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How Many Species of Insects and Other Terrestrial Arthropods Are There on Earth?

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Abstract

In the last decade, new methods of estimating global species richness have been developed and existing ones improved through the use of more appropriate statistical tools and new data. Taking the mean of most of these new estimates indicates that globally there are approximately 1.5 million, 5.5 million, and 7 million species of beetles, insects, and terrestrial arthropods, respectively. Previous estimates of 30 million species or more based on the host specificity of insects to plants now seem extremely unlikely. With 1 million insect species named, this suggests that 80% remain to be discovered and that a greater focus should be placed on less-studied taxa such as many families of Coleoptera, Diptera, and Hymenoptera and on poorly sampled parts of the world. DNA tools have revealed many new species in taxonomically intractable groups, but unbiased studies of previously well-researched insect faunas indicate that 1–2% of species may be truly cryptic.

INTRODUCTION

As May (34, p. 514) noted, "To a good approximation, all species are insects." Not surprisingly, the question of just how many species of organisms there are has largely revolved around the number of insect species and their allies, with many more novel methods of estimating numbers of species developed for insects than for other hyperdiverse groups such as nematodes, mites, or fungi.

In this review, I build on a number of previous reviews of how many species there are on Earth (16, 23, 24, 35–37, 52, 55–59). In these reviews, many authors (23, 24, 35–37, 52, 56–59) have estimated all species of eukaryotes with special attention to insects and other arthropods, whereas only a few have just discussed insects (16) or insects and other arthropods (55, 61). I follow recent classifications (64) (**Figure 1** and Appendix) and include the subphyla Chelicerata, Myriapoda, and Hexapoda in the terrestrial Arthropoda, noting that there are a few terrestrial Crustacea. Insects are the largest class in the Hexapoda. I describe previous methods of estimating global species richness for insects plus a number of newer, independent, statistically robust estimates and others that have improved on previous methods (61). Several new estimates have measures of uncertainty, and all have clearly stated assumptions that can be tested. Averaging these estimates suggests there might be 1.5 million species of beetles, 5.5 million species of insects, and an additional 1.3–1.5 million other terrestrial arthropods (61), and this is discussed later.

In recent years, potential new support for hyperestimates of insect species has come from DNA studies that have shown previously unresolved species complexes may constitute numerous species. Such cryptic diversity has been called the biodiversity wildcard (6). Finally, with indications that 80–90% of species are yet to be described, questions of where these undescribed species are to be found and which groups they may belong to are important, as they may guide where future taxonomic research should be focused.

HISTORICAL PERSPECTIVES

It is perhaps surprising, given our fascination with the extraordinary diversity of life on Earth, that it was not until the 1980s that the question of just how many species share our planet was explored in a scientifically rigorous way. In his seminal review on this topic, May (35) suggested different aspects of ecological theory, including food webs, relationships between body size and number

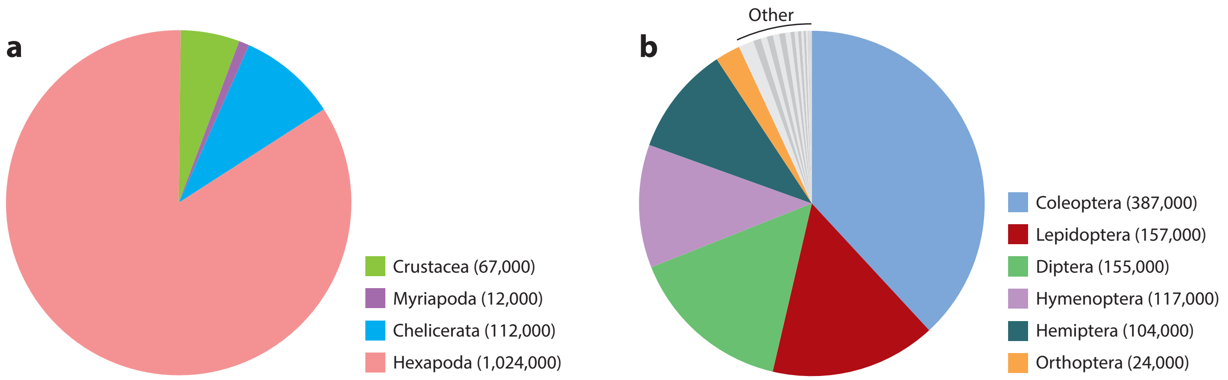

Figure 1

Relative proportions of named species in (*a*) the four subphyla constituting the Arthropoda and (*b*) the orders in the Insecta, with numbers in parentheses. A full breakdown of orders within the Arthropoda is in the Appendix. Data from the Catalogue of Life summarized by Zhang (64).

