

Predicting species numbers using species–area and endemics–area relations

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Received 4 February 2003; accepted in revised form 28 May 2004

Key words: Butterflies, Endemics, Endemics–area relation, Lepidoptera, Patch occupancy model, Species–area relation

Abstract. Current ecological theory predicts an allometric relation between the number of species with restricted range size (endemics) and area (the endemics–area relation EAR), a pattern similar to the common species–area relation (SAR). Using SARs and EARs we can estimate species loss after habitat loss. A comparison of the predictive power of both approaches (using a patch occupancy model and data from European butterflies) revealed that the EAR approach is less reliable than the SAR. Contrary to current theory it appeared that EARs are relations in their own right that describe spatial distributions of endemic species. They do not simply follow from the underlying SAR. The implications of these results for the applicability of SARs and EARs in biodiversity forecasting are discussed.

Introduction

The study of species–area relationships (SARs) has a long tradition in ecology and the construction of SARs is one of the most frequently used methods to estimate species numbers at different spatial scales (Rosenzweig 1995, 2001; Lomolino 2000). Additionally, SARs are frequently claimed to be of major importance in biodiversity forecasting and in predicting future species loss (e.g. Pimm and Askins 1995; May et al. 1995; Harte and Kinzig 1997; Pimm 1998; Ney-Nifle and Mangel 1999, 2000; Harte 2000; Veech 2000).

The most often used model to describe the relationship between species number S and area A is the Arrhenius model (Arrhenius 1921), a power function of the form

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

where S_0 denotes the intercept value at unit of area and z the slope (Rosenzweig 1995). If such a model is able to describe a given SAR it should be possible to estimate how many species will be lost if the area where these species originally lived is partly destroyed (Wilson 1992; May et al. 1995; Kinzig and Harte 2000; Ulrich and Buszko 2003a, b, 2004a, b). If S_R is the species number in a remnant area A_R ($S_R = S_0 A_R^z$) we can divide this latter function through Eq. (1) and get, after simple rearrangement

$$\frac{S_R}{S} = \left(\frac{A_R}{A}\right)^z. \quad (2)$$

Eq. (2) predicts that the fraction of species $f_{\text{SAR}} = (S - S_R)/S$ lost after habitat loss of $(A - A_R)/A$ should be

$$f_{\text{SAR}} = 1 - \left(1 - \frac{A_R}{A}\right)^z. \quad (3)$$

Harte and Kinzig (1997) and Kinzig and Harte (2000) argued that Eq. (3) tends to overestimate real species loss after small to moderate habitat loss. To correct for this they derived a so-called endemics–area relation (EAR). They assumed that an area is subsequently subdivided into smaller parts and that in each part the original allometric species–area relation ($S \propto A^z$) holds. This assumption refers in particular to a situation where species have similar scale invariant spatial distribution patterns (Harte et al. 1999).

Endemics are species that have very restricted range sizes. Harte and Kinzig (1997) formalized this and labeled all species as being endemic if they occur in only one of the subareas of a total larger area. Kinzig and Harte (2000) argued that for such defined endemics E a power function SAR model holds, similar to the Arrhenius model:

$$E = E_0 A^{z'} \quad (4)$$

with z' being the slope of the EAR.

Equation (4) implies (Kinzig and Harte 2000) that the fraction of species lost after habitat destruction should be

$$f_{\text{EAR}} = 1 - \left(\frac{A_R}{A}\right)^{z'}. \quad (5)$$

Kinzig and Harte (2000) argued that the EAR approach is better suited to predict patterns of species loss during a process of habitat destruction than the conventional SARs. They should therefore have potential applications in conservation studies and diversity forecasting.

However, critical tests whether species spatial distributions are indeed self-similar and whether SARs and EARs are able to predict species losses are astonishingly scarce. A literature survey revealed that the same few papers are cited as corroboration of the applicability of SARs (May et al. 1995; Pimm and Askins 1995; Pimm 1998) for predicting species loss. Only Ulrich and Buszko (2003a), using data on Polish butterfly species, dealt with EARs and found them not to be superior over the classical SAR approach in predicting species numbers. In a recent paper (Ulrich and Buszko 2004a) we showed that for butterflies the use of SARs and EARs in biodiversity forecasting might lead to different predictions about diversity loss and prioritizing schemes for conservation. However, due to the potential implications for biodiversity forecasting

the applicability of both the SAR and the EAR approach deserves further attention.

