

Biodiversity and the Species Concept—Lineages are not Enough

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Received 15 April 2016; reviews returned 13 October 2016; accepted 14 October 2016

Associate Editor: Roberta J. Mason-Gamer

Abstract.—The nature and definition of species continue to be matters of debate. Current views of species often focus on their nature as lineages—maximal reproductive communities through time. Whereas many authors point to the *Evolutionary Species Concept* as optimal, in its original form it stressed the ecological role of species as well as their history as lineages, but most recent authors have ignored the role aspect of the concept, making it difficult to apply unambiguously in a time-extended way. This trend has been exacerbated by the application of methods and concepts emphasizing the notion of monophyly, originally applied only at higher levels, to the level of individuals, as well as by the current emphasis on molecular data. Hence, some current authors recognize units that are no more than probable exclusive lineages as species. We argue that biodiversity is inherently a phenotypic concept and that *role*, as manifested in the organismal extended phenotype, is a necessary component of the species concept. Viewing species as historically connected populations with unique role brings together the temporal and phenotypic natures of species, providing a clear way to view species both in a time-limited and time-extended way. Doing so alleviates perceived issues with “paraphyletic species” and returns the focus of species to units that are most relevant for biodiversity. [Coalescence; Ecological Species Concept; Evolutionary Species Concept; General Lineage Concept; lineage; phenotype; species.]

The numerous ways in which species have been defined and the apparent inability of biologists to agree on something so fundamental has been described as the “species problem.” The problem is longstanding; already Darwin (1859, p. 44) lamented that, “No one definition has as yet satisfied all naturalists.” The current deluge of massively parallel genomic sequence data and new approaches that are being applied to resolve species boundaries (e.g., Carstens et al. 2013) mean that the topic has as much relevance as ever. It is important that the ideas behind our current views of species continue to be scrutinized because their application will have lasting effects on our assessment and understanding of biodiversity.

We view species as arbitrary just in the sense that there are various real historical assemblages of individuals that exist and that a choice must be made among them as to which will be called “species” (Simpson 1961). Other authors such as Holsinger (1984), Mishler (2010), and Hull (in Grene 2002) have also viewed species as arbitrary in this sense. If species are arbitrary in this way, then given the degree of focus on them in biology and more broadly, we need to choose carefully the entity that receives this designation.

A large body of literature exists dealing with the nature of species; it is not our intent to review that comprehensively, especially since excellent reviews exist (Luckow 1995; Mayden 1997; de Queiroz 1998; Wilkins 2009). However, we do wish to highlight here some important points in the discussion. One key point that has emerged is the distinction between the primarily ontological notion of what a species is and the more epistemological aspect of the operational

criteria by which one can be recognized in nature (Mayr 1957; Frost and Kluge 1994; Richards 2010). Along the same lines, Mayden (1997) and de Queiroz (1998) distinguished between species *concepts* and *criteria* (definitions) in that the concept is “an idea about the kind of entity ... designated by the term species,” whereas a criterion is “a standard ... for judging whether a particular entity is or is not a species” (de Queiroz 1998). The conflation of these ontological/epistemological aspects has undoubtedly led to some confusion (Hull 1997; Mayden 1997; de Queiroz 1998; Richards 2010), but not all species concept problems can be ascribed to this and not all authors even agree on the distinction (e.g., Ereshefsky 2009). We find the distinction useful and will frame our discussion with it in mind, considering both the conceptual aspects of species and the implications they have when put into practice.

The idea of *lineage* as important to the view of species can be traced back at least to Darwin (1859), but its instantiation in a formal species concept appears to have begun with Simpson (1951). Although overshadowed for some time by the *Biological Species Concept* (BSC) of Mayr (1942), the view of species as lineages has gained popularity over the past three decades, perhaps fueled by phylogenetic thinking at higher taxonomic levels. It has been discussed most recently in a series of papers by de Queiroz (1998, 1999, 2005a, 2005b, 2005c, 2007, 2011). The centrality of lineage as the basis for species circumscription also has been emphasized in many empirical studies (e.g., Leaché and Fujita 2010; Brown et al. 2012; Ruane et al. 2014; Shirley et al. 2014), indicating that the “species as lineage” view has become common in practice. While we agree that population

lineages are a relevant aspect of species, we also agree with Pigliucci (2003) that they are not *sufficient* for a species concept and will argue for an alternative view.

Here we review the details of a lineage-based species concept and, restricting our discussion to sexually reproducing organisms, argue that: (i) although often invoked, the lineage rationale for species is used inconsistently, in that it is usually equated with monophyly but need not be; (ii) a lineage concept with no other criterion cannot conceptualize a species in time; (iii) broadly viewed ecological role (manifested empirically as extended phenotype) is an essential part of the species concept, allowing for both time-limited and time-extended conceptualization, and aligning well with the notion of biodiversity; and (iv) the details of the species concept matter because alternative approaches can circumscribe different entities and, therefore, differently affect important conclusions related to evolution, community ecology and assembly, and conservation.

THE CENTRAL PLACE OF POPULATIONS AND THEIR EXTENT THROUGH TIME AS LINEAGES

With respect to sexually reproducing organisms, most—but not all—species concepts that have been advanced since the beginning of the 20th century (therefore, since the “New Synthesis” of evolution and genetics) have viewed species in terms of *populations*. The majority of concepts reviewed by Mayden (1997), for example, construe species in terms of populations or reproductive communities. If populations are accepted as fundamental, real entities in nature, then it is the relationship of populations to each other that is really at issue when conceptualizing a species.

