New approaches narrow global species estimates for beetles, insects, and terrestrial arthropods

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It has been suggested that we do not know within an order of magnitude the number of all species on Earth [May RM (1988) *Science* 241(4872):1441–1449]. Roughly 1.5 million valid species of all organisms have been named and described [Costello MJ, Wilson S, Houlding B (2012) *Syst Biol* 61(5):871–883]. Given Kingdom Animalia numerically dominates this list and virtually all terrestrial vertebrates have been described, the question of how many terrestrial species exist is all but reduced to one of how many arthropod species there are. With beetles alone accounting for about 40% of all described arthropod species, the truly pertinent question is how many beetle species exist. Here we present four new and independent estimates of beetle species richness, which produce a mean estimate of 1.5 million beetle species. We argue that the surprisingly narrow range (0.9–2.1 million) of these four autonomous estimates—derived from host-specificity relationships, ratios with other taxa, plant:beetle ratios, and a completely novel body-size approach—represents a major advance in honing in on the richness of this most significant taxon, and is thus of considerable importance to the debate on how many species exist. Using analogous approaches, we also produce independent estimates for all insects, mean: 5.5 million species (range 2.6–7.8 million), and for terrestrial arthropods, mean: 6.8 million species (range 5.9–7.8 million), which suggest that estimates for the world's insects and their relatives are narrowing considerably.

biodiversity | body size | Coleoptera | species richness

Beetles account for roughly 25% (350,000–400,000 species) (1) of all described species (~1.5 million species), making this the most species-rich order known on Earth and supporting the philosopher Haldane's famous observation that God has "an inordinate fondness for beetles" (2, 3). Therefore, because this is a single lineage, an understanding of their global species richness, and that of the insects and other arthropods of which they form a part, is particularly important. There have been several reviews that discuss the merits of different estimates of the species richness for these taxa as well as of other organisms (1, 4–9), but none have been able to use these to derive mean estimates with some measure of error associated with these means. Here we compare global species estimates for beetles, insects, and terrestrial arthropods from eight different methods of estimation (here called methods 1–8). One of these (method 8) we introduce here, called the "body size and year of description" method, is based on the observed tendency for larger species of organisms to be described and named before smaller species, resulting in a decline in the mean body size of named species over time (10, 11). We use data for beetles from the Natural History Museum (NHM) world collection in London and the British fauna to test this method. There has been some discussion as to whether global species estimates are converging (12) or not (13), and here we test this further.

Methods

British Beetle Body Sizes. The most recent checklist (14) was used for the list of names of British beetles and the year they were described. Body lengths were calculated as mean values of the body-size ranges provided by Joy in 1932 (15). For the ~700 species added to the British list since then, a range of electronic and literature sources was used to derive body sizes. Body sizes could not be found for ~20 species (only 0.5% of species), and estimates of body sizes for these species were made using the mean body sizes of either other species in the same genus or of similar genera in the same subtribe or tribe. The year of description of each species was traced using the checklist of British beetles (14). We note that the year of description for a species is not necessarily the same year a species is recognized as occurring in Britain, because a species may be described elsewhere in Europe and it may take many years before it is recognized as being present in Britain. Some of the more recent changes in the new British checklist (14) reflect such additions. For example, *Asaphidion curtum* (Carabidae) was described by Heyden in 1870 elsewhere in continental Europe but was not recognized in Britain until 1986 (16), even though it has no doubt been present for a very long while, as it is very similar to *A. flavipes* (L). Our body size–year plots reflect the year of description and not when a species was discovered in Britain. Disentangling these two different dates would be a very complex task.

Body Sizes of Beetles in the NHM. Data from the curated named species of beetles in the NHM collection were made in June 2011. The collection of named beetle species is housed in 8,891 drawers across 972 cabinets. Every three cabinets, a single drawer was selected from across those cabinets using random numbers. In total, 189 drawers were selected for data collection. Some cabinets contained no curated beetles, and these were ignored. The number of drawers in cabinets varied between 15 and 20, and in some instances the drawer selected either was empty (drawers are left empty throughout the collection to allow easy expansion as new specimens are added) or held unsorted specimens. In these cases, the next drawer of the curated collection was selected. When selected, the drawer was removed from the cabinet and the names of all named species and their body lengths were recorded. Body lengths were measured from the anterior-most part of the head, excluding the antennae, to the posterior-most point of the

Significance

Many suggest we are approaching a sixth mass extinction event, and yet estimates of how many species exist, and thus how many might become extinct, vary by as much as an order of magnitude. There are few statistically robust methods to estimate global species richness, and here we introduce several new methods, including one that builds on the observation that larger species are often described before smaller species. We combine these, giving equal weight to each, to provide mean global species estimates for the most speciose order, class, and phylum on Earth, beetles, insects, and arthropods (terrestrial). We attempt to aid conservation planning by broadening the range of methods used and bringing greater stability to global estimates for these taxa.

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

Method	Beetles	Insects	Terrestrial arthropods (ref.)	Year	Concept
1. Host specificity	12.2		30.0 (17)	1982	Made assumptions about insect host specificity to trees, number of tropical tree species, ratio of beetles to other insects, and those found in the canopy versus the ground
	4.9–40.7		7.3–81.4 (8)	1988	Subsequent remodeling using additional data produced a range of estimates (the upper and lower ones being included here) depending on the assumptions
	0.6–2.2		2.4–10.2 (18)	2000	Subsequent remodeling using additional data, again producing a range of estimates (with the upper and lower estimates given here)
	1.5–1.9		6.1–7.8 (19, 20, 44)	2012–2013	Two new models use Monte Carlo simulations to account for uncertainty associated with model variables incorporating a wide range of host-specificity and other data; models were rerun here to give beetle-only figures
2. Ratios of known to unknown		4.9–6.6 (21)		1990	Ratio of butterflies to other insects in the British fauna (67:22,000) and upscaling with estimates of 15–20,000 world butterfly species
	0.9–1.2	**5.4–7.2**		This paper, 2015	Here updated using 24,043 for British insect species (22)
3. Plant:beetle ratios	**1.2–1.3**			This paper, 2015	Modeling of the number and regional distribution of all plants (23) suggests 2.1% of the world's plants are found in North America (excluding Mexico); the beetle faunal list is 25,160, with a projected total (including undescribed species) of 28,000 (24)
4. Higher taxonomic ratios		2.6 (37)		2011	Higher taxonomic classification has a predictable pattern and is used to predict species richness
5. Taxonomists' estimates		5 (34)		1991	Asked a range of insect taxonomists how many species they thought existed for their group
6. Educated guesses and guesstimates		0.02 (42), 3, 100			
7. Proportion of new species		1.84–2.57 (43)		1991	Estimating the proportion of new species in intensively sampled Hemiptera from Sulawesi and using this to add to existing described species for the world
		3–6.7 (9)		1993	Remodeled to take into account incomplete sampling
8. Body size and year of description	**1.7–2.1**		**5.9–7.4**	This paper, 2015	Mean body size of a sample of beetle species in the Natural History Museum compared with the mean body size of British beetles over time; estimates for arthropods are based on a modeled ratio of 1 beetle to 3.9 other arthropod species derived from other host-specificity estimates (19, 20, 44)

Estimates are in millions, with new estimates from this paper in bold. We have not included any estimates (here called "guesstimates") where there was no clear basis for the figure. Estimates within three time periods (1980–1989, 1990–2000, and 2001–present) are shaded, with the darkest shading for the earliest period and the lightest for the current period.

abdomen or elytra for the largest and smallest individuals in a series and the mean was determined.

Number of Beetle Species in the NHM. The database of the NHM's beetle collection at the time of sampling (2011) comprised 179,649 species, excluding subspecies, recognized synonyms, and manuscript names. This is roughly half of the world's described beetles. Currently the collection has 188,735 full species (December 19, 2014), suggesting roughly 2–3,000 species are being added a year. Like all large taxonomic collections, specimens where they have been identified to species have been added to the collection including new species. However, with almost 9,000 drawers, it is impossible for the curators to make sure that all parts of the collection are taxonomically correct and reflect the current systematic arrangements of species. Some of the taxa listed as species in the collection may now have been synonymized but corrections to the collection have not always been made. We have no reason to believe that the size distribution of the beetle species in the NHM is not representative of all currently described beetle species.

Year of Description Against Body Size for Beetles in the NHM. To test whether the negative correlation between year of description and body size found for British beetles (12) was also true for the NHM's beetle collection, the year of description was sought for a subsample of the beetles that were databased for this study. Tracking down the year of description for the species in the sample was largely done through a number of the global species databasing systems that are currently available as well as through publications. Families for which year of description were recorded were completed in alphabetical order up to and including Phengodidae. Families where it was difficult to find the year of description for more than 95% of species were not included in this analysis to avoid biasing the sample.

Results

The different methods of estimating global species richness for the focal taxa and the resulting estimates are summarized in Table 1 and are summarized here. Method 1: The host specificity of insects to trees (8, 17, 18) has been recently reexamined (19, 20) and here, using the same modeling, we provide estimates for beetles alone. Method 2: The ratio of butterflies to other insects in the British fauna scaled up using estimates for all butterflies in the world (21) has been updated here using new estimates of the British insects (22) to give estimates for beetles and insects of the world. Method 3: Recent modeling of the number and regional distribution of all plants (23) suggests 2.1% of the world's plants are found in North America (excluding Mexico). The beetle faunal list of this region is 25,160 with a projected total (including undescribed species) of 28,000 (24). Here we assume that the ratio of beetle to plant species is similar across the world, scaling up to give an estimate of the number of beetle species in the world. Figures for methods 4–7 (higher taxonomic ratios, taxonomists' estimates, educated guesses, and proportion of new species) are from the literature and are discussed further below.

Method 8: Because Gaston (11) found that larger species of British beetles were generally described earlier than smaller species, we used a plot of the cumulative $\log_e$ mean body size for British beetles against year to test where the mean body size of a sample of the NHM's world collection of beetle species fitted. We found that the 95% confidence intervals for the mean body size of a sample of 2,652 named beetle species in the NHM encompass the 95% confidence intervals for the mean body size of all named British beetles described by the years 1758 and 1762, when 352 species and 437 species had been described, respectively (Fig. 1; see also Fig. S1, where we have used cumulative species instead of year for the *x* axis). We suggest that the ratio of the number of beetle species in the NHM collection to the number of British species described in 1758 or 1762 can be used as multiplication factors (e.g., 179,649/352 = 510.4 and 179,649/437 = 411.1) for converting the number of British beetle species currently described into a global estimate (under certain assumptions, as discussed below). If we assume that the 4,069 described British beetle species (14) represent the complete fauna, then using these British-to-global multiplication factors for the years 1762 and 1758, we estimate that there are 1.7–2.1 million beetle species globally (4,069 × 411.1 = 1.7 million and 4,069 × 510.4 = 2.1 million). The negative relationship between body size and year of description ($r = -0.404$, $n = 3{,}637$, $P < 0.001$) found by Gaston (11) we retested with a more complete and up-to-date British beetle database and, as Gaston had previously shown, adding the newer recent species reduces the slope ($r = -0.370$, $n = 4{,}069$, $P < 0.001$). We also found a weak negative relationship between body size and year for a sample of NHM beetles ($r = -0.150$, $n = 917$, $P < 0.001$). Therefore, this suggests that the tendency for larger species to be described before smaller species possibly may be a widespread phenomenon.

To examine how global species estimates have changed over time, we present mean estimates of global species richness for three time periods, 1980–1989, 1990–2000, and 2001–present for

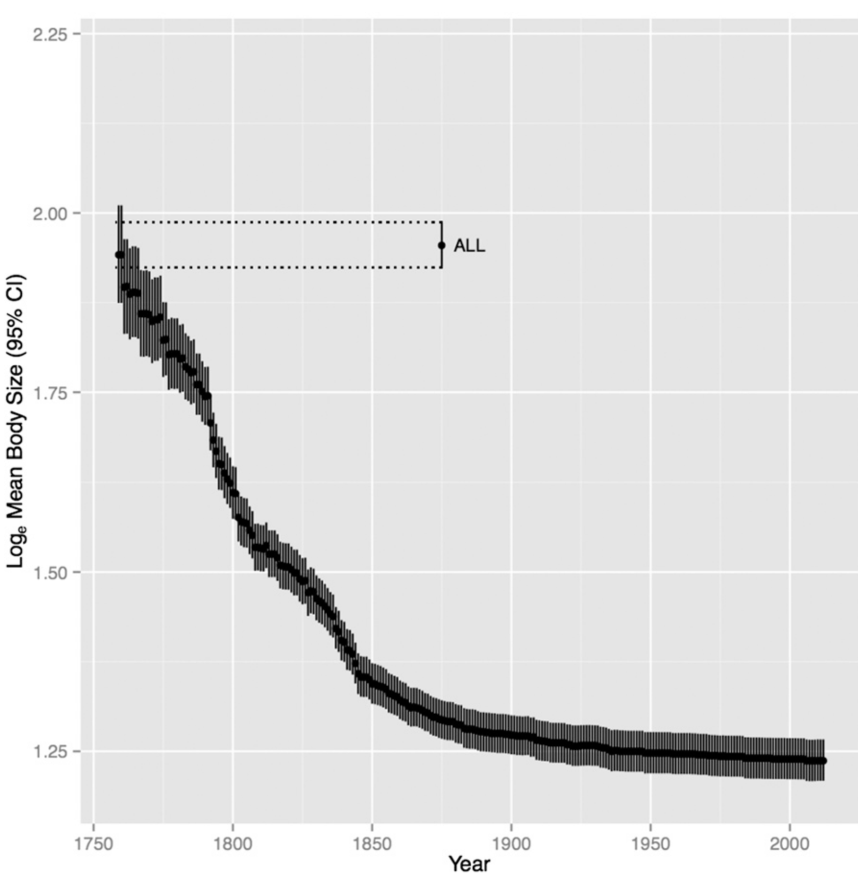

Fig. 1. Cumulative $\log_e$ mean [with 95% confidence interval (CI)] of British beetle body size for each year from 1758 to 2014, and for mean body size (with 95% CI) for a sample of beetles from the Natural History Museum, London (ALL). Note that the horizontal axis is arbitrary for ALL but that the dotted horizontal lines indicate where the 95% CIs intercept the years for the British data (see also Fig. S1).

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Table 2. **Calculations of means of global species richness for each taxon are based on those estimates from Table 1 in three time periods: 1980–1989, 1990–2000, and 2001–present**

	Time period	Beetles	Insects	Arthropods
Mean global estimates, mean (range; maximum/minimum)	1980–1989	17.5 (4.9–40.7; 8.3) $n = 2$		36.8 (7.0–80.0; 11.4) $n = 2$
	1990–2000	1.6 (0.6–2.2; 3.7) $n = 1$	4.7 (1.8–6.7; 3.7) $n = 4$	6.0 (2.0–10.0; 5.0) $n = 1$
	2001–present	1.5 (0.9–2.1; 2.3) $n = 4$	5.5 (2.6–7.8; 3.0) $n = 4$	6.8 (5.9–7.8; 1.3) $n = 2$

These means represent the means of estimates made in individual studies, with some of these estimates being point estimates and others being measures of central tendency for probability distributions (e.g., medians). Confidence intervals for probabilistic estimates are not used here. *n*, number of studies.

beetles, insects, and terrestrial arthropods, giving equal weight to the eight methods (Table 2). Each method has its own differently calculated measures of uncertainty and, therefore, rather than providing SEs for the means for each period, we have chosen to provide the upper and lower estimates as a measure of the variation.

Discussion

We have made several assumptions that require further explanation in our new method of estimating global species richness from the body sizes of British beetles and those in the NHM (method 8). We have assumed that British beetles are representative of beetles worldwide both in terms of their taxonomic composition and body-size distribution and offer two sets of evidence that support this. First, Spearman's rank correlations of the number of species in different families of beetles sampled from trees from the Palearctic, Southeast Asian, Central American, and Australian biogeographic regions suggest that the beetle faunas of these regions are similarly structured taxonomically ($\rho = 0.44–0.71$ across the pairwise correlations, with all correlations being highly significant, $P < 0.001$) (25). This reflects the fact that beetles are a relatively old group, with most families appearing in the geological record before the breakup of Gondwana (26). Second, at the regional scale, faunal species richness of the United Kingdom appears to be similar to that of other Western European countries of a similar size and latitude (Fig. S2). We have also assumed that the cataloguing of British beetles is near-complete. Addition of species to the British list will therefore increase estimates of global beetle species. Our assumption that the body size of British beetles reflects that of the rest of the world remains to be tested. Body-size variation in insects, particularly interspecific variation with temperature and nutrition, has received considerable attention (27), but evidence on how the size distributions of assemblages change with latitude is inconclusive (28–30). Although Bergmann's rule for endotherms suggests that species are larger toward the poles, there is insufficient evidence to suggest that the same is true for insects (31).

This is not the first time that the body sizes of organisms and the observation that larger species are described first have been used to estimate global species richness. Although cautioning against the idea, May (5) noted that in a log–log plot of the body sizes of all organisms a straight line might be plotted backward from the larger size classes to extrapolate the number of species on Earth. Plotting back to a minimum body size of 0.2 mm (6) and 0.1 mm (32) gives estimates of roughly 10 million species and 20 million species, respectively. Testing this model would require complete biotas of parts of the world to be measured and identified to species.

The suggestion that current global species estimates for all organisms are converging (12) around 5 ± 3 million species has been challenged (13). However, our findings lend support to this claim if insects and terrestrial arthropods are seen to be the largest contributors of species. Ranges of estimates for both groups have reduced considerably since the 1980s (Table 2). Our figures for the number of all beetle species from our mean body size and year of description method compare well with those from other methods (Table 1), with a mean of 1.5 million species.

In compiling our list of methods and estimates in Table 1, we chose to include only those with a clear methodology and testable hypotheses and not to include others, which are effectively guesses (7, 9, 33) and cannot be tested further. In this context, although some consider that estimates based on surveys of taxonomists (34) are "unscientific," we find it remarkable that the estimate of 5 million insect species made in this way is so close to our new average for insects. Sophisticated statistical methods exist for eliciting expert opinion, and new estimates derived this way on the diversity of life on coral reefs (35) suggest this may be a fruitful area for further exploration. Two other recent methods that have clear methodologies deserve some scrutiny. Costello et al. (36) used description-rate models to estimate that there may be only 1.6–1.7 million terrestrial species on Earth, which is of the same order as what we suggest here for beetles alone. They provide no estimates for the three taxa we discuss here, but many of the invertebrate groups where they do have estimates (butterflies, moths, crickets, scarab beetles, wasps, and dragonflies) are generally larger organisms and are well-studied. Not surprisingly, the estimates for how many undescribed species there may be for these groups are low. It may well be that their sample of described species is biased toward better-known groups with larger individuals of more completely described faunas and floras, hence resulting in low estimates for global species richness. Mora et al. (37) observed consistent patterns in the numbers of higher taxa, which increased predictably from phyla through to genera. Supposing that the number of species per genus is constant globally—an assumption for which there are no theoretical grounds (38)—they then extrapolated to the species level to predict that there are 8.7 million ($\pm$1.3 million SE) species of all eukaryotes on Earth, with about 75% being terrestrial. This approach makes the assumption that the pattern observed across higher taxa can be extended to species, but it is important to note that taxonomic divisions above the species level are arbitrary human constructs, and this stands in stark contrast to the species concept, which, although the details are debated (39), ultimately reflects biological concepts. It may very well be that the patterns observed in the higher taxa reflect little more than human tendencies for grouping and that these patterns should not be extended to the lowest taxon, which is arguably much less arbitrary and more biological in nature.

The question of how many species exist is complicated by the possibility of cryptic species, with many new species being revealed only through genetic analysis (40). Although molecular methods are at the forefront of resolving the problem of cryptic species, recognizing synonyms where species are accidentally described more than once is also a problem in all groups and arguably has the potential to inflate estimates considerably, especially for insects (12). The net effect or balance of such considerations is far from being resolved.

All methods of estimating global species richness have their weaknesses, most because they are based on assumptions that often have not been sufficiently tested. However, we are encouraged by the fact that the estimates from the different methods we have shown here are surprisingly similar and that their range has reduced down to a factor of 2–3 compared with as much as a factor of 10 in the 1980s and 1990s. Because there are currently so few methods to estimate how many species we share the planet with (36, 37), we believe that our body size and year of description method is an important discovery that can be tested further. Finally, why there are so many species of beetles, aside from the Creator's obvious predilection for them, appears to reflect the Jurassic origin of numerous modern lineages, high lineage survival, and diversification into a wide range of niches, including the utilization of all parts of plants (26, 41).

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