Species as a Heuristic: Reconciling Theory and Practice

Tom Wells[1], Tom Carruthers[2], Pablo Muñoz-Rodríguez[1], Alex Sumadijaya[1,3], John R.I. Wood[1,2], and Robert W. Scotland[1,*]

[1]*Department of Plant Sciences, University of Oxford, Oxford, UK;* [2] *The Herbarium & ToL, Royal Botanic Garden, Kew, Richmond, UK; and* [3]*Research Center for Biology National Research and Innovation Agency, Cibinong Science Center, Indonesia*
[*]Correspondence to be sent to: Department of Plant Sciences, University of Oxford, Oxford, UK;
E-mail: robert.scotland@plants.ox.ac.uk

Abstract.—Species are crucial to most branches of biological research, yet remain controversial in terms of definition, delimitation, and reality. The difficulty of resolving the "species problem" stems from the tension between their theoretical concept as groups of evolving and highly variable organisms and the practical need for a stable and comparable unit of biology. Here, we suggest that treating species as a heuristic can be consistent with a theoretical definition of what species are and with the practical means by which they are identified and delimited. Specifically, we suggest that theoretically species are heuristic since they comprise clusters of closely related individuals responding in a similar manner to comparable sets of evolutionary and ecological forces, whilst they are practically heuristic because they are identifiable by the congruence of contingent properties indicative of those forces. This reconciliation of the theoretical basis of *species* with their practical applications in biological research allows for a loose but relatively consistent definition of species based on the strategic analysis and integration of genotypic, phenotypic, and ecotypic data. [Cohesion; heuristic; homeostasis; lineage; species problem.]

As perhaps the most recognized, observed, counted, measured, and studied unit in biology, species are of pivotal importance to our understanding of Earth's biodiversity. In spite of their centrality to biological research a widely accepted definition of what species are and how they can be delimited continues to elude us. This "species problem" has repeatedly complicated what should be a relatively simple question—"Is a given group of organisms meaningfully described by the term species, or not?"—turning it into an apparently intractable debate that combines complex biological processes and intricate philosophical concepts (Richards 2010, p. 1).

Heuristic frameworks offer a means of overcoming challenging problems that lack easy prospects of resolution. Often using trial and error, heuristics are able to provide an answer through the strategic analysis of the available data. They may provide an answer that will be in some sense provisional and not necessarily optimal but is sufficient as a working definition that can be used to make progress.

In this article, we suggest that the explicit recognition of the term *species* as a heuristic can provide a realistic and useful link between the *theoretical ideas of what species are* and the *practical ways by which species can be recognized and delimited*. Rather than separating theory from practice as has often been the case in contemporary systematics (Mayden 1997; de Queiroz 1999; Richards 2010, p. 144), this approach enables some reconciliation between the two. It can thereby alleviate the considerable philosophical burden of the species problem without compromising on theoretical integrity.

In making this proposal, we do not support the idea that species have no reality outside the human mind, nor that their delimitation is arbitrary, nor that there can be multiple, equally valid definitions based on the preconceptions of individual researchers. Instead, a reality of sorts exists which should be aimed for, but the practical difficulties of determining when exactly speciation has occurred mean that our attempts to recognize a species will always be provisional, amounting to the best approximation based on analysis of the available data.

We consider that this should not be a cause for concern, given species are not unique in this regard, and heuristics underpin a number of biological and other scientific research methods. Finally, we outline why we believe this is an important way of thinking about species, focusing on how it might influence the science of species delimitation—taxonomy.

THE SPECIES PROBLEM: VARIABILITY AND COMPARABILITY

The major obstacle to resolving the species problem remains the difficulty of finding a theoretical definition sufficiently flexible to accommodate the variability inherent in evolving biological organisms, while also being consistent enough to provide useful comparability across different groups of organisms (Hull 1997). This apparent dichotomy can give the impression of a schism between evolutionary theory and taxonomic practice, often leading to the suspicion that species and the process of describing them are arbitrary, rooted in antiquated systems of hierarchy and therefore constructs of the human imagination that do not reflect the complexity of evolutionary processes or biodiversity (Haldane 1956; Raven 1976; Mishler and Donoghue 1982; Nelson 1989; Hey 2001; Mallet 2001; Mishler 2010).

Despite the problems in their theoretical definition species retain an important place in contemporary biology—which relies on our ability to recognize and compare them. Understanding species richness and distribution patterns underpins important scientific insights including the latitudinal biodiversity gradient (Hillebrand 2003), biodiversity hotspots (Myers et al. 2000), biogeography (von Humboldt 1805; de Candolle 1855; Wallace 1876; Brundin 1972) and, not least of all, the theory of evolution by natural selection itself (Darwin 1859). The term *species* also remains invaluable for understanding the different processes that drive speciation (e.g., Gao and Rieseberg 2020), providing an epistemological framework for understanding patterns of relationship that retains its power even in the face of complex and diverse evolutionary phenomena (Brower 2019). The utility of species as a unit of biodiversity is also evident in the field of conservation, where rightly or wrongly, species are still widely treated as both the means of quantifying and monitoring ongoing biodiversity loss, and the prime target for conservation action (Maclaurin and Sterelny 2008; Rounsevell et al. 2020). Accurate and consistent species definitions, counts, and comparisons are thus key to understanding patterns of biodiversity and the processes that underpin them (e.g., Faurby et al. 2016), as well as the planning and legal frameworks used for their conservation (e.g., Cracraft 1997; Agapow et al. 2004; Isaac et al. 2004). Disagreement about what species are and how they should be delimited impacts negatively on all these activities.

