

Reviews

The Species as a Reproductive Community Emerging From the Past

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Abstract

Biologists and philosophers of science have been unable to fully resolve the decades-long controversy as to what kind of unit of living biodiversity should receive the valued label “species”: reproductive communities (among sexual organisms), genealogical groups, or clusters of organisms that share traits. Among these choices, which represent a spectrum from process to history to observable outcome (respectively), the latter (more operationalist) concepts are not viable. *Species of sexual organisms must embody or imply cohesive and integrating processes such as interbreeding and shared ecological pressures* if they are to have sufficient power to bear the burden we give them: to predict or explain traits across the genome and among organisms. This commitment to cohesive process is needed whether biologists use species as taxonomic containers to synthesize data, as minimal phylogenetic units, or as actors in evolutionary diversification. These varied uses can be satisfied via a concept of reproductive community, but not the strict Biological Species Concept (BSC). Its two drawbacks are a focus on the contemporary and a restriction to intrinsic factors. Current reproductive compatibility may predict future matings, but it does not explain well the traits and genes that living organisms already have. The organisms alive today were shaped by isolating factors of the past, not those of the present, to whatever extent those differ. *The most broadly-useful species concept must therefore see species retrospectively, as reproductive communities of the past.* As well, the BSC’s exclusion of extrinsic factors renders each of its units incomplete in explanation and synthesis. *Reproductive communities in nature were isolated not just by intrinsic (genetic) differences, but also by purely extrinsic (e.g., geographic) factors.* Such reproductive communities were and are real, natural entities whose integrated and self-reinforcing cohesive processes constrained genealogical descent and aligned the distribution of many traits. This Retrospective Reproductive Community Concept (RRCC), formalized mathematically in multispecies coalescent models, justifies the traditional practice of taxonomists using morphological data to seek the echoes of past reproductive cohesion. However, which reproductive communities naturally deserve to be ranked as species, and which as demes or populations, is a vexing question. *There is no natural, discrete and broadly informative species rank that applies universally, or perhaps even usually. To whatever extent species rank is justified, it is as justified for asexual organisms as for sexuals.* The presence or absence of sex is just one example of the variability biologists confront. Because cohesive processes vary among clades, *a useful and broadly-applicable species concept cannot specify detailed cohesive mechanisms.* Nor can it perfectly align the named species of taxonomy with units of evolution, because the latter are not structured to match taxonomy’s partition of boxes. *Taxonomic species should approximate, but can only approximate, evolutionary units.* Settling on retrospection, letting go of a natural meaning for species rank, and accepting taxonomy as approximation allow biology to turn to the far more daunting task: listening to the natural world to understand the many interacting processes that built distinction and identity, that shaped the reproductive communities emerging out of the past into the present day.



1. Introduction

The word “species”, ubiquitous in the biodiversity sciences, continues to have an unsettled meaning. Does it refer to a living evolutionary unit, a unit of phylogenetic history, an ecological unit, or merely a collection of similar organisms? The literature debating species concepts (summarized by de Queiroz, 2007; Harrison, 1998; Mayden, 1997; Wilkins, 2018; Zachos, 2016) is so large, tangled, and seemingly endless that some have suggested the unqualified word is unsalvageable, and might best be deleted from our vocabulary (Ereshefsky, 1992). It is, however, deeply entrenched. “Species” appeared on average at least once per abstract in the journal *Evolution* this year, exceeded by only two nontrivial words (“population” and “selection”). Biologists have referred almost all of their data to named units called species. Given the frequency of its use, the word “species” is unlikely to be abandoned any time soon, but given its ambiguity, biologists need either to accept and beware of a multiplicity of meanings, or — our goal here — to resolve which meanings best serve them.

Our account centres on cohesive processes and time frames. We begin with processes (and patterns) and historical context.

1.1. Process: Species as cause or effect

Biologists’ attention to species began long ago with the simple observation that organisms are bundled by their similarities into distinct clusters. In a particular area, the many bigleaf maples will be distinct in numerous traits from the many vine maples, and from the red cedars, black bears, sockeye salmon, and monarch butterflies. Although one could conceive of a world with forms of organisms grading insensibly into one another, biodiversity is structured more discretely (Dobzhansky, 1935): organisms form clusters in multidimensional trait space. Taxonomists recognize these bundles in describing biodiversity; evolutionary biologists and others build their explanations of biodiversity around them.

If biologists had agreed to use the word *species* to mean “a trait-sharing cluster of organisms” (e.g., Mallet, 1995; Nelson & Platnick, 1981; Sokal & Crovello, 1970) then declaring something a distinct species would have been a simple matter of making a statement about similarities and differences. These “species” would have only the modest burden to reflect observation, leaving the explanation of why or how they came to exist as a job for evolutionary biology and ecology. However, even centuries ago, biology’s species concepts extended beyond traits to include ideas of mating and descent (Wilkins, 2018). As 20th century evolutionary biologists began to study what produced the clusters, they sought to embed their understanding of evolutionary process into the very concept of species, applying the word not to the patterns but to their causes, and thus defining species in terms of interbreeding and reproductive

isolation. Thus, species were conceived of as communities of organisms exchanging genes through sexual reproduction (Dobzhansky, 1935, 1950; Hennig, 1966; Mayr, 1942). To phylogeneticists seeking to reconstruct the history of genetic descent, however, it seemed an unnecessary burden to embed processes of interbreeding in their elemental historical units, and so alternative species concepts were proposed that consider only genealogical history, independent of the cohesive processes that molded that history. Species in these genealogical concepts are the smallest recognized or recognizable monophyletic (or exclusive) units (Baum, 2009; Baum & Shaw, 1995; Mishler & Donoghue, 1982; Rosen, 1978). In many cases these three alternative concepts of species — a cluster of organisms delimited by traits, a reproductive community, and a genealogical unit — might coincide in delimiting the same set of organisms, but not always. When different sets of organisms are delimited as “species” depending on the species concept used by the researcher, then the meaning or truth of our claims about species, and their practical implications, vary accordingly.

The disciplinary interest (evolutionary process, phylogeny, taxonomy, ecology, physiology) of a biologist does not directly predict their preferred concept of species, as biologists also vary in their preference for operationalism — whether recognized units should minimize commitment to theories of cause and instead more directly reflect observable outcomes. The triad of reproductive community, genealogical lineage, and trait-sharing cluster not only forms a causal sequence (Fig. 1), but also a sequence from hypothesis to predicted observations, from theoretical commitment to operationalism: a hypothesis of *reproductive community* predicts a *genealogical lineage*, which predicts a *cluster of organisms with distinctive traits*. Some biologists have chosen to conceive species operationally, as trait-sharing clusters, whether their interests are in speciation (Mallet, 1995), phylogeny (Nelson & Platnick, 1981; Nixon & Wheeler, 1990) or predictive classifications (Sneath & Sokal, 1973). Because these authors define their species concepts in terms of observable trait differences, which would represent evidence (not concept) in others’ frameworks, some have suggested that operationalist authors are confusing evidence and concept (de Queiroz, 1998, 2007; Hey, 2006; Mayden, 1999). While some biologists may have been so confused, at least some of these authors put forth their concepts with conscious operationalist intent. The question is not whether operationalist species concepts are species concepts, but rather how suitable they are.

We will argue that the more operationalist species concepts are not viable. For species to carry the burden of explanation and organization that biologists give them, they must go beyond patterns of traits and even beyond histories of genes to include a sense of cohesive processes (e.g., sex and ecology; Boyd, 1999; Dobzhansky, 1935; Dupré, 2008, 2022; Mayr, 1942; Templeton, 1989; R. A. Wilson, 1999) — whether the species so delimited are used by speciation biologists, phylogeneticists, or biologists more broadly. That

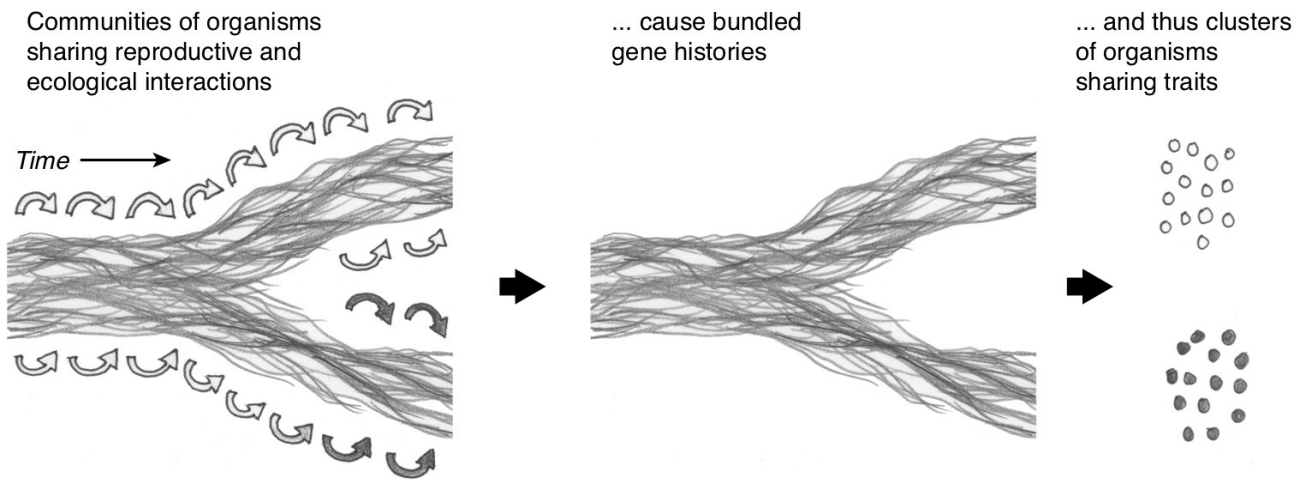


Figure 1. Reproductive communities held together by cohesive processes cause genealogical history to be bundled, and thus clusters of organisms to be similar in traits. However, process, genealogy, and traits are not so easy to separate. At each generation, traits affect the community's cohesion. Gene histories and trait clusters are both products of the acting community and components of the actor itself, feeding back generation by generation (curled arrows in first panel)

is, if it is to be broadly useful, a species must be (in some sense) a reproductive community bound by cohesive forces.¹

1.2. Time: Species in the past, present, and future

An answer to the question “What is a species?” could enlighten biologists and philosophers and yet still not settle the species concept debate. The Evolutionary Species Concept (*sensu lato*, de Queiroz, 1998, 2007; Mayden, 1997; Simpson, 1951, 1961; Wiley, 1978), for example, has become widely accepted. De Queiroz's (2007) phrasing that species are “separately evolving metapopulation lineages” aptly incorporates many perspectives in evolutionary biology, its four words alluding to isolation, process, integration, and history. Many biologists do indeed consider species to be such independently evolving lineages, and so this concept arguably succeeds as a general portrait of species as they exist through time. It does not, however, resolve the puzzle that has long troubled biologists. Most biologists addressing species empirically are concerned with a different version of the question “what is a species?”, namely “how should we conceive of species as they exist at this moment?” These biologists seek guidance in choosing among the discordant species delimitations provided by interbreeding, genealogy, and traits. The reassurance that these delimitations eventually coincide over evolutionary time doesn't help the biologist on the ground (or at sea) attempting to understand species limits today. We argue that varying delimitations are not just the mistakes of different methods seeking the same answer; they represent different concepts of living species and their boundaries.

To resolve how biologists should best see and describe a species lineage as it passes through the present moment, in the evolutionary flash-bulb of contemporary research, time frames must be considered carefully (e.g., Baum, 1998; Gannett, 2003; Millstein, 2009), with more precision than in the temporally-ambiguous concept of “a separately evolving metapopulation lineage”. Should we interpret this as meaning that the lineage has recently been evolving independently, that it is evolving independently at this moment, or that it will continue to evolve independently in the future? Each of these claims has different import in our causal theories. If a species had an essence, a kernel of identity that endured unaffected, then clarity about time and verb tenses would be unimportant: it was, it is, it will be. It is too easy to slip into thinking that a species does have such a kernel, to look at a line in a phylogenetic diagram and imagine its persistent essence of identity. But there is no essence, just genes and bodies tumbling through time. They have no commitments to one another, no agreed alliances, just qualities that affect the likelihood of interactions moment by moment. These qualities derive from events at varying points in the past, while the fates of descendants in future generations depend on multiple processes unfolding at different rates. Confronted with multidimensionality, biologists seeking to explain, understand, or predict need to choose a species concept whose time frame is suitable for their purposes. What statements a biologist can correctly make about a living species, and what methods should be used to infer its boundaries, depend on how this ambiguity in time frames is resolved.

The task we set ourselves is to understand what set of contemporary organisms a biologist should point to and

¹ Among sexual organisms. We discuss asexuals in section §7.

say, “This is a species”. That is the unit neontological taxonomists seek to delimit; the unit under whose name biologists file their observations of physiology, ecology, and behaviour; the unit used as the building block of inferred phylogenetic trees and explanations of trait evolution; the unit seen in evolutionary theory as a living actor; and the unit valued in conservation biology as the holder of unique genetic resources. It is that unit whose identity and edges we seek to clarify.²

We propose two alternative concepts of extant species as reproductive communities. They are discordant with each other because they frame time differently: one retrospective and short term, the other instantaneous and prospective over the long term. The first sees species as cohesion-molded lineages of the past (RRCC, the Retrospective Reproductive Community Concept), the second as communities reproductively isolated at this moment and possibly projected to retain integrity into the future (BSC+, an extension of the Biological Species Concept of the Modern Synthesis).³

It is the former, retrospective concept that should, we argue, guide the delimitation of species used generally throughout biology. The rationale is simple: The traits and genes of living organisms are best explained and understood by the processes that shaped them. Those processes lie in the past. By taking a retrospective view, the RRCC largely achieves unification among species concepts based on interbreeding, genealogy, and traits, because reproductive communities of the past align with genealogy and current traits as closely as cause aligns with effect. The contemporaneous or prospective BSC and BSC+ remain, however, outside of this club of concordance. There is no generalized concept that can successfully unite all of the disparate species concepts except by sacrificing clarity and utility, because the concepts’ different time frames give them different roles in explanation and data synthesis, and (important for the taxonomist) discordant delimitations at any given moment. Biology’s two goals for species — to serve broadly in explanation and synthesis, and to embody current evolutionary processes — are incompatible. The distinct units that satisfy each, however, can be brought into a common framework.

1.3. Our argument

We begin by arguing that most of biology, including taxonomy and phylogenetics, needs species that acted as real objects, molded by both intrinsic and extrinsic cohesive processes (sections §§2 and 3). Conceiving species by the instantaneous forces integrating them at this moment (§3)

has value in some contexts, but for broad use in explanation and data synthesis, species should be viewed retrospectively, as reproductive communities (among sexual organisms) of the recent past (§4). In this retrospective view, the species rank is poorly defined or arbitrary in many or most lineages (§5), not clearly distinct from demes, populations, or other reproductive communities or clades. If a natural species rank is suggested in some taxa by special patterns of evolutionary change, it may be equally applicable to asexual lineages (§7). Even without a natural species rank, retrospective units are compatible with the needs of speciation biology, phylogenetic diversification studies, and conservation biology (§6). The best units for broad use as species are therefore those bound by cohesive processes and viewed retrospectively. Mysteries will remain: species are much richer than our prescription of process and retrospection. Their full nature varies, species by species, as a result of the diverse cohesive processes that shape them (§§7, 9).

Threaded throughout is a dialog between the taxonomic species of classification and the theoretical species of evolutionary biology (taxic vs. functional species of Baum, 2009; T vs. E species of Zachos, 2016; species taxa vs. species individuals of Dupré, 2022). For each, we will seek its best version: how should taxonomic species be conceived, and how should evolutionary species be conceived? We attempt to hold them concordant as long as we can, not for sentimentality, but because the taxonomic species derives its value from the evolutionary (sections §§2, 3.1, 4, 8.1), and both can (if well-conceived) serve to explain and predict trait distributions. In the end, an approximate match is the best that can be achieved (§8).

