Understanding and confronting species uncertainty in biology and conservation

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Recent essays on the species problem have emphasized the commonality that many species concepts have with basic evolutionary theory. Although true, such consensus fails to address the nature of the ambiguity that is associated with species-related research. We argue that biologists who endure the species problem can benefit from a synthesis in which individual taxonomic species are used as hypotheses of evolutionary entities. We discuss two sources of species uncertainty: one that is a semantic confusion, and a second that is caused by the inherent uncertainty of evolutionary entities. The former can be dispelled with careful communication, whereas the latter is a conventional scientific uncertainty that can only be mitigated by research. This scientific uncertainty cannot be 'solved' or stamped out, but neither need it be ignored or feared.

For researchers, few ideals are as sought after as those of the independent observer; preferably, a scientist should discover and transmit his or her story, and not be a part of it. But what if that cannot be arranged? In some fields, most notably quantum physics and human behavioral research, observation *per se* can have a direct effect on outcomes, so that studies must be designed to incorporate those effects. Of course, research in these fields does not come to a halt. Neither does research halt in other fields where the impact of the observer cannot be avoided or ignored safely, but rather is addressed directly as part of the research program. Here, we argue that biological research on species will benefit from an explicit recognition of the inherent limitations that biologists experience as investigators of species.

Many evolutionary biologists, systematists and ecologists struggle with the related questions of how to identify species and how to define the word 'species'. These persistent questions constitute what is known as the 'species problem'. The problem is not new. Indeed, Darwin drew upon the persistence of wide taxonomic disagreements to support his arguments for the evolution of

species, but the problem endures with a steadily increasing literature on how to define 'species'. A recent listing of species concepts found 24 in the modern literature [1] and new books appear steadily [2–4].

In recent years, a recurring claim with regard to the species problem is that most species concepts have strong implicit similarities, and that most are consistent with the idea that species are evolving lineages or evolving populations [1,3,5,6]. We agree with this consensus. However, we remain concerned that it does little to address the fundamental cause of the species problem, which is the inherent ambiguity of species in nature. Here, we focus directly on the nature of this ambiguity and review a modern synthesis under which species-related research and conservation efforts can proceed without suffering from, and without fear of, the ambiguity of species.

Background and synthesis
Prominent in species debates are questions regarding the role played by human investigators in the creation of species taxa, particularly with regard to taxonomic rank designations. Darwin argued that decisions to apply the taxonomic rank of species were sometimes arbitrary, and that species are not different essentially from varieties [7]. Spurway drew upon the ways that animals learn to identify different kinds of organism to argue that species designations are caused by basic human instincts, and that we could not expect to find a universally applicable definition of 'species' [8]. Haldane supported this view [9], and it has been articulated more recently from different directions by Levin [10] and Nelson [11]. Yet, these skeptics notwithstanding, the view has emerged since Darwin that species have special properties that set them apart from taxa of other ranks, and that species are objective and real to some extent because of these properties. Dobzhansky's *Genetics and the Origin of Species* portrayed species as real genetical and evolving entities that could be studied with modern genetic approaches [12]. Huxley's *The New Systematics* [13] is

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the historical touchstone for modern systematic research programs that see species not just as categories with representatives in museums, but also as dynamic evolving entities that exist independently of human observers and of human-assigned categories [14,15].

These two ideas – that species are categories that are created essentially by the biologists who study them, and that species are objective, observable entities in nature – have long been in conflict. On the one hand, we have species taxa that have been identified traditionally on the basis of distinctive characteristics. On the other hand, we have an idea of a species as a kind of entity in nature, an evolutionary unit made up of related organisms that are evolving together. Over the years, various authors have recognized this fundamental distinction [3,16–22]. Yet, is it possible that these two perspectives on species can be joined? That has been the intended purpose of some popular species concepts, and much of the modern debate over species concepts has been a struggle over how best to describe species in a way that preserves both the accepted taxonomic traditions and the modern understanding of evolutionary processes. Both the Biological Species Concept of Mayr [23,24] and the Phylogenetic Species Concept of Cracraft [25,26] are intended to help biologists identify species taxa that are real evolutionary role players in nature. Neither view admits a distinction between species taxa and species as evolutionary entities.

