



ELSEVIER

Original article

Regional species richness of families and the distribution of abundance and rarity in a local community of forest Hymenoptera

Werner Ulrich ^{*,1}*Department of Animal Ecology, Nicolaus Copernicus University Toruń, Gagarina 9, 87-100 Toruń, Poland*

Received 30 September 2004; accepted 7 October 2004

9 Abstract

Recent investigations about the relationship between the number of species of taxonomic lineages and regional patterns of species abundances gave indecisive results. Here, it is shown that mean densities of species, of a species rich community of forest Hymenoptera (673 species out of 25 families) were positively related to the number of European species per family. The fraction of abundant species per family declined and the fraction of rare species increased with species richness. Species rich families contained relatively more species, which were present in only one study year (occasional species), and relatively fewer species present during the whole study period (frequent species). © 2004 Published by Elsevier SAS.

Keywords: Hymenoptera; Parasitoids; Community structure; Rarity; Species richness; Singletons; Ecological drift

18 1. Introduction

The question of how evolutionary history influences the distribution and abundance of species at local and regional scales has recently gained much interest. A series of studies dealing with birds and mammals showed that vulnerability to extinction is not randomly distributed and that species poor lineages contain higher proportions of regionally rare species, which are potentially in danger of becoming extinct (Russel et al., 1998, Purvis et al., 2000a, 2000b). On the other hand, Schwartz and Simberloff (2001) reported an opposite trend for North American vascular plants. They found that species poor taxa contain fewer numbers of regionally rare species.

All of these studies dealt with abundance or spatial distribution patterns at regional or continental scales and used regional or global rarity as a metric for estimating extinction probabilities. However, whether species richness of taxa influences patterns of abundance and therefore of community structure at the local, ecosystem scale is largely unknown. Additionally, there is an obvious lack of analyses about

groups others than vertebrata (Schwartz and Simberloff 2001). 38 39

The present paper tries to fill this gap in our knowledge. A local community of forest Hymenoptera is used to infer whether regional species richness is related to patterns of local abundance. Hymenoptera are one of the largest arthropod taxa. In Europe, about 16,000 species in 80 families have been described so far (Ulrich, 1999a) and local habitats like forests contain more than 500 species (Hilpert, 1989, Ulrich, 1998). This extraordinary high local and regional species richness makes the group an ideal candidate for the study of the relation between species richness of lineages and local abundance patterns. 40 41 42 43 44 45 46 47 48 49 50

2. Methods 51

The compilations of Ulrich (1999a, 1999b, 2001a) are used to infer species numbers of European Hymenopteran families and included the recent new estimate for the Ichneumonidae of Horstmann (2002). In total, about 16,000 species of European Hymenoptera have been described (Ulrich, 2001a). However, the exact number of Hymenoptera is even for Europe still unknown and the percent of undescribed species may be up to 20% for some families of Microhymenoptera (Ulrich 1999a, Horstmann 2002, personal com- 52 53 54 55 56 57 58 59 60

* Corresponding author. Tel.: +48-56-611-4469.

E-mail address: ulrichw@uni.torun.pl (W. Ulrich).

¹ www.uni.torun.pl/~ulrichw.

61 munication). However, the problem of taxonomic incom- 117
 62 pleteness affects nearly all larger families of this group to a 118
 63 more or less equal degree (Ulrich, 1999a, 1999b). The use of 119
 64 estimates given in Ulrich (1999a, 2001a) instead of numbers 120
 65 of described species does not change the results presented 121
 66 below (data not shown). 122

67 Data about local Hymenopteran densities and species 123
 68 numbers are based on a long-term quantitative sampling 124
 69 program for estimating arthropod densities and biomasses in 125
 70 a beech forest (*Fagus sylvatica*) located on a limestone 126
 71 plateau approximately 420 m above sea level in the vicinity 127
 72 of Göttingen in Lower Saxony, Germany (Schaefer, 1991). 128
 73 The vegetation can be classified as a Melico-Fagetum subas-
 74 sociation *Lathyrus vernus*. The herb layer is well developed
 75 and consists mainly of spring geophytes that usually disap-
 76 pear in summer. *Mercurialis perennis* and *Allium ursinum*
 77 dominate. A distinct shrub layer is missing. Ulrich (1998,
 78 2001a) provided detailed descriptions of the study site and
 79 the sampling program.

