

## Recent Developments in Species Delimitation and Taxonomy Considered in the Context of the Unified Species Concept

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**ABSTRACT:** Species delimitation and species taxonomy are important to most subfields of herpetology. I have argued that a previous controversy about the definition and concept of species resulted in a large part from different authors treating different properties that lineages acquire during divergence as necessary properties of species and therefore treating the species category as a stage in the evolution of lineages. I also proposed that a unified species concept could be achieved by not treating any of the properties in question as necessary properties of species so that all separately evolving metapopulation lineages are species. Although the proposed unified species concept has become increasingly accepted, the traditional interpretation persists. I discuss two cases of such persistence in the field of species delimitation. In one case, a protracted speciation model assumes the traditional interpretation of species by not considering separately evolving lineages to be “true” species until they cross some “conversion” threshold. Use of this model has led to the conclusion that species delimitation methods based on the multispecies coalescent model delimit intraspecific population structure rather than species. Consideration of the results upon which that conclusion was based in the context of the unified concept reveals that the method in question accurately delimited species. In another case, a proposed heuristic criterion for delimiting species, the genealogical divergence index, adopts the traditional interpretation of species by treating an index value above a certain threshold as a necessary property of species—one that is closely related to the traditional monophyly and exclusivity criteria. In the context of the unified species concept, this index is more appropriately used as a coalescent measure of lineage divergence than as a species criterion. In the field of species taxonomy, I have recently proposed a revised concept of subspecies based on the unified species concept. The revised concept makes the subspecies category more significant biologically and avoids problems associated with previous uses that caused some authors to reject that category. Nonetheless, recent authors have continued to avoid recognizing subspecies taxa, causing them to adopt to misleading taxonomies that obscure the existence of lineage structure within many species.

**Key words:** Ephemeral species; Genealogical divergence index; Incipient species; Multispecies coalescent model; Protracted speciation model; Subspecies

SPECIES delimitation and taxonomy have relevance not only to systematic herpetology but also more generally to all branches of herpetology that use species as basic units of study and comparison. To develop appropriate methods for delimiting species and representing them taxonomically, one needs first to have a concept of what species are, and that issue has been controversial. Approaching the second millennium of the Common Era, numerous definitions of the term “species” had been proposed, and many were considered to describe alternative species concepts (see Mayden 1997; de Queiroz 1998; Harrison 1998). I previously reviewed those definitions and concluded first, that most if not all conformed to a single general concept of species—the idea that species are segments of inclusive population-level lineages—and second, that their incompatibilities resulted primarily from alternative definitions treating different properties acquired by diverging lineages (e.g., intrinsic reproductive isolation, gene-tree monophyly, fixed character-state differences) as necessary properties of species (de Queiroz 1998). I then proposed that the incompatible species definitions and concepts could be reconciled by treating those different properties not as necessary properties of species but as contingent properties, leaving only the common general concept as a unified species concept. Subsequently, I have addressed implications of that proposal for various related topics including philosophical issues concerning species (de Queiroz 1999), Ernst Mayr’s

writings on species (de Queiroz 2005a), species in the future of taxonomy (de Queiroz 2005b), three different species problems (de Queiroz 2005c), the problem of species delimitation (de Queiroz 2007), Darwin’s species concept (de Queiroz 2011), and the controversial subspecies category (de Queiroz 2020, 2021).

After publication of my article on the relevance of the unified species concept to the problem of species delimitation (de Queiroz 2007), there have been some influential proposals in this field that are incompatible with the unified concept. Here I examine two such proposals about species delimitation in the context of the unified concept with the intent of providing a perspective on what they do and do not tell us about separately evolving lineages. The first is a protracted speciation model and how it bears on species delimitation methods based on the multispecies coalescent model. The second is a proposed genealogical divergence index (*gdi*) as a criterion for delimiting species. Although I criticize these approaches from the perspective of the unified species concept, I also discuss current limitations of species delimitation methods based on the multispecies coalescent model. In addition, I address a common aversion to the recognition of subspecies taxa that results in less informative taxonomies and persists despite the proposal of a revised subspecies concept (de Queiroz 2020, 2021) that removes the problems with subspecies upon which that aversion was based.

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### SPECIES DELIMITATION UNDER THE MULTISPECIES COALESCENT MODEL

One of the most promising recent advances in species delimitation has been the development of objective methods

for inferring separate lineages from genetic data based on the multispecies-coalescent model (MSCM; Rannala and Yang 2003). This model is important because it explicitly incorporates the distinction between gene trees and species trees (e.g., Maddison 1997). That distinction, although widely accepted, had not been incorporated into previous methods for inferring phylogenetic relationships among species (species trees), which effectively assumed that a single gene tree, or a tree inferred from the concatenated sequences of multiple genes, or the most common topology among multiple gene trees would approximate the species tree (e.g., Edwards 2009). On the contrary, theoretical considerations have shown that under certain conditions these methods will lead to inferences of incorrect species trees and that the appropriate solution to this problem is the MSCM, which models phylogeny as gene trees evolving within a species tree (e.g., Degnan and Rosenberg 2009; Edwards 2009).