As Hey (2001) and various others have pointed out, population is a somewhat vague concept, often overlooked in its details. A population is perhaps most often defined by probability of reproduction among an assemblage of individuals relative to other such assemblages. Specific definitions include those of Mayr (1966): “the community of potentially interbreeding individuals at a given locality” and Van Valen (1976): “a group of individuals in which adjacent individuals at least occasionally exchange genes with each other reproductively, and in which adjacent individuals do so more frequently than with individuals outside the population.” Population dimensions can change over time, meaning that use of population as the basic organizational unit above the level of the individual inevitably introduces some uncertainty into the application of species concepts (Dobzhansky 1950).

Interbreeding is a process; through time it generates a pattern that can be traced using historical analysis. A local population may be viewed as one whose members occasionally interbreed with those of other such populations. To the extent that this happens, local populations will not be fully distinct from each other in their present properties or historical pattern. Hence,

in order to ensure a greater degree of separation, many authors have emphasized that the unit most relevant to species is a larger interbreeding population group (Simpson 1951) or *metapopulation* in the sense of de Queiroz (1998). The latter used it to “distinguish species, which are traditionally considered to reside at the higher end of the population level continuum, from populations at the lower end of the continuum, such as demes and family groups.” Local population/subpopulation separation and reuniting over relatively brief time intervals disqualifies the smaller units from being called distinct species (de Queiroz 1998)—they all collapse into the broader maximal reproductive unit. Hence, it is actual interbreeding, or its absence, that is being emphasized in the notion of metapopulation and, therefore, species.

Darwin (1859) depicted connections through time between species and their “offspring.” While he did not specifically use the word “lineage,” he did write of “species ... being lineal descendants of other species” (p. 29) and referred to “lines of descent” many times (de Queiroz 2011). Within an evolutionary framework it eventually became common to speak of populations and species through time and the term “lineage” came to be used in this broad way (e.g., Simpson 1951). Swinnerton (1921), for example, equated lineage broadly with “line of descent.” As de Queiroz (1999) noted, lineage has sometimes been used to refer to *clade* in the sense of a branched metapopulation sequence, but he restricted lineage to a single metapopulation through time and explicitly did not allow branching of metapopulations, since that would mean that two metapopulations (and therefore lineages) were present. In some cases authors have not been precise in their use of lineage, so that it is difficult to know exactly what entity they had in mind; de Queiroz cited one clearly alternative use of the term (Wilson 1995). We accept that lineages in the sense of de Queiroz (1998) exist apart from our ability to discover them (cf. Wiley 1978; Frost and Kluge 1994), which gives them an objective reality.

THE RELATIONSHIP OF LINEAGE TO SPECIES

Simpson (1951, 1961) formalized his *Evolutionary Species Concept* (ESC) as “a phyletic lineage (ancestral-descendent sequence of interbreeding populations) evolving independently of others, with its own separate and unitary evolutionary role and tendencies.” Subsequent authors who discussed the ESC have also described it in terms of a lineage (Wiley 1978, 1981; Frost and Hillis 1990; Frost and Kluge 1994; Mayden 1997; de Queiroz 1998, 1999; Wiley and Mayden 2000; de Queiroz 2005a, 2005c, 2007). When these authors used *lineage* they meant a single unbranched population sequence through time (as in de Queiroz 1998).

Van Valen (1976) used *lineage* in a similar sense as de Queiroz (as a population through time), but explicitly allowed for groups of such lineages to comprise species. Similarly, it is clear for authors such as Wilson (1995)

and Davis and Nixon (1992) that they are concerned with recognizing as species groups of populations that are related because of their historical connectivity in a broader sense (see below), rather than strictly as a single nonbranching metapopulation through time. In the view of these authors, species can comprise more than a single noninterbreeding population. In these cases, other criteria are then required as part of the concept to define the limits of the species even in a single time.

Because they are created and constrained by interbreeding relationships, lineages have an inextricable relationship to the process of interbreeding and, therefore, to concepts that employ interbreeding criteria; de Queiroz (2005b) discussed the relationship of the lineage concept of species to the BSC. In fact, such a lineage concept is *very* similar to Dobzhansky (1935) or Mayr (1942) species concept ("groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups") in the groups they would circumscribe because they are "two sides of the same coin," or, as Poulton (1904) put it, "Syngamy and epigony are but two sides of the same phenomenon – reproduction" (Mallet 2003).

When species are defined as lineages, they are inherently time-extended "individuals" (or "complex wholes"; Rieppel 2007) because lineage is fundamentally a time-extended notion. If we equate species to lineages, some of that objectivity is thus inherent. However, it is only with Hennig's (1950, 1966) strict lineage approach (hereafter, HSC), where every lineage splitting results in two new species (see also Frost and Kluge 1994), that such species can be viewed as nonarbitrary and not requiring other criteria to specify their end in the time dimension. This is because lineage splitting events necessarily define the beginning and end of each species in Hennig's approach. As Rieppel (2010) stated, this approach is logically sound but biologically problematic. One reason that it is problematic is that many view species as at least sometimes persisting through splitting events. Especially in the case where a peripheral local population becomes distinct, to what degree we can say the remainder of the original species is changed has been discussed at some length (Wiley 1978; Ax 1987; de Queiroz 1999). Strict application of Hennig's rule would mean that the remainder of the original species in this case needs to be viewed as a new entity (a new species). Hennig (1966) understood the consequences for this scenario (as well as for species that exhibit change between splitting events) but held to the logical consistency of his approach. In a single paragraph, Wiley (1978, p. 21–22) appeared to agree with this view, but then also seemed to allow for species persistence through cladogenesis. If an approach allows persistence of a species through lineage splitting, then additional criteria are necessary to delimit species in the time dimension.