Materials and methods

The present paper uses a patch occupancy approach for studying EARs and SARs (Griffiths 1992; Leitner and Rosenzweig 1997; Hanski 1999; Ulrich 2002a). This has the great advantage of allowing the generation and analysis of multiple replicable spatial distribution patterns. Additionally, sample areas used in such models can be 'well-shaped' (Harte et al. 1999; Maddux and Athreya 1999), i.e. they can have the same spatial properties as those that were assumed for the theoretical derivations of SAR and EAR patterns (Harte et al. 1999; Kinzig and Harte 2000; Lennon et al. 2002).

Initially 200 model communities with species numbers between 50 and 500 were computed. Dominance–rank orders of these communities followed in all cases the power fraction model of Tokeshi (1996). This model has the great advantage of being able to generate communities following a wide range of realistic rank order distributions by varying only a single shape generating parameter k (Ulrich 2002b, 2004a, b). It is therefore an ideal tool for the study of ecological processes that involve communities with different dominance–rank order distributions. In the present study I used randomly assigned k -values between -0.3 and 1.0 leading to distribution patterns similar to those found in nature (a classical lognormal RAD is generated by a k -value of 0.1). Abundances were in every case adjusted so that the least abundant species had exactly one individual. All computations were done with the program RAD (Ulrich 2002b). Computational details are fully described in the online manual of this program (Ulrich 2002b).

The individuals of these 200 model communities were placed at random into the cells of a grid with an area of 1000×1000 cells. To introduce habitat heterogeneity carrying capacities of the grid cells varied and were assigned by a superposition of trigonometric functions (Burrough 1983) leading to a fractal grid similar to ones formed by a fast Fourier transformation (Hastings and Sugihara 1993). For each species a different grid was used.

After placement, an area of 32×32 adjacent cells was sampled by the nested design Harte and Kinzig (1997) and Harte et al. (1999) used to derive their EAR approach. For each sample species numbers, numbers of endemics and the slope and the intercept of the SARs and EARs were determined. Species occurrences in the cell groups of the nested design were used to determine the numbers of species lost after the elimination of a certain area. Placement and computation were done with the PatchOccupancy program (Ulrich 2002a, 2004b).

Additionally, I used data on European butterfly species provided by the Red Data Book of European Butterflies (Swaay and Warren 1999) to infer SAR and EAR patterns. Butterflies in the sense of this Red Data Book are all species

of the families Hesperidae, Papilionidae, Pieridae, Lycaenidae, and Nymphalidae. Appendix D of this compendium is a species \times country matrix and gives occurrence data for each European country and for some Mediterranean islands. Due to different SAR slopes, SARs and EARs were constructed separately for Mediterranean countries and for countries north of the Alps and Pyrenees and the Eastern European countries (in the following termed M- and NE-countries). This division is identical to the one of Ulrich and Buszko (2003b), where a complete list of countries of both groups is given. The total butterfly fauna of Europe contains 576 species, 524 are found in the Mediterranean region and 376 in Northern and Eastern Europe.

In line with the definition of Harte et al. (1999) those species were classified as being endemics, which occur in only one country, irrespective of country size. The NE-countries contain 110 such endemic butterfly species, the M-countries 243.

SARs and EARs were constructed by a subsequent accumulation of countries. Habitat loss was simulated by the exclusion of certain countries and their butterfly fauna. This process implies also the elimination of the endemic species of these countries and the pattern of species loss was used to compare the predictions of Eqs. (3) and (5). The ordering of countries in such processes influences the resulting SAR. Theoretically a random addition of countries should result in a more concave SAR shape than the addition of contiguous countries (Rosenzweig 1995). However, Ulrich and Buszko (2003b) showed that M- and NE-country SARs followed power functions without detectable lower concavity. The processes of country accumulation and exclusion were repeated 20 times with a randomly reshuffled sequence of countries. According to Colwell and Coddington (1994) this number of reshufflings should be sufficient to eliminate the variance introduced by the ordering of countries.