Contemporary Approaches to the Species Problem

Three contemporary approaches to species conception are based on pluralism (e.g., Mishler and Donoghue 1982; Kitcher 1984; Dupré 1993, 1999; Ereshefsky 1998, 2001), lineages (e.g., de Queiroz 1988, 1998, 1999, 2005, 2007; Mayden 1997; Hey 2006; Padial and De la Riva 2021), and cohesion (e.g., Templeton 1989; Boyd 1991, 1999; Pigliucci 2003; Rieppel 2007, 2009; Wilson et al. 2007; Maclaurin and Sterelny 2008). These approaches differ in how they reconcile the theory and practice of species, for example, pluralist approaches recognize different but equally valid kinds of species that are defined in different ways. In contrast, lineage and cohesion approaches both attempt to treat species as coherent and broadly comparable entities but differ in whether they emphasize separation and divergence between species (e.g., de Queiroz 2007) or the forces that result in species cohesion and clustering (e.g., Templeton 1989). Below, we assess the relative merits and failings of these approaches in terms of reconciling theoretical ideas of what species are with the ways they might be practically identified and delimited. We suggest that these approaches implicitly contain an element of the heuristic approach. Later, we outline why we believe an explicitly heuristic approach can be used practically, is theoretically appropriate and can improve the way

biologists define, think about and use species in their research.

Pluralism and Pragmatism

A pluralistic approach to species definition recognizes multiple competing definitions or concepts as equally valid ways of dividing biodiversity into different units. These divisions might be based either on the specific biology of a particular group of organisms (e.g., Dupré 1993, 1999; Ereshefsky 1998), or, more prosaically reflect differing research priorities and preoccupations (Kitcher 1984). As Ereshefsky (1998) puts it: "…contemporary biological theory provides ample evidence that the tree of life is segmented by biological forces into different types of species taxa. Consequently, there is no single unitary species category, but a heterogeneous collection of base taxa referred to by the term 'species'." As a result, pluralists argue that the only acceptable response to evolutionary theory is to acknowledge that there are many different types of species, and that different definitions can or should be used to account for this variation. To do otherwise, they argue, is to risk obscuring the complexity of evolutionary relationships and processes (e.g., Mishler and Donoghue 1982; Willis 2017).

This assertion has itself resulted in many different suggestions as to how biodiversity should be described and delimited in practice. Mishler and Donoghue (1982) for example, suggest treating species like all other taxa, as "assemblages of populations united by descent," with a simple requirement for monophyly and the abandonment of any sense of equivalence or comparability between different species. By endeavoring to align systematic practice with evolutionary theory as rigidly and completely as possible, this and other similar frameworks (e.g., Pleijel and Rouse 2000; Hey et al. 2003; Mishler and Wilkins 2018) reject any notion that there can be a unified taxonomic rank like *species* that might allow for broad comparability.

An alternative approach, which allows for at least a limited form of comparability, is simply to encourage researchers to state the criteria and definitions they are using in their species delimitations, so that other researchers understand the nature of the species under discussion and what comparisons are possible (Mishler and Donoghue 1982; Ereshefsky 2010). Though theoretically coherent, this approach does not align well with the reality of contemporary biological practice. Biologists, ecologists, conservationists, or biogeographers seeking to make meaningful comparisons between groups of organisms are reliant on the existing work of countless other researchers. Differences of opinion about the optimal species concept are virtually ubiquitous, even within taxonomic groups such as birds (Cracraft 1997), insects (Marris 2007), or flowering plants (Rieseberg et al. 2006). It is therefore unreasonable to expect those undertaking broad biological comparisons to identify and reconcile all the potentially conflicting criteria used by other researchers to delimit species in different

groups of organisms before they can conduct their own research.

As such, many pluralists take a more pragmatic approach. Ereshefsky (2010) for example, admits that although in an ideal world, we might do away with the term *species* and replace it with a series of more explicit terms like "ecospecies," "morphospecies," and "phylospecies" (Ereshefsky 1998), this suggestion is impractical and the overarching term should be retained. Similarly, Dupré (1999) meticulously outlines the theoretical impossibility of a monist species concept, before acquiescing in a "feeble monism" in recognition of the importance of a *general reference system* "…within which evolutionists, economists, morphologists, gardeners, wildflower enthusiasts, foresters, and so on can reliably communicate with one another."

