Detecting biodiversity hotspots using species–area and endemics–area relationships: the case of butterflies

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Abstract. Using data of the Red Data Book of European Butterflies we establish the species–area relationship ($S = 8.5\ A^{0.23}$) and the endemics–area relationship ($S = 0.5\ A^{0.18}$) of European butterflies. Applying confidence limits as tools for the identification of hotspot countries we show that in the case of butterflies hotspots of endemism and hotspots of overall species richness do not coincide. We introduce plots of residuals from species–area relationships shifted upwards by the 95% confidence limits of the intercept (α-values) as a new tool for identifying and ranking of hotspots.

Introduction

The identification of ecological hotspots, regions with extraordinary high species diversities, has become an important task in conservation biology (Myers 1990; Olson and Dinerstein 1998; Myers et al. 2000; Kapos et al. 2001; Bonn et al. 2002). The majority of schemes to the identification of hotspots focused either on total species numbers or on numbers of endemic or threatened species (Smith and Theberge 1986; Myers et al. 2000). Additionally 'charismatic' or 'flagship' species, taxa like large cats, butterflies, parrots or hummingbirds, with high touristic or emotional value that might attract public attention were taken as surrogates for total diversity (Andelman and Fagan 2000, Williams et al. 2000). However, there is growing concern about the shortcomings of schemes that use endemic or threatened species as surrogates for total species diversity in the evaluation process of areas and for the identification of ecological hotspots (Prendergast et al. 1993, Andelman and Fagan 2000, Bonn et al. 2002).

A common tool for the identification of ecological hotspots is the use of species–area relationships (SARs) where species numbers are regressed against area. Areas that score high above the resulting regression line are then classified as being hotspots (Veech 2000; Hobohm 2003). However, a series of studies that focused on networks of areas for conservation pointed to the shortcom-

ings of this approach. The conservation of such defined hotspots does not necessarily conserve total species diversity best (Fagan and Kareiva 1997; Kerr 1997; Pimm and Lawton 1998; Reid 1998; Andelman and Fagan 2000). Using SARs of endemic species (so-called endemics–area relations, EARs) or SARs based on threatened species only does not seem to improve the outcome (Bonn et al. 2002).

Studies that focused on hotspot identification techniques relied largely on complementary analyses (Williams 2000) based on algorithms for the best choice problem (Church et al. 1996; Williams et al. 1997). These techniques to be of value demand good quality data sets of spatial distribution patterns. Such data are for most animal groups, in particular arthropods, still unavailable. But the number of studies that try to evaluate the applicability of SARs for the identification of ecological hotspots is also still limited (Rosenzweig 1995; Pimm and Lawton 1998; Veech 2000; Kier and Barthlott 2001; Hobohm 2003; Ulrich and Buszko 2003a). Veech (2000) studied the applicability of the SAR approach in detail and found the way of constructing them had a major influence on site choice. In particular, it is largely unknown to what extent networks of hotspots that were identified by SARs and EARs are able to preserve global or continental biodiversity.

Butterflies are an often used target taxon for conservation studies. The limited number of species and the availability of large quantitative data sets make them an ideal candidate for comparative studies and biodiversity forecasting efforts (Dennis 1993; Pullin 1995; Thomas et al. 2001; Ulrich and Buszko 2003a, b; Ulrich and Buszko 2004). For European butterflies the Red Data Book of European Butterflies (Swaay and Warren 1999) and the Distribution Atlas of European Butterflies (Kudrna 2002) laid the foundation for detailed analyses of species spatial distributions and the applicability of SARs in biodiversity forecasting and the identification of hotspots (Ulrich 2004; Ulrich and Buszko 2003a, 2004). The recently launched program for the identification of prime butterfly areas in Europe is based on it, but focuses on a restricted number of 34 target species (Swaay and Warren 2003). The program tries to identify prime areas for conservation on the basis of occurrences of threatened or endemic species, habitat directives by the Bern convention and limited distribution. These efforts need detailed knowledge about small scale patterns of species distributions and seem applicable to only a very limited number of arthropod taxa.

