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Grids versus regional species lists: are broad-scale patterns of species richness robust to the violation of constant grain size?

Petr Keil · Bradford A. Hawkins

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Abstract Where distribution maps do not exist ecologists often use regional species lists to examine geographic patterns of species richness, despite the fact that inconsistent grain sizes across areas may complicate interpretation of the results. We compare patterns of species richness of European butterflies and dragonflies using regional species lists (varying grain size) and regular grids (constant grain size). We asked if species lists give results comparable to the gridded data when used in simple macroecological analysis of environmental correlates of species richness. We generated two equal-area grids (220 × 220 km and 440 × 440 km) to map the richness gradients and model species richness as a function of actual evapotranspiration (AET) and range in elevation. Then we used species checklists of 33 administrative regions of unequal sizes to construct the same environmental models while accounting for differences in area. Analysis of butterfly checklist data produced comparable results to the analysis of gridded data. In contrast, dragonfly checklist data had a distorted spatial pattern and much weaker associations with environmental variables than the gridded data. The robustness of checklist data appears to be variable, even within a single geographical region, and may not generate patterns congruent with those found using equal-area grids.

Keywords Species richness · Species-area · Shape · Checklist · Grid · Europe · Evapotranspiration · Topography

Introduction

Studies of broad-scale biodiversity patterns are usually performed using gridded data with equal or nearly equal cell sizes, and it has been argued that holding the spatial resolution of

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P. Keil (✉)
Department of Ecology, Faculty of Science, Charles University, Vinicna 7,
12844 Praha 2, Czech Republic
e-mail: pkeil@seznam.cz

B. A. Hawkins
Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697, USA

the data constant is essential to avoid potentially misleading patterns and statistical models (the *assumption of constant grain size*; Whittaker et al. 2001). For example, the effect of varying area (Arrhenius 1921) and the effect of varying shape (Kunin 1997; Heegaard et al. 2007) can obscure the true pattern of species richness. Further, richness data are most often generated by overlying species range maps or by compiling geographically extensive survey data of individual records. Although there is discussion in the literature about the relative merits of map-based versus survey-based data (e.g. Hurlbert and White 2005; Hurlbert and Jetz 2007; Hawkins et al. 2008), reliance on either data source restricts the taxonomic scope of biodiversity studies to well known groups of organisms such as vertebrates, some vascular plants and a few invertebrate taxa (e.g. Hawkins et al. 2003a). But if the assumption that grain must be constant could be relaxed or if there was a reliable way to account for the effect of area, it would potentially increase the availability of richness data for many more organisms, especially for insect groups and tropical regions.

There is a strong tradition of generating regional or national checklists throughout the world, and they have been published for all major groups of plants and animals. Because they are easily maintained and updated, they also tend to be relatively accurate representations of the richness of target taxa within their geographic scope. Moreover, regional checklists are excellent for socioeconomic and historical analyses (Konvicka et al. 2006); whereas climatic and physical geography predictors are available for almost any unit we want to use, economic and historical predictors may be available for administrative units only. The problem with such species lists, however, is that their extent is determined by political or administrative criteria (sometimes by biogeographic boundaries), so they do not meet the constant grain size assumption of diversity analyses. This raises the possibility that variability of species richness arises as simple consequence of unequal areas covered by regional species lists. Despite this potentially serious issue, workers are beginning to use data sets based on regions with unequal areas in an effort both to identify the environmental factors driving diversity gradients and to guide conservation decisions (Barcena et al. 2004; Clarke and Funk 2005; Kier et al. 2005; Beck et al. 2006; Konvicka et al. 2006; Kalmar and Currie 2007; Feuerer and Hawksworth 2007; Baselga 2008; Hof et al. 2008; Keil et al. 2008b; Qian 2008). The common practice to account for the effect of unequal grain size is to use the area as covariate in regression models, either untransformed (Qian 2008), log-transformed (Kalmar and Currie 2007) or using more complex transformations (Keil et al. 2008b; Palmer et al. 2008). Given the rapidly increasing use of regional checklists to study diversity gradients, it is time to evaluate the validity of this approach.