The outcome is that though many researchers take a pluralist view of species in theory, they do not tend to adopt the methodological recommendations of pluralists in practice. Most researchers instead adopt varying forms of compromise between what de Queiroz (1999) describes as *ontological* and *epistemological* extremes of definition. This is sometimes known as the "Cynical Species Concept" (Kitcher 1984), or "whatever a competent taxonomist chooses to call a species" (Regan 1926 in Wilkins 2009: 222). The result is the unsatisfactory situation where researchers compare species but have no standardized concept of what is meant by the term *species*. At a practical level, the confusion between operational criteria and theoretical definitions has led to an emphasis on the differences between species concepts, rather than their similarities (de Queiroz 2007), which has in turn reinforced the sense of an irresolvable incomparability and the suspicion that species might not be "real" at all.

Diverging Lineages

Rather than treating different species concepts as equally valid ways of dividing the Earth's biodiversity into different types of species, an alternative view is that these concepts are all merely different methods of identifying the same thing (Mayden 1997; Hey 2006). This is the contention underlying the *Unified Species Concept* (USC) (de Queiroz 2005, 2007). de Queiroz (1998, 1999, 2005, 2007) redefined the majority of existing species concepts as simply criteria for delimiting and identifying species, but not actual definitions of what they are. He argued that at their core, what these operational criteria all shared in common was the theoretical concept of species as *Separately Evolving Metapopulation Lineage Segments* (de Queiroz 2007). That is, segments of ancestor-descendant series (Simpson 1961; Hull 1980) composed of connected subpopulations (Levins 1970; Hanski and Gaggiotti 2004) with a shared evolutionary trajectory (Simpson 1951, 1961; Wiley 1978). Where pluralists see evidence for many different types of species therefore, the USC merely identifies different diagnostic properties. This separation between theory and practice allows species to be more or less comparable

units, even where different sets of properties or criteria are used to delimit them.

The crucial issue for species recognition and delimitation under the USC is that symptoms of divergence arise in a *contingent* manner (de Queiroz 2007). That is, evidence of lineage separation does not necessarily occur for all possible contingent properties, or if it does occur, does not do so simultaneously, or even in a regular or consistent order (de Queiroz 1998, 2007 Fig. 1). As a result, at each stage of divergence, species may or may not be distinguishable using diagnostic characters, may or may not be reproductively isolated, may or may not have adapted to distinctive ecologies, and may or may not pass through polyphyletic, paraphyletic, or monophyletic stages. This explains why any attempt to establish a single universal value or threshold for species recognition is unlikely to succeed. Instead, de Queiroz (2007) states that multiple lines of evidence based on different contingent properties should be used in combination to provide corroborating evidence, and thus stronger support for lineage separation and speciation.

This approach is at least implicitly heuristic in that it requires the strategic assessment of a representative set of properties taken to be indicative of lineage divergence. In the vast majority of cases, this presents no problems, since most species are sufficiently diverged from their ancestors and closest relatives to possess a number of different contingent properties, such that different operational methods (morphological, reproductive, ecological, or phylogenetic) will tend to arrive at more or less the same conclusion, despite being based on different types of evidence (Wilson et al. 2007).

For more recently or partially diverged lineages however, the likelihood of disagreement between delimitations based on different criteria increases, necessitating a decision about thresholds of *necessary and sufficient* levels of divergence. We may agree therefore, that we are talking about the same things (*Separately Evolving Metapopulation Lineage Segments*), but if we each continue to resort to our own chosen criteria and thresholds, it is hard to argue that much progress has been made in escaping the loss of comparability resulting from competing species definitions.

This problem is evident in de Queiroz's (2020) attempts to resolve a disagreement over species delimitation in two genera of North American reptiles. Separate authors had cited the USC in support of their opposing positions on whether to recognize distinct species or not. Burbrink and Guiher (2015) and Yang and Rannala (2010) each felt that the lineages in their investigation showed *sufficient divergence* to warrant recognition at the rank of species, while in both cases Hillis (2019, 2020) disagreed. de Queiroz's (2020) proposed solution of a new definition of subspecies as *incompletely separated lineages* may indeed provide a useful way to recognize partial lineage divergence, but it also highlights the fact that the operational challenge of judging exactly how much divergence is necessary and sufficient for species recognition has merely been extended under the USC.

As de Queiroz (2020) admits, "lineage separation is not always an all or nothing situation." However, he had also previously explicitly stated that "any evidence of lineage separation is sufficient to infer the existence of separate species. To the extent that the possession (by a set of populations) of even a single relevant property provides such evidence, it may be considered evidence for the existence of a species." (de Queiroz 2007).

What these contradictory statements reveal is that while the USC goes a long way towards providing a unified theoretical definition of *species*, ultimately it leaves us no closer to an established framework for their delimitation in practice. In describing species as *Separately Evolving Metapopulation Lineage Segments*, de Queiroz may have implied they were real ontological entities comparable across the tree of life, but the operational focus on degrees of divergence ultimately risks leaving them in the realm of subjective human constructs. Splitting the theoretical idea of what species are from the practical ways they can be identified allowed the USC to illuminate the commonality and comparability of evolving and variable species. The failure to account for this variability under a consistent operational framework has, however, undermined the USC and failed to dispel the doubts surrounding the reality of species as more or less comparable units of biodiversity.