The present paper instead establishes the species–area relationships of the whole butterfly fauna as well as of threatened and of endemic species. On this basis we study the applicability of the SAR approach to the identification of prime areas for conservation and to the problem of how many species might be protected in a limited amount of area. It will be shown that SARs are indeed able to identify target areas and a new scheme for identifying target areas is presented.

Materials and methods

Butterflies as treated in the Red Data Book of European Butterflies (Swaay and Warren 1999) are all species of the families Hesperiidae, Papilionidae, Pieridae, Lycaenidae, and Nymphalidae. Appendix D of the Red Book is a species × country matrix that gives species numbers and distribution classes for each mentioned European country, region, and for some Mediterranean islands. It contains 575 species out of 47 countries, regions or islands (see Ulrich and Buszko 2003a for a comprehensive list of the countries).

From these data we constructed species–area curves for all species and for endangered and endemic species only. According to common practice we classified all species of the IUCN class 1 as being endangered. These are species, which occur on less than 1% of the area under consideration (countries or islands). We classified all species as being endemic if they occur only in one country, region or island listed in the Red Data Book (Ulrich and Buszko 2003a).

For constructing SARs we used the power function first proposed by Arrhenius

$$S = S_0 A^z \tag{1}$$

where S_0 denotes the expected species number per unit area (the intercept in a double log plot), S the number of species and A the area considered. z is the scaling exponent that ranges for most mainland SARs between 0.05 and 0.3 (Rosenzweig 1995; Lomolino 2000). For fitting of this model we used the linear regression module of STATISTICA 5 (Statsoft 1997) with ln-transformed species number and area data. Errors given in the text refer always to standard errors. We used double sided t-tests for comparing means of independent samples.

Recently Hobohm (2003) used residuals of SARs for a ranking of hot spots (called α-values by him). While this seems a sound method it gives no criterion when to except an area as an ecological hotspot. Most often the 95% confidence limits of the regression are used as a criterion to identify hotspots (Veech 2000). However, this criterion runs into problems at very large or very small areas due to the expanding of the confidence limits. Here we use the 95% confidence limits of the intercept value of the SAR for constructing boundaries to separate ordinary from extraordinary areas with respect to species richness (Figure 1). These boundaries are then defined as

$$\ln(S_{\text{upper}}) = \ln(S_0) + \text{CL}_{0.95} + z\ln(A) \tag{2}$$

and

$$\ln(S_{\text{lower}}) = \ln(S_0) - \text{CL}_{0.95} + z\ln(A) \tag{3}$$

where $\text{CL}_{0.95}$ denotes the 95% confidence limit of the ln-transformed intercept of the SAR.
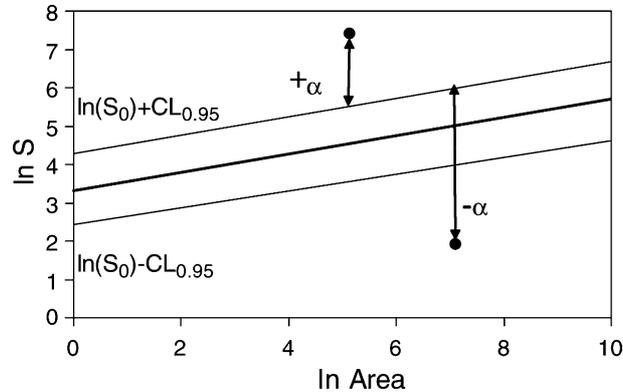
Figure 1. The vertical distance (positive or negative) of data points from the regression lines of species–area curves shifted upwards by the 95% confidence limit of the intercept (α-values) can serve as a metric to define ecological hotspots. α-values above zero indicate extraordinary species richness.

