

The population ecology and social behaviour of taxonomists

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The ecology and social habits of taxonomists (those individuals who describe new species) have significant implications for understanding how many more species there are to discover (henceforth 'missing species'). The diversity of different taxa is interesting in itself, and determining where missing species live will be vital in setting conservation priorities.

We assembled readily available data on the rates of species descriptions for six groups of taxonomists: those describing flowering plants (World Checklist of Selected Plant Families; http://www.kew.org/wcsp/; accessed 1 August, 2011); marine snails of the genus Conus [1]; spiders (Planetary Biodiversity Index - World Spider Catalog; http://research.amnh.org/oonopidae/catalog/; accessed 1 August, 2011); amphibians [Frost, D.R. (2011) Amphibian Species of the World: an online reference. Version 5.5 (31 January, 2011); http://research.amnh.org/herpetology/amphibia/index.php; accessed 1 August, 2011]; birds (http:// www.zoonomen.net/avtax/frame.html; accessed 1 August, 2011); and mammals (http://www.bucknell.edu/msw3/; accessed 1 August, 2011). In the accompanying supplementary material online, we provide scripts for the R software package to allow others to analyse these data sets.

Conventional wisdom is highly prejudiced. It suggests that taxonomists were a formerly more numerous people, are in 'crisis' [2], are becoming endangered [3] and are generally asocial. We consider these hypotheses and reject them to varying degrees.

There is one striking common feature in the rates of species description for the taxa we analyse: since approximately 1950, they have increased and, for all but birds, that increase has been essentially exponential (Figure 1a). This confounds attempts to predict the total numbers of species from the expected declining rates of description as the pool of missing species diminishes.

How can these rates increase? This question motivated us to count the numbers of taxonomists. They, too, are increasing exponentially (Figure 1c). Only when one adjusts the 'catch' (the number of species described) by the 'effort' (the number of taxonomists at work) does one see a generally consistent decline, most obvious since 1900 (Figure 1d). This decline allows statistical estimates of the number of missing species [4,5].

For some groups (mammals and spiders in particular, Figure 1d), the numbers of species described per taxonomist

increase until approximately 1900 (Figure 1d), despite an inevitably declining pool of missing species. One probable underlying cause (an increase in taxonomic efficiency) could involve many factors. Generally, over time there has been easier circumscription of taxa owing to increasing numbers of species with which to compare (i.e. being able 'to see more of the puzzle'), changing patterns of specialisations by taxonomists, or the synergies of working together in groups.

We note that these trends in taxonomic efficiency probably continued beyond the point when numbers of species described per taxonomist began to decrease. Certainly, since 1950, modern travel and data-sharing technology have facilitated better access to the remote places where many species occur and increasing access to the literature and specimens housed in herbaria and museums around the world. Given this, the currently decreasing numbers of species described per taxonomist over the past 50 years probably represents the effect of a declining pool of missing species.

Driving the decrease in the pool of missing species is a trend for increasing specialisation of taxonomists over time. Figure 1e–i plots the percentage of taxonomists in a given interval that described species in more than one family ('now general') or did so within their careers ('ever general'). Those who describe species in more than one family, even within their lifetimes, have been in a minority for birds and plants since approximately 1950 and mammals since approximately 1900. Spider taxonomists typically describe species in more than one family within a lifetime, but not within any given 5-year interval (Figure 1h). Counter to these trends, amphibian taxonomists are becoming more generalised over time (Figure 1g).

Finally, although lone taxonomists still practice, the mean dates of a species described by just one taxonomist cluster around 1900, whereas dates for three or more describers, cluster in the past few decades (Figure 1j–o).

Do our results simply reflect a trend towards giving junior collaborators credit? The data reject this too. Counting only the numbers of unique senior authors in a time interval produces graphs almost identical to those in Figure 1a-d, because the great majority of secondary authors on species descriptions are senior authors on other descriptions.

In short, the numbers of all taxonomists are increasing rapidly for the taxa we compiled, as are the numbers of taxonomists who are the senior authors on species

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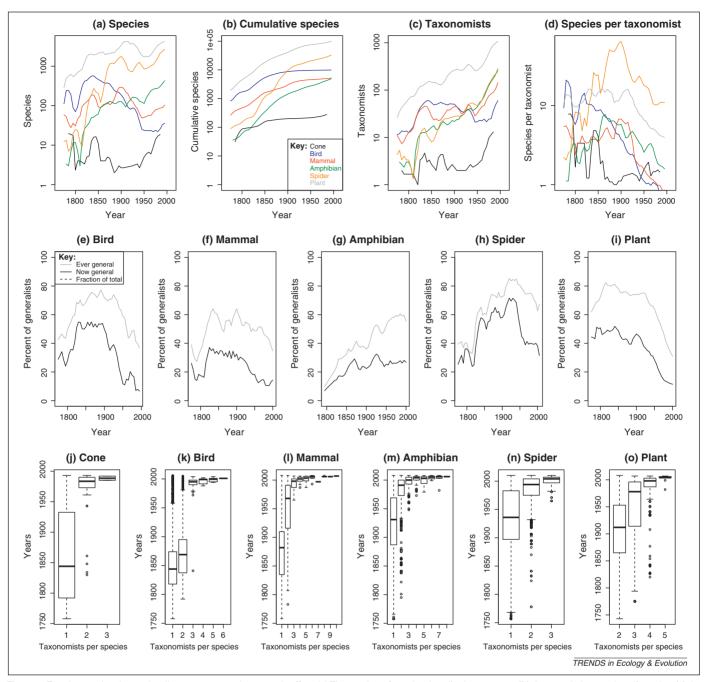