of species, and host specificity, might provide an answer. For example, he noted that there might be a negative log-linear relationship between the number of animal species of different body size classes. Because most very large species are described, one could use a line fitted to the number of species in the larger size classes to predict backward. Extrapolating back to 0.2 mm (roughly the smallest size for eukaryotes) gives a total of approximately 10 million species below this line (36).

Earlier estimates in the eighteenth and nineteenth centuries reflected a lack of exploration and understanding of the diversity of life across the planet. Linnaeus (32), for example, in *Species Plantarum*, was one of the first to attempt to catalog the diversity of plants on a global scale. Having listed more than 6,000 species, he concluded that the global total should be no more than 10,000 species (50). For insects, the earliest estimate was by Ray (49), who suggested that there might be 2,000 species in Britain and 20,000 worldwide. In a first reasoned estimate, Kirby & Spence (31) suggested that there might be 110,000–120,000 plants and fungi on Earth and, given in Britain there appeared to be roughly 6 insect species for each plant species, there might be 600,000 insect species worldwide. From the early 1800s, there was no further update until Sabrosky (51), who, summarizing the views of several authors in the 1950s, suggested the number of insect species could be 2–10 million but gave no reasons for this estimate. Erwin (13) reinvigorated the debate by using ratios of numbers of insects to plant species, as Kirby and Spence (31) had. He suggested using ratios of numbers of insects to plant species, and he suggested that there might be as many as 30 million tropical arthropod species (see the section below titled Host Specificity). This estimate, published at a time of increasing concern for the fate of global biodiversity through forest loss and other forms of environmental change, stimulated a renewed interest in how many species of insects there might be.

HOW MANY SPECIES ARE CURRENTLY DESCRIBED?

Determining just how many valid named species of insects and other terrestrial arthropods exist has been difficult because of high levels of synonymy. However, the most recent estimate of 1,013,825 named insect species compiled in the Catalogue of Life (64) is based on numerous separate catalogs for different taxa where synonyms have been identified for 827,017 species (equivalent to 82% of the estimated total). **Figure 1** shows that, in terms of named species, insects are the dominant group of arthropods, with Coleoptera, Lepidoptera, Diptera, and Hymenoptera being the most speciose insect orders. Rates of description of new species generally have been low, with roughly 7,000 species of insects described each year between 1979 and 1988 (23), although the rate may have since increased through online publishing. Even if there has been an increase in the rate of description, taxonomists are a long way from naming all species of insects, and a high proportion of species are likely to become extinct before they can be named (9). What we do know is that there has been disproportionate research effort into more charismatic groups such as birds and mammals, which has resulted in a much lower average number of research papers per known species of insects (35). The same is true within insect taxa as well with some groups, such as Papilionidae, Lucanidae, and Cicindelidae, having been relatively well studied with few new species being currently added while other groups, such as many families of beetles, parasitic wasps, and flies, have been almost completely ignored.

DIFFERENT METHODS OF ESTIMATING GLOBAL SPECIES RICHNESS OF INSECTS

In the following section, current methods of estimating global species richness are briefly discussed (**Table 1**). Some estimates (14, 40, 48, 51) appear to have no clear testable methodology and thus

Table 1 Summary of methods of estimating global species richness of beetles, insects, and terrestrial arthropods