### Protracted Speciation Model

As a result of this advance in the theory of estimating the phylogenetic relationships among species, several software packages implementing the MSCM were developed (e.g., Liu and Pearl 2007; Kubatko et al. 2009; Heled and Drummond 2010), and shortly thereafter methods based on the MSCM were extended to the related problem of species delimitation (Yang and Rannala 2010; reviewed by Carstens et al. 2013; Rannala and Yang 2020), where they are now seeing wide application. However, in an influential study, Sukumaran and Knowles (2017), hereafter S&K, criticized those methods, arguing that they overestimate the number of species because they incorrectly interpret evidence for population structure within a species as evidence for separate species. Examining S&K's study in the context of the unified species concept reveals that although their criticism of species delimitation methods based on the MSCM is appropriate under traditional species concepts, which only consider separately evolving lineages to be species after those lineages evolve some specified property (e.g., intrinsic reproductive isolation, gene tree monophyly, a fixed character-state difference), that criticism does not apply under the unified species concept, according to which all separately evolving lineages are species (de Queiroz 2005b, 2011).

S&K evaluated methods based on the MSCM by using one such method, BPP (Yang and Rannala 2010; Yang 2015; Flouri et al. 2018), and datasets simulated under a protracted speciation model (PSM; Etienne et al. 2014). Under the PSM, a lineage-splitting event does not correspond to a speciation event, and not all lineages arising from such splits develop into "true" species. Instead, there is a lag between an initial lineage-splitting event and the "conversion" of the resulting lineages, termed "incipient" species, into "true" or "good" species (Fig. 1).

The PSM is based on traditional species concepts rather than the unified concept. The idea that a lineage does not become a "true" species until sometime after it comes into existence as a lineage reveals the species concept implied by the PSM to be a generalized version of those species concepts in which a lineage is only considered a species after it evolves some additional property (i.e., other than being a lineage). The required property is deliberately left unspecified under the PSM, which is the reason that its implied species concept is generalized, although S&K mentioned the evolution of reproductive isolation as an example. As noted above (see Introduction), that way of conceptualizing species was explicitly rejected



FIG. 1.—Species under the species concept implied by the protracted speciation model versus under the unified species concept. The tree composed of thick gray, blue, and green branches represents a population-level lineage history upon which a gene genealogy, represented by thin purple lines, is conditioned (as in the simulation study by S&K). Under the PSM, all splits in the population-level tree represent the initiation of speciation and the origin of "incipient" species, but speciation is only considered "completed" when an "incipient" species is "converted" into a "true" species, represented by a color change along a branch in the population-level tree. Thus, in this diagram, there are three "true" PSM species represented by the sets of gray, green, and blue branches (the first of which is paraphyletic). By contrast, under the unified concept of species, all separately evolving lineages are species, and therefore all splits in the population-level tree result in species, of which there are eight at the most recent time (bottom of the diagram). Diagram redrawn from Fig. 1 of Sukumaran and Knowles (2017).

to achieve a unified species concept (de Queiroz 1998). In this context, S&K's finding that BPP (a method based on the MSCM) tended to overestimate the simulated number of species (Fig. 2A) is a direct result of the PSM used to generate the simulated data. BPP delimited species as separately evolving lineages (Fig. 2B), but under the PSM only some of those lineages were considered species. Therefore, the number of species was overestimated, at least in the context of the PSM and its implied traditional species concept.

In contrast to the PSM, under the unified species concept all separately evolving lineages are species (de Queiroz 2005b, 2011). Thus, in Fig. 1, there are eight species (separate lineages) at the most recent time (bottom of the figure) under the unified species concept, not three, as would be recognized under the PSM. Because of this difference, the performance of BPP under the unified species concept (rather than the PSM) is reflected not in Fig. 2a, but in Fig. 2B. There, the number of species-as-lineages inferred by BPP closely matches the number of simulated lineages. In fact, rather than markedly overestimating the number of species, BPP tended to slightly underestimate that number (in the context of the unified species concept).

Moreover, the results of S&K's study are to be expected given the way in which the study was designed. Under their simulations, population-level trees were simulated under a conventional birth–death process, then the lineages ("incipient" species) in those trees were converted into "true" species across a range of specified rates. That conversion, however, had no effect on the gene genealogies simulated on the population-level