Biologists of many stripes have contributed to understanding species and species concepts — speciation biologists, taxonomists, population geneticists, phylogenetic biologists, systematists, and conservation biologists (see Acknowledgements). Our goal is not to analyze each discipline’s contributions, but rather to understand what concepts of species best serve them. As we have considered this problem, we have been surprised to realize how much the disciplines share, all needing a process-based and retrospective view of biology’s basic units of biodiversity.

2. Species must be bound by cohesive processes

Any general-purpose species concept must be based on more than genealogy or traits; it must be based on the forces that shape genealogy and traits (e.g., interbreeding

² The question “What is a species?” is asked with varied intentions. It can be asked with or without time frame specified, as discussed above. The asker might intend to centre it on ideas (what abstract concept might biologists want as a referent for this word?), or on the natural world (these things that biologists find in the world, what are they?). (See §9 about the tension between idea-centric and nature-centric approaches.) The asker might understand species as reproductive communities, but seek to know which of the latter can be called species as opposed to populations (rank; see §5).

³ The RRCC could be seen either as a process-laden extension of the Phylogenetic Species Concept, or a retrospective modification of the Biological or Evolutionary Species Concepts. It does not include a sense of species rank, and so arguably, it is not a species concept at all. It is implicitly the concept of units in multispecies coalescent studies.

potential; multi-trait ecological selection). This is already accepted implicitly by most speciation and population biologists, but it has not been so widely accepted, at least explicitly, among those working in taxonomy or phylogenetic systematics. Nonetheless, their basic units likewise need to be bound by such cohesive processes in order to hold the implications that taxonomists and phylogeneticists hope them to have.

2.1. Taxonomic species as data synthesizers

Even as biologists and philosophers debated the subtleties of abstract species concepts, taxonomists continued their prosaic task of “organizing” biodiversity, building a classification of taxa that serves as a shared resource for all of biology. In the process, they have discovered, distinguished, and named well over 1 million species (Chapman, 2009; Mora et al., 2011). These named species are fundamental to our descriptions and theories of the biological world. While these taxonomically recognized species could be viewed as mere temporary sketches outside the discussion of species concepts, we suggest that their pragmatic value is synthetic, central to biology, and the very reason biologists place so much importance on the word “species”.

Named species serve as anchors to which biologists attach data about different characteristics gleaned from different specimens, permitting a synthetic view of the species’ form, function, and place in phylogeny. Under the name “*Drosophila melanogaster*”, biology has placed data of many kinds — behaviour, gene sequences, chromosomes, ecology, development. For the most part, these trait observations were made on different specimens. As biologists, our interpretation that those traits occur together in any given specimen of the species depends on our confidence in placing the specimens into the same species. This shared placement allows us to infer, therefore, that the specimen whose courtship was observed likely also has a particular chromosome count, a particular developmental mechanism of neuronal connections, and came from a larva that consumed a particular kind of food. Our taxonomic concept of “*Drosophila melanogaster*”, i.e., how it is distinguished, determines what specimens are placed within it, and thus what observations come together in this synthesis. The synthesis that taxonomy enables is fundamentally predictive: by placing a specimen in *D. melanogaster*, biologists predict it will have many or most of the traits observed previously in other specimens.

Biologists’ use of named species in data synthesis highlights the fundamental role that taxonomy plays for all of biology (and beyond) as it discovers and distinguishes species. *Almost all of biology stands or falls depending on the extent to which specimens are well placed together into species and more inclusive taxa*, i.e., whether each named taxon synthesizes correctly the sharing of traits, and the

position in phylogeny. Although this pragmatic perspective also matches the fundamental goals of phenetics (Sneath & Sokal, 1973), its success depends on evolutionary process.

2.2. Taxonomy’s need for cohesive process

For named (taxonomic) species to serve as containers for data synthesis, the species concept they embody must make some commitment to processes of cohesion, giving the species’ members a mechanism for sharing properties (Boyd, 1999).

Reproductive communities serve well in data synthesis to the extent that their members are genealogically connected through interbreeding and share a common selective regime. Their self-reinforcing cohesion (section §3.1) strengthens and maintains the boundaries within which many other traits can evolve, adding to the distinctiveness of the lineage. Identifying an organism as a member, even if by a few diagnostic traits, allows us some confidence in predicting many other unobserved traits and qualities.

Trait-sharing clusters, however, do not suffice for data synthesis, whether delimited under a morphological (e.g., Sokal & Crovello, 1970) or a genotypic (e.g., Mallet, 1995) species concept. A cluster, as a simple empirical observation from a set of observed traits (phenotypic or genotypic), cannot predict that its members are similar in any other traits or loci without a biological model to constrain the outliers in unstudied dimensions. A single monarch butterfly specimen could conceivably have recently obtained genes for photosynthesis or ciliary photoreceptors through introgression from plants or mammals, but we assume such events are unlikely when we use the taxonomic species to build a picture of the shared traits of monarchs.⁴ Without some measured or assumed process (that, for instance, limits interbreeding or lateral transfer), no limits can be placed on the distributions of traits other than the diagnostic ones, and a trait-sharing cluster cannot synthesize data among specimens. The processes assumed need not be enumerated, well understood, or as strong as panmictic sexual interbreeding, but *some* cohesive process must be implied. A unit that does not embody process or mechanism (i.e., an operationalist’s unit) has no power to direct inference, crumpling against the weakest challenge (Maddison & Maddison 1992, p. 70).

Inferred genealogical groups can serve effectively in data synthesis, as long as their implied claim of monophyly or exclusivity encompasses most or all of the genome, which requires that they invoke cohesive processes. The value of a genealogical unit is straightforward: genealogy predicts similarities and differences in genes, genetic variants are traits themselves and control phenotypic traits, and thus genealogy should almost always be the best predictor of current trait distributions among organisms. However, biologists deal with *inferred* genealogies, based on a subset of

⁴ Obviously, this is an extreme example, but it shows that if unstudied traits are entirely unconstrained by a biological model, then there is no point in building a taxonomic classification at any level, from species to families to domains, except to summarize the few traits already observed and used in diagnoses.

genes or a subsample of organisms. In strictly asexual lineages, groupings that reflect the history of a few studied loci are necessarily predictive for all traits, but in sexual organisms, different loci can have different histories (Avice et al., 1983; Tajima, 1983). To have the power to predict the distributions of unstudied traits, an inferred genealogical species must claim monophyly, or some milder genetic coherence, *across the genome and among all organisms claimed to compose it.*⁵ Without a complete census of genes and specimens, a genome-wide claim requires a theory of cohesion among genes.

Not only do taxonomic species require cohesive processes, the more informed taxonomists are about those processes, the better their species can serve in synthesis. Species as trait-sharing clusters could be recognized without any commitment to their causes, just as higher taxa were recognized by pattern cladists without a commitment to evolution (Nelson & Platnick, 1981). This is the operationalist approach. However, phylogeneticists abandoned such a process-neutral framework not because they were seduced by the unknowable, but because better data and better models of process allowed them to achieve results (about history) more powerful and informative than unexplained patterns. The root of the problem with operationalist species is that there are many ways to build clusters (UPGMA? PCA? NJ? DBSCAN?). Do biologists choose one method arbitrarily and stick with it forever? Cluster methods vary in their ability to reflect the patterns predicted by different processes. As biologists' understanding of population genetic processes advances, unchanging cluster methods would fail to track that understanding. Their clusters would become less and less relevant to evolutionary biologists, and more and more evidently inadequate for synthesis. But, if the clustering methods change in order to adapt to new understandings of process, then the paradigm implicitly has a process-based species concept hiding behind the curtain, directing, justifying, and thereby accompanying species delimitation.⁶

The fact that a taxonomist can use a clustering method without intentionally inferring details of a process model for their particular species does not change the importance of their delimitation descending from the best available concepts of cohesive processes.⁷ That descent is needed to confer a biological meaning on the species delimited — and thus affirm that they are relevant to evolutionary model-

ling, that they are informative about more than just the traits already measured. A species concept that claims to avoid process assumptions by referring only to outcomes (traits, genealogies), but which is justified via a cohesive process, is a theory in operationalist's clothing. For clarity and honesty, it would be better to admit to process explicitly in the species concept itself.

Although our stance may seem to promote theory against pragmatism, it is in fact fully pragmatic (in the sense of “prioritizing utility” rather than “without meaning”). Every day, biologists (and humans in general) use taxonomic species for data synthesis. The success of this deeply useful effort depends on species having meaning beyond the traits of the taxonomic diagnosis. An inferred species, to be useful, must make biological claims explicitly or implicitly; it must be more than simply the output of a cluster method.⁸ The biological claims are often weak and full of errors, because biodiversity is messy and our knowledge is limited (e.g., sections §§4.9, 8.2). Nonetheless, the taxonomic species must at least approximate a unit with evolutionary integrity. Whether cohesive processes are invoked explicitly in the concept, in its justification, or its inference, they must be assumed. There is no refuge in operationalism or in unexamined pragmatism.

2.3. Phylogenetics assumes cohesive processes

Cohesive processes need to be invoked in the concept or inference of a species for it to serve as an effective container for data synthesis, but are they required for a species to serve as the fundamental unit of phylogenetic analyses? Yes, and for similar reasons. Phylogenetics needs its basic units to go beyond bare genealogical history and to include mechanisms of cohesion. We have no choice but to accept process theories if our units are to have power.

Phylogenetic analysis of sexual species needs to assume that inter-locus and inter-organism cohesive processes are present, binding the trees of different genes to be predictably correlated. Without such processes, a genealogy of an unobserved locus could deviate completely from the observed gene trees, and the phylogeny would not guide our understanding of species, their descent, or their trait evolution, except for the few loci and organisms already studied. Access to full genomic data does not salvage a process-free approach because we could not place phylogenetically

5 Species concepts are challenged when different regions of the genome show discordant similarities (e.g. Fontaine et al., 2015; Martin et al., 2013), e.g., loci controlling mating traits group populations A and B, but the rest of the genome groups A and C. Both taxonomic data synthesis (above) and retrospective explanation (§4) would be best served by the grouping that reflects more of the genome.

6 By “understanding” we mean well-established in the paradigm, not cutting-edge and contentious. The clusters would best avoid presupposing processes currently being tested.

7 We are not saying that species taxonomy requires elaborate theories of process. Rather, we are saying that, just as phylogeneticists decided, at least a slight commitment to process is needed for power, and the better understood the process, the more taxonomy's units will be accurate and informative.

8 Operationalism can be useful if partial (concepts minimize theoretical commitment, but still maintain some), to guard against unwarranted inference, but in absolute form (concepts entirely barren of theoretical commitment), its units are pointless. Operationalization, though, is always required. A species concept's units must be testable through observations.

all of the knowledge gained from other specimens, not fully sequenced, without assuming population cohesive mechanisms.

The full power of phylogenomics depends on inter-locus cohesive processes. Without them, the shattering of the genome's history into many separate gene trees by recombination would require biologists to infer thousands of gene trees, each likely to be poorly resolved, and each unable to inform character mapping or each other. By accepting (and assuming) that the different loci are to varying degrees linked together, and descended in reproductive communities bounded by isolation, adjacent loci can inform each other about their gene trees, and the pooled power of many loci can contribute to a species tree. This pooling of loci — whether by concatenation (Gatesy & Springer, 2014; Leigh et al., 2008) or by multispecies coalescence (Degnan & Rosenberg, 2009; Heled & Drummond, 2010; Liu et al., 2009) — implicitly invokes reproductive communities and their cohesive forces. Even if one's goal is not a resolved species tree, but only the inference of the distribution of gene trees (Hahn & Nakhleh, 2016), a model of inter-locus cohesion contributes important power to the result.

3. Species as reproductive communities

We have arrived to the **first of the major conclusions** of this paper: *For sexual organisms, both data-synthesizers and phylogenetic biologists need to conceive of their fundamental units as reproductive communities bound by cohesive processes.* Modern Synthesis authors (e.g., Dobzhansky, 1935; Mayr, 1942) were thus fundamentally correct in choosing the reproductive community as biology's basic taxonomic unit. To be most broadly useful, a species concept should be based on population and speciation biology's best knowledge about the processes of cohesion and isolation. A reader might thereby guess that we are leading taxonomy and phylogenetics to the Biological Species Concept (BSC, Mayr, 1942). We are not. A different concept better channels speciation biology's knowledge, a concept that celebrates the BSC's focus on cohesive processes, but that looks backward in time like the Phylogenetic Species Concept (Baum & Shaw, 1995; Mishler & Donoghue, 1982).

The question that we are asking is how biologists should see living organisms, at this moment in time, as divided into reproductive communities called "species".⁹ We will

explore three alternative species concepts, beginning with the classic Biological Species Concept:

The Biological Species Concept (BSC) — An extant species is a set of living organisms currently sharing interbreeding compatibility (i.e., if purely extrinsic barriers were removed, they could successfully interbreed) but lacking compatibility with others.

While compatibility may be a central factor shaping reproductive communities, we see such a compatible set as neither an evolutionary actor (arguably not deserving the label "community") nor sufficiently broadly explanatory in studies of extant biodiversity, because it excludes extrinsic factors from species identity and delimitation.¹⁰ The best possible version of the BSC incorporates extrinsic factors:

The Biological Species Concept Plus (BSC+) — An extant species is a set of living organisms whose intrinsic reproductive compatibilities and extrinsic context (e.g., geography) together allow them to interbreed while isolating them from other such groups. Their isolation is complete and enduring, i.e., their descendants are expected to maintain integrity as a lineage. This concept differs from the BSC primarily in acknowledging the role of extrinsic factors in isolation.

The units of the BSC+ are in fact evolutionary actors, but their definition relies on contemporaneous (i.e., at this moment) properties and thus limits their utility. We therefore advocate the following for most purposes in biology and as the basis for named taxonomic species (§4):

The Retrospective Reproductive Community Concept (RRCC) — An extant species is a reproductive community of the recent past, extending to the present, within which there was sufficient interbreeding (or other cohesive processes) to maintain coherence in genealogy and traits (and outside of which these forces were insufficient for broader coherence). This concept focuses on history, but it goes beyond simple genetic history to incorporate cohesive processes. Its units are evolutionary actors and serve in explanations of the organisms alive today.

3.1. Reproductive communities are real

Before considering these alternative framings of species-as-reproductive-communities, we first step back to briefly outline the cohesive processes that shape such communi-

⁹ Thus, we are not concerning ourselves with how a lineage through time might be segmented sequentially into diachronic species. We see a species as diachronic, but our focal question (§1.2) concerns its presentation in the current moment, and how neontological taxonomists, speciation biologists, and others might see its boundaries.

¹⁰ We will use the word "intrinsic" for isolation arising from genetic differences, "extrinsic" for purely external factors that act even if there are no genetic differences among the isolated populations, such as simple geographic distance (allopatry). This usage varies from others (e.g., Coyne & Orr, 2004), in which "extrinsic" is broader, including anything dependent on environment, even if it also depends on genetic differences. Our usage highlights the purely extrinsic factors.

ties in sexual organisms.¹¹ These processes affect, and are affected by, reproductive interactions, ecology, and other aspects of the organisms and their environments. By weaving together the community's members genetically and phenotypically, cohesive mechanisms give the community integrity and distinction in form, space, and through time, making a unit that serves well both as an actor in evolutionary models and as a container for taxonomic data synthesis.