Results

The model approach

As predicted by Harte et al. (1999) power functions described SARs and EARs in the fractal grids well (Figure 1). The slope values obtained for SARs ranged between 0.11 and 0.87, values also found in nature (Rosenzweig 1995). The variance explanation of the power function SAR model was in the mean 90%, that of the power function EAR model 89%.

Above 10% area loss the SAR approach overestimated real species loss by a factor of 2.5 ± 2.30 (Figure 2a). As predicted by Harte and Kinzig (1997) the EAR approach worked better but still overestimated observed species loss by a factor of 1.90 ± 1.50 (Figure 2b). In both cases the pattern of overestimation was constant above 10% species loss. Despite the close fit of the power function to both SAR and EAR patterns, predictive powers scattered in both cases widely around the mean (indicated by the error bars in Figure 2). The variance

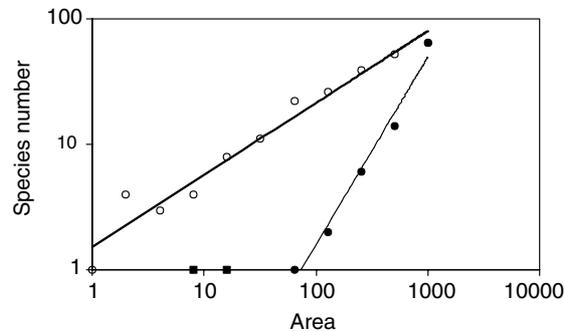


Figure 1. A typical species–area (open circles) and its associated endemics–area (filled circles and squares) relation of the model communities used here. Both follow allometric functions. The two data points denoted by filled squares show outliers that were not used to compute EARs. The SAR slope z is 0.57, the corresponding EAR slope z' 1.49 ± 0.27 (mean \pm standard deviation). Eq. (5) predicts a steeper EAR slope of 1.61, a value that is in this case not significantly different from the empirical one (at the 1% error level).

of the EAR approach was lower at higher fractions of area lost. This result implies that for any reliable estimate of species loss multiple replicates have to be used, a task that seems impossible to perform in the case of real habitats under threat.

Below 10% area loss both approaches had an even wider scatter of predictions (Figure 2a, b) ranging from no species loss to a loss that was even higher than the total species number in the grid. This scatter reduces the applicability of both approaches as a tool for predicting species loss at low levels of habitat loss significantly.

Endemics–area relations of European butterflies

Figure 3a, b show the endemics–area relations for M- and NE-countries, respectively. In the Mediterranean region (Figure 3a) small countries tend to have higher numbers of endemic species than expected by the EAR (the open squares). The latter predicts that countries below 10,000 km² should have no endemics. Leaving these countries aside the Mediterranean EAR can be described by an allometric function with a slope of 1.48 ± 0.05 . The EAR slope of the NE-countries is 0.63 ± 0.07 (Figure 3b).

It is easy to simulate habitat loss with the present butterfly data. A simple exclusion of countries or combinations of countries and a counting of the remaining number of species leads to precise information about species loss in relation to habitat loss. These data can be compared with the predictions either of the traditional SAR approach (Eq. (3)) or of the endemics–area approach (Eq. (5)). Figure 4 compares the predictive power of both methods (given as predicted versus observed species loss) at different degrees of habitat loss.