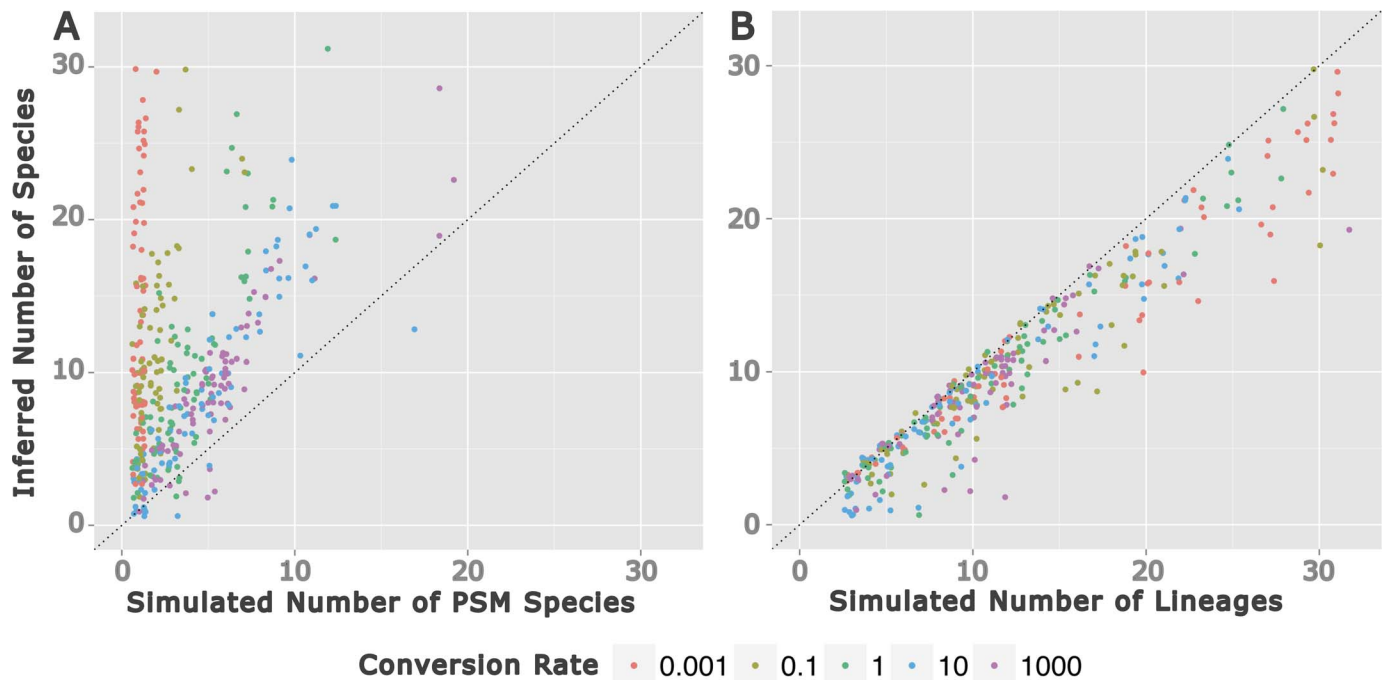


FIG. 2.—Performance of species delimitation under the MSCM in the results of S&K. When species were simulated under the PSM and delimited using BPP, the method systematically overestimated the number of PSM species across a range of species conversion rates (rates at which “incipient” species are converted into “true” species), with greater overestimation at lower conversion rates (A). By contrast, BPP accurately estimated or slightly underestimated the number of separate lineages (B). Under the unified species concept (USC), all separately evolving lineages are species, and in this context BPP accurately estimated or slightly underestimated the number of species (B, where “USC species” can be substituted for “lineages”). Diagram modified from Fig. 2 of Sukumaran and Knowles (2017), illustrating the results of simulations run for a fixed duration of 5.0 time units, a species-initiation rate of 0.5, and extinction rates of 0.0 and 0.2.

trees or on the sequence data simulated on the gene genealogies. Because the simulated gene genealogies and sequence data contained no information about whether a lineage had been “converted” into a “true” species, it would have been impossible for BPP (or any other species delimitation method) to correctly infer the numbers of simulated “true” species from those data (Leaché et al. 2019). That being the case, it seems more constructive to employ a species concept and associated model of speciation that has direct implications for species delimitation using objective analytical methods, such as those based on the MSCM. The unified species concept (and conventional birth–death speciation model) meets this need by emphasizing lineage separation, which can be assessed objectively using genetic data (e.g., Knowles and Carstens 2007; Yang and Rannala 2010; Carstens et al. 2013).

#### Speciation as a Process

The general notion of protracted speciation (as opposed to the PSM discussed above) is appealing in the context of the idea that speciation is more appropriately conceptualized as a time-extended process than as an event or outcome (e.g., Bush 1993; de Queiroz 1998; Hendry 2009; Santini et al. 2012). The PSM, however, is at odds with this idea in that the “conversion” of a lineage from an “incipient” species to a “true” species happens within one generation (Leaché et al. 2019). Nonetheless, the PSM is consistent with the idea inherent in most traditional species concepts that an inclusive population lineage does not become a species until it evolves a specified property. That idea leads to the interpretation that initial lineage separation represents the beginning of the speciation process (at least in some

cases) and acquisition of the specified property represents the end (“completion”) of that process and the attainment of “full” or “good” species status, as manifested in the PSM. Although this traditional interpretation might seem intuitively appealing, it is what created the incompatibilities among the traditional species concepts, because each required the acquisition of a different property before a lineage would be considered a species. Rejection of that general approach to conceptualizing species is therefore necessary to achieve a unified species concept (de Queiroz 1998).