80 From 1980 to 1987 Hymenoptera of this forest were 129
 81 quantitatively sampled with emergence traps (Ulrich, 1998,
 82 1999b, 2001a). Each trap covered a forest floor of 0.25 m²
 83 (1984 and 1985; in both years five such traps were run), 1 m²
 84 (1981 and 1982; 12 traps, 1983 and 1986: four traps, and
 85 1987: 16 traps), and 3.2 m² (1981: 10 traps). In total
 86 43,695 specimens from 720 species and 30 families of Hy-
 87 menoptera were sampled during the eight study years and of
 88 them 695 species could be identified at least to genus level.

89 A study that is based on emergence densities, have to 130
 90 control for individuals that were enclosed under the traps 131
 91 during placement but did not emerge. These individuals 132
 92 might bias mean densities, hence samples obtained directly 133
 93 after the placement of traps were therefore excluded. Ex- 134
 94 cluded were also all nest-building aculeate species because 135
 95 they were not sampled quantitatively (in total 22 species out 136
 96 of the families Vespidae, Formicidae, Sphecidae, Megachil- 137
 97 idae, and Apidae). The following analysis is therefore based 138
 98 on catches of 33,806 individuals from 673 species. 139

99 Mean annual emergence densities per species were com- 140
 100 puted as the total number of individuals per family and year 141
 101 divided by the area sampled by the traps and by the actual 142
 102 number of species of the respective family found in the 143
 103 forest. All species represented by only a single individual 144
 104 (singletons) were classified as rare. In total 198 species 145
 105 belong to this group. All species of the upper density quartile 146
 106 were classified as abundant. These are all species (in total 147
 107 159) of which at least 20 individuals were obtained. The 148
 108 second density quartile contains all species (148) represented 149
 109 by 5–19 individuals.

110 Following Ulrich and Ollik (2004) all species, which were 150
 111 found in only one of the sampling years, were classified as 151
 112 being occasional (in total 338 species). Frequent species are 152
 113 those found in at least six of the eight study years (in total 153
 114 72 species). 154

115 The use of frequencies of rare or abundant species might 155
 116 be misleading at low total species numbers due to Poisson 156

sampling errors. To minimize such errors such frequencies 117
 were computed only for families having more than 10 Euro- 118
 pean species. Therefore, (Figs. 2–4) leave out the Embolemi- 119
 dae (two European species, one rare species in the beech 120
 forest) and the Heloridae (one European species present also 121
 in the forest). 122

The non-parametric statistics, the non-linear and the mul- 123
 tiple regression (GLM mode) modules of STATISTICA 5 124
 (Statsoft, 1997) were used for statistical analysis. Errors refer 125
 always to standard deviations. Species numbers, body weight 126
 and density data were log-transformed prior to multiple re- 127
 gression. 128

3. Results 129

A regression between mean local density per species and 130
 log species richness of European Hymenopteran families 131
 explained 17% of the total variance when only families found 132
 in the forest were included (Fig. 1A). Including all European 133
 families raised the coefficient of determination to 31% 134
 (Fig. 1B). Spearman's rank coefficient indicates in both cases 135
 to a significant positive correlation between mean density 136
 and log species richness ($p < 0.01$). 137

Hymenopteran families do not only differ in species rich- 138
 ness but also include a wide range of body sizes ranging from 139