But, hidden partly in the debates over the nature of species lies a direct and complementary connection between species as taxa and species as entities. The connection represents a conceptual linkage that circumvents many aspects of the species problem and that leads directly to ways that research can proceed without species conflicts. To see this connection, consider that newly devised species taxa serve as hypotheses that might be supported by new data and that, notwithstanding the rule of precedence, might require later revision. Growing collections, improving methods of morphological analysis, and the increasing use of ecological, behavioral and genetic data have moved biologists necessarily away from the view of taxa as fundamentally static to a view in which species taxa can be revised on the basis of increasing information from diverse sources [13–15,27,28]. This view, that our ideas regarding a particular species should be subject to examination in light of data from natural populations, has also emerged in the population genetic literature [29,30]. In particular, Templeton argues that population genetic data should be used to test whether populations do indeed exist as cohesive species [31].

These twin strands of thought on the hypothesis-testing aspect of species designations, from the perspectives of both systematics and population genetics, lead to the idea that a species taxon can serve as a hypothesis of a species as an evolutionary and ecological unit in nature [3,32–35]. This synthesis draws directly upon the practice in systematics in which taxa are subject to revision, but, in addition, there is the idea that a species taxon presents a general hypothesis that all existing organisms that would be assigned to that taxon actually constitute a biological entity in nature.

In principle, species taxa that are used as hypotheses

might be simply confirmed or rejected, although more typical outcomes are likely to be fuller descriptions of the evolutionary processes that occur among the organisms that would be identified as members of a taxon. Some species taxa can be expected to be highly explanatory as evolutionary hypotheses, in which case they are likely to be affirmed by the discovery of additional characters that are shared uniquely among the organisms assigned to the taxon. At some point following research on these evolutionary processes, a taxon might come to be paired with a full description of the population or populations that it represents, including the degrees of isolation and distinction that occur among populations. Also, the degree or quality of correspondence between a taxon and its evolving counterparts might be used to devise more taxa as necessary.

The ambiguity of species entities

From a purely ontological perspective, entities are real things that have a location in space and time, and that can be acted upon or can change [36]. Entities have a different kind of existence than do categories, such as taxa, which have defining properties. To be clear, by way of a deliberate example, consider the species taxon *Ursus maritimus* (polar bear). The defining properties of this taxon were described first by Constantine Phipps [37]. Today, many animals that we assign to this taxon live in zoos, but most constitute a circumpolar arctic population, comprising multiple connected regional populations; that is, an evolving entity [38]. Even if this entity were to disappear, and the natural population of polar bears were to become extinct, the species taxon would still exist as a set of defining characteristics and would still have representatives in museums or zoos.

Species are but one kind of multi-organismal entity, and organisms can also be components of social groups within species as well as parts of commensal interspecies assemblages. Biologists also recognize ecological entities that consist of many different kinds of organisms, and individual organisms are parts of ecosystems, both on very local and broad scales. To complete the point, we need not be monistic with regard to species entities and so might wish to consider different kinds of species entities as a function of how they arise and persist. Templeton [39] articulated two general processes that will cause a group of organisms to evolve together: gene exchange and ecological equivalence (or demographic exchangeability). Both processes, alone or together, can cause genetic drift and adaptations to be shared by a group of organisms, and cause that group to evolve cohesively and separately from other such groups.

Our perceptions of an evolving group of organisms will be least ambiguous for those taxa whose only representatives exist in a single, small distinct population (e.g. a species restricted to a single lake or mountain peak). But even small populations that appear cohesive and well bounded in some respects might not be in others. The population of finches of the species taxon *Geospiza fortis* that lives on Isla Daphne Major in the Galapagos is not separated completely from populations on other islands, neither is it completely separate from populations that are

assigned to other taxa [40,41]. Episodic hybridization results in gene flow, and introgressing traits from other species are sometimes favored by natural selection. In this case, detailed genetic and ecological data reveal both the presence of a cohesive evolving population, as well as ways in which that population is not entirely separate from other populations, some of which are assigned to the same taxon and others to different taxa.

We might expect that large populations, especially if they are subdivided geographically, will often comprise multiple evolutionary entities. A taxon might include organisms that are found in isolated populations, each of which is evolving separately. Such populations might be connected tenuously by occasional gene flow, and thus might share some common selective sweeps (i.e. fixations of advantageous mutations) and adaptations [42], but they might still occur mostly as separate populations. In these contexts, the nature of the evolutionary entity could be inherently ambiguous, and even intensive field research will not reveal a clear demarcation. In short, all the organisms of a species taxon will often not constitute an evolutionarily cohesive entity, particularly for species taxa with representatives that are widespread or have disjunct distributions [43].

Understanding species uncertainty

Using species taxa as a framework to study evolving species in nature reveals two different kinds of uncertainty that might persist in species-related research and discussions.