De Queiroz's 1998 version of a lineage concept of species (the *General Lineage Concept*, hereafter GLC) defined species as "segments of population level evolutionary lineages." While his formulation allows

application of various additional criteria to specify the extent of the lineage segment in a particular case (and in fact anticipates that a sequence of additional species-marking features will arise), *it requires none of them* (they are not inherently part of the concept), meaning that it does not explicitly conceptualize species in time. Hence, it must be viewed as explicitly a pure lineage concept. The same is true of de Queiroz's (2005c) *Unified Species Concept*, which appears to be identical to the GLC. The GLC clearly specifies the time-limited (single time) extent of a species because it is a maximal interbreeding unit (metapopulation). However, because it leaves the temporal extent of a species indefinite, this flexibility restricts the GLC from being a full species concept (under de Queiroz's definition of *concept* as specification of an entity). In other words, it explicitly conceptualizes only the "width" (time-limited extent) and not the "length" (time-extended extent) of species.

This egalitarian approach opens the door to arbitrariness in duration of species because any of a number of species criteria *could* be employed to mark the beginning and end of species; since no one criterion is inherent, none would *have* to be used. For example, under de Queiroz's GLC it would be in theory possible (albeit unlikely) to regard a continuous population lineage from a single-celled ancestor to an elephant as a single species, since that could be specified as the relevant segment of the metapopulation lineage. Simpson (1961, p. 165) argued that it is necessary to "chop up" the lineage somehow but felt that such an operation is arbitrary, to the extent that he viewed species "through time" and "in time" as different things:

In such cases, a distinction cannot be made in practice between "species" in the basic genetical or evolutionary sense and in the sense of subdivisions in a continuous ancestral-descendent line. I do not here favor or propose a special term for the latter sort of taxonomic group. I do maintain that it is desirable and useful to realize that these are two quite different things, and that the "species" of paleontological taxonomy may be of either sort.

Kunz (2012) also argued that anagenesis and cladogenesis would yield two types of species. We disagree with this distinction. Ironically, Simpson (1951, 1961) had a meaningful way of "chopping up" lineages built into his concept—change in *role*. If role was inherent in the original ESC, what happened subsequently such that this notion was lost in later discussions of the ESC?

THE RISE OF HISTORY AS A CRITERION FOR SPECIES: THE LOSS OF "ROLE"

A key distinction between Simpson's (1951, 1961) description of a lineage-based concept (his ESC) and nearly all subsequent authors' versions and views (Wiley 1978; Frost and Hillis 1990; Frost and Kluge 1994;

de Queiroz 1998) is the presence in the former of the phrase “with its own separate and unitary evolutionary role” or its equivalent. All later authors have emphasized the lineage nature of species, but have downplayed any other fundamental characteristics of species. Interestingly, although Wiley removed “role” from his recast version of the ESC (“a single lineage of ancestral descendant populations of organisms which maintains its identity from other such lineages and which has its own evolutionary tendencies and historical fate”), later in the same paper he did appeal to role to distinguish lineages (Wiley 1978, p. 21).

With the rise of “population thinking” advocated by evolutionary synthesists such as Mayr and Simpson, populations as fundamental units in nature became integral parts of our way of viewing species, as noted above. The idea of population lineages through time was also further developed, building on the idea of lineages such as those depicted and discussed by Darwin (1859; cf. de Queiroz 2011). Whereas before Darwin the delimitation of species focused largely on phenotypic uniqueness (see below), with the advent of a phylogenetic paradigm the possibility arose of delimiting them, at least conceptually, by their unique history.

Increasingly over the past few decades our ability to reconstruct hierarchic phylogenetic patterns has led to an emphasis on thinking about taxa as historical entities. This is certainly true for groups above the species level, which are most often today viewed (rightly, we argue) as real historical (monophyletic) groups of species defined as all the descendants of a common ancestral species. The general model for the tree of life follows from the notion of divergence with modification through time, yielding a hierarchic pattern of relationships. Early on in phylogenetic studies the emphasis was on phenotype (primarily morphology) for evidence of relationship, but increasingly it has shifted to analysis of genotype because of the wealth of character information available in the genome.

With respect to level, the reconstruction of phylogenetic patterns was initially focused at the species level and above, with terms such as *monophyly* and *paraphyly* being used to describe the relations among species as they comprise higher level taxa. With the advent of molecular data, reconstruction of hierarchic relationships was pushed in the tree of life toward the level of individuals, almost inevitably, because the fundamental unit of sampling for the genome is the *individual organism*. Previously, with phenotypic characters such as morphology, it had been (and remains) standard practice to code characters for *species* based on a broad sampling of individuals. The problems with the interpretation of a hierarchic taxon pattern reconstructed from individual sexually reproducing diploid individuals whose genomes may reflect the reticulating pattern of their genealogy have been pointed out at some length, as has the misapplication of terms such as “monophyly” and “paraphyly” to describe the relationships among such

individuals (e.g., Platnick 1977; Willmann 1983; Ax 1987; Nelson 1989; Lidén 1990; Nixon and Wheeler 1990; Davis and Nixon 1992; Davis 1996; Wiley and Mayden 2000; Rieppel 2010; Kunz 2012), although this usage persists (e.g., Velasco 2008, 2009; Mishler 2010; Lockhart et al. 2014; Pazhenkova et al. 2015). The problem exists because individual sexually reproducing organisms do not show the same kind of hierarchic relationships as taxa (reviewed in Rieppel 2010). Note, however, that if we recognize (meta)populations as the fundamental evolutionary units and view species as assemblages of them, then monophyly *can* apply to species, to the extent that those populations (which would need to be noninterbreeding with each other) exhibit hierarchic relationships (under a model such as shown in Fig. 1). In that case, it would be the *population* within which the concept of monophyly does not apply.