Method	Number of beetle species[a]	Number of insect species[a]	Number of terrestrial arthropod species[a]	Year	Reference
Host specificity	12.2	—	30	1982	13
	4.9–40.7	—	44.5 (7.3–81.4)	1988	55[b]
	—	—	6	1996	4
	0.6–2.2	—	2.4–10.2	2000	43
	—	—	**6.4 (3.6–11.4)**	2011	21
	—	—	**7.8 (3.7–13.7)**	2011	21
	—	—	**7.8 (2.9–12.7)**	2013	22
	1.1 (1.5–1.9)	—	—	2015	61
Ratios of known to unknown	—	5.8 (4.9–6.6)	—	1990	60
	1.1 (0.9–1.2)	**6.3 (5.4–7.2)**	—	2015	61
	1.3 (1.2–1.3)	–	—	2015	61
Higher taxonomic ratios	—	**2.6**	—	2011	39
Proportion of new species in samples	—	2.2 (1.8–2.6)	—	1991	27
	—	**5.9 (5–6.7)**	—	1993	56
Discovery curves	—	2.7 (2.1–3.4)[c]	—	2001	11
Body size and year of description	**1.9 (1.7–2.1)**	—	**6.7 (5.9–7.4)**	2015	61
Expert opinions—taxonomists' estimates	—	5	—	1991	16
Other	—	6.3 (2.5–10)	—	1952	51[d]
	—	—	50	1988	14[d]
	–	2	—	2000	40[d]
	—	5.5 (5–6)	—	2007	48[d]
Mean (minimum–maximum confidence intervals of estimates used), *N*	**1.5 (0.9–2.1), 4**	**6.1 (5.0–7.2), 2[e]** **4.9 (2.6–7.2), 3**	**7.0 (6.7–7.3), 2**	—	—

[a]Estimates are in millions, with those used to calculate mean values in bold; where earlier estimates from a particular method have been superseded by later estimates, only the latter are in bold and used in calculations for mean estimates.
[b]The intention of Stork's (55) analysis of Erwin's methodology was to show that one could come up with almost any figure depending on how the assumptions are manipulated. Data compiled from Reference 8 (with some corrected figures from the literature) and Reference 61.
[c]Estimate not used in calculating means, as their methodological basis is unreliable.
[d]Estimate not considered as they do not have a methodological base and should be ignored.
[e]Mean estimate without including higher taxonomic ratios estimate (see text for further explanation).

have been referred to as guesstimates (61). Given that there are now other more reasoned estimates with testable assumptions, there is no need to use these estimates further.

Host Specificity

One of the first to use a reasoned methodology and set of testable assumptions was Erwin, who sampled beetles by knockdown insecticide, fogging 19 individuals of a moderately common

Central American tree, *Luehea seemannii* (13). He collected and sorted 955 species of beetles and added an estimate of 206 for weevil species, which had not been sorted, rounding up to 1,200 species. He assumed that host-specificity levels were 20%, 5%, 10%, and 5% for herbivores, predators, fungivores, and predators, respectively, indicating that 163 species were specific to this tree. He guessed that there were 50,000 tropical tree species and postulated that if they each had similar numbers of host-specific beetle species, there should be around 8 million beetle species. He then assumed that beetles constitute 40% of all arthropod species and that the canopy is twice as rich as the ground fauna, so adding these other components gave a total of 30 million species of tropical arthropods. Several authors since have shown that Erwin's guess for host specificity was too high (4, 42, 43, 55). With a much larger amount of data for each of Erwin's assumptions, Hamilton and colleagues (20–22) used Latin hypercube sampling, a specialized form of Monte Carlo simulation wherein probability distributions are sampled in a stratified random manner to test where the greatest uncertainty lay. Two models gave predicted medians of 6.1 million and 7.8 million tropical arthropod species globally, with 90% confidence intervals of 3.6 to 11.4 million and 3.9 to 13.7 million, respectively. These models lend little support to hyperestimates of tropical arthropod species richness, with both models suggesting probabilities of <0.00001 for estimates of 30 million or greater (20, 21). A third model using probability-bounds analysis gave similar results but with larger 90% confidence intervals (22).