In this paper we examine the possibility that violation of the constant grain size assumption does not greatly distort spatial richness patterns at the sub-continental extent. We compare species richness patterns generated for European butterflies and dragonflies using (i) gridded data based on species' range maps with two differently sized equal-area cells as base units and (ii) data based on national checklists with regions of variable sizes as base units. We also generate environmental models of richness using well-known environmental correlates of diversity to evaluate the robustness of the models to how the data are handled (constant vs. variable grain size). We are not focused here on comparing species richness gradients or environmental correlates of butterfly and dragonfly richness (see Hawkins and Porter 2003 and Keil et al. 2008a for detailed environmental models for each group). Rather, our goal is to test the reliability of the checklist data, separately for each of the two taxa. We selected these two insect groups in Europe to conduct for analysis because of their popularity amongst naturalists and hence reliability of both the distribution maps and the national checklists.

Materials and methods

The gridded data (constant grain size)

For both butterflies and dragonflies we used two spatial resolutions (Fig. 1). The 220 × 220 km grid system of Hawkins and Porter (2003) is hereafter referred as GRID220. This grain provides reasonably good detail and reliability within Europe, but it does not correspond to the spatial resolution of the data based on regional checklists (whose average region size is 160,000 km^2—equivalent to a 400 × 400 km grid). This could be a confounding problem since diversity patterns are frequently scale-dependent (Whittaker et al. 2001). Hence, we used the 220 × 220 km grid to generate a 440 × 440 km grid, hereafter referred as GRID440 (Fig. 1). Both grids were overlaid on range maps, and the presence of each species was recorded. The butterfly richness data were generated using the range maps for 372 species in Tolman (1997), and the dragonfly data were based on the 131 range maps in Dijkstra and Lewington (2006). For more detailed description of the data-generating procedure see Hawkins and Porter (2003); Keil et al. (2008a). For each grid cell we also generated data for annual actual evapotranspiration (AET; Ahn and Tateishi 1994), and the difference between the lowest and the highest altitude (range in elevation). AET has been shown to be strongly associated with the western Palearctic diversity gradients of both groups (Hawkins and Porter 2003; Keil

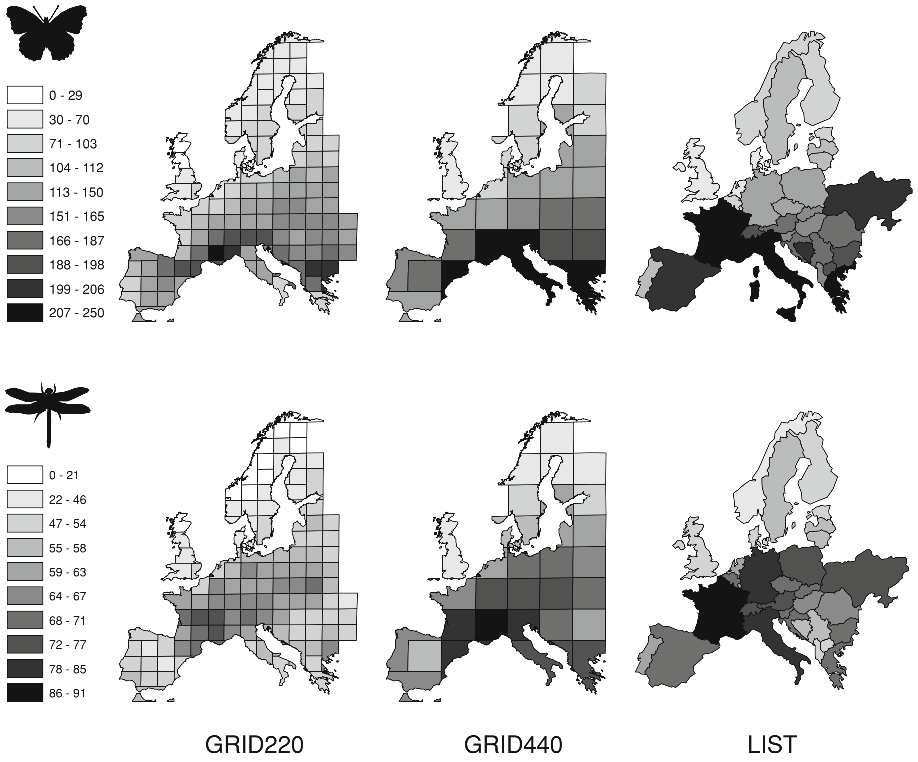

Fig. 1 Spatial patterns of dragonfly species richness in the 220 × 220 km grid (GRID220 data), 440 × 440 km grid (GRID440 data) and in the regional units (LIST data)

et al. 2008a). Range in elevation, a proxy for meso-scale climatic gradients up mountain sides, is also often associated with diversity patterns in mountainous areas (e.g. Rahbek and Graves 2001; Ruggiero and Hawkins 2008). Because of the strong right-skew of the distribution of elevation range we used its natural logarithm in all analyses, although non-transformed data gave similar results.