In this paper α-values refer to deviations from S_{upper} as shown in Figure 1. Then, positive values of α indicate ecological hotspots.

Results

The European butterfly SAR is well fitted by a power function of the form $S = (8.5 \pm 10)\ A^{0.23 \pm 0.04}$ (Figure 2a). Among the smaller countries the Principality Liechtenstein and Andorra have more species than expected from the SAR. Madeira, the Azores and Ireland appear to be comparably species poor. Despite the fact that the larger southern European countries and the Asian part of Turkey belong to the group of ecological hotspots defined by Myers et al. (2000) the SAR is unable to separate these countries from others. Portugal and Cyprus even range below the regression line. Apparently, they are less species rich in butterflies than expected from their classification as belonging to a hotspot region. Instead the SAR identifies in particular mountain countries like Andorra, Switzerland, Liechtenstein, Slovenia, Macedonia or Albania as being extraordinary diverse.

The SAR of endangered species only (Figure 2b) follows also a power function. The slope of this function ($z = 0.32 \pm 0.07$) is significantly ($p(t) < 0.01$) higher than that of the species number SAR. Numbers of endangered (S_E) and total species numbers (S) are highly correlated ($r = 0.76$, $p(t) < 0.01$). However, the proportion of endangered species (S_E/S) is independent of total species number S ($r = -0.09$; ns). This proportion was also independent of area ($r = 0.04$; ns) and of the number of endemic species ($r = 0.05$; ns). Hence, there is no trend towards higher proportions of endangered species in countries with higher numbers of endemics.
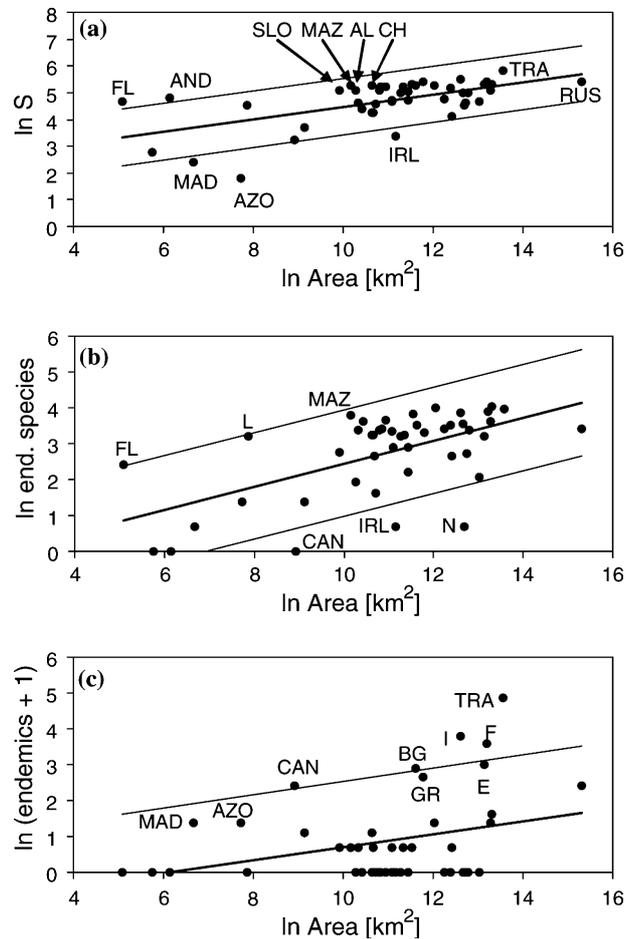
Figure 2. (a) The species–area relationship of European butterflies in a double log plot together with S_{upper} and S_{lower} regression lines. Regression: $S = (8.5 \pm 10)\ A^{0.23 \pm 0.04}$; $R^2 = 0.36$, $p(t) < 0.001$; (b) the species–area relationship of endangered European butterflies (species of the IUCN abundance class 1) in a double log plot together S_{upper} and S_{lower} boundaries. Regression: $S = (0.5 \pm 2)\ A^{0.32 \pm 0.07}$; $R^2 = 0.35$, $p(t) < 0.001$; (c) the endemics–area relationship of European butterflies in a double log plot together with S_{upper} and S_{lower} boundaries. Regression: $S = (0.5 \pm 2)\ A^{0.18 \pm 0.08}$; $R^2 = 0.10$, $p(t) = 0.03$. Countries and islands: Albania (AL), Andorra (AND), Madeira (MAD), Azores (AZO), Bulgaria (BG), Canary Islands (CAN), France (F), Greece (GR), Ireland (IRL), Italy (I), Luxemburg (L), Macedonia (MAZ), Norway (N), Principality Liechtenstein (FL), Slovenia (SLO), Spain (E), Switzerland (CH), Russia (RUS), Turkey Asian part (TRA). Note that the endemics are given as species number + 1.

