1 **Empirical and Philosophical Problems with the Subspecies Rank**
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41 "The reader may now be tempted to agree with Hamilton (1975) that "common usage" is
42 preferable to all these "metaphysical" ruminations. As understandable as this temptation is, I
43 suspect that sooner or later common usage will have to be sacrificed if we are to understand the
44 evolutionary process."

45

46 David Hull 1980

47

48 **ABSTRACT:**

49 Species-level taxonomy is derived from methodological sources (data and techniques) that assess
50 the existence of spatio-temporal evolutionary lineages via various species concepts. These
51 concepts determine if observed lineages are independent given a particular methodology
52 supposedly connected to ontology, which relates the metaphysical concept to what "kind" of
53 thing a species is. Often, species concepts fail to link methodology and practice back to ontology.
54 This lack of coherence is in part responsible for the persistence of the rank of subspecies, which
55 in modern usage often functions as a placeholder between the evolutionary events of divergence
56 or collapse. Thus, prospective events like lineage merger or collapse determine if a subspecies is
57 subsumed into an existing species or achieves species rank given unknowable future information.
58 This is conditioned on evidence that the lineage already has a detectably distinct evolutionary
59 history. Ranking these lineages as subspecies seems attractive given the observation that many
60 lineages do not exhibit intrinsic reproductive isolation. We argue that the use of subspecies is
61 indefensible on philosophical and empirical grounds. Ontologically, the rank of subspecies is
62 either identical to that of species or undefined in the context of evolutionary lineages
63 representing spatio-temporally defined individuals. Some species concepts more inclined to
64 consider subspecies, like the Biological Species Concept, are disconnected from ontology and do
65 not consider genealogical history. Even if ontology is ignored, methods addressing reproductive
66 isolation are often indirect and fail to capture the range of scenarios linking gene flow to species
67 identity over space and time. The use of subspecies and reliance on reproductive isolation as a
68 basis for an operational species concept can also conflict with ethical issues governing the
69 protection of species. We provide a way forward for recognizing and naming species that links
70 theoretical and operational species concepts regardless of the magnitude of reproductive
71 isolation.

72 Keywords: Ontology, genomics, gene flow, reproductive isolation, species, subspecies
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75 **1 INTRODUCTION: GENE FLOW AND THE SPECIES PROBLEM**
76 It is now understood that the history of life on Earth is not easily represented as a
77 bifurcating process (Mallet et al., 2016; Wen et al., 2016), and that many organisms fail to
78 maintain genomic exclusivity with closely related or even long extinct relatives (Reich, 2018).

79 Extreme examples of non-bifurcating histories have shown that some species or even entire
80 clades may have been produced from reticulating ancestral taxa over millions of generations in
81 the past (Abbott and Rieseberg, 2012; Baack and Rieseberg, 2007; Frantz et al., 2013).
82 Incomplete reproductive isolation provides a biologically interesting landscape of possibilities
83 for speciation, such as adaptive introgression (Figueiró et al., 2017; Leroy et al., 2020; Schmickl
84 et al., 2017) or when spatially-dependent genetic incompatibilities change over the landscape
85 (Barnard-Kubow and Galloway, 2017). Absence of reproductive isolation after speciation,
86 reflected as continued introgression across parts of the genome, is now well established (Wu,
87 2001; Wang et al., 2019). While degree of reproductive isolation may increase with time since
88 divergence, the spatial nature of isolation and the portion of the genome involved in speciation
89 varies widely. Gene flow therefore makes the boundaries between many species indistinct or
90 "fuzzy." When researchers categorize individuals into taxonomically coherent species, this
91 uncertainty is likely to present difficulty.
92   The "gray zone" of speciation (de Queiroz, 1998) highlights the broad set of empirical
93 outcomes where sometimes uncomfortable taxonomic decisions must be made or are
94 alternatively, ignored altogether. In the gray zone of "incomplete" genealogical exclusivity,
95 uniquely identified lineages may remain connected by occasional or ongoing introgression,
96 making determination of species status difficult when relying on overall measures of gene flow
97 to delimit species (Jackson et al., 2017; Leaché et al., 2019; Nosil, 2008; Roux et al., 2016).
98 Degree of gene flow might be negatively correlated with age of divergence, which on the surface
99 could help identify where lineages are in the gray zone. However, a correlation between time and
100 gene flow may be disconnected by divergent selection at loci due to sexual and ecological
101 pressure (Gavrilets, 2004; Nosil, 2012; Singhal and Moritz, 2013).
102   In some groups, reproductive isolation scales with time of divergence (Bolnick and Near,
103 2005; Singhal and Moritz, 2013) but not in others (Burbrink et al., 2021). Pre- and postzygotic
104 isolation may also accumulate at different rates (Stelkens et al., 2010; Uy et al., 2018). Over long
105 periods of time with continuous or intermittent connection between lineages, one should ask:
106 how have these lineages retained their identity for so many generations in the face of gene flow
107 if they are not distinct evolutionary entities (i.e., species)? This is contrasted against known rates
108 of species reversal or extinction by hybridization, which can occur in just a few generations for
109 range-limited taxa such as various fish groups and Darwin's finches (Hendry et al., 2006;
110 Rudman and Schluter, 2016; Seehausen, 2006; Seehausen et al., 1997; Taylor and Larson, 2019;
111 Vonlanthen et al., 2012) to thousands of generations for species with continental ranges like
112 ravens (Kearns et al., 2018). For other taxa, partial reproductive isolation may be a stable
113 evolutionary endpoint and indicate why species showing ancient divergences with gene flow fail
114 to collapse (Servedio and Hermisson, 2020). In the gray zone of speciation, there are thus crucial
115 questions about how taxonomists should address naming geographic lineages with spatial
116 overlap and introgression across the genome given the complexities of demography, selection,
117 and hybridization (Jackson et al., 2017; Leaché et al., 2019; Roux et al., 2016).

The indefinite nature of many species boundaries has long been recognized (Darwin, 1859; Hey, 2001; Hull, 1976; O'Hara, 1993). To resolve this taxonomic conundrum, many researchers in the 20th century (particularly during and immediately after the Modern Synthesis) inferred reproductive isolation and applied the rank of subspecies to diagnose, define, and delimit populations with fuzzy boundaries (Mayr, 1982, 1965). The use of subspecies to represent geographic variation has a long history in systematics from the late 19th century through to the present. As early as the 1950s, however, problems with the subspecies solution had been identified (Cracraft, 1983; Frost and Kluge, 1994; Gillham, 1956; Rosen, 1979; Wilson and Brown, 1953).

From a perspective where subspecies are considered entities and not artificial constructs (Cracraft, 1983), the rank preserves the identity of evolutionary lineages and underscores that those lineages are not fully reproductively isolated and therefore not ready for full taxonomic recognition as full species. Subspecies then represent a placeholder category, expecting either that historical lineages will cease to be unique (collapse) or will eventually become species (incipient species), but without differentiating between these contrasting scenarios in the present day. Both situations implicitly rely on speculation rather than evidence regarding the future trajectory of reproductive isolation (O'Hara, 1993; Zink and McKitrick, 1995). As we explain below, neither view of prospective subspecies taxonomy serves to identify lineages properly or reveal future processes of divergence. We therefore provide a description of what species are, what subspecies are not, and why the lure of the subspecies rank should be resisted if we are to move forward with clear taxonomies that better describe the reticulated tree of life.

As we outline below, synthesizing decades of thought on the philosophical and practical literature of the "species problem," species are historical entities that are phylogenetically diagnosable and exist as ontological individuals, occupying a unique position in the process of evolution. As such, they are not required by any modern understanding of evolutionary theory to be reproductively isolated as ontological individuals exhibit leaky or fuzzy boundaries across both space and time. We assert that the following are indefensible: 1) philosophically, to accept the existence of subspecies as ontologically distinct entities within species; 2) biologically, to recognize subspecies as arbitrary divisions of clines when such units lack an evolutionary basis and phylogenetic diagnosis; and 3) operationally, to use the subspecies category as a pragmatic tool to advance aims such as field-guide identifications or conservation policy and management.

