Correspondence

Quantifying the use of species concepts

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Humans conceptualize the diversity of life by classifying individuals into types we call 'species'[1]. The species we recognize influence political and financial decisions and guide our understanding of how units of diversity evolve and interact. Although the idea of species may seem intuitive, a debate about the best way to define them has raged even before Darwin[2]. So much energy has been devoted to the so-called 'species problem' that no amount of discourse will ever likely solve it[2,3]. Dozens of species concepts are currently recognized[3], but we lack a concrete understanding of how much researchers actually disagree and the factors that cause them to think differently[1,2]. To address this, we used a survey to quantify the species problem for the first time. The results indicate that the disagreement is extensive: two randomly chosen respondents will most likely disagree on the nature of species. The probability of disagreement is not predicted by researcher experience or broad study system, but tended to be lower among researchers with similar focus, training and who study the same organism. Should we see this diversity of perspectives as a problem? We argue that we should not.

Our survey consists of 19 questions designed to gauge thoughts on species, along with information about each researcher. After ethical approval and circulation (Supplemental information), we received 402 responses from researchers in 39 countries. The results, including questions not analyzed here, can be explored interactively using a freely-available online dashboard (Supplemental information).

We found that most respondents (86%) conduct their research with one of 16 species concepts in mind (see Supplemental information for description of concepts), with the remainder tending not to use a concept (Figure 1A). The pattern of concept use revealed low consensus among respondents, as the diversity of concepts was high (Figure 1A). Specifically, there is a 79% chance that two randomly drawn respondents would use different concepts (Table S1).

Although each concept is distinct, some differ less than others. Highly similar concepts include different versions of the biological species concept — where species are recognized based on reproductive isolation — the evolutionary species concept — where species are cohesive evolutionary units — and the phylogenetic species concept — where species are historically related groups. Because these 'variant concepts' are similar, we merged them to see how the results are affected; the chance of disagreement is lower, but still substantial, at 61% (Table S1).

Why do researchers think so differently? One possibility is that experience helps develop a more consistent idea of species. Surprisingly, concept proportions were similar across six career stages, indicating that researcher experience does not strongly influence concept use (Figure 1B).

In contrast, the focus and evolutionary scale of research both explain variation in concept use. There was a small difference when respondents were grouped by whether or not they study species formation (i.e. speciation). Speciation researchers