Most often hotspots are defined in terms of endemic species (Myers et al. 2000). Figure 2c shows that the SAR approach clearly separates southern from northern and eastern European countries with respect to numbers of endemic species. The southern European countries Greece, Italy, and Spain, as well as

the islands Madeira, the Azores, and the Canary Islands range above the S_{upper} regression line. Additionally, the approach detects France, Bulgaria and the Asian part of Turkey as being exceptionally rich in endemic species. Many of the northern European countries instead lack any endemic species. Total numbers of species and numbers of endemics appeared to be correlated only at species numbers above 180 (Figure 3).

Figure 2 points therefore to two aspects of species richness, total species numbers and numbers of endemics. In the case of butterflies both numbers are only loosely correlated. Instead numbers of endangered species appeared to be highly correlated with total species number. Figure 4 shows a new way to visualize these findings for a better detection of the different aspects of species richness. Plots of α-values of endemics or endangered species against α-values of total species numbers and numbers of endangered species are able to define 3 groups of countries that might be potential targets for conservation. Classes I and II contain countries with high numbers of endemics or high total numbers of species only. Class III instead appears to be the most interesting group while being species rich and rich of endemics or endangered species. Interestingly, only the Principality Liechtenstein falls within this last group while it is species rich and rich in endangered species (Figure 2c). This result again emphasizes that overall species richness and richness in endemics are distinct concepts.

