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BIODIVERSITY RESEARCH

Local species richness of Central European hoverflies (Diptera: Syrphidae): a lesson taught by local faunal lists

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ABSTRACT

Published quantitative descriptions of local species assemblages represent a rich and little explored source of information exploring macroecological patterns. We used this source of data to estimate determinants of syrphid species richness in Central Europe. We examined the influence of three census-related covariates and five environmental variables on the observed or standardized (by rarefaction) species richness of 163 local syrphid assemblages. We also compared a large data set collected by a single author with a compilation of various sources. The covariates had mostly significant effects: increasing sample size and increasing sampling effort caused an asymptotic increase in species richness. The most effective collecting technique was entomological net, followed by malaise and colour traps. After taking into account the influence of covariates, the effects of geographical environmental variables (altitude, latitude and longitude) were more important than the effects of habitat variables. Syrphid richness exhibited a hump-shaped response to altitude and a latitudinal peak in the central areas of Central Europe. Our approach illustrates the potential of literature data for studying large-scale variation among local species assemblages.

Keywords

Central Europe, diversity determinants, geography, local assemblages, macroecology, multiple regression, species richness.

INTRODUCTION

Researchers in macroecology depend on reliable information on species distribution across large areas. They typically work with such data sources as distribution atlases, recording databases and maps in identification guides (Blackburn & Gaston, 1998; Gaston & Blackburn, 1999). Despite the recent boom in large-scale biodiversity surveys, comprehensive data of sufficient quality remain scarce, arguably limiting our knowledge. In particular, they tend to be limited to a relatively few popular groups of organisms such as mammals, birds, butterflies and vascular plants (e.g. Jetz & Rahbek, 2002; Hawkins & Porter, 2003; Kotze *et al.*, 2003; Rugiero & Kitzberger, 2004; Thomas *et al.*, 2004). They are often biased towards large-scales. Distribution data on scales of hundreds to thousands of square kilometres are available from all continents (cf. Hawkins *et al.*, 2003; Mathias *et al.*, 2004), but only a few regions and groups possess such maps at tens to hundreds of square kilometres (e.g. Dennis & Hardy, 2001; Titeux *et al.*, 2004). Most importantly, distribution data rarely contain information on species abundance. Many crucial macroecological patterns, including the abundance–distribution relationship (Brown, 1995), would hardly have been discovered, had there not been independent studies of abundance patterns in local communities.

Published quantitative descriptions of local communities, however, represent rich and little explored sources of information. There are perhaps myriads of such descriptions, covering a broad array of taxa and conducted for diverse purposes, ranging from pest monitoring through biodiversity inventories to the pure curiosity of naturalists. Although explored in studies of local patterns since the early days of quantitative ecology (Preston, 1962a,b), few studies have collated this information to test macroscale hypotheses. Naturally, working with published faunal lists suffers with many difficulties. They are typically buried in inaccessible local literature, and are time-consuming to collate for large areas. Griffiths *et al.* (1999) pointed out that they suffer from unequal sampling efforts and vary in spatial scale among studies. Another potential bias emerges when comparing surveys using collecting techniques differing in effectiveness and selectivity (Southwood, 1978). However, these biases can be quantified, and it is possible to control for their effects statistically. Storch and Kotecky (1999) used published faunistic surveys to analyse the structure of bird communities in the Czech Republic, and to a limited extent, the same method was used by Sanders (2002) to

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examine ant species richness patterns in the western United States.

We believe that by overlooking published faunistic lists, ecologists discard valuable sources of data that might, at the very least, allow the testing of some ecological patterns in taxonomic groups not represented in more traditional sources.

Here, we apply the approach for exploring determinants of species richness for Central European hoverflies (Diptera: Syrphidae). Hoverflies are a suitable group for such a study because they are species rich, ecologically diverse (Sommaggio, 1999) and more popular among naturalists than any other Dipteran family. Despite their popularity, understanding their distribution and structure of local assemblages is much less advanced than, for example, in butterflies or birds.

We tested here the hypothesis which assumes that species diversity parallels variation in the physical environment (Wright *et al.*, 1993). Despite the limited capability of such studies to reveal the underlying ecological processes (Ricklefs, 2004), we believe that even looking for a pattern is valuable (Gaston & Blackburn, 1999), especially in less-studied groups of organisms.

We collated data from published faunal lists, and used them to explore the following diversity-environment patterns:

(1) Species richness should decrease with elevation, but the response may be hump-shaped, reaching highest values in middle altitudes (see review by Rahbek, 1995).

(2) Species richness should decrease towards high latitudes (Pianka, 1966; Brown, 1995; Rozenzweig, 1995; Gaston & Blackburn, 2000; Hillebrand, 2004).

(3) Species richness should vary across different types of biotopes, and it should be possible to discern species-poor biotopes from species-rich ones (Bankowska, 1980; Humphrey *et al.*, 1999).

(4) Different collecting methods should vary in their efficiency of measuring insect diversity (Southwood, 1978; Buffington & Redak, 1998; Standen, 2000; Kitching *et al.*, 2004). It should therefore be possible to discern effective and less effective methods.

We examine these patterns on the level of the local species richness, *sensu* Srivastava (1999) (i.e. that richness is measured on a scale small enough that all the species could encounter each other within ecological time, and so possibly interact).