2 BRIEF HISTORY OF SUBSPECIES AND REPRODUCTIVE ISOLATION

The rank of subspecies has a long history of discussion and implementation under fundamentally different concepts. These concepts range from those without explicit evolutionary interpretation to those being essentially the same as species. Subspecies represented as trinomials have been applied at least since 1844 (Remsen, 2010; Simpson, 1961) and were considered to be essentialistic, similar to the rank of species at that time (Mayr, 1982). After Darwin (1859), subspecies were often considered as natural entities and not classes. Subspecies were thought to be incipient species by some authors (Rensch, 1929, 1928; Rothschild and Jordan, 1895, 1903)

which are part of species, or *Rassenkreise* (circle of races; polytypic species or differences at the ends of isolation by distance; Reydon and Kunz 2021). Gloger, Bergmann, and Allen viewed subspecies as adaptive geographic variants to address ecogeographic phenomena (Mallet, 2013; Mayr, 1982). Subspecies descriptions increased throughout the late 19th to mid-20th century biased towards European and North American mammals, birds, butterflies, and to a lesser degree reptiles and amphibians (Burt, 1954; Frost, 2020; Frost and Hillis, 1990; Gillham, 1956; Mayr, 1946; Padial and De la Riva, 2021). This taxonomic bias is notable given the small contribution of these groups to the overall biodiversity of life on Earth but also expected given the emphasis on studying these organisms in the Northern Hemisphere (Mora et al., 2011).

In many cases, previously diagnosed morphological species named by earlier researchers were demoted to subspecies and considered geographic variants of widespread species (Stresemann, 1975). Proliferation of subspecies names continued through the middle 20th century, when arbitrary sections of clines and minute phenotypic variants were formally named in many groups (Burt, 1954; Gillham, 1956; Huxley, 1938; Padial and De la Riva, 2021). For example, in reptiles, subspecies were described at their highest rate after the 1950s and declined rapidly towards the end of the 20th Century (Uetz and Stylianou, 2018). This is paralleled in ornithology, where subspecies descriptions increased from the late 19th Century, peaked in the mid-20th Century, and declined rapidly towards the 21st century (Remsen, 2010).

Wilson and Brown (1953) struck back at the widespread proliferation of subspecies by showing that 1) they are often defined by an arbitrary choice of characters that can differ widely over geographic space, 2) the same characters often occur in different areas of a species' range, 3) microgeographic races are a common outcome of elaborate and extensive trait variation due to local adaptation, and 4) there is a lack of a lower limit for defining these entities. Essentially, any number of arbitrary traits can be used to group individuals into an arbitrary number of subspecies. However, champions of the subspecies idea continued (Mayr, 1954; Parkes, 1982; Smith and White, 1956). In fact, the years immediately following Wilson and Brown (1953) and Brown and Wilson (1954) saw a "cline" of opinions from authors wanting to eliminate the rank to those wanting to produce more refined definitions. Some authors considered only established allopatric forms as subspecies whereas others devised rules to handle arbitrary descriptions (Burt, 1954; Edwards, 1954; Gosline, 1954; Inger, 1961; Starrett, 1958).

The taxonomic rank of subspecies has been defined and redefined for many decades (Amadon, 1949; Braby et al., 2012; Mayr, 1965; Patten, 2015; Rand and Traylor, 1950), though there has been little consistency in the criteria used to delimit subspecies boundaries. Various rules have been proposed to delimit subspecies other than as arbitrary handles of convenience. Some authors consider them to not be evolutionary lineages, equivalent to evolutionary lineages, former evolutionary lineages, or rank-free evolutionary lineages (Amadon, 1949; Braby et al., 2012; de Queiroz, 2020; Hillis, 2020; Mayr, 1965; O'Brien and Mayr, 1991; Rand and Traylor, 1950). Often they are simply recognized as unique para- or peripatric subdivisions within the range of a species defined by phenotypic similarities that are composed of fertile individuals. Other authors only consider allopatric populations as candidate subspecies (Edwards, 1954; Haig

198 et al., 2006). A recent review of the many ways subspecies rank is defined suggests that they
199 show ecological, morphological, or genetic trait differences often over geographic space with
200 some degree of reproductive (in)compatibility (Reydon and Kunz, 2021).
201   Several methodological approaches using morphological, ecological, or genetic data to
202 decide when lineages should be delimited as subspecies have been applied over the last 70 years.
203 For example, Amadon (1949) and Patten and Unitt (2002) proposed a threshold where 75% or
204 more of individuals examined differ at particular traits between populations. O'Brien and Mayr
205 (1991) recommended that subspecies be allopatric and receive no migrants, but also possess
206 exclusive phenotypic characters defining a unique natural history. Other definitions regard
207 subspecies as distinct populations with at least one phenotypic trait diagnosable in at least 95%
208 of individuals (Remsen, 2010). Tobias et al. (2010) used a phenotypic yardstick when measuring
209 morphological and vocal traits in birds to generate a minimum threshold for sympatric and
210 parapatric species. Köhler (2021) advocated combining mtDNA tree structure with sequence
211 divergence thresholds to delimit species vs. subspecies, though no criteria are given for the
212 spatial distribution of taxa or degree of reproductive isolation. Rather, taxa are ranked in a tree
213 and then genetic divergences are assessed over various ranges of values thought to represent
214 species or subspecies. Others have suggested that subspecies be allopatric, divergent along at
215 least one axis of genetic, morphological, or ecological variation, but "less" than what would be
216 expected for closely-related species existing in sympatry (Descimon and Mallet, 2009).
217 Additionally, subspecies have been conceived to reflect a range of incomplete adaptive
218 divergence within species that do not rise to the "level" of specific differentiation (Braby *et al.*,
219 2012).
220   Others have recently tried to establish the link between phenotypic and genomic
221 differentiation of populations when identifying subspecies (Patten, 2015). These "subspecies
222 genes" (the term used by Patten 2015) are considered discoverable using genomic methods. In
223 parapatric populations "subspecies genes" are thought to provide evidence that these entities
224 represent incipient species. For parapatric subspecies, allelic introgression is expected to vary
225 widely with neutral alleles moving extensively between populations and adaptive alleles
226 remaining local to each subspecies (Braby et al. 2012). Most recently Dufresnes et al. (2021)
227 suggested that the distribution of cline widths among diagnostic SNPs be used to determine if
228 lineages represent species or subspecies. Here, Poisson or binomially distributed densities
229 centered on widths of 0 km indicate the presence of two unique species with genes likely tied to
230 reproductive isolation, whereas Gaussian-distributed densities centered on larger widths are
231 indicative of subspecies.
232   It is clear that most modern proposals identifying subspecies as being different from
233 species rely on perceived lack of reproductive isolation (Braby et al., 2012; Mayr, 1982, 1965).
234 However, most described species have never directly been tested for degree of reproductive
235 isolation in any meaningful way (Cracraft, 1983; Mayr, 1963). For example, avian taxonomic
236 classification committees for North and South American birds, which follow the biological
237 species concept (BSC), use a range of criteria to delimit species. A review of how bird species

were delimited in practice found that diagnosability was the most frequently applied criterion (Sangster, 2014). As Mayr (1963) points out, the application of the typical morphological species concept (species differ enough morphologically to be considered unique) is simply serving "as secondary indications of reproductive isolation." It follows then that this view of morphological, behavioral, and molecular differentiation are often surrogates for identifying reproductive isolation applied to determining subspecies rank where isolation is incomplete. Therefore, most instances of species and secondarily subspecies description fail to directly test for reproductive isolation but rather infer it given degree of difference in measured characters.

While reproductive isolation is usually not tested, this does not mean that such testing is impossible given genomic data and modern computational methods. Reproductive isolation is fascinating as a biological process, even though it is not in of itself a "trait" possessed by any species (Coyne and Orr, 2004), but rather as a measure of interaction as a result of speciation. However, studying reproductive isolation necessarily requires the presence of two entities. This underscores the obvious point that historical lineages have to be defined independently of reproductive isolation to be able to quantify the supposed lack of independence (Cracraft, 1983; Nelson and Platnick, 1981). Identifying these independent lineages is a necessary first step before quantifying hybridization over a landscape.