Figure 1. Trends over time in species discovery rates and taxonomic effort. (a) The number of species described per 5 years, (b) the cumulative number of species, (c) the number of taxonomists involved in species descriptions and the (d) species per taxonomists. Data are three-period moving averages to show trends. (e-i) The percentages of taxonomists who described species in more than one family in their careers ('ever general') or within that 5-year interval ('now general'). Data are three-period moving averages to show trends. (j-o) The average dates when increasing numbers of taxonomists were involved in describing species.

descriptions. For most taxa, taxonomists are becoming taxonomically specialised, and more taxonomists are involved. Although we cannot tell from the data here, it is likely that this collaboration involves different skills and abilities now than in the past, where description meant a simple account of morphology.

How can these results fit with evidence that those who only do taxonomy are becoming scarce [2,3,6]? Clearly, taxonomic description no longer belongs to those who do nothing else; species description is much more widely practiced. Geography probably matters, as anecdotal evidence indicates the numbers of traditional taxonomists are increasing in developing countries but declining in developed ones. However, we cannot tell whether the increase in breadth of taxonomic practice is a cause or a consequence of the decline in those who do nothing else.

For our examples, the numbers of species described per taxonomist have dropped for over a century, despite increasing taxonomic effort, collaboration and specialisation. For the relatively well-known taxa we survey, this surely reflects the diminishing pools of missing species. It might not be general, however. The patterns for speciose but more poorly known taxa, probably including insect groups such as beetles and parasitic wasps, might be very different.

Update

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.tree. 2011.07.010.

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Letters

Climate change responses: forgetting frogs, ferns and flies?

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We were pleased to see Gardner et al.'s recent paper in TREE on a third universal response to climate warming [1]. Indeed, we have noticed the same trend, and have presented similar comments on the topic (Sheridan, J.A. and Bickford, D, unpublished data). We agree with Gardner et al. [1] that there is strong evidence of a third pervasive response to climate change; size reduction has been found in too many organisms experiencing climate change to be a simple coincidence. Gardner et al. present an excellent suite of potential studies that can examine this trend and help identify proximate causes of the observed declines. However, we suggest that although birds provide an excellent endothermic study system, ectotherms offer a richer group from which to draw conclusions and offer research hypotheses aimed at understanding the mechanisms behind shrinking organisms. We feel that studies of size declines in ectotherms should receive equal attention for several reasons.

First, ectotherms represent the vast majority of both species diversity and biomass across ecosystems and they are integral parts of trophic networks in all ecosystems. How they respond to warming, both on ecological and evolutionary scales, will have widespread and important impacts. If they are being affected in large-scale ways by the same or similar mechanisms, one might be able to predict and mitigate against those effects.

Second, there are two explicit thermodynamic and metabolic rules of ecology that are well known in ectotherms: the temperature metabolic rate rule [2] and the temperature-size rule [3]. The former states that ectotherms burn more metabolic energy when it is warmer and need more energy to achieve and maintain adult body size at higher temperatures [2]. Large-scale implications of this are that ectothermic organisms will have to consume more metabolic energy to maintain their body size as temperatures increase. It is unlikely that increased consumption is sustainable, so it is reasonable to expect that ectotherms will decrease in size with continued climate warming, as has been shown for toads [4] and tortoises [5]. The temperature-size rule relates larval development and temperature; animals mature earlier and at smaller sizes when they experience warmer temperatures [3,6]. Continued increases in global temperatures are likely to result in faster development times and smaller sizes of ectotherms. This theoretical framework provides ample experimental and model-based approaches to test hypotheses about the ultimate mechanisms of body size reductions.

Third, although body size changes in endotherms are real and have been observed in many taxa [7–9], many of the endothermic size reductions are secondary effects of climate change (altered diet or nutrition, to cite the main example from [1]). Size declines of ectothermic animals and plants, by contrast, are more likely to be direct results of changes in temperature and precipitation associated with climate change. Precipitation is predicted to become increasingly variable across the globe, and to decrease in some areas [10]. This reduction in predictable rainfall is likely to reduce plant size, as has been shown for North American species [11], and is also likely to affect food availability for both faunal and human populations. Studies on the mechanisms directly affecting size changes in ectotherms and primary producers might, therefore, have broader impact than studies on secondary changes in endotherms.

As noted by Gardner *et al.*, there is much work yet to be done on understanding the mechanisms of this trend, how it plays out across the tree of life, and what it will mean for ecosystem functioning and human livelihood. A broad perspective and theoretical framework are necessary to understand fully observed trends in organism size change, and to develop effective mitigation strategies.

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