

## Species–area relationships of butterflies in Europe and species richness forecasting

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Species–area relationships (SARs) of European butterfly species (Rhopalocera) appear to follow power functions with Mediterranean butterflies having a much higher slope value ( $z = 0.49$ ) compared to the slope for the northern and eastern European countries ( $z = 0.10$ ). A simulated process of species extinction by a stepwise density dependent random elimination of species affected species–area patterns differently. For Mediterranean countries SAR slopes decreased, for other European countries slopes increased during the extinction process. Comparisons of species numbers before and after extinction with those predicted by a classical SAR approach differed widely and revealed that SARs are not able to predict future species numbers at local scales. For Mediterranean countries the classical SAR approach underestimated the number of species remaining after simulated extinction, for all other European countries SARs highly overestimated species numbers. These contrasting patterns indicate that changes in SAR patterns do not unequivocally point to changes in species diversity or community structure as assumed by current theory. On the other hand, the results strongly indicate that simplified applications of SARs for forecasting might give misimpressions about species loss and future biodiversity if the initial community structure, especially relative densities and numbers of species with restricted range size, are not taken into account.

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Butterflies are major study subjects of ecologists and conservationists. They are relatively easy to sample and to identify and for most European countries and North America detailed distribution maps and at least semi-quantitative abundance data are available (frequently given as abundance or distribution classes) (Karsholt and Razowski 1996). This makes them one of the most often used taxa for conservation studies and monitoring (Dennis 1993, Pullin 1995, Thomas et al. 2001).

Species–area relations are most often described by an allometric function of the form

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

where  $S$  is the number of species in an area  $A$  and  $S_0$  and  $z$  are the parameters of the model.  $S_0$  can be interpreted as the expected mean number of species per

unit of area (Rosenzweig 1995). This model stems either from the classical derivation of allometric SARs from lognormal type relative abundance distributions (Preston 1962, May 1975, Sugihara 1980) or from recent application of fractal geometry to the study of species–area patterns (Harte et al. 1999). Although a series of other models have also been proposed to describe SARs, it seems that at least above regional scales allometric models provide the best fits to most data sets (Connor and McCoy 1979, Rosenzweig 1995, Lomolino 2000, Ulrich 2001, Ulrich and Buszko 2003).

Current ecological theory assumes that the slope value of the power function model tells something about regional patterns of species spatial distribution (Rosenzweig 1995, Hanski and Gyllenberg 1997, Crawley and Harral 2001, Rahbek and Graves 2001, Willis and Whittaker 2002). At regional scales mainland

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SARs typically have  $z$ -values between 0.1 and 0.2. Islands are characterized by relatively higher numbers of endemic species or species with restricted range sizes. For islands allometric SARs with higher slope values ( $> 0.3$ ) are therefore predicted (Rosenzweig 1995). Habitat fragmentation shifts mainland patterns of habitat distribution towards island patterns and these changes in habitat structure should be accompanied by changes of SAR patterns. If habitat fragmentation results in changes of species spatial distribution patterns so that more species have restricted range sizes, slope values should be higher than before fragmentation (Ulrich 2000, Rosenzweig 2001). For instance, Rosenzweig (2001) reported that SAR slopes of Australian lizards changed during a process of fragmentation. Lizards in the network of the West Australian wheatbelt reserves have a SAR slope of 0.26, higher than expected for the typical mainland pattern ( $z < 0.2$ ) but yet not as high as for the near true islands ( $z = 0.36$ ). In this case fragmentation influenced local extinction patterns of lizards and resulted in more restricted range sizes where species are confined to habitat reserves.

However, local and regional species extinction might affect SAR patterns in a different way. Ecological theory assumes that endemic species or species with restricted range sizes are most prone to extinction (Gaston 1994, Kunin and Gaston 1997). These are often species of low local abundance (Hanski et al. 1993, Gaston 1996, Gaston and Curnutt 1998). Such an extinction pattern should result in a rising proportion of abundant and widespread species. Now imagine a finite universe of species. Then slope and intercept of SARs must be connected (Gould 1979, Niklas 1994). If rare species have higher probabilities of extinction

mean species numbers per unit of area ( $S_0$ ) would be less affected than the total number of species  $S$ . Such an extinction pattern would result in a decrease in slope values of power function SARs (Leitner and Rosenzweig 1997). Just this pattern (but reported in a slightly different form) was recently found by Lawesson et al. (1997) (see also Ma et al. 2002). They studied plant species richness patterns of young and old Danish beech forests. Older forests accumulated more rare or remnant species resulting in a high slope of power function SARs. Younger forests still on the way to accumulating such species contained relatively more abundant species with good colonization abilities and their slope values were much lower.