METHODS

The data

We gathered over 100 faunistic papers from the region of Central Europe, surveying particular localities for syrphid fauna. From this pool, we selected only those studies reporting abundance for every species found during the survey and providing a description of the habitat, census technique and sampling effort. This reduced the scope of papers suitable for the analyses, but allowed using the species-abundance distributions and numbers of individuals as measures of the sampling effort. We ended up with 163 syrphid assemblages in 33 published faunistic papers (Cepelak, 1967; Cepelak *et al.*, 1967; Claussen, 1982; Chemini *et al.*, 1983; Barkemeyer, 1984; Stollar, 1984, 1995, 1997; Dirlbek, 1986; Malec, 1986; Cepelak & Cepelak, 1987; Kralikova, 1987, 1993, 2002; DeCleer, 1990; Löhr, 1991, 1995; Pellmann & Koja Nahnall, 1991; Rozkosny & Vanhara, 1992, 1993; Leopold & Cölln, 1994; Kralikova & Degma, 1995; Kula & Scholz, 1995; Stuke, 1995; Borcherding, 1996; Precht *et al.*, 1996; Kula & Laska, 1997; Mazanek & Bicik, 1997; Hondelmann, 1998; Ssymank, 2000, 2002a,b; Reddersen & Jensen, 2002), dealing altogether with 121,722 identified individuals of 341 species (Fig. 1 and Appendix S1 in Supplementary Material). The word 'assemblage' is hereinafter used for data originating from one particular locality.

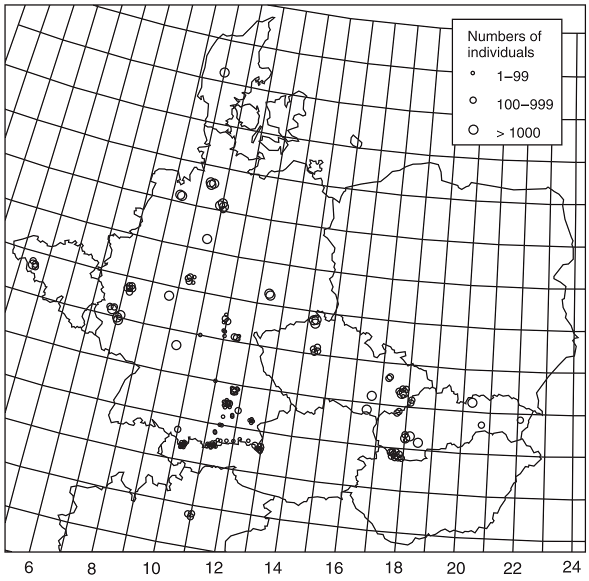

Figure 1 Locations of all local syrphid assemblages used for analysis of determinants of species richness of Syrphidae in the region of Central Europe (LAMBERT'S CONFORMAL CONIC PROJECTION). See Appendix S1 in Supplementary Material for detailed description of every assemblage.

Table 1 lists the explanatory variables characterizing each assemblage. Data from the same locality sampled for more than one year were merged (the abundances were summed), assuming that main patterns are more or less preserved from year to year (Gilbert & Owen, 1990). The nomenclature followed Ssymank *et al.* (1999).

To check for robustness of the emerging patterns, we followed three lines of evidence:

(1) Complete analysis of 163 assemblages. The response variable was untransformed species richness, as reported in source papers.

(2) Restriction of analyses by excluding weakly sampled assemblages. We included only assemblages containing > 100 individuals (84 assemblages) and analysed them both as raw data (herein *Restricted analysis*) with untransformed species richness as the response variable, and as rarefied data (*Rarefaction analysis*). Rarefaction allows standardization and comparison of data sets gathered with unequal sampling efforts (Krebs, 1989; Gotelli & Colwell, 2001). We estimated a theoretical number of species of each assemblage if it consisted of 100 individuals and used it as the response variable. We understand that rarefaction should not be used for collections obtained by different methods (Krebs, 1989), but we attempted to control for collecting methods statistically (see succeeding discussions).

Table 1 Independent variables characterizing syrphid assemblages analysed for determinants of syrphid species richness. Variables: individuals, effort and humidity are treated as covariates in all analyses

Variable	Type	Description	Groups (for categorical variables)
Individuals	Continuous	Number of individuals collected	
Effort	Continuous	In hours*	
Method	Categorical	sampling method employed	Net– collected using sweeping net Malaise– collected by malaise trap Colour– colour-based traps (dishes, sticky traps) Combined– a combination > 2 methods
Humidity	Categorical	Wetness of collecting site	Dry– dry habitat (steppe, heathland, etc.) Meso– mesophilous habitat Wet– wetlands, streamsides, ponds Mixed– a combination of the above
Openness	Categorical	Openness of the collecting site	Open– open habitat (meadow, steppe) Semi-open– open mosaic of shrubs, trees Forest– forest Mixed– a combination of the above
Altitude	Continuous	Altitude of the locality	
Latitude	Continuous	Latitude of the locality	
Longitude	Continuous	Longitude of the locality	

*Hours per person/malaise trap/colour dishes multiplied by number of persons/traps/dishes.

(3) Comparison of results obtained by single author with broader compilation. We build on the fact that 85 out of 163 surveys were performed by single author (Ssymank, 2002a,b), using the identical method (entomological net). We compared untransformed species richness in these data (*Ssymank analysis*) with the rest of data (*Ssymank excluded analysis*).

Table 2 The best multiple regression model for the *complete analysis* explaining the variability in raw species richness of Central European Syrphidae. The model was constructed by iterative additions and deletions of environmental variables in covariate models (see Methods for more details). It explained 91.7% of total deviance (variation in species richness)

Complete analysis	Effect	d.f.	AIC	*P*
Null model		162	3661.87	
Individuals§	↑	1	927.28	****
Method	†	3	773.47	****
Effort§	↑	1	619.93	****
Altitude‡	↑↓	2	517.87	****
Latitude‡	↑↓	2	449.5	****
Longitude‡	↓↑	2	429.17	**
Effort§ × individuals§		1	355.6	****

†Colour < combined < malaise < net.
‡Dependent variable entered as second-degree polynomial.
§Dependent variable entered as natural (ln) logarithm.
F-test for significance of model terms: ****$P < 0.00001$, ***$P < 0.0001$, **$P < 0.001$, *$P < 0.01$.

Regression analyses

We employed a regression approach to assess how environmental and census-related variables affect the detected species richness: generalized linear models (GLM) assumed a Poisson distribution of the response variable (log-link), computed in S-PLUS 2000 (1999, cf. Chambers & Hastie, 1991). For selecting among alternative models, we combined traditional significance testing with the information-theory approach using the Akaike Information Criterion (AIC) that selects models that attain a good fit to data while penalizing complex models containing redundant terms.