Failure for reproductive isolation to occur between lineages continuously distributed over the landscape usually results in some form of a hybrid zone. These zones can be examined to understand if reproductive isolation is actually occurring given the observed hybridization. Thus, if endogenous or exogenous selection is present, then species boundaries are likely to be preserved. Realistically, the degree of reproductive isolation, extent of linkage disequilibrium, and amount of backcrossing is not easily determined given that hybrid zones change widths, extent, and location through time (Ryan et al., 2018). Reproduction through a hybrid zone could reflect true neutrality where species might collapse, be reinforced in the case of selection against hybrids (tension zones), or reveal gradients of environmental selection from one parental species through to the range of the other parental species (Barton and Gale, 1993; Barton, 1979; Endler, 1977; Gompert et al., 2017; Harrison and Larson, 2014; Nachman and Payseur, 2012). Moreover, hybrid zone widths alone may not be reflective of the degree of reproductive isolation since the sizes and location of the zone may change over several orders of magnitude considering variation in dispersal rates and historical climate change (McEntee et al., 2020). Therefore, there may be no clear pattern suggestive of lineage collapse or complete reproductive isolation indicated by these studies.

Changes in hybrid zone shapes and locations over time might be common (Buggs, 2007; Ryan et al., 2018; Wielstra, 2019), as revealed by evidence from the fossil and pollen records, niche modeling through time, displacement of extant populations of one species from the expanding range of another, or genome-wide evidence from displaced lineages. There is ample evidence that hybrid zones of various shapes and sizes have existed from the present through to the late Miocene between extant species (Barth et al., 2020; Burbrink et al., 2021; Hewitt, 2011). In birds, fertile hybrids can be produced well past speciation, even among taxa sharing a

278 common ancestor 5-17 million years ago (Price and Bouvier, 2002). Importantly, evidence from
279 the predicted origin of hybrid zones along with continuous or repeated instances of contact
280 suggests that hybrid zones have formed and reformed many times, yet the identity of the
281 interacting lineages remain intact despite gene flow (Wang et al., 2019). As pointed out by
282 Servedio and Hermisson (2020), partial reproductive isolation may be a long term stable reality
283 for most species. Gene flow may never reach a point of species collapse or absolute reproductive
284 isolation, therefore rendering the subspecies category again superfluous where evolutionary
285 histories of species are maintained over many millennia. This is in contrast to documented
286 species collapse that occurs just in a few generations upon contact (Rudman and Schluter, 2016;
287 Seehausen et al., 1997; Taylor et al., 2006; Vonlanthen et al., 2012).
288   Complete reproductive isolation is not the universal indicator of speciation, nor is it
289 necessary or even common for "good" species that form and maintain their evolutionary
290 distinctiveness over time. Defining what is meant by reproductive isolation is often complex
291 given differential introgression throughout the genome and unique interactions over time and
292 space along hybrid zones. At least for methods described above that use some quantification of
293 hybridization or gene flow, only arbitrary breaks along a continuum of reproductive
294 compatibility can "determine" when evolutionary lineages represent subspecies or species
295 (Dufresnes et al., 2021; Hillis, 2020; Tobias et al., 2010). Unfortunately, none of these proposals
296 have considered how subspecies and species actually differ with regard to ontology or process
297 (Burbrink and Ruane, 2021; de Queiroz, 2022).
298
3 ONTOLOGY OF SPECIES AND ITS CONSEQUENCES FOR SUBSPECIES
300
301 3.1 *Are species ontological individuals?*
302   Because the subspecies rank is inherently tied to the species problem, we compare the
303 ontology of species and subspecies with regard to how we detect, diagnose, delimit, and define
304 them given various species concepts. We hold that species are natural concrete objects and are
305 not abstractions (Ghiselin, 1997, 1974; Hey, 2001; Nathan and Cracraft, 2020). That is, they are
306 real entities that exist in the real world. Species are fundamental units of evolution that are also
307 the fundamental rank in the taxonomic hierarchy (Bock, 2004), and de Queiroz (1997) notes that
308 this special status decouples species from the hierarchy of taxonomic ranks. Therefore, this rank
309 occupied by species in the otherwise-arbitrary hierarchy of taxonomy coincides with a
310 biologically meaningful unit, unlike other ranks such as genus and family. Thus, species are real
311 and are the aim of discovery of taxonomy, while the remaining higher ranks are applied to
312 named clades of increasing inclusiveness as an approximation of their evolutionary history
313 (Hennig, 1966). However, if species are parts of clades at different levels of inclusiveness, and
314 these clades are also considered as individuals, then assigning species to higher named taxa is not
315 classification, in the sense of class versus individual (de Queiroz, 2005, 1988).
316   The recognition of species as ontological individuals has a long history (Baum, 1998;
317 Bernier, 1984; Brogaard, 2004; Coleman and Wiley, 2001; Ereshefsky, 1992; Frost and Kluge,

318 1994; Ghiselin, 1987, 1981, 1974; Hennig, 1966; Holsinger, 1984; Hull, 1976; Kitcher, 1984;
319 Mayden, 2002; Mishler and Brandon, 1987; Queiroz, 1999; Rieppel, 2009; Rieppel and Grande,
320 2007; Wiley, 1980). The implications of individuation versus the treatment of species as
321 classes/natural kinds have been detailed elsewhere (Frost and Kluge, 1994; Mayden, 2002). To
322 review, if species are ontological individuals, they must fit specific criteria for the category. We
323 consider the criteria for individuation to be the following: Is it ostensively defined? Is the thing a
324 particular? Are there instances of the thing? Is it bounded in space and time, with the boundaries
325 fuzzy? Do the parts exhibit cohesion? Is the thing a mereological sum (Table 1)?
326
327 Table 1. Criteria that differentiate ontological categories of individual and class.

Individual	Example
Particular Thing	*Lithobates heckscheri*
No Instances	One lineage of *L. heckscheri*
Defined Through Ostension	Can point to unique diagnostic characters
Bound in Space and Time	Distributed only in SE North America, diverged from closest living relative ~15–10mya
Cohesive	Individuals of *L. heckscheri* are connected via tokogenic processes
Mereological Sums	Composed of other individuals; individual organisms of *L. heckscheri* are parts of the whole lineage
Class	Example
Universal Thing	Hydrogen (H) atom
Instances Exist	H atoms are exactly the same
Defined Through Intension	H defined by strict rules

Not Spatio-Temporally Bound	H originated with the universe, found across universe
Not Cohesive	Single H affected at a time
Not Mereological Sums	Not parts of wholes, the parts of H are also class objects

328

329   Species are particular things, so there are no instances of them. They are not universals
330 like "chairs," of which there are many instances. The River Frog *Lithobates heckscheri* is a
331 unique thing, a particular of which there are no instances. Species are not defined by a specific
332 list of characteristics or rules that will always *define* a species, that is, they are not intensionally
333 defined. Contrast that with hydrogen, which is always defined by the presence of a single proton
334 and a single electron. Species have diagnostic features that allow us to *point to* and say "that is
335 *Lithobates heckscheri*." As such, species are ostensively defined and are *diagnosed* rather than
336 defined. Species are spatio-temporally bound, they have beginnings (speciation) and ends
337 (extinction). The boundaries in space and time are fuzzy. The fuzziness refers to geographic
338 distribution and tokogenetic reticulation. Consider hydrogen again, which likely appeared at the
339 beginning of the universe and continues to exist throughout the space of the universe. The parts
340 of species exhibit cohesion through the tokogenetic nexus and respond to similar processes in
341 similar ways.
342   If species are individuals and their parts are also individuals, then species are
343 mereological sums. Each organism within a species is a particular thing, an ontological
344 individual. If each organism is a part of a species, then species would be a whole ontological
345 individual composed of its parts, the specific organisms as ontological individuals. Based on the
346 criteria for arguing that a thing fits the ontological category individual, species are individuals.
347   Given that species are individuals, we can ask, what kind of individuals are they:
348 replicators, interactors, or replicator continua? Species, as lineages, exhibit tokogeny through
349 time. Replication among organisms is required for persistence of the individual in this case.
350 These criteria meet the definition of replicator continua (Hull, 1990; Lidén, 1990). Of further
351 interest is the question of transitive properties in hierarchical fashion. Specification hierarchies
352 have set-like organization in which they are equal members of higher sets in the hierarchy. For
353 example, the New York Yankees are equally members of the eastern division as they are the
354 American League. Species, however, do not possess these transitive properties. A single cell
355 lacks transitive properties to the tissue it in part makes up, the organ it contributes to, or the
356 organism it is part of, for example. Does a single parietal epithelial cell of a Bowman's capsule
357 inform us of medullary countercurrent osmotic maintenance, the endocrine insertion of
358 aquaporins, the composition of the filtrate itself, or the properties of the organism with said
359 kidney? No, because these hierarchical levels above that cell possess emergent properties.
360 Species (*and cells*) are examples of scalar hierarchies and thus can suffer from over-reductionism