The study of slope and intercept values of power function SARs might therefore tell something about the way a process of species loss proceeds or how species respond to habitat loss. Based on the arguments above we consider four theoretical possibilities (Fig. 1): 1) Global extinction of rare, locally restricted, and endemic species is more likely than extinction of widespread species. The mean local species richness is then relatively unaffected so the intercept remains constant (or decreases slightly) but global species richness decreases. So the SAR slope must also decrease (Fig. 1A). In other words, species extinction affects local species numbers less than regional ones. This possibility is consistent with a pattern where local abundance and range size are positively related (Gaston 1994, Kunin and Gaston 1997). 2) If there are relatively few species with restricted range size, which become globally extinct, but many widespread species, which become locally extinct in some areas, overall species richness is less affected than local species richness. Therefore, the

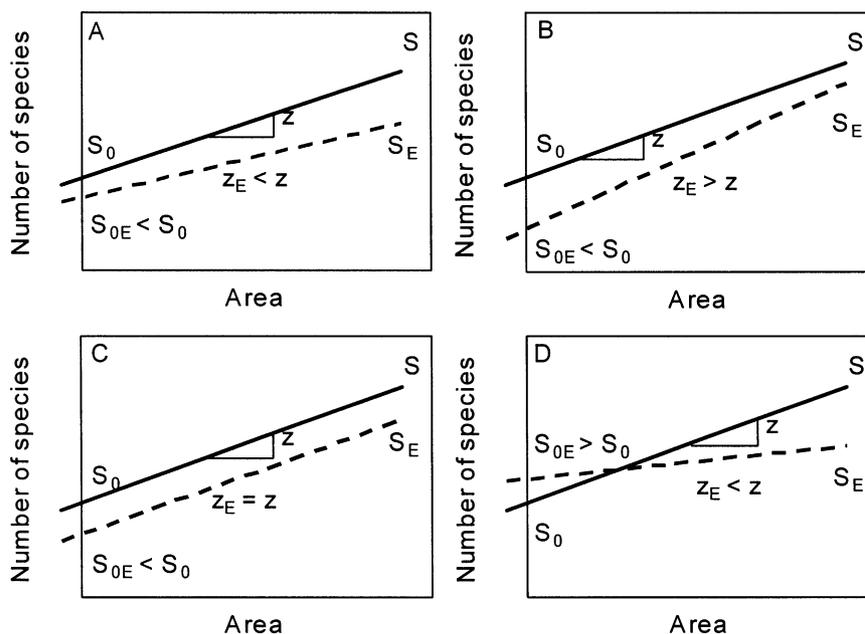


Fig. 1. Four ways that species extinction might influence species area relations.  $S$ ,  $S_0$  and  $z$  are the parameters of the power function model (see eq. (1) in the text).  $S_E$ ,  $S_{0E}$  and  $z_E$  are the parameters after extinction. Both axes are supposed to have logarithmic scales. Further explanation in the text.

SAR slope must increase (Fig. 1B). 3) Restricted and widespread species have approximately equal chances of becoming globally extinct. In this case the SAR slope remains constant but the intercept decreases (Fig. 1C). This pattern would only be possible if there is no relation between local abundance and range size because any such relation would immediately influence the relation between slope and intercept after species extinction. 4) Finally, the slope value might decrease but the intercept increase. Such a pattern implies that a process of habitat destruction would let local diversity to increase. We may think of a fragmentation process in which species fill open niches in the remaining habitat patches (Fig. 1D). In this case the relation between local abundance and range size should be weakened.

The study of species–area patterns might therefore tell something about the way extinction processes affect species spatial distribution patterns. The aim of the present paper is to study such changing patterns of SARs for European butterflies. Butterfly SARs are not well studied even though SARs are one of the major tools for estimating regional species numbers, identifying ecological hotspots or depauperate regions (Kerr 1997, Veech 2000, Kinzig and Harte 2000). Therefore, changes in SAR patterns have potential implications for conservation strategies that are urgently required for some butterflies (Pullin 1995, Thomas and Abery 1995).