Type I uncertainty

One persistent component of the species problem is that 'species' is a confusing homonym, with different meanings that are disparate ontologically and yet related semantically. Three ontologically distinct meanings predominate in the literature of the species problem: (1) 'species' is the name of a taxonomic rank; (2) 'species' is the word that we apply to a particular taxon of that rank (e.g. the species taxon *Homo sapiens*); and, finally, (3) 'species' is a word that we apply to an evolving group of organisms. The potential for confusion between the first two meanings, the taxonomic rank and particular taxa, has been recognized for some time [18,44,45]. Less widely realized is that confusion also arises between the second and third meanings, between the ideas of a species as a taxon (i.e. a category of organism or a group of organisms with a shared set of traits) and a species as an evolving group of closely related organisms. Although biologists and philosophers have recognized that evolution creates entities that comprise multiple related individuals [23,36,46,47] it has been understood only at times that such things are not literally the same things as taxa (i.e. kinds of organisms) [3,16,17,34]. That one word, 'species', is sometimes used to refer to a taxonomic rank, at other times a particular taxon, and at other times an entity in nature, causes confusion and requires that authors and speakers take care to articulate their meaning when they use the term.

Type II uncertainty

The second kind of uncertainty arises from basic limitations of empirical scientific research. This uncertainty is caused by the inherently ambiguous correspondence between a species taxon and the entity or entities for which it is used as a hypothesis. Even with clarity over the distinction between a taxon and an evolutionary entity, it might be very difficult to assess empirically the actual correspondence for a particular taxon. This practical, empirical uncertainty is conventional in the sense that scientists are rarely fully assured of a correspondence between their hypothesis and reality. At base, this uncertainty arises because of the subjective component of devising categories. Species taxa are devised by investigators and are partly a function of biologists' tools, circumstances and inclinations. For species that can be observed easily and have distinguishing morphological characters, this subjective element will seem remote and biologists can agree on the organisms to be included in a species taxon. However, for many organisms that live in soil or water, or within or upon other larger organisms, the subjective element might be large. Two investigators working with a common sample of organisms might well disagree on the weight to be given to particular patterns of variation in such cases, and thus on the designations and descriptions of new species taxa. When we turn to the field, and use species taxa as hypotheses, we see also that the uncertainty is difficult to mitigate. In short, species entities are very difficult to study, for they are evolutionarily and demographically dynamic. They will often not be very distinct and the degree to which they are distinct can change over time [5] if, for example, separated populations exchange genes occasionally (as is the case with the Galapagos finches).

Confronting species uncertainty

Across the breadth of species-related research, biologists vary in their use of species taxa. In systematics, taxa are the essential starting point for classification and phylogenetic research. In population biology, some taxa are also used in the course of ecological or genetic research on the structure of evolving populations, although only a few can be examined in this way. In the continuum of research programs, which lies between focused taxonomic research on the one hand, and research that is focused on particular populations in nature on the other, there lies a great deal of research by ecologists, evolutionary biologists and conservation biologists that rely upon taxa as indicators of evolutionary entities. For example, many multi-species studies, including ecosystem studies and biodiversity assessments, rely strongly upon species taxon counts. Such counts suffer several limitations depending on the context, but one that is typically overlooked is the usually unknown correspondence between taxa and evolutionary entities [22,48,49].

What do we gain by considering species taxa explicitly as hypotheses of species entities in nature, and by dividing our species-related uncertainty into semantic (type I) and empirical (type II) components? For research on natural populations, for evolutionary and ecological questions or for efforts to conserve biological diversity, we gain a

general research protocol that is not hindered by some of the traditional species-problem debates. Of course, the method is not thereby made easy or simple. No synthesis can do that because species in nature are difficult subjects. However, we can appreciate that the difficulty of studying species is a conventional scientific difficulty; it is caused by the need to devise and test hypotheses, just as in other fields with difficult subjects.

The framework of treating species taxa as hypotheses of species entities leads us to distinguish those aspects of species uncertainty that are inherent to research and discovery of biological diversity, and to set aside some aspects of species-related debate that are avoidable. Two basic questions are inescapable. First, by what criteria shall species taxa be identified? For systematists, this question lies at the heart of species-concept debates [2,15,50,51]. However, when a taxon is to be a tool for the study of evolutionary entities, then the question becomes the following: what criterion will aid best in the discovery of the locations, boundaries and properties of evolutionary entities? Importantly, the answer might not be the same for all kinds of organisms.