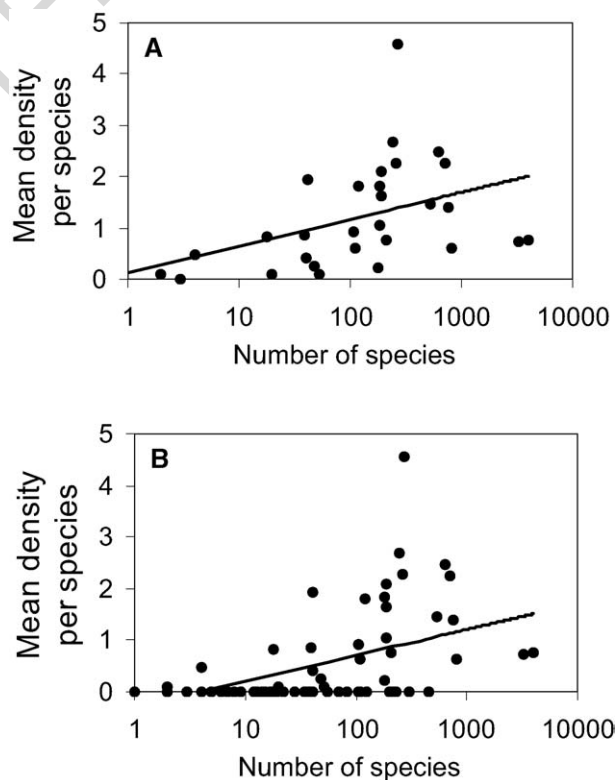


Fig. 1. Plots of mean local emergence densities (individuals m⁻² species⁻¹) of forest Hymenopterous species on the corresponding number of European species per family. (A) Only families found in the beech forest. Least square regression: $Y = (0.22 \pm 0.09)\ln(X) + (0.14 \pm 0.49)$; $R^2 = 0.17$; Spearman's rank $r = 0.51$; $p(t) = 0.004$. (B) All European families included. Least square regression: $Y = (0.22 \pm 0.04)\ln(X) - (0.29 \pm 0.16)$; $R^2 = 0.31$; Spearman's rank $r = 0.60$; $p(t) < 0.0001$.

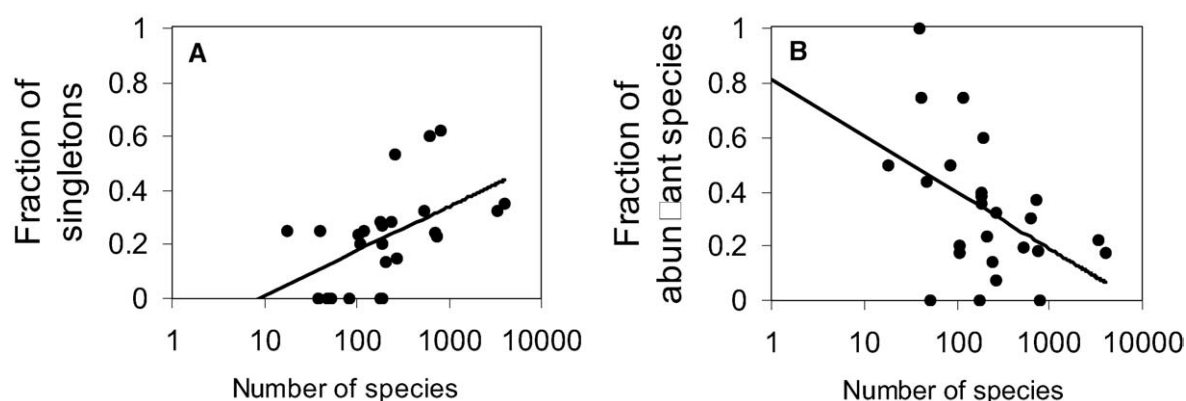


Fig. 2. (A) Plots of the fraction of singletons on the corresponding number of European species per family. Non-linear least square regression: $Y = (0.07 \pm 0.02)\ln(X) - (0.15 \pm 0.13)$; $R^2 = 0.28$; Spearman's rank $r = 0.58$; $p(t) = 0.002$. (B) The fraction of abundant species (the upper quartile) was negatively correlated with the corresponding number of European species per family. Non-linear least square regression: $Y = (-0.09 \pm 0.04)\ln(X) + (0.81 \pm 0.19)$; $R^2 = 0.22$; Spearman's rank $r = -0.48$; $p(t) = 0.02$.