Ratios of Known to Unknown

Raven (46) noted that for mammals, birds, and other large and well-documented animals, there are roughly twice as many tropical as temperate species and suggested that if the same ratio holds true for other organisms then, with 1.5 million species described and with two-thirds of these being temperate, the global total for all eukaryote organisms would be 3 million plus. Using ratios of faunas to floras to predict numbers of species has a logical ecological and biogeographical basis. Taking a similar approach, Stork & Gaston (60), and Stork et al. (61) in a recent update, argued that ratios of the number of butterfly species to other insect species in Britain (67:24,043) could be used against the number of butterfly species in the world (15,000–21,000) to estimate the number of insect species in the world as 5.4 million to 7.2 million, and for beetles, 900,000 to 1.2 million species.

New modeling of the rates of species description suggest there are 405,000 species of plants (30). Further, 2.1% of the world's flowering plants are found in North America (excluding Mexico) (30), and with the beetle faunal total projected to be 28,000 for the same region, global numbers of beetle species alone are estimated at 1.2–1.3 million species (61).

Higher Taxonomic Levels

One novel approach to estimating global species richness is based on the observation there is a consistent numerical trend that links the numbers in each category of Linnaeus's taxonomic classification with a consistent increase at each lower taxonomic level. Analyzing the 1.2 million species currently cataloged and noting that the higher taxonomic levels are more completely classified, Mora et al. (39) predicted that there are 8.74 million species [standard error (SE) $\pm$ 1.3 million] on Earth, with 7.77 million (SE $\pm$ 0.96 million) of these being Animalia of which 2.6 million are insects. A problem with this method is all higher taxonomic levels above species arguably are artificial and genera, tribes, and orders, for example, may be higher or lower in some groups than others. How do we equate tribes, for example, in different insect orders let alone across groups such as nematodes or fungi? Such differences may be further exacerbated depending on whether the most active or early taxonomists for a particular taxon were so-called lumpers or splitters. How to assess this potential level of error is not clear, and whether the fundamental concept for this method is sound is not clear either.

Proportion of New Species in Samples

One attempt at estimating global species richness is based on assessing the proportion of new species in a new collection from a single location and extrapolating globally (27). Here, the authors examined 1,690 species of Hemiptera collected on a year-long expedition to Sulawesi (Indonesia) and estimated that 62.5% were new species. They then used two methods to estimate global species richness from their data. First, they argued that if the same proportion of undescribed species was found worldwide, then with 79,000 described species of Hemiptera, the world total would be 184,000–193,000. They suggested that Hemiptera constitute 7.5–10% of the canopy insect fauna, and extrapolating for all insect species gives figures of 1.84–2.57 million. Second, they further suggested that there were about 500 tree species in the region sampled and that if these had produced 1,056 new Hemiptera species, then 50,000 tree species worldwide (13) would produce 105,600 new species of Hemiptera. Adding on the described species would give 187,300 species and, extrapolating up again, a global estimate for all insects of 1.87–2.49 million that was very close to their previous estimate (27). However, they provided no evidence that the proportion of new species would be the same elsewhere in the world. In addition, because on average, common species tend to be sampled first, the authors may not have adequately sampled Hemiptera in the region; this suggests their estimates are too low (23, 56).

Discovery Curves

Estimates of species richness from discovery curves have been used for more than 50 years, with the estimate being the predicted asymptote for accumulative number of species against time (45, 54, 63). Using birds as a test group, Bebber et al. (5) found that unless the species discovery curve has an asymptote, estimates will have very large margins of error and are not statistically rigorous. One such estimate of 2.05–3.4 million insect species has been derived using discovery curves of Braconidae in the Palearctic (11). An important improvement to discovery curve estimates is correcting for the number of taxonomists describing species at any one time (30) (see also References 10 and 44). Costello et al. (10) used a stochastic process model to fit a discovery curve for 580,000 marine and terrestrial animal species from the Catalogue of Life and estimated that there may be only 1.6–1.7 million terrestrial species of eukaryotes on Earth. The insect groups they used included Lepidoptera, Orthoptera, Scarabaeidae, Vespidae, and Odonata, which are among the largest and most studied insect groups. Because larger species tend to be described first (15, 61), these groups are therefore not representative of the remaining insect groups in terms of the percentage remaining to be described. Not surprisingly, their global species estimates are low (61).