Are SARs able to point to target areas for conservation? To answer this question we plotted species numbers of those countries or country combinations that scored high in Figure 4 against area. This allows then a ranking of priority regions (Figure 5). The plot reveals some interesting patterns. Andorra and the Principality Liechtenstein together contain more than 1/3 of all European butterflies (208 species) on an area of only 0.005% (628 km^2). The small Atlantic islands (Canary Islands, Madeira, the Azores) and the three small mainland countries Andorra, Liechtenstein and Luxemburg together even contain 248 species (42% of European total) on only 0.12% of total area (13,755 km^2). These countries together with Greece contain 340
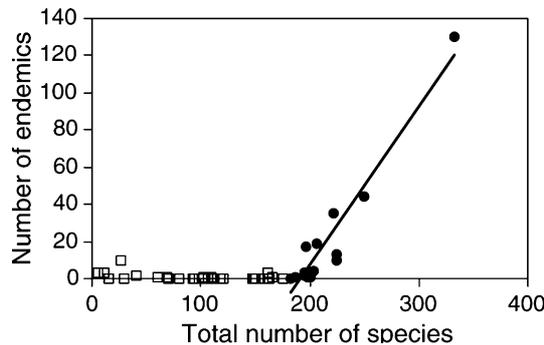
Figure 3. Total species numbers and number of endemics of European butterflies are correlated only at species numbers above 180. Regression line: $E = 0.89S - 172$; $R^2 = 0.91$.
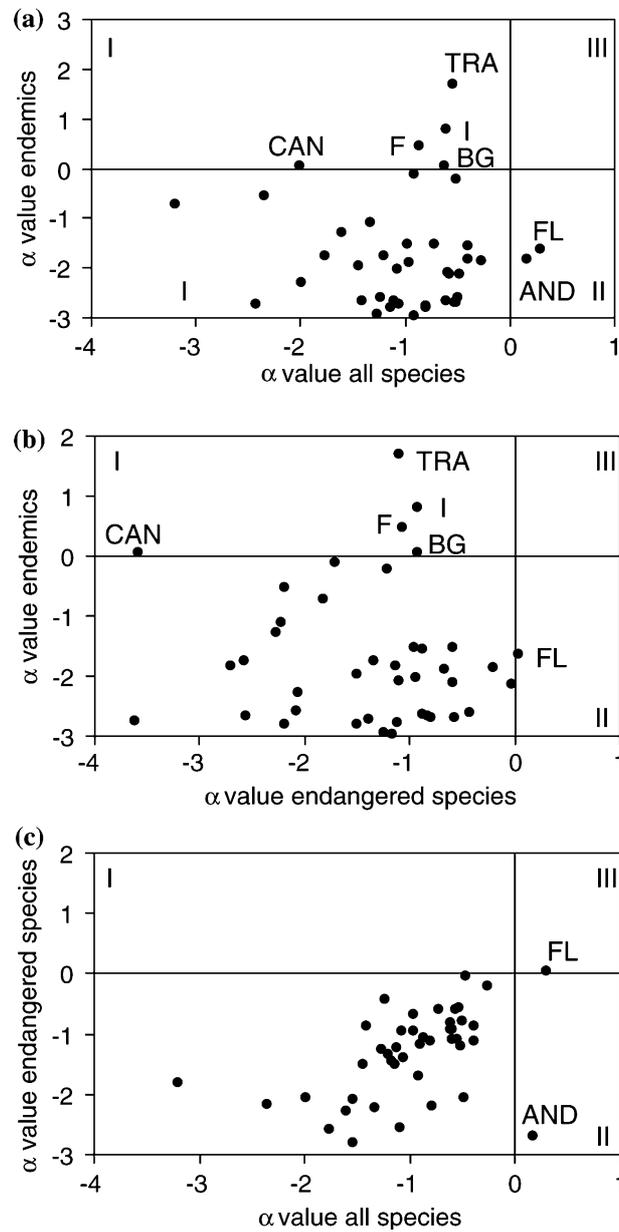
Figure 4. From plots of α-values of endemics against α-values of all species (a) and of endangered species (b) and plots α-values of endangered species against α-values of all species (c) it is possible to classify areas into three groups: a group with high numbers of endemics (I), a group with high total numbers or numbers of endangered species (II), and a group with high scores of both previous classes (III). Countries as in Figure 1. Only the Principality Liechtenstein belongs to group III with respect to the number of endangered species.
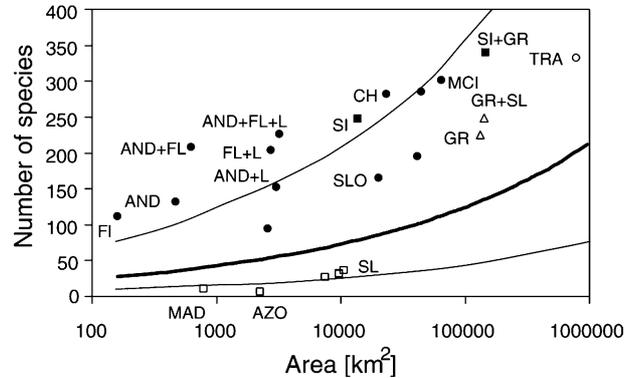
Figure 5. Numbers of species or endemics hotspots as defined in Figure 1 in comparison with the expectation of the species–area relationship of European butterflies (bold line; light lines are S_{upper} and S_{lower} boundaries). Black circles denote hotspots of species as derived from Figure 1A: Andorra (AND), Luxemburg (L), Principality Liechtenstein (FL), Slovenia (SLO), Switzerland (CH); MCI denotes three data points combining species numbers of AND, L, and FL with Slovenia or Switzerland or both. Open squares give islands that are endemics hotspots: Madeira (MAD) and the Azores (AZO). SL denotes combinations of MAD, AZO and the Canary Islands (CAN). Open triangles show Greece (GR) and Greece plus SL islands (GR + SL). The open circle gives the European part of Turkey (TRA). The black square AND + FL denotes Andorra and the Principality Liechtenstein combined. The black square SI denotes small islands and countries combined (AND + FL + L + Can + AZO + MAD). SI + GR denotes small islands and countries (SI) together with Greece.