To control for the effect of census technique procedures on the resulting species richness, we considered individuals, effort and method as covariates. We first assessed their separate effects, checking, in the case of individuals and effort, for the linearity of the relationship by constructing the regressions also as second-degree polynomials and natural logarithms. Next, for each analysis we constructed a multiple-regression model based on forward selection of covariates (the covariate model). We used successive exclusion of redundant terms via stepwise backward deletion, and checked model terms for first-order interactions.

We then computed single-term regressions of environmental variables: humidity, openness, altitude, latitude and longitude, and finally constructed the best multiple-regression models for each analysis (Tables 2, 3 & 4; Fig. 3), involving both covariates and explanatory variables, employing stepwise forward selection and deletion as described previously for the covariate model.

RESULTS

Complete analysis

In regressions of covariates (Appendix S2 in Supplementary Material), species richness increased with individuals and effort. It tended to approach asymptote near 10^3 individuals and 10^2 hours (Fig. 2). Regarding method, entomological net was

Table 3 The best multiple regression models for the *rarefaction analysis* (56.2% of deviance explained) and the *restricted analysis* (69.5% of deviance explained). Only assemblages with > 100 individuals were included. In the rarefaction analysis, the model explains the variability in species richness standardized by rarefaction. In the restricted analysis, the same scope of assemblages was used but the response variable was raw species richness. Both models were constructed by iterative additions and deletions of environmental variables in covariate models (see Methods for more details)

Rarefaction analysis	Effect	d.f.	AIC	*P*	Restricted analysis	Effect	d.f.	AIC	*P*
Null model		83	307.78		Null model		83	1140.88	
Method	†	3	276.92	**	Individuals¶	↑	3	698.26	****
Effort¶	↑	1	242.7	****	Method	‡	1	590.55	****
Individuals	↓	1	226.16	*	Altitude	↑	1	516.2	****
Altitude	↑	1	185.41	****	Latitude§	↑↓	2	470.93	**
Latitude§	↑↓	1	158.61	**	Longitude§	↑↓	2	435.32	**

†Colour < combined < malaise < net.

‡Combined < colour < malaise < net.

§Dependent variable entered as second-degree polynomial.

¶Dependent variable entered as natural (ln) logarithm.

F-test for significance of model terms: ****$P < 0.00001$, ***$P < 0.0001$, **$P < 0.001$, *$P < 0.01$.

Table 4 The best multiple regression models for the *Ssymank analysis* (72.8% of deviance explained) and the *Symank excluded analysis* (86.7% of deviance explained). Both models were constructed by iterative additions and deletions of environmental variables in covariate models (see Methods for more details)

Ssymank analysis	Effect	d.f.	AIC	*P*	Ssymank excluded analysis	Effect	d.f.	AIC	*P*
Null model		80	239.528		Null model		81	1104.539	
Individuals§	↑	1	75.436	****	Individuals§	↑	1	626.125	****
Effort	↑	1	69.307	*	Method	†	3	479.124	****
					Altitude	↑	1	388.821	****
					Longitude‡	↓↑	2	339.088	***

†Combined < colour < malaise < net.

‡Dependent variable entered as second-degree polynomial.

§Dependent variable entered as natural (ln) logarithm.

F-test for significance of model terms: ****$P < 0.00001$, ***$P < 0.0001$, **$P < 0.001$, *$P < 0.01$.

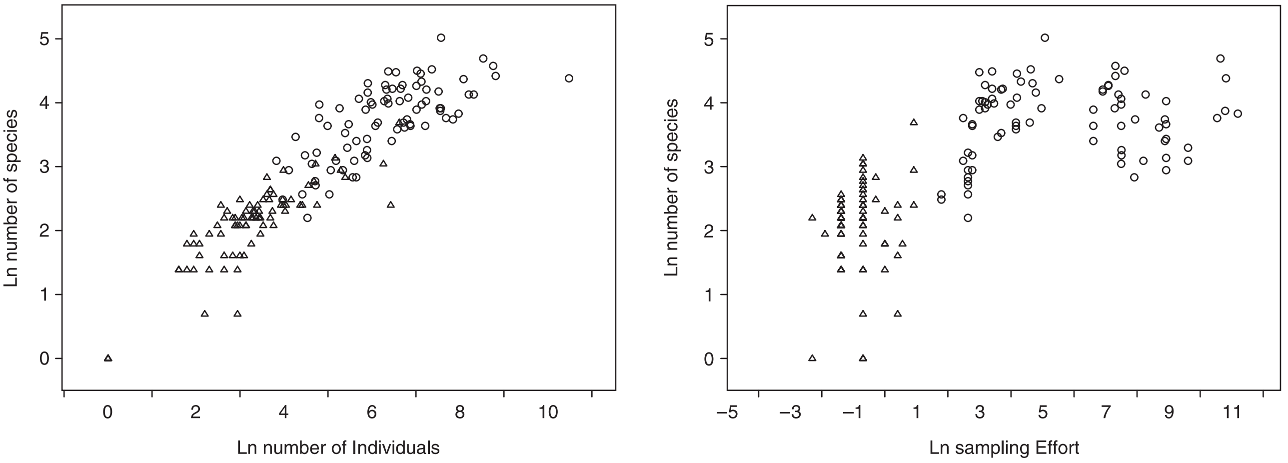

Figure 2 Patterns of detected syrphid species richness accumulation with increasing number of individuals and/or increasing sampling effort as collated from faunistic papers from the region of Central Europe. Triangles represent assemblages collated from Ssymank (Ssymank, 2002a,b). Circles represent the rest of assemblages.