Body Size and Year of Description

Gaston (15) showed that the mean body size of British beetles (arguably the best-known beetle fauna in the world) decreases year by year from the earliest described species to the most recently described, with the decreases becoming smaller each year. Stork et al. (61) suggested it might be possible to measure the mean body size of the world's described beetles and plot where in time it fitted on Gaston's plot of mean body size of British beetles against year and thus estimate what proportion of the world's beetles remain to be described. To test this, they calculated the mean body size of a random sample (2,652 species) of the world's most comprehensive beetle collection (179,649 species in 2010) in the Natural History Museum, London (NHM). Stork et al. (61) found that the 95% confidence intervals for the mean body size of the NHM beetles fitted the 95%

confidence intervals for the mean body size of all named British beetles described by the years 1758 and 1762 on Gaston's plot, when 352 species and 437 species had been described, respectively. They suggested that the ratio of the number of beetle species in the NHM to the number of British species described in 1758 or 1762 may be used for converting the number of British beetle species into global estimates of 1.7 million and 2.1 million species (4,069 × 179,649/437 and 4,069 × 179,649/352, respectively). Using a ratio of 1 beetle to 3.9 other arthropod species derived from other methods (20–22) gives estimates of 5.9–7.4 million species of arthropods.

Expert Opinions—Taxonomists' Estimates

Taxonomists have often given estimates for how many species there might be for their given taxa, and one survey of taxonomists suggested a total of 5 million insect species (16). Probably most taxonomists base their estimates on their extensive knowledge of collections around the world of their focal taxon and the frequency with which they encounter new taxa. They also are probably influenced by estimates from other taxonomists whose knowledge they respect. Sophisticated statistical methods now exist for eliciting expert opinion, and new estimates derived this way on the diversity of life on coral reefs (8) suggest this may be a fruitful area for further exploration with other taxa.

HOW DO WE USE THIS RANGE OF ESTIMATES TO DERIVE WORKING GLOBAL ESTIMATES?

In this review, I have described a number of different methods for estimating global species richness, each with its own caveats and assumptions, and some more reliable than others. These are shown in **Figure 2** and summarized in **Table 1** with mean estimates (with upper and lower values) shown for all of these and for the group of estimates that I have indicated are the most reliable. These latter figures are the same as or close to those in Reference 61, which focused on the species richness of beetles and argued that because this taxon accounts for around 40% of all described species of arthropods, estimating the global richness of this taxon was important. Stork et al. (61) presented four new and independent estimates of beetle species richness, which produce a mean estimate of 1.5 million beetle species. Using these methods and other recent methods, they also derived estimates for all insects [mean of 5.5 million species (range, 2.6–7.8 million)] and for terrestrial arthropods [mean of 6.8 million species (range, 5.9–7.8 million)]. In **Table 1**, I show mean values for those estimates that I consider more reliable, and the figure for beetles is the same. For insects, I have some doubts about the higher taxonomic ratio method, as discussed in the section titled Higher Taxonomic Levels, and have estimated the mean of estimates with and without this method, giving 4.9 with and 6.1 without—I therefore concur with the mean estimate of 5.5 from Reference 61. The three estimates for terrestrial arthropods using host specificity are all from the same data set, and here, I have used a single mean from these in calculating the mean of estimates of 7.0 million species—slightly higher than the estimate in Reference 61.

After six decades, estimates of global richness for marine, coral reef, and terrestrial species have all failed to converge (8). Correcting for two incorrect numbers in the supplementary material in Reference 8 (4.7 m for arthropods added for Reference 37 and median value of 4.8 m for insects from Reference 43), and again using least-squares regression as in Reference 8, the R^2 values are nonsignificant for insects and arthropod estimates together ($R^2 = 0.089$, $P = 0.202$, 20 observations), for insects (0.032, 0.601, 11), for insects without unreliable estimates (0.005, 0.872, 8), and for arthropods without unreliable estimates (0.555, 0.055, 7), confirming that, as previously suggested (8), estimates for these groups are not converging. The exception is for terrestrial arthropods ($R^2 = 0.578$, $P = 0.017$, 9 observations) (**Figure 2**), but this is due to two