Cohesive Clusters

An alternative attempt at tackling the issue of sufficiency in species delimitation might be characterized as flipping the entire problem on its head by thinking less about *divergence,* and more about *cohesion*. In this vein, a number of authors have argued that species are more than simply divergent or isolated lineages (e.g., Simpson 1951; Wiley 1978; Pigliucci 2003; Rieppel 2007, 2009; Freudenstein et al. 2017) but are more akin to loosely, but coherently united clusters of organisms with a shared set of properties indicative of cohesion. The idea that species form cohesive clusters appears to be borne out by social animals that form herds, swarms, flocks, or shoals (e.g., Emlen 1952; Hoare et al. 2000; Krause and Ruxton 2002); as well as external actants such as obligate parasites (e.g., De Bekker et al. 2014), specialized mutualists such as pollinators (Wiebes 1979; Kato et al. 2003; Pellmyr 2003), and even mimics (Rieppel 2007). This clustering is the basis of the *Cohesion Species Concept* (Templeton 1989), but is also implicit in earlier concepts, such as Simpson's (1951) original definition of the *Evolutionary Species Concept* (ESC), which described species as having their own "separate and unitary evolutionary role and tendencies."

Templeton's (1989) description of the *cohesion mechanisms* underlying species integrity identified the basic task in species delimitation as one of identifying the mechanisms that help to maintain an evolutionary lineage in a state of extended equilibrium or *homeostasis*. The two key terms he used for this approach were *genetic* and *demographic* exchangeability, the relative importance of which will vary based on the biology of the organisms in question. Genetic exchangeability expresses the possibility of gene flow (predominantly by sexual reproduction) between organisms, and incorporates mate recognition and other pre- and postzygotic isolation barriers. It is largely derived from evolutionary relatedness and genetic similarity resulting from common descent and leads to the sharing of similar phenotypic characters and ecological tolerances—demographic exchangeability. Tracing the properties indicative of these cohesion mechanisms allows us to identify the "most inclusive group with the potential for cohesion"—a species (Templeton 1989).

Similarly, the notion of species as *homeostatically sustained clusters of properties and relations* (Boyd 1991, 1999; Wilson et al. 2007) emphasizes the overlapping sets of properties that unite species. This *Homeostatic Property Cluster* (HPC) definition of *biological kinds* in relation to species, advocates the necessity of using *flexibly delimited clusters of properties* to identify them. No single property, nor specific set of properties, is strictly necessary or sufficient for membership of a species, but rather overlapping subsets of properties cohesively unite them. This is in many respects broadly analogous to the USC's call for the combined analysis of multiple contingent properties indicative of lineage divergence. Thinking in terms of loose clusters of properties however, attempts to reduce the role of sufficiency through a focus on cohesion, or *homeostasis*, brought about by shared *underlying causal mechanisms,* rather than any preoccupation with isolated properties of divergence. To this end, the HPC method sets out a specific way of assessing criteria for the recognition of a species' cohesion based on the identification of *causally basic properties,* and their *diagnostic properties* (Wilson et al. 2007). Diagnostic properties will tend to cluster together because they share causally basic roots. While this clustering may not be perfect, it will display a homeostatic integrity, or cohesion, drawn from shared underlying mechanisms.

Instead of leaving the choice of properties indicative of lineage divergence to individual researchers then, cohesion-based approaches to the species problem do provide some guidelines about what properties to use and how to integrate them. Nonetheless, cohesion—like divergence—comes in degrees. The integration of multiple lines of evidence is not always straightforward, while deciding how to handle contradictory signals in different data will to some extent require a return to decisions based on necessity and sufficiency. In practice therefore, deciding when exactly cohesion has broken down is perhaps no easier than finding precisely when two lineages have diverged. In this sense, cohesion methods—like those based on divergence—require a heuristic estimate of the species boundary.

The Case for Species as a Heuristic

How then can we escape from under the theoretical weight of the species problem and seek to reconcile

different theoretical ideas about species with how we identify and use species in practice? One approach to making decisions that appear intractable is by using heuristics. The psychologist Herbert Simon originally outlined the role of heuristics in decision-making and problem-solving in connection with what he termed the "bounded rationality" that arose from the limits of human judgment in scientific discovery (Kulkarni and Simon 1988; Simon 1989). More recently, heuristics have been described as "a repertoire of fast and frugal rules for decision-making under uncertainty" (Gigerenzer and Selten 2001). While generally seen as sacrificing the optimum for speed, there is evidence heuristics enhance decision-making (Marewski and Gigerenzer 2012), especially in situations where there is limited sampling (Gigerenzer and Brighton 2009; Gigerenzer and Selten 2001). The definition of a heuristic that we use here is: *a framework that relies on the strategic analysis of a subset of relevant data to make decisions that would otherwise be intractable, either as a result of the decision-maker's limitations, or the difficulties in data compilation and assessment.*