The breadth of processes that shape the boundaries of reproductive communities is reflected in the expansive literature of speciation biology including case studies, conceptual frameworks, theories, and methods (e.g., Barraclough, 2019; Coyne & Orr, 2004; Wilkins, 2007). Pre-zygotic barriers include such forces as geographical isolation (allopatry), spatial or temporal niche separation (e.g., phenological shifts), physiological or behavioural isolation (e.g., song or habitat preference, isolation due to pollinators), mechanical isolation, divergence in gamete recognition systems, and others. Post-zygotic barriers include all factors that reduce survival or reproduction of hybrids, whether acting on first or later generations of hybrids, and whether strictly genetic or influenced by the environment. These barriers can be simple or complex, spread quickly or slowly, with or without the action of selection, sometimes promoted by ecological interactions (Stankowski & Ravinet, 2021). Barriers may accumulate more or less as a function of overall divergence (Roux et al., 2016) or may be compounded when the establishment of new barriers is facilitated by the presence of previous barriers (e.g., “snowballing” of post-zygotic barriers, Moyle & Nakazato, 2010; Orr, 1995). The broad agenda of speciation research is to uncover common themes in the who-what-when-where-and-how of the origin and spread of isolating barriers (Coyne & Orr, 2004).

A reproductive community's story is about more than its interbreeding boundaries. Its many traits, ecological and otherwise, also build its identity and integrity (Barraclough, 2019; Cadena & Zapata, 2021; Lande, 1980; Mishler & Donoghue, 1982; Templeton, 1989; Wu, 2001; see Fig. 2d). Ecological and developmental interactions can contribute to reproductive isolation through reinforcement (Butlin, 1989), but they can also contribute directly to other aspects of cohesion, distinction, and identity (Barraclough, 2019). Organisms, through habitat preferences or differential survival, place themselves in a landscape that imposes a selective regime, which then can lead to a feedback loop of deepening adaptive commitment (e.g., Kay et al., 2011; Lowry,

2012; Seehausen & Wagner, 2014). A small ecological difference in sister lineages can thus become a difference in adaptive zones (Simpson, 1944; Webb et al., 2002; Wiens, 2004), leading to crisp distinctions between the lineages in many traits, especially if environmental differences are multidimensional (e.g., prairie vs woodland). Multi-trait distinctions can also arise from epistasis and developmental integration, linking the fates of different traits. Together these various forces can differentiate diverging lineages across their genomes (Wu, 2001).

Isolating barriers, adaptive zones and other interacting and self-reinforcing factors (Barker, 2019; Boyd, 1999) give a reproductive community active integrity and a unique identity, making it a natural and real object (Baum, 1998; Ghiselin, 1974; Hull, 1987; Mishler & Brandon, 1987; Wilkins, 2007). It may not have the sharply defined multidimensional boundaries and stable persistence of a chair, an organism, or a river, but it is at least as real as a cloud, a city, or a school of fish. Its identity is formed by its ecological, developmental, and reproductive distinctiveness. When a reproductive community is distinguished by more traits, and those distinctions are maintained actively by evolutionary processes, that community is more real as an object (Baum, 1998) and more usefully recognized in our theories. Hull (1987) called a species a “genealogical actor in an ecological role”, but portraying a species' identity as solely genealogical is too narrow. Cohesive forces are not just the script it reads, and ecology is not just a role it plays. These are as much a part of its identity as its genealogical structure (§§2, 4.4, 5.1).¹²

3.2. Intrinsic reproductive compatibility (BSC)

The exclusion of purely extrinsic factors from the classic formulations of the Biological Species Concept (Dobzhansky, 1935; Mayr, 1940, 1942) prevents its units from serving as comprehensive explainers in our theories, and from serving as actors in evolution.¹³ Dobzhansky's (1935) definition explicitly focuses on isolating properties of the organisms themselves:

A species is a group of individuals fully fertile inter se, but barred from interbreeding with other similar groups by its physiological properties (producing either incompatibility of parents, or sterility of the hybrids, or both).

11 Mishler and Brandon (1987) usefully distinguish between cohesion (parts behave alike) and integration (parts interact actively). Under “cohesive processes” we include those that build and maintain both cohesion and integration. As the distinction is not vital to most aspects of our argument, we subsume both under “cohesive processes” in order to minimize words.

12 Our enthusiasm for the reality of reproductive communities and our references to monophyly (§4.1) and to simple clean units like those in many multispecies coalescent models (§4.2) might leave the impression that our argument relies on an orderly world without discordance, fuzziness, or intermediate conditions. It does not. We do believe in the reality of reproductive communities, but we know that they are rife with discordance, and not clean or simple objects with simple trajectories. Our discussion uses simple cases to reduce the words needed, but our conclusions hold even as disorder rises (as we discuss, e.g., §§4.6, 4.9, 5.2, 8.2).

13 There are many variants of the BSC; we address its original formulations to highlight the consequences of their focus on intrinsic factors and current properties.

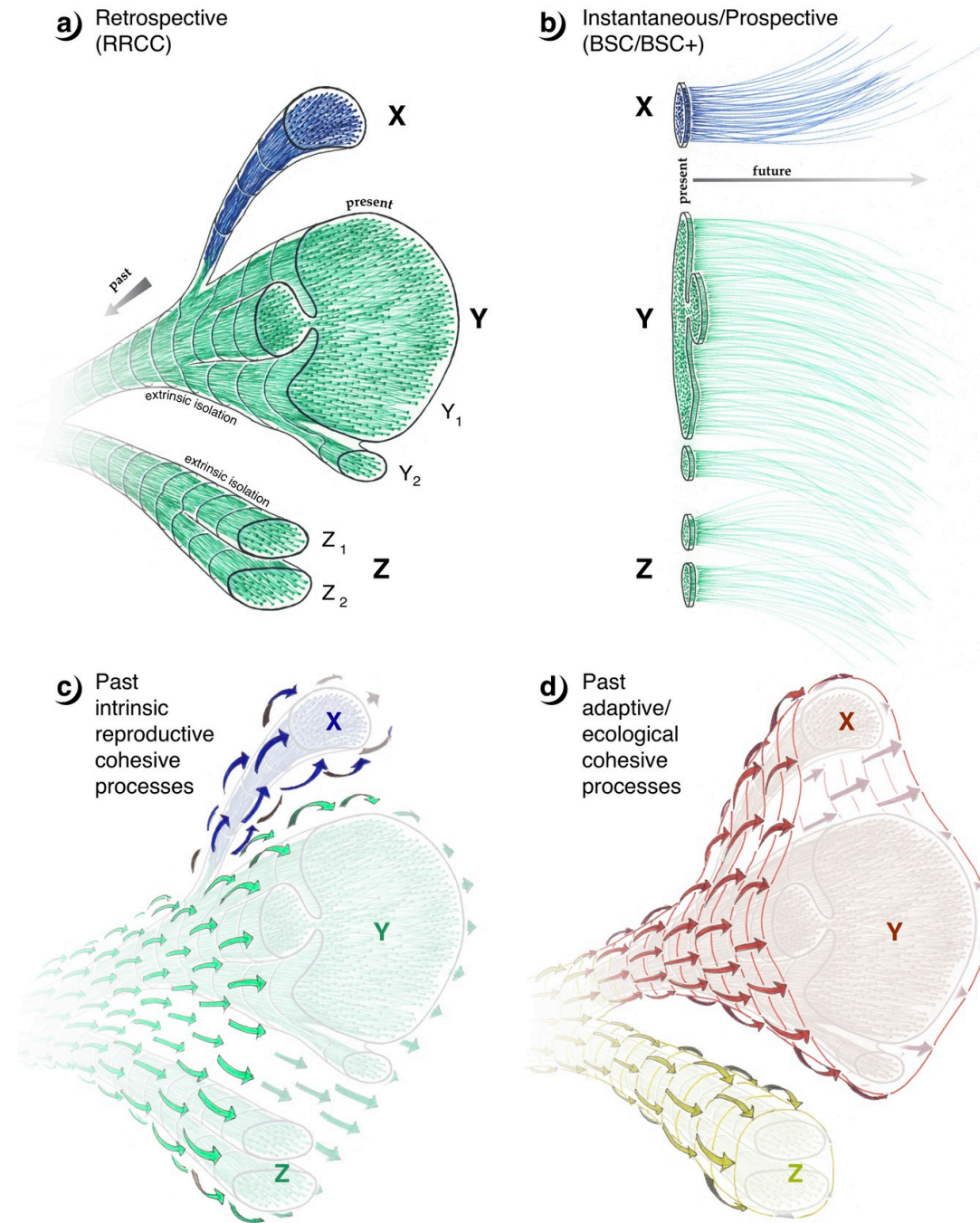


Figure 2. Species as reproductive communities emerging from the past (a, c, d) or as communities at this instant, and possibly projecting into the future (b). Reproductively incompatible genotypes shown by dark blue versus teal green colours. **(b) The instantaneous/prospective Biological Species Concept (BSC) and derivative BSC+** delimit units by the instantaneous state of cohesive forces at this moment in time. They seek units whose current reproductive isolation is complete, foretelling integrity into the indefinite future. The wispy lines projecting into the future suggest Y+Z are expected to reunite or maintain integration, and thus would be considered a single BSC+ species. **(a, c, d) The Retrospective Reproductive Community Concept (RRCC)** seeks retrospective units reflecting past cohesive processes that explain living organisms and their traits. Although gene flow among branches is not shown, it may be present to some degree among parts of Y and Z. Purely extrinsic barriers (e.g., geographic distance) shown by black wire frame in (a); annuli mark spans of many generations. Intrinsic reproductive cohesion shown by arrows in (c); incompatibilities by differences in colour. Ecological and other adaptive cohesive processes (e.g., an adaptive zone) shown by arrows and annuli in (d), involving the organisms' commitment to a habitat and that habitat's selection on them. Two distinct ecologies are represented by darker red-brown and paler olive green in (d). In this example, X, Y, Z, Y₁, Y₂, Z₁, Z₂, and X+Y could all be considered reproductive communities of the recent past.

The longer form of Mayr's definition states:

A species consists of a group of populations which [...] intergrade or hybridize wherever they are in contact or which are potentially capable of doing so (with one or more of the populations) in those cases where contact is prevented by geographical or ecological barriers.

To be different species by these criteria, populations must differ in traits that limit interbreeding. They are the same species if they could interbreed should any extrinsic barriers be removed. Later authors have taken a similar approach in treating populations as conspecific if their isolation comes only from extrinsic factors rather than genetic differences (e.g., Templeton, 1989, p. 12, "intrinsic cohesion mechanisms").

It might seem natural that species definitions would rely only on the properties and behaviours of the organisms, and not on factors entirely outside of the organisms, say, geographic distance. Surely a species' identity and its distinctions from others must arise from and depend on differences in its organisms and their qualities? As tempting as this stance may be, it renders species incomplete as actors and explainers. As it evolves, a species' edges are in fact determined by both intrinsic properties and extrinsic context, the latter at times acting alone, even when relatives share the same intrinsic properties. Even objects that we believe to have a deeply internal and persistent identity, such as ourselves, have boundaries sometimes shaped by external forces. Hairs that fall from our heads on their own accord, by the body's intrinsic actions, leave the body and move outside of its boundary. Hairs that are clipped by scissors, the action of an extrinsic force, are just as surely separated from ourselves.¹⁴ Extrinsic factors participate in forming the boundaries of natural entities. A reproductive community (the individual of Ghiselin, 1974), is both constitution and circumstance, bounded by its own self-generated traits (e.g., reproductive compatibility) and by the contexts in which it finds itself (e.g., geographic barriers).

In other words, intrinsic compatibility on its own is not enough to unite populations into an evolutionary unit. The sharing of reproductive compatibility makes a group of populations an abstract set (insofar as they share a trait, special though it may be), but it does not alone make them an evolutionary actor that behaves with integrity as a unit. Selection on one population, for instance, will not lead to any effects on the others if they are disconnected because of large geographical distances or habitat barriers. They are not integrated in the sense of Mishler and Brandon (1987). If together they were monophyletic, they could at least claim the status of a historical unit, but if paraphyletic and lacking active integrity, and with no reasonable prospect for integration in the future, they are not acting as a unit, and cannot be considered such, even if they have intrinsic re-

productive compatibility. Excluding extrinsic factors from a species concept and pinning identity and boundary to only one set of intrinsic factors, regardless of whether those factors are ever put into action, treads perilously close to the very essentialism that Mayr fought.

We therefore suggest that the intrinsic-factors-only BSC is inappropriate for delimiting units for use broadly throughout biology (§§2.2, 2.3), despite the central role that intrinsic reproductive isolation plays in speciation (§6.1). To resolve an evolutionary unit that respects what actually happens in the natural world and thereby achieves comprehensive prediction and explanation of genealogy and traits, biologists' recognition of species must be based on all factors, intrinsic and extrinsic, that determine its behaviour (Wiley, 2002). Basing species on all isolating and cohesive factors has the important side benefit of making them more easily determined; there is no need to undertake the difficult task of teasing apart intrinsic effects from others either empirically (e.g., Westram et al., 2022) or conceptually (Wiens, 2004). Our **second major conclusion** is therefore that *reproductive communities should be seen as isolated not just by intrinsic (genetic) differences, but also by extrinsic (e.g., geographic) factors.*

3.3. Reproductive communities of the moment (BSC+)

Expanding the BSC to the BSC+ by incorporating purely extrinsic isolating factors can permit its units to be comprehensive evolutionary actors, but it presents a different challenge: What then is the distinction between populations and species? With the strict BSC the answer was relatively straightforward, since full intrinsic isolation is an ultimate conceivable barrier to interbreeding and can serve as an absolute criterion for the definition.¹⁵ However, if geographic isolation alone can delimit species, as it can for populations, then what is the difference between the two?

Species and populations have long been seen as differing in the time scales of their integrity and independence: the species stands in stately patience over phylogenetic time as ephemeral populations bounce around inside its walls. The cohesive processes that maintain a species may be slow acting, with gene flow only occasionally uniting its populations, its isolation only occasionally challenged by contact, but nonetheless its isolation is settled, complete. Species thereby have integrity, and play independent roles in evolutionary process, over the long term (Barraclough, 2019; Simpson, 1961, p. 177). In contrast, a population is immediate, held together by interbreeding that is actual, ongoing, generation by generation (Carson, 1957), but its integrity and isolation might not last, as shifts in gene flow and ranges might lead populations to re-unite. The contrast can also be expressed in terms of rates: A population derives from high rates of interbreeding at small spatial scales,

¹⁴ Implied here is a possible distinction between identity and boundary — see §4.5.

¹⁵ The BSC's clarity of the distinction between species versus populations is lost in versions that permit hybridization.

contrasting against low rates at broader scales (among populations). A species derives from low rates of gene flow among populations and of rearrangements of population structure, providing slow cohesion, and extremely low rates (often zero) among species, providing (more or less permanent) isolation.

Thus, an expectation that isolation is complete, settled, and long-enduring is what distinguishes a species from a population in the Modern Synthesis. This sense of long-term integrity can be incorporated explicitly into a species concept (the BSC+) that also generalizes the BSC by including extrinsic factors, as follows:

A contemporary long-view species is a reproductive community composed of individuals at this point in time united by factors (such as reproductive compatibility, ecological pressures, and geographic context) such that their descendants are likely to be interbreeding, more likely than with others, into the indefinitely distant future, and whose point of eventual subdivision cannot be anticipated.

Forecasting is invoked to clarify the rank of species, which is reserved for units expected to have integrity indefinitely and thus sitting at one end of a spectrum. Metapopulations, populations and demes would also lie on this spectrum, with lesser time spans of projected integrities. Other authors have also characterized the BSC as prospective (Baum, 1998; de Queiroz & Donoghue, 1988; Harrison, 1998; O'Hara, 1993),

Although we do see the BSC and BSC+ as looking into the future, our primary argument does not depend on their prospection, but rather on their restriction of focus to the present. Because these concepts consider only the instantaneous state of cohesive processes at the present moment, they do not serve biology as well as a retrospective concept that integrates cohesive processes through time back into the recent past (§4). The critical contrast could thus be stated as instantaneous focus vs. backward time-integration, rather than prospection vs. retrospection.