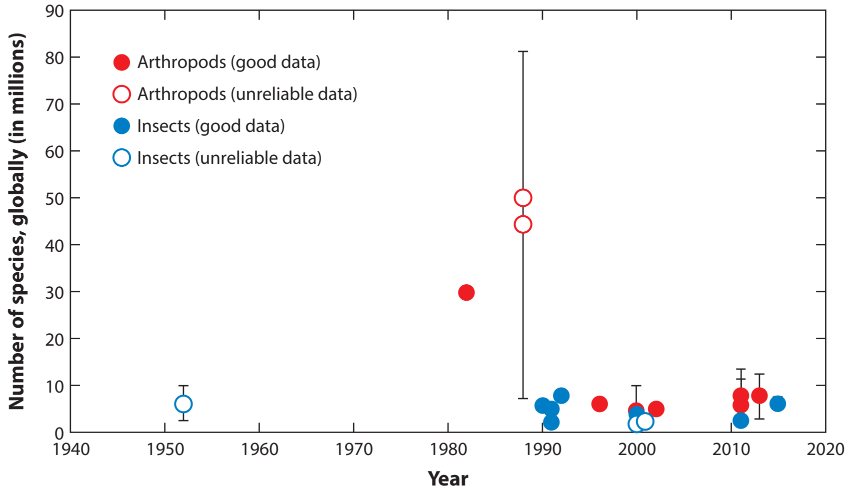

Figure 2

Estimates of the global species richness of insects and terrestrial arthropods, in millions of species, against year (data from **Table 1**).

unreliable estimates (14, 55) and the 30 million species estimate (13), which should be considered an outlier. However, as has been previously argued (61), because the narrow range (0.9–2.1 million) of estimates for beetles were from four different methods (host specificity relationships, ratios with other taxa, plant–beetle ratios, and body size), this represented a major advance in homing in on the richness of this taxon as well as of insects and terrestrial arthropods. In addition, some of the newer estimates in **Table 1** and **Figure 2** (20–22) have confidence intervals and build on many previous attempts to determine how many species of insects and arthropods exist.

UNDERSAMPLING AND GEOGRAPHICAL DISTRIBUTION OF INSECTS

To date, there have been no attempts to predict how the world's insect species may be distributed across different biogeographical regions, and here, I suggest that estimates of how plant species are distributed (30) may be used as a first guide (**Table 2**). Such an analysis indicates that the ratio of tropical to temperate species may be higher than previously thought (e.g. 46), with the estimates suggesting less than 15% of insect species are north temperate and that 85% of species are found in the tropics and south temperate regions. More than 1.6 million species of insects may be in the neotropics with similar figures for the combined Australasian region and the Indo-Malayan regions and less than a million species for Afrotropical region (**Table 2**).

If, as the mean global estimates in **Table 1** show, roughly 20% of species have been named, then we have massively undersampled the world's insect fauna, particularly in the tropics. Many insect species are known from either one location or single specimens (57) because of lack of sampling and the fact that there are always a high proportion of single individuals in samples (41). It tends to be assumed that tropical insect species have narrow geographic ranges because poor collecting has generated a paucity of evidence to the contrary (17). An analysis of the distribution of 159 species of pimpline ichneumon wasps sampled by a network of Malaise traps operated at 17 sites throughout Costa Rica between 1986 and 1990 found that about 40% of the fauna could be collected at any one of the sampling sites (17). What is clearly needed to address the problem

Table 2 Estimates for the numbers of terrestrial arthropod, insect, and beetle species in different biogeographical regions (38) based on the percentage distribution of the world's plant species (29a, 30) (for example, for Australasia, the number of arthropod species is 13.10% of the total of arthropod species worldwide—890,799)