Modern phylogenetic work often focuses on molecular data and analysis of gene trees. When most authors apply the GLC using molecular data they confine themselves to recognizing monophyletic clades on gene trees as species. The extreme application of this is the *Genealogical Species* approach of Baum and Shaw (1995), which seeks assemblages of individuals for which *all* gene trees are monophyletic (or, more properly, the individuals are *exclusive* (in the sense of de Queiroz and Donoghue 1990) for all loci). However, the GLC paradigm described by de Queiroz (1998) explicitly does not require monophyly or exclusivity; as long as interbreeding has ceased between two extended population groups they are species, regardless of the gene tree relationships among their individuals. While monophyletic gene trees are *evidence* of lineage formation, “paraphyletic species” (with respect to their gene trees) are perfectly consistent with the GLC of de Queiroz (1998). We believe that this mismatch between theory (of lineages) and application (by monophyly) is due to conflation of the meaning of *lineage* as a time-extended metapopulation *sensu* de Queiroz (1998) with the common usage of *lineage* as clade, in this case usually in a gene tree.

The extent to which gene trees reflect the relationships among the units in which they reside (e.g., species) has been the subject of a great deal of interest ever since the possibility of discordance between species trees and their included gene trees was described (Tajima 1983; Neigel and Avise 1986). The requirement of monophyly for species (or even subspecies; Zink 2004) follows from the coalescence observation that, given enough time, gene trees for a lineage will transition from paraphyly to monophyly (Neigel and Avise 1986). Most recently, approaches have been developed to utilize allelic data sampled from extant individuals under the coalescent model in order to estimate the number of, and limits among, lineages, accommodating population processes that result in gene tree heterogeneity. These techniques have been heavily used in the recent spate of species delimitation approaches and algorithms. The use of these with putatively neutral genetic markers alone (i.e., without phenotypic data partitions), while

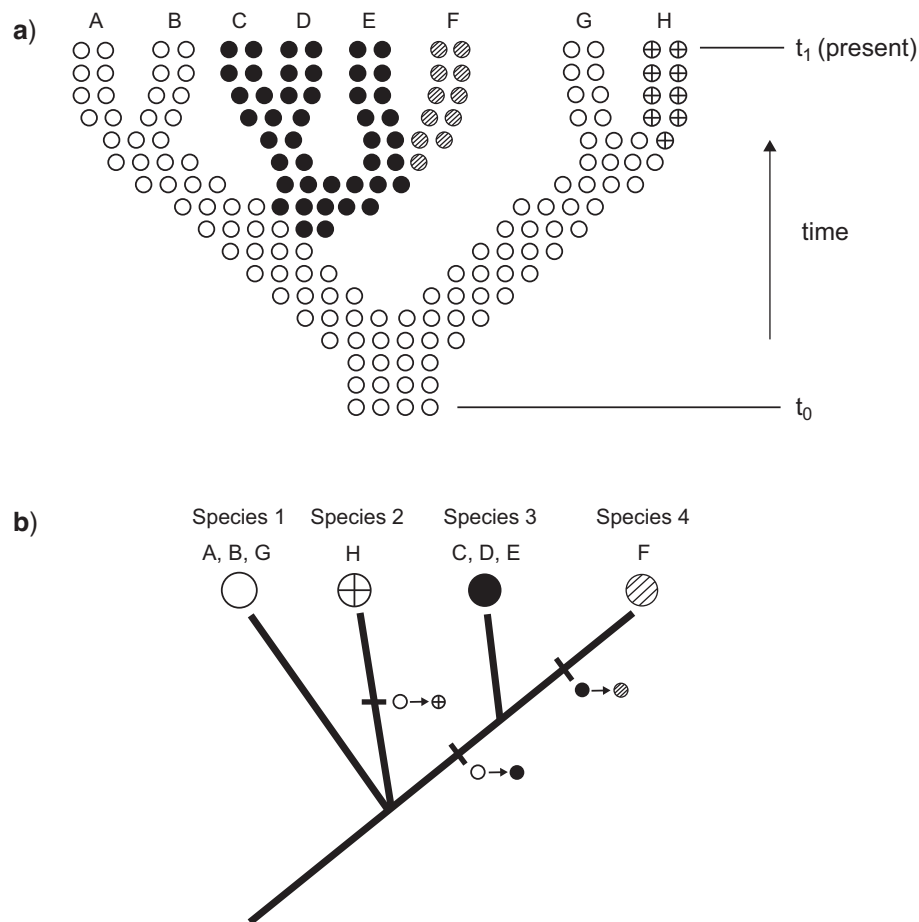


FIGURE 1. A simplified population phylogeny through time (a) and its corresponding species cladogram (b). The differently filled circles indicate different states of a phenotypic character that determines role. A group of adjacent circles at a particular time represents a metapopulation (i.e., the limits of interbreeding). Character state transformations are indicated on the cladogram.

frequent, implicitly equates species with lineages (e.g., Pons et al. 2006; O'Meara 2010; Yang and Rannala 2010; Ence and Carstens 2011); this is often justified by reference to de Queiroz's GLC. Whereas the coalescence approach mitigates the requirement for gene tree monophyly to hypothesize lineage formation (Knowles and Carstens 2007), some signal of exclusivity is needed among the loci or a lineage could not be identified. Changing population sizes through time, selection, and gene flow/migration will affect coalescence, altering the picture given by the neutral model and complicating the application of this approach.

While it is not clear that de Queiroz intended for lineage recognition to be the sole and sufficient basis for species circumscription, given that he described the relevance of secondary species criteria, it has been increasingly applied in this way (e.g., Knowles and Carstens 2007; Leaché and Fujita 2010; Fujita et al. 2012; Bagley et al. 2015; Barej et al. 2015; Johnson et al. 2015; Laakkonen et al. 2015; Murphy et al. 2015; Salerno et al. 2015; Saitoh et al. 2015; Guarnizo et al. 2016; Rato et al. 2016). It is the exclusive use of history—species defined only as lineages—that we disagree with, in part because

it represents a shift from the fundamental conception of species as inherently phenotypic entities in place for the past 2500 years and, at least in some cases, misaligns the notion of species with their key position as units of biodiversity involved in particular interactions with their environment. Others have also questioned the key place given to history in the definition of species (e.g., Doyle 1995).