The Red Data Book of European butterflies (Rhopalocera) (Swaay and Warren 1999) provides a unique database for the study of SARs and the effects of species extinction. It provides for each European country detailed species lists of butterflies together with semiquantitative abundance data. These data allow non-nested SARs to be constructed and support realis-

tic simulations of species extinction patterns. This makes it possible to predict future faunal composition after species loss and allows comparisons of pre and post extinction SAR patterns to be made. The aim of the present paper is to undertake such a comparison and to predict future species–area relationships.

## Materials and methods

Butterflies as treated in the Red Data Book of European butterflies (Swaay and Warren 1999) are all species of the families Hesperidae, Papilionidae, Pieridae, Lycaenidae, and Nymphalidae. Appendix D of the Red Book is a species  $\times$  country matrix that gives distribution classes for each European country and for some Mediterranean islands (Tables 1 and 2).

From these data species–area curves were constructed separately for Mediterranean countries and for countries north of the Alps and the Pyrenees and the eastern European countries (termed M- and NE-countries in the following text). Both regions constitute sufficiently separated faunistic provinces having a species overlap of only 160 species (28%). France and Bulgaria might both be classified as belonging to the NE- or to the M-country group. Their faunal lists and the SARs of M- and NE-countries do not clearly point to the correct position of both countries (see below). The present study places both countries into the NE-countries. However, when they were included into the M-country group computations did not produce patterns different from those reported below (data not shown). Tables 1 and 2 show the classification used in this study and provide condensed raw data for both country groups. The total butterfly fauna of Europe

Table 1. Mediterranean countries and their butterfly fauna. The distribution classes refer to the 4 distribution classes in the Red Data Book of European butterflies (Swaay and Warren 1999) and denote percent of area colonized.

| Country                | Distribution class |           |           |            | Sums       |
|------------------------|--------------------|-----------|-----------|------------|------------|
|                        | <1                 | <5        | 10–15     | >15        |            |
| Albania                | 7                  | 46        | 98        | 11         | 162        |
| Andorra                | 1                  | 6         | 34        | 79         | 120        |
| Azores                 | 4                  | 0         | 1         | 1          | 6          |
| Bosnia and Herzegovina | 30                 | 50        | 71        | 32         | 183        |
| Canary Islands         | 1                  | 7         | 13        | 5          | 26         |
| Cyprus                 | 4                  | 6         | 14        | 17         | 41         |
| Macedonia              | 44                 | 42        | 70        | 42         | 198        |
| Greece                 | 27                 | 57        | 54        | 87         | 225        |
| Croatia                | 39                 | 72        | 58        | 14         | 183        |
| Italy                  | 47                 | 92        | 55        | 56         | 250        |
| Malta                  | 0                  | 0         | 4         | 12         | 16         |
| Madeira                | 2                  | 4         | 3         | 2          | 11         |
| Portugal               | 18                 | 23        | 22        | 49         | 112        |
| Turkey Asian part      | 53                 | 96        | 90        | 93         | 332        |
| Turkey European part   | 40                 | 57        | 30        | 1          | 128        |
| Yugoslavia             | 46                 | 75        | 50        | 30         | 201        |
| Spain                  | 25                 | 29        | 28        | 124        | 206        |
| <b>Sums</b>            | <b>156</b>         | <b>28</b> | <b>23</b> | <b>133</b> | <b>524</b> |

Table 2. North and eastern European countries and their butterfly fauna. Distribution classes as in Table 1.