Even though the descendants of a reproductive community won't remain united forever, the forecast of the BSC+ is projected to indefinite time to indicate that there is as yet no *particular* foreseen break in the community. If instead there were a strong predictor of a specific divide, a factor that made it likely, for example, that in the future the descendants of eastern individuals would no longer be interbreeding with the descendants of western individuals, then that would justify considering them as currently two BSC+ species.

We see the BSC+ as an improvement upon the strict BSC, as its incorporation of extrinsic factors makes its units complete evolutionary actors, but we will not advocate for its broad use. Its primary drawback is its focus on the present (and perhaps future) rather than the past (§4). In addition, the cost of its completeness is that biologists would have to accept *all* full barriers as species-worthy, even if purely extrinsic and however numerous. A population in Vladivostok and another in Newfoundland, with none intervening, should be considered separate BSC+ species if their vagility is low enough to support a forecast of isolation, even if they

are not genetically or ecologically differentiated and have no intrinsic reproductive barriers. This conclusion is unsettling taxonomically, and could add considerably to the taxonomist's burden, but would be required for the BSC+ to be consistent in recognizing extrinsic factors. In the retrospective view, such hyper-splitting is permitted but not required or recommended (§5).

4. Species should be seen retrospectively

The authors of the Modern Synthesis were correct to advocate a species concept centred on cause and mechanism, giving biology process-bound reproductive communities as its focal units. Where the BSC and BSC+ run astray is in their reliance on causes of the present, rather than causes of the past. Current reproductive compatibility is predictive — it suggests who is likely to be interbreeding with whom in the present, next summer, or in 1000 years — but it does not explain well the traits and genes that living organisms already possess. Such traits arose from evolutionary parameters and processes *of the past*. While past parameters may often match present ones, to whatever extent they do not, the past parameters better guide our understanding of the organisms in front of us. This renders the in-this-moment BSC+ units inappropriate for the taxonomic species used broadly throughout biology to synthesize current traits, and inappropriate as units to study genetic history and trait evolution. For those purposes, we have to turn our gaze backward, and see species as reproductive communities emerging from the past (Fig. 2 a, c, d), shaped by both intrinsic and extrinsic factors.

4.1. Why retrospection: Time lags and chance events

Current parameters of reproductive communities (e.g., compatibilities, migration rates) can fail to explain current traits whenever conditions have changed (as they will during evolution). The new conditions may take many generations to leave their mark on gene lineages and traits. Perhaps a climatic or geological event causes a habitat barrier to arise, strongly isolating eastern populations from western populations — or perhaps the reverse, previous isolation undone. Perhaps different selective sweeps occurred separately in allopatric populations, each dragging along only a small portion of the genome but generating intrinsic reproductive isolation because of Bateson–Dobzhansky–Muller effects (Wang & Hahn, 2018). These events in principle could almost instantly change the parameters of the model of current reproductive isolation, extrinsic or intrinsic, among these populations, and change the expectations of its effects on genomes. Current reproductive isolation, and the forecast of future interbreeding, will have changed dramatically, but most of the genome will not have yet responded to the new potentials. The lag could be long, if, for instance, a new isolating trait were confined to a recombination cold spot, allowing most of the genome to remain open to gene flow (Schluter & Rieseberg, 2022). Ge-

nealogies and most traits will continue to reflect processes that acted further in the past.

This time lag may be most severe for the very processes and factors that bind and delimit species — longer distance gene flow, occasional contact with sisters, intrinsic reproductive isolation. These processes, compared to those delimiting populations, play out over the longer term. It may take many generations for a neutral variant or an adaptation to spread across a species' range (and thus characterize a species). The strong intrinsic reproductive isolation that enforces species boundaries may be only occasionally activated. The effects of these processes develop slowly over time, and yet species concepts like the BSC declare species separate as soon as isolating mechanisms are in place, long before their consequences have been realized in patterns of genes and traits.

Even if conditions remain constant over time, retrospective explanation is likely to make reference to different *kinds* of processes than prospective prediction — in particular, stochasticity from extrinsic factors. A lineage that had a 95% chance of continued integrity might have nonetheless split into two, far earlier than expected, by a catastrophic climatic event, leaving a strong imprint on the present structuring of biodiversity. Retrospective units would reflect that event, unexpected as it may have been. But the BSC+, looking forward, would not envision many of the chance events that might happen in the future, particularly those from outside forces (climate, tectonics, contact with a new predator or disease). Of course, chance events in the future could be expected, but exactly which ones will occur, and the directions they will take (east or west? together or apart?), would not be predictable. Looking forward, many chance processes would add only the fog of uncertainty rather than foretell a specific structuring of biodiversity. Looking backward, though, the realized chance events that did produce a structuring of biodiversity must be part of any account of history, and thus they determine the delimitation of retrospective units.

Paraphyly of reproductively compatible populations is a classic “problem case” illustrating discord between the BSC and retrospective views (Bremer & Wanntorp, 1979; Mishler & Donoghue, 1982; Rosen, 1978). A single population (e.g., X in Fig. 2a; also, as in 3f) could evolve intrinsic reproductive isolation from a paraphyletic series of related populations (Y+Z in Fig. 2a) isolated from one another by extrinsic events. Because populations Y and Z in Fig. 2 remain reproductively compatible with one another, these would be interpreted as a single species under the BSC. So might the BSC+, looking forward, if they are projected to reunite in the future (Fig. 2b). Looking backward, however, for most purposes of explanation and data synthesis, their re-

productive compatibility is not a valid reason to hold them together as a single unit. A paraphyletic group misrepresents the causal flow of past genetic descent, which would lead to inaccurate explanation and synthesis unless there were a strong counterbalancing force that had shaped variation more deeply and broadly across the genome than did recency of common ancestry. A multidimensional adaptive zone shared by and unique to Y and Z might have been enough to overcome their genealogical disunity and to have shaped them alike, but no such force is part of our scenario in Fig. 2. (Indeed, 2d shows X and Y united ecologically instead.) The reproductive compatibility of Y and Z didn't provide a counterbalancing force, because in these scenarios there were extrinsic barriers. Compatibility remained an unfulfilled potential, not put into effect, inactive because of extrinsic isolation. Unfulfilled potentials do not a species make; the counterbalancing forces must have acted, shaping the variation we see today. Without a selective force broadly affecting traits and holding Y and Z alike, that paraphyletic assemblage, as a “unit”, explains little about the organisms in front of biologists. Y + Z should not be lumped together as one distinct unit; it would generally mislead about the evolution of traits except the reproductive.¹⁶

Taxonomists must choose between prospective and retrospective units because they lead to differences in how extant organisms are sorted into taxa. The **third major conclusion** of this paper is therefore this: *The best general species concept is retrospective, based on reproductive communities of the past.* Retrospection is necessary for a species concept to serve in most explanations and in data synthesis (see also §§4.6–4.8, and Sober, 1984; W. P. Maddison, 1997; O'Hara, 1993, Maddison in Vlijm, 1986; Zachos, 2016). Retrospection does not, however, guarantee simple unambiguous units (e.g., §4.9), nor does it offer a clear path to ranking taxa as species (§5).

4.2. Reproductive communities looking backward (RRCC)

A retrospective view of reproductive communities would therefore serve most biologists seeking to understand the current traits of organisms and how they evolved. This leads us to propose the following definition for the Retrospective Reproductive Community Concept (RRCC)¹⁷:

A reproductive community viewed retrospectively is and was composed of cohesive processes and organisms in ancestral-descendant sequence through the generations, from the past to a current moment, over which the organisms were united by factors (such as reproductive compatibility and ecological context) such that their descendants were likely to (and did) continue interbreeding and shar-

16 Paraphyly may be acceptable as a temporary approximation, but will only rarely be optimal. Retaining a plesiomorphic ecology, for example, would likely not be enough to justify a paraphyletic group. Despite the phrasing of §2.1, taxonomic synthesis is not simply making generalizations over sets of organisms; it is an evolutionary inference (§4.6), for which the lineages tracing genealogy could account for plesiomorphies and would typically provide more accuracy. See further comments about paraphyly in §§3.2, 4.9, 5.2, 5.5.

17 It might also be abbreviated as RC² or R2C2.

ing a selective trajectory in subsequent generations, more likely with each other than with others outside the community. It extends back in time, fading as the more distant generations are no longer needed to explain extant genealogical structuring and trait similarities.

The concept does not require constant panmixia, and accommodates small-scale fluctuation (e.g., the “cholla skeleton” portions in Fig. 3d, 3e, 3h) by time-averaging; more complex scenarios are discussed in §4.9. This concept does not include criteria for species rank, and thus its formal name does not include “species” (see §5).

In the spirit of taxonomy, we diagnose this concept’s distinctions from others. It nearly matches the monophyly-oriented Phylogenetic Species Concept (Mishler & Brandon, 1987; Mishler & Donoghue, 1982), separately considering grouping and ranking (§5), but in grouping it goes beyond genealogy to include cohesive processes. On the other hand, it is easily derivable from the BSC and Templeton’s (1989) Cohesion Species Concept by reorienting those toward the past and adding extrinsic isolating factors. Indeed, biologists using multispecies coalescent methods who favour the BSC may recognize the RRCC as their species concept. The RRCC is also closely akin to the Evolutionary Species Concept (Barracough, 2019; de Queiroz, 1998, 2007; Hey, 2006; Mayden, 1997; Simpson, 1951, 1961; Wiley, 1978, 2002), but the RRCC clarifies time frames, restricting claims about independence to the past tense. The RRCC descends from all of these concepts.

The RRCC may not have been named explicitly until now, but it is consistent with morphological taxonomy (§4.8) and articulates a concept already in wide use with genetic data. Retrospectively viewed reproductive communities are the units of multispecies coalescent models and genomic species delimitation methods, depicted as tubes within which genes descend (Degnan, 2018; Degnan & Rosenberg, 2009; Knowles & Carstens, 2007; W. P. Maddison, 1997; Smith & Carstens, 2020; Sukumaran & Knowles, 2017; Yang & Rannala, 2010; Yu et al., 2011). A living species (or, more generally, a unit of the RRCC) is represented by the recent part of a terminal tube of a multispecies coalescent diagram, fading into the past (Fig. 2acd), its depth depending on the cohesive processes (§4.9). In current models, these tubes represent the processes that shaped genealogy rather than the genealogy itself (W. P. Maddison, 1997), but richer models (e.g., §4.4) would see the tubes as a continuing interplay between causes (cohesive processes) and results (genealogies). The cohesive and isolating processes implicitly represented by the walls of these tubes are all-inclusive, intrinsic and extrinsic, just as with the BSC+. Not only is a comprehensive view of isolation the target, it is the only feasible target. Filtering

the action of only intrinsic factors in genetic or phylogeographic data would be nearly impossible.

The RRCC considers both a single moment and the passage of time. It stands in the present day, looking at the cross section of a lineage as it arrives to the present, but also looks back into that lineage’s past as a diachronic object. A metaphor may help. A living species is like a train you see as you arrive onto the platform: large, intricate, still hissing, smelling faintly of hot oil, its passengers exiting in mid-conversation. You see it front of you, at this moment, but you know that it has just arrived. You sense the traces of its recent past, and *that past is deeply part of what the train means to you.*¹⁸

4.3. Unification of species concepts

The backward-looking view of the RRCC approximately resolves the longstanding conflict among alternative species concepts — reproductive, genealogical, morphological, genotypic — based on interbreeding, genetic history, and trait similarities. Species concepts based on reproductive cohesion can be approximately concordant with those of genealogy and traits, as long as they represent reproductive communities *of the past*. Those past communities molded the genealogical units and trait-sharing clusters that biologists see today, and thus match them as closely as cause matches effect. This match should hold, not eventually (de Queiroz, 2007), but at any given moment of time.

Mayden (1997) and De Queiroz (1998, 2007) proposed a more comprehensive unification, suggesting that all species concepts could be unified under the Evolutionary Species Concept (Mayden, 1997), or as stated by de Queiroz (2007), the concept of “separately evolving metapopulation lineages”. De Queiroz argued that metapopulation lineages will, as they evolve separately, eventually come to be distinct in all aspects — traits, genealogy, and reproduction — such that disparate species concepts would eventually have concordant delimitations. An asymptotic expectation does not, however, adequately guide biologists’ species delimitation at this moment. Many extant lineages have not yet reached the asymptote, and so the concepts’ disunity remains. Any unification of the prospective (BSC or BSC+) and retrospective (phylogenetic or RRCC) views would have to be a low-resolution compromise, as their different goals lead them to different species delimitations.

The RRCC remains discordant with the BSC and BSC+, in principle at least. In practice, many lineages appear to have reached the de Queiroz asymptote, i.e., such that retrospective units of genealogy and trait similarities are also currently reproductively isolated (e.g., Rieseberg et al., 2006). Other lineages have not reached a concordant asymptote (Mishler & Donoghue, 1982), thus forcing biologists to se-

¹⁸ We are not suggesting the world is non-Markovian. Biologists have only the present to study; nothing more is left of the past. However, the BSC and BSC+ do not summarize all of the present. They convey only cohesive processes, and only those currently operating. Inside the train are many remnants of its past that are not part of our initial view. A complete census of traits would suffice if we had it, but we don’t, and so a model of the molding cohesive processes of the past is needed to guarantee breadth of prediction.

lect among the disagreeing species concepts for use in the general species taxonomy. Better to choose the broadly useful RRCC and praise whatever concordance exists with current and future isolation, rather than attach the label “species” to the instantaneous BSC+ and bemoan its lack of utility in explaining the world in front of us.

4.4. Body and breath

What is a species made of? Organisms? Genes? Yes, and more. A species is also made of processes, traits, and environmental context. The reproductive community X fading into the past in Fig. 2 shows symbols for organisms, genetic connections, extrinsic isolation (2a), reproductive isolation (a, c), and ecological adaptation (d). All of these together compose the community. The community is its organisms, their genes, their traits, their genealogical connections, and the intrinsic and extrinsic forces that isolate the community and shape it. A reproductive community is an actor, and its actions produce... the actor, generation after generation (Fig. 1; Barker, 2019).¹⁹ Genetic descent gives the organisms their traits; their traits are selected and determine breeding relationships; the outcomes of selection and interbreeding determine the genetic descent (§3.1). Beings and processes are inextricable (Dupré, 2022; Rieppel, 2009). A reproductive community is both body and breath, substance and action.

To infer a reproductive community is therefore in principle to infer everything that gave it integrity and identity (§3.1), including the cohesive and isolating processes of mating, ecology, and geography. Current methods of coalescent species delimitation are not yet adequate to the full task. The models remain simple, with processes such as secondary contact and introgression only beginning to be explored (e.g., Smith & Carstens, 2020; Yu et al., 2011). More critically, units are inferred only by the match of their predictions of gene descent to the sequence data available. While the genealogical outcomes hold considerable power to reveal the processes that shaped them, the inference of process would benefit from data directly pertinent to the mechanics of the process. Since those processes include reproductive isolation, commitments to adaptive zones, and geographical isolation, the methods would best measure and model mating traits, ecological differences, and geographic context (Cadena & Zapata, 2021) in addition to gene sequences. The goal of this would not be to determine contemporary isolation, but to characterize, richly and with understanding, the past factors that contributed integrity to the reproductive communities.