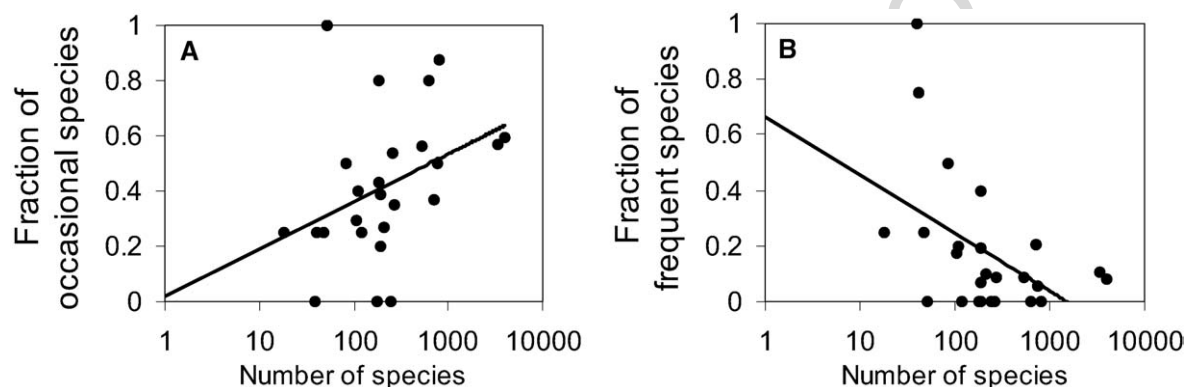


Fig. 3. (A) Plots of the fraction of occasional species (species found in only one of the study years) on the corresponding number of European species per family. Non-linear least square regression: $Y = (0.07 \pm 0.04)\ln(X) + (0.17 \pm 0.21)$; $R^2 = 0.14$; Spearman's rank $r = 0.49$; $p(t) = 0.01$. (B) The fraction of frequent species (species found in at least six study years) was negatively correlated with the corresponding number of European species per family. Non-linear least square regression: $Y = (-0.09 \pm 0.03)\ln(X) + (0.67 \pm 0.19)$; $R^2 = 0.23$; Spearman's rank $r = -0.44$; $p(t) = 0.03$.

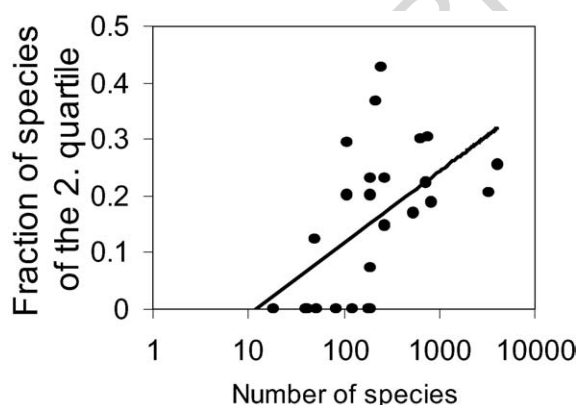


Fig. 4. Plots of the fraction of species with intermediate densities (species of the second quartile) on with the corresponding number of European species per family. Non-linear least square regression: $Y = (0.05 \pm 0.02)\ln(X) - (0.12 \pm 0.10)$; $R^2 = 0.27$; Spearman's rank $r = 0.61$; $p(t) = 0.001$.

140 very small Mymaridae to large Ichneumonidae or Symphyta.
 141 Any species number–density regression has therefore to control
 142 for possible underlying density–body weight relationships (Gaston and Kunin, 1997). In order to do this multiple
 143 regression was used with log-transformed species number
 144

and body weight data as independent variables. (Table 1) 145
 shows that after separating the body weight effect, the rela- 146
 tion between mean log-density and log species number still 147
 remains significant ($p_{\text{species number}} = 0.03$). 148

The fraction of singletons was positively (Fig. 2A; Spear- 149
 man's $r = 0.58$; $p = 0.002$) and the fraction of abundant 150
 species negatively (Fig. 2B; Spearman's $r = -0.48$; $p = 0.02$) 151
 correlated with species richness. These results hold after 152
 controlling for mean body weight. The significance levels for 153
 the species richness effect were in both cases below 0.02 154
 (Table 1). 155

Larger families contained higher proportions of occa- 156
 sional (Fig. 3A; Spearman's $r = 0.49$; $p = 0.01$) but lower 157
 proportions of frequent species (Fig. 3B; Spearman's r 158
 $= -0.44$; $p = 0.03$). Again both results hold after controlling 159
 for mean body weight (Table 1). 160