The identification of genetic lineages before features such as phenotypic difference and intrinsic reproductive isolation come into being may suggest the existence of nascent or incipient species (cf. Folk and Freudenstein 2015). To the extent that such units eventually become species (under whatever concept/definition), they may certainly be valuable for study of the processes involved with speciation and they are useful as initial hypotheses of species worthy of further investigation. However, nascent species are also nascent “non-species,” since there is no guarantee that they will proceed to become real species—they may also be just “evolutionary ephemera” (Singhal and Moritz 2013). Taxonomically, phenotypically defined presumed nascent (or incipient) species have often been treated as subspecies (Mayr

1982). The limits of populations, and thus of species, can change through time and are dependent on future events. Ultimately, only species that have intrinsic reproductive isolating mechanisms yield entities that have a high probability of continued separation, since any other populations could easily reunite if brought into contact; even dissolution of intrinsic barriers is not unknown. While we do not go so far as to advocate the requirement of intrinsic reproductive isolation in a species concept, we question the wisdom of recognizing assemblages that are no more than probable genetic lineages as species (e.g., [Leaché and Fujita 2010](#); [Carstens and Satler 2013](#)), especially given the ambiguity of lineage identification with these approaches ([Carstens et al. 2013](#); [McKay et al. 2013](#)). [O'Hara \(1993\)](#) argued for the prospective nature of species concepts, which is rooted in the tentative nature of populations. However, the circumscription of species is solely a current and retrospective process with respect to the data we collect and analyze; we cannot anticipate the future of such taxa and they must be based on currently observable patterns. Hence, they must satisfy criteria regarding what they are now and not what they might be in the future.

SPECIES AS FUNDAMENTAL UNITS OF BIODIVERSITY: WHY ROLE AND PHENOTYPE MATTER

Although the process of describing biotic diversity has been ongoing in some sense for centuries (since at least the time of Aristotle and Theophrastus), it is only with the increasing threat and reality of its loss in the last few decades that a real focus on the concept of biodiversity has come to the fore. While biotic diversity can be valued and assessed at various levels, including that of the individual organism and the genetic locus, the key level remains the species ([Wilson 1988](#)). A recent consideration of different ways of assessing biodiversity concluded that species richness, while not perfect, is the best metric ([Maclaurin and Sterelny 2008](#)). This does not mean that other levels of biodiversity, such as gene diversity within species, do not exist or are not important, but just that the key level of focus is the species. Species are inextricably linked to the notion of biodiversity because for perhaps most biologists and even for the public at large, they are viewed as the fundamental units of natural biotic diversity. The idea of species as basic phenotypically distinguishable groups in nature is common and has a long history. Species, or something closely approximating them (assemblages of individuals that share a recognizable similarity among themselves and difference from other such groups), are the basic units of folk taxonomies ([Atran 1990](#)). The units that the classical authors discussed, those of the medieval herbalists, and of flora and fauna writers in the post-Renaissance era, approximate many of the units that we still recognize as species. Phenotypic distinguishability was thus the first species criterion. However, we do not advocate following such a tradition just because it has always been that way.

We argue rather for the crucial importance of *role* (and its manifestation as phenotype) because of its inherent relevance to biodiversity. The critical value of biodiversity lies in the myriad roles (in the sense of [Simpson 1951, 1961](#)) that organisms exhibit that make them part of complex biotic systems. This diversity is a direct result of the different morphological, chemical, and behavioral properties that organisms display. We view role broadly as the ways in which individuals interact with their environment and the total complement of expressed properties (beyond genotype) that they exhibit; it is an organism's correspondence to the concept of ecological niche *sensu* [Hutchinson \(1957\)](#); an *n*-dimensional hypervolume composed of all biotic and abiotic organismal interactions).

We assert that role is a necessary part of the species concept and that Simpson was right to include it as part of the definition of the ESC. Although [Wiley and Mayden \(2000\)](#) interpreted Simpson's use of role to mean no more than "individuality," [Simpson \(1961, p. 154\)](#) explicitly described roles as "definable by their equivalence to niches" and further stated that "morphological resemblances and differences (as reflected in *populations*, not individuals) are related to roles if they are adaptive in nature [emphasis in original]." This is a clear connection between the ecological part that species play and their definition. [Hull \(1965\)](#) felt that Simpson did not provide sufficient criteria to circumscribe role, but this is an operational criticism rather than a conceptual one—that is, Hull did not object to the idea of role but to Simpson's characterization of it. [Van Valen \(1976\)](#), in an explicit refinement of [Simpson's \(1961\)](#) concept that is known as the former's *Ecological Species Concept*, described a species as "a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range" (p. 154). However, Van Valen did not fully develop this concept; he called it "a vehicle for conceptual revision, not a standing monolith." [Levin's \(2000\)](#) ecogenetic concept is also similar to this view in that ecological function is part of his specification. Later in his career even [Mayr \(1988\)](#) came to view role as critical with his emended definition of species as "a reproductive community of populations (reproductively isolated from others) that occupies a specific niche in nature."

Although at first the notion of role may seem elusive, the idea is no vaguer than that of population and, therefore, lineage; both ideas can be difficult to apply empirically. Diversity in expressed organismal properties is specifically due to diversity in their *phenotypes* rather than genotypes per se, since many genotypic changes are not expected to lead to expressed changes. Synonymous third base position changes in coding DNA are expected to yield no difference in amino acid sequence, for example, but situations exist in which such a change *could* lead to alternative splicing and thus have a phenotypic effect. Although the traditional view has been that phenotypic change is the direct result of underlying genotypic change, we now

know that not all phenotypic change can be attributed directly to genotypic change; our ever-increasing knowledge of epigenetic determination of phenotype falsifies an exclusive correspondence (e.g., Cortijo et al. 2014). Beyond even epigenetic manipulation of the genome, extra-genomic determinants of organismal properties have been described (cf. Freudenstein et al. 2003; Bonduriansky and Day 2009; Danchin et al. 2011). Whatever their basis, as long as such attributes are heritable by some mechanism, they may affect organismal properties and thus species role. Hence, we are invoking a very broad “extended phenotype” (Dawkins 1982) as the raw material for role determination and when we refer to phenotype from this point forward we mean it in this broadest sense.

