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Regional patterns of diversity and estimates of global insect species richness

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The total number of insect species in the world is an important if elusive figure. We use a fresh approach to estimate global insect species richness, based on biogeographic patterns of diversity of well or better documented taxa. Estimates generated by various calculations, all variations on a theme, largely serve to substantiate suggestions that insect species are likely to number around 10 million or less.

Keywords: biodiversity; diversity; insects; species richness.

Introduction

The global number of extant species has been seen as a fundamental descriptor of life on Earth. It is a figure we do not know. Several methods have been used to generate estimates for one or more major taxa (i.e. the most speciose): the bases of these methods include patterns of species taxonomic description, host relations, and body size distributions (Erwin, 1982; May, 1988, 1990, 1992; Thomas, 1990; Gaston, 1991, 1992; Hawksworth, 1991; Hodkinson and Casson, 1991; Hammond, 1992). No single approach has any logical supremacy, all have at least one step which is founded on weak assumptions, and all by definition are extreme extrapolations. A broad range of methods needs to be employed in order to generate estimates which are based on different assumptions and empirical data. This approach hopefully will give rise to a set of estimates which demonstrate some agreement on the numbers of species in a given taxon.

In this paper we use a simple but as yet little explored approach to estimating global numbers of extant insect species. We use estimates of insect numbers from comparatively well-known regions to generate global estimates using large scale spatial patterns in the species richness of other taxa. Such an approach has been advocated in the past, but applied in little more than an illustrative manner (e.g. Stork and Gaston, 1990; Hammond, 1992; Stork, 1993).

Biogeographic regions

For a number of comparatively well-known taxa, information is available which enables the numbers of species occurring in each of a standard set of biogeographic regions to

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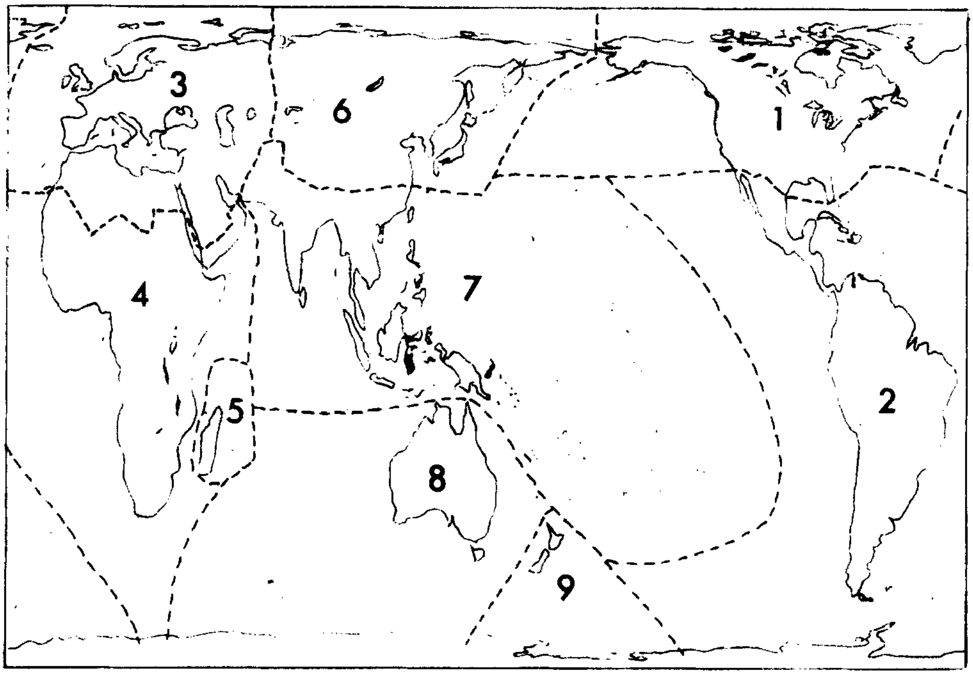