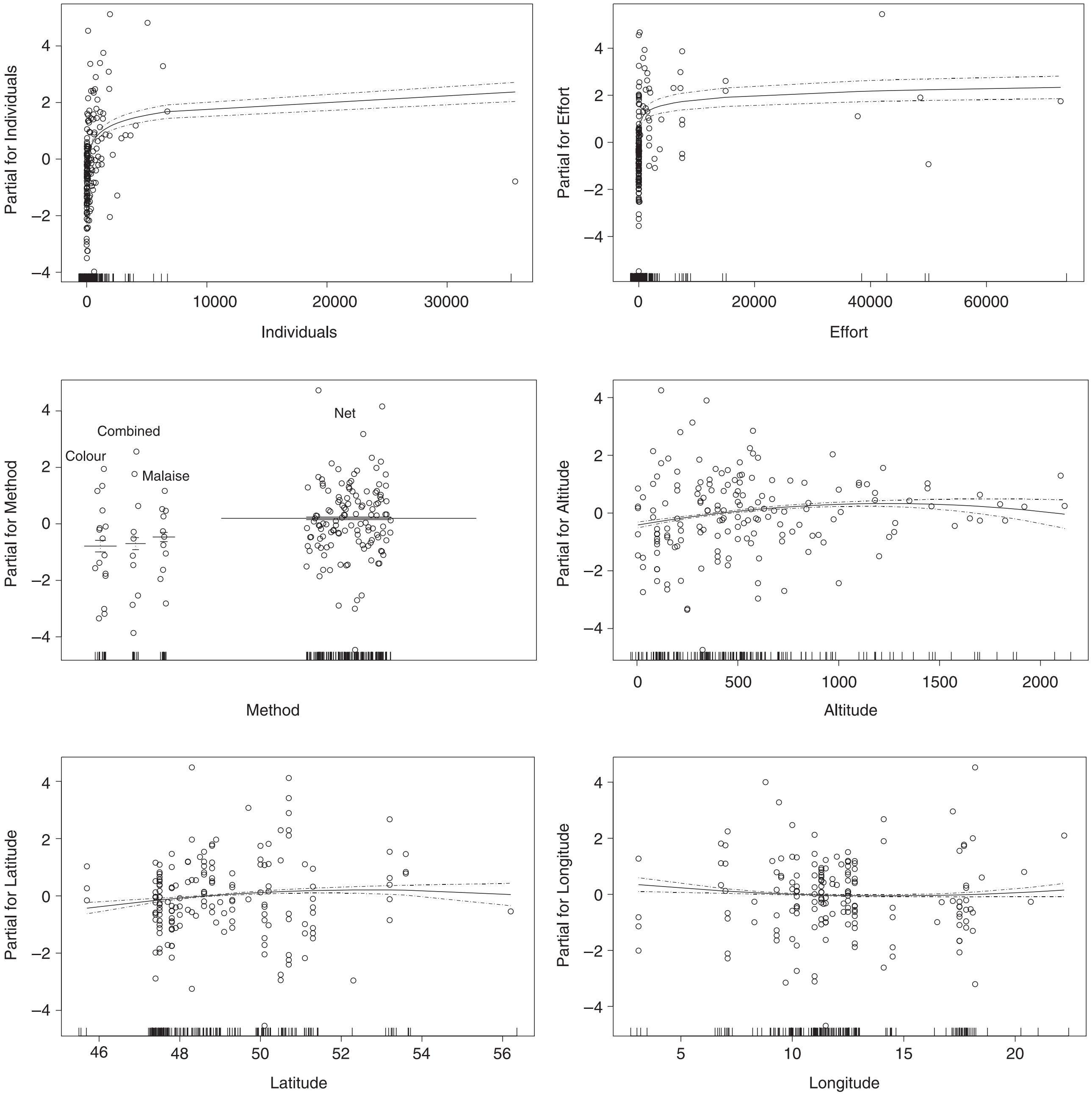

Figure 3 Example of a multiple-regression best model for determinants of species richness of local assemblages of Central European Syrphidae. Complete data set. The thick lines are partial effects of individual predictors on residuals (dots) fitted after including all other predictors to the model, the broken lines are standard errors.

the least efficient, whereas malaise traps and combined techniques were the most efficient. Covariate model included all the covariate terms, plus a non-additive interaction of individuals and effort. Here, the net was the most efficient method, followed by the malaise traps, combined techniques and colour traps.

Single-term regressions of environmental variables (Appendix S2 in Supplementary Material) revealed the effect of humidity (the highest richness in mixed habitats, followed by dry, mesophilous and wet habitats), whereas openness had no effect. Regarding geographical variables, richness decreased with altitude, and both longitude and latitude generated polynomial responses. In single-term additions into the covariate model, humidity lost its significant effect, the effect of altitude became hump-shaped, whereas latitude retained its convex polynomial effect.

The environmental predictors entering the best models were altitude, latitude and longitude (Fig. 3, Table 2). Altitude exhibited a hump-shaped polynomial response with richness peaking around 1000 m, latitude followed a hump-shaped polynomial with richness peaking around the 52nd parallel, and longitude followed a U-shaped polynomial with a minimum around the 13th meridian (Fig. 3).

Analyses excluding weakly sampled assemblages

Species richness increased with individuals in restricted analysis, but decreased in rarefaction analysis. Similarly, it increased with effort in restricted analysis, but followed a hump-shaped pattern in rarefied analysis (Appendix S2 in Supplementary Material). Ordinary net was most efficient method in both cases. In the covariate models, richness increased with individuals in restricted analysis, but decreased in the rarefaction analysis. Effort had a positive effect in the former, but no effect in the latter. For method, the high efficiency of ordinary net was retained in both covariate models.

In single term regressions of environmental variables (Appendix S2 in Supplementary Material), both analyses revealed that richness was highest in mixed humidity habitats. There was a hump-shaped response to latitude and a linear increase with altitude. The three effects were retained in single-term additions to the covariate model.

In the multiple regressions (Table 3), rarefaction analysis, altitude caused a linear increase of species richness, latitude caused a polynomial increase, whereas the contribution of longitude was not significant. In the restricted analysis, richness again linearly increased with altitude, whereas the response to latitude was fitted by a concave polynomial peaking around the 52nd parallel, and to longitude by a convex polynomial with a minimum around the 13th meridian.

