduction. This approach needs prior investigations about deviations from a self-similar pattern of species accumulation (from a power function SAR). For this you need detailed maps of species spatial distributions. So, why should we apply SARs as predicting tools if we already have to know the spatial distribution patterns and can exactly tell which species will become extinct after destroying a certain area? One answer to this question lies surely in our inability to foresee exactly the progress of habitat reduction. Thus, we have to rely on estimates. Additionally, for only a few larger groups of animals or plants are detailed continental wide distribution maps available (Konvicka, Maradova, Benes, Fric, & Kepka, 2003; Storch, Konvicka, Benes, Martinkova, & Gaston, 2003). However, to establish SAR patterns you do not need the whole map. In most cases a few detailed mapped regions are necessary to infer the type of SAR and to estimate the necessary model parameters.

Our simulation caused continuous changes in the slope of power function SARs during the area reduction process. A similar pattern had already been reported by Ney-Nifle and Mangel (2000). They used a patch occupancy approach and found that spatial effects like range sizes, fragmentation patterns and edge effects influenced SAR pattern leading either to higher or to lower species loss than predicted by the initial SAR pattern. In particular, they found that smaller edge effects during area loss (introduced by more aggregated patterns of area loss) reduced species loss. This seems to contradict our finding that the aggregated elimination design (with its lower sum of edges) caused a higher species loss than the fractal design. Unfortunately, Ney-Nifle and Mangel (2000) used highly unrealistic patterns of habitat loss (square or rectangular cuts). Therefore, their results cannot be directly compared with those of the present study and with the ones of Seabloom et al. (2002).

Nevertheless, each of these three studies found that the way area loss proceeds will influence SAR patterns and species loss. Additionally, Ulrich and Buszko (2003b) simulated species loss of European butterflies and found that the initial spatial distributions of species, in particular those of species with restricted range sizes, might strongly influence the way species loss proceeds.

Of course, our simulation is still highly artificial. In reality, habitat reduction proceeds by losing small irregular areas but not by eliminating whole biogeographic units like UTM grids. Our simulation also does not account for small island effects or dispersal, which might counteract habitat reduction (Lomolino & Weiser, 2001). However, our simulation was not intended to give a realistic model for species loss at various ecological scales. Our aim was to point to some potential pitfalls in the use of standard methods for predicting species loss. For this task a rather coarse-grained reduction pattern seems appropriate. SARs are used to predict species loss at regional scales where local differences in species numbers are levelled (May et al., 1995; Pimm & Askins, 1995; Brooks et al., 1997; Pimm & Lawton, 1998; Brook et al., 2003). Additionally, the self-similarity approach to SARs relies on a coarse grained grid where local differences in species richness are of minor importance (Harte et al., 1999a; Plotkin et al., 2000b). Hence, in particular this SAR model should predict species loss well when applied to grid cell reduction patterns as in this study. The failure of the allometric SAR model instead casts doubts to its applicability to more natural ways of habitat loss.

The present results do not point to unequivocal conclusions. SARs might be powerful tools in biodiversity forecasting. However, they have to be constructed in a case-specific manner. There are no standard solutions. On the other hand, our results also imply that conscious landscape planning might reduce the negative effects of habitat conversion on biodiversity to a certain extent. Highly aggregated patterns of land conversion should be avoided. However, we also strongly feel that we should not overestimate the possibility to avoid negative effects on biodiversity simply by changing patterns of habitat destruction instead of conserving habitats.

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