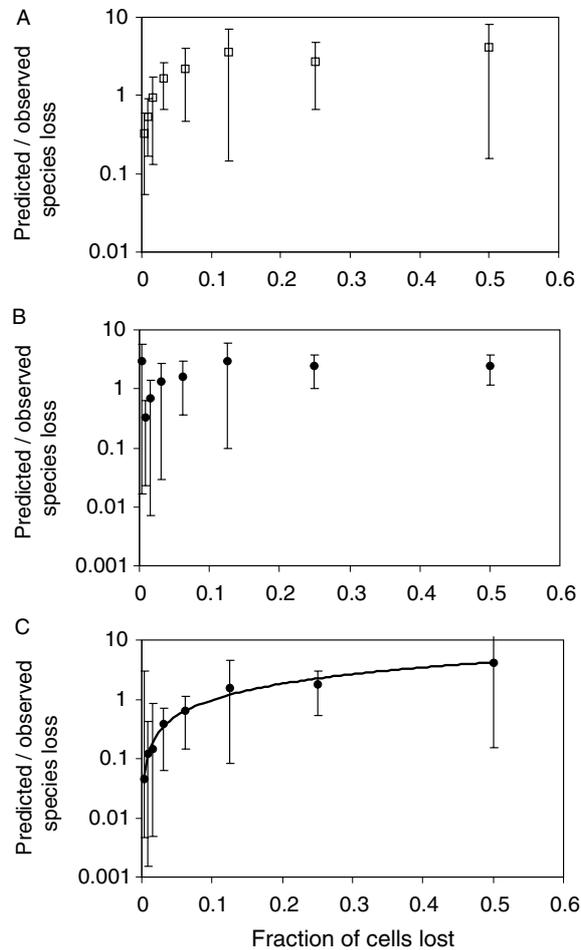


Figure 2. Predictive power (measured as the quotient of expected and observed species loss) using (a) the classical SAR, (b) the EAR approach with observed slopes, and (c) the EAR approach with expected slopes (Eq. (4)) of the 200 model communities used in this study. Error bars denote one standard deviation. Above 10% of cells eliminated the SAR approach overestimated the observed species loss by a factor of 2.5. EARs overestimated this loss by a factor of 1.9 (b) and 1.44 (c), respectively. The regression line in (c) indicates the close correlation between predictive power and fraction of habitat lost using expected z' -values ($y = 7.9x^{0.91}$; $R^2 = 0.98$).

Below 10% habitat loss predictive powers of both approaches scatter widely around the expected value of 1 mainly due to the low number of species expected to become extinct. Above 10% habitat loss a remarkable difference between M- and NE-countries appears. For the M-countries, where both the allometric SAR and the EAR fit closely to the data, both approaches predict species loss reasonably well. In the mean they overestimate real species loss, the

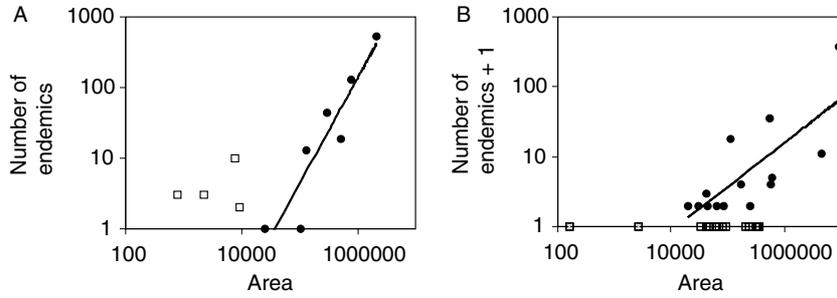


Figure 3. (a) EAR of Southern European (Mediterranean) butterfly species (area in km²). Open squares: countries below 10,000 km². The regression line was drawn only through filled circles: $S = 0.000002 \text{ area}^{1.48 \pm 0.05}$; $R^2 = 0.87$. (b) EAR of Northern and Eastern European butterfly species (area in km²). Open squares: 17 countries without endemic species. The regression line was drawn only through filled circles: $S = 0.0025 \text{ area}^{0.63 \pm 0.07}$; $R^2 = 0.58$. Note that the y-axis in (b) is number of endemics + 1.