Figure 1. The approximate limits to the biogeographic regions used in this study. 1 – Nearctic: N. America north of Mexico; 2 – Neotropics: Central and South America including Mexico; 3 – Western Palaearctic: Europe, Scandinavia, former USSR east to Tashkent, N. Africa, and Middle East (inc. Afghanistan); 4 – sub-Saharan Africa: Africa excluding area mentioned in (3); 5 – Madagascar, including Seychelles, Comoros, Reunion and Mauritius Islands; 6 – Eastern Palaearctic: former USSR east of Tashkent, Mongolia, China south to Yangtzee River, Japanese Archipelago and Korea; 7 – South East Asia: from Pakistan, India, Nepal and Bhutan through to Papua New Guinea and east to Pacific islands, including Hawaii; 8 – Australia, including Tasmania; 9 – New Zealand: including neighbouring islands.

be determined, either from summary information on regional occurrences or, more commonly, from species checklists. We have collected such information (Table 1) using the biogeographic scheme employed in the organization of some of the collections in the Entomology Department of The Natural History Museum, London (Fig. 1). No inference as to the faunal and floral distinctiveness/reality of these regions should be made in the context of the data analysed. Taxa were chosen for analysis largely on the basis of the quality and availability of the species richness information. Only those of a sufficiently high taxonomic level that they are well represented world-wide were considered. For the purpose of this study, sub-species were ignored, as were species found solely in the Antarctic or the Arctic.

The proportions of species of various taxa occurring in each biogeographic region, not unexpectedly, show a substantial degree of consistency. Less than 10% of species in each taxon occur in the Nearctic, Western Palaearctic, Madagascar, or New Zealand. Approximately 10–20% occur in sub-Saharan Africa. Whilst the Neotropics are commonly championed as the most speciose biogeographical region, there is much variation in the proportion of species they contain in different taxa (28.9–53.2%). Patterns in S.E. Asia are complex; proportions range form 12.7% to 44.9%.

Reasonable estimates can be made of the numbers of insect species occurring in the two best studied of the biogeographic regions considered here, the Nearctic and Australia.

For the Nearctic two estimates have been published of about 150 000 (Taylor, 1983; Kosztarab and Schaefer, 1990), and Stork (1993) has suggested a figure of around 200 000. Even allowing for substantial conservatism in these numbers it is very doubtful that the total would exceed 500 000. For Australia estimates have been somewhat more varied. Taylor (1983) gave a figure of about 110 000 which seems rather on the low side, whilst Stork (1993) suggests one of about 400 000. Monteith's (1990) remark that the projected estimate by taxonomists of the number of beetle species in Australia is about 20–40 000 would tend to support the lower end of this span of estimates of total species richness for the region. The same can be said of Colless and McAlpine's (1991) observation that the Australian dipterous fauna comprises a probable total of some 10 000–12 000 species. Again it seems doubtful that the entire insect fauna would exceed a total of 500 000 species.

We can take a range of apparently reasonable estimates (encompassing those suggested by the various workers) of the numbers of insect species in the Nearctic and Australia, assume that these constitute similar proportions of global species numbers as we have documented for other taxa (Table 1), and generate estimates of global insect

Table 1. Percentages of the total number of species of various taxa recorded from different biogeographical regions. In no cases were sub-species considered. For birds, only the breeding ranges of non-pelagic species were considered. Percentages sum to more than 100 where species occur in more than one biogeographic region. The limits and key to the biogeographic regions are described in Fig. 1. Sources: higher plants – Groombridge (1992); dragonflies – Tsuda (1984); dynastine beetles – Endrödi (1985); tiger beetles – (Pearson and Cassola 1992, D.L. Pearson, personal communica-tion); swallowtail butterflies – (Collins and Morris 1985); amphibians – Frost (1985); birds – Sibley and Monroe (1990); mammals – Corbet and Hill (1991)