Nonetheless, under the unified concept, speciation is still appropriately viewed as a time-extended process. For one thing, lineage separation usually does not happen in an instant. The reduction in gene flow during lineage separation can be gradual, as in parapatric or clinal speciation (e.g., Endler 1977; Bush and Howard 1986) and in allopatric speciation when extrinsic barriers to gene flow develop gradually (e.g., uplift of mountains, rising sea levels, rifting of tectonic plates). Moreover, the fact that species result from a continuous process does not require that they come into existence (as “full” or “good” or “true” species) only after the process is “complete.” To use an organism-level analogy, we consider organisms to exist before the process of reproduction is “complete.” For example, embryos are considered organisms even though they have not yet hatched or been born, and juveniles are considered organisms even if they have not yet become independent of their parents (e.g., in organisms that provide postnatal nutrition to their young). Considering a separately evolving metapopulation lineage not to be a species until it crosses some “conversion” threshold makes the species category analogous to the category “adult” rather than the category “organism”

(de Queiroz 1998), which is at odds with the widely held view that the species category is one of the fundamental categories of biological organization (e.g., Mayr 1982). The unified species concept, by contrast, brings the species category into line with that view.

### Incipient and Ephemeral Species

The unified species concept also bears on the supposed distinction between “incipient species,” as well as “ephemeral species” (e.g., Rosenblum et al. 2012), on the one hand, and “true species,” “full species,” and “good species” on the other. Implicit in this terminology, particularly when the two categories are contrasted (as in the case of the PSM), is the idea that an incipient or ephemeral species is not truly, not fully, or not yet a species. That idea is rejected under the unified concept, according to which all separately evolving metapopulation lineages are species (de Queiroz 2005b, 2011). Under the unified concept, a species may persist for a short time or a long time, it may be young or old, and it may be differentiated from other species in various ways and to various degrees, but in all cases, as long as it is a separately evolving metapopulation lineage, it is a species. Thus, in contrast to how incipient and ephemeral species are treated under traditional species concepts and the PSM, under the unified species concept, incipient species and ephemeral species are “full,” “good,” and “true” species (although those adjectives are no longer necessary). An incipient species is a species at an early stage of its existence (analogous to an embryonic or hatchling organism), whereas an ephemeral species is a species of relatively short duration (analogous to an organism that dies as an embryo, larva, hatchling, or juvenile). Both are just as much species as later stage and longer enduring species.

### Current Limitations of Species Delimitation under the MSCM

In arguing that BPP accurately delimited species conforming to the unified species concept in the study by S&K (see Protracted Speciation Model), I do not mean to suggest that BPP and other species delimitation methods based on the MSCM will invariably delimit species-as-lineages correctly. The simulations performed by S&K were based on a simple model that did not include parameters representing several phenomena thought to be important in natural populations, including gene flow between lineages and population structure within lineages. (The “population structure” in S&K’s simulations corresponded to separate lineages that had not yet been “converted” into “true” species, which is not considered population structure under the unified species concept. Under the unified concept, population structure occurs within lineages rather than between them and takes the form of phenomena such as subpopulations with reduced but ongoing gene flow between them, isolation-by-distance, and other departures from panmixia). BPP and other species delimitation methods based on the MSCM often use analogous simplifying assumptions (Barley et al. 2018). Thus, the reasonably accurate delimitation of species-as-lineages by BPP in the study by S&K (Fig. 2B) is to be expected, given that the data were simulated using a model that closely matches (except for the “conversion” of “incipient” species into “true” species) the model used by BPP. However, if one or more of BPP’s assumptions were to be

violated in an empirical dataset, the method might yield incorrect species delimitations.

For these reasons, it would be useful to conduct a simulation study similar to that of S&K but replacing the PSM, particularly the element corresponding to the conversion of lineages into “true” species, with a model that incorporates some form of population structure within (as opposed to between) lineages. That is, it would be useful to assess how BPP and other species delimitation methods based on the MSCM perform when the assumption of panmixia within lineages is violated, an occurrence that is expected to be common in empirical datasets. Toward that end, a study by Barley et al. (2018) is important, because it used a concept of species as separate lineages rather than the generalized traditional species concept implied by the PSM. Although based on simpler one- and two-species models (compared with the larger numbers of lineages, in some cases >30, modeled by S&K), Barley et al. (2018) evaluated the impact of several different kinds of model violations (subpopulations with migration and isolation-by-distance for one-species models; decreasing gene flow, recent gene flow, and a population bottleneck for two-species models) on the performance of two different species-delimitation methods based on the MSCM, BPP, and STACEY (Jones 2017).