4.5. The Once and Future Species

Our argument that retrospective and prospective views see different boundaries for contemporary species challenges the usual intuitions about the temporal continuity of an object. A species lineage comes from the past, passes through the present moment, and continues into the future, just like a chair or a person (Ghiselin, 1974). If a species is an object with such continuity through time, then there might seem to be no need to specify a time frame precisely when speaking of its boundaries. Why should its instantaneous boundary at this very moment depend on whether we are looking forward or backward? Shouldn't its causal flow have a single cross section as it passes through this moment?

The story recounted for any natural object's past differs from its future foretold not only because the plot will have moved on to the next chapter, but also because the storyteller sees different kinds of events and answers different questions in recollection than in anticipation. This is true for our personal stories — looking backward we see accidents, looking forward we see aspirations. Retrospection and prospection differ in accounts of natural objects as well, and in similar ways (§§4.1, 4.2). Unforeseeable events of chance can figure prominently in retrospective histories, but in prediction they are, well, unforeseeable (§4.1). History invokes causes generating results in the short term, because its explanation need only arrive to the present moment, while prediction of long-term fate correspondingly emphasizes causes that are slower acting and more intrinsic (§4.2). Thus, a history of reproductive communities emphasizes extrinsic factors and chance events, using a shallow window reaching back only to the first one or two divergence events (deeper than that, and phylogenetic explanation takes over). In contrast, a characterization of the momentary isolation of a living population emphasizes intrinsic factors and ongoing extrinsic factors. It would also assess the long-term durability of those factors, if an attempt is made to project integrity into the indefinite future. These different views see different boundaries of the reproductive community.

A species can be seen as existing through time, but not simply as a sausage with each representative generation a slice. Biologists say “A species is...” and picture a lineage diachronically, enduring through time, in the present tense grammatically but not temporally, an identity with persistence. Biologists may believe that this view of a species directly implies what a species “is” synchronically, at this moment, in the true present tense, but it doesn't.²⁰ The species' identity through time, as biologists and philosophers have characterized it to date, does not adequately define the momentary boundaries to the precision that taxonomists need.

¹⁹ And thus, our previous framing of species as causes that explain rather than outcomes being explained (Wilkins, 2022) is too one-sided. Species are both, cause and effect.

²⁰ This temporal equivocation of “is” may be central to the persistence of the “species problem”.

In the present, and at the fine scale studied by taxonomists, a diachronic species' edges shimmer differently with eyes focused for different questions.²¹ Giving an example in which one researcher considers breeding looking forward but another considers genealogy looking backward, Gannett (2003) argues:

Asking different research questions results in different populations [...] Populations are variably constituted in different contexts of investigation because different theoretical interests determine what particular sets of relations are privileged. [...] Dynamic breeding units and genealogical units are not identical.

Exactly how to characterize this is unclear to us. We (and we think most evolutionary biologists) are inclined to see species identity, or at least some portion of it, as persisting through time (perdurantism, Reydon, 2008; Rieppel, 2009).²² But, in the face of differing boundaries depending on temporal view, should we see identity as hierarchical, a reproductive community having a broad diachronic identity but multiple synchronic sub-identities, different when viewed forward versus backward? Or should we instead see boundary and identity as disconnected, that there is only a single identity with multiple alternative view-dependent boundaries? That there is a single boundary with (somehow) multiple views? That reproductive communities are constructed rather than real (Gannett, 2003)? Regardless, it's not just an issue of alternative methods seeking to infer the same thing. *Something* different is being inferred looking forward and backward, whether identity or boundary or view or invention, in a manner that matters to those delimiting species.

We thus disagree with the view (de Queiroz, 1998, 2007; Mayden, 1997) that the many species concepts proposed reflect merely alternative inference methods under a single unifying concept of separately evolving metapopulation lineages. That view would imply that the methods' varying delimitations represent errors on a common answer they all seek. The BSC, BSC+, and RRCC are, however, asking different questions: "What contemporaneous set of organisms has intrinsic reproductive compatibility *at this moment*?" (BSC); "What set has integrity from all factors, *at this moment and likely into the future*?" (BSC+); "What set has been maintaining its integrity *in the recent past*?" (RRCC). We agree with de Queiroz and Mayden that biologists should take care not to equate a difference in kind of evidence with a difference in concept. Nonetheless, the BSC, BSC+, and RRCC remain separate concepts, useful for different purposes.

4.6. General purpose taxonomic units must be retrospective

The aptness of retrospective units for general-purpose (taxonomic) species can be illustrated by a thought experiment of a distant future in which taxonomic tradition has been replaced by a vast database and inference engine to satisfy taxonomy's role in synthesizing knowledge and modeling biodiversity. Dystopian though it may be, this thought experiment illustrates the fundamental logic of taxonomic species in organizing trait correlations, and their need to be retrospective units.

In this distant future, biology's taxonomic database and inference engine is called "TAXONOMATIC", containing not only all of biology's observations for all specimens, but also a tree-of-life-sized coalescent model (lineages, divergences, introgression, etc.), a map onto which all specimens are placed (precisely or approximately).²³ When a biologist submits new gene sequences and observations, TAXONOMATIC not only places the specimen on the coalescence map (while also adjusting the map/model itself if needed), but also supplies predictions of unobserved traits. Thus, if an input observation included red eyes, a black abdomen, and a particular gene sequence, TAXONOMATIC would add it to the model in Coalescence Region 16.20.24.16 [formerly known as *Drosophila melanogaster*]. It would also predict that the specimen has four pairs of chromosomes, and two power-supplying wings. TAXONOMATIC does more than taxonomy's job, predicting unobserved traits. It also does evolutionary biology's job, explaining observed traits as it adjusts its model with new data.

TAXONOMATIC's accurate synthesis requires neither named species, nor discrete units at all, as long as the coalescent model reflects the (fuzzy or not) reproductive communities accurately enough to predict gene tree correlations. Although we associate taxonomy with parcelling biodiversity into discrete boxes, when relieved of the constraints of its traditions, taxonomy's fundamental goal can be satisfied without discrete or named species at all.

Also, and more pertinent to our argument for retrospection, TAXONOMATIC's methods would be entirely retrospective. It would use hemiplasy-aware character mapping on the multispecies coalescent model (Hahn & Nakhleh, 2016) to make its predictions of unobserved traits, as well as to explain the evolution of observed traits. TAXONOMATIC builds and uses a model of the *past* reproductive communities, bound as tightly or as loosely as they had been. While current reproductive isolation may aid in the model's inferences and explanations, it would do so only to the extent it informs the past isolation embedded in the model. Current reproductive isolation would otherwise offer little help for

21 So too do our personal physical boundaries shift from bones to boundary layers to family as our eyes shift from questions concerning X-rays to wind chill to extended phenotypes. This is not an example of temporal parallax, but nonetheless shows the question-dependency of an object's boundaries.

22 We have some hesitation about persistent identity; see comments in §1.2 on the lack of a kernel.

23 We call it a "coalescent model" for simplicity, but it would go beyond neutral coalescence to address also selection, migration, mutation, etc.

TAXONOMATIC's basic functions of organizing and explaining biological data.

4.7. The mistake of seeking cause in the present

If the argument for retrospective units is so strong, why is current reproductive isolation the *de facto* definer of species in much of evolutionary biology? It is clear why inter-fertility among living organisms matters to those who seek to manipulate or manage populations for conservation or agriculture, but one might expect a historical view to come more naturally in evolutionary studies.

One answer may lie in biologists' penchant to look for cause *in the present day*. Gould and Lewontin (1979), for example, pointed out that adaptationist biologists tend to study current utility and assume that the original selective pressure was the same. The same urge to find evolutionary explanations in contemporary causes may also have led biologists into the error of looking for interspecific character correlation without phylogeny. Formally, this is a confusion about statistical independence (Felsenstein, 1985), but it may be provoked by a tendency to seek causes and effects in the visible correlations in "the thin slice of time in which we live our lives" (W. P. Maddison & FitzJohn, 2014). Perhaps, too, the authors of the Modern Synthesis sought contemporary causes (current reproductive isolation) for contemporary patterns (bundles of trait similarities). Even though the uniformitarian assumption of equal contemporary and past causes is a parsimonious default, embedding it into a species concept constrains it as a fixed assumption. The causes that should be sought are those in the past, and they must be permitted to differ from those we can measure in living populations.²⁴

The lack of access to genetic data in the mid 20th century may also help explain the Dobzhansky-Mayr focus on current interbreeding potential. The study of reproductive compatibilities promised results. Compatibilities *could* be measured in living populations, albeit with difficulty. In comparison, reconstructing the history of reproductive communities seemed far more difficult in 1940, absent the widespread genetic data we have today. The tables have turned, as signalled by the rise of coalescent-based species delimitation methods (Knowles & Carstens, 2007; Yang & Rannala, 2010). The more empirically accessible unit is now that of the RRCC. Biologists' ability to infer reproductive communities of the past is increasing much more rapidly than their ability to assess current potential reproductive isolation. Indeed, even if one's interest is in the mechanisms of isolation rather than species delimitation, it is often easier to trace the mechanisms' past effects through achieved genetic differentiation than their current effects in grueling and delicate mating experiments.

Nonetheless, the hold that current reproductive isolation has on biologists is strong. When considering whether to treat a recognizable form as a distinct species, we find ourselves jumping instinctively to the question, "But is it reproductively isolated?", in the present tense. We want units with explanatory power — based on process — but we also want to be able to see that process happening in front of us, today. We can't expect to have both. In distinguishing species, biologists must tear their eyes away from the thin slice of the present and seek their explanatory framework (i.e., taxonomy) in the past.

4.8. The relevance of classical morphological taxonomy

Conceiving species as reproductive communities of the past confirms the relevance of the millions of species already inferred through morphological differences. A peculiar effect of the BSC was to render the units delimited by most taxonomic practitioners only marginally relevant to the species concept that long dominated evolutionary biology's conversation. The BSC focuses on current compatibility in the behavioural, physiological, and structural mechanisms of interbreeding, but most taxonomists have access only to preserved morphology. While this disconnect between species in principle and species in practice might have indicated an antiquated irrelevance of taxonomists, it rather reflects limits on the relevance of the BSC.

Many practicing species taxonomists, despite their limited data, have implicitly sought units that reflect cohesive processes. The first author, when first beginning morphology-based taxonomy, learned that one should have at least two different kinds of characters distinguishing a species (e.g., colour and structure). Two kinds of traits would likely be under different genetic control, and thus their alignment would suggest linkage disequilibrium, i.e., evidence of isolation of reproductive communities in the recent past. Taxonomists also pay attention to geographic distributions, e.g., sympatry versus allopatry, for hints about interbreeding or isolation. These and other written or unwritten guidelines show that the frequent intent of classical taxonomists has been to reflect reproductive communities, not simply trait-sharing clusters.

The fact that taxonomists' data is almost entirely morphological might at first glance seem to rob them of the chance to infer interbreeding, but if their goal is to infer interbreeding *of the past*, it does not. Reproductive communities of the past *do* leave effects on trait similarities and differences of the present, and thus are in principle accessible through classical taxonomy. That is not to say that morphology easily and accurately resolves past reproductive communities, but that its evidence has value of similar nature to genetic sequence data. Current reproductive isolation also provides evidence, but its power (beyond being

²⁴ We acknowledge that observation of current reproductive isolation may better indicate cohesive processes of the recent past than does, say, the number of marginal setae, but it cannot be assumed as an automatic indicator, and the analysis must be framed as an inference of history.

just another trait) is limited to suggesting (the more relevant) isolation in the recent past.

In seeking traits unique to a lineage, traits from different aspects of the phenotype, and clues in geographic distributions, the classical morphological taxonomist is, in broad terms, using the same methods and asking the same question as practitioners of modern genomic species delimitation methods: what are the echoes of the reproductive communities of the recent past? Genotypes and phenotypes both carry these echoes, and can serve as alternative data types for a single retrospective species concept. This shared perspective of morphological taxonomy and genetic species delimitation has led to their uniting in the field of integrative taxonomy (Dayrat, 2005; Hedin & Milne, 2023; D. R. Maddison & Sproul, 2020; Padial et al., 2010; Puillandre et al., 2012; Riedel et al., 2013; Schlick-Steiner et al., 2010).

The empirical inaccessibility of the BSC and BSC+ is not just a nuisance for taxonomists; it reveals the limited utility of units that make few predictions about measurable traits in most of the genome. The very fact that reproductive communities of the past (RRCC) are so directly testable by both morphology and genes across the genome, that they leave such an imprint, is precisely why they are so much more useful for organizing our knowledge of biodiversity than BSC units. Taxonomic species inferred by their morphological traces have been relevant all along.

4.9. Monophyly, modelling, and messes

We hinted (§4.1) at the possibility that RRCC units must be monophyletic, but more accurate would be to say that the most usefully recognized reproductive communities should predict (at least approximate or partial) monophyly. The usual definitions of monophyly are not easily applied to a population or a species (Rieppel, 2010), but definitions based on gene genealogies have been formulated (e.g., Baum, 2009; Baum & Shaw, 1995). Whatever precise definition of monophyly might be chosen, it is clear that a reproductive community viewed retrospectively is not necessarily monophyletic (or exclusive) genealogically. A “tube” in a multispecies coalescent diagram represents such a community, providing well-defined boundaries of cohesion, and yet it doesn’t guarantee that all of its extant members’ gene lineages coalesce together before the shallowest ancestral divergence. A clade in a multispecies coalescence phylogeny does not imply monophyly in the gene trees; it suggests it probabilistically and approximately.

A coalescent modeller can build an accurate model of the cross sections of tubes as they arrive at the present day —

the leading edge of the coalescent tree diagram; the current and instantaneous presentation of reproductive communities — even if those communities are far from monophyletic in a traditional genealogical sense. Among the messy scenarios shown in Figure 3 are two extremely recently separated sisters (Fig. 3b, surely little differentiated), a large remnant from a peripheral isolate (Y in Fig. 3c, and thus in traditional terms paraphyletic, perhaps), a product of introgression (Y in Fig. 3g, partially mixed ancestry), and a fully hybrid population (H in Fig. 3i, dual ancestry). Despite youth or a mixed past, each of these can behave as a single living unit in a coalescent model with full accuracy if it was recently panmictic, homogenizing whatever came from its ancestry.²⁵

A set of organisms can be an adequate and accurate unit for coalescent modelling, that is, a *historically sufficient unit*, if any statements made about the evolutionary relationships between one of its member organisms and any contemporaneous organisms outside of the unit are the same for all of its members.²⁶ In stochastic models, the phrase “statements made about” can be interpreted as “model parameters concerning”, i.e., the unit’s members must share the same values of any parameters concerning genetic links outside the group (and thus, in effect, can be members of the same “tube” or clade in the coalescence model). Each of the recently split, introgressed, and hybrid units highlighted in the previous paragraph is historically sufficient because its components are homogeneous with respect to relationships outside the group.²⁷ However, a group like Y in Fig. 3h would not be a historically sufficient unit, because alleles introgressed from X have not spread throughout Y. There would be statements about relationships between organisms from northern Y (toward the top of the diagram) and X that don’t apply to those from southern Y, e.g.: “northern individuals of Y have genes recently introgressed from X”. If a model were to force the same statements to be made about northern and southern Y by uniting them (i.e., force them to have the same model parameters), it would lose accuracy.

We are speaking, however, of the instantaneous state of living populations, the leading edge of the coalescent tree, and therefore these historically sufficient units have the same shallowness that led us to argue against the BSC and BSC+ as general species concepts. Yes, they are momentary units to model and discuss, but that does not make them adequate as explanatory in general use. To be units that would serve well as general-purpose taxa, as “good species”, they need to extend backward through a duration of time, long enough to have molded a shared identity.

25 This is a claim about ontological status, not epistemological. The units could be difficult or impossible to discover with available data, and they may offer little prediction or explanation.