Region	Predicted % of world's plant species	Number of vascular plants	Number of arthropod species	Number of insect species	Number of beetle species
Australasia	13.10	52,728	890,799	720,521	196,515
Afrotropical	17.73	71,363	1,205,639	975,179	265,971
Central America	11.18	45,000	760,240	614,918	167,713
Indo-Malayan	13.36	53,774	908,479	734,822	200,416
North America	2.10	8,453	142,800	115,503	31,502
Neotropics	29.46	118,577	2,003,279	1,620,348	441,935
Oceanic	3.54	14,249	240,720	194,706	53,104
Palearctic	9.53	38,358	648,040	524,165	142,961
Total	100	402,500	6,799,996	5,500,163	1,500,118

The number of flowering plants for North America given here and derived from Joppa et al. (30) is considerably lower than the recent estimate of 18,600 species for this region by the Missouri Botanical Gardens (**http://www.missouribotanicalgarden.org/media/fact-pages/flora-of-north-america.aspx**). This suggests that more work needs to be done to determine how plant species are distributed globally; hence the figures given in **Table 2** for how insect species are distributed are just a first estimate.

of undersampling is longer-term sampling using a variety of methods across a wide range of locations (55).

THE CASE FOR MUCH GREATER NUMBERS OF SPECIES OF MITES

There has been some debate as to whether the diversity of the soil fauna and mites in particular has been overlooked, with some suggesting there might be several hundred thousand or even a million mite species (23). Mites are generally very small, with the smallest adults being 80 μm but most species measuring 400–800 μm (19). As Walter (62) has suggested, most species of mites fall below the size that May (36) used in his body size estimates of global diversity and therefore should be hyperdiverse. Halliday et al. (19), in a careful review, suggested that about 48,200 species of mites had been described (at year 2000) with estimates for the faunas of Britain and North America north of Mexico as 2,590 and 28,800, respectively. They used multiplication factors based on the increase in species numbers from reviews of selected groups to derive these figures. These estimates are not too dissimilar to the number of described beetle species from Britain and estimated numbers of beetles from North America of 4,069 (12) and 28,000 (33), respectively. Like beetles, mites are ecologically diverse, and comparisons with beetle diversity might be valid. There might be 1.3 million species of non-insect terrestrial arthropods (61), and because spiders are likely to number roughly 122,000 (2), there well may be a million species of mites (1.3 million − 122,000 = roughly 1 million).

CRYPTIC DIVERSITY

The possibility that global species estimates might be underestimated because of cryptic diversity was first raised by Adis (1). Enormous advances in revealing cryptic diversity have come from using DNA methods. Well-documented examples of DNA analyses of single species of butterflies reveal many hidden species (7, 25), but what these sometimes show is that once separated by barcoding, morphological differences for species can be found in adults or other life stages, such as the larval stage (7). Consequently, the real level of truly cryptic species that cannot be separated morphologically even once their presence had been detected using DNA and other tools may be much lower, particularly for poorly studied groups.

Determining just what is the level of real cryptic species is not necessarily straightforward. Using average numbers of cryptic species from taxonomic studies using molecular assessment is not a valid approach to determine the rate of hidden species because taxonomists do not necessarily select species groups randomly, as they generally have some prior evidence that there is hidden diversity within a particular group that requires the use of DNA tools (3). More indicative of the level of potential cryptic diversity are those studies in which whole or large parts of faunas are selected randomly for DNA analysis (e.g., 29). Several such studies of European beetles and bees reveal little change in the apparent number of species after DNA barcoding. For beetles, DNA barcode sequences ≥500 base pairs were obtained from 15,948 individuals of 3,514 species (53% of the German fauna) representing 97 of the 103 families: 92.2% could be unambiguously assigned to single species, 6.8% were assigned to more than 1 barcode, creating 395 barcode identification numbers (BINs), and 2.6% shared BINs with another species (26). Overall, there was a potential increase in the number of species of 2.2% (26). In a similarly large sample for bees, there was a net increase in BINs of 8%, with some species sharing the same BINs and others separated by 2 to 4 BINs (53). Of course DNA barcoding may not reveal all cryptic species, and in that case, the percentage of truly cryptic species may be higher than I have suggested.