The complex and highly inter-related nature of biological systems perhaps explains the frequency of heuristic concepts and methods in systematic, evolutionary, and biogeographical research. Perhaps the most well-known example is the set of algorithms used to calculate the "best tree" of phylogenetic relationships. Since the number of possible trees increases exponentially with increases in the number of taxa, calculations quickly become impossible without heuristic search methods based on strategic sampling and trial and error (Andreatta and Ribeiro 2002). In biogeography, the delimitation of biomes—one of the most powerful tools for understanding the distribution patterns of different taxa (Whitaker 1962; Crisp et al. 2009; Särkinen et al. 2012; Hughes et al. 2013)—is also inherently heuristic, since it is based on the integrated observation of key vegetation types with a limited number of topographical and climatic characteristics (Santos and Capellari 2009). A similar case can also be made about many other key biological concepts, including genes (Pearson 2006; Noble 2008), biodiversity (Maclaurin and Sterelny 2008), and the individual (Gilbert et al. 2012). Meanwhile, specific methods including multiple sequence alignment, phylogenetic inference and models of character evolution, diversification or biogeography are all inherently heuristic (Jukes and Cantor 1969; Hasegawa et al. 1985; Tavaré 1986; Nee et al. 1994; Ronquist 1997; Ree et al. 2005; Alfaro et al. 2009; Rabosky 2014). No reasonable researcher considers these methods to align exactly with reality, but nor are they thought to represent artificial phenomena. When applied with an understanding of their heuristic nature, they can act as a useful tool to improve our understanding of complex phenomena such as phylogenetic relationships (Soltis et al. 2000; Pennington et al. 2010; Nevado et al. 2016), the ages of different taxa (Baldwin and Sanderson 1998; Muñoz-Rodríguez et al. 2018, 2019), the rates at which different clades have diversified (Hughes and Eastwood

2006; Givnish et al. 2009), and the processes that have shaped geographical distributions (Crisp et al. 2009; Särkinen et al. 2012; Hughes et al. 2013).

In line with the common use of heuristics in biological research therefore, we argue that explicitly recognizing the term *species* as a heuristic can alleviate many of the apparent difficulties in defining what species are. This is possible because a heuristic notion of species fits with both what we know about species theoretically, and the way they are delimited and used by biological researchers in practice. Recognizing species as a heuristic makes sense in practice because diagnosis and delimitation can only ever be based on the analysis of a representative set of samples and properties. Equally treating species as heuristic is also appropriate in theory because species are constantly changing but relatively stable networks of variable entities maintained by homeostatic forces. Finally, the use of species as a means of understanding broader biological phenomena means that species themselves act as a heuristic tool, something that helps to clarify how they might best be defined and delimited.

Species are Heuristic in Practice:

The practice of species delimitation is always carried out using a subset of all the potentially relevant data (Fig. 1). The analysis of these data is undertaken selectively, in that we choose what samples to analyze and which properties to assess. We cannot and do not include all the potential individual organisms, nor all of the potentially available diagnostic properties because of the limitations we face as humans working in a particular time and place (Fig. 1).

Our location in space and time exerts an influence on our ability to perceive species in that our understanding of Earth's biodiversity is primarily based on the extant individual organisms alive today or in the recent past—a tiny subset of the organisms that have belonged to the lineage of a given species. Spatially, these extant individuals will also be scattered over Earth's various ecosystems, many of which are remote and hostile to the small numbers of humans actively engaged in biological research. A taxonomist or other biologist studying a given species is therefore only likely to be able to analyze a limited subsample of living and preserved specimens relevant to their enquiries (Fig. 1).