| Country                  | Distribution class |           |          |            | Sums       |
|--------------------------|--------------------|-----------|----------|------------|------------|
|                          | <1                 | <5        | 10–15    | >15        |            |
| Austria                  | 26                 | 47        | 57       | 57         | 187        |
| Belgium                  | 29                 | 17        | 28       | 29         | 103        |
| Bulgaria                 | 34                 | 51        | 65       | 46         | 196        |
| Belarus                  | 30                 | 38        | 46       | 4          | 118        |
| Switzerland              | 26                 | 74        | 58       | 37         | 195        |
| Czech Republic           | 25                 | 26        | 39       | 60         | 150        |
| Germany                  | 29                 | 35        | 38       | 46         | 148        |
| Denmark                  | 14                 | 1         | 14       | 40         | 69         |
| Estonia                  | 5                  | 14        | 15       | 64         | 98         |
| France                   | 49                 | 58        | 44       | 71         | 222        |
| Finland                  | 15                 | 22        | 7        | 57         | 101        |
| Great Britain            | 14                 | 8         | 11       | 27         | 60         |
| Hungary                  | 9                  | 30        | 33       | 85         | 157        |
| Ireland                  | 2                  | 5         | 8        | 14         | 29         |
| Latvia                   | 28                 | 18        | 19       | 44         | 109        |
| Lithuania                | 18                 | 15        | 23       | 55         | 111        |
| Liechtenstein            | 11                 | 28        | 55       | 12         | 106        |
| Luxemburg                | 25                 | 26        | 25       | 18         | 94         |
| Moldavia                 | 38                 | 18        | 10       | 14         | 80         |
| Norway                   | 2                  | 17        | 20       | 54         | 93         |
| Netherlands              | 26                 | 9         | 8        | 27         | 70         |
| Poland                   | 35                 | 33        | 33       | 48         | 149        |
| Romania                  | 34                 | 57        | 36       | 48         | 175        |
| Russia                   | –                  | –         | –        | –          | 225        |
| Russia northeastern part | 38                 | 45        | 39       | 39         | 161        |
| Russia southeastern part | 54                 | 69        | 27       | 45         | 195        |
| Sweden                   | 8                  | 18        | 17       | 64         | 107        |
| Slovakia                 | 29                 | 34        | 52       | 48         | 163        |
| Slovenia                 | 16                 | 53        | 43       | 53         | 165        |
| Ukraine                  | 56                 | 43        | 41       | 64         | 204        |
| <b>Sums</b>              | <b>114</b>         | <b>30</b> | <b>7</b> | <b>165</b> | <b>376</b> |

contains 576 species, 524 are found in the Mediterranean region and 376 in northern and eastern Europe.

The Red Data Book uses the IUCN criteria to estimate abundances of species per country according to four distribution classes: 1) distribution <1% of area under consideration, 2) distribution between 1 and 5% of area, 3) distribution of 5–15% of area, and 4) distribution >15% of area (Tables 1 and 2). To simulate extinction species occurrences were eliminated from the raw data matrix by a random process. Extinction probabilities were weighted by the distribution category. Species of distribution class two was given a 3 times lower probability to go extinct than those of category 1. Those in class 3 got a 10 times lower probability and class 4 species had a 15 times lower probability. At each step of the elimination process one species occurrence in one of the countries (country chosen at random) was eliminated according to the above given probabilities and the whole process was continued until in both country groups only 10% of the total fauna remained. Such a pattern is similar to the one that is expected in nature where rare species or species with restricted range sizes have higher probabilities to go locally extinct. The specific extinction probability values were chosen to reflect best the 4 distribution categories of the Red Data Book. Other

assumptions concerning extinction probabilities result of course in different SAR-parameter values during the extinction process. Various tests with other values, however, did not affect the general patterns reported below (data not shown).

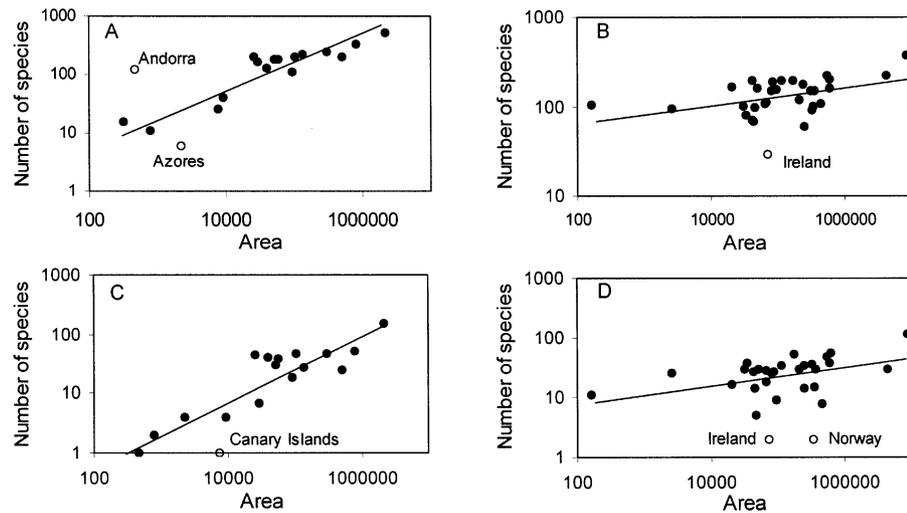
For statistical analysis the whole simulation process was replicated 50 times each for both country groups.