Single author vs. compilation

In Ssymank analysis, only the covariates individuals and effort had significant (positive) effects on species richness in single term regressions (Appendix S2 in Supplementary Material) and in the best model. None of the environmental variables showed a significant effect when added in the covariate and the best models.

In *Ssymank-excluded analyses*, the only significant effect of covariate was increase of richness with individuals, and there was positive increase with altitude and a hump-shaped relationship to latitude. In multiple regression (Table 4), the effect of latitude was lost, a hump-shaped effect of longitude became significant, and altitude caused a linear increase of species richness, which contrasted with the hump-shaped pattern found in complete analysis.

DISCUSSION

Our approach illustrates the potential utility of using data from local faunal surveys for studying macroscale patterns in little-studied groups. It allowed a comparison of the efficiency of different data collecting methods, and pointed to some pitfalls in comparing data from secondary sources. Most importantly, controlling statistically for variation in study method unmasked several unexpected patterns of syrphid species richness.

Effects of collecting methods

Predictably, the highest proportion of total variability in syrphid species richness was explained by the sampling effort and the number of individuals. Responses of species richness to increasing collection size/effort were mostly asymptotic curves, as expected in thoroughly sampled assemblages (Figs 2 & 3) (Gotelli & Colwell, 2001). However, there was an exception in the rarefaction analysis, in which the number of species decreased with increasing sample size. As rarefaction suppresses the sample-size effect, increasing numbers of individuals should not have any influence. The inversion of the relationship was likely caused by one extremely large collection from a relatively species-poor assemblage (80 species, but 35,658 individuals, see Appendix S1 in Supplementary Material). After removing this assemblage from the data set, the number of individuals did not influence rarefied species richness.

Regarding the efficiency of collecting methods, the most interesting result was the consistently good performance of the entomological net. The likely reason is that experienced researchers search effectively for rare species, and hence detect relatively high proportions of species in short periods of time. The higher effectiveness of malaise traps compared to colour-based traps corroborates the findings of Kitching *et al.* (2004) who used these two methods in an extensive survey of many Dipteran families in a tropical forest. Malaise traps usually catch more individuals on an order of magnitude than colour traps, which results in a higher probability of detection of rare species (Kitching *et al.*, 2004). The relatively low efficiency of combined sampling might be caused by the small number of such studies ($N = 10$); just by chance they may have been carried out in species-poor habitats, and it is notable that four of them were assemblages from communal waste dumps (Dirlbek, 1986).

Single author vs. compilation

In quite uniformly executed surveys by Ssymank (Ssymank, 2002a,b), only census-related covariables but no environmental predictors affected species richness. This was understandable in the case of latitude, as Ssymank's data cover 3.2 latitudinal degrees in southern Bavaria, contrasting with 10.5 degrees in the complete analysis. Less expectably, the analysis of Ssymank's data did not reveal any effects of habitat and altitude. A likely explanation is that the majority of the collections were small (mean number of individuals = 59; maximum = 752) and based on low effort (mean effort = 0.55 h; maximum = 2.5), far below the asymptotic values for numbers of individuals and effort (Fig. 2). Also, the low effort did not likely cover seasonal variation in composition of the assemblages.

This is further supported by comparing *Ssymank excluded* and *complete* analyses. The two gave nearly identical results, which show that the patterns associated with habitat types and geography in the succeeding discussions were unmasked only after we included larger area and large collections. It would be ideal to build an inference on data collected by identical method, and by a single collector. For macroscale patterns, however, such data will hardly ever exist because of obvious constraints imposed by the need to cover large areas effectively.

Habitats and geography

Habitat type had only a marginal effect on species richness. In contrast, Bankowska (1980) described considerable differences in species richness among various habitats in Poland, and Humphrey *et al.* (1999) found lower richness in closed-canopy forests than in open-canopy forests. The weak effects in our study could be due to several reasons. First, our coarse habitat categories, adopted for the sake of statistical tractability, could have been too coarse to detect any pattern; they were certainly much coarser than the fine differences among forest stands analysed by Humphrey *et al.* (1999). Second, the authors of individual surveys may not be consistent in describing their collecting sites. This seems to be a serious pitfall of all analyses that use secondary sources, and we urge authors of future surveys to provide as detailed as possible descriptions of their sites, perhaps accompanied by photographs. Third, species *richness* may not vary among habitats, but differences can still be apparent at the level of community structure; for instance in the relative abundances of species belonging to different trophic guilds (Papp, 2002). Finally, it is still possible that within the region covered by the study, variation in species richness because of geography exceeds any habitat-associated variation.

The latter claim is supported by the fact that including altitude, latitude and longitude in the model suppressed any variation because of habitat type. This suggests that even within the relatively restricted region covered by this study, geographical position plays a major role in the determination of syrphid local species richness (MacArthur, 1972); a similar pattern was recently found for birds and butterflies in the Czech Republic (Storch *et al*., 2003). This starkly contradicts Willis and Whittaker (2002), who claimed that species diversity on the local level should be mainly influenced by local habitat structure.

The variable with the strongest effect was altitude. The response was hump-shaped in complete analysis, and linear for all analyses with restricted data. The difference was clearly the result of exclusion of many high altitude assemblages, mostly surveyed by Ssymank (2002a, 2002b), from the latter two analyses. The high altitude assemblages tended to contain few individuals (mean numbers 85 ± 81.3 SD above 1000 m, vs. 876 ± 1061.3 below 1000 m). As a result, the rarefaction, the restricted and the Ssymank excluded analyses spanned a shorter altitude gradient. The high richness of syrphids in mountains has already been noticed by Bankowska (1980) and Haslett (1997). Our results extend their conclusion for the whole of Central Europe. It hence seems that syrphid species richness does not follow the trivial linear decrease with altitude documented for considerable number of organisms (Rahbek, 1995).