361 in practice (Frost and Kluge 1994). In sum, species are replicator continua individuals that
362 exhibit a scalar hierarchy.
363
364 3.2 *Are subspecies real things?*
365   A way to answer this is to ask if subspecies exist without human perception. A
366 distributional segment of some species has blue organisms, while the rest are brown elsewhere.
367 Sentient extraterrestrial beings land on Earth and perceive these blue organisms. Those blue
368 organisms were there before the aliens perceived them and will be blue after the aliens depart. So
369 the distributional segment of blue organisms is a real thing. Are they also subspecies? If they
370 exist as ostensively defined (they are blue), then calling them a subspecies would be an error in
371 diagnosis: they are species. Conversely, if extraterrestrial beings perceived variation among
372 individuals by different prescriptions then the previously defined "blue" subspecies was never
373 real, and it maintains that the subspecies is not something recognized by alien life forms.
374   There is another level to the reality of subspecies and it has to do with the name.
375 *Agkistrodon contortrix contortrix* is a real name, just as Hamlet and Clarissa Dalloway are real.
376 However, the things they represent are fictional. We see a dissonance between subspecies as
377 trinomial names and the biological entities they have been purported to be.
378   If subspecies are considered a kind of evolutionary unit, the recognition of subspecies as
379 a class would reject that claim because evolution as a process would not exist for subspecies: no
380 evolutionary processes, then no evolutionary unit. We are left with the realization that if
381 subspecies are indeed real things, and are individuals, then they are species.
382
383 3.3 *Are subspecies ontological individuals?*
384   Here we take a skeptical approach to the notion that subspecies ***are not*** ontological
385 individuals. We use the specific criteria for the category ontological individual (as noted above
386 for species) to challenge the idea that subspecies cannot be individuated. So the questions below,
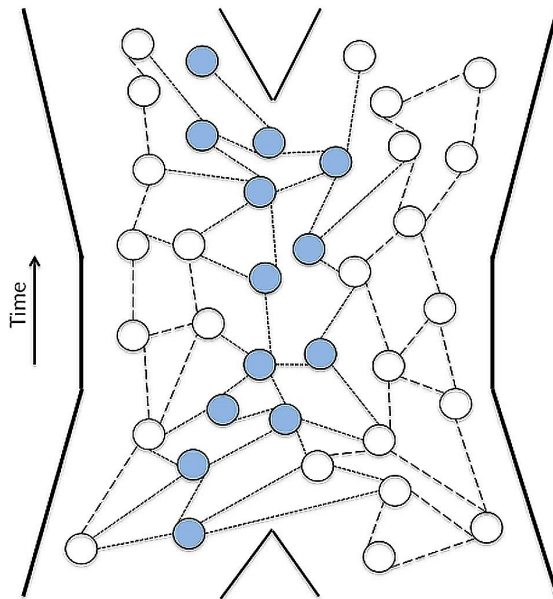387 directly and one criterion at a time, evaluate subspecies as individuals.
388   Are subspecies ostensively defined? This question stands out for subspecies because the
389 way many workers name subspecies is based on some theoretically localized morphological
390 variation (that species is blue over there, but not here), thus you can point to the blue feature and
391 name it. Given that a subspecies can be diagnosed in this way, it is actually a species; the
392 subspecies rank does not stand as a distinct and separate real, concrete individual apart from the
393 species. There are not, in fact, *two* taxonomic ranks that both independently represent real
394 biological units.
395   Are they particular things without instances? There are two ways to address this.
396 Subspecies could be instances of species, but if species have instances then species must be
397 classes. However, species are not classes, they are individuals, and do not have instances. If
398 subspecies are defined by specific rules, say the presence of blue members, and demes or
399 populations of blue members exist in unconnected space, then subspecies would be a class with
400 instances of each other. If subspecies are unique evolutionary units, and thus particulars, then

401 subspecies would be an individual and a part of a whole. That means they would also be
402 diagnosed and not defined by a set of rules. As such, subspecies would again be
403 indistinguishable from species.
404   Are subspecies spatio-temporally bound, with the boundaries fuzzy? If subspecies are
405 evolving units such as incipient species or as lineages collapsing via hybridization, then they
406 certainly would be bound in time and space with fuzzy boundaries. Incipient species and
407 collapsing lineages reflect lineage dynamics as diverging and merging parts of the tokogeny,
408 respectively. We assume which parts of the tokogeny are named as subspecies based on
409 reproductive connectivity, but where do these subspecies begin and end? And how do these
410 processes differ from the process of lineage reticulation? We are left to conclude that markers of
411 spatio-temporal boundaries are artificial (i.e., where and when are organisms blue) and in fact
412 simply reflect a normal process of lineages that are species.
413   Do subspecies exhibit cohesion? We think they must, but only partially, regardless of
414 how they are delineated within a species. If they were fully cohesive, they would be recognized
415 as species. However, in the delineation, other cohesive parts of the whole lineage (the species)
416 are intentionally left out. So, some parts/members of the subspecies may be responding
417 cohesively with extralimital parts, thus rendering the cohesion partial (Fig.1).
418

420 **Fig. 1.** A schematic illustrating the partial cohesion, partial boundedness, and the partial participation as interactors of a
421 subspecies within a lineage. The tokogenetic nexus depicted contains all circles (organisms) and their replicating connection
422 between them is illustrated through lines. The blue dots depict the delimited individuals through time to be members of a
423 subspecies with which other members of the tokogeny reproduce but are not included (dotted lines), illustrating partial
424 participation within a real ontological individual.
425

426   Are subspecies mereological sums? Subspecies must be individuals composed of parts
427 which are individuals to be such. Subspecies are certainly composed of ontological individual

428   parts (i.e., each organism). If the subspecies does not have instances and is spatio-temporally
429   bound, then such an entity composed of these parts would be a mereological sum. Would that
430   entity still be a subspecies? No, that entity would be a species.
431   Are subspecies interactors, replicators, or replicator continua? They may be partial
432   interactors in the sense that some members of the subspecies are interacting with other members
433   inside, but at the same time other members are interacting with members outside of the
434   delineated subspecies. They may also be partial replicators, if we consider replicators as
435   reproductive organisms. Like interactors, it is easy to see that reproduction would occur among
436   members within the subspecies as well as with members outside the subspecies.
437   Can subspecies exhibit scalar hierarchies? Making that claim would require taking parts
438   from the whole (species) and saying the parts represent a scalar hierarchy, which is an error.
439   Subspecies are more like specification hierarchies, in which they are extensions of a set, and this
440   is a characteristic of classes. If they were scalar hierarchies, then they must be species or a
441   monophyletic clade above species.
442
443   3.4 *Subspecies as incipient or collapsing species.*
444   Specifically, for those subspecies that are allopatric historical lineages, these are no
445   different from species. For those subspecies considered historical lineages as either incipient and
446   merging species, they, too, are ontologically no different than species or part of the phylogeny.
447   We note that assessing these processes with real data under any concept (e.g., BSC, Evolutionary
448   Species Concept, and Phylogenetic Species Concept), however, implicitly contain prospective
449   statements (O'Hara, 1993). For example, a group of populations that qualify as a species in the
450   present moment is predicted to continue instantaneously into the near future. Even if they begin
451   to merge over time and eventually cease to be distinct species, this will not happen immediately,
452   as they are spatio-temporally distinct. Even at nearly instantaneous temporal scales, interpreting
453   subspecies as incipient species already suggests that spatio-temporally independent lineages are
454   cohesive and therefore species, and subspecies as former historical lineages that are in the
455   process of merging are also species.
456   Considering species as the units of evolution that are also concrete individuals, we then
457   ask if they can be discovered under a single or multiple concepts. The idea of monism suggests
458   species are discoverable by one single concept (Hull, 1999). This is in opposition to pluralism,
459   where a single species concept cannot account for various processes that generate species in
460   different groups. Monism aligns well with concretism and suggests that among the plethora of
461   species concepts used today, there is really only one that is practical for defining species (see
462   (Nathan and Cracraft, 2020). Alternatively, perhaps the appropriate species concept has not been
463   discovered yet. (Reydon, 2006, 2005) suggests that a pluralistic view of species may be at the
464   heart of debates about the species problem. Under this pluralistic view, species may be
465   considered as four different kinds of entities: 1) synchronic — equivalent to biological species,
466   2) diachronic — segments of the tree of life, equivalent to phylogenetic species, 3) classes
467   sharing similar properties, or 4) classes of evolving populations or groups. Here, the first two

categories are considered individuals and may not actually be different kinds of entities but rather viewed as time-limited or time-extended (de Queiroz, 1998, 1988). The second two are classes. Within diachronic species, there exist two other categories differentiating between lineages and clades. The former are lineages that are reproductively compatible (Reydon and Kunz, 2021), and these authors treat both lineages and clades as biologically relevant. Subspecies would be diachronic and also equivalent to species in that regard.