The above results seem contradictory. Species rich fami- 161
 lies had higher mean densities per species than species poor 162
 ones. On the other hand, in these families frequencies of 163
 abundant species were lower and frequencies of singletons 164
 higher. Such a pattern is only possible if there are accompa- 165
 nying changes in abundance patterns of species with interme- 166

Table 1

Multiple regressions using frequencies and log-transformed mean densities as dependent and log-transformed species numbers and mean body weights as independent variables point to species richness as a major variable that influences patterns of local abundances

	Beta	Std. Error	B	Std. Error	<i>t</i>	<i>p</i>
Mean density						
Constant			0.47	0.48	1.04	0.310
Body weight	-0.18	0.19	-0.11	0.11	-0.97	0.340
Species richness	0.42	0.19	0.26	0.11	2.23	0.030
Fraction of abundant speices						
Constant			1.05	0.31	3.27	<0.01
Body weight	0.24	0.20	0.04	0.03	1.25	0.220
Speices richness	-0.47	0.22	-0.09	0.04	-2.41	0.020
Fraction of singletons						
Constant			-0.20	0.23	-0.86	0.400
Body weight	-0.01	0.19	-0.01	0.03	-0.04	0.960
Speices richness	0.55	0.19	0.08	0.03	2.96	<0.01
Fraction of occasional species						
Constant			-0.35	0.37	-0.94	0.360
Body weight	-0.26	0.20	-0.04	0.03	-1.28	0.210
Speices richness	0.42	0.20	0.09	0.03	2.04	0.050
Fraction of frequent species						
Constant			0.94	0.29	3.24	<0.01
Body weight	0.33	0.19	0.05	0.03	1.71	0.100
Speices richness	-0.49	0.19	-0.09	0.03	-2.58	0.020
Fraction of species in the second quartile						
Constant			-0.22	0.17	-1.33	0.200
Body weight	-0.15	0.19	-0.01	0.02	-0.79	0.430
Speices richness	0.55	0.19	0.05	0.02	2.95	<0.01

167 diate densities that counterbalance these opposite trends.
 168 This was indeed the case. (Fig. 4) shows a strong correlation
 169 of the fraction of species of the second abundance quartile
 170 with species number per family. Again, this correlation re-
 171 mained statistically significant after controlling for mean
 172 body weight (Table 1).

173 4. Discussion

174 There are apparently no comparable studies that tried to
 175 relate local patterns of abundance and community structure
 176 to the species richness of taxonomic units. However, recent
 177 investigations on the relation between species richness of
 178 taxa and abundance patterns at the regional scale gave inde-
 179 cisive results while either pointing to a negative relation in
 180 plants (Schwartz and Simberloff, 2001) or to a positive rela-
 181 tion in some mammals (Purvis et al., 2000a). The present
 182 study shows that both trends might be observed in the same
 183 data set when using different measures of abundance. This
 184 has potential implications for studies that try to assess extinc-
 185 tion risks for instance on the basis of IUCN abundance and
 186 frequency classes. Using total abundances or frequency
 187 classes might give contrary impressions about the depen-
 188 dence of extinction vulnerability on taxon size.

189 The 'mystery of singletons' in arthropod samples has
 190 gained much attention (Novotny and Basset, 2000, Ulrich,
 191 2001b). The high number of singletons has mainly been
 192 explained by high local and regional dispersion abilities
 193 resulting in higher numbers of transient species or tourists

194 and by sampling artifacts (Shmida and Wilson, 1985, Hub-
 195 bell and Foster, 1986, Novotny and Bassett, 2000). The above
 196 results point to species richness of taxonomic lineages and
 197 therefore to evolutionary history as an additional variable
 198 that might influence rarity at the local scale.

199 Table 1 does not point to any body weight effect on density
 200 as reported in other studies (Gittleman and Purvis, 1998;
 201 Belgrano et al., 2002). Indeed, the local density–body weight
 202 distribution has a negative slope (Ulrich, 2001a, Ulrich,
 203 2004). However, the size differences between and inside the
 204 taxa that form the classical 'Microhymenoptera' are rela-
 205 tively small and the body size effect is weak (Ulrich, 2001a).
 206 Additionally, the lumping of species into families with wider
 207 size distributions further levels the body weight effect.