Another unexpected result was the concave latitudinal pattern. It remained significant despite the inclusion of the altitude effect in the best models, revealing a slight increase of species richness, irrespective of altitude, near the 52nd parallel in Central Europe. One interpretation might be again the presence of species-poor Ssymank assemblages in the southern part of the studied region. Alternatively, the central latitudes may host a higher number of species as a result of the mixing of northern and southern biogeographical elements (Schmitt & Hewitt, 2003), already observed by classical biogeographers (e.g. Maran, 1953; De Lattin, 1967; Culek *et al*., 1996). To obtain better insight into the situation, however, our analysis should be extended for the whole of Europe.

An even more enigmatic relationship is the concave response of species richness to longitude. A similar (and similarly weak) pattern applies for butterflies, if analysed on the level of individual states (Konvicka *et al.* in review), whereas Hawkins *et al.* (2003) and Hawkins and Porter (2003) report an eastward increase of butterfly and bird richness within the study region, associated with increasing evapotranspiration. However, the longitudinal effect was weakest of the three geographical effects.

Conclusions and further directions

For large scales and well-known organisms, the patterns of regional richness are extractable from various accessible sources of information. However, in studies of the large-scale variation of species richness among local assemblages, and particularly in the case of less popular organisms, both descriptive biogeography and modern macroecology suffer from a major deficit of knowledge. Our study showed that using the faunistic literature could give us some of this much needed information. Nevertheless, it also showed that results of such collations may be sensitive to the particular selection of authors and studies. Some of our results, such as the rich syrphid fauna of mountain belt, have already been noted by traditional naturalists, and our approach allowed rigorous testing of its validity. On the other hand, such patterns as increased richness in central latitudes of Central Europe were unexpected, and elucidating them will require further exploration, perhaps by extending this approach to the whole of Europe. Similarly, analysis of less detailed faunistic papers, such as those reporting abundances only on an ordinate scale, might yield some further interesting insights, especially when compared with the more detailed ones.

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SUPPLEMENTARY MATERIAL

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/DDI/DDI172/DDI172sm.htm

Appendix S1 Overview of the data used
Appendix S2 Results of all single-term regressions

REFERENCES

Bankowska, R. (1980) Fly communities of the family Syrphidae in natural and anthropogenic habitats of Poland. *Memorabilia Zoologica*, **33**, 3–93.

Barkemeyer, W. (1984) Über die Syrphiden (Dipt., Syrphidae) in den Hochmoorresten der nordwestlichen Bundesrepublik Deutschland. *Zoologische Jahrbuch Systematik*, **111**, 43–67.

Blackburn, T.M. & Gaston, K.J. (1998) Some methodological issues in macroecology. *American Naturalist*, **151**, 65–83.

Borcherding, R. (1996) Zur Schwebfliegenfauna von Kleinschmalkalden (Thüringer Wald). *Abhandlungen und Berichte des Museums der Natur Gotha*, **19**, 121–132.

Brown, J. (1995) *Macroecology*. University of Chicago Press, Chicago, IL.

Buffington, M.L. & Redak, R.A. (1998) A comparison of vacuum sampling versus sweep-netting for arthropod biodiversity measurements in California coastal sage scrub. *Journal of Insect Conservation*, **2**, 99–106.

Cepelak, J. (1967) Prispevok k poznaniu sezonnej dynamiky pestric Zadielskej doliny (Syrphidae, Diptera). [Contribution to knowledge of the seasonal dynamics of syrphids in Zadielska dolina]. *Zbornik Vychodoslovenskeho Muzea*, **8**, 176–179.

Cepelak, J. & Cepelak, S. (1987) Ergebnisse der Forschung der höheren Zweiflüglern (Diptera, Brachycera) im Gebirge Biele Karpaty I. Velka Javorina. *Biologia*, **42**, 1011–1019.

Cepelak, J., Gunarova, V. & Slameckova, M. (1967) Prispevok k poznaniu niektorych skupin vyssich much. [Contribution to knowledge of some groups of higher flies]. *Acta Facultatia Rerum Naturalium Universitatia Comenianae — Zoologica*, **12**, 155–181.

Chambers, J. & Hastie, T. (1991) *Statistical models in S*. Chapman and Hall, London.

Chemini, C., Daccordi, M. & Mason, F. (1983) Ditteri Sirfidi raccolti due siti forestali presso Ala (Provincia di Trento). *Studi Trentini Di Scienze Naturali*, **60**, 125–135.

Claussen, C. (1982) Schwebfliegen aus der Haseldorfer Marsch W Hamburg nach Gelbschalenfängen (Diptera, Syrphidae). *Entomologische Mitteilungen aus dem Zoologischen Museum Hamburg*, **115**, 203–218.

Culek, M., Grulich, V. & Povolny, D. (eds) (1996) *Biogeograficke cleneni Ceske republiky* [*Biogeographic division of the Czech Republic*]. Enigma, Prague.

DeCleer, K. (1990) Faunistich-ecologische studie van de ongewervelde fauna in het natuurreservaat De Gulke Putten (West-Vlaanderen, Wingene). I. Zweefvliegen (Diptera: Syrphidae) en een bespreking van de malaiseval als bemonsteringtechniek. *Phegea*, **18**, 71–88.

De Lattin, G. (1967) *Grundriss der zoogeographie*. G. Fisher, Jena.

Dennis, R.L.H. & Hardy, P.B. (2001) Loss rates of butterfly species with urban development. A test of atlas data and sampling artefacts at a fine scale. *Biodiversity and Conservation*, **10**, 1831–1837.

Dirlbek, K. (1986) Dipterofauna prazskych skladek komunalniho odpadu. [Dipterous fauna of the Prague communal waste depositions]. *Casopis Narodniho Muzea — Rada Prirodovedna*, **155**, 160–173.

Gaston, K.J. & Blackburn, T.M. (1999) A critique for macroecology. *Oikos*, **84**, 353–368.

Gaston, K.J. & Blackburn, T.M. (2000) *Pattern and process in macroecology*. Blackwell Science, Oxford.