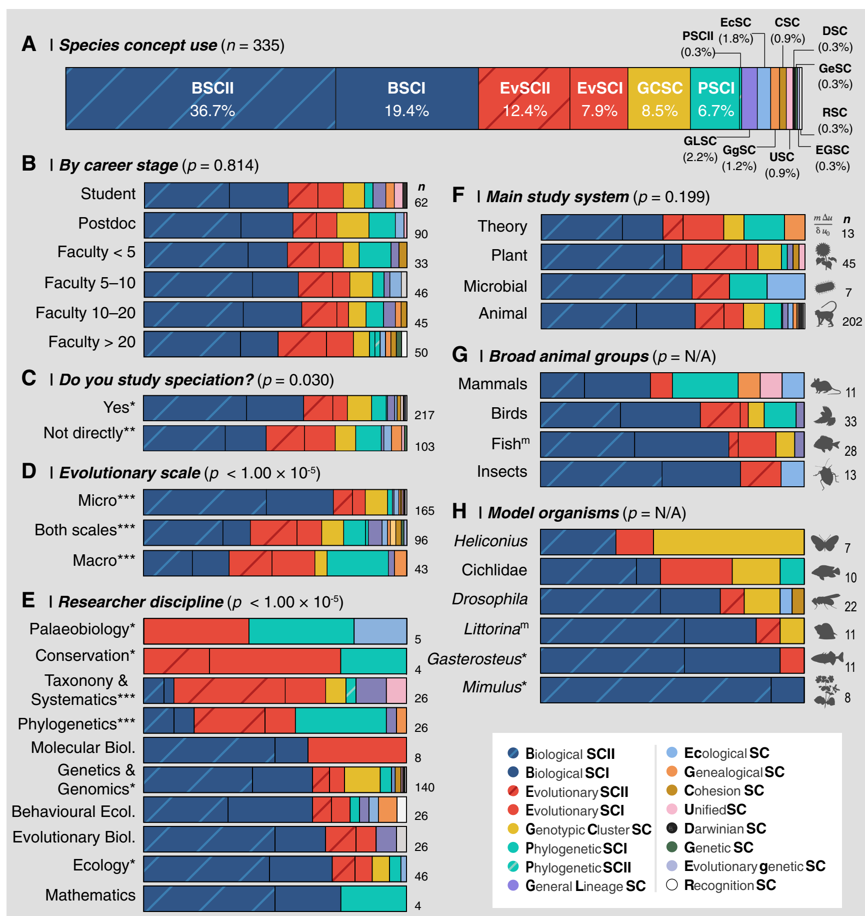

Figure 1. Concept use among the survey respondents.
Proportion of respondents using each concept for (A) all respondents who use a concept, and with researchers grouped by researcher characteristics (B–E) or study system (F–H). Variant concepts are colored the same, with the more recently proposed variant shaded with diagonal hatching. The chance of disagreement for each group (and other summary statistics) can be found in Table S1. The *p*-values for each sub-heading are from Fisher's exact tests comparing concept use across groups. Stars next to each group indicate that the proportion of BSC use (variants combined) is higher or lower than expected by chance based on the observed sample sizes (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, mmarginal: $p < 0.07$). N/A: test was not performed because some researchers study multiple organisms. Sample sizes (*n*) are provided for each group. Descriptions of each concept and full references are available in supplemental information.

were more likely to use a biological species concept than those that do not study speciation directly (Figure 1C). The evolutionary scale of research had a stronger effect (Figure 1D): microevolutionary researchers, who study population-level change over short time scales, are much more likely to use a biological species concept than macroevolutionary researchers, who study change across deep time and broad taxonomic groups.

Researcher discipline also explained variation in concept use. Disciplines formed two main groups: those where the biological species concept dominated and those where it was rare or absent (Figure 1E). Biological species concept-rich disciplines tended to be those more focused on understanding ecological and or evolutionary processes. Disciplines traditionally focusing on the history, identification and classification of organisms more commonly used Evolutionary and Phylogenetic species concepts. The chance of disagreement tended to be lower in groups enriched for biological species concept use — in some cases <50% with variant concepts combined (Table S1).

The effects of study system varied with taxonomic scale. First considering broad classifications of study system, there was no major difference in concept use between researchers that study animals, plants, microbes or theory (Figure 1F). Patterns were also similar among researchers that nominated a broad animal group, though biological species concept use was higher in researchers that study fish or insects compared with those that study birds or mammals (Figure 1G). Biological species concept use was highest in some groups of researchers studying specific model organisms in speciation research translating to a lower chance of disagreement (Figure 1H and Table S1).

Although it is difficult to infer causation from these results, they indicate that concept use is shaped by various factors that are essentially cultural differences between groups of biologists. They also enabled us to quantify the 'species problem' for the first time. Assuming that the respondents are broadly representative, we can conclude that any two biologists will most likely disagree on the nature of species to some extent. However, when measured in terms of the number of concepts used, the disagreement is not as extensive as one might have expected, as ~90% of researchers follow one of six concepts— or one of four when versions of the same concept are combined.

In general, we think that unifying variants of the same fundamental concepts would help make working with species concepts easier. For example, the two versions of the biological species concept are fundamentally similar, differing only by how much reproductive isolation is needed to recognize species[4]. Given that there is nothing explicit about this criterion in the phrasing of the original biological species concept — and because concepts are not strict definitions — we could apply one version in different ways. Similar arguments might be made for unifying other concepts.

Rather than struggling to reconcile differences between more divergent concepts — others have tried without broad acceptance[5] — it might be more helpful to ask: is having multiple species concepts really a problem? The goals of biologists are extremely diverse, and the diversity of concepts can be seen as a solution to our collective needs[6]. Concept diversity can instead be viewed as a strength because it allows us to see biodiversity from different perspectives. The real problem arises when we fail to disclose the concept we are using. When we are explicit, others can adjust when interpreting results or making decisions.

To help put the disagreement about species into perspective, Lowry and Gould[7] drew an analogy with an eastern parable about a group of blind men encountering an elephant. Each man touches a different part of the elephant, such as its ears, tail, trunk, or tusk. They then discuss their individual experiences, only to find that they disagree on the true nature of the elephant. In some versions of this tale, the group breaks out into a fierce debate that leads nowhere — a scenario that is reminiscent of the species debate. In a more positive version, members of the group stop arguing, listen to one another, and combine their perspectives to 'see' the whole elephant. Rather than fanning the embers of an exhausted debate, we hope this survey helps researchers to understand and embrace other perspectives as we work toward a more complete understanding of biodiversity.

SUPPLEMENTAL INFORMATION

Supplemental information including experimental procedures and one table can be found with this article online at https://doi.org/10.1016/j.cub.2021.03.060.

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AUTHOR CONTRIBUTIONS

S.S. and M.R. conceptualized the study, analyzed the data and wrote the paper.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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