208 Nevertheless, there are two possible caveats in the present
 209 study. First, the analysis assumes that eclector samples are
 210 sufficiently accurate to allow comparisons to be made con-
 211 cerning differences in mean densities among families. Previ-
 212 ous studies (Thiede, 1977, Funke, 1983, Ulrich, 2001a) have
 213 shown, that parasitic Hymenoptera (the vast majority of the
 214 species) spend at least one stage of their live cycle (often the
 215 pupal stage) in the soil or near the ground. These species
 216 should be sampled quantitatively. Based on a mix of sample
 217 techniques Ulrich (2001a) showed that of the 720 species
 218 found in the forest less than 20 spend their whole live cycle in
 219 the canopy of trees. Furthermore 20–30 bi- or polyvoltine
 220 species spend at least one generation solely in the canopy.
 221 These species (5–6% of total) are potentially undersampled.
 222 Because these species come from different families their low
 223 frequency should not influence overall density estimates.

224 A second caveat might be a possible sample bias against
 225 species rich families. If species of these families are under-
 226 represented in local samples (for instance due to their very
 227 low densities) estimates of mean species densities would also
 228 be biased towards higher mean densities in species rich
 229 families. However, this would only be a problem if there
 230 were severe sample bias, but there is no indication, that this
 231 occurred. Jackknife estimates of total species numbers and
 232 local species—area curves point to rather equal rates of
 233 unrecorded species among families (Ulrich, 2001a and in
 234 preparation). In fact, due to the well known negative abun-
 235 dance—body weight relation (Ulrich, 1999c) this type of
 236 sample bias is more related to mean body weight. In this
 237 respect, such a bias might occur in the Ichneumonidae with
 238 its mainly larger species of low mean abundances (Ulrich,
 239 1999c). However, to account for the correlation in (Fig. 1) the
 240 fraction of unrecorded species in the largest families must be
 241 at least five times the fraction in smaller families. The close
 242 linear regression between local (forest) and European species
 243 numbers (Ulrich, 2001a and in preparation) makes such a
 244 bias improbable.

245 Recently, Magurran and Henderson (2003) and Ulrich and
 246 Ollik (2004) found that the division of local communities
 247 into frequent and occasional species might improve our un-
 248 derstanding of what factors influence local patterns of spe-
 249 cies abundances. The present works adds to this picture.
 250 (Fig. 3) showed that at the local scale, species rich lineages
 251 have higher proportions of occasional but lower proportions
 252 of frequent species. Frequent species are either those that
 253 persist in a community over longer time periods or have high
 254 migration abilities so that local extinctions are immediately
 255 counterbalanced. Differences between small and large lin-
 256 eages in regard to patterns of temporal persistence in a
 257 community might therefore tell something about their evolu-
 258 tionary history. Unfortunately, up to now it proved to be
 259 impossible to work out an unequivocal phylogenetic system
 260 of Hymenopteran lineages at and above the family level
 261 (Downton et al., 1997; Ronquist, 1999; Carpenter, 2000; Vil-
 262 helmsen, 2001). Furthermore, there is no consensus about the
 263 status and the phylogenetic position of most of the super-
 264 families (Ronquist, 1999). This poor state of the art prohibits
 265 a deeper analysis of the evolutionary significance of the
 266 present findings. In particular, it would be of interest to see
 267 whether patterns of local abundance are not only related to
 268 species richness but also to the phylogenetic age of a lineage.

269 Nevertheless, the patterns reported here call for an expla-
 270 nation. Of course, one might think about a simple statistical
 271 artifact. Local and regional species numbers of Hy-
 272 menopteran families are highly correlated (Ulrich, 1999b,
 273 2001a), and regionally species rich families are most often
 274 also species rich at the local scale. Now assume that temporal
 275 variability is a simple log-normally distributed random num-
 276 ber. Then species of species rich families will have a higher
 277 probability to reach very high densities. One hundred nu-
 278 merical simulations of this simple model using the observed
 279 species numbers and realistic ranges of maximum and mini-

280 mum densities resulted in 24 statistically significant (at p 280
 281 < 0.05) correlations between regional species richness and 281
 282 mean local density per species. This model might therefore 282
 283 account for the relationship of (Fig. 1), but fails to explain the 283
 284 remaining patterns. In particular, it predicts a positive corre- 284
 285 lation between species richness and the fraction of abundant 285
 286 species contradicting the observed pattern (Fig. 2). 286