Considering species as evolving individuals should be recognized as the dominant and necessary basis for evolutionary classification. However, the BSC continues to cast a long shadow over species delimitation, though instances where the criterion of reproductive isolation is actually rigorously tested empirically when delimiting species are rare (Cracraft, 1983). For the most part, phenotypic differences served to indirectly determine if species are potentially interbreeding (Sokal and Crovello, 1970) until the rise of genetic data. The vast majority of named species are likely also distinct evolutionary entities, as taxa delimited based on apparent reproductive isolation are probably separate species in most instances. Of course these species may also contain multiple independently evolving lineages (cryptic species). In contrast, this operational basis for classification is also associated with the use of "subspecies" for numerous lineages in the gray zone of speciation, a trend that is still being advocated in several major groups (Braby et al., 2012; Hillis, 2019; Patten, 2015). However, as noted here and by previous researchers (Cracraft, 1983; Frost et al., 1992), prioritizing a particular form of cohesion over evolutionary history represents a major starting point for problems with recognizing species and, in particular, promotion of the subspecies rank.

From a classification point of view, where members of a particular class are defined by essential properties, lineages connected by some gene flow could be problematic. But, ontologically, species are not classes. Species represent the basal category of taxonomy (systematization), yet are defined ontologically as individuals (de Queiroz, 1988; Griffiths, 1974). Further subdividing this category has no meaning given that anything below this category is not defined as an individual or simply refers to arbitrary classifications. Logically, if one can group populations and those are identified as spatio-temporal individuals that are cohesive with fuzzy boundaries then this entity cannot be further subdivided as species. Along the continuum of "subspecies" definitions, they either represent nothing concrete in nature or they are species. We thus assert that species are a reasonably indivisible unit; not that variation does not occur within species, but that it does not make sense to consider the existence of infraspecific evolutionary units in taxonomy.

Our assertion thus derives from the nature of species as concrete natural objects which are ontological individuals. This illustrates that taxonomy is the process of identifying the singular real, distinct entities in nature produced by evolution, which are named as species. The category of species is not arbitrary, while taxonomic ranks above the species are arbitrary. Crucially, this implies that there logically cannot be a ontologically meaningful subspecific entity that is recognized taxonomically. If the subspecies is an ostensively defined individual, it is redundant with the species, and is itself a species; de Queiroz (2020) makes this argument. If

508   the subspecies is an intensionally defined class, then it is describing intrinsically different levels
509   and hierarchies of biological phenomena, which taxonomy is explicitly not attempting to address,
510   such as ecology, behavior, and phenotype. Obviously, species can contain geographically
511   structured genetic sublineages, populations, demes, and individuals, all of which vary from one
512   another in biologically meaningful ways. But the aim of taxonomy is to reflect an evolutionary
513   classification beginning with the fundamental unit of evolution, the species. Infraspecific
514   variation, even if biologically meaningful (e.g., local adaptations) are of a qualitatively distinct
515   nature; we cannot identify any potential subspecific entity that is (i) real, and (ii) not a species.
516   If this were not true, and taxonomy were used to delimit hierarchical, class-based
517   infraspecific variation, there would thus be no logical reason to stop at a single rank below the
518   species. There would instead be an explicit need for an infinite number of infraspecific ranks,
519   sub-subspecies, sub-sub-subspecies, etc., down to taxonomic recognition and nomenclatural
520   allocation of individual organisms within species, or even individual cells or alleles within
521   individuals, as each of these represents the potential substrate for future evolutionary variation or
522   distinctiveness. One might also argue for the taxonomic recognition of other non-species entities
523   that provide the context for evolution, such as ecological communities, colonial organisms, or
524   multi-species consortia such as biofilms. Rather, we argue that the existence of ontologically
525   meaningful subspecies is logically impossible.
526
527   **4 RECENT PROPOSALS REVIVING SUBSPECIES**
528   Most modern definitions of subspecies, particularly those that consider genetic data,
529   attempt to bridge evolutionary history with reproductive isolation (Braby et al., 2012; Hillis,
530   2020). Conceptualizing subspecies under a variety of processes that can be modeled and applied
531   to classify evolutionary history can be problematic. Spatially, subspecies can be peripatric,
532   parapatric, or, by some authors, only allopatric. They can also be incipient species, merging
533   historical lineages, or be unrelated to historical processes that generate unique lineages. As
534   various authors have pointed out for over 40 years, these definitions are almost always
535   unsatisfactory (Frost and Kluge, 1994; Rosen, 1979). As noted by ourselves and other previous
536   authors, this creates a "burden of heritage" in many modern taxonomies (Crifasi, 2007; Pyron
537   and Burbrink, 2009; Torstrom et al., 2014).
538   Several recent proposals have been written to revive the use of subspecies in systematics.
539   Hillis (2020) suggested that continuously distributed geographic races that represent formerly
540   isolated lineages be considered subspecies. He favors naming those formerly distinct
541   evolutionary lineages that are apparently being subsumed within the species as subspecies,
542   denoting both historical lineage independence and current non-independence given a lack of
543   reproductive isolation (Hillis, 2019). After lineages collapse into single species, evidence of their
544   existence will become artifacts represented only by ghost admixture (Ottenburghs, 2020).
545   However, extinct taxa are still named as species regardless of how they become extinct, even if
546   by hybridization. Therefore, there is no reason to not consider these overlapping lineages as
547   species given that they can still currently be detected as spatio-temporal individuals regardless of

548 gene flow. That they can be detected indicates they are unique evolutionary lineages; they are
549 species regardless of what happens in the future. The benefits of naming species now and
550 properly enumerating biodiversity at the correct scale of classification is much greater than the
551 uncertain drawbacks of either collapsing species or waiting for them to become "more" of a
552 species at some time in the future.
553   A primary objection to the Hillis (2020) proposal is that he treats the existence of real,
554 historical lineages as an empirical epiphenomenon ("subspecies") that is distinct from their
555 ontological divergence into separate individuals ("species"). Specifically, a subspecies as Hillis
556 proposes operates like a class to which organisms belong, rather than an individual. Indeed, he
557 states "A third solution is to use the subspecies category to refer to geographic races. Why would
558 we want to do this? Many applications, such as field guides, rely on the appearance of organisms
559 for identification" and "the subspecies category (or common names) can be used effectively to
560 differentiate geographic races within a species whenever that is practical or important."
561 Consequently, subspecies are at least permitted (if not required) to be classes defined
562 intensionally by the possession of characteristics such as geographic origin, external
563 morphology, or specific allele frequencies. Yet, these classes are nevertheless defined *within*
564 ontological individuals (species). This logical incompatibility is not necessarily fatal, but we
565 suggest it is incongruous when trying to understand the evolutionary process and use taxonomy
566 to express phylogeny.
567   Despite strong advocacy for subspecies from authors such as Hillis (2019, 2020),
568 theoretical work that explains how subspecies form and transition into species has been absent.
569 The lack of a theoretical basis for identifying how "subspeciation" and the maintenance of
570 subspecies differs from speciation is evident (but see de Queiroz 2020). This is in part a
571 consequence of the lack of a consensus view on how to define subspecies and how to delimit
572 them, as described above. By contrast, evolutionary theory on populations and species, the
573 hierarchical scales below and above subspecies, have a rich legacy and remain active areas of
574 research in speciation and macroevolution. Without a theoretical basis, the relevance of
575 subspecies in evolutionary biology is relegated to a taxonomic rank decoupled from process.
576   de Queiroz (2020, 2021) provides a distinct approach offering viewpoints grounded in the
577 theory of phylogenetic taxonomy. Importantly, he points out that there is nothing necessarily that
578 differentiates between ranks; all historical evolutionary lineages are nested within each other.
579 What he therefore argues is that separately evolving meta-population lineages (species) may
580 themselves contain population-level lineages (subspecies) that are of the same fundamental kind,
581 all "species." Therefore, a species may have multiple incompletely separated subspecies that are
582 nevertheless distinct ontological individuals, species within species. This is analogous to a family
583 containing subfamilies; both describe a fundamentally similar level of variation. In a system of
584 phylogenetic nomenclature (de Queiroz, 1997; Laurin, 2008), ranks are not needed, and we can
585 view all of these historical lineages as ontological individuals nested along the phylogeny.
586   We differ from de Queiroz in discarding the label of "subspecies" primarily due to
587 historical baggage, although we both seem to recognize the same individuals as "species." What

