Taxonomic inflation: its influence on macroecology and conservation

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Species numbers are increasing rapidly. This is due mostly to taxonomic inflation, where known subspecies are raised to species as a result in a change in species concept, rather than to new discoveries. Yet macroecologists and conservation biologists depend heavily on species lists, treating them as accurate and stable measures of biodiversity. Deciding on a standardized, universal species list might ameliorate the mismatch between taxonomy and the uses to which it is put. However, taxonomic uncertainty is ultimately due to the evolutionary nature of species, and is unlikely to be solved completely by standardization. For the moment, at least, users must acknowledge the limitations of taxonomic species and avoid unrealistic expectations of species lists.

The problem of defining species has troubled biologists for a long time. Recently, attention has focused on fundamental properties, such as what species are [1,2] and how they arise [3,4], and there has been less interest in how species are to be described and delineated (but see [5,6]). In spite of major differences of opinion about species delimitation, we tend to use species as although they were completely clear-cut. For example, species provide data points that are used to test hypotheses about broadscale ecological patterns (macroecology). In conservation, the status of threatened species is enshrined in legislation, and substantial funding is provided by governments and international agencies for species-based conservation. Assessments and management plans are frequently based on counts of species. Regardless of the pros and cons for each species concept (Box 1), species uncertainty presents a serious challenge to all biological endeavours that are based on taxonomic lists, and compromises many biodiversity studies [7]. A key question is whether we have taxonomic tools that are suitable for the many uses to which species are put. If not, what can be done?

Problems with species lists

An important source of uncertainty in species lists stems from a recent trend away from the broad-brush biological species concept (BSC) towards more fine-grained phylogenetic species concepts (PSC, Box 1). Even under a single species concept, taxonomic groups might be prone to different splitter versus lumper taxonomic cultures. For

example, ant taxonomists, following a campaign to eradicate INFRASPECIFIC NAMES (see Glossary) [8], generally describe new morphological forms with restricted distributions as separate species. By contrast, butterfly systematists, influenced by TRINOMINAL NOMENCLATURE promoted at the turn of the 19th century (e.g. [9]) typically adopt a POLYTYPIC SPECIES concept (Box 1), and describe many local subspecies within widely distributed species. The result is that regional or global species counts of butterflies and ants are not comparable.

Taxonomic knowledge is very incomplete. Most species await description [10], whereas other taxa have been redescribed many times [11]. This uneven coverage implies that species lists will be unstable; species numbers will vary particularly in little-studied groups. Yet taxonomic instability is a feature even of well known groups. Primate species have increased so rapidly as a result of the application of new species concepts (Box 2) that another term seems necessary. We here use 'taxonomic inflation' (*c.f.* [11,12]) for cases in which many existing subspecies are raised to species level.

One characteristic of inflation is that taxonomic changes are biased toward certain groups. Without bias, species uncertainty could be treated as random error in macroecology and conservation. However, the chance that a species has been described is much greater for large-bodied, wide-ranging species, such as primates [13]. Furthermore, whether a species is reviewed by taxonomists is influenced by where it lives, and whether it is charismatic or easy to study. For example, taxa sharing

Glossary

Comparative methods: techniques for studying correlated evolution among traits of species or higher taxa, while controlling for the fact that close relatives are expected to be similar as a result of shared ancestry (e.g. [38]). Species data points are typically used, but the methods are appropriate for any set of taxa whose phylogeny can be estimated.
Evolutionarily significant unit: a population that merits separate management based on it having ecological and genetic variation of adaptive significance and/or unique evolutionary history [31].
Infraspecific names: names for taxa below the species level (subspecies, varieties and forms).
Phylogenetic diversity: the total amount of evolutionary history (branch length) represented by a species or group of species.
Polytypic species: literally 'a species with many types'; a species consisting of many divergent geographical races or subspecies, each of which intergrades with other subspecies of the same species wherever they meet.
Trinominal nomenclature: the practice, in zoology, of appending subspecific names to the Linnaean binomen of genus and species. For example, in the trinomen *Gorilla gorilla beringei*, the name 'beringei' indicates a subspecies.