287 Nevertheless, it remains to be shown whether stochastic 287
 288 models might explain the observed relationships. In this 288
 289 respect it would be interesting to see whether the neutral 289
 290 model approach of Hubbell (2001) predicts similar relation- 290
 291 ships between regional species diversity and patterns of local 291
 292 community structure. Hubbell (2001) showed that his eco- 292
 293 logical drift model results in close positive correlations be- 293
 294 tween regional and local abundances and phylogenetic age. 294
 295 Additionally, his model predicts that phylogenetic older lin- 295
 296 eages should be more species rich. From these two assumed 296
 297 patterns it is only a short step to the prediction of a positive 297
 298 relationship between local abundance and species richness of 298
 299 lineages. However, whether the other patterns reported here 299
 300 also follow from ecological drift is still not clear. To study 300
 301 this, intensive and CPU-time consuming simulations with 301
 302 larger assemblages under different speciation regimes are 302
 303 necessary. 303

304 Of course, the present results refer only to one community 304
 305 of forest Hymenoptera; it remains to be shown whether they 305
 306 can be generalized. For this task complete local abundance 306
 307 data about other species rich taxa like Diptera, Carabidae, 307
 308 Lepidoptera, Arachnida, or Aves are necessary. 308

309 Last, the present results shed light on a neglected group of 309
 310 species, those having intermediate densities. Most studies 310
 311 dealing with conservation and biodiversity concentrated on 311
 312 rare species (Gaston and Kunin, 1997). It seems that to get 312
 313 unequivocal results about patterns of rarity and abundance 313
 314 these intermediate species have to be included into our analy- 314
 315 ses. 315

Acknowledgements 316

317 I thank K. Horstmann, E. Diller, the late R. Hinz, and H. 317
 318 Hilpert for the determination of the Ichneumonidae and some 318
 319 Diapriidae. This work was in part supported by a grant from 319
 320 the Deutsche Forschungsgemeinschaft and a grant from the 320
 321 Polish Science Committee (KBN, 3 F04F 034 22). The au- 321
 322 thor received a scholarship from the Friedrich-Ebert- 322
 323 Foundation. 323

References 324

- 325 Belgrano, A., Allen, A.P., Enquist, B.J., Gillooly, J.F., 2002. Allometric 325
 326 scaling of maximum population density: a common rule for marine 326
 327 phytoplankton and terrestrial plants. *Ecol. Lett* 5, 611–613. 327
 328 Carpenter, J.M., 2000. On the higher-level phylogeny of Hymenoptera 328
 329 (Insecta). *Contr. 19th Ann. Meeting Intern. Willi Hennig Society,* 329
 330 Leiden. 330