The second question is when does one decide that there is one, or more than one, evolving entity? Two kinds of answer come fairly readily. One is simply not to decide whether or where to draw lines of demarcation, but rather to present the full picture that research has revealed, and to do so in its full complexity rather than to reduce that complexity artificially. A second kind of resolution, which might be demanded because of practical concerns, is to make a decision regarding demarcations, while also recognizing the decision as an oversimplification demanded by the practical concerns.

The principal aspect of the species problem that is avoided by our proposed synthesis is the traditional debate over a 'best' species concept. Consider that if taxa are to serve as hypotheses, then there are several common species concepts and associated taxonomic criteria that could provide a good starting point for the study of populations. In particular, the use of reproductive traits and the use of diagnostic characters are both well motivated by evolutionary theory, and each is expected to provide a rough guide to the presence of evolutionary units in nature [6]. This is not to say that one is as good as another in a particular context, simply that each is justifiable in principle, and that it remains to investigators to make that justification for their particular subjects of research.

A key inspiration of the species-concept debate is the often-described need for species-related clarity. These appeals say in part that we need a common concept of species to handle the uncertainties that arise in species-related research. Although true in strictly systematic contexts, the same arguments have also been applied in reference to the study of evolving populations in nature [26,52,53]. However, no species concept or protocol can remove the inherent difficulty and ambiguity of research on evolving populations. The demarcation of two different sources of species uncertainty leads to a fairly straightforward parsing of conventional demands for species-related clarity into those that are tractable and those that are not.

The common assertions, that we must be able to both count species and to distinguish species, are directly answerable: (1) species taxa can be counted, and they are distinguished in the course of their devising; whereas, (2) evolutionary entities will often be truly indistinct, and will sometimes not be countable strictly or distinguishable unambiguously no matter how thoroughly they are studied [34].

Identifying units for conservation

The contrast between species taxa and evolutionary entities is stark when considering conservation. Species taxa can often be preserved in the sense of having living representatives by culturing organisms in zoos and botanical gardens; that is, by maintaining living counterparts to the taxon representatives that are kept in museums. But if species taxa are to have representatives living in nature, then they must be part of evolving populations. In recent decades, this simple realization of the fundamental insufficiency of taxa as the focus of conservation efforts has shifted those efforts towards research on how best to conserve evolving populations [54].

For population-based conservation efforts to be effective, goals must be articulated clearly both in terms of what kinds of populations are to be conserved and in terms that recognize the inherent difficulties and ambiguities. To appreciate how such apparently offsetting demands (for conservation criteria that recognize inherent ambiguities) can be implemented, and to appreciate the issues raised by their application, we consider the entity-based idea of an evolutionary significant unit (ESU) [55−58]. An ESU is a population, or group of closely connected populations, that belong to a species taxon. Furthermore, an ESU shows evidence of being genetically separate from other populations, and contributes substantially to the ecological or genetic diversity found within the species taxon as a whole.

In recent years, the ESU concept has been applied broadly to salmon populations on the west coast of the USA, as well as to a variety of other species [58,59]. The intent in defining salmon ESUs has been to identify entities that are on largely independent evolutionary trajectories. Although it is problematic to predict which ESUs will be important to the future evolution of the taxon, conservation of as many ESUs as possible should minimize anthropogenic constraints on natural evolutionary processes and maximize the probability that the taxon and some of its populations will persist into the future. However, this formulation provides no specific, quantitative standards and offers no guarantees that type II uncertainties will be resolved. Thus, several variations of the ESU concept have been proposed, and the concept has been criticized as being too broad [60], too narrow [61,62] or non-operational [52,63]. Two different kinds of approach have been suggested to address the apparent vagueness of the ESU concept. One suggestion is that, for the purposes of efficiency, ESU status should be decided using a uniform standard of genetic cohesiveness and uniqueness. For example, Moritz [60] suggested a specific genetic cutoff (based on mitochondrial DNA monophyly and nuclear gene differences) for conferring ESU status. The obvious concern that application of that standard will

appear arbitrary in many applications, or capricious in the face of other kinds of evidence of cohesiveness and uniqueness is perhaps answered by the considerable need for a readily applicable, if imperfect, yardstick. Given that mitochondrial DNA diversity will often be a poor indicator of demographic boundaries [64–66], this particular proposal might not be ideal. However, this does not mean that some standardized method might not provide a reasonable balance between biological realism and the needs for efficiency.