species (57% of European total) on 1.3% of area (145,712 km^2). Other country combinations of similar area appeared to be much less effective in accumulating species. Of course, the Asian part of Turkey is very rich in endemic species. However, it should be noticed that many of these species are not endemic if we take the surrounding Asian countries into account. Compared to its area the total species numbers do not deviate significantly from expectation (Figure 5).

Discussion

The Mediterranean region and the Asian part of Turkey have several times been identified as being ecological hotspots (Médail and Quézel 1997; Mittermeier et al. 1997; Olson and Dinerstein 1997, 1998; Myers et al. 2000; Hobohm 2003). This classification was mainly based on the diversity of vascular plants. It was therefore a surprise to see that our species–area relationships did not clearly identify the Mediterranean countries in general as being exceptionally species rich. Even the Asian part of Turkey, that lies at the boundary of two hotspots, the Mediterranean and the Caucasian, appeared not to be particularly species rich (Figure 2). Instead, the EAR approach clearly

identified these countries and the whole Mediterranean basin as being rich in endemics.

A second surprising result is that the Atlantic and Mediterranean islands, although relatively rich in endemic species, appeared to have rather limited overall species diversity. Madeira, the Canary Islands, the Azores and to a lesser extent Cyprus and Malta proved to be less divers than expected from the SAR. This contrasts sharply with the work of Médail and Quézel (1999) and Myers and Cowling (1999) who classified these islands as hotspots for vascular plants. We expected therefore that butterflies as phytophagous insects follow the plant pattern. On the other hand these authors did not classify the Balkan region as being a plant hotspot whereas butterfly species numbers are relatively high (Figure 2).

One reason for our failure to identify the larger southern European countries as being hotspots might be our use of residuals from the SAR in a log space. Most previous approaches used absolute species numbers or numbers of endemics to identify hot spots. However, even a plot of SAR residuals against country area at a linear scale (Figure 6) does not unequivocally point to the Mediterranean countries as being hot spots. While Greece and Italy score high, species numbers of France and Spain do not deviate in particular from expectation and score similar to Hungary or the Czech Republic. Portugal, Cyprus and Malta even range below the regression. It seems that more important than geographic range is whether a country is predominantly mountainous or not and whether it is an island or a mainland.
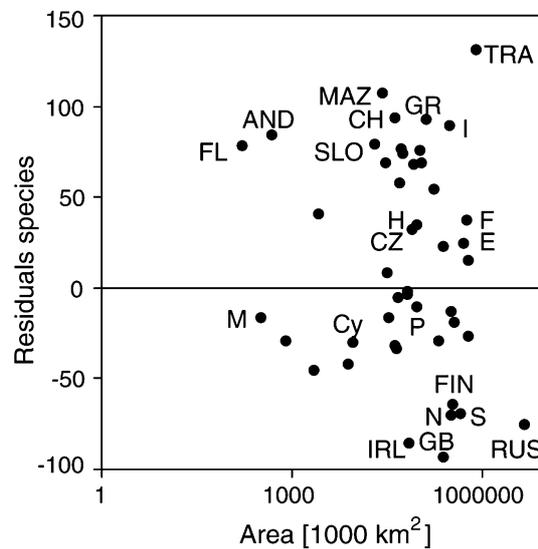
Figure 6. Residuals (total species numbers) from the SAR of European butterflies (regression line of Figure 2a). Countries: Czech Republic (CZ), Cyprus (Cy), Finland (FIN), Hungary (H), Great Britain (GB), Malta (M), Sweden (S); other countries as above.