The results of this study were more nuanced (than those of S&K): the methods were found to be robust to minor model violations, but more prone to errors with larger ones (see also Zhang et al. 2011; Luo et al. 2018). In addition, the two methods exhibited different sensitivities to model violations: BPP was more prone to mistake population structure (within lineages) for separate species, whereas STACEY was more prone to mistake two species with gene flow for a single species. Similarly, Mason et al. (2020) found that a different coalescent-based species delimitation method, Bayes-factor delimitation with SNAPP (Leaché et al. 2014), incorrectly delimited two species for a single lineage with isolation-by-distance and sampling gaps.

No species-delimitation method is (or can be) infallible. Current methods based on the MSCM can lead to erroneous delimitations in some circumstances, but they can also lead to correct delimitations, and their behavior is at least somewhat predictable given their simplifying assumptions (e.g., Zhang et al. 2011; Barley et al. 2018; Luo et al. 2018; Mason et al. 2020). Moreover, the fit of empirical datasets to current implementations of the MSCM can be assessed (e.g., using posterior predictive simulations; Reid et al. 2014; Barley et al. 2018), so that users can be aware of situations when they should be cautious about accepting the results of species-delimitation analyses. Finally, if species-delimitation methods using the MSCM are like other model-based methods in the related field of phylogenetics, we can expect future improvements to those methods through modifications of current implementations of the MSCM—that is, by replacing unrealistic assumptions with more realistic ones. In my opinion, replacing the unrealistic assumption of panmixia within species with a more realistic assumption of isolation-by-distance, particularly one in which the relationship between geographic and genetic distance can be estimated from the data and includes panmixia as a special case, would represent an important improvement. Admittedly, this opinion was formed in the context of my ignorance about how difficult that approach would be to program, although isolation-by-distance has already been incorporated into related methods for inferring population genetic clusters (e.g., conStruct; Bradburd

et al. 2018) and simulating population-genetic data (e.g., SLiM; Haller and Messer 2019). Other complicating processes, such as gene flow and different modes of speciation, are also being modeled (e.g., delimitR; Smith and Carstens 2020).

#### GENEALOGICAL DIVERGENCE INDEX

A recently proposed heuristic criterion for delimiting species is the *gdi*, which estimates the genetic divergence between two taxa (candidate species) due to the combined effects of genetic isolation and gene flow (Jackson et al. 2017a). In its original formulation, the *gdi* is calculated from coalescent simulations based on the estimated migration rates and divergence time between two candidate species (lineages), by using the software PHRAPL (Jackson et al. 2017b). It is the proportion of simulated gene trees in which the two gene copies sampled from the candidate species for which the *gdi* is being calculated are more closely related to each other than to the one gene copy sampled from the candidate species to which it is being compared. Leaché et al. (2019) provided a method for calculating the *gdi* analytically, rather than from simulations, from estimates of the divergence time, the population sizes, and the migration rates for two candidate species. The *gdi* is scaled to vary between 0 (no divergence) and 1 (strong divergence).

Based on *gdi* values obtained from currently recognized species and populations not currently recognized as species in a meta-analysis of 178 datasets (Pinho and Hey 2010), Jackson et al. (2017a) proposed the following criteria for delimiting species:  $gdi > 0.7$  suggests that the lineages being compared are separate species;  $gdi < 0.2$  suggests a single species;  $0.2 < gdi < 0.7$  indicates ambiguity. Jackson et al. (2017a) acknowledged that the *gdi* is not an ideal metric for delimiting species, both because it varies continuously and because there is no definitive boundary between the *gdi* values for populations versus species. Nonetheless, the *gdi* and its associated criteria have become popular in species delimitation studies, including several herpetological examples (e.g., Chan and Grismer 2019; Malleret et al. 2022; Burriel-Carranza et al. 2023).

In the context of the unified species concept, the *gdi* is a useful coalescent measure of the divergence of one lineage relative to another, but it is not an appropriate metric for delimiting species. For one thing, the *gdi* is just another way of assessing the amount of difference between lineages, the species criterion adopted by Darwin (1859) and his contemporaries, who applied the criterion subjectively and primarily to differences in morphology. That subjective morphological criterion was later replaced by criteria that are more objectively defined or that relate more directly to the biological bases of lineage separation and divergence (de Queiroz 2011). Although arguably less arbitrary, those other criteria, like an accepted amount of morphological difference, represent thresholds crossed by diverging lineages that were treated as necessary properties of species under traditional species concepts. That way of conceptualizing species (as a stage in the process of lineage divergence) was explicitly rejected to achieve a unified species concept (de Queiroz 1998). In this context, a *gdi* of 0.7 is just another threshold crossed by diverging lineages, and like the other thresholds that have previously been adopted as necessary for species status (e.g., intrinsic reproductive isolation, a fixed character-state difference, reciprocal monophyly), it is not considered necessary under the unified species concept. A

separately evolving lineage with a *gdi* of  $< 0.7$  (or even 0.2) is still a species.