	Biogeographic regions								
	1	2	3	4	5	6	7	8	9
higher plants	6.5	32.4	n/a	16	n/a	n/a	19	5.7	n/a
amphibians	4.9	46.2	2.1	15.6	3.9	4.2	21.1	4.5	0.1
birds	6.1	36.5	6.4	19.0	2.4	6.7	29.7	6.0	1.1
mammals	8.4	30.0	9.2	20.9	2.3	7.7	27.0	6.5	0.1
dragonflies	8.5	28.9	5.1	13.5	3.8	10.1	40.8	5.5	0.3
tiger beetles	5.5	n/a	n/a	18.0	8.9	n/a	n/a	3.8	0.7
dynastine beetles	4.8	53.2	2.1	13.2	4.9	1.0	12.7	12.6	0.4
swallowtails	5.4	30.4	6.1	13.3	2.8	11.2	44.9	3.0	0.0

Table 2. Estimates (in millions) of the global number of insect species based on various estimates of the numbers of insect species in the Nearctic (1) and Australian (8) regions and the proportions of the respective global totals the richness of other taxa in these regions constitutes (e.g. the Nearctic contains 6.5% of the world's higher plants, assuming that it also contains 150 000 insect species, then there are 150 000/0.065 = 2.3 million species of insects in the world). The proportions in regions 1 and 8 of the global total numbers of species of the taxa used in these estimates are given in italics.

	Higher plants	Amphibians	Birds	Mammals	Dragonflies	Dynastines	Tiger beetles
Nearctic	6.5%	4.9%	6.1%	8.4%	8.5%	4.8%	5.5%
150 000	2.3	3.0	2.5	1.8	1.8	3.1	2.7
250 000	3.8	5.1	4.1	3.0	2.9	5.2	4.5
500 000	7.7	10.2	8.2	6.0	5.9	10.4	9.1
Australia	5.7%	4.5%	6.0%	6.5%	5.5%	12.6%	3.8%
150 000	2.6	3.3	2.5	2.3	2.7	1.2	3.9
250 000	4.4	5.6	4.2	3.8	4.5	2.0	6.6
500 000	8.8	11.1	8.3	7.7	9.1	4.0	13.2

species richness. When contrasted with the range of estimates of insect species numbers which are commonly quoted (5–80 million), the results of such an analysis are reasonably consistent (Table 2). Estimated numbers of insect species in the Nearctic of 150 000, 250 000 and 500 000, yield estimates of global richness, respectively, of 1.75–3 million, 3–5 million and 6–10 million. Likewise for Australia, estimates are generated of 1.25–4 million, 2–6.5 million and 4–13 million. Neither for the Nearctic nor Australia are the estimates of global insect species richness based on individual insect taxa markedly different from those based on non-insect taxa.

In support of this approach, it is noteworthy that Colless and McAlpine (1991) suggest that the Australian dipterous fauna and the Australian insect fauna as a whole both comprise about 5% of the respective world totals. Five per cent falls well within the range of proportions of other taxa occurring in this area (Table 1).

The same process as used to generate the above estimates can be performed in reverse to ask what kinds of estimates of the numbers of insect species in each biogeographic region result from different estimates of the global total number of insect species and the proportions of species of other taxa found in the different biogeographic regions. We have done this for global total numbers of insects of 2 to 30 million (Table 3). The

Table 3. Table to show the estimates of numbers of insects in each biogeographic region (1–8) arising from global estimates of insect numbers, generated using the greatest and smallest proportions from other taxonomic data

	2 M	5 M	10 M	20 M	30 M
1	170 000	425 000	850 000	1 700 000	2 550 000
	96 000	240 000	480 000	960 000	1 440 000
2	1 064 000	2 660 000	5 320 000	10 640 000	15 960 000
	578 000	1 445 000	2 890 000	5 780 000	8 670 000
3	184 000	460 000	920 000	1 840 000	2 760 000
	42 000	105 000	210 000	420 000	630 000
4	418 000	1 045 000	2 090 000	4 180 000	6 270 000
	264 000	660 000	1 320 000	2 640 000	3 960 000
5	178 000	445 000	890 000	1 780 000	2 670 000
	46 000	115 000	230 000	460 000	690 000
6	224 000	560 000	1 120 000	2 240 000	3 360 000
	20 000	50 000	100 000	200 000	300 000
7	898 000	2 245 000	4 490 000	8 980 000	13 470 000
	254 000	635 000	1 270 000	2 540 000	3 810 000
8	252 000	630 000	1 260 000	2 520 000	3 780 000
	60 000	150 000	300 000	600 000	900 000