26 Historical sufficiency is defined in more general terms than needed for coalescence modelling so that it can apply broadly. Thus, traditional monophyletic groups are historically sufficient units as well.

27 The unit can have heterogeneity with respect to internal structure (e.g., it could be a clade of many species), but all components must agree on external relationships. In Fig. 3d, Y is currently structured, but since its generations immediately after the split from X were panmictic, all living members of Y have the same relationships to those of X.

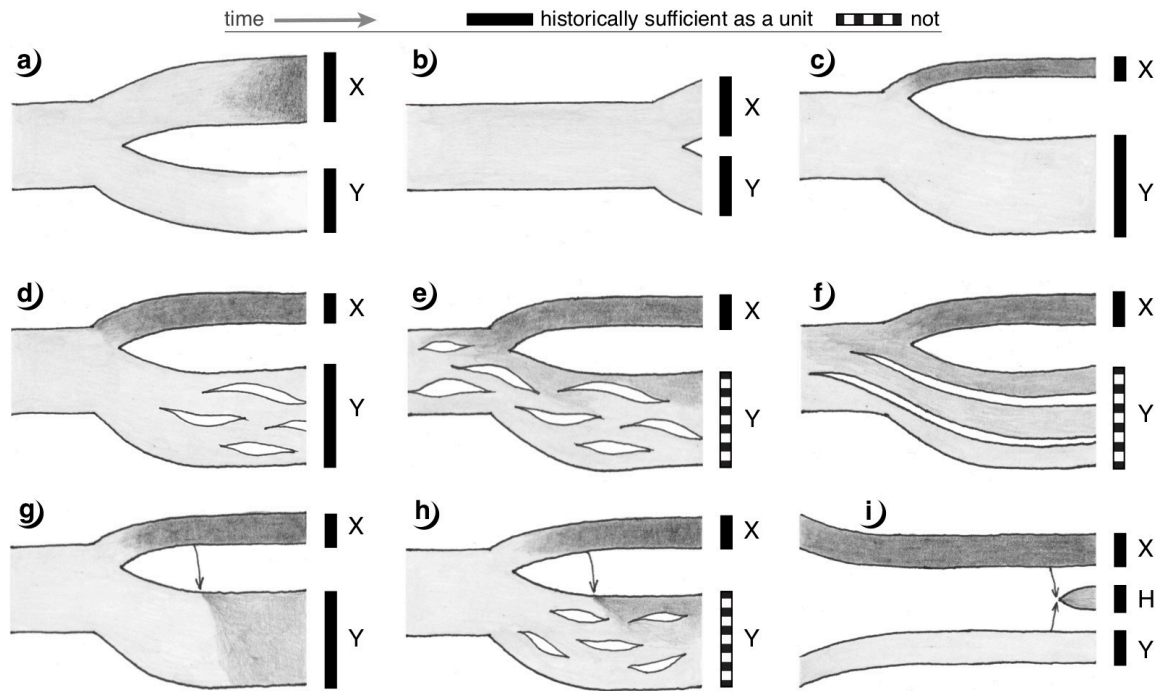


Figure 3. **Untidy situations.** Present-day groups X and Y marked as to whether each is a historically sufficient unit (HS, see §4.9) or not. **(a)** A tidy situation: panmictic ancestor, daughters long diverged, novel traits evolving to distinguish them. **(b)** Panmictic ancestor whose daughters are recently diverged. Both X and Y are discrete (HS) even though they are not yet distinctive in traits. **(c)** Despite X being a tiny isolate, its large sister Y is HS if it is panmictic. **(d)** Even though Y is currently structured, it is HS because it was panmictic after the split from X. **(e)** One daughter Y retains structure from ancestor, and thus is not HS because some of its parts share more with X. **(f)** Paraphyly of Y renders it not HS. **(g)** Y is HS despite introgression from X, as long as the introgressed alleles have spread uniformly throughout Y. **(h)** Introgression from X has made Y not HS because its population structure has limited allele spread. **(i)** Hybrid lineage H is HS despite having arisen from two parental lineages.

Thus, among the historically sufficient examples in Fig. 3, neither H in 3i, nor X and Y in 3b, are likely to have endured long enough to acquire distinctiveness after their formation. There may be no good taxonomic solution in these scenarios. In them, no time-integrated retrospective unit had sufficient integrity and duration to form an unambiguous unit of broad utility. The only thing to be done is to present the coalescent diagram, and say, “That was the history. It does not divide easily into units that are both living and broadly useful”.

Biologists may, arguably, sometimes be justified in recognizing a unit with multiple origins, and thus far from monophyletic in any traditional sense. A hybrid population formed recently by allopolyploidy (perhaps as in Fig. 3i; e.g., Soltis et al., 2012) can be a historically sufficient unit in shallow time, but in deeper time it would lack genealogical coherence. Nonetheless, it could more or less instantly be a highly explanatory unit in genomic, physiological, and ecological aspects, without the need for the passage of time, because of the unique traits shared by the population’s members, both as polyploids and as hybrids from a particular parental pair (Mishler & Brandon, 1987). This argument could justify the recognition not only of very recently formed hybrids, but even perhaps polyphyletic units. If that same parental pair hybridized at multiple sites, the collection of products might form a unit usefully recog-

nized taxonomically because of their many shared traits, even if they remain isolated and polyphyletic (and see comments about paraphyly in §4.1).

5. Which reproductive communities to rank as species?

When inferring a species, it is not enough to determine which individuals grouped themselves into a reproductive community; one also needs to determine whether that community has distinction deserving the rank of species, as opposed to, say, the rank of population. These two hurdles (grouping and ranking) are not separate by all species concepts — the strict BSC has the same criterion, complete intrinsic reproductive isolation, for both grouping and ranking — but other concepts, including the RRCC, and forms of the BSC that allow for hybridization between ‘good’ species (Rundle et al., 2001), explicitly or implicitly see grouping and ranking as separate tasks (Mishler & Brandon, 1987).

The species rank is not specified in the retrospective view as far as we have described it, either in the RRCC definition above, in the related Phylogenetic Species Concept (Mishler & Donoghue, 1982), or in coalescent species delimitation theory (Sukumaran & Knowles, 2017). Complete contemporary reproductive isolation could be used as an

auxiliary criterion to set rank,²⁸ but we will argue that its utility would be doubtful. In the worst-case scenario, the species rank has no natural meaning in an explanatory, retrospective framework; in the best-case scenario its meaning arises out of how change tends to be concentrated on lineages. We begin by picturing the best of all possible worlds.

5.1. The best of all possible worlds: Multi-trait revolutions

The interconnectedness of cohesive processes (§3.1) leads to multidimensional evolutionary change. Suppose that, in this best of worlds, a lineage spends most of its time in quiet stasis or gentle drift. A new adaptation then shifts habitat slightly, provoking a new selective regime, pushing the lineage into a new adaptive zone, distancing it from its relatives ecologically and possibly geographically, and promoting intrinsic reproductive isolation. The cascade of changes — which we will label a “multi-trait revolution” — might span much of the genome, disrupting past reproductive and ecological interactions, and causing the lineage to lurch to a new stable state.²⁹

If such punctuational change were the common mode of evolution, then most changes in traits would occur in clusters, in concert with many others. Nature would offer us not only bundles of genealogical descent (reproductive communities) but also bundles of more-or-less coincident trait changes (Fig. 4a, 4b). Reproductive communities that differ by such a concert of trait distinctions could be distinguished by biologists as species, and that distinction would have strong explanatory power. There need not be a single universal mechanism of multi-trait revolutions; mechanisms could vary across the tree of life, leading to a sort of patchwork pluralism (Mishler & Brandon, 1987; Mishler & Donoghue, 1982) in the biological meaning of the species rank.

The best-case scenario would not only have changes concentrated on lineages at points of multi-trait revolutions, but also these revolutions would occur more or less synchronously in isolated relatives. Thus, in Fig. 4a, the evolution of reproductive isolation in X would be accompanied (or quickly followed) by the evolution of diverse other traits, and similar revolutions would have happened in Y and Z, thereby leaving X, Y, and Z all with distinctive autapomorphies worthy of species distinction. Every organism could be placed into a distinct unit of species rank. None of the subunits would show such multidimensional distinction; if any did (e.g., Y₂), then each of the others

(e.g., Y₁) would (in the best of all possible worlds) have had its own revolution, and that would be the level of species.

The possibility that most substantial recent lineages are marked by multi-trait evolutionary bursts is the best hope we see for a natural species rank. The authors differ in their optimism: WPM is doubtful³⁰; JW is more hopeful. The frequency and magnitude of such multi-trait revolutions is an empirical question. Multidimensional distinctions can evolve rapidly (Moyle & Nakazato, 2010), but we lack data on how ubiquitous they are across the tree of life (Baack et al., 2015).

5.2. Worlds less than the ideal

Biologists ranking units as species must be prepared to do so in a world that is not the best of all possible worlds. Two flaws could erode this best-case scenario. The multi-trait revolutions could be too infrequent to mark all recent substantial lineages, for instance leaving a series of populations indistinctly different from one another and yet paraphyletic with respect to a peripheral isolate. The multi-trait revolutions may vary continuously (and not bimodally) in size, from many traits to very few, leaving a broad gradation of distinctions among lineages. Wherever these apply, a natural rank of species, arguably, would not exist.

Insufficient frequency of multi-trait revolutions (Fig. 4b) would leave biologists with no clear path to a complete subdivision into species units. Suppose, as seems likely, that reproductive communities split more often (at least into demes) than multi-trait revolutions happen. Some extant communities (Y and Z in Fig. 4b) could be indistinctly different from each other, and little changed from the ancestors that they share with a “lucky” relative (X) that had subsequently undergone multidimensional concerted change. By its multi-trait revolution, X might be called distinct at the species rank. Y and Z would not deserve to be called separate species from one another, if species rank depended on having a unique multi-trait revolution. However, because of their paraphyly, uniting them as the same species would (likely) not be justified either (§4.1). The organisms of Y and Z would not be part of any species.³¹

If change occurs gradually rather than in bursts, or if bursts vary in size continuously down to one or two traits, then we do not see how the rank of species could be natural, at least not as biologists have usually seen it, as a special and discrete level of biological organization. Sister lineages (e.g., Y₁ and Y₂ in Fig. 4c) could present any number of distinctions, from one to many, depending on how recently they were isolated (the speciation continuum, Singhal et

28 I.e., past isolation would be used to delimit groups; present or future isolation to rank them.

29 We are not saying that such revolutions exist, nor, if they do, that they follow mechanisms proposed by Mayr (1963) or others. Indeed, we portray this imaginary world in order to clarify that the real world likely fails to consistently provide a natural rank of “species”.

30 Perhaps because, as a taxonomist, he would prefer to believe that his frequent failure to find the species rank among a continuum of differences is biodiversity’s fault rather than his own.

31 Sukumaran et al.’s (2021) method is compatible with this view.

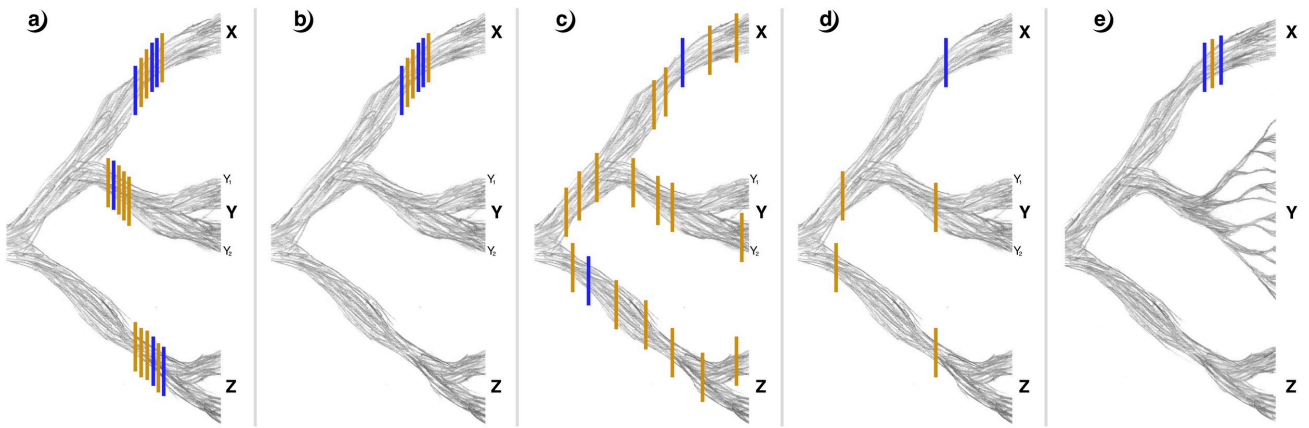


Figure 4. Possible distributions of changes in traits (blue and brown bars) on a tree of separating reproductive communities. A natural rank of species could exist if changes occur frequently and in clusters. Blue lines: novel traits contributing to intrinsic reproductive isolation; brown lines: various other novel traits (ecological, etc.). (a) In the best of all possible worlds, change is clustered, and clusters of change are frequent enough that every organism belongs to a lineage marked by its own recent multi-trait revolution. (b) Change is clustered, but not as frequent as extrinsic lineage isolation. (c) Changes are not so clustered, but more frequent than lineage separation. (d) Changes are not clustered, less frequent. (e) Isolation of lineages is primarily extrinsic, and some (Y) are finely divided into demes distinct only in neutral markers.

al., 2018). Biologists could quantify such distinctions as a continuous variable — let’s call it “speciesness” — and rank as full species those reproductive communities passing some threshold of speciesness. Even if speciesness measured something real and natural, the qualifying threshold of speciesness that biologists use to mark species rank would not, most likely, mark a threshold in the natural world itself. The threshold value would not be embedded in the evolutionary process; diverging sister lineages would not experience a sea change as they pass the value. The threshold would, most likely, be designated arbitrarily, or based on taxonomic utility (§5.4).

If species rank were merely a threshold in a continuous variable, it would impose an arbitrary discreteness on a natural world that is continuous. A measure of “speciesness” as a continuous variable could have biological meaning, but the species rank *as a binary choice* would be arbitrary.⁵² For a species rank that biologists treat as discrete to be naturally so (i.e., distinctions are either very few or very many), a lucky pattern of extinction would need to accompany gradual change.

5.3. Reproductive isolation as ranking criterion?

If (hypothetical) multi-trait revolutions are not conveniently-enough placed on lineages to serve as a general cri-

terion for species rank, then we have to look elsewhere to justify a natural and discrete rank of species. We will consider one last option: to use reproductive isolation, either current or past, as an auxiliary criterion to set the rank of a reproductive community. We will conclude that it cannot save the naturalness of the species rank, except perhaps weakly and partially.

The completeness of populations’ *current* reproductive isolation has little value for most explanation and synthesis. Not only has current isolation not yet had time to shape genomes (§4), but evolutionary explanation does not depend much on whether a living unit’s isolation has crossed the threshold from partial and temporary to complete and permanent. A reproductive community arrives to the present day held together by whatever held it together: geographical isolation, ecological specialization, reproductive isolation. Its ragtag assemblage of cohesive processes needed only to have helped it reach the present day intact, even if barely. The isolation it achieved nonetheless predicts trait correlations and explains the distinction of the community’s living members. It does so equally well whether or not it carries forward into the future a promise of long-enduring reproductive isolation. The great bulk of a reproductive community’s ability to predict and explain comes from its past isolation, not its current isolation.