## Results

### General SAR patterns

The species–area relations of European butterflies are well described by the allometric model of the form  $S = S_0 A^z$  (Fig. 2). All fits of the power function model in Fig. 2 are significant at  $p(t) < 0.05$ . We also tested another often used alternative to the power function, the logarithmic model ( $S = z \ln(A) + S_0$ ). This model gave even better fits in the case of the NE-countries ( $R^2$  power function: 0.23,  $R^2$  logarithmic model: 0.29) but performed worse in the case of the M-countries ( $R^2$  power function: 0.82,  $R^2$  logarithmic model: 0.77). However, the logarithmic SAR model resulted always in highly negative estimates of the intercept  $S_0$ . The intercept value should give an estimate of the expected

Fig. 2. Species–area relationships of butterflies in Europe. A: all Mediterranean species. The regression function is  $S = 0.54A^{0.49}$ ;  $R^2 = 0.82$ ;  $p < 0.0001$ . B: all species of northern and eastern European countries:  $S = 42.5A^{0.10}$ ;  $R^2 = 0.23$ ;  $p = 0.01$ . C: endangered Mediterranean species only (species of distribution class 1):  $S = 0.4A^{0.56}$ ;  $R^2 = 0.76$ ;  $p < 0.0001$ . D: endangered species of northern and eastern European countries:  $S = 4.7A^{0.14}$ ;  $R^2 = 0.20$ ;  $p = 0.05$ . Note the different scale of the y-axis in B.



number of species per unit of measurement (the species density; in this case species numbers  $\text{km}^{-2}$ ). The smallest countries had in both country groups areas of ca 200–300  $\text{km}^2$  (Liechtenstein and Monaco). Negative intercepts of the logarithmic model indicate therefore that below these areas the model does not longer fit. Additionally, for both country groups the logarithmic model markedly underestimated species numbers of the largest countries (data not shown).

The power function model resulted for the NE-countries in an estimate of the species density of  $43 \pm 18$  species  $\text{km}^{-2}$  (mean  $\pm$  standard deviation) (Fig. 2). For the M-countries a much lower species density was predicted (ca  $1 \pm 1$  species  $\text{km}^{-2}$ ).

SAR slopes for the M- and for the NE-countries differ significantly (Fig. 2). The Mediterranean SAR has a slope of  $0.49 \pm 0.06$ . The SAR of the NE-countries has a slope of only  $0.10 \pm 0.04$  ( $p(t) < 0.0001$ ). The regression identifies three outliers of very high or very low species diversity. Andorra has a comparably high butterfly diversity, the Azores and Ireland seem to be depauperate. Because outliers might have an overproportional influence on parameters of least square regressions these three countries were omitted in the following analysis.

### Simulating species extinction

The simulated extinction process described above affected species–area relations of both country groups in a striking and opposite manner. For Mediterranean countries slope values continuously decreased during simulated species extinction (Fig. 3). The opposite pattern occurred in the case of northern and eastern European countries. There, slope values increased and peaked at ca 20% species remaining. At even lower species numbers when only the most abundant and

widespread species remained slope values sharply decreased during further extinction (Fig. 3C).

For both M- and NE-countries intercept values decreased during the extinction process. This theoretically expected result holds until ca 75% of all species were eliminated. At lower species numbers intercept values varied more irregularly. Such a pattern is expected if at low species numbers Poisson sampling errors and especially the exclusion of countries with zero counts influence species numbers overproportionally.