- 331 Downton, M., Austin, A.D., Dillon, N., Bartowsky, E., 1997. Molecular
332 phylogeny of the apocritan wasps: the Proctotrupomorpha and Evani-
333 omorpha. *Syst. Entomol.* 22, 245–255.
- 334 Funke, W., 1983. Arthropodengesellschaften mitteleuropäischer Wälder.
335 Abundanz und Biomasse–Eklektorfauna. *Verh. Ges. Ökol* 11, 111–129.
- 336 Gaston, K., Kunin, W.E., 1997. Concluding comments. In: Kunin, W.E.,
337 Gaston, K. (Eds.), *The Biology of Rarity*. Chapman & Hall London, pp.
338 262–272.
- 339 Gittleman, J.L., Purvis, A., 1998. Body size and species-richness in carni-
340 vores and primates. *Proc. R. Soc. Lond. B. Biol. Sci.* 265, 113–119.
- 341 Hilpert, H., 1989. Zur Hautflüglerfauna eines südbadischen Eichen-
342 Hainbuchenmischwaldes. *Spixiana* 12, 57–90.
- 343 Horstmann, K., 2002. Bemerkungen zu einer Liste der aus Deutschland
344 nachgewiesenen Ichneumonidae. *Nachrbl. Bayr. Entomol* 51, 75–80.
- 345 Hubbell, S.P., Foster, R.B., 1986. Commonness and rarity in a neotropical
346 forest: implications for tropical tree conservation. In: Soule, M. (Ed.),
347 *Conservation Biology: Science of Scarcity and Diversity*. Sinauer Sun-
348 derland, pp. 205–231.
- 349 Hubbell, S.P., 2001. *The Unified Theory of Biogeography and Biodiversity*.
350 University Press, Princeton.
- 351 Magurran, A.E., Henderson, P.A., 2003. Explaining the excess of rare
352 species in natural species abundance distributions. *Nature* 422, 714–716.
- 353 Novotny, V., Basset, Y., 2000. Rare species in communities of tropical insect
354 herbivores: pondering the mystery of singletons. *Oikos* 89, 564–572.
- 355 Purvis, A., Gittleman, J.L., Cowlishaw, G., Mace, G.M., 2000a. Predicting
356 extinction risk in declining species. *Proc. R. Soc. Lond. B. Biol. Sci.* 267,
357 1947–1952.
- 358 Purvis, A., Agapow, P.-M., Gittleman, J.L., Mace, G.M., 2000b. Nonrandom
359 extinction and the loss of evolutionary history. *Science* 288, 328–330.
- 360 Ronquist, F., 1999. Phylogeny of the Hymenoptera (Insecta): the state of the
361 art. *Zool. Scr.* 28, 3–11.
- 362 Russell, G.J., Brooks, T.M., McKinney, M.M., Anderson, C.G., 1998. Taxo-
363 nomic selectivity in bird and mammal extinctions. *Conserv. Biol.* 12,
364 1365–1376.
- Schaefer, M., 1991. Fauna of the European temperate deciduous forest. In:
Röhrig, E., Ulrich, B. (Eds.), *Temperate Deciduous Forests*, vol. 7.
Ecosystems of the World, Amsterdam, pp. 503–525.
- Schwartz, M.W., Simberloff, D., 2001. Taxon size predicts rates of rarity in
vascular plants. *Ecol. Lett* 4, 464–469.
- Shmida, A., Wilson, M.V., 1985. Biological determinants of species diver-
sity. *J. Biogeogr.* 12, 1–20.
- Statsoft Inc, 1997. *Statistica for Windows (Computer program manuals)*.
Tulsa, OK.
- Thiede, U., 1977. Untersuchungen über die Arthropodenfauna in Fichten-
foresten (Populationsökologie, Energieumsatz). *Zool. Jahrb. Syst.* 104,
137–202.
- Ulrich, W., 1998. The parasitic Hymenoptera in a beech forest on limestone
I: species composition, species turnover, abundance and biomass. *Polish
J. Ecol.* 46, 261–289.
- Ulrich, W., 1999a. The numbers of species of Hymenoptera in Europe and
assessment of the total number of Hymenoptera in the world. *Polish J.
Entomol.* 68, 151–164.
- Ulrich, W., 1999b. Regional and local faunas of Hymenoptera. *Polish J.
Entomol.* 68, 217–230.
- Ulrich, W., 1999c. Abundance, biomass and density boundaries in the
Hymenoptera: analysis of the abundance–body size relationship and
differences between forest and open landscape habitats. *Polish J. Ecol.*
47, 73–86.
- Ulrich, W., 2001a. Hymenopteren in einem Kalkbuchenwald: Eine Mod-
ellgruppe zur Untersuchung von Tiergemeinschaften und ökologischen
Raum-Zeit-Mustern. *Schriftenr. Forschenzentr. Waldökosysteme A* 171,
1–249.
- Ulrich, W., 2001b. Ecological characteristics of rare species: the case of
parasitic Hymenoptera. *Polish J. Ecol* 49, 379–389.
- Ulrich, W., 2004. Allometric ecological distributions in a local community
of parasitic Hymenoptera. *Acta Oecol* 25, 179–186.
- Ulrich, W., Ollik, M., 2004. Frequent and occasional species and the shape
of relative abundance distributions. *Div. Distr* 10, 263–269.
- Vilhelmsen, L., 2001. Phylogeny and classification of the extant basal
lineages of the Hymenoptera (Insecta). *Zool. J. Linn. Soc* 131, 393–442.