Pointing to phenotype as the basis for role and to phenotypic difference as critical in species distinguishability raises the empirical question of how much phenotypic difference is required to shift role. This question is similar to one that might be asked of a purely lineage-based approach—how does one know when one has a distinct lineage? How distinct does the lineage have to be? These questions reflect the epistemological challenge of applying such concepts. The answer is that one needs enough evidence (of lineage or role) to build a persuasive case for a particular real-world instance. In practice, we often do not know the ecological effect of particular character changes. Therefore, we suggest that any fixed change in expressed organismal properties provides evidence for a hypothesis of role shift. Ultimately it is the task of the investigator to identify phenotypic changes that actually shift roles. Species circumscribed in this way, or in any other way, always remain hypotheses subject to further test.

UNITING ROLE AND HISTORY

Although Darwin (1859) avoided giving a precise definition of species in the *Origin*, it is clear that the notion of distinguishability was important to him when he stated, “the amount of difference is one very important criterion in settling whether two forms should be ranked as species or varieties.” At the same time, Darwin recognized that species must also exist as units through time, as depicted in the only illustration in the *Origin* (de Queiroz 2011). Subsequently, Poulton (1904) recognized four key aspects by which groups such as species had been circumscribed: common morphology, interbreeding, common ancestry, and geographic range distinction. Common ancestry is equivalent to the lineage history of a group. Ability to interbreed and common morphology are both phenotypically based features. Geographic range is not an inherent property of individuals or larger groups but typically is the result of shared lineage history (it could be limited by phenotype). Hence, these four aspects distill down to differences in phenotype and/or lineage history.

We restate and simplify Simpson (1951) and Van Valen’s (1976) concept as follows: *A species is a lineage or group of connected lineages with a distinct role.* Here we mean lineage in the sense of de Queiroz (1998). By “connected lineages” we mean that any population in the group may be traced to any other population in the group through lineages without leaving the assemblage (= “convex group” of Estabrook 1978). Hence, connected lineage segments may form a branched assemblage but do not necessarily form a clade—that is, the assemblage can be paraphyletic. To illustrate this point, consider the pattern of connected populations in Figure 1a that are depicted with differently filled circles to indicate that they are marked by distinct roles. Assuming that these populations are noninterbreeding, under a pure lineage concept there are eight species present (A, B, C, D, E, F, G, H). Phenotypically, there are four types indicated by the symbols and, when more than one population of a type is present, each is connected to the other similar populations, such that there are four species under our approach (A + B + G, C + D + E, F and H). Under our role-based view, a species can include the two metapopulation lineages resulting from any metapopulation division, whereas under the strict lineage approach it cannot because lineages must be unbranched (de Queiroz 1998). In general, we would expect a greater number of species to be recognized under a pure lineage view than under our approach because each persistently noninterbreeding population is a species under the former.

Importantly, our approach allows paraphyletic assemblages of populations (i.e., C + D + E or A + B + G; Fig. 1a) to be species, as long as they share a role. They represent ancestral species that have given rise to other species. The corresponding cladogram (Fig. 1b) depicts such a species as a branch with no apomorphies, but with a unique combination of characters. Our concept would not, however, allow polyphyletic groups of populations to be a species, in the sense that if the most recent common ancestral population of the assemblage is not included in the species, we would not consider the assemblage to comprise a species, even though the populations share a role, because it would suggest that the role had originated in parallel and is not homologous. The requirement for connectivity would exclude those populations from being a part of the same species. In this way, we recognize the importance of historical continuity of reproduction for species membership and homology of role. It is in this sense that lineage information (history) is most important.

Age of a lineage and degree of change in role might be expected to be coupled, at least loosely, as indicated by Figure 5.4 in de Queiroz (1998), in which reproductive separation is followed through time by the successive satisfying of various species criteria, including diagnosability. However, there is no reason that lineage divergence and role divergence would need to be strictly linked. Lineage divergence could occur without role change and the latter could occur without the former (resulting in the pattern known as

anagenesis). One could imagine a scenario in which fragmentation of an ancestral population results in new allopatric populations that happen not to interbreed. The resulting population lineages would exist through time and exhibit a hierarchic historical pattern. The tree of population lineages could be extensive, with many present-day populations at the tips. However, the populations might not differ in their role—in any of their expressed properties. Each of these noninterbreeding populations would represent species under a pure lineage concept. Wiley (1978) imagined a much simpler scenario of two sibling lineages that are identical in their features, and also held that they should be considered distinct species because lineage splitting equates to speciation. Simpson (1961, p. 161) and then Hull (1965) questioned the idea of sister lineages being recognized as species if their roles did not differ. A key question for us in these cases is how much biodiversity is present in such a situation. We argue that, from the perspective of species richness, the answer would be “one species,” the minimal amount of biodiversity, in spite of the fact that multiple lineages are present. Moreover, considering the recognition of diversity in practice, and supposing such indistinguishable lineages were recognized, these “species” could not be expected to embody any of the benefits of biodiversity that we have outlined. This is the problem encapsulated by nonphenotypically distinct lineages—besides whatever burden they might place on future taxonomists inundated with doubtful names—they are necessarily without practical relevance for any other organism, human, or otherwise. It would be difficult to argue that the loss of such a species would negatively impact an ecosystem if a phenotypically identical sister species were available to occupy its place.