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Box 1. Species concepts and taxonomic inflation

There are almost as many concepts of species as there are biologists prepared to discuss them [39]. However, two ideas have particularly important practical implications: the biological and phylogenetic species concepts.

The biological species concept

Under the biological species concept (BSC), species are taxa that can overlap geographically because they are reproductively isolated. However, many distinct taxa hybridize; such taxa are normally considered separate species if they retain genetic integrity when in contact, and hybrids are rare. If not in contact, taxa 'potentially' (i.e. likely to be) reproductively isolated are considered separate species [40]. Whereas subspecies and phylogenetic species that hybridize contribute to global and regional biodiversity, only overlapping, reproductively isolated entities can increase local diversity. The practical effect of the BSC is to designate geographically differentiated populations that intergrade at their boundaries as subspecies or geographical races within overall 'polytypic species'; by contrast, such subspecies might be considered to be full species under the PSC. From the late 1930s onwards, Dobzhansky and especially Mayr promoted this inclusive, polytypic species concept [40], which led to a period of relative taxonomic stability for many vertebrates by the 1960s–1980s (Box 2, Figure I).

The phylogenetic or 'diagnostic' species concept

Under the phylogenetic species concept (PSC), species are considered to be populations differing by at least one taxonomic character from all others, and within each of which there is 'a parental pattern of ancestry and descent' [41]. The PSC is considered to apply even if diagnosable forms are not reproductively isolated. This seems to conflict somewhat with the definition, unless one excludes all introgressants from membership in species, because 'a parental pattern of ancestry and descent' between such taxa is certainly likely to result from hybridization. In practice, the PSC is applied to geographically differentiated forms, but not to local morphs. The PSC is a recent innovation, promoted widely since 1989 [1,41], and has been particularly influential in the classification of vertebrates. On average, the PSC has recognized 48% more species than has the BSC [26], and it is unclear what are the limits to diversity under the PSC [1,2] – taxonomic inflation can be much greater in well analyzed and charismatic taxa, such as primates (Box 2).

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geographical ranges with practising systematists are more likely to be reinvestigated (e.g. [14]). Given the negative relationship between biodiversity and systematic expertise [15], many cryptic species will probably never be identified. Geography is important in other ways: research funds for conservation are increasingly focused in 'hotspots' (e.g. [16]). Distinctive populations in these areas are more likely to be designated as species [17], making hotspots appear even hotter.

Implications for macroecology

Species are fundamental units in macroecology. Examples of patterns in macroecology include the tendency for geographical ranges of species to be larger at higher latitudes [18] and the tendency for abundance to be greater in the centre of the range of a species than at its edge [19,20]. Tests of such patterns typically assume that species are discrete equivalent entities in a way that is unbiased relative to the hypothesis being examined. However, explanations for these patterns differ in the species concept assumed. For example, one explanation for the geographical pattern of the abundance of species is

that migration among populations (the rescue effect) is greater in the centre of the range than at the edges [19]. The implicit species concept requires demographic exchangeability within the range of the species, but not outside. As such, its assumptions are closer to the BSC, whose species have well defined edges, rather than the PSC, whose species frequently exchange individuals and genes with neighbouring species (Box 1). Conversely, Brown *et al.*'s explanation is that the species is less abundant at the edge because it is suboptimally adapted to these areas [20]. This hypothesis assumes something similar to a PSC, because it depends on a lack of locally adaptive race formation within species. The fact that ecological hypotheses, as well as biologists, have differing species concepts is a previously unrecognized dimension of the species problem. It might be easier to test hypotheses if the species list reflected underlying reality, but it would be frustrating if the prevailing species concept of the taxonomy used differs from that assumed in the hypothesis. In an ideal world, each hypothesis would be tested using the most appropriate rank in the taxonomic hierarchy.

An obvious effect of taxonomic inflation on macroecology is larger sample size. Generalizing about the effects on hypothesis testing is difficult, but we can make some simple predictions:

• For hypotheses assuming a BSC, inflation should increase error variance rather than enhancing information content, thus reducing power. For example, correlations between life-history traits and extinction risk [21] will be weaker using a PSC, because phylogenetic species are likely to vary more in extinction risk than in life history, whereas biological species should vary in both.