More specifically, the *gdi* is closely related conceptually to the exclusivity species criterion (Avice and Ball 1990; Baum and Shaw 1995), according to which a lineage is considered a species if the copies of each of several genes in the (extant) members of that lineage coalesce (unite in a common ancestral gene copy) more recently with one another than they do with the copies of that gene in organisms of a different lineage. In addition, both the *gdi* and the exclusivity species criterion are closely related conceptually to the monophyly criterion (Rosen 1979; Mishler and Donoghue 1982), according to which the members of a lineage must form a monophyletic group to be considered a species. Both the *gdi* and the exclusivity criterion represent a special case of the monophyly criterion in which the criterion is applied to gene copies rather to organisms or populations; however, because many genes are contained within each organism or population, the *gdi* and exclusivity differ from monophyly as applied at those higher levels of biological organization in being based on concordance among multiple genes. They also differ from one another in the fraction of genes that must exhibit concordance (all or most for exclusivity—see Baum and Shaw 1995;  $gdi$  of 0.7 =  $P$  of 0.8 or 80%—see Leaché et al. 2019). The *gdi* also differs from traditional exclusivity in being estimated from population parameters rather being assessed directly from inferred gene trees. In any case, none of those thresholds (e.g.,  $gdi > 0.7$ , monophyly or exclusivity in all or most genes) are considered necessary properties of species under the unified species concept.

In addition, the *gdi* has certain properties that highlight its more appropriate interpretation as a coalescent measure of divergence than as a species criterion. Because the *gdi* is inversely related to population size, comparing population lineages with very unequal population sizes can lead to the inference that Lineage A is a different species from Lineage B, but Lineage B is not a different species (or is ambiguously delimited) from Lineage A (Leaché et al. 2019; see Leaché 2021 and Gaughran et al. 2025 for empirical herpetological examples). This is an expected outcome given that the time to reach monophyly is inversely related to population size (Neigel and Avice 1986; Rosenberg 2003). Thus, if speciation occurs via a founder event, or if it occurs via markedly unequal division of an ancestral species (in terms of population sizes), the expectation is that the smaller species (lineage) will reach monophyly in some stipulated fraction of its genes sooner than will the larger species (lineage). Therefore, the *gdi* of the smaller species relative to the larger species will be greater than for the reciprocal comparison. The result that Lineage A is a different species from Lineage B, but Lineage B is not a different species from Lineage A is obviously undesirable for a species criterion. By contrast, the result that the *gdi* of Lineage A compared with Lineage B is much greater than the *gdi* of Lineage B compared with Lineage A is perfectly acceptable for a coalescent measure of divergence. It indicates that Lineage A has progressed farther along the path to monophyly in its gene trees than has Lineage B, an outcome that is expected if Lineage A is smaller than Lineage B.

#### SUBSPECIES

One of the biggest complicating factors in species delimitation is gene flow (e.g., Jackson et al. 2017a), and arguably

the biggest problem regarding gene flow is that the amount varies continuously (e.g., de Queiroz 2021). At one end of the continuum, two lineages that have exchanged no genes for thousands of generations are clearly different species (under the unified concept), and at the other end, a lineage within which gene flow is so extensive there is no evidence of population structure is clearly a single species. However, most real cases lie somewhere in between. Often the most troublesome cases are those in which there is not only strong evidence of differentiation indicative of more than one lineage but also strong evidence of substantial admixture where the lineages come into contact. Not surprisingly, such cases often lead to controversies regarding the numbers and boundaries of species. Some North American herpetological examples involve the Copperheads (*Agkistrodon contortrix* species complex), Cottonmouths (*Agkistrodon piscivorus* species complex), Cornsnakes (*Pantherophis guttatus* species complex), and Ratsnakes (*Pantherophis obsoletus* species complex), each of which some authors consider to constitute multiple species (e.g., Burbrink and Guiher 2015; Myers et al. 2020; Burbrink and Ruane 2021; Burbrink et al. 2021) and others to constitute a single species, with the admixing lineages treated as subspecies (e.g., Hillis 2020; Hillis and Wüster 2021; Hillis et al. 2021; Marshall et al. 2021).

The subspecies category, however, has been controversial. It has been criticized repeatedly because of previous abuses, including (but perhaps not limited to) the recognition of subspecies for artificial partitions of gradual, continuous variation, for single-character differences that are not necessarily indicative of underlying genetic discontinuities, and for phenotypes that represent individual variation rather than population-level differences (e.g., Frost and Hillis 1990; Hillis 2020; de Queiroz 2020). Consequently, the subspecies category has been disparaged repeatedly and its use shunned by many recent authors (e.g., Frost 1995; Grismer 1999, 2002; Burbrink et al. 2022). Moreover, the traditional concept of subspecies (e.g., Mayr 1966, 1969)—that is, geographically contiguous groups of populations that differ (phenotypically or genetically) from other such groups, but are not reproductively isolated from them—is incompatible with the unified species concept because it is tied to a species concept that treats intrinsic reproductive isolation as a necessary property of species.