A different kind of suggestion is that the current ESU criteria should be replaced by a single, better criterion that would, inherently by its nature, dispel uncertainty. The principal claim of this sort is that ESUs should be groups of individuals that share a unique character, or suite of characters, that distinguish them from individuals of other ESUs [52,63]. In other words, an ESU should be identified by the criteria used in one version of the Phylogenetic Species Concept [67,68], not for reasons of efficiency (which could also be claimed), but because such criteria are inherently unambiguous indicators of real evolutionary entities. These proposals, which equate the presence of a disjunct pattern of characters with the presence of an evolving population, have two limitations. First, they assume accuracy on the part of taxonomic criteria and overlook the reasons why species taxa will often be a poor guide for elucidating evolutionary entities. Second, by directly equating ESUs with species taxa they have nothing to offer to the question of how best to conserve diversity below the species level.

In the case of Pacific salmon, the recognized species taxa that are based on diagnostic characters are considerably more inclusive than ESUs that have been identified, each of which is limited to the populations in a restricted geographic area [58]. For this species, taxa based on diagnostic characters appear to be too coarse a guide for identifying evolutionary entities, which is not surprising given the highly structured populations of anadromous fish. In other contexts, it might happen that a strong focus on diagnostic characters could lead to taxa that are less inclusive than true evolutionary entities, either because of the vagaries of sampling or because of the near infinity of possible characters to examine [69].

Policy implications of species uncertainty

If conservation efforts do focus on evolving populations and treat species taxa as research guides, then the ambiguity of evolving populations and their uncertain connection to taxa will often be manifest. If biologists making conservation recommendations are revealed as being uncertain in their species assessments, will this hinder the legal and policy-making components of species conservation? Perhaps if biologists admitted uncertainty over species, then they could not play as constructive a role in conservation efforts [70]. For two reasons, we think that such a concern is misplaced.

First, the traditional practice of treating species taxa as the primary focus of conservation efforts has a cost, quite apart from that associated with the possible misidentification of evolving populations. A strong reliance on taxa as conservation units creates a pressure to devise new species taxa as a strategy to serve conservation goals, or to shift the rank of a taxon solely as a way to preserve biodiversity [71]. In other words, legitimate conservation concerns, combined with a reliance on taxa as conservation units, can have the unfortunate consequence of shifting taxonomic decisions away from biological criteria and towards political or economic concerns.

Second, the uncertainty of species entities is not different in kind to that associated with other scientific subjects. Importantly, many scientific pursuits have high levels of uncertainty and also play a highly visible role in the formation of public policy. Consider droughts, for example, which, as phenomena, are not circumscribed easily, their intense environmental and financial impact notwithstanding. Meteorologists, hydrologists and policy planners have worked to develop practical guidelines for drought identification, even as they debate how best to do so [72]. Consider as well the difficulties associated with medical diagnosis and the identification of health-risk factors. Physicians must make judgment calls regularly in the care of their patients, and they must also provide public health guidelines that are as unambiguous as possible, often in the face of substantial inherent ambiguity.

The question of how best to identify populations for conservation has much in common with questions of how to identify droughts, and to prevent or treat disease, and with other areas where imperfect scientific knowledge is used to shape public policy. The choices of what to conserve must often be made with regard to populations that are not separate completely from others, or when information regarding the relationships and degrees of distinction among populations is very incomplete. Such decisions, although difficult because of the uncertainties that are not mitigated easily, are not different in kind from those decisions made in other contexts where scientists have imperfect knowledge or where nature does not present clear boundaries.

Prospects

Biologists cannot hope to avoid or eradicate species uncertainty. Whether such hope arises from a wish to 'solve' the species problem, or from a wish to simplify the tasks of biodiversity conservation, or from fear that policy-making and legal institutions cannot accommodate uncertainty about species, we should recognize that there is not a single species concept, nor a research protocol, that can remove the inherent difficulty and uncertainty that accompanies research on evolving populations. These are conventional scientific uncertainties, and we cannot shelter ourselves from them.

The first reward of treating species taxa as hypotheses and by recognizing the inherent uncertainties of species-related research is a research protocol that is conventionally hypothetico-deductive. But beyond this aspect, which already characterizes the work of many investigators, the largest gains will be in the area of explanation. Researchers of biological diversity are sometimes entangled by species-problem-related questions that come from colleagues and biologists in other specialties, as well as from laypersons, students and professionals in fields who rely

upon the conservation recommendations of biologists. By explaining how research begins with taxa and proceeds to the study of populations, many species puzzles can be explained in the familiar language of the uncertain relationship between our hypotheses and the realities of nature.

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