Strength of *past* reproductive isolation might be a worthy criterion for ranking an RRCC unit as an evolutionary

⁵² If the chosen threshold were at one extreme, e.g., “differing at all loci” or “with integrity expected to endure indefinitely” (as in the BSC+), then arguably it is more natural than some intermediate threshold, say, 50%. Even still, divergent sister populations at 99% are not that different from those at 100%, and so the black and white image is still a misrepresentation. If biologists recognized that species rank were merely a point on a continuum, and treated it as such, then the misrepresentation might be inconsequential. At the same time, they would have to acknowledge that the choice of whether or not a unit is a species matters less than implied by the intensity of their attention to the rank.

species if it reflected distinction across the genome, rather than in just a few reproductive traits. That requires that the mechanisms of cohesion and isolation were active (not just unrealized potential) and enduring, extending deep enough into the past to mold the genome. Realized isolation could be measured by its effects, e.g., a reproductive community could be ranked as a species when it has achieved coalescent distinction (exclusivity) in all or the majority of loci (Baum, 2009; Baum & Shaw, 1995).

Setting aside concerns of about the naturalness of thresholds (§5.2), such a coalescent criterion for species rank would offer statistical predictivity about genealogy. However, the cost of automatically recognizing such units might exceed their value, especially when their exclusivity was achieved by purely extrinsic isolation. Many small and isolated demes in ponds or on mountainsides could satisfy this criterion for species (e.g., Fig. 4e), even though they might be isolated only by allopatry and differ only in neutral markers, having no special distinctiveness as evolutionary actors. This has been described as the over-splitting problem of coalescent methods (Leaché et al., 2018; Sukumaran & Knowles, 2017), which we discuss further in §5.4.

At issue is not the reality of reproductive communities (which we affirm), but rather the reality or naturalness of the species rank (Donoghue, 1985; Mishler, 2022; Mishler & Brandon, 1987; Mishler & Donoghue, 1982; Wilkins, 2018, 2022; Zachos, 2016, 2022). The BSC and BSC+ promise to both delimit and rank species by current complete reproductive isolation, but their units lack broad utility in biological synthesis, phylogenetics, and evolutionary explanation. Broad utility requires a retrospective approach, but that does not provide a species rank except perhaps for those (few? many?) reproductive communities that have undergone some special process (e.g., a multi-trait revolution). While an auxiliary criterion such as current complete reproductive isolation might be used to confer species rank on a reproductive community, the limits of the rank's meaning would need to be recognized. Such a species rank would amount to an annotation informative for special purposes, and not a broadly predictive endorsement.

5.4. Taxonomy in the real world

Evolutionary biologists could leave many organisms unplaced to species, instead placing them in unranked reproductive communities, but taxonomists don't have that luxury. Taxonomists have the task of placing all organisms into the organizational framework used by biologists broadly, and thus into smallest recognized units, which in general happen to be called "species". However biologists might conceive of *evolutionary species*, taxonomists have

different constraints on what to rank as *taxonomic species* (Baum, 2009; Dupré, 2022; Zachos, 2016; see also §8).

If there is no natural species rank that applies universally, then taxonomists are given license to (in fact required to) balance the value of naming a taxon for synthesis and explanation against pragmatic and cognitive limits. At the one extreme, biologists could, in principle, recognize and name *all* reproductive communities of the recent past, including those that lack distinctiveness in traits (§5.2) and coalescence (§5.3). The costs of doing so outweigh the benefits, however. Reproductive communities are too numerous: nested (Holsinger, 1984), almost fractally (Zachos, 2016), from local demes to metapopulations, many of them small (e.g., Ehrlich & Raven, 1969; Larson et al., 1984). While demes may share adaptive alleles (Morjan & Rieseberg, 2004), they might, at most loci, behave as separate reproductive communities. There is little value in recognizing such local demes indistinctly different from others. Taxonomy cannot afford the burden for such little return.

Freed from a theoretical commitment, the rank of species can continue to be used in taxonomy, but meaning nothing more than "among real evolutionary units, this one is important to name".³³ The value of a species rank wouldn't derive from its naturalness, but from its cognitive or information-storage value: to emphasize one level of the hierarchy and to guarantee a sortable partition with human-readable labels.³⁴ Taxonomists would focus on information efficiency, to convey as many trait distinctions in as few named taxa as possible. Until there are accepted quantitative cost/benefit models for taxonomic informatics, taxonomists could therefore continue as they have, with trait differences sufficient to recognize a taxon determined by the clade's taxonomic traditions (Baum, 2009; Mishler & Donoghue, 1982; Regan, 1926; Wilkins, 2022; Zachos, 2016). Alternatively, rank could be guided by conservation prioritization (§6.3). We therefore cannot give clear guidance as to whether 1, 2, 3, or more species would best be distinguished in Fig. 2. Lumping versus splitting is not a quaint sign of confusion; it represents an unavoidable puzzle of trade-offs in a world not anchored by a natural species rank.

This analysis of ranking speaks to concerns in the literature that species delimitation methods over-split by mistaking population structure for species structure (Derkarabetian et al., 2022; Leaché et al., 2018; Sukumaran & Knowles, 2017). Ideally, over-splitting would be solved by methods that set rank by modelling biological features of lineages beyond coalescent structure (e.g., ecological and mating traits). Proposed solutions (Derkarabetian et al., 2022; Pei et al., 2018; Sukumaran et al., 2021) do not do this directly, but rather calibrate rank by user judgement imported from past experience or other systems; this judge-

³³ In ascribing low meaning, we refer, of course, only to the assignment of rank. The unit itself, as a reproductive community, could have rich biological meaning.

³⁴ This gives permission to name subspecies in principle. If rank is arbitrary, then whether to treat species as the smallest recognized unit is settled simply by convention. The choice to name subspecies should therefore hinge on taxonomic utility and tradition group by group, not on ideological commitment.

ment could involve diverse biological considerations. Even were ranking methods to directly model processes beyond coalescence, we would not envision them confirming a natural and discrete species rank, which we see as not existing in many or most lineages. Rather, such methods would automate what biologists judge as the most important features to convey in taxonomic species, balanced against the cost of recognizing them — the aforementioned trade-off of utility versus cost. In the retrospective framework, over-splitting is not a violation of a deep and binary evolutionary meaning, but rather a lesser sin, of contravening taxonomic practice and its pragmatic trade-offs.

5.5. Taxonomic species can make only limited promises

Even if biologists were to settle on some criterion of distinctiveness in traits or reproduction to set the rank of species, taxonomy can't guarantee that all of its species meet that criterion. This is a simple consequence of two requirements: that taxonomic units should be clades or coherent reproductive communities of the past (i.e., approximately monophyletic; §§4.1, 4.9), and that all organisms should be placed in one and only one species (i.e., a partition). These two requirements constrain how related units can be ranked. A lineage promoted to species rank (for whatever reason — reproductive isolation, multi-trait revolution, taxonomic utility) automatically promotes its sisters and cousins. If X in Fig. 2 or in Fig. 4e is ranked as a species, then Y and Z would need to be treated also as separate species, regardless of how similar they are.

Thus, a species might have received its rank “undeservedly” because the rank was assigned to its sister. A taxonomic species does not, and cannot, guarantee any quality — not current reproductive isolation, not a certain level of trait distinction, not a certain degree of coalescent exclusivity — other than (approximate) monophyly. Taxonomic species could promise a special property other than monophyly only if taxonomy were to abandon either historical coherence (monophyly or reproductive community) or a partition of organisms into species.

5.6. If biodiversity's units lack a natural rank of species

This world, most likely, has some reproductive communities delimited by multi-trait revolutions, and thus naturally possessing a special rank, but many more lacking such distinction. We thus see no way to assign a natural rank that applies universally within the retrospective framework of synthesis and explanation.⁵⁵ This is not a reason to avoid retrospection. It is more important to choose units that serve broadly in explanation and data synthesis, even though we don't know what rank to assign to a unit, than

to choose a unit with a clear rank but with limited explanatory power. We are not, of course, the first to discuss the possibility that the species rank is without a general biological justification (Mishler, 2022; Mishler & Brandon, 1987; Mishler & Donoghue, 1982; Wilkins, 2022; Zachos, 2016).

This is a discomfiting result. Biologists, ourselves included, want to have a universal level at which to declare “new”, give a name, and alphabetize, and they want that level to be natural, objective, and broadly relevant. Biologists want to be able to count species objectively for studies in diversification (§6.2). The BSC tempted us with the promise of a natural rank justified by evolutionary principles, but its units are not complete evolutionary actors. The BSC+ is complete, but its instantaneous snapshot of process is of limited explanatory value. The most useful units, those of the RRCC, can accept an auxiliary criterion like multi-trait revolution to set rank, but that must be a secondary (and sometimes discarded) criterion.

The **fourth major conclusion** of this paper is therefore this: *There is no rank of species under the retrospective concept of reproductive communities that is natural, discrete, and universal, unless special processes consistently generate genome-wide revolutions in adaptive and reproductive traits. Completeness of reproductive isolation does not justify the species rank.*

6. Units for biodiversity sciences

For data synthesis and evolutionary explanation, the RRCC may be most apt, but concepts based on interbreeding potential (BSC, BSC+) also have an important place in biology. Ecologists need to know current reproductive compatibilities in order to model the dynamics of living populations. We here explore how several disciplines — speciation biology, phylogenetic diversification studies, and conservation biology — might value different species concepts, and accommodate the lack of a natural species rank in the RRCC (see also Mishler, 2022 and Thiele et al., 2021 for a vision of biology without an “objective” species rank).

6.1. Does speciation biology need a species concept?

A worldview in which reproductive communities are seen as real but the species rank as not (§5.6) might seem to challenge speciation biology. Can speciation biology be a coherent discipline if achieving species status isn't objectively defined? It can (in fact, it has), with little problem. Indeed, if there is any discipline that has little need to be constrained by a fixed species concept, it is speciation biology.

Speciation biology may refer to species in its statement of purpose, but more as landmarks for orientation than as critical concepts for day-to-day research. The field fo-

⁵⁵ It is not clear that the prospective framework (BSC/BSC+) fares any better with respect to a natural species rank. Reproductive isolation is a continuum; it does not cleanly partition biodiversity.

cuses on the processes by which reproductive isolation is achieved, on genomic structuring, physiological responses, and ecological selection. Extrinsic factors are considered (e.g., Mayr, 1940; Schemske, 2010; Sobel & Chen, 2014), whether or not they are included in any formal definition of species. These mechanisms are studied both retrospectively (e.g., phylogeography) and contemporaneously (e.g., gamete compatibility). As mechanisms are studied, little attention is usually placed on declaring whether or not a lineage has achieved species status. Many classic speciation systems (freshwater sticklebacks and other fishes of post-glacial lakes - Schluter, 1996, Apple maggot flies - Filchak et al., 2000; prairie sunflowers Ostevik et al., 2016) have hosted highly productive research despite the varied forms not being judged as separate species in evolutionary terms or not declared as such taxonomically. Indeed, avoiding reference to species status as a fixed and fully defined achievement gives speciation biology the flexibility to have a more nuanced view of diversification.

The word “speciation” already carries alternative meanings, corresponding to the three senses of reproductive community we have discussed: “the acquisition of intrinsic reproductive isolation” (BSC), the more inclusive “the process of lineages becoming permanently isolated” (BSC+), and “a branch point on a phylogeny” (corresponding to the RRCC). These alternatives do not align; when speciation in one sense occurs, it need not occur in the others (Rabosky, 2016; Rabosky & Matute, 2013). Judging from the diverse mechanisms and varied outcomes studied by speciation biologists, an expansive definition would seem to best characterize the field:

*Speciation is the set of processes by which reproductive communities diverge and gain independence and distinction, from the initial stages of trait acquisition, ecological divergence, or the origin of reproductive isolating factors, to the widespread establishment of distinctive traits, ecologies, and interbreeding relationships.*³⁶

Speciation is occurring whether or not any lineage ever achieves complete reproductive isolation. Despite the etymology of the name, the aptness of studying these processes does not depend on the existence of a discrete and natural rank of species. The word “speciation” is therefore like the word “knitting”, about a process of making, without presupposing the form or completion of the product.

Our view that current reproductive isolation should neither define the boundaries of general-purpose species (§§3, 4) nor set their rank (§5.3) in no way negates the centrality of reproductive isolation to an understanding of speciation. Research focussing on reproductive isolation in extant populations is vital; it permits experimentation and provides rich data about mechanisms and processes that we can obtain no other way. However, the label “species” need not, and should not, be tied to contemporary reproductive isolation. Speciation biologists can, of course, choose to apply the label “species” to currently isolated sets of organisms, but that would be a field-specific use of the term, as those sets would not appropriately serve as named species for use in biology more broadly.

Whether or not it dictates a species concept, speciation biology plays a central and necessary role in biology’s delimitation of species. Whenever a species taxonomist or other biologist delimits species in their own group, to interpret their data and make inferences, they must rely on general theories of how cohesive and divisive processes act. Those theories, developed by speciation biology, are the necessary foundation for methods to reconstruct reproductive communities of the past.

6.2. Phylogenetic diversification without ranked species

A rank-free RRCC might appear incompatible with phylogenetic studies of species diversification, but the latter can adapt to units without a natural rank of species. Inference methods (e.g., Louca & Pennell, 2020; W. P. Maddison et al., 2007; Magallón & Sanderson, 2001; Mitter et al., 1988; Rabosky, 2014) currently model events of speciation as if they produce units that are objectively countable (naturally discrete and equivalent). The potential arbitrariness of species rank (§5) may have little effect on inference of deep-time processes, but it could strongly affect our estimates of shallow-time parameters.³⁷ However, the models would not need objectively ranked species if they were re-framed in terms of divergence and extinction of reproductive communities bearing varied cohesion-related traits or degrees of isolation.

Rank-free diversification models could be developed by adding to existing birth-death models a new category of event, a lineage’s acquisition of reproductive isolation. Data required for parameter estimation would include not only the “observed” phylogeny, but also the current intrinsic isolation status of the extant reproductive communities

³⁶ This definition applies to sexual organisms. It can be extended to encompass both sexual and asexual organisms (§7), e.g., *Speciation is the set of processes by which phylogenetic communities derived from a recent common ancestor diverge and gain distinction in genes and traits (including, in sexuals, those concerning interbreeding), from the initial stages of separation and divergence, to the widespread establishment of distinctive traits, interactions, and ecologies.*

³⁷ To be honest, most of the data input into such methods currently does not involve objectively ranked species (Faurby et al., 2016; Willis, 2017). If diversification studies presently assume that taxonomists’ behaviour of lumping and splitting is phylogenetically uniform or randomized, perhaps they would be equally willing with explicitly RRCC units.

that form the terminal branches.⁵⁸ Such models could be based on that of Sukumaran et al. (2021; see also Sukumaran & Knowles, 2017 and Quinn, 2022), who model divergence of multispecies coalescent tubes and onto them map the acquisition (as if trait evolution on a phylogeny) of what they call “species status” (perhaps, full reproductive isolation). A more sophisticated model would allow the degree of reproductive isolation of each lineage to be a continuous variable. Even better would be to model the acquisition of individual traits that contribute to isolation and cohesion — a change in habitat preference, a shift in mating behaviour, and so on — component by component (§3.1; feedback arrows of Fig. 1, 2cd). One advantage of trait-by-trait mapping is that it could account for the fact that isolation is a multilateral relationship among populations, not a unilateral declaration by a single lineage (Coyne & Orr, 2004). A model even more sophisticated (but rather difficult to infer) would dissolve the distinction between the phylogeny and the traits that shape phylogeny. A phylogenetic branch would be a model of the intrinsic traits and extrinsic factors that provided cohesion and isolation. As these traits and factors change with time, the walls they form would shift and split, forming divergent lineages and eventually a phylogenetic tree. Such an approach would be the natural synthesis of phylogenetic biology and speciation biology, integrating retrospection and prospecting.

6.3. Valuable and actionable units in conservation biology

Conservation biology needs both retrospective and prospective units: retrospective to indicate what units had past integrity, giving them distinctness and thus *value* worth preserving, and prospective to guide *actions* needed to preserve them.