I attempted to resolve the taxonomic controversies mentioned above by revising the concept of subspecies to make it consistent with the unified species concept, thereby also making it more meaningful biologically (de Queiroz 2020, 2021). Given that species are separately evolving lineages, the obvious phenomenon upon which to base such a redefinition is that of incomplete lineage separation, which implies the existence of sublineages within a more inclusive lineage. Thus, according to my proposal, subspecies are incompletely separated species (metapopulation lineages) within a more inclusive species (metapopulation lineage). Adopting this revised concept of subspecies resolves the taxonomic controversies mentioned above because in this context the authors on both sides are right. For example, Eastern Copperheads and Broad-banded Copperheads are species (different lineages), but they are also subspecies (incompletely separated lineages within a more inclusive lineage).

This revised concept of subspecies contrasts with the traditional concept in a subtle yet fundamental way: it treats the subspecies as a category within the species category rather

than as a mutually exclusive category. Part of the reason that the distinction is subtle is that it involves both similar and different meanings of the prefix “sub-.” Under both traditional and revised concepts, the prefix “sub-” indicates a relationship of inclusion: subspecies are included within species. However, under the traditional concept of subspecies, because the categories species and subspecies are treated as mutually exclusive (i.e., an entity cannot be both species and a subspecies), the prefix “sub-” carries a connotation of “not fully” or “less than completely.” Just as a subadult is not fully an adult, a subspecies is not fully a species. By contrast, under the revised concept of subspecies, because the categories species and subspecies apply to entities of the same fundamental kind, the prefix “sub-” designates only the relationship of inclusion. Just as a subset is a set within a set, and a subclade is a clade within a clade, a subspecies is a species within a species. In other words, subspecies are a kind of species (incompletely separated species); they are not entities that are not quite or not yet species. Under this revised concept of subspecies, subspecies are not “elevated” to species because the subspecies category is not a rank separate from and “lower” than the species category. A subspecies conforming to this revised concept is a species.

For those who oppose use of the term subspecies because of its historical baggage, it may be helpful to consider the revised concept from a different perspective. Rather than considering the revised concept as the modification of an existing subspecies concept to make it more acceptable in the context of modern biology, the proposal can instead be considered the choice of an etymologically appropriate term for an important but previously unnamed concept. That is, if we consider it useful to have a term for the concept of an incompletely separated population-level lineage within a more inclusive population-level lineage, then given that the term species is used for population-level lineages, it makes sense to use the term sub + species for incompletely separated sublineages within a species. Rather than considering the revised subspecies concept a modification of the definition of an existing term, it can instead be considered the formation of a new term (for an important biological concept) that happens to be a homonym (an identically spelled word with a different meaning) of a term previously associated with questionable taxonomic practices.

On the subject of taxonomic practices, I also want to clarify that the proposal in question is about the biological concept of subspecies; it is not about the use of trinomina, which have been used traditionally to represent subspecies in taxonomies, although it obviously has relevance to that practice. In the context of the revised subspecies concept, trinomina are simply a means (device) that can be used to represent subspecies taxonomically but need not be used for that purpose. A subspecies is an incompletely separated species (population lineage) regardless of how it is named or otherwise represented in a taxonomy, that is, for the purpose of communication. In some cases, representing subspecies with trinomina may be appropriate, while in others, representing them with binomina may be preferable, provided that incomplete separation is indicated in some other way (see de Queiroz 2020 for additional discussion and examples). However, if trinomina are to be used, they should be applied to entities conforming to the revised subspecies concept, or if they are not, that should be clearly indicated; for example, see those designated as “legacy” subspecies in de Queiroz and Chan (2025).

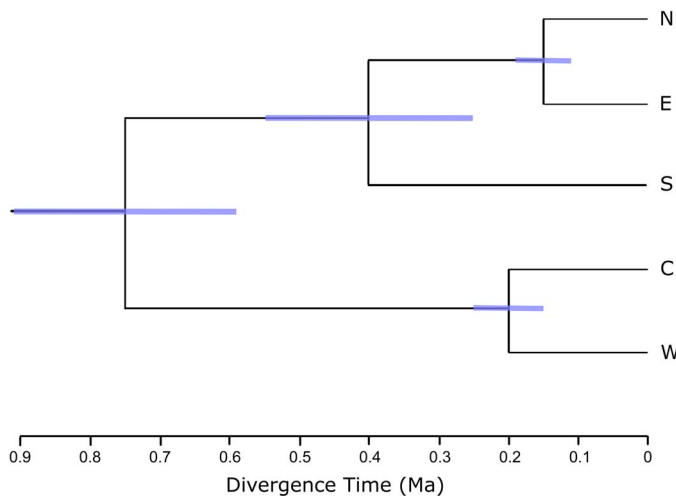


FIG. 3.—Unnamed lineages within a species. The hypothetical phylogenetic tree illustrated is similar to those inferred in several recent herpetological studies in that it represents the phylogenetic relationships and estimated divergence times among lineages that are not recognized taxonomically within a single (recognized) species taxon. Horizontal blue bars centered on branch points represent confidence limits for the divergence-time estimates. Abbreviations for the names of the hypothetical lineages are as follows: N = northern, E = eastern; S = southern; C = central; W = western. Avoiding the recognition of subspecies for the individual lineages or monophyletic groups of lineages (e.g., N + E, C + W) within the recognized species taxon could be incorrectly interpreted as indicating that the species lacks sublineage structure.