Gilbert, F. & Owen, J. (1990) Size, shape, competition, and community structure in hoverflies (Diptera: Syrphidae). *Journal of Animal Ecology*, **59**, 21–39.

Gotelli, N.J. & Colwell, R.K. (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters*, **4**, 379–391.

Griffiths, G.H., Eversham, B.C. & Roy, D.B. (1999) Integrating species and habitat data for nature conservation in Great Britain: data sources and methods. *Global Ecology and Biogeography*, **8**, 329–345.

Haslett, J.R. (1997) Insect communities and the spatial complexity of mountain habitats. *Global Ecology and Biogeography Letters*, **6**, 49–56.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guegan, J.F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105–3117.

Hawkins, B.A. & Porter, E.E. (2003) Water–energy balance and the geographic pattern of species richness of western Palearctic butterflies. *Ecological Entomology*, **28**, 678–686.

Hillebrand, H. (2004) On the generality of the latitudinal diversity gradient. *American Naturalist*, **163**, 193–211.

Hondelmann, P. (1998) Zur Schwebfliegen-fauna (Diptera, Syrphidae) von Agrarökosystemen am Beispiel der Lößbörden Südniedersachsens. *Drosera*, **98**, 113–122.

Humphrey, J.W., Hawes, C., Peace, A.J., Ferris-Kaan, R. & Jukes, M.R. (1999) Relationship between insect diversity and habitat characteristics in plantation forests. *Forest Ecology and Management*, **113**, 11–21.

Jetz, W. & Rahbek, C. (2002) Geographic range size and determinants of avian species richness. *Science*, **297**, 1548–1551.

Kitching, R.L., Bickel, D., Creagh, A.C., Hurley, K. & Symonds, C. (2004) The biodiversity of Diptera in Old World rain forest surveys: a comparative faunistic analysis. *Journal of Biogeography*, **31**, 1185–1200.

Kotze, D.J., Niemelä, J., O'Hara, R.B. & Turin, H. (2003) Testing abundance–range size relationships in European carabid beetles (Coleoptera, Carabidae). *Ecography*, **26**, 553–566.

Kralikova, A. (1987) Pestrice (Diptera, Syrphidae) studijnej plochy Dvorcany pri Nitre, so zvlastnym zretelom na afidofagne druhy. [Hoverflies (Diptera, Syrphidae) of the study site Dvorcany near Nitra, with special referrence to aphidophagous species]. *Rosalia (Nitra)*, **4**, 271–291.

Kralikova, A. (1993) Hoverflies (Diptera: Syrphidae) of the area of the danube water works construction site. *Biologia*, **48**, 541–548.

Kralikova, A. (2002) Hoverflies (Diptera, Syrphidae) in Javorina (Belianske Tatry Mts) and seasonal dynamics of some species. *Biologia*, **57**, 235–241.

Kralikova, A. & Degma, P. (1995) Faunistic-ecological analysis of hoverflies (Diptera: Syrphidae) in some landscape elements of the Danubian lowland with a special reference to the aphidophagous species. Part II. *Ekologia (Bratislava)*, **14**, 237–246.

Krebs, C.J. (1989) *Ecological methodology*. HarperCollinsPublishers, New York.

Kula, E. & Laska, P. (1997) Hoverflies (Diptera, Syrphidae) in forest stands of Decinsky Sneznik Hill. *Folia Facultatis Scientiarium Naturalium Universitatis Masarykiana Brunensis*, **95**, 97–103.

Kula, E. & Scholz, A. (1995) Hoverflies (Syrphidae, Diptera) of spruce forest in the polluted area. *Dipterologica Bohemoslovaca*, **7**, 111–118.

Leopold, J. & Cölln, K. (1994) Die Schwebfliegen (Syrphidae) der Streobstwiesen von Wehlen (Kreis Bernkastel-Wittlich). *Fauna Flora Rheinland-Pfalz*, **7**, 637–671.

Löhr, P.-W. (1991) Schwebfliegen (Diptera, Syrphidae) der Großgemeinde Mücke im Vorderen Vogelsberg. *Beitrage Zur Naturkunde in Osthessen Naturkde*, **27**, 103–110.

Löhr, P.W. (1995) Syrphiden (Diptera, Syrphidae) aus einem Naturgarten im Veorderen Vogelsberg (Hessen) nach Farbschalen- und Malaisefallen. *Volucella*, **6**, 195–222.

MacArthur, R.H. (1972) *Geographical ecology: patterns in the distribution of species*. Harper & Row, New York.

Malec, F. (1986) Auffällige Grossinsekten als Indikator-Arten für nordhessische Halbtrockenrasen. *Naturschutz in Nordhessen*, **9**, 73–91.

Maran, J. (1953) *Puvod a slozeni fauny Ceskoslovenska*. [*The origin and composition of Czechoslovakian fauna*]. Orbis, Prague.

Mathias, P.V.C., Mendonça, C.V., Rangel, T.F.L.V.B. & Diniz-Filho, J.A.F. (2004) Sensitivity of macroecological patterns of South American parrots to differences in data sources. *Global Ecology and Biogeography*, **13**, 193–198.

Mazanek, L. & Bicik, V. (1997) Syrphids (Diptera, Syrphidae) of Litovelske Pomoravi and the Vsetinske vrchy Hills. (ed. by J. Vanhara and R. Rozkosny) *Dipterologica bohemoslovaca*. Vol. 8. Folia Facultatis Scientiarium Naturalium Universitatis Masarykiana Brunensis, *Biologia*, **95**, 115–128.

Papp, L. (2002) Dipterous guilds of small-sized feeding sources in forest of Hungary. *Acta Zoologica Academiae Scientarum Hungarica*, **48**, 197–213.

Pellmann, H. & Koja Nahnall, M. (1991) Untersuchungen zur Fauna der Syrphidae (Diptera) im Botanischen Garten der Universität Leipzig. *Entomologische Nachrichten und Berichte*, **35**, 181–187.