upper end of this range coincides with the oft-quoted estimate of 30 million insect species made by Erwin (1982). On this basis, the numbers of insect species in the Nearctic would have to be three or more times greater than the upper estimate suggested earlier, and that for Australia about two or more times greater. Global estimated totals of 2 million can be argued to be far too low on many grounds, and such a conclusion is substantiated here, with some estimates on this basis being less than the known numbers of insect species in the Nearctic or Australia.

National inventories

Similar calculations to those using biogeographic figures can be performed for smaller areas at a national scale. Estimates of total numbers of insect species are available for several nations, along with figures for the number of species in other taxa which occur there and the proportions these represent of the associated global totals (Table 4). The nations considered are temperate, and comprise very small geopolitical boundaries compared to the biogeographical boundaries used previously. The proportions of species of most taxa which occur within their bounds are therefore low, making any extrapolations substantially more tenuous, and resulting in great variability in the estimates of the magnitude of global insect species richness which they generate (Table 5). These estimates range from 0.9 to 28.1 million species. Using the upper estimates of the

Table 4. The percentages of the global totals of various taxa which occur in different countries, and the estimated total numbers of insect species occurring in those same regions. Principal sources: Gaston (1992 and references therein), Groombridge (1992)

	Higher plants	Amphibians	Reptiles	Birds	Mammals	Estimated no. of insects
Japan	2.05	1.30	0.97	2.78	2.14	70–100 000
Canada	1.15	1.00	0.63	4.73	3.31	55 000
Britain	0.62	0.15	0.09	2.43	1.00	23 500
Finland	0.42	0.13	0.08	2.56	1.43	22 500
Switzerland	1.15	0.45	0.22	2.23	1.79	31 500

Table 5. Estimates (in millions) of the global number of insect species based on various estimates of the numbers of insect species in different nations and the proportion of the global total numbers of species in several taxa found in those regions

	Higher plants	Amphibians	Reptiles	Birds	Mammals
Japan	3.4–4.9	5.4–7.7	5.7–10.3	2.0–3.6	3.3–4.7
Canada	4.8	5.5	8.7	1.2	1.7
Britain	3.8	15.7	26.1	1.0	2.4
Finland	5.4	17.3	28.1	0.9	1.6
Switzerland	2.7	7.0	14.3	1.4	1.8

numbers of insects in Japan, they have a mean of 7.3 million. Plainly, however, many of the estimates are ridiculously low (e.g. some are less than or little different from the number of described species; Gaston, 1991; Hammond, 1992).

Discussion

Estimation of the global numbers of insect species from the patterns of distribution of other taxa has several potential limitations. Foremost it presupposes that insect species are distributed globally in a similar fashion to better known taxa. If, for example, insects demonstrated overall steeper latitudinal increases in species richness than these other taxa then substantial under estimation of their species richness might result. There seems little evidence for such a claim, but it cannot be ruled out. Data from the taxa used in this study show no significant correlation between total global species number and proportion found in the principal tropical regions (Neotropics, sub-Saharan Africa, South East Asia), suggesting that, more broadly, more speciose taxa do not have relatively more species living at lower latitudes (unpublished results).

Second, the approach taken here assumes that there is no substantial under-estimation or over-estimation of the proportions of species in well-known taxa in particular biogeographic regions. For several of the taxa used, the relative numbers of species in tropical regions seem likely to increase, however, it remains doubtful that this effect will be sufficiently substantial as to alter the broad pattern of the results obtained.

Accepting the estimates generated at their face value, they serve in the main to substantiate suggestions that insect species are more likely to number around 10 million or less than around 30 million or more (e.g. May, 1990, 1991; Gaston, 1991, 1992; Hodkinson and Casson, 1991; Stork, 1993). Where markedly higher figures were generated they tended to be associated with those calculations for which the errors in extrapolation would be expected to be greatest (e.g. from small temperate countries).

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