Whereas we argue against recognizing species solely on the basis of historical lineage, such entities can represent hypotheses for which phenotypic differences may be sought and in this way the combination of history and phenotype makes for a powerful and truly integrative approach (e.g., Tan et al. 2010; Barrett and Freudenstein 2011; Edwards and Knowles 2014). Molecular studies may uncover candidate species that await verification of phenotypic difference (e.g., Rato et al. 2016). Many studies of this type have been cast in terms of discovering “cryptic species.” Leavitt et al. (2015), for example, reported “dozens of putative cryptic species” based on molecular criteria in a group where previously one or two species had been recognized. The definition of “cryptic species” varies among authors from species that are *difficult to detect* (but potentially detectable) based on phenotypic (usually morphological) features (Perez-Ponce de Leon and Nadler 2010) to those that are *indistinguishable* for morphological features (Egge and Simons 2006). To the extent that species are phenotypically distinct but this difference is difficult to perceive, such units may be consistent with our view of species. If, however, the entities that are being recognized are only genotypically identified lineages and have no distinguishing phenotypic features, we would

argue against their recognition. The term “molecular taxonomy” has been used recently to describe the latter approach (Johnson et al. 2015).

DOES IT MATTER? IMPLICATIONS OF OUR ESC COMPARED TO A PURE LINEAGE APPROACH

Beyond the theoretical issues of how we may view species, the question arises as to what extent the differences matter. We argue that they do matter in the sense that we perceive more or less diversity in a place or clade, differently assess imperiled populations, and make conclusions about the evolutionary process differently. In this section, we detail some of the differences with respect to our ESC approach compared to a pure lineage approach.

One way in which the difference matters is in implications for neontological and paleontological views of species, which have often been seen as being in tension (Thomas 1956; Imbrie 1957; Simpson 1961). In the extreme, Simpson (1951), as noted above, argued that paleontological and neontological species are fundamentally different. How this can be so is unclear to us, since presumably the same sort of species has existed at any particular time. Including role as an inherent part of the species concept has the benefit of reconciling these perspectives, since role differs among species at a particular time and changes with time because it is directly dependent on character change. Empirically, phenotype can be evaluated both in and through time, meaning that the same criteria apply to species in both the time-limited and time-extended views.

Another practical difference lies in the treatment of geographically isolated populations. Under a concept that strictly equates species with lineages, persistently geographically isolated populations that are otherwise no different from other populations are distinct species, since it is the absence of actual interbreeding among populations that generates and defines lineages. Hence, the notion of a “disjunct population” of a species ceases to exist under a pure lineage concept. The HSC and GLC would fall into this camp. Although the BSC is otherwise similar to a pure lineage concept in relying on actual interbreeding in many cases, presumably neither Mayr (1942) nor Dobzhansky (1935) would have agreed with elimination of the idea that the ability to interbreed (or not) was important in their definitions, emphasizing as they did the importance of intrinsic isolating mechanisms. Acceptance of persistently geographically isolated populations with no other differences as species has been viewed as problematic by some authors (Van Valen 1976; Mallet 1995; Wiens 2004) and would certainly lead to a proliferation of species relative to those that are commonly circumscribed today.

The results of applying a pure lineage concept versus our approach depend on the particular situation. For much of the duration of a long-lived species, it may be a lineage in the sense of an extended metapopulation and may be phenotypically distinct, and thus be relatively

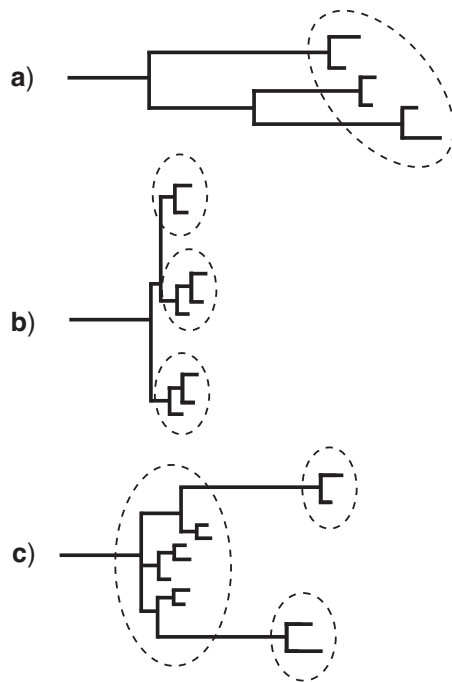


FIGURE 2. Situations in which species circumscription can be challenging. Branch length indicates degree of historical change (lineage formation), whereas lateral distance among clades indicates degree of phenotypic differentiation. a) Lineage formation with little phenotypic change. b) Phenotypic change with little lineage formation. c) The progenitor–derivative scenario, here with two lineages emerging from a progenitor. Dashed ovals indicate the species we would circumscribe in each case.

easy to recognize empirically. Hence, for species that originated long ago, almost any species discovery procedure would probably work and any concept would also. The challenging parts of the tree of life are near the points at which species are originating; those are the places where systematists are most often working to understand “difficult” groups and “species complexes.” That is where the details of a concept and associated empirical operations matter most. It is the difficult cases that prove illuminating. Barley et al. (2013) provided a very useful characterization of situations involving cryptic species that are challenging for species delimitation procedures (their Fig. 1; adapted and expanded here as Fig. 2). They characterized two situations as particularly difficult—lineage formation without morphological change and morphological change with little genetic differentiation—and we add to this the progenitor–derivative case. We consider each of these in turn.

1. *Lineage formation with little or no phenotypic change* (Fig. 2a): Sometimes called “non-adaptive radiation” (Gittenberger 1991), this pattern results in historical patterning of lineages through time, but apparently with little biotic or abiotic selective pressure to fix changes. This is the case that is often being termed “cryptic species,” where detected gene lineages are perceived as significant, even with no phenotypic differences. Such lineages within species have been

the domain of phylogeography (Avice 2000) but are now being recognized as more significant because of a greater ability to resolve structure with larger amounts of data and because of the emphasis on gene tree monophyly. While these lineages are interesting phylogeographically, they are of little significance as taxa, and unless phenotypic differences can be found we argue that they should not be recognized as species.