The accumulated specimens in Natural History collections can allow for useful cross-comparison in time and space, thereby reducing some of our observational difficulties (Latour 1999, p. 38). Even this has its limitations however, since Natural History collections tend to reflect the interests and idiosyncrasies of the collectors and researchers who have contributed to them. These include particular geographic or taxonomic focuses, funding opportunities, political and historical boundaries, storage considerations, physical inaccessibility, and the prizing of the rare over the common. Natural History collections are, therefore, intrinsically partial and biased, and they are also often incomplete.
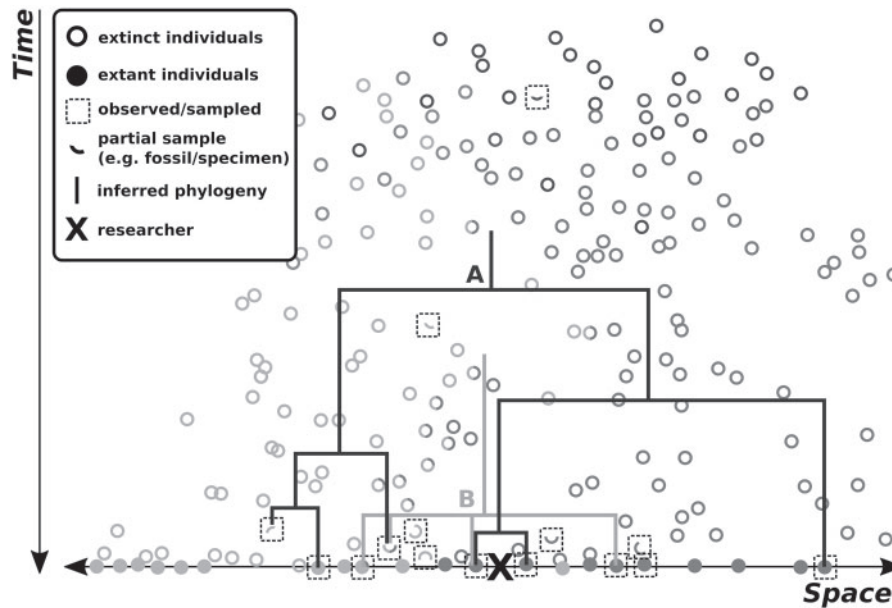
FIGURE 1.   Stylized diagram depicting location in time and space of individuals of one ancestor (black) and two descendent species (dark and light grey) in relation to a hypothetical researcher (X) and their observations. Circles combining two shades depict instances of hybridization and introgression. Overlaid phylogenies (A: high genome coverage; B: barcode marker/organelle) show potentially conflicting topologies of relationships inferred as a result of different taxon and genome samplings. The majority of individuals that have ever belonged to the three hypothetical species are beyond the perception of the researcher. The researcher's spatial location within part of the geographical range of one species also results in a bias in sampling towards the accessible minority. Both of these factors have a knock-on effect when it comes to inferring evolutionary relationships through phylogenetic analysis of different genomic regions taken from different groups of individuals. Historic introgression might cause two species to be lumped together when analysed with a barcode or organelle marker (b) for example, while spatially biased sampling within the more widespread species may imply a level of phylogenetic divergence that some researchers might treat as evidence of a third species (a), despite a lack of corresponding phenotypic or ecological change.

Herbarium specimens of large plants such as tropical trees are obviously incomplete, but the loss of ecological and behavioral context involved in transferring any organism from its natural environment as a preserved specimen to an institution is an inherent weakness of all aspects of collection-based research.

Fossils also offer a means of collapsing space and time to make inferences about both extant and extinct species (Fig. 1). The fossil record is even patchier than our imperfect collections of extant organisms however, containing only parts of organisms, from particular ecologies in particular epochs, and—crucially to contemporary researchers—little or no DNA.

Phylogenetic and other analyses of DNA sequence data have unarguably revolutionized how we undertake systematic and taxonomic research, and they also offer a lens into the distant past (Fig. 1). Nonetheless, material for DNA sequencing is almost always extracted from an even smaller subsample of our subsample of collected specimens, and the section of the genome used is itself almost always partial—either in the form of particular genes and barcode markers, or organelles, SNPs, transcriptomes, and consensus sequences. At the same time, as described above, phylogenetic analyses are themselves inherently heuristic.

A separate issue for our ability to accurately identify and perceive species is that, although we have invented tools with which to supplement our natural senses—such as those that allow us to perceive light, sound, and chemicals beyond our natural range—it remains the case that fundamental limits are placed on our powers of perception, which are necessarily circumscribed by our sensory abilities. We will never be able to experience or understand the world in the manner of an organism like a sightless catfish "tasting" its murky surroundings, let alone a plant, subterranean fungus or microscopic bacterium. Nor is our sight any clearer from a definitional point of view either, since the criteria used in the majority of species concepts are, like physical forces, not directly observable phenomena. We cannot see gene flow, reproductive isolation, ecological niches, or genealogical relationships, and we must rely instead on proxies to infer them. Our senses thus directly limit our ability to untangle and interpret the behavior and relationships that are key to species recognition and, as a result, our inferences about them cannot be anything other than heuristic.

In light of this, the discovery of new specimens, properties, or techniques may lead us to adjust our previous delimitations, but no decision can ever be based on all the potentially relevant or actually available data. The integration of different types of data is therefore key to improving the accuracy of species delimitation, especially in the face of low sampling or high uncertainty (Pante et al. 2015; Gratton et al. 2016; Sukumaran and Knowles 2017; Federman et al. 2018;

Hundsdoerfer et al. 2019; Parker et al. 2021), consistent with the principles of both the USC and cohesion-based approaches. Decisions about what types of potentially available data or properties should be integrated in these analyses are strategic, in that they will be based on our existing knowledge about the group of organisms in question.

Treating Species as a Heuristic is Consistent with Theoretical Ideas of What Species Are:

Beyond the intrinsic limits of human experience and perception, extrinsic limits are also placed on our ability to delimit species by their own nature as constantly changing yet more or less stable collections of individual organisms experiencing similar environmental and ecological forces. This state of "punctuated equilibrium" in the course of ongoing evolution raises a fundamental question about the nature of identity in the course of change; an issue that Rieppel (2009) described in terms of a Heraclitus Paradox: if all the elements of which something is composed are exchanged or replaced, can it still be considered the same entity? At any given point in time, the network of individuals within a species will change and eventually be entirely replaced, but as long as the forces holding them in place—what Templeton termed "cohesion mechanisms"—remain in existence, the species continues to exist. This underpins why cohesion mechanisms and evidence of lineage divergence are effective means of identifying species, despite the continual change in their constituent organisms. We are forced to use proxy characters not just because of practical limitations, but because of the theoretical nature of species as dynamic networks of variable and evolving entities.