• For hypotheses assuming a PSC, or when the hypothesized process persists at lower hierarchical levels, analytical power will be increased with taxonomic inflation. For example, Darwin [22] noted that species in species-rich genera tend to have a greater number of distinct varieties, suggesting that processes causing a genus to diversify continue to operate within species. Therefore, testing for correlates of diversity on an evolutionary timescale [23] could be more conclusive using inflated taxonomies, although available evidence is mixed [24].

• When inflation is biased with respect to the hypothesis under test, type I errors (false positives) are likely because extra data are effectively pseudoreplicates. For example, if inflation is greater in large-bodied taxa, correlations of body size with either species richness or geographical range will be compromised. Conversely, if splitting is greater within more diverse taxa, correlates of diversity could be exaggerated.

Macroecological hypotheses are routinely tested using species-level comparative datasets. Taxonomic instability complicates data collection because it is not always clear how study populations relate to species names. Fully synonymic checklists are helpful, but even when the original study taxon and the name in the database share the same Latin binomial, ecological data might be assigned wrongly if the taxon was subsequently split. Incorrect

Box 2. Taxonomic inflation in the Primates

Groves' Primate Taxonomy [42] is an ambitious attempt to apply the phylogenetic species concept (PSC) to an entire order of mammals. The new list has greatly inflated the number of recognized primate species. However, primate species numbers have been increasing exponentially for the past two decades (Figure I). From 1995–1996, the range of species numbers in different treatments was ∼25% of the total. Because of this level of uncertainty, Harcourt et al. [43] abandoned species taxa altogether in favour of genera. Most lists were not explicit about the species concept employed, and it seems likely that the steady growth during the 1990s (∼ six species per year) reflects the gradual adoption of the PSC among primate families and genera.

The period of recent inflation contrasts strongly with the stability seen for at least two decades before 1985. Since then, the number of species has doubled, yet this increase includes only ∼30 new discoveries, most of which were first described as subspecies and only recently elevated to full species rank. Available evidence suggests that even a stabilization of emphasis on the PSC will not halt inflation: whereas Groves [42] lists 16 titi monkeys (Callicebus spp.), a more recent list [44] contains 28.

Recent increase in primate species numbers is highly non-random. For example, the three major continents contained approximately equal numbers of primate species during the 1980s. The number of neotropical species actually fell during the 1960s and 1970s as the result of a revision of the tamarins (Saguinus spp.) [45], but the subsequent increase has been far more rapid in the Neotropics than anywhere else [24]. Nevertheless, in Groves [42], neotropical species make up a smaller fraction of the total than at any time in the previous decade. New discoveries have also been distributed far from randomly: nearly half were strepsirrhines (eight lemurs and six lorisoids) and a third (ten) were platyrrhines (New World monkeys).
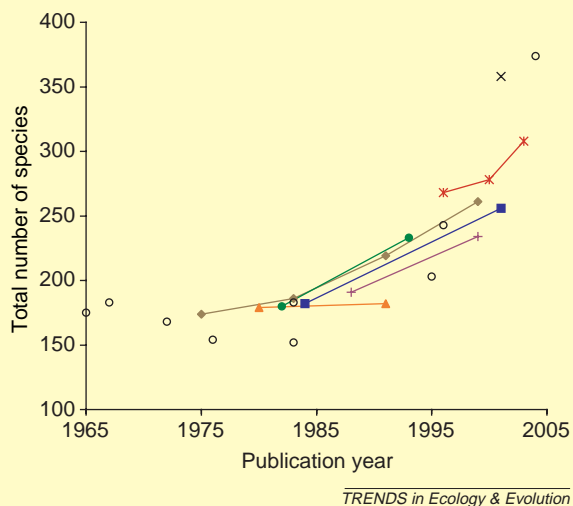

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Figure I. Primate species numbers in: Groves' Primate Taxonomy (cross: [42]); The Encyclopaedia of Mammals (squares [46,47]); Walker's Mammals of the World (diamonds: [48–51]); A World List of Mammalian Species (triangles: [52,53]); Mammal Species of the World (filled circles: [54,55]); Primate Adaptation and Evolution (plusses: [56,57]); The IUCN Red List of Threatened Animals (stars: [58–60]); and eight independent taxonomies (open circles: [61–69]).

assignment of data can bias hypothesis testing, particularly for traits that are evolutionarily labile. Taxonomic inflation also results in purely species-level data becoming rapidly outdated, necessitating the reclassification of literature data whenever taxonomic opinions change.