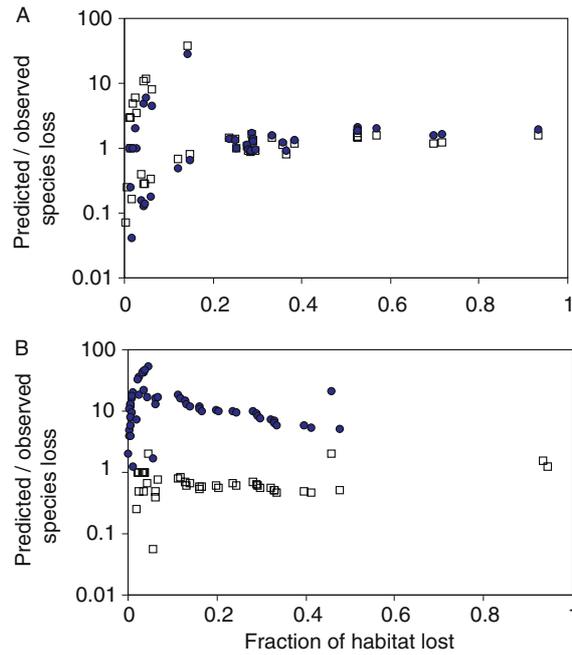


Figure 4. (a) Predicted versus real species loss of M-countries (a) and NE-countries (b) in relation to habitat loss (simulated by the elimination of countries and combinations of countries). Open squares stem from predictions by the SAR approach (Eq. (3)), black circles were computed using the empirical EAR (Figure 6). Note that the EAR approach is strictly valid only at less than 50% habitat loss. However, for comparison with the SARs estimates at higher degrees of habitat loss were also included.

SAR approach by about $27 \pm 9\%$ and the EAR approach by about $38 \pm 22\%$. On the other hand, in the case of the NE-countries the EAR totally failed (Figure 4b). In the mean it overestimated real species loss by a factor of 10. The SAR approach worked better but underestimated species loss by about $66 \pm 6\%$.

Discussion

The present results show that the endemics–area approach proposed by Harte and Kinzig (1997) and Kinzig and Harte (2000) for estimating species loss during habitat destruction does not give better results than the use of classical species–area curves. The EAR method was especially developed to predict species loss after small to moderate habitat loss. In these cases only a few species will become extinct. Figures 2 and 4 show that below 10% area loss predictions scatter widely making any precise diversity forecasting impossible. The observed variance is larger than expected from simple Poisson errors due to low species numbers that become extinct. A second factor influencing the variances of the predictions appears to be habitat structure that leads to aggregated species spatial distributions and large differences in local species numbers. Predictions about species loss from regression lines will therefore be heavily influenced by which small patches are lost.

This latter point leads to the general question about the applicability of species–area and endemics–area relations for predicting species numbers. Despite the frequent claims of theoreticians about the usefulness and importance of SARs in biodiversity forecasting (May et al. 1995; Kinzig and Harte 2000; Harte 2000), both methods still await critical tests by field ecologists (Ulrich and Buszko 2004a, b). From a theoretical point of view the low R^2 values found for many SARs [the 100 SARs of the compilation of Connor and McCoy (1979) have a mean coefficient of determination of only 0.48] make even moderate extrapolations beyond the range of measurements doubtful especially due to the large confidence ranges for species numbers at small and large area scales. Estimates of species loss, however, rely on such extrapolations.

In this respect it is astonishing how well the SAR and the EAR methods worked in the case of at least the southern European butterflies. The mean error level of less than 40% for M-countries is much less than even for the model approach. M-country SAR and EAR closely followed power functions ($R^2 = 0.82$ and 0.87 , respectively) (Figure 3; Ulrich and Buszko 2003a). However, in the case of the NE-countries, where the variance explanation of both models is much lower ($R^2 = 0.23$ and 0.58 , respectively) (Figure 3b; Ulrich and Buszko 2003a), the SAR approach still worked reasonably well ($66 \pm 6\%$ underestimation) whereas for the EAR large systematic errors occurred. Therefore, the goodness of fit of the SAR might influence the applicability of EARs more than that of SARs. However, many more comparable studies are necessary to validate this speculation.

Why did the SAR approach work for the butterflies better than expected from the grid model? One reason is surely that the spatial resolution of the model was finer than that of the real data. For comparisons spatial resolution is best measured in terms of species numbers per unit area. For the model this was 2.25 species per cell. The smallest Mediterranean area dealt with in the Red Data Book of European Butterflies instead has an area of 316 km² and contains 16 butterfly species. At this resolution averaging effects already lower the high variance in diversity between habitat patches and lead to a better fit of the power function model. Nevertheless, it is interesting to see that between 20 and 50% habitat loss the predictive power of the SAR was for the real data set always better than for the model communities. The fits of the power function model were in both cases similar as were the species numbers dealt with. One explanation for this may be that the grid structure of the model was coarser than the landscape structure of the M-countries. Therefore, the averaging of species numbers in the real landscape might result in more precise estimates. This would improve the power of SARs to predict species numbers.