588   de Queiroz defines as subspecies, we simply take to be the event horizon of ontological
589   definitions of species, suggesting that this can fulfill most needs of the term. Where de Queiroz
590   would call an incompletely separated lineage a "subspecies," we would simply reiterate that
591   there exists a continuum of divergence between species. This ranges from weak to strong
592   reproductive isolation. In summary, we believe that there are few significant disagreements
593   between our view and de Queiroz's, other than that we find his continued support of the word
594   "subspecies" to be an unnecessary complication with an excessive burden of heritage.
595   We note there remains another option which Hillis (2020) and de Queiroz (2020, 2021)
596   proposals consider but do not address directly. An ontologically complete philosophy could
597   recognize all spatio-temporally discrete population units as species (Kizirian and Donnelly,
598   2008; D. Kizirian, *pers. comm.*). This status could be gained and lost instantaneously; a newly-
599   formed allopatric island population or geographic population isolate would therefore
600   immediately become a "species," but also immediately merge back into the ancestral species
601   upon re-connection (Murray and Crother, 2016). While such proposals have occasionally been
602   considered (e.g., Collins 1991), they are generally rejected as being empirically unwieldy and
603   causing taxonomic inflation beyond the level with which most researchers are comfortable. In
604   fact, Hillis (2021) criticizes de Queiroz (2020) by suggesting that the latter's proposal would
605   result in something akin to this scenario, in which ever-finer population structure is delimited as
606   species. de Queiroz (2021) denies this, but admits that his own threshold for demarcating the
607   continuum between "structure" and "subspecies" remains poorly defined.
608
609   **5 SUBSPECIES PRESENT PROBLEMS FOR CLASSIFICATION AND**
610   **COMPARATIVE METHODS**
611   Determining if evolutionarily distinct groups are unique "enough" to merit species status
612   given degree of reproductive isolation disregards historical uniqueness of lineages. In many
613   cases, upholding the primacy of reproductive isolation can distort evolutionary history by
614   applying an incorrect taxonomy to paraphyletic groups (see Fig. 2). In instances where biological
615   species group non-sister lineages because of failure to be reproductively isolated, the result is
616   paraphyly (Rosen, 1979; Frost & Kluge, 1994). Application of the subspecies rank to indicate the
617   presence of lineages with gene flow has unfortunately been used to derive paraphyletic
618   classification of the North American Ratsnakes as a valid taxonomic solution (Hillis and Wüster,
619   2021)**.** Some authors indicate the that concept of paraphyly properly only applies to inter-species
620   relationships (Nixon and Wheeler, 1990; Wiley, 1981), though as Velasco (2008) notes, the idea
621   of recognizing and naming non-sister populations, subspecies, or species as taxa is undesirable if
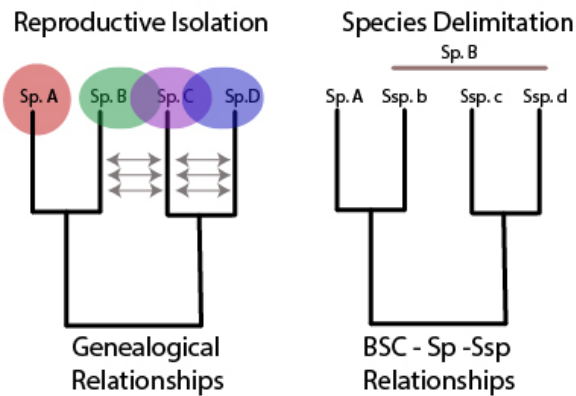622   the goal is to generate a taxonomy reflective of genealogical history.
623   Interestingly, the problem of considering paraphyletic taxa has been recognized by some
624   authors (Lee, 2003; Tobias et al., 2010) and yet interbreeding is prioritized over accurately
625   reflecting evolutionary history. However, if accurately representing evolutionary history and
626   providing names to reflect that history is a primary goal of systematists, then species concepts
627   that group and rank individuals without regard to phylogenetic/genealogical history such as the

628 BSC, Ecological Species Concept (Van Valen, 1976), Cohesion Species Concept (Templeton,
629 1989), Recognition Species Concept (Paterson, 1985), or Genetic Species Concept (Mallet,
630 1995) are problematic and poorly communicate that history.
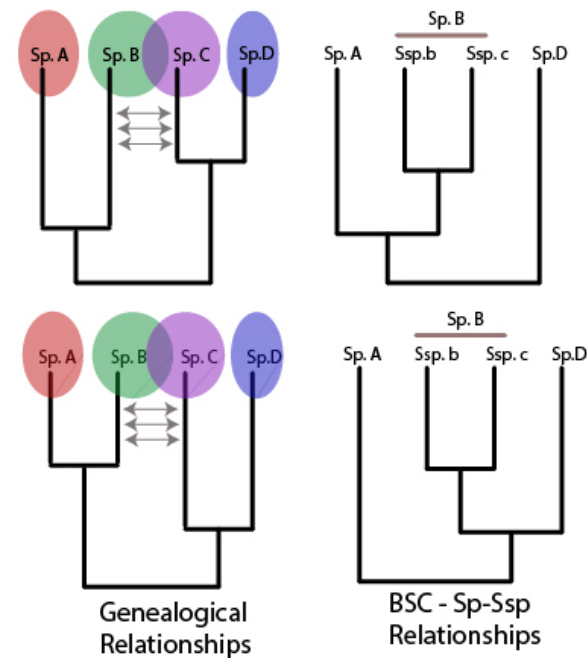631   Maintaining paraphyletic species also affects tree inference and downstream application
632 of trees for other avenues of research. Applying the rank of subspecies can prevent accurate
633 study of evolutionary history if terminal tips are composed of grouped non-sister lineages for
634 inferring phylogeny (Ruane et al., 2014). Additionally, many subspecies continue to persist in
635 taxonomies that do not represent lineages but rather as classification artifacts or handles of
636 conveniences (i.e. legacy subspecies). These legacies are not lineages and therefore placing those
637 on trees will not reflect lineage divergence.
638   This creates a difficult problem for tree inference and classification above the species
639 when terminals in a phylogeny could be a combination of species as lineages, lineage subspecies,
640 species containing non-sister subspecies, and legacy subspecies (Yaxley and Foley, 2019). Only
641 the first two categories of terminal units would be useful for inferring phylogeny, and for tree
642 construction, lineage subspecies are equivalent to species. Of course, this affects downstream
643 approaches for inferring gene flow, incomplete lineage sorting, historical demography, and
644 macroevolutionary and macroecological processes such as trait evolution, biogeographic
645 inference, diversification and community assembly (Smith et al., 2018). No tree-based inference
646 method gives expectations for how terminal taxa (or OTUs) form, and thus cannot accommodate
647 tree distortion (Velasco, 2008) potentially misleading phylogenetic comparative methods.
648

Fig. 2. Examples of how recognizing subspecies can distort representations of phylogenetic history. On the left hand side of both A and B panels, the overlap between colored circles indicates lack of reproductive isolation (RI) and is illustrated over the correct genealogical relationships with a thin gray arrow representing hybridization after speciation. A) Demonstrates a paraphyletic outcome where species are delimited using the biological species concept (BSC) and subspecies are recognized. On the right hand side, the three species (B–D) are considered subspecies of B given lack of RI and force a paraphyletic representation of lineages (species and subspecies -Sp-Subsp Relationships). The sister lineage of species A, subspecies b, is incorrectly constrained to be a lineage within species B. B) Demonstrates an outcome where species are delimited due to lack of RI and the species, B and C, are constrained to be subspecies of B. Two polyphyletic outcomes are shown where species B is constrained to include two lineages (subspecies b and c) and is either the sister taxon of A or D. However, in either topology species B will contain at least one lineage that is not sister to that species. For example, if species B were considered as sister to species A, then species C can no longer be correctly inferred as the sister lineage to species D.