An important property of taxonomic inflation is that species richness in large areas will increase faster than that in small areas. At the limit, global species richness increases with every subspecies elevated to species rank, whereas local diversity changes only with new discoveries (Box 1). Species-area curves, turnover in community composition and plots of regional against global geographical range would become steeper following taxonomic inflation. These quantitative effects of inflation will depend on the relative geographical range sizes of split taxa. If most splits are asymmetrical (i.e. 'new' species tend to have small ranges) then maximal global range sizes will be relatively unaffected, but the variance will change as a result of the larger number of narrow-range endemics. Predominantly symmetrical splitting will lead to fewer wide-ranging species, with unpredictable consequences.

Implications for conservation biology

Much conservation planning depends on numbers of species, reflecting richness, diversity, endemism, threat and many other attributes that can be compared across locations and taxa [16,25]. If different taxonomic cultures operate regionally or depend on the group studied, conservation priorities might track taxonomic fashion rather than fundamental biological parameters. Taxonomic inflation will cause particular problems in assessing whether rates or risks of extinction have changed over time. Species numbers will increase (because more are recognized), potentially masking extinction, but taxonomic inflation will also result in a higher proportion of threatened or extinct species, because the average geographical range and population size will decline [26]. These effects will make global targets, such as the recent pledge in the Convention on Biological Diversity (http://www.biodiv.org) to slow the loss of biodiversity by 2010, very hard to meet, as they confound our attempts even to measure the loss of species reliably.

In area-based conservation planning, the problem becomes more unpredictable. Two recent studies [27,28] show how location of hotspots of endemic species richness move spatially with changing species concepts, leading to the conclusion that hotspots might sometimes be more apparent than real [28]. Biodiversity hotspots based on overall local species richness will be less prone to change than those based on endemics: endemics are defined by having small ranges, and an inflated taxonomy will therefore have inflated values of endemism.

A different kind of problem occurs when species are valued more highly than subspecies or local populations. This encourages elevation to species rank of populations that need protection, regardless of whether there is scientific support for this status. This phenomenon has been described in the black turtle Chelonia agassizi [17], but is likely in many other taxa. Such inflation will be biased towards charismatic, large-bodied, rare and endangered forms (such as primates, Box 2) that attract high public, scientific and conservation interest.

The issues for conservation biology are complex, especially because of the different processes in listing and priority setting versus those for implementing species recovery. Sometimes, local interests might lead to a population being given separate listing, even though survival might be more likely when the population is managed as a component of a viable metapopulation.
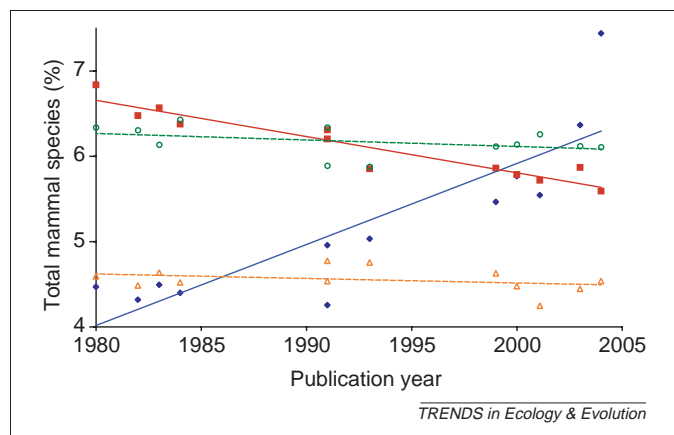
Figure 1. Percentage of total mammal species in four Orders across 12 published taxonomies [46,47,49–55,59,60,69]. Lines are least squares regressions. In 1980, Primates (diamonds) were the sixth most speciose order of mammals. Now they are third, exceeded only by rodents and bats. Numbers of artiodactyls (triangles) and marsupials (circles) have increased at a similar rate to the mammalian average, but carnivores (squares) have remained stable in total number and, thus, have declined as a fraction of the total.