Pianka, E.R. (1966) Latitudinal gradients in species diversity: a review of concepts. *American Naturalist*, **100**, 33–46.

Precht, A., Cölln, K. & Jacobi, J. (1996) Zum Standortbezug von Malaise-Fallen Eine Unterschung am Beispiel der Schwebfliegen (Diptera: Syrphidae). *Fauna Flora Rheinland-Pfalz*, **8**, 449–508.

Preston, F.W. (1962a) The canonical distribution of commonness and rarity. *Ecology*, **43**, 185–215.

Preston, F.W. (1962b) The canonical distribution of commonness and rarity. *Ecology*, **43**, 410–432.

Rahbek, C. (1995) The elevational gradient of species richness: a uniform pattern? *Ecography*, **18**, 200–205.

Reddersen, J. & Jensen, T.S. (2002) The Syrphidae, Coccinelidae, and Neuroptera (s. lat.) of a large Danish spruce forest. *Entomologiske Meddelelser*, **70**, 113–127.

Ricklefs, R.E. (2004) A comprehensive framework for global patterns in biodiversity. *Ecology Letters*, **7**, 1–15.

Rozenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge.

Rozkosny, R. & Vanhara, J. (1992) Diptera Brachycera of forest steppe near Brno (Hady Hill). *Acta Scientiarum Naturalium Academiae Scientiarum Bohemicae Brno*, **27**, 1–76.

Rozkosny, R. & Vanhara, J. (1993) Diptera (Brachycera) of the agricultural landscape in southern Moravia. *Acta Scientiarum Naturalium Academiae Scientiarum Bohemicae Brno*, **26**, 1–64.

Rugiero, A. & Kitzberger, T. (2004) Environmental correlates of mammal species richness in South America: effects of spatial structure, taxonomy and geographic range. *Ecography*, **27**, 401–416.

Sanders, N.J. (2002) Elevation gradients in ant species richness: area, geometry and Rapoport's rule. *Ecography*, **25**, 25–32.

Schmitt, T. & Hewitt, G. (2003) The genetic pattern of population threat and loss: a case study of butterflies. *Molecular Ecology*, **13**, 21–31.

Sommaggio, D. (1999) Syrphidae: can they be used as environmental bioindicators? *Agriculture, Ecosystems and Environment*, **74**, 343–356.

Southwood, T.R.E. (1978) *Ecological methods*, 2nd edn. Chapman & Hall, New York.

Srivastava, D.S. (1999) Using local-regional richness plots to test for species saturation: pitfalls and potentials. *Journal of Animal Ecology*, **68**, 1–16.

Ssymank, A. (2000) Steobst- und Intensivobstbestände: Vegetation, Blühphänologie und Syrphidendiversität (Diptera, Syrphidae) im Drachenfelser Ländchen. *Decheniana (Bonn)*, **153**, 109–128.

Ssymank, A. (2002a) Vom Karwendel bis zur Donau — Dipterologische Notizen und Biologie der Schwebfliegen (Diptera, Syrphidae) in Bayern Teil II. *Volucella*, **6**, 175–193.

Ssymank, A. (2002b) Beiträge zur Faunistik und Biologie der Schwebfliegen in Bayern (I) (Diptera, Syrphidae). *Entomofauna*, **23**, 125–144.

Ssymank, A., Doczkal, D., Barkemeyer, W., Claussen, C., Löhr, P.-W. & Scholz, A. (1999) Syrphidae. *Checkliste der dipteren deutschlands*. Studia dipterologica — (Suppl. 2). (ed. by H. Schumann, R. Bährmann and A. Stark), pp. 195–203.

Standen, V. (2000) The adequacy of collecting techniques for estimating species richness of grassland invertebrates. *Journal of Applied Ecology*, **37**, 884–893.

Stollar, S. (1984) Sezonny vyskyt pestricovitych (Diptera, Syrphidae) habrovych dubrav. [Seasonal occurrence of hoverflies (Diptera, Syrphidae) in hornbeam-oak stands]. *Biologia*, **39**, 627–632.

Stollar, S. (1995) Flower flies (Diptera, Syrphidae) in agroecosystems. *Dipterologica Bohemoslovaca*, **7**, 183–187.

Stollar, S. (1997) The hoverflies (Diptera, Syrphidae) at Mochovce, the construction area of a nuclear power station. *Folia Facultatis Scientiarium Naturalium Universitatis Masarykiana Brunensis, Biologia*, **95**, 181–184.

Storch, D., Konvicka, M., Benes, J., Martinkova, J. & Gaston, K.J. (2003) Distribution patterns in butterflies and birds of the Czech Republic: separating effects of habitat and geographical position. *Journal of Biogeography*, **30**, 1195–1205.

Storch, D. & Kotecky, V. (1999) Structure of bird communities in the Czech Republic: The effect of area, census technique and habitat type. *Folia Zoologica*, **48**, 265–277.

Stuke, J.H. (1995) Beitrag zur Fauna ausgewählter Insektengruppen auf nordwestdeutschen Sandheiden. *Drosera*, **1**, 53–83.

Thomas, J.A., Telfer, M.G., Roy, D.B., Preston, C.D., Greenwood, J.J.D., Asher, J., Fox, R., Clarke, R.T. & Lawton, J.H. (2004) Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science*, **303**, 1879–1881.

Titeux, N., Dufrene, M., Jacob, J.P., Paquay, M. & Defourny, P. (2004) Multivariate analysis of a fine-scale breeding bird atlas using a geographical information system and partial canonical correspondence analysis: environmental and spatial effects. *Journal of Biogeography*, **31**, 1841–1856.

Willis, K.J. & Whittaker, R.J. (2002) Species diversity — scale matters. *Science*, **295**, 1245–1248.

Wright, D.H., Currie, D.J. & Maurer, B.A. (1993) Energy supply and patterns of species richness on local and regional scales. *Species diversity in ecological communities. Historical and geographical perspectives* (ed. by R.E. Ricklefs and D. Schluter). University of Chicago Press, Chicago.