662
6 PRAGMATIC ISSUES WITH SUBSPECIES IN ETHICS, POLICY, AND CONSERVATION

Based on our above discussion of the philosophical and empirical issues with the subspecies category, there are also several crucial considerations for biodiversity ethics, policy implications, and conservation management. The intersection between values, conservation, and taxonomy is complex and has received extensive attention in the past (Mace, 2004; Moritz, 1994). Based on our formalization of the philosophical and empirical nature of species and the inapplicability of subspecies, we offer a few additional comments.

Some authors have suggested that subspecies may play a useful role in conservation management through greater applicability of policy and legal protections. For instance, Phillimore and Owens (2006) concluded that *"subspecies may, in fact, be of considerable conservation utility, as proxies for the sub-structure found within species."* Yet, as subspecies cannot be defined coherently as the outcome of evolutionary processes, it is just as likely that legal protections and management practices will be misled by a focus on arbitrarily named intraspecific taxa (Zink, 2004). Correspondingly, if "subspecies" are found to represent evolutionary significant units (ESUs) in a phylogenetic context produced by historical evolutionary processes (*sensu* Crandall et al., 2000), we have argued that this is *prima facie* evidence that they are, in fact, species. Ranking them as such therefore increases their capacity for legal protection under nearly all policy frameworks worldwide.

Accordingly, if one adopts a historical, phylogenetically based species concept that recognizes species as the fundamental unit and primary product of the evolutionary process (Hull, 1976; Nathan and Cracraft, 2020), this reduces the potential for idiosyncratic mismatches between policy aims and empirical taxonomic conclusions. Generally, no one would argue for taxonomic decisions to be made for the sole purpose of achieving a policy outcome, which would undermine both the legal process and scientific method. Rather, some have suggested that recognition of "subspecies" can promote policy aims of conserving ESUs (e.g., Braby et al., 2012). There are two major problems with this.

The first is that it saddles the science of taxonomy with additional aims and considerations that are outside of its remit. The goal of taxonomy, we reiterate here, is to discover species as the fundamental unit of evolution and infer relationships among those units. If ESUs or subspecies represent evolutionarily distinct, historical phylogenetic units, then they should simply be recognized (and protected) as species. If subspecies do not represent distinct historical evolutionary units, then the rank is being utilized for pragmatic or utilitarian reasons to recognize geographic or morphological (etc.) variants solely for policy and management.

For instance, (Frankham et al., 2012) concluded: *"if species are delineated using the diagnostic phylogenetic species concept, genetic rescue of small genetically isolated populations may require crosses between species, with consequent legal and regulatory ramifications that could preclude actions to prevent extinction. Consequently, we conclude that the diagnostic phylogenetic species concept is unsuitable for use in conservation contexts, especially for*

702 *classifying allopatric populations."* This seems untenable and at best misaligned with, if not
703 outright contradictory to, the empirical aims of taxonomy as a science (Pyron and Mooers,
704 2022). The policy implications of a taxonomic decision are subordinate to scientific accuracy.
705   The second, more pragmatic issue is that formal taxonomic recognition is obviously not
706 an intrinsic requirement of legal policy, which can be modified at will, or conservation
707 management, which typically has a specific geographic or population context. As noted by Braby
708 et al. (2012), many major legislative frameworks are not dependent on trinomial nomenclature.
709 Appendix III of CITES allows for international protection of specific geographic populations of
710 species regardless of taxonomy. The Australian Environmental and Biological Conservation Act
711 (EBPCA), American Endangered Species Act (ESA), and Canadian Species At Risk Act
712 (SARA) all provide facilities for protecting geographic or genetic segments without formal
713 taxonomic recognition, at least for some groups such as vertebrates. Essentially every state in the
714 USA protects most or all wildlife *in toto,* while many have provisions that allow protection for
715 specific populations or geographic units without requiring them to have trinomials. The same is
716 true of most administrative entities throughout the world. In Canada, the Committee on the
717 Status of Endangered Wildlife in Canada (COSEWIC) "wildlife species" can be defined as
718 infraspecific geographic or genetic variation without formal taxonomic recognition, and at least
719 24 designatable units of Sockeye Salmon (*Onchorhynchus nerka*) are recognized and protected
720 within the Fraser River Drainage Basin alone (COSEWIC, 2017). Thus, no alteration of
721 empirical taxonomic practice is needed to address any fundamental issue in conservation policy
722 (Haig et al., 2006).
723   Non-historical infraspecific units could also make conservation *more* difficult if we want
724 to prioritize species delimitation, but current protections of poorly designated subspecies limit
725 sampling efforts to properly designate species. As noted by Frankham et al. (2012), taxonomic
726 conclusions have policy and regulatory implications that may subsequently affect management
727 and research dynamics. Thus, the most evolutionarily accurate taxonomy is presumably desired
728 to facilitate effective conservation and study. In contrast, the persistence or erection of inaccurate
729 subspecies or species designations can only act to obscure or hamper effective action. If
730 biodiversity has intrinsic value, then the most accurate taxonomy that reflects the real existence
731 and extent of that biodiversity is obviously most desirable for management and policy.
732   The debate over nature's value and biodiversity in particular, addressed in part by the
733 philosophical field of environmental ethics (Brennan and Lo, 2021), is far from settled. There is
734 surprisingly little agreement over basic questions such as whether biodiversity has intrinsic value
735 (as an end unto itself), or only instrumental value (as a means to an end) such as ecosystem
736 services or commercial material (see Maier, 2012; Vellend, 2014). Crucially, is the value of life
737 centered on the individual organism (Agar, 2001), or does it emerge at higher levels, such as the
738 species (Lockwood, 1987)? Put another way, do we simply consider each individual panda bear
739 valuable, or is the ontological individual *Ailuropoda melanoleuca* also valuable in its own way,
740 distinct from individual pandas? Is that value instrumental, based for instance on the role it plays
741 in Chinese forests, or intrinsic, simply because it exists? Would that value extend to infraspecific

742 units such as "subspecies?" Regardless of how one answers these open questions (Callicott,
743 1989; Norton, 1995), we suggest that subspecies frequently confound these deep moral issues in
744 conservation and environmental ethics.

745   As noted by Karl and Bowen (1999), taxonomy is often connected to a powerful mantle
746 of values in a conservation context, one which is not intrinsically supported by its existence as an
747 empirical science but arises unavoidably based on the ethics of policy and management for
748 threatened and endangered biodiversity. Agar (2001), in his defense of the intrinsic value of
749 individual living things, noted that locating value above the level of the individual (e.g., claiming
750 that species themselves are morally considerable) had the unusual implication that different
751 species concepts thus had differing ethical standings. Frankham et al. (2012) made this explicit
752 as quoted above, concluding that the PSC was "unsuitable" for "conservation contexts," and that
753 species concepts based on reproductive isolation such as the BSC or Differential Fitness Species
754 Concept (DFSC) minimize "harm" and maximize "potential benefit" for conservation aims.
755 Arguing the reverse, Russello and Amato (2014) concluded that *only* the PSC was sufficiently
756 operationalized to function effectively for conservation and management purposes.

757   The unavoidable implication is that the PSC is harmful and thus ethically inferior for use
758 in conservation, and therefore that our value systems in relation to biodiversity provide a moral
759 guide to taxonomic action. If taxonomic rank is derived from the degree of reproductive
760 isolation, and considering the complex nature of hybridization, then with regard to conservation
761 Allendorf et al., (2001) is correct in stating "*Any policy that deals with hybrids must be flexible*
762 *and must recognize that nearly every situation involving hybridization is different enough that*
763 *general rules are not likely to be effective.*" While not solving the problem of population or
764 species protection, it has to be realized that there is an unintended feedback loop when
765 recognizing rank given the variation in what is meant by reproductive isolation over space and
766 time and across the genome with regard to conservation status. On the other hand, extinction via
767 hybridization at least acknowledges species existence as unique evolutionary lineages with
768 reticulation (de Queiroz, 2005; Rhymer and Simberloff, 1996)**.**

769   Resolving these questions is clearly beyond the scope of the present review (see Pyron
770 and Mooers 2022). However, we make several basic observations based on our definition of
771 taxonomy as the discovery and classification of natural, concrete species as the fundamental unit
772 and primary outcome of the evolutionary process. If, as Lockwood (1987) and Agar (2001)
773 suggest, value is located in individual organisms, the moral implications derived from species
774 concepts is lessened or alleviated, and the inapplicability of subspecies is primarily limited to the
775 philosophical and empirical issues described above. One might question, however, the ethical
776 implication of privileging one set of arbitrarily delineated yet morally equivalent individuals as a
777 subspecies, especially if by doing so they receive differential conservation (Zink, 2004).