The regional data (varying grain size)

Hereafter we refer to the data generated using regional checklists as the LIST data. Species richness of butterflies in each European country was taken from Ulrich and Buszko (2003) whose primary source was the Red Data Book of European Butterflies (van Swaay and Warren 1999). These data were collated by 50 "national compilers" using published local distribution data as well as direct fieldwork of thousands of amateur lepidopterists (van Swaay and Warren 1999). Another possible source of checklist data would be the Fauna Europaea database, which we used for dragonflies. We prefer to use the Red Data Book data here because (i) they are more accurate (more local experts involved) and (ii) they have been recently used in other macroecological studies (Ulrich and Buszko 2003; Konvicka et al. 2006). Further, the results based on either of the data sources are nearly identical. The dragonfly LIST data are from the Fauna Europaea database (http://www.faunaeur.org) and were generated using national checklists combined with expert opinion (Fauna Europaea Odonata coordinator J. van Tol—personal communication). The few taxonomic discrepancies between the sources for the LIST data and the GRID data are provided in the Appendix.

To compare how these regional data sets differ from the range-derived gridded data we also created alternative "national checklists" based on range maps. For both butterflies and dragonflies we overlaid a political map of Europe on range maps of individual species (Tolman 1997; Dijkstra and Lewington 2006) and scored presence of each species in each country. We regressed the these richness values against the LIST data so that we could identify any potential bias caused by the source of the data.

We attempted to avoid using smaller or relatively remote islands in our study. Hence, the Republic of Ireland was excluded. In case of dragonflies, Corsica, Sardinia and Sicily were also excluded (Fauna Europaea reports species richness of Corsica, Sardinia and Sicily separately from that of the French and Italian mainland). This was not possible in case of butterflies—the Red Data Book reports species richness of France and Italy with the associated Mediterranean islands included. See Fig. 1 for the geographic extent of our study.

For each country in the LIST data we compiled the same environmental variables as for the GRID data and also included the area of each region [km^2]. The value of AET for each country was calculated as the arithmetic mean of all cells in the Ahn and Tateishi's (1994) grid that were lying in the country of interest. Range in elevation and region area were obtained from a world atlas.

Data analysis

In all analyses we used species richness as the response variable. We first mapped the data to evaluate visually the geographic patterns generated by each data set.

For the GRID220 and GRID440 data we also generated ordinary least squares (OLS) regression models using AET and ELEVRANG both as individual predictors and in combination. For the LIST data we included area as a third variable and we modeled species richness as function of all combinations of AET, ELEVRANG and area. To account for potential nonlinear effects of area (Arrhenius 1921) we used area (i) as a linear untransformed predictor, (ii) as its natural logarithm and (iii) square-root transformed. We then ranked all models within each data set according to their Akaike Information Criterion (AIC). Finally, we tested if the regression coefficients obtained from the GRID220 and GRID440 are significantly different from regression coefficients from the LIST data using Welch's *t*-test for unequal sample sizes and unequal variances.

An awareness of the potential analytical and inferential consequences of spatial dependence and spatial autocorrelation in ecological data has been developing in the past 15 years (Legendre 1993), including discussion of how spatial autocorrelation may influence interpretation of regression models (see e.g. Lennon 2000; Beale et al. 2007; Diniz-Filho et al. 2007). However, the environmental models based on our grid and similar grids have been found to explain the spatial structure in the data very well (Hawkins and Porter 2003; Hawkins et al. 2003b; Keil et al. 2008a), especially at the broad scale over which our regression models are constructed. Moreover, residual spatial autocorrelation does not bias structural relationships between richness and the environment (Diniz-Filho et al. 2007). Further, the spatial regression methods used to control residual spatial autocorrelation assume stationarity of slopes across the full spatial extent of data, but geographically weighted regressions identified significant non-stationarity ($P < 0.05$) in the richness-AET relationships in five of the six data sets (only the list data for Odonata were stationary), precluding the use of spatial modeling. It has also recently been shown that the regression coefficients arising from eight commonly used spatially explicit regression methods are essentially uninterpretable ecologically and offer no advantages over the results obtained using OLS (Bini et al. 2009).