Species–area relations are frequently used to estimate species numbers after species extinction or habitat loss (May et al. 1995, Harte and Kinzig 1997). If  $S_E$  denotes the total species number in a region of  $A_E$ , the expected species number  $S_x$  of any part  $x$  of the region can be computed by solving

$$\frac{S_x}{S_E} = \left( \frac{x}{A_E} \right)^z \quad (2)$$

Fig. 4 compares for M- and NE-countries these estimates with the observed values after 75% of species had been eliminated. Both country groups differ strikingly. In the M-countries the simple use of species–area relations overestimates in most cases simulated species loss (Fig. 4A). For smaller countries or regions with  $< 10\,000 \text{ km}^2$  (like Monaco, Madeira, the Canary Islands or Cyprus) the SAR approach predicts a highly depauperate fauna where  $< 5\%$  of species remain. In reality, between 8 and 31% of species remained. But even for larger countries like Spain or Portugal the SAR approach gave highly inaccurate estimates about species loss. However, the opposite picture came up for the N-countries. There, the SAR approach always underestimated real (simulated) species loss irrespective of country size (Fig. 4B). Three countries (Liechtenstein,

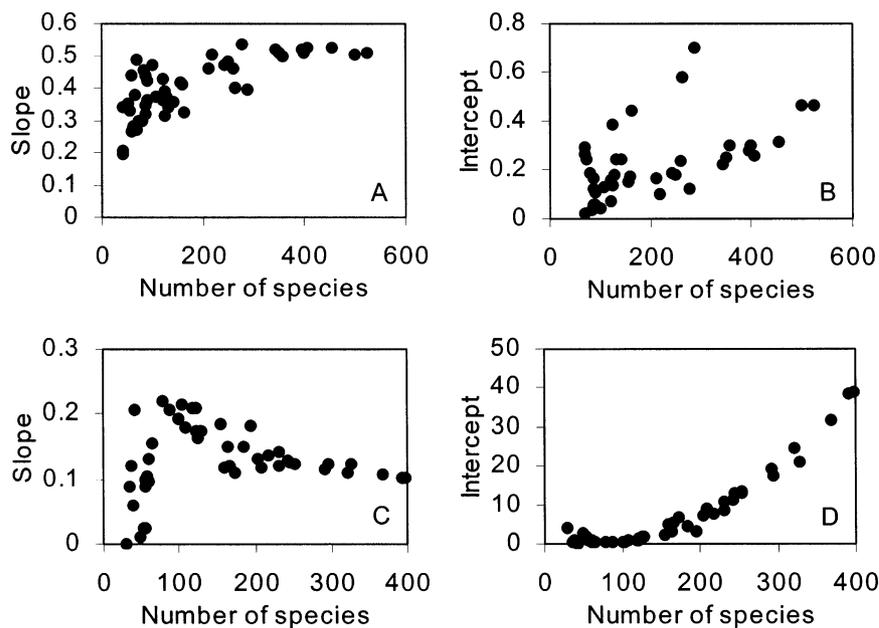


Fig. 3. Dependence of slope (A, C) and intercept (B, D) of butterfly SARs on species numbers during the simulated extinction process. A, B: Mediterranean countries; C, D: other European countries. Data points are means of 50 runs of the species extinction process as described in the materials and methods section. The right most data points are the initial values before the extinction process.

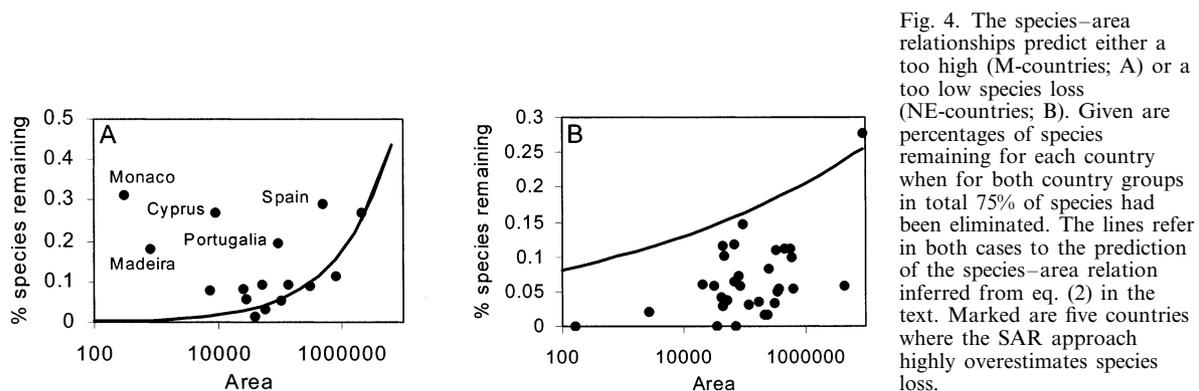


Fig. 4. The species–area relationships predict either a too high (M-countries; A) or a too low species loss (NE-countries; B). Given are percentages of species remaining for each country when for both country groups in total 75% of species had been eliminated. The lines refer in both cases to the prediction of the species–area relation inferred from eq. (2) in the text. Marked are five countries where the SAR approach highly overestimates species loss.