778   Alternatively, perhaps species have intrinsic value. This is a big "if," but one that has
779 frequently been examined in the environmental ethics literature (Sandler, 2012; Smith, 2016). If
780 this is the case, then a logical inference might be that the taxonomy most in accord with the
781 moral value of biodiversity would be one which recognizes the fundamental units of evolution as

782 species, as we argued for above. Thus, subspecies or other ranks erected based on intrinsic
783 reproductive isolation would distort interpretation of nature's value via the same implied
784 distortions of phylogenetic and evolutionary history outlined by Rosen (1979) and Velasco,
785 (2008). This is the mirror-image conclusion of Frankham et al. (2012).
786   Finally, perhaps species have only instrumental value, such as for their ecosystem
787 services or their various values to humankind. This would not affect the status of species as
788 ontological individuals produced by the evolutionary process, and thus the instrumental value
789 judgment of species would be orthogonal to the practice of taxonomy as an empirical science. If
790 subspecies are inappropriately confounded with ESUs (see discussion in Braby et al. 2012) as
791 non-historical entities erected for purposes related to conservation value (e.g., Frankham et al.
792 2012), this again burdens taxonomic ranks with non-historical secondary considerations which
793 they were not designed to address. As described above, the pragmatic aims of such approaches
794 can usually be addressed with non-taxonomic policy and management solutions. Therefore we
795 argue that in any of these cases, the taxonomic solution most congruent with the value of
796 biodiversity is one which diagnoses and delimits the naturally arising, fundamental units of that
797 biodiversity as an outcome of the evolutionary process.
798
799 **7 TAXONOMIC SOLUTIONS FOR SPECIES FAILING TO SHOW REPRODUCTIVE**
800 **ISOLATION**
801   Our discussions above are not concerned with species delimitation *per se;* whether or not
802 subspecies exist is orthogonal to how species are delimited, a question which has many
803 approaches (Carstens et al., 2013). Nevertheless, readers may rightfully ask how this
804 understanding should affect their interpretation of empirical data. Correspondingly, we wish to
805 counteract three potential misreadings of our discussion. First, the decision of whether an
806 independently evolving metapopulation lineage exists as a species may not easily be answered
807 objectively. In nearly all instances, investigators will still have to make a decision with some
808 degree of subjectivity. Here, we reiterate previous authors that such determinations must appeal
809 to empirical data that are derived from an understanding of the evolutionary history of
810 populations with explicit reference to their historical genealogical relationships (Leaché et al.,
811 2019). However, the question still carries a philosophical component. Thus, we do not simply
812 advocate treating population clusters identified within species using methods such as BPP,
813 PHRAPL, or STRUCTURE as species (see Sukumaran and Knowles, 2017); the computational
814 method cannot make the decision as to whether the entities delimited as species (by such
815 technique) correspond to actual species.
816   Second, intraspecific genetic and phenotypic variation is widespread and abundant. This
817 provides the rich texture of evolutionary biology, and population-level differentiation is one of
818 the primary avenues by which we learn about the evolutionary process. Taking our modestly
819 reductionist view of the ontological nature of species does not in any way compress or limit the
820 study of populations across the phylogeography-phylogenetics continuum (Edwards et al., 2016).
821 Rather, we argue that there is a philosophical limit of the resolution of taxonomy as a science in

822 recognizing the evolutionary individual, the species, as the fundamental unit. Note that we are
823 not (as explained above) saying that there is a *threshold* of divergence beyond which incipient
824 lineages become species; this is a continuum in nature. Rather, there is an epistemological event-
825 horizon beyond which we cannot meaningfully *detect* this divergence; diagnosable lineages
826 should be delimited as species. Groups below this level cannot be recognized taxonomically, but
827 nonetheless remain potent sources of data for ecology and evolution.
828   Thus, during species delimitation we are attempting to ascertain detectable infraspecific
829 variation which has accumulated to such a degree as to cross the detectable "species event-
830 horizon" and merit taxonomic recognition. We argue that it makes no sense to speak of
831 infraspecific groups beyond that boundary; otherwise we are asking about the taxonomic status
832 of non-taxonomic entities. We have shown above that if such entities are historical and
833 independent, they are simply species, and the boundary in that instance should be adjusted
834 accordingly. If the populations are not historical and independent (e.g., incompletely diverged
835 sub-lineages or populations diagnosed by non-phylogenetic characteristics), then pasting them on
836 as subordinate units to an evolutionary system of classification is a counterproductive attempt to
837 fuse non-equivalent processes and patterns. However, studying, describing, and understanding
838 such infraspecific genetic and phenotypic variation is still an invaluable pursuit.
839   Finally, we note that subspecies are a regulated rank in the International Code of
840 Zoological Nomenclature (ICZN, 1999). Beyond advocating for cessation of further descriptions
841 or utilization of subspecies, we are not suggesting any major or substantive alteration of Code-
842 based taxonomic practice. Just because subspecies names are regulated by the Code does not
843 mean that subspecies are real biological entities or phenomena, or that taxonomists have to use
844 them; it simply provides rules and recommendations for their formation, availability, and validity
845 as nomina in the species series. We contend that subspecies should not be used in active or new
846 taxonomies. However, the existence of subspecies in historical literature provides a rich vein of
847 taxonomic hypotheses to be tested using new genomic datasets and methods, and the Code
848 continues to provide a robust framework for their interpretation in a coherent taxonomy.
849

850 **ACKNOWLEDGEMENTS**

854

855 **AUTHOR CONTRIBUTIONS SECTION**

856 **Frank Burbrink** and **R. Alex Pyron** wrote the initial draft of the ms. All co-authors, **Chris**
857 **Murray, Brian Crother, Sara Ruane, Brian Smith**, and **Edward Myers** contributed by editing
858 and adding to each section and developing the table and figures.
859

860 **DATA ACCESSIBILITY STATEMENT**
861 There are no data associated with this review manuscript.
862

COMPETING INTERESTS STATEMENT
None declared.

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1233   **FIGURE LEGENDS**
1234   **Figure 1.** A schematic illustrating the partial cohesion, partial boundedness, and the partial
1235   participation as interactors of a subspecies within a lineage. The tokogenetic nexus depicted
1236   contains all circles (organisms) and their replicating connection between them is illustrated
1237   through lines. The blue dots depict the delimited individuals through time to be members of a
1238   subspecies with which other members of the tokogeny reproduce but are not included (dotted
1239   lines), illustrating partial participation within a real ontological individual.

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1241   **Figure 2.** Examples of how recognizing subspecies can distort representations of phylogenetic
1242   history. On the left hand side of both A and B panels, the overlap between colored circles
1243   indicates lack of reproductive isolation (RI) and is illustrated over the correct genealogical
1244   relationships with a thin gray arrow representing hybridization after speciation. A) Demonstrates
1245   a paraphyletic outcome where species are delimited using the biological species concept (BSC)
1246   and subspecies are recognized. On the right hand side, the three species (B–D) are considered
1247   subspecies of B given lack of RI and force a paraphyletic representation of lineages (species and
1248   subspecies -Sp-Subsp Relationships). The sister lineage of species A, subspecies b, is incorrectly
1249   constrained to be a lineage within species B. B) Demonstrates an outcome where species are
1250   delimited due to lack of RI and the species, B and C, are constrained to be subspecies of B. Two
1251   polyphyletic outcomes are shown where species B is constrained to include two lineages
1252   (subspecies b and c) and is either the sister taxon of A or D. However, in either topology species
1253   B will contain at least one lineage that is not sister to that species. For example, if species B were
1254   considered as sister to species A, then species C can no longer be correctly inferred as the sister
1255   lineage to species D.
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