Finally, just as diagnostic properties are used as proxies for the forces involved in speciation, species themselves constitute a proxy to better perceive and understand the patterns and processes of evolution. Particular species, or species groups, can be used to understand evolution at both the micro- and macro-evolutionary level, whether as model organisms for understanding particular genetic pathways, or in species counts for assessing local biodiversity richness, or as input data in models of dispersal and diversification. Not only does this make species a form of heuristic in their own right, it also defines what we need species to be—that is representative units of earth's biodiversity that allow comparisons and inferences.

Benefits of Treating Species as a Heuristic:

Commonly highlighted issues arising from the *species problem* are at least partially reduced by acknowledging species are heuristic. Whether we believe them to be "real" or purely nominal entities is not important if we accept that species are heuristic estimates of observable phenomena. Instead, the approach outlined here leads us to a looser definition of species as clusters of closely related individuals responding in a similar manner to comparable sets of evolutionary and ecological forces, which can be recognized by the congruence of contingent properties indicative of those forces. The exact means of speciation may differ, some species may be more genetically isolated from their neighbors than others, while levels of morphological distinctiveness or reproductive isolation will vary, and ecological niches may be more or less well defined. In combination however, these properties serve to distinguish more or less discrete biological entities exerting a unique impact on each other and their surrounding environment.

This definition of species is not entirely new. In addition to being compatible with both extended lineage definitions such as the *Evolutionary Species Concept* or the *Unified Species Concept* and cluster concepts such as the *Cohesion Species Concept* and *Homeostatic Property Cluster*, it finds ready parallels in notions of consilience (Whewell 1860, 1847; Crowe et al. 1994; Richards 2010; Snyder 2005a, 2005b), compatibility (Estabrook and McMorris 1977; Meacham 1981; Meacham and Estabrook 1985), reciprocal illumination (Hennig 1966), congruence (Patterson 1988, 1982; Wilson 1965), and the triple helix (Lewontin 2000). The benefit of an explicit recognition of the heuristic nature of species lies in removing the association with subjectivity while avoiding resorting to pluralism. Rather than separating theory from practice by proposing a monist definition and a pluralist approach to delimitation as many have done before (e.g., Wilkins 2009; Richards 2010), treating species as a heuristic reconciles the two: *species* is a heuristic concept, and we use heuristics when we identify species or use them to make further inferences about the biological world. As such, the fact that we cannot hope for a perfect perception or definition of species does not mean that they are arbitrary constructs, but merely that our approach to describing them requires a certain degree of flexibility, which is best accomplished by recognizing that *species* as a heuristic.

A heuristic approach to species delimitation also enables us to be strategic about how we focus our efforts in contemporary biological research. A lack of comprehensive sampling or fine-grain data need not hold us back if delimitations are provisional and based on "a practical method not guaranteed to be optimal or perfect, but sufficient for the immediate goals" (Wood et al. 2020). Perhaps the most pressing goal in contemporary systematics is the completion of an inventory of life on earth. This formidable challenge is evident enough for the two largest groups of known terrestrial organisms—insects and flowering plants – which together account for 75% of currently described biodiversity and each possess large proportions of potentially undiscovered species (Mora et al. 2011). It is even more pronounced however, for more challenging groups like fungi and microbes, where simply getting an estimate on what is unknown presents serious difficulties (Schmit and Mueller 2007; Locey and Lennon 2016). The current slow progress in species discovery (Goodwin et al. 2020) makes for a

stark contrast with the rate of predicted and documented global change that is already having a negative impact on biodiversity. The latest estimates suggest that 25% of plant and animal species are threatened with extinction in the coming decades (Díaz et al. 2019), for example, and that 600 known species of plants may have become extinct in recent times (Humphreys et al. 2019). As a result, whether our priority is improving the basis for conservation action, or merely understanding Earth's biodiversity for its own sake "we will need to do the best we can, as soon as we can" in attempting to complete the inventory of life on Earth (Raven et al. 2020), and this will be more achievable with a heuristic approach.

CONCLUSION

What Are Species in Theory?

Species are sections of branches on the tree of life—*lineage segments*. They are also cohesive entities, genealogically related and displaying an imperfect but more or less stable homeostasis through time—*separately evolving metapopulations* or *homeostatic property clusters*. They exert a unique and distinct influence on themselves and their conspecifics, as well as on other organisms and the environment they inhabit. It is this common influence and its derivation from shared characteristics inherited through common genealogical relationships that differentiate species from the populations within them, as well as from the higher taxa above them. It is also what makes species such a valuable unit of research. Put heuristically therefore, species are clusters of closely related individuals, responding in a similar manner to comparable sets of evolutionary and ecological forces.

How Do We Delimit Species in Practice?