Results

An average number of species per unit of observation (grid cell or country) in all data sets was roughly two times higher in butterflies than in dragonflies (Table 1). Regressions of the LIST data generated using national checklists against the data generated using range maps showed no systematic bias due to the different data sources either in terms of slope or intercept (Fig. 2). The relationships were linear with strong explanatory power showing that, relative to each other, none of the data sources systematically over- or under-estimated species richness.

The mapped richness patterns at both 220 and 440 km grain revealed a decrease in butterfly richness towards the north, with maximum richness found in cells covering the Pyrenees, Alps and southern Balkans (Fig. 1). The GRID dragonfly diversity patterns appeared similar to that found for butterflies, although the decrease in richness found in the

Table 1 Summary of values of species richness in the various data sets used in the study. SD is standard deviation

Dataset	Mean	Median	SD
Butterflies LIST	150.1	157	51.2
Butterflies GRID440	138.1	132.5	58.3
Butterflies GRID220	116	115	47.1
Dragonflies LIST	62.7	64	11.9
Dragonflies GRID440	59.6	64	18.3
Dragonflies GRID220	49.9	54	15.8

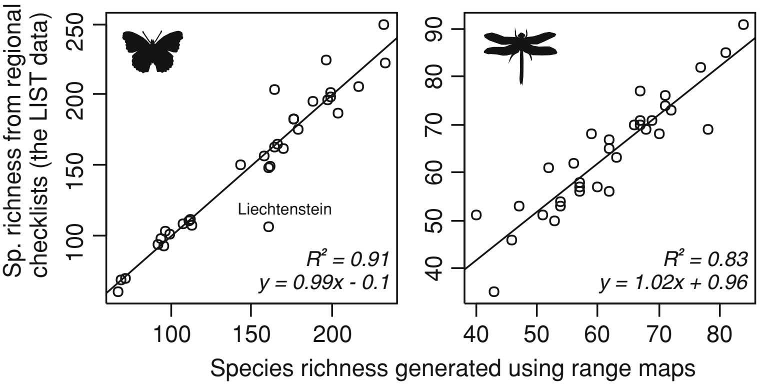

Fig. 2 Comparison of species richness data generated using checklist data and/or expert opinion (the LISTS data) and data generated using range maps in Tolman (1997; butterflies) and Dijkstra and Lewington (2006; dragonflies). Dots represent individual European countries

southern peninsulas was slightly stronger (Fig. 1). However, much of this gradient was lost in the mapped LIST data, and the richness patterns appeared substantially more erratic, except for lower richness in the British Isles and parts of Scandinavia (Fig. 1).

The best regression models (according to AIC) based on the GRID220 and GRID440 were very similar for butterflies and dragonflies (Tables 2, 3)—species richness was best modeled using both AET and ELEVRANG, and these models had very high coefficients of determination (Tables 1, 2). When AET and ELEVRANG were tested separately AET explained substantially more variance than ELEVRANG, indicating that AET (or water-energy balance) is a stronger correlate of species richness than the elevation range across the full geographic extent of the data. In the case of dragonflies the single-term ELEVRANG model had minimal explanatory power (Table 2).

The species richness of butterflies based on the LIST data was best modeled by a combination of AET, ELEVRANG and an area term. The variance explained was similar as in the GRID models (Table 2). Interestingly, the model containing only area had no explanatory power (Table 2) showing that the species-area relationship in butterflies is obscured by the environmental gradient across Europe.

Attempts to model the LIST species richness of dragonflies resulted in models explaining much less variation than models based on the GRID data ($R^2 = 0.47$ in the best LIST models versus $R^2 = 0.83$ in the best GRID440 model (Table 3). Similar to the GRID models it was not possible to discern if the AET-Area or the AET-ELEVRANG-Area model is better.