Moldavia, and Ireland) totally lost their butterfly fauna under simulated extinction, whereas the SAR predicted that ca 10–15% should remain. On average the SAR approach underestimated real species loss by a factor of 5.

Even if species losses differ from those that are expected from SARs the ranking of countries might remain the same. In other words species rich countries might remain relatively species rich and species poor relatively species poor. To test how the simulated species extinction process affects this relative species richness distribution of the countries at each step of species elimination we calculated Spearman's rank order correlations between initial and simulated species numbers (Fig. 5). For M-countries the ranking of countries remains constant until ca 60% of species had been eliminated. For NE-countries rank order began to change at a markedly earlier stage. Although all correlation coefficients remained significant at the 5% error level, Fig. 5 indicates that a species loss of > 75%

would also cause a marked reordering of countries in respect to their species diversity.

## Discussion

Butterfly species–area relationships of northern and southern European countries appeared to differ. Although both could be described by the power function model the slope value for the NE-countries is much lower than for the M-countries Wilcox et al. (1986) studied species–area relations for butterflies of the Great Basin and showed that SARs follow power functions with a slope of 0.15. Steffan-Dewenter and Tschardtke (2000) corroborated this finding in their study of German calcareous grasslands. The slope value for NE-countries reported here is therefore in accordance with those reported for other mainland butterfly communities. They are also in line with slopes found for other taxa (Rosenzweig 1995, Lomolino 2000).

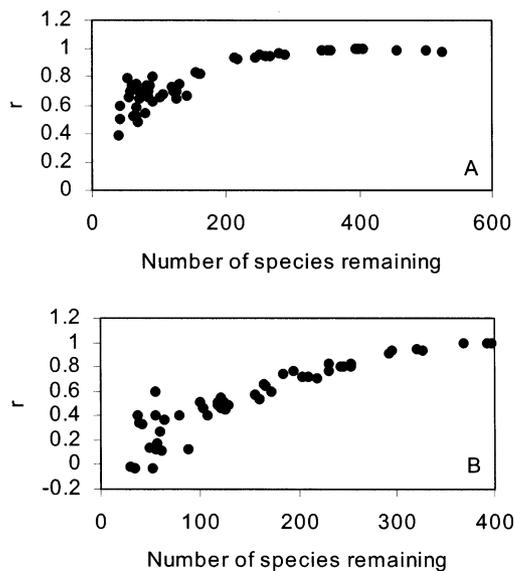


Fig. 5. The correlation coefficient (Spearman's rank correlation) between species number per country at each stage of the simulated extinction process and the original species number decreases during species elimination. This decrease is more pronounced for NE-countries (B). In Mediterranean countries (A) correlation coefficients  $r$  remained above 0.9 until 60% of species were eliminated. For NE countries the elimination of only 25% was enough to drop  $r < 90\%$ .

For islands Davies and Spencer Smith (1997) and Ricklefs and Lovette (1999) reported only slightly higher slopes of butterfly SARs (0.20–0.26). These values are lower than expected for typical islands (Rosenzweig 1995). Davies and Spencer Smith (1997) related these low slope values with the overall high ability of butterflies to disperse. Itamies (1983) found a much higher slope of 0.67 in his study of Lepidoptera on Baltic islands; however, this deviating result is best explained by the fact that his study islands represented series of successional stages with the larger islands being in a mid or late stage of succession (Itamies 1983, Steffan-Dewenter and Tschardt 2000). The Mediterranean SAR slope ( $z = 0.49$ ) reported in this study is therefore even steeper than those expected for typical islands.