Clearly the inclusion of the qualifying adjectives "closely," "similar," and "comparable" in the theoretical definition of species outlined above is intentionally imprecise. We do not provide any empirical thresholds for particular criteria or properties, since we have reiterated the futility of attempting to do so. While there can be no set of universal criteria or properties applicable to species delimitation, a heuristic approach does provide clear guidelines for their selection and assessment.

Since species are clusters of closely related individuals, responding in a similar manner to comparable sets of evolutionary and ecological forces, species are identifiable by the congruence of contingent properties that act as proxies for those forces. A heuristic method of species delimitation is therefore one based on an integrated assessment of congruence in traits indicative of genotypic, phenotypic, and ecotypic cohesion.

In an ideal sense, well-supported monophyly based on molecular phylogenetic analysis and a comprehensive taxonomic and genomic sampling strategy represents the best evidence for genotypic cohesion. Similarly,

population genetics and genomics can both provide methods for assessing genotypic cohesion at a fine scale. Monophyly alone is however insufficient for species delimitation if we are to avoid recognizing intraspecific phylogenetic lineages with little in the way of morphological or ecological differentiation (Freudenstein et al. 2017). Molecular phylogenetic or population genetic analysis should, therefore, always be integrated with some form of assessment of congruence with both morphological and ecological data. By insisting that molecular phylogenetic analysis be carried out in conjunction with assessment of morphological and ecological data, our definition also avoids precluding species generated by processes that do not automatically or immediately result in monophyly, such as hybrid speciation, polyploidy, or paraphyly in the case of recent ancestor-descendant speciation. Where molecular phylogenetic analysis is impractical due to inadequate samples or easily sequenced material, or where it fails to resolve well-supported relationships, species delimitation remains possible, but should be based on a strong hypothesis of phylogenetic relatedness resulting from multiple and unambiguous phenotypic and ecological traits.

Phenotypic characters remain the most obvious and readily available means of identifying and delimiting species (Pante et al. 2015). What is more, since the shared possession of a set of traits is derived from genealogical relatedness, and is influenced by selective ecotypic pressures, morphological data are also capable of providing evidence for all three forms of cohesion. Shared morphological traits, like a particular beak size or shape can therefore serve as evidence both of genealogical relationships and a shared ecological niche (Wilson et al. 2007). This explains why species delimitations were and are possible in the absence of notions of evolution or modern scientific methods, as well as why many species delimitations have remained stable in the face of these developments.

Finally, the assessment of particular ecological adaptations or niches is notoriously difficult. They can either be hard to disentangle from phenotypic traits themselves, or else present serious difficulties in terms of empirical measurement. Possible examples include assessments of mutualistic specialization like pollinator relationships or dispersal mechanisms, sensitivities to particular chemicals, and distribution patterns aligned with geographical features or ecological clines. For some of these properties, advances in the sophistication and availability of technologies such as camera traps, sophisticated sensors, computer modeling and increased knowledge of gene function are enabling more detailed study and analysis. In most cases however, a heuristic approach based on proxy and inference remains more than sufficient.

Limitations, Potential Criticisms, and Final Remarks

We do not claim that recognizing and treating species as a heuristic is an infallible panacea for the species

problem. Different researchers will inevitably continue to disagree about where exactly the boundaries between species should be drawn. A heuristic notion of species cannot surmount this, but as de Queiroz (2007) hoped for the USC, the argument should be focused on the weight of the evidence presented, rather than disagreements over what exactly a species is or is not. As such, the heuristic nature of species delimitation will be familiar to most taxonomists in their attempts to make judgements about species boundaries, since much of this framework simply reflects an explicit statement of what has been implicit in most contemporary approaches to species delimitation. What is gained is an understanding of why that approach is effective and appropriate, despite the theoretical disputes.

Nonetheless, for research areas such as conservation and biogeography that use species data in a comparative way, it could be argued that treating species as a heuristic potentially endangers rather than ensures comparability. This is particularly the case if "heuristic" is misunderstood as a return to the Cynical Species Concept, where species are whatever a taxonomist says they are. The result would be that species are no more comparable than they were under a pluralist approach. If this were the case, then no progress has been made, and the sense of nagging doubt that stalks the term *species* will remain.

We hope we have shown however, that by focusing on reconciling the theoretical ideas of what species are, what we need them to be in our research and the ways they can be identified, a heuristic approach to species delimitation should in fact better guarantee comparability among them. If species are treated as clusters of closely related individuals, responding in a similar manner to comparable sets of evolutionary and ecological forces, they are comparable enough to make inferences about those forces and the patterns they have led to. This definition also provides a unifying framework for how the different types of data available to contemporary researchers should be integrated, rather than leaving it up to the individual to choose which type of properties they should focus on. By reconciling evolutionary theory with taxonomic practice, heuristics allow us to make necessary taxonomic decisions about species in the face of uncertainty. These decisions have proven to be one of the most useful and powerful tools for the study of evolution, systematics, biodiversity, and ecology. They are neither perfect, nor definitive, but they are preferable to continued attempts to define our way out of the species problem.

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