In order to manage biodiversity, conservation biologists must focus on the current status and interbreeding potential of organisms. They may need to understand what organisms can potentially interbreed (BSC), for example, to rebuild connectivity between fragmented populations, or to rescue a declining population by borrowing genetic material (Frankham, 2015; Whiteley et al., 2015). They also need to know the currently active boundaries of isolation (both intrinsic and extrinsic) to model population dynamics and integrity. Often these would involve projections over the short term (i.e., population level projections), but projections over the long term are also key to conservation planning (metapopulation or BSC+ level projections). These assessments may need to consider graded probabilities of interbreeding or permanence, rather than the simple isolated-or-not assessment of the BSC or the permanent-or-not assessment of the BSC+, but their approach would be prospective.

While this compels conservation biology to look at current potentials to manage populations and sets of inter-

fertile organisms (whether or not they are called species), conservation biologists also need the retrospective view of the RRCC. Conservation biology’s first question is, “what should be saved?”. This choice would be based on distinctiveness in genes and other traits of the populations at present, best summarized or predicted by the retrospective unit (RRCC). Even though the RRCC provides no natural rank of species, conservationists could still choose a threshold of genomic or phenotypic distinction for a conservation unit, which could provide a non-evolutionary but nonetheless objective criterion for species rank. Particular retrospective communities passing the distinctiveness threshold could be named as species to highlight them as conservation targets (Garnett & Christidis, 2007; Thiele et al., 2021).

Thus, conservation biology needs to be pluralistic: RRCC units to help choose targets for intervention, populations (and perhaps the BSC+) to model likely outcomes, and BSC units to take action.

7. Different ways to be a species (with or without sex)

In phrasing the RRCC vaguely enough to encompass a breadth of cohesive processes involving reproduction, ecology, and development (§3.1), we were not simply expressing uncertainty about what processes play the greatest roles. We were implicitly allowing that the processes could vary from clade to clade, from lineage to lineage. In principle, there is no reason to require, when recognizing units, that their cohesive processes be identical across all of biodiversity. The steps forward that we have taken with the RRCC, prescribing process and retrospection, may be as far as can be gone towards a universal concept.

7.1. Variation in process

Different groups of organisms differ in their mating systems, dispersal abilities, ecological tolerances, developmental plasticities, and genomic structuring. It is to be expected therefore that they might also differ in how those processes contribute to cohesion. In some groups, more than others, allopatric isolation may have more of an effect, ecological selection may be a more powerful diversifying dimension, or reproductive systems may be more fragile to discord.

Varied processes can shape reproductive communities, but also varied processes might give them a justifiable species rank. Within a single clade of diversifying reproductive communities, some lineages may be marked by a shift in adaptive zone; others by a shift in mating mechanisms. Depending on what a biologist seeks to highlight, these different processes can serve as alternative lines at which to draw the rank of species.

⁵⁸ Branching would represent extrinsic isolation. Reunification of lineages would be possible until intrinsic reproductive isolation is established.

Variation in process leads to our **fifth major conclusion**: *A general-purpose species concept requires process and retrospection, but it cannot specify detailed cohesive mechanisms, because different lineages can have different ways to form species* (Mishler & Brandon, 1987; Wilkins, 2007; Zechos, 2016).

7.2. Species in asexual lineages

Just as different groups of organisms show variation in ecological or developmental processes, they also show a continuum of sexuality from panmixia to obligate asexuality. Strictly asexual lineages, at one end of the continuum, are excluded from consideration as species under the BSC or BSC+. They are also excluded by the RRCC as defined above (§4.2), which is directed toward sexual lineages, but the RRCC could easily be broadened to include asexuals.³⁹

Under a retrospective concept, designating asexual lineages as species is as justifiable as it is for sexual lineages. Asexual clades can serve as well as sexual reproductive communities, perhaps better, as units in data synthesis, phylogenetic studies, and evolutionary explanation. Strictly asexual lineages lack the special kind of integration provided by recombination in sexuals, but they form perfect clades, cleaner in genealogical descent, and therefore perhaps more precise as trait predictors. With asexuals, “it’s clades all the way down”, right to the individual organism.

Asexual lineages form perfect groups, and so the only puzzle is rank — which clades to single out and mark as species. Rankability, though, does not obviously favour sexual over asexual species. In asexuals, there are clades within clades; in sexuals, there are more integrated reproductive communities within less integrated reproductive communities (Holsinger, 1984). The choice of which of the nested levels to consider species seems equally fraught. Sexual lineages lack a universal natural species rank in retrospective evolutionary explanation (§5). The processes that might confer natural rank of species on sexual lineages, such as those involving adaptive zones (§5.1), could equally well occur in asexual lineages. If so, then the naturalness of asexual species’ rank would match that of sexuals.

Are there signs that some levels of asexuals’ genealogical hierarchy stand out as forming predictive units for many traits? Those who study asexual organisms often see variation structured so (Barraclough, 2019; Holman, 1987; Mishler & Brandon, 1987). One can find sets of asexual organisms forming a multidimensional morphological cluster, having their own ecological role and a coherent geographic range (as described in Templeton, 1989; examples in Bierzychudek, 1985; Gilabert et al., 2014; Rushworth et al., 2018). A biologist can learn their appearance, their habitat

preference, and their geographic range, and can then go into the field and predictably find more individuals, behaving as they are expected to behave. This correlated variation is not the delusion of a taxonomist intent on inventing order; it appears to delimit a real thing on the landscape, as distinctive as a sexual species is within its clade. The distinctiveness of the asexual unit may depend on extinction of intermediate lineages, or it may depend on the same ecological forces and developmental interactions that align traits in sexuals (§§3.1, 5.1; see also Barraclough, 2019; Wilkins, 2007).

The implications of considering asexual species go beyond taxonomy. For evolutionary biology, there is value in bringing asexuals into the conversation about species and speciation (Barraclough, 2019). The study of systems that lack or are polymorphic for sex has the potential to contribute to our understanding of speciation in both sexual and asexual lineages, much as the study of hybrid zones serves as a window on a breadth of evolutionary processes (Harrison, 1990). Specifically, asexual lineages can help us to understand the contributions of mechanisms other than sexual reproduction in structuring biodiversity across the tree of life. Divergence and diversification can and do occur regardless of whether sexual incompatibility evolves (Rabosky, 2016; Rabosky & Matute, 2013). Even if one’s goal is to understand evolution of sexual lineages, the study of asexuals can serve as a “control” for theories that involve sexual interactions (e.g., Whitton et al., 2017). For instance, a theory that explains a pattern of diversification by some consequence of mechanisms of reproductive isolation might be challenged if asexual lineages show similar patterns.

The **sixth major conclusion** of this paper is this: *Ranking asexual lineages as species is as justified as ranking sexual reproductive communities as species*. In both cases, the rank could be conferred by abrupt shifts in adaptive and ecological cohesion, not necessarily by a special boundary of reproductive isolation.

8. Taxonomic species and evolutionary species

Named taxonomic species need not match the theoretically important units in evolutionary biology (“evolutionary species”, Baum, 2009; Dupré, 2022; Zechos, 2016), but their schism should be resisted by biologists as far as possible. Biology’s taxonomic trait syntheses, phylogenetics’ reconstructions, and evolutionary biology’s explanations are all best served by the same basic units (§§2, 4), reproductive communities of the past. Taxonomic species succeed to the extent that they are evolutionary species. Nonetheless,

³⁹ To bring sexuals and asexuals to a shared vocabulary, we might use the phrase “*phylogenetic community*” to refer either to clade (among asexuals) or past reproductive community (among sexuals). In both, there are processes that held the community members’ collective genomes as an integrated, isolated unit (among sexuals, those of a reproductive community; among asexuals, the linked descent of all loci from a common ancestor).

problems of rank (§5), messiness of evolution (§4.9), and lack of knowledge prevent a direct alignment between taxonomy's partition and evolution's reproductive communities. The title of this paper must therefore accommodate two meanings of "species", evolutionary and taxonomic. In either, the species is a reproductive community emerging from the past. Evolutionary species are those reproductive communities marked naturally by (perhaps) a multi-trait revolution, while taxonomic species are those selected for naming by taxonomists according to their conventions of distinctiveness and allocation of effort.⁴⁰

8.1. Classes versus individuals

The philosophical debate about whether species are kinds (or classes) or individuals (Haber, 2016) is, in effect, a battle between seeing them as taxonomic units versus evolutionary units. An evolutionary species is an individual (Baum, 1998; Ghiselin, 1974; Haber, 2016; Hull, 1976, 1987; Mishler & Brandon, 1987; Wiley, 2002; our §3.1), as evident in biologists' descriptions of its actions — it adapted, it suffered a bottleneck, it broke apart, it retained integrity in the face of introgression, it went extinct. A taxonomic species can be such an individual, but biologists also treat it as a class (or set, or natural kind in the sense of Boyd, 1999, but not Ghiselin, 2002) over which to make generalizations about organisms, whenever they use it as a container to accumulate data from different specimens into a synthetic view of the organisms' traits (§2.1). The species-as-class and the species-as-individual are not the same formally: a class doesn't engage in actions (though its members do), while an individual (made of parts) does.⁴¹ However, biologists can maintain both views as a painless pluralism, insofar as the units can agree on what organisms a species contains (as members of the class, or as parts of the individual).

Species can be successfully treated as both individuals and classes (Baum, 1998; Boyd, 1999; Dobzhansky, 1950; Ereshefsky, 1992) because the former justifies the latter. A species is more useful as a class for making generalizations the more its parts form (or had formed) an integrated evolutionary individual, whose cohesive processes generated concordant distributions among traits and thus made generalizations successful.⁴² This is, in effect, Boyd's (1999) concept of a homeostatic property cluster. The integrity of the species as an individual is the cause; the utility of the species as a class is its effect.

8.2. Approximation and error

A taxonomic classification can lead to subsequent errors to whatever extent its species do not reflect evolutionary units. Some level of mismatch is inevitable (Baum, 2009; Zachos, 2016), because biodiversity isn't divided into the simple partition that classification demands.⁴³ Nature instead provides fuzzy or overlapping units (§4.9, Zachos, 2016), or units distinct as reproductive communities but whose other properties cannot be guaranteed (§5.5). A classification's errors go beyond its inability to match the true texture of biodiversity. Its taxa are subject, as well, to the usual scientific errors of observation and inference.

The consequences of inaccuracies in species classification can be severe. A poorly delimited or identified taxon can lead to observations being assigned to the wrong rows in the vast implicit spreadsheet of biology (species × traits). Misplaced observations might be critical in some studies, not in others. In most cases, they will be placed in the correct phylogenetic neighbourhood. In parts of the tree of life where biologists are just barely starting to uncover biodiversity, our tolerance for minor misplacements should be high. As a clade is studied in more detail, then studies that use the taxonomy would require more stringency on the accuracy of species limits and specimen placement.

A non-taxonomist, depending on their interests, might therefore need the classification to convey the uncertainty in how any given species is delimited or any given specimen is identified (Monckton et al., 2020). Error is a natural part of science. Species descriptions and identifications are not, however, typically accompanied by informative error bars. Proposals have been made for uncertain status (Donoghue, 1985), but there is no canonical system used to convey taxonomic uncertainty, except for the coarse and vague use of "cf.", "aff." in specimen identifications, or placement as an unnamed species in a genus. Biologists on the ground might be well served by better methods for assessing and communicating uncertainty in delimitation and identification, as well as in describing edges that are in fact not discrete (e.g., through introgression). Indiscrete edges do not necessarily hold back subsequent work, as long as they are conveyed clearly (Hahn & Nakhleh, 2016).

Acceptance of the inevitability of approximation and error is liberating. Taxonomists can continue as they have: *"No one has seen an organism like this before; no one has looked at this diversity in decades. Let me sort it to the first*

40 Taxonomy, requiring that all organisms be placed to species, may be sometimes forced to recognize species that are not distinct reproductive communities, if tangled processes fail to provide them (§4.9).

41 The same is true of a human versus the set of her cells: Susan's cells crave oxygen; Susan craves chocolate; the set of Susan's cells does neither, standing serenely in abstraction.

42 This analysis overstates the contrast in perspectives. As shown by TAXONOMATIC (§4.6), taxonomic data synthesis is not simply generalization over a class, but is a complex inference invoking the processes that make a lineage an individual.

43 Classification might approximate evolutionary units more closely if it abandoned the partition-of-boxes model. Objects can be real even if they are indiscrete or have overlapping boundaries. We think of cities as real things, but not as boxes — rather, as points of concentration attenuating outwards that can overlap. Whether or not biologists could adapt to an alternative abstraction eventually, species classification is likely to remain as a simple partition for the foreseeable future.

and second decimal places before you worry about the fourth and fifth. That will be acceptable progress for now." For many poorly known clades, gaining a rough cut of biodiversity is a valuable starting point. While this may appear to relegate taxonomists to mere stage-setters, they could equally well be thought of as pathbreakers (E. O. Wilson, 1985). Rough-cut taxonomic species may have to persist decades or centuries. Better that we work to accommodate and understand their errors, rather than work only on building error-free dreams.

Our **seventh major conclusion** is: *Taxonomic species should approximate, but can only approximate, evolutionary units.* Their reality as evolutionary units does not, however, imply the reality of the species rank, which for many or most lineages is a taxonomic convenience, not a natural property.

9. Conclusion

The “species problem” arises from a collision of alternative disciplines and questions applied to a complex and dynamic system, which biologists view both in snapshot and as a movie. Many biologists who contemplate species (ourselves included) are attached to multiple perspectives, and thus in their discussions the word “species” sometimes flickers iridescently among meanings.

We have presented the case that biology’s general-purpose species, as we look at them today, should be seen as historical lineages, of the past (as in the phylogenetic species concept), whose boundaries were formed by cohesive and isolating processes (as in the biological species concept). Like Templeton (1989), we make reference to cohesion but have been intentionally inclusive and vague about exactly what its processes are. For instance, we have not clarified the relative contributions of different cohesive processes, how deep into the past the retrospection should extend, exactly how much introgression would compromise lineage distinctness, or how to deal with discordant patterns shown by different sections of the genome (e.g., Bougie et al., 2021; Fontaine et al., 2015; Martin et al., 2013; Wang & Hahn, 2018; though, see footnote 5 in §2.2). These issues do not change the basic conclusion, however. Even if biodiversity has considerable disorder, even if its units are hard to discover, biology’s general-purpose units should be retrospective and process-based.

As much as we would like to specify precise cohesive mechanisms in definitions of “species” and “reproductive community”, we can’t, and we shouldn’t. A dash of ambiguity is not only necessary but perhaps even fruitful (Ami-tani, 2022; Bush, 1994). The meanings of those words must be tied to evolutionary process, and must evolve as our understanding of mechanism evolves — we should not expect their meanings to be frozen in the 1940s or in the 2020s. As Kuhn (1970) argued, the units most central to our theo-

ries cannot be defined in advance and then studied for the processes that make them and that they participate in; the very sense of the units is tied up with our theoretical understanding of them. If we commit to a simple measurable defining property for species (intrinsic reproductive isolation? genealogical exclusivity?) to reflect biology’s preoccupation of the moment, it will inhibit our theories adapting to new understandings of the mechanisms that structure biodiversity.

A concept of species, or of reproductive communities in general, cannot be merely a definition. It must be a theory, at least in part. The two properties we have prescribed (retrospection, cohesive process) are necessary, but not sufficient, for a general species concept. What fills in the rest of a concept (clade by clade) — what are the cohesive processes, how they shape reproductive and phylogenetic communities at various levels, and whether any communities have special properties that would naturally give them the rank of species — is for biology to continue discovering. The RRCC is an *open* concept, intentionally incomplete, only partially constraining the nature and boundaries of a reproductive community, leaving them to vary lