NEW ESTIMATES FOR TERRESTRIAL ARTHROPOD SPECIES-RICHNESS IN AUSTRALIA

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Australia makes up a little under 6% of the total landmass of earth, but its biota is a large and unique component of the biosphere. Arthropods, particularly insects, dominate terrestrial ecosystems, and the Australian land arthropod fauna is no exception. In comparison to the vertebrates and angiosperms, the arthropod fauna of Australia is poorly known. Commonly cited estimates of insect species-richness refer to the number of described and undescribed species held in collections. Given the size of the continent, the paucity of sampling and survey work in all but the east coast and south west, and the narrow endemism displayed by many taxa, these estimates are at best very conservative. We have surveyed the literature and canvassed taxonomic experts to derive a new estimate of the number of terrestrial arthropod species in Australia of 253 000, with almost 205 000 of these being insects. Estimating total species richness for very diverse groups is difficult, and we rely on a poll of experts and a method that extrapolates from the rate of species discovery from recent taxonomic research. The largest components of terrestrial arthropod species richness are in the Araneae (spiders), Acari (mites) and the five largest insect orders: Hemiptera (true bugs), Hymenoptera (wasps, bees and ants), Diptera (flies), Lepidoptera (moths and butterflies) and Coleoptera (beetles). These revised estimates provide an indication of how much more taxonomic research is needed in Australia to describe this fauna, and where large gaps in our knowledge still lie. An outline estimate of the resources required to describe the remaining fauna is also presented. We also discuss the reconciliation of our taxonomic estimate with those suggested by three recent ecological biodiversity surveys.

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Documenting life on earth is one of the great intellectual challenges facing humanity today (Wilson 1985, 2000; Wheeler 1995). The scope of this challenge has only been addressed in detail recently (May 1986, 1988, 1992, 2000), beginning with a touchstone paper suggesting that the number of species on earth was much larger than previous estimates and most of these species were insects in the canopies of tropical forests (Erwin 1982). Estimates of global insect diversity span the range of a few million to 80 million (Hammond 1995; Stork & Gaston 1990; Nielsen & Mound 2000), with a consensus between four and ten million (Wilson 1988; May 2000). The highest estimates rely on extrapolations that assume a rate of host specificity for herbivorous rainforest insects that is much greater than empirical data suggests (Novotny et al. 2002).

Australia spans a latitudinal range from the tropics to the temperate zone, and has a geological history characterised by isolation that predisposes it to a high percentage of biotic endemism (Mummery & Hardy 1994). Occupying almost 6% of the land surface of the earth, it has a similar proportion of described species of higher plants, and some vertebrate and insect taxa (Gaston & Hudson 1994). In contrast to the vertebrates and higher plants, Australia's invertebrate fauna, including terrestrial arthropods, is poorly documented (Nielsen & West 1994). We are discovering that many elements of Australia's invertebrate fauna are endemic to small geographic ranges (Harvey 2002), suggesting higher levels of beta and gamma diversity than for other elements of the fauna. Australia is the only country with the combination of first world economy and mega-diverse fauna (Common & Norton 1992), so it is here that world leadership in biodiversity knowledge and management is possible (Williams et al. 2001).

There have been a number of previous estimates of the size of the Australian insect fauna, the largest component of terrestrial arthropods. Tillyard (1926) estimated 37 000 species. It is difficult to interpret how he made this calculation, but it appears to be based on an estimate of the species in collections plus an allowance for unknown species in the very species-rich orders. Waterhouse (1971) extrapolated a total of 80 000–100 000 Australian species from the 54 000 species known at that time, a total quite similar to that of Taylor (1979), who conducted a detailed poll of experts to arrive at a figure of 108 000. Taylor clearly distinguished the process through which subsets of species in nature are accessed to collections, then a subset of those species in collections are described in revisions. The Commonwealth Scientific and Industrial Research Organisation's *Insects of Australia* (CSIRO 1991) also makes an estimate of the number of species for each insect family and order, giving a lower grand total for insects of 84 270 species. However, there are inconsistencies in the way the number of species was calculated between chapters. Some authors report the number of described species (eg Thysanura), some report the described species, plus those undescribed species known in collections (eg Ephemeroptera), while others clearly add to that number to account for the species in nature not yet in collections (eg Diptera). An increase in the size of the fauna was made in Nielsen and West (1994), who calculated a figure of 140 000, but did not describe the method they used.

Our purpose here is to revise the estimate for the number of terrestrial arthropod species in Australia and the proportion that are already described. Rather than being an esoteric 'numbers game' this information is critical for determining where the large gaps in our knowledge still lie, for determining research approaches and priorities, and for the allocation of finite research funds by granting bodies.

Materials And Methods

Estimates of the total number of species in an area can be made using a wide variety of methods, ranging from direct counts of described species to more indirect and theoretical abstractions (May 1994). Here we rely on expert taxonomic estimates (Tables 1 & 2) for the groups under study. These in turn rely on a knowledge of the number of described and undescribed species in collections, and a direct estimate of those additional species awaiting discovery. This last figure is often derived using a method that relies on calculating the rate at which new species are described in recent revisionary studies, and use of this rate to estimate the size of the total fauna based on the current number of described species (Table 3). We term this the 'revision multiplier' approach first used to our knowledge by Halliday et al. (1997). We compare estimates by taxonomic experts with those based only on the revision multiplier method for the very largest groups: Araneae, Hymenoptera, Coleoptera, Lepidoptera and Diptera.

Taxa under consideration here are limited to terrestrial arthropods, comprising the Arachnida, Myriapoda, Crustacea, Onychophora, and Hexapods (Insecta, Collembola, Protura and Diplura). We have included those species that are largely terrestrial but have an aquatic stage in their lifecycle (for example Odonata), and entirely aquatic groups such as water mites. The species concept we employ is a morphological one, only including species that can be clearly identified by discontinuities in morphology of preserved specimens. We recognise that detailed analyses will reveal even greater number of genetic species (see for example Rowell et al. 1995 and Rockman et al. 2001 on Australian Onychophora), but our understanding of how this may increase the species' estimates is not yet clear. For some groups, the number of described species has been derived from the Australian Biological Information Facility (ABIF) web site of the Australian Biological Resources Study (ABRS) <www.environment.gov.au/abrs/abif.htm>.

Results

The numbers of described species and estimated total species are provided separately for the non-insect groups (Table 1) and the insects (Table 2). Examples of the multiplication factors derived from recent revisions in a number of insect groups and Araneae are given in Table 3. A summary of the results presented in Tables 1 and 2 is given in Table 4. In calculating totals, the midpoint of ranged estimates was used.

For two of the five largest groups (Tables 1 & 2) expert estimates are generally very close to those derived using the revision multiplier method (Table 3). For Diptera, taxonomic experts estimate 30 000 species while the revision multiplier method predicts 30 744 (6432 x 4.78) species; and for Lepidoptera, taxonomic experts estimate 20 000 while the revision multiplier method indicates 20 748 (10 586 x 1.96) species. However, some disparities are also evident, and there

TABLE 1. Current number of described species and estimate for the true species richness for non-insect groups of Australian terrestrial arthropods by various taxonomic experts (MH = Mark Harvey)

Taxonomic category	No. of described Australian species	Estimated total Australian species	Reference/Authority
Arachnida			
Scorpionida	42	150	MH
Araneae	2399	20 000	Raven, Todd-Davies, York-Main, MH
Amblypygida	4	10	MH
Schizomida	46	80	MH
Palpigradida	0	5	MH
Pseudoscorpionida	149	750	MH
Opilionida	194	1200	MH
Acarina	2871	20 000	Halliday (1997)
Total Arachnida	**5705**	**42 195**	
Myriapoda			MH
Symphyla	29	200	Greenslade
Pauropoda	40	400	Greenslade
Polyxenida	4	25	MH
Sphaerotheriida	27	100	MH
Chordeumatida	9	75	MH
Polyzoniida	5	100	MH
Siphonophorida	3	75	MH
Polydesmida	122	1000	MH
Spirostreptida	62	300	MH
Julida	8	8	MH
Scutigerida	5	20	MH
Geophilida	30	250	MH
Scolopendrida	50	100	MH
Craterostigmatida	1	1	MH
Lithobiida	25	75	MH
Total Myriapoda	**407**	**2539**	
Crustacea			
Amphipoda	23	100	Friend (1982, 1987)
Isopoda	?	400	MH
Decapoda	?	300	MH
Total Crustacea	**23**	**800**	
Onychophora	72	250	MH
Hexapoda (Entognathous)			
Collembola	322	2000–3000	Greenslade
Diplura	28	38	ABIF
Protura	32	32	ABIF

are possibly taxon-specific reasons for these differences (see Discussion). For beetles, taxonomic experts estimate an average of 90 000 species in Australia while the revision multiplier method predicts 14% more species, *viz.* 102 596 (22 901 x 4.48). For Araneae, taxonomic experts suggest there are 20 000 species, however the revision multiplier method predicts 17% fewer species, *viz.* 16 577 (2399 x 6.91). For the Hymenoptera, this difference is even greater in that taxonomic experts suggest 43 800 species, while the revision multiplier method predicts 34% fewer species, *viz.* 28 766 (8013 x 3.59).

Discussion

There has been no previous estimate of the size of the terrestrial arthropod fauna of Australia, however the grand total for insects of almost 205 000 is higher than the previous most recent grand total estimate (Nielsen & West 1994) by about 32%. It is also much larger than the figures reported in the Biodiversity theme report of the Australian State of the Environment Report for 2001 (Williams et al. 2001). Our total falls below the Australian component of Stork's (1993) 'guestimate' of 400 000 for Australia and New Zealand.

TABLE 2. Current number of described species and estimate for the true species richness for Australian insect groups by various taxonomic experts

Taxonomic category	No. of described Australian species	Estimated total Australian species	Reference/Authority
Insecta			
Archaeognatha	10	14	ABIF
Thysanura	28	38	ABIF
Ephemeroptera	84	333	ABIF
Odonata	320	330	ABIF
Plecoptera	179	196	ABIF
Blattodea	534	587	ABIF
Isoptera	263	455	Evans
Mantodea	104	114	ABIF
Dermaptera	87	121	ABIF
Orthoptera	1835	2800	Rentz
Phasmatodea	105	115	ABIF
Embioptera	25	28	ABIF
Psocoptera	253	278	ABIF
Phthiraptera	463	648	ABIF
Hemiptera	4453	11 580	Martin, Gullan, Hollis, Fletcher, Cassis
Thysanoptera	500	1000–2000	Mound
Megaloptera	24	26	ABIF
Neuroptera	551	800	New
Coleoptera	22 901	80 000–100 000	Oberprieler, Slipinski, Weir, Calder
Strepsiptera	42	58	ABIF
Mecoptera	27	30	ABIF
Siphonaptera	84	92	ABIF
Diptera	6432	30 000	Yeates, Bickel
Trichoptera	588	800	Wells
Lepidoptera	10 586	20 000	Edwards, Horak
Hymenoptera	8013	43 800	Austin, La Salle
Total Insecta	**58 491**	**204 743**	

TABLE 3. Rates of increase of species description for diverse groups of terrestrial arthropods (i.e. 'revision multipler estimate' – see text for discussion).

Group	Species before revision	Species after revision	% Increase	Reference/Authority
Araneae				
Nicodamidae	7	22	314	Harvey (1995)
Hersiliidae	4	55	1375	Baehr & Baehr (1987, 1988, 1989, 1992, 1993, 1995, 1998)
Lamponidae	22	185	841	Platnick (2000)
Mygalomorphae	149	348	234	Raven (1994)
Average Increase (%)			**691**	
Hymenoptera				
Hyptiogastrinae (Gasteruptiidae)	31	107	345	Jennings & Austin (1997a, 1997b, 2002)
Stephanidae	9	21	233	Aguiar (2001)
Braconidae (various genera)	24	76	317	Austin (1990), Austin & Dangerfield (1992, 1993), Austin & Wharton (1992), Austin et al. (1993), Dangerfield & Austin (1995), Quicke et al. (1998), Saeed et al. (1999).
Scelionidae (3 genera)	64	266	353	Austin (1986, 1995), Iqbal & Austin (2000), Dangerfield et al. (2001)
Rhapalosomatidae	2	11	550	Austin et al. (in prep.)
Average increase (%)			**359**	
Diptera				
Bombyliidae *Comptosia*	26	138	530	Yeates (1991)
Bombyliidae *Docidomyia*	5	25	500	Yeates (1996b)
Bombyliidae *Neosardus*	5	20	400	Yeates (1996a)
Bombyliidae Anthracini	7	28	400	Yeates & Lambkin (1998)
Therevidae *Agapophytus*	10	40	400	Winterton & Irwin (2001)
Dolichopodidae Sciapodinae	41	264	643	Bickel (1994) & pers. comm.
Average increase (%)			**478**	
Lepidoptera				
Fraus	8	25	212	Nielsen & Kristensen (1989)
Paralaea	4	13	225	McQuillan et al. (2001)
Cadra	2	7	250	Horak (1994)
Lophocoronidae	3	6	100	Nielsen & Kristensen (1996)
Average increase (%)			**196**	
Coleoptera				
Pselaphinae	400	1600	400	Chandler (2001)
Pseudomorphinae	58	249	429	Baehr (1991, 1997)
Colydiidae	51	172	337	Slipinski (unpublished)
Tenebrionidae *Apterotheca*	7	44	628	Bouchard (2002)
Average Increase (%)			**448**	

Given that Australia occupies around 6% of the land area of the earth, the new estimate is proportionally compatible with a grand total for earth of 4–6 million (May 2000; Novotny et al. 2002). Australia does not have significantly large areas of tropical rainforest, however the small areas remaining are extremely important foci of species diversity and endemism in the Australian biota (Rainforest Conservation Society of Queensland 1986; Moritz et al. 2001; Yeates et al. 2002). South-western Australia is acknowledged as a globally significant biodiversity hotspot (Myers et al. 2000) and there is significant invertebrate endemism in temperate Australian habitats that we are only just discovering (Harvey 2002). These findings are compatible with the notion that global species-richness is 'pear-shaped', with the southern continents having a greater share of biodiversity than similar areas in the northern hemisphere (Platnick 1991; Eggleton 1994).

Revision multiplier methods

There are a number of reasons to believe that the 'revision multiplier' method may be inaccurate in practice, at least for some groups. For example, the average multiplication rate will depend on the particular revisions that are chosen as a sample to derive an average. The examples in Table 3 are representative of recent revisions, and exclude those outliers that would give a spurious rate, such as those that describe an entirely new genus and species (giving an infinite rate at species level), those that describe a large number of new species in an otherwise small genus of 1–2 described species (giving an overestimate), or those that add a single species to an otherwise well-known group such as butterflies or heliothine moths (giving an underestimate). In addition, there are usually a number of species recognised in revisionary works that are not formally named because of the lack of suitable material. Excluding these unnamed species underestimates the true rate of discovery. Further, descriptive research is mostly carried out as part of externally funded research and/or postgraduate training. Such studies are often restricted to groups that can be adequately treated in a 2–3 year time frame, and these are often not the highly diverse, problematic groups that require a longer time commitment. For this reason, groups that are truly species-rich, such as the Staphylinidae (Coleoptera), Chloropidae (Diptera) or Eulophidae (Hymenoptera), are absent from the rate figures thus tending to underestimate the true rate in some cases.

The revision multiplier undoubtedly also generates different biases depending on how many researchers have studied the group historically. This may be the reason, at least in part, for the difference in the apparent under-estimate for the Hymenoptera compared with the estimates of taxonomic experts. Historically, there have been very few taxonomic studies of Australian Hymenoptera, and those undertaken have mostly focused on the larger more obvious aculeate wasps, ants and bees. However, the huge species diversity within this order exists disproportionately among the parasitoid families. Most parasitoid families have been vastly understudied compared with other insect groups because of their tiny size (many in the 0.5–2 mm size range). Indeed, the expert taxonomic estimate for Hymenoptera given here may still be a significant under-estimate, given that several studies for other regions of the world have estimated the species richness of the Hymenoptera to be much closer to and even higher than the Coleoptera (La Salle & Gauld 1991). The biological basis for this huge number of Hymenoptera, in particular the parasitoid families, is that: 1) many parasitoids display a relatively high degree of host specificity; 2) different groups have specialised in exploiting all host life history stages; and 3) they have radiated into all available insect and arachnid groups to exploit as hosts. The same influences may also affect estimates in parasitoid dipteran families such as Tachinidae and Bombyliidae. The discrepancy between the multiplier effect and the taxonomic experts in Araneae may be due to the relatively few major taxonomic revisions on large families undertaken over the past decade or so. For example, Harvey (unpublished data) is currently revising the family Oonopidae, which currently contains only nine named Australian species. The total fauna is estimated to contain over 200 new species, thus producing a multiplier effect of over 2300%. The inclusion of such data would skew the figures towards that estimated by the taxonomic experts.

Although the revision multiplier method is probably inaccurate at least for some groups, it does provide a snapshot of current taxonomic research. The figures in Table 3 indicate that, for the larger terrestrial arthropod groups in Australia, the rate of increase is still very high, and not beginning to decrease to a point that would signal that our knowledge is approaching completeness. Recent discoveries such as the fascinating stygial groundwater biodiversity of the Australian arid zone (Humphreys 2001) reinforces how much we still have to learn about Australia's invertebrate diversity.

Scoping the problem

Given that we have described about one in four Australian terrestrial arthropod species in the last two hundred years (Table 4), how long will it take to describe the remaining fauna? Assuming these numbers are approximately correct, and a similar rate of discovery (60 000 species in 230 years) is maintained, we will describe that last new species of Australian terrestrial arthropod in the year 2700. Given the rates of deforestation and habitat degradation in Australia, it is likely that many of these species will be extinct long before they are discovered (see for example Regan et al. 2001). This is clearly an undesirable outcome and one that will deny us access to important information for management of our natural heritage and realisation of potential economic benefits. Current targets from Environment Australia (2001) propose a 1% per year increase in the number of taxa described for invertebrates. For terrestrial arthropod species, this amounts to around 600 per year, and at that numeric rate the fauna would be described in 2300. The actual current rate of discovery of terrestrial arthropod species in Australia is unknown.

One possible realistic scenario for approaching the task at hand is to form 20 research teams dedicated to the project of understanding Australia's terrestrial arthropod biodiversity. These teams would comprise three people, a research systematist, technical support officer and illustrator (*vide* Platnick 1999). They would operate in the areas where need is greatest, in the five largest insect orders, mites and spiders, and be stationed in institutions around Australia such as the state museums, CSIRO and the Universities. Salary costs with modest overhead components and research expenses would amount to around $300 000 per annum for each team. For all 20 groups, the budget would amount to $6 000 000 dollars per annum. If each group was to achieve an average annual output of 200 species, 4000 species could be described per year across all groups. This output will require all the efficiencies achievable through technological advances in data handling, communication, and imaging. In this way, the entire terrestrial arthropod fauna could be described in approximately 45 years. In another sense, this is a very small insurance premium against 'bio-ignorance' of the Australian biota. In a global context, the aim of the All-Species Foundation (www.all-species.org) is to discover and describe all species on earth in the span of a single human generation, a rate about twice as fast as the one we propose above.

Describing species is the taxonomic component of a comprehensive 'encyclopaedia' of Australian life, and is of little use in and of itself, except to the discipline of taxonomy. However, the process of discovery we envisage has far greater relevance to the rest of biology and society. Specimen material feeding into such a process would be products of biodiversity survey work for a variety of reasons and add different kinds of information (Cracraft 1995, 2000), such as discovering areas of endemism for conservation, the effects of invasive species,

TABLE 4. Summary statistics for the number of described species for groups of terrestrial arthropods, estimated size of the fauna (from Tables 1 and 2), and the proportion yet to be described.

Group	No. of species described	Total fauna	% Described	No. remaining to be described
Arachnida	5705	42 195	13.5	36 490
Myriapoda	351	2129	16.5	1778
Crustacea	23	800	2.9	777
Onychophora	72	250	28.8	178
Entognathous Heaxapoda	382	2570	14.9	2188
Insecta	58 491	204 743	28.6	146 252
Terrestrial Arthropods	65 024	252 687	25.7	187 663

the native suite of biological control agents, bioprospecting and the distribution and abundance of groups providing essential ecological services such as pollination. In addition, such an encyclopaedia would include systematic information on relationships, that allow us to predict biological attributes, which we believe will be of tremendous value to all biologists. Given increases in knowledge sharing and capacity, taxonomists will assign the hypothesis they call 'species' with much more information and with much greater relevance. Biologists will be able to discover and study biodiversity patterns at many scales with a greater amount of available distributional data. Resource managers would back decisions with more complete and precise information. Furthermore, the general public will have much greater access to the vast and amazing biodiversity of this continent.

Ecological Surveys versus Taxonomic Estimates

Some recent broad-scale surveys of invertebrate faunas for terrestrial habitats suggest a larger total Australian fauna than our taxonomic estimates suggest. A three-week survey of arthropods along a single altitudinal transect in the wet tropics of North Queensland (Monteith & Davies 1991) collected an estimated 5100 species of insects, representing about 2.5% of the fauna of the entire continent we estimate here. We find it difficult to believe that such a high proportion of Australia's insects could be collected in such a spatially, temporally and ecologically restricted survey. Similarly, a canopy fogging survey of arthropods from four species of *Eucalyptus* in two localities (Scheyville, NSW, and Karragullen, WA) found 1500 species (Majer et al. 1994, 2000) of insects, representing about 0.75% of the total fauna. Endopterygote larvae were not sorted in these samples, thereby the species totals are under-estimates. Given that there are over 500 species of eucalypt in Australia, it is difficult to rationalise such a high proportion of the fauna being discovered in such an ecologically limited survey. Flight intercept traps and canopy fogging apprehended 1171 species on a single Australian rainforest tree species (Basset & Arthington 1992). This is also an under-estimate given that Acari, Collembola, and most Hymenoptera, Diptera and Lepidoptera adults were not sorted to species.

It is a significant challenge to directly compare the results of these intensive surveys with estimates generated for broad taxonomic groups for the whole continent. More detailed information is required on species distributions and host specificity (see Novotny et al. 2002), especially for species-rich families of phytophages and parasites. Future research might profitably proceed along two main avenues: 1) determine the level of host specificity in plant feeding insects in dominant plant communities; and 2) the level of beta and gamma diversity in different ecosystems and different guilds of species.

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