Conservationists should explicitly separate listing activities from recovery planning, and recognize that different units are appropriate to each process [29]. Recent efforts to generate explicit rules for taxa to be included on the UK bird lists [30] and for designation of population units for conservation action [6,31] are direct responses to these different demands.

Prospects

Clearly, there are big problems with species lists. The situation will remain acute because scientists will probably always disagree about species concepts. For the most part, disagreement is epistemological rather than data driven. In fact, we predict that taxonomic inflation will affect more and more taxa as the PSC gains popularity. However, philosophical trends are frequently reversed; in future, the fashion might switch back from splitting to lumping and, indeed, there is a diversity of philosophies now in operation. We speculate that other, nonbiological, drivers of taxonomic change might exist. For many decades, primates were the sixth most speciose order of mammals. Recently, they have overtaken artiodactyls, carnivores and marsupials (Figure 1), thus raising the profile of primates and increasing their suitability as a model system. Carnivore biologists, who have maintained a relatively stable taxonomy, might well feel piqued at the loss of prestige of their organisms.

If taxonomic instability is here to stay, what can be done? One obvious solution is to abandon species altogether. To some extent, this is already happening: for example, by analyzing data at the level of populations [32]. Some recent studies (e.g. [33,34]) have instead used Phylogenetic Diversity as an alternative measure of biodiversity. Phylogenetic diversity is suitable for some applications, such as identifying biodiversity hotspots [35], but not in most macroecology. Here, existing methods suffice. For example, in modern Comparative Methods, close relatives with similar traits have reduced influence, so analyses are relatively insensitive to taxonomic

inflation, except in traits directly affected by changes in taxonomy (e.g. geographical range). Recently, conservationists have focussed on ranks in the taxonomic hierarchy other than species; for example, the use of Evolutionarily Significant Units was advocated in recent US legislation. However, abandoning species could be dangerous because of the public perception of species, and possible effects on funding decisions.

One way to continue using species lists in conservation while avoiding the problems of species uncertainty is to agree on a standardized list. As we have seen, this approach is advocated by several bird organizations (e.g. [30]), and has many obvious virtues for describing and managing biodiversity. However, this does not necessarily solve the problem for macroecologists. A static list would almost certainly contain a mixture of species concepts, making it unsatisfactory for testing many hypotheses. The alternative (to tailor taxon lists to be relevant to the hypothesis) has two drawbacks. First, it would be difficult to choose a list objectively, given existing knowledge. Second, if macroecologists and conservationists used different species lists, macroecological results might not apply to the taxa recognized by conservationists. This could compromise the exciting and useful new field of testing for correlates of extinction risk [21]. Nonetheless, a standard list is a useful reference point for all species-related issues, and we recommend their use. Possible developments that would enable the continued use of species lists include online, global synonymic checklists. These could be tailored to enable data retrieval according to the classification and species concept defined by the user and, ultimately, linked to the standard list as well as to museum collections. The technology is readily available, but would require long-term institutional investment [36].

Conclusion

Macroecology would become more useful if its practitioners were explicit and more sensitive about the choices of taxonomic lists and types of data that they analyze, to make their hypotheses and tests more robust to taxonomic uncertainty. Conservationists could benefit by separating macroecological patterns from the process of conservation. Patterns such as the distribution of global species richness are sensitive to taxonomic inflation; therefore, regional conservation priority should be based on relatively stable species lists. Conservation action, such as recovery plans, can often be independent of species altogether: ideally, it should make little difference to conservationists whether the mountain gorilla *Gorilla gorilla beringei* is classified as a species, subspecies or local population [37].

Acceptance of darwinism implies that evolution will result in a continuum of living organisms in space and time, modified by variable extinction of intermediates. Species are part of this continuum, rather than being particularly unique taxonomic entities. The pre-darwinian, albeit useful, nomenclature that we use to classify this lumpy continuum should not trick us into believing that the species we name are necessarily sensible evolutionary, ecological or conservation units.

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