With that clarification in mind, both the revised concept of subspecies and the device of trinomina are often not being used in cases where they would convey useful information about biologically significant divisions within species. Herein, I mention examples involving North American lizard (non-snake squamatan) species, because I have recently reviewed the taxa in question as part of my duties as a member of the committee that publishes the list of scientific and standard English names of North American amphibian and reptile species (Nicholson 2025). In reviewing those taxa (de Queiroz and Chan 2025), I encountered several cases of excellent phylogeographic studies in which the authors inferred sublineages within lineages that they recognized as species (and designated with binomina), but they did not recognize the sublineages taxonomically. Examples include *Phrynosoma cornutum* (Finger et al. 2021), *Phrynosoma hernandesi* (Leaché et al. 2021), *Sceloporus occidentalis* (Bouzid et al. 2021), *Sceloporus magister* (Pavón-Vázquez et al. 2024), and *Elgaria coerulea* (Leaché et al. 2024).

In those studies, the entities in question (sublineages) were clearly interpreted as population-level lineages. In many cases, the authors explicitly referred to those entities as “lineages,” and in all cases the authors inferred phylogenetic relationships among the sublineages by using methods for inferring species trees (Fig. 3) and estimated divergence times and migration rates between them, as well as their population sizes. In some cases, the sublineages were largely congruent with previously recognized subspecies, and in many cases, taxonomic names were available that could have been applied to them. Importantly, the studies in question provide evidence both for the existence of sublineages within the lineages recognized as species and for incomplete separation of those sublineages where they come into contact. That is, the entities conform closely

to the definition of subspecies under the revised concept (de Queiroz 2020).

In each of the cases in question, choosing to recognize a single species without taxonomic subdivisions—that is, choosing not to recognize subspecies—gives a false impression of internal homogeneity (specifically, the lack of sublineage structure) when the taxonomy is adopted in subsequent publications, such as checklists, field guides, and citizen-science networks—homogeneity that is contradicted by the studies themselves. Given the existence of a subspecies concept that has been redefined to make it biologically meaningful and that directly addresses the increasingly common finding of incompletely separated lineages within species, avoiding the recognition of subspecies simply because of past abuses (e.g., Pyron and Burbrink 2009; Burbrink et al. 2022) is counterproductive. That practice contradicts the fundamental taxonomic goal or representing biological diversity, which is manifested not only as maximally inclusive metapopulation lineages (species) but sometimes also as sublineages within them. It can be particularly damaging in the context of biodiversity conservation, which tends to prioritize taxonomically recognized entities (e.g., the US Endangered Species Act).

#### CONCLUSIONS

The problems that I have discussed concerning species delimitation and taxonomy all appear to be tied to taxonomic traditions. Both the protracted speciation model and use of the *gdi* as a species criterion are tied to a tradition of treating the species category as a stage in the evolution of lineages, a stage that is not reached until some threshold is crossed in the process of lineage divergence. As I have argued herein and elsewhere, that tradition must be rejected both to achieve a unified concept of species and to make the species category consistent with its interpretation as one of the fundamental categories of biological organization, analogous to the lower level categories “cell” and “organism.” That change also effectively removes the species category from the hierarchy of taxonomic ranks, placing it firmly in the hierarchy of biological organization (de Queiroz 1999). In the case of subspecies, avoidance of the subspecies category is tied to a long tradition of questioning the usefulness of that category dating back at least to Darwin (1859), who referred to it as a “doubtful category” (p. 120), as well as to the traditional treatment of the subspecies category as a taxonomic rank. That tradition must also be rejected to achieve a consistent (with the unified species concept) and more biologically significant concept of subspecies, a concept that treats the subspecies category not as a taxonomic rank but as a subcategory of the species category—subspecies are incompletely separated species (lineages) within a more inclusive species (lineage). This revised subspecies concept should remove the doubts previously associated with that category and permit the taxonomic representation of lineage diversity within species. In general, it seems best not to treat taxonomic traditions (including both acceptance of and opposition to certain practices) as conventions that must be adopted; instead, it seems more useful to treat taxonomy as a set of methods for representing patterns of biological diversity that need to be reevaluated continually under the guidance of that purpose. Rather than starting with a set of taxonomic conventions and trying to determine the best way to apply them to a set of results, we should start with a set of results that we wish to represent taxonomically and then try to determine the best way

to represent them—even if that involves rejecting or modifying existing conventions or developing entirely new ones.

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