The two country groups seem to differ in species density. For the NE-countries  $43 \pm 18$  species  $\text{km}^{-2}$  was predicted. For most countries only rough estimates of this value are available but it is likely that in the mean the power function SAR overestimates species density. For instance for Poland, where a detailed distribution atlas is available (Buszko and Kartanas 1998, Ulrich and Buszko 2003) the true value is  $< 10$  species  $\text{km}^{-2}$ . For the M-countries the SAR-based estimate of  $S_0$  of only  $1 \pm 1$  species  $\text{km}^{-2}$  is probably much too low with realistic values ranging around 5–10 species (Fig. 2). These contrasting results indicate that for smaller areas below  $100 \text{ km}^2$  a different SAR model

has to be constructed. For the NE-countries lower species numbers than predicted imply that SAR slopes (when fitted by an allometric model) are higher at scales below  $100 \text{ km}^2$ . Similar changes in SAR-patterns (but at lower scales) have recently been reported by Plotkin et al. (2000) and Ulrich and Buszko (2003). For the Mediterranean countries the occurrence of more species than predicted by the SAR indicates a pattern similar to the small island effect reported by Lomolino and Weiser (2001).

The way species extinction was simulated in this study is, of course, somewhat artificial. It treats all regions equally and assumes similar density dependent extinction probabilities irrespective of species numbers and (probably more important) possible changes of relative abundances. However, we are not able to follow real large-scale extinction processes in detail and have to rely on simulations to model future species loss and spatial patterns. The model used here is in fact very similar to the way SARs have been derived from patterns of species relative abundances (Sugihara 1980, Tokeshi 1993) or patterns of species spatial distributions (Harte et al. 1999, Harte 2000). Of course, more elaborate models for species extinction patterns would give more precise estimates of future species numbers, but it seems unlikely that they will change the main results of the present study with respect to the difference between northern and southern European countries and the inaccuracies of the classical SAR approach to biodiversity forecasting.

For Mediterranean countries our results indicate that species loss should affect both slope and intercept values of the SAR. Both are expected to decrease. But this decrease is not monotonic. Values fluctuate to a great deal during species elimination (Fig. 3A and B). Such a pattern makes it very difficult to attribute changes in SAR patterns found to any underlying change in community structure or to factors leading to species extinction. Additionally, the same species elimination process resulted in a totally different picture for the NE-countries. There, slope values initially increased.

Because the species extinction process was for both country groups the same in affecting the rare species of each country with higher probability the initial distribution of these rare species seems to be decisive. Tables 1 and 2 show that the fraction of rare species is nearly the same for both country groups (ca 30%) however the number of endemic species differed. In the M-countries 243 species (43%) were confined to only one country, in the NE-countries there were only 110 (29%) such species (Ulrich and Buszko unpubl.). The higher probability of eliminating these species in the M-countries resulted in decreasing slopes because regional species numbers were more affected than local ones. The whole process is therefore similar to the theoretical model one described in the introduction. In contrast the NE-countries have high numbers of widespread species and thus

elimination affected local species numbers more than regional. The effect was an initial rise in slope and a pattern similar to model two.

These contrasting results imply that changing patterns of species–area relationships cannot be unequivocally referred to a certain mechanism. Our simulation shows that the same process of species extinction can result in patterns similar to model one or model two. The outcome seems to depend on the initial distribution of relative abundances and range sizes. Observed changes in species–area relations therefore do not allow conclusions to be drawn about the processes that led to these changes.

A third major result that can be inferred from the present study is that a too simplified application of species–area relations might lead to highly inaccurate estimates about future species loss. SARs are one of the most often used tools for biodiversity forecasting (Lomolino 2000, Rosenzweig 2001) and have been applied to estimate bird and plant species loss (Pimm and Askins 1995, Harte and Kinzig 1997, Brooks et al. 1997, Pimm 1998). However, Pimm and Lawton (1998) pointed to situations where SARs might give wrong impressions about which areas to protect. Harte and Kinzig (1997) and Kinzig and Harte (2000) gave some examples where SARs overestimated species loss after habitat destruction and developed a slightly modified approach using only endemic species. Ney-Nifle and Mangel (2000) modelled changes in species–area relations in model landscapes and also found the SAR approach to be unreliable if no additional data on species range sizes or species spatial distributions were available. All of these critiques relied on model landscapes and theoretical species spatial distributions. The present approach is based on real distribution patterns of European butterfly species and simulated patterns of species loss. It appears that SARs are not able to predict future species loss at the local scale. Depending on the initial situation SARs either under- or overestimated true species loss.

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