2. *Phenotypic change with little historical signature* (Fig. 2b): This involves the decoupling of role or phenotypic distinction from lineage formation as it is viewed from a gene tree perspective, and is likely the result of a few loci that have cascading phenotypic effects or are under strong selection. A number of recent studies have shown the surprising degree to which phenotypic divergence can occur even in the presence of substantial gene flow (Morjan and Rieseberg 2004; Rieseberg et al. 2004; Jordan et al. 2005; Poelstra et al. 2014), meaning that population boundaries may be more porous than we expect even when phenotypic distinction exists. In these cases, we might expect lineage estimation from gene trees to indicate a lack of clear pattern even though distinct phenotypes persist as fixed characters in population groups. This may also be true in adaptive radiations, where distinct morphological types may be present with little evidence of genetic lineage formation (Barley et al. 2013). Unless there is evidence that a particular phenotypic type is arising independently in different populations, we would recognize these types as species.

3. *Progenitor–derivative species* (Fig. 2c): The case of a progenitor–derivative relationship, in which a subset of a former metapopulation lineage becomes distinct for a novel phenotype and forms a new lineage while leaving the ancestral type with the plesiomorphic features, is problematic for the coalescence approach. The problem occurs when the two resulting metapopulations are highly dissimilar in size, resulting in very different coalescence times. Paraphyletic assemblages of populations are in fact what one would expect in such scenarios, specifically with peripatric speciation or speciation following long-distance dispersal; the expectation of these patterns has been described by previous authors (e.g., Rieseberg and Brouillet 1994; Crisp and Chandler 1996; Harrison 1998; Hudson and Coyne 2002). Though not monophyletic for its gene trees, the “paraphyletic residuum” may easily be a lineage *sensu* de Queiroz. With enough time, the assumption is that the patterns will resolve to “reciprocal monophyly” due to chance extinction of individuals, but this can be a very long time in groups with large effective population size (N_e) in the residual population(s), and may be long in groups even with smaller N_e if neutral expectations (e.g., lack of selection) are violated. Under approaches such as the autapomorphic version of the PSC (de Queiroz and Donoghue 1988; Adams 1998), such residual groups of populations would lose the species status that they previously had by virtue of character transformation that occurs in a small part of the whole (cf. Wiley 1978, p. 22; Sites and Marshall 2004).

Such paraphyletic species are not just hypothetical constructs. Molecular systematic and evolutionary studies recover patterns of paraphyletic species with some frequency and some authors are concerned about the perceived “problem” (Harrison 1998). Studies by, for example, Patton and Smith (1994), Nikulina et al. (2007), Syring et al. (2007), Feinstein et al. (2008), Martinsen et al. (2009), and Kadereit et al. (2012) have revealed such patterns. Some authors have even expressed concern about conflict with nomenclatural codes, suggesting that “Paraphyly is difficult to reconcile with a nomenclatural Code that presumes that all individuals are members of monophyletic groups” (Grube and Kroken 2000), although monophyly is not even mentioned in the current botanical or zoological codes (McNeill et al. 2012; ICZN 1999). While the molecular pattern should prompt researchers to investigate these groups more carefully, especially seeking phenotypic features that may correlate with lineage groups, under our view there is no reason to reject species status for paraphyletic assemblages of populations; we argue that they should not be denied species status in the intervening period while waiting for genetic coalescence to occur.

Ultimately, the way that we view species influences how we view evolution. In our way of viewing species, speciation is the fixation of a new role in a lineage, whereas under pure lineage concepts speciation is population division (= cessation of interbreeding); the possibility of anagenesis does not exist there. We do not argue that true anagenetic speciation is necessarily common or easy to demonstrate, but its possibility should not be ruled out and our approach accommodates it.

Although our focus here has been on sexually reproducing organisms, much of biodiversity comprises asexual individuals (notably bacteria and archaea). Workers dealing with those organisms have struggled to define a meaningful species concept, but recent arguments have been made for something similar to what we advocate here—combining elements of genetic relatedness and phenotype (e.g., Rosselló-Móra and Amann 2001, 2015). Asexual organisms form clear lineages and to the extent that they differ in role, our approach to species should be applicable to them as well as to sexual groups.

It was not our intention to propose a new species concept here; as with de Queiroz, we believe that all of the elements already exist in previous proposals. We see the way of viewing species outlined here as only a modification of some previous well-known ones. We view it as a clarification of Simpson’s ESC and Van Valen’s *Ecological Species Concept*. Sandler (2012), in his treatment of the ethics of species, used as a working concept, “groups of biologically related organisms that are distinguished from other groups of organisms by virtue of their shared *form of life*. A species’ form of life refers to how individuals of the biological group typically strive to make their way in the world.” This is in essence our view, since it includes both relationship and role. If it needs a name to distinguish it, we would

suggest the “phenophyletic” view, emphasizing the dual aspects of role/phenotype and lineage that it embodies. On balance, we argue that this concept of species aligns better with ideas of biodiversity, reconciles notions of species in time, and yields an entity of more general significance than that resolved under a strict lineage concept.

FUNDING

This work was supported by National Science Foundation [DEB-0842076 and DEB-1406732].

ACKNOWLEDGMENTS

We thank the following individuals for comments on the manuscript and discussion of species issues: Mac Alford, Andy Anderson, Craig Barrett, David Baum, Marymegan Daly, Jerrold Davis, Kevin de Queiroz, Jeff Doyle, Roberta Mason-Gamer, Brent Mishler, Tod Stuessy, and anonymous reviewers. They do not necessarily agree with our conclusions.

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