There has been some discussion as to whether there are differences in the proportion of cryptic species in different parts of the world and different groups (6). Purported biogeographical differences in the distribution of cryptic species with higher percentages in the tropics than temperate regions might well be the result of centuries of more intensive taxonomic study that temperate insects have received compared to those from the tropics. Janzen et al. (28), for example, DNA barcoded 100,000 insect specimens of selected target groups, revealing 3,500 species, and they found that there was a 9.1%, 54.6%, and 69.1% increase in identified species for Lepidoptera, Braconidae, and Tachinidae, respectively. These figures are probably, as one might expect, with far fewer species being detected for the more well-known Lepidoptera than the other two groups. They noted that after separation by barcoding many but not all of these cryptic species subsequently could be distinguished by subtle morphological and/or ecological traits. As discussed above, use of good traditional morphological methods of taxonomy and intensive study with large numbers of specimens from many locations are likely to separate most species previously found to be cryptic.

Inevitably, cryptic species are likely to be more evident in geographically widespread species or those in areas of evolutionary flux, such as islands. Levels of synonymy in different groups range considerably with some well-studied families of butterflies having 50–80% synonymy, whereas for moths of the family Noctuidae, it is 20%, with other groups of insects showing similar levels, depending on how well studied the group is (18). Because, no doubt, there are still hidden synonymies in our current catalogs of insects and these could be balanced by species that need further separation (cryptic diversity), I see no need to adjust the global species estimates either upward or downward for either at this stage.

CONCLUSIONS

In this review, I summarize a range of different methods of estimating global species of insects, many of which have testable assumptions and estimates of error, and provide consensus estimates of 5.5 million and 7.0 million for insect and terrestrial arthropod species, respectively. Much higher estimates seem improbable, but several problematic areas may change this view. First, much more extensive sampling of previously overlooked areas of the world may reveal many more species, although some estimates do attempt to take this into account. Second, increasingly more sophisticated and rapid DNA techniques may show that there are many more cryptic species than we have previously considered. These are key areas for further research.

APPENDIX

Numbers of described species in the major taxa constituting the Arthropoda in the Catalogue of Life from Zhang (64); Insecta are broken down into orders in the shaded region of the table.

Taxon	Extant species described
Phylum Arthropoda	1,214,295
Subphylum Chelicerata	111,937
Class Pycnogonida	1322
Class Arachnida	110,615
Order Opiliones	6,484
Order Scorpiones	1,947
Order Solifugae	1,113
Order Pseudoscorpiones	3,454
Order Palpigradi	82
Order Ricinulei	58
Order Opilioacarida[a]	35
Order Holothyrida[a]	27
Order Ixodida[a]	891
Order Mesostigmata[a]	11,424
Order Trombidiformes[a]	25,797
Order Scarcoptiformes[a]	16,299
Order Araneae	42,473
Order Amblypygi	161
Order Thelyphonida	110
Order Schizomida	260
Subphylum Myriapoda	11,885
Class Chilopoda	3,100
Class Symphyla	187
Class Pauropoda	835
Class Diplopoda	7,753
Subphylum Crustacea	66,914
Subphylum Hexapoda	1,023,559
Class Collembola	8,130
Class Protura	804
Class Diplura	800
Class Insecta	1,013,825
Order Archaeognatha	513
Order Zygentoma	560
Order Ephemeroptera	3,240

Order Odonata	5,899
Order Orthoptera	23,855
Order Phasmida	3,014
Order Embioptera	463
Order Grylloblattodea	34
Order Mantophasmatodea	15
Order Plecoptera	3,743
Order Dermaptera	1,978
Order Zoraptera	37
Order Mantodea	2,400
Order Blattodea[b]	7,314
Order Psocoptera	5,720
Order Phthiraptera	5,102
Order Thysanoptera	5,864
Order Hemiptera	103,590
Order Hymenoptera	116,861
Order Strepsiptera	609
Order Coleoptera	386,500
Order Neuroptera	5,868
Order Megaloptera	354
Order Raphidioptera	254
Order Trichoptera	14,391
Order Lepidoptera	157,338
Order Diptera	155,477
Order Siphonaptera	2,075
Order Mecoptera	757

[a]These six orders form the two superorders of the mites—Parasitiformes and Acariformes.
[b]Blattodea now includes the termites (Isoptera).

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