Numbers of endangered species and total species richness appeared to be highly correlated. Both approaches identified the same countries as being species rich. It seems therefore that at least for butterflies the use of endangered species only might serve as an appropriate surrogate for total species richness. If this result holds for other groups it seems also that species diversity might be an appropriate surrogate for assessing numbers of threatened species.

On the other hand, total species richness and numbers of endemics appeared to be correlated only at high species numbers. As found in other studies (Prendergast et al. 1993; Bonn et al. 2002) centers of endemism and centers of species diversity did not coincide (Figures 2 and 4). Additionally, the use of endemism hotspots as a surrogate of overall diversity would only cover a small part of total butterfly species richness in Europe.

EARs are commonly believed to have much higher slopes than the underlying SARs (Harte and Kinzig 1997; Harte 2000; Kinzig and Harte 2000; Ulrich and Buszko 2003b). Based on the assumption of self-similar species spatial distributions Harte and Kinzig (1997) even argued that EAR slopes should always have values above 1. The EAR slope of $z = 0.18$ is even lower than the SAR slope of $z = 0.23$. If we leave out all countries without endemic species, the EAR is best fitted by a power function ($E = (0.28 \pm 0.85) A^{0.27 \pm 0.17}$; $R^2 = 0.16$; $p(t) = 0.03$). In the latter case SAR and EAR slopes do not significantly differ. Apparently butterflies do not fit into the predictions derived from self-similarity theory.

The present paper also shows that the use of residuals from S_{upper} regression lines of SARs as defined in Figure 1 (α-values) might be a method for the identification and for the ranking of ecological hotspots (Figure 4). It appeared that there are no European countries that are overall species diversity and at the same time endemism hotspots (no species of class III in Figure 4b). Hence, in butterflies both concepts have clearly to be separated. Conservation efforts have to consider this. It seems necessary to work out separate conservation priority schemes for total diversity and for the diversity of endemics. On the other hand, the high correlation between overall and threatened species diversity shows that conservation schemes focusing on total diversity might also be appropriate for threatened species.

The question of how much biodiversity can be preserved by a minimum amount of area is central to conservation biology. In the case of butterflies it was interesting to see that preserving only 0.005% of Europe (Andorra and the Principality Liechtenstein) is able to preserve more than 30% (208 species) of all European butterflies. Only about 1.5% of area would be necessary to preserve nearly 60% of total butterfly diversity while the SAR predicts at such an area only about 130 species (23%). It seems that the SAR approach used in this study is able to identify prime areas for conservation even without detailed small scale knowledge of species occurrence patterns.

However, we should also be aware of some pitfalls in the argumentation. The small populations in Andorra or Liechtenstein rely at least in part on the surrounding area. Regional butterfly populations frequently form distinct

metapopulations and local survival might depend on the viability of the whole metapopulation network (Hanski 1999). At least for some species the area necessary for survival might therefore be significantly larger than country area. Detailed studies in Andorra and Liechtenstein are necessary to establish more precisely the ability of both countries to preserve a significant part of the butterfly diversity in Europe.

Additionally, there is no unequivocally objective measure of ecological value. Here we use 95% confidence limits to separate hotspots from 'ordinary regions'. While this follows common practice the use of 90 or 67% limits would be as sound. However, practitioners and politicians need some fix criteria for planning and decision taking and in this context it seems appropriate to rely on a ranking of area and a predefined cut-off criterion. We hope that our criterion proves to be useful for other taxa too and helps to identify priority regions for biodiversity conservation.

Acknowledgments

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