Although the explanatory power of AET and ELEVRANG in the LIST based models for dragonflies was very poor (Table 3), none of the regression coefficients obtained from the GRID440 models differed significantly from the regression coefficients obtained from the LIST models in either butterflies and dragonflies ($P > 0.1$; Welch's *t*-test). When comparing the GRID220 models with LIST models, we also found no significant differences in regression coefficients. The only exception was ELEVRANG, which had significantly higher coefficients in LIST models than in the GRID220 models ($P < 0.001$; Welch's *t*-test). Models with area included in square-root or logarithmic scales performed similarly, and clearly better than models with a linear area term in all analyses (Tables 1, 2). However, although including area improved the statistical power of the LIST regression models, particularly for dragonflies, the improved fits have no ecological explanatory

Table 2 Regression models of species richness (S) of European butterflies from grid-based (GRID220 and GRID440) and regional checklist-based data (LIST)

Variables in the model	Model formula	AIC	R^2
(a) Butterflies GRID220			
AET, ELEVRANG	$S = 0.33\mathrm{AET} + 9.5\mathrm{ELEVRANG} - 90.7$	702.5	0.78
AET	$S = 0.36\mathrm{AET} - 39.2$	718	0.75
ELEVRANG	$S = 21.5\mathrm{ELEVRANG} - 28.5$	845.4	0.22
None (Null model)	–	871	0
(b) Butterflies GRID440	–		
AET, ELEVRANG	$S = 0.4\mathrm{AET} + 17.3\mathrm{ELEVRANG} - 154$	200.3	0.86
AET	$S = 0.47\mathrm{AET} - 56.9$	210	0.81
ELEVRANG	$S = 39.7\mathrm{ELEVRANG} - 144.1$	248	0.37
None (Null model)	–	261.2	0
(c) Butterflies LIST	–		
ln(Area), AET, ELEVRANG	$S = 9.8\ln(\mathrm{Area}) + 0.37\mathrm{AET} + 20\mathrm{ELEVRANG} - 281.2$	210.4	0.81
Sqrt(Area), AET, ELEVRANG	$S = 0.08\mathrm{sqrt}(\mathrm{Area}) + 0.42\mathrm{AET} + 15.3\mathrm{ELEVRANG} - 186.4$	210.6	0.82
Linear area, AET, ELEVRANG	$S = 0.0001\mathrm{Area} + 0.4\mathrm{AET} + 19.3\mathrm{ELEVRANG} - 0.02$	212.4	0.80
Sqrt(Area), AET	$S = 0.13\mathrm{sqrt}(\mathrm{Area}) + 0.52\mathrm{AET} - 131.1$	214.8	0.77
Linear area, AET	$S = 0.0001\mathrm{Area} + 0.5\mathrm{AET} - 0.014$	217.6	0.76
AET, ELEVRANG	$S = 0.3\mathrm{AET} + 28.1\mathrm{ELEVRANG} - 196$	220.3	0.74
ln(Area), AET	$S = 14.2\ln(\mathrm{Area}) + 0.5\mathrm{AET} - 232.8$	220.8	0.73
AET	$S = 0.44\mathrm{AET} - 50.3$	236.9	0.54
ELEVRANG	$S = 41.1\mathrm{ELEVRANG} - 153.7$	237.4	0.53
ln(Area), ELEVRANG	$S = 2.8\ln(\mathrm{Area}) + 39.7\mathrm{ELEVRANG} - 175.6$	238.8	0.54
Linear area, ELEVRANG	$S = 0.00001\mathrm{Area} + 41.5\mathrm{ELEVRANG} - 156$	239.3	0.53
Sqrt(Area), ELEVRANG	$S = 41.4\mathrm{ELEVRANG} - 0.0009\mathrm{sqrt}(\mathrm{Area}) - 155$	239.4	0.53
Best area	$S = 120.2 + 0.07\mathrm{sqrt}(\mathrm{Area})$	260.2	0.07
None (Null model)	–	260.7	0

Akaike Information Criterion (AIC) and coefficients of determination (R^2) are provided for comparing models. Models are ordered according to AIC. The term ELEVRANG represents ln(range in elevation). The Null model is a model that contains no explanatory variable and no variability in species richness is explained ($R^2 = 0$)

power, as the differences in area are artifacts of human political history rather than ecologically meaningful differences in the size of the base units.