The high variability in local patch diversity meant that, for the model species and for the butterflies, some small patches had more endemic species than expected from EARs. In the case of SARs such a pattern had recently been identified by Lomolino and Weiser (2001) and by Crawley and Hurrall (2001). Whether this 'small island effect' (Lomolino and Weiser 2001) is simply a stochastic effect caused by the high variance at small scales or whether dispersion and rescue mechanisms lead to increased species numbers remains unclear. Several authors reported guild specific changes of species numbers in habitat fragments compared to undisturbed areas of similar size (Andr n 1994; Golden and Crist 1999; Kruess and Tschardtke 2000; Zschokke et al. 2000; Summerville and Crist 2003). Such changes cause deviations from the overall SAR pattern and make predictions of species numbers at small scales less precise. Unfortunately, a systematic study of deviations from the power function SAR is only at the beginning (Plotkin et al. 2000; Lennon et al. 2002; Ulrich and Buszko 2003a, b, 2004a). The ultimate result of such efforts might be an extension of the power function model that contains guild specific correction factors correlated especially to dispersion abilities (Hanski 1999; Zschokke et al. 2000) and body weight (Andersen et al. 1997).

In the case of the 'small island effect' the total number of species that will survive after habitat destruction will be higher than predicted by the SAR or the EAR. For instance, the EAR approach predicts according to Eq. (5) that no endemic butterfly species should occur in Mediterranean regions below an area of 30,000 km². Figure 3a instead shows 4 small islands (Cyprus, Canary Islands, Azores, and Madeira) with 2–10 endemic species. In the case of the mainland, the EAR predicts for Albania, Portugal, Bosnia and Herzegovina, and Croatia at least one endemic species to occur, whereas in these countries no endemics exist (Swaay and Warren 1999). Interestingly, no such 'small island effect' could be detected for the NE-countries (Figure 3b). The study of EARs reveals therefore hidden patterns that would be overseen by constructing only

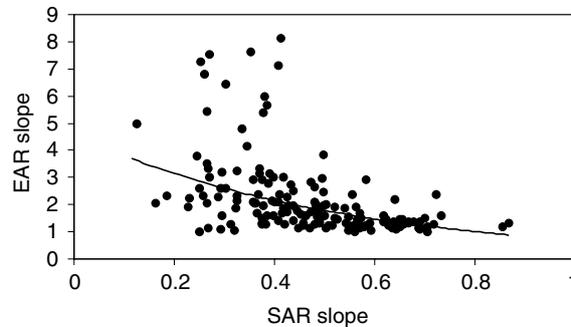


Figure 5. EAR slopes z' versus SAR slopes z of 200 model communities of the grid approach. The regression line denotes the best fit regression: $z' = 4.6e^{-1.89z}$; $R^2 = 0.30$, $p < 0.01$.

classical SARs. Unfortunately, up to now only a few studies reported species–area data of endemics (e.g. Pearson and Cassola 1992; Balmford and Long 1994; Kinzig and Harte 2000; Ulrich and Buszko 2003a). This limited knowledge makes detailed comparisons of EARs and SARs still impossible.

Harte and Kinzig (1997) and Harte et al. (1999) developed the EAR concept from the underlying SAR and argued that both relations are closely connected. In other words the SAR should determine EAR patterns. The above results indicate that this is not the case. Figure 5 shows that although SAR and EAR slopes of the model approach were significantly correlated this correlation is not very close. In particular at SAR slope values below 0.4 there is a remarkable scatter in the EAR slopes and both are not correlated ($r = 0.1$; $p(t) > 0.5$). This scatter could not be explained by grid properties, model fit or species number of the model (no significant covariation, data not shown). However these are the SAR slopes that are most often found in nature (Rosenzweig 1995). EARs seem therefore to be relations in their own right that describe spatial distributions of species with restricted range sizes.

Acknowledgments

I thank Prof J. Buszko for critical and valuable suggestions on the manuscript. Miss H. Pearson kindly improved my English. This work was in part supported by a grant from the Polish Science Committee (KBN, 3 F04F 034 22).

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