Discussion

Our results suggest that there is no clear answer to the question of the reliability of checklists to generate species richness data at broad extents. For butterflies we find that the strong statistical links between richness and climate are mostly maintained. We note that the explanatory power of the LIST regression models is only slightly lower than those generated from the GRID440 data with a similar average area. It could be argued that the checklist data generate patterns and models sufficiently robust that they could be used if butterfly distribution maps did not exist.

Table 3 Regression models of species richness (S) of European dragonflies from grid-based (GRID220 and GRID440) and regional checklist-based data (LIST). Presentation as in Table 2

Variables in the model	Model formula	AIC	R^2
(a) Dragonflies GRID220			
AET, ELEVRANG	$S = 19.6 + 0.12\text{AET} - 3.5\text{ELEVRANG}$	488	0.71
AET	$S = 0.6 + 0.115\text{AET}$	502.3	0.67
None (Null model)	–	624.8	0
ELEVRANG	$S = 42.9 + 1.03\text{ELEVRANG}$	626.3	0.004
(b) Dragonflies GRID440			
AET, ELEVRANG	$S = 9.8 + 0.16\text{AET} - 2.47\text{ELEVRANG}$	128	0.83
AET	$S = 0.15\text{AET} - 3.9$	128.4	0.82
ELEVRANG	$S = 18.4 + 6\text{ELEVRANG}$	180	0.09
None (Null model)	–	181	0
(c) Dragonflies LIST			
ln(Area), AET	$S = 4.2\ln(\text{Area}) + 0.07\text{AET} - 15.3$	148.1	0.46
ln(Area), AET, ELEVRANG	$S = 4\ln(\text{Area}) + 0.06\text{AET} + 0.78\text{ELEVRANG} - 17.2$	150	0.47
Sqrt(Area), AET	$S = 18.6 + 0.03\text{sqrt}(\text{Area}) + 0.07\text{AET}$	150.8	0.42
Linear area, AET	$S = 0.25 + 0.0004\text{Area} + 0.07\text{AET}$	152.7	0.38
Sqrt(Area), AET, ELEVRANG	$S = 21 + 0.03\text{sqrt}(\text{Area}) + 0.08\text{AET} - 0.65\text{ELEVRANG}$	152.7	0.42
Linear area, AET, ELEVRANG	$S = 0.25 + 0.0004\text{Area} + 0.07\text{AET} + 2.9\text{ELEVRANG}$	154.7	0.38
ln(Area), ELEVRANG	$S = 1.12 + 2.8\ln(\text{Area}) + 4.1\text{ELEVRANG}$	156.2	0.31
Best area	$S = 24.7 + 3.5\ln(\text{Area})$	158.5	0.22
Sqrt(Area), ELEVRANG	$S = 27.1 + 0.02\text{sqrt}(\text{Area}) + 4.2\text{ELEVRANG}$	159.6	0.24
Linear area, ELEVRANG	$S = 0.3 + 0.0002\text{Area} + 4.4\text{ELEVRANG}$	160.2	0.23
AET, ELEVRANG	$S = 17.9 + 0.03\text{AET} + 4\text{ELEVRANG}$	160	0.23
ELEVRANG	$S = 22.7 + 5.6\text{ELEVRANG}$	160.1	0.18
AET	$S = 39.1 + 0.05\text{AET}$	161.2	0.15
None (Null model)	–	164.7	0

This is not the case for dragonflies. First, even by visual inspection (Fig. 1) the species richness pattern is distorted when using the checklists. Second, Hawkins et al. (2003a) found that climate-richness regressions on average explain 60–70% of the variance in richness across a wide range of plant and animal groups, which means the amount of dragonfly richness explained by AET in the gridded data is typical, and dragonflies conform to the view that contemporary climate exerts a powerful influence on diversity patterns (Keil et al. 2008a). On the other hand, if we had only checklist data available for analysis, we would conclude that dragonfly richness is only weakly associated with AET and that we do not know what really influences their species richness distribution. This would be an error, especially if we were interested in evaluating potential effects of climate change on European dragonflies.

It is somewhat surprising that the butterfly and dragonfly results differ so strongly, since both have very similar underlying diversity patterns (Hawkins and Porter 2003; Keil et al. 2008a). The inconsistency of the results is probably not due to the analytical protocols, as both groups were handled identically. Moreover, we have shown here that makes little difference whether range maps or national checklists are used to generate the LIST data.

We can further discount the issue of scale sensitivity of the richness patterns. Although we expected (and found) some differences in the regression models between the GRID220 and GRID440 data, the average areas in the GRID440 data and the LIST data were similar. And even after controlling for this difference in average grain by comparing directly the LIST and GRID440 data, the LIST dragonfly data performed poorly. Having discounted the issues of data handling, analytical protocols and spatial scale, three possible reasons for the inconsistency in the dragonfly results remain. First, dragonfly species richness per country is usually half that of butterflies (Table 1) and the incorrect addition or omission of few species from lists can distort resulting patterns more severely in dragonflies than in butterflies. Second, both area and shape vary in the LIST data. It was shown that elongated areas capture more species than areas of regular shape (Kunin 1997), and that complexity of a perimeter influences species richness within an area (Heegaard et al. 2007). Regressing out area is not enough in cases when the shape matters (it obviously did not matter that much for butterflies). Finally, even though dragonflies are one of the most popular insect groups, and Europe is one of the best surveyed continents, there may still be lack of distributional data from regions with less tradition in natural history, in particular the Balkans. We excluded Bosnia and Herzegovina, Serbia, Montenegro, Albania and Macedonia from the analyses and the R^2 of the best model [ln(Area), AET, ELEVRANG] indeed increased to 0.54 which is, however, still low. Unfortunately, with only two data sets at our disposal it is not possible to explore analytically specific characteristics of the data that might account for the inconsistency of our results.

One might note that even though the models based on the dragonfly LIST data performed poorly in terms of explained variance, the regression coefficients were not significantly different. One could conclude that we have found the same relationship although the uncertainty with LIST data is higher. This may be true for strong relationships like the species-energy correlation. However, more subtle relationships can be missed with regional checklist data since levels of uncertainty are substantially higher. We are also unable to evaluate the possibility that the analyses of checklist data might be more robust over larger geographical extents. The spatial extent of our analysis is fairly small, and the environmental gradients within Europe are narrow compared to the global gradients in climate and elevation. It is possible, and even likely, that differences between gridded and checklist data might be much weaker at the global extent, since the 'noise' in the richness data caused by binning at multiple grain sizes will be relatively minor compared to the variability in richness generated by the very strong environmental gradients captured when comparing countries ranging from the poles to the equator. Future studies can evaluate the spatial extent at which we can be reasonably certain that using checklists does not distort the patterns themselves or their statistical evaluations. Until then, workers should be wary of using checklists uncritically and should carefully take into account the limitations of checklists when using them. At the continental scale at least it is currently impossible to judge the extent that the results of analyses based on checklists can be trusted. This is unfortunate, since it restricts the taxa that can be studied to those for which distribution maps exist. But the warning of Whittaker et al. (2001) should not be ignored; the constant grain assumption can be important in some cases, even if we cannot currently predict when.

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Appendix

Mismatches between the sources for the GRID data and the LIST data

Butterfly species complexes represented by one map in Tolman (1997) but which are two or more species in van Swaay and Warren (1999): *Spialia sertorius* (Hoffmannsegg), *Pyrgus carlinae* (Rambur), *Meleageria coridon* (Poda), *Agrodiaetus dolus* (Hübner), *Plebeius pylaon* (Fischer von Waldheim), *Aricia agestis* (Denis & Schiffermüller), *Lasiommata megera* (Linnaeus). Butterfly species complexes represented as one species in van Swaay and Warren (1999) but which have two maps in Tolman (1997): *Pontia daplidice* (Linnaeus). Butterfly species listed only in van Swaay and Warren (1999): *Pyrgus bellieri* (Oberthür), *Agrodiaetus fulgens* (De Sagarra), *Neolycaena rhymnus* (Eversmann), *Clossiana selenis* (Eversmann), *Triphysa phyrne* (Pallas), *Melanargia pherusa* (Boisduval), *Tomares callimachus* (Eversmann).

The set of dragonfly species that were treated in Dijkstra and Lewington (2006) (the source for the GRID data) was identical to the set of species in Fauna Europaea (the source for the LIST data) except for *Pyrrhosoma elisabethe* (Schmidt) and *Cordulegaster picta* (Selys) that are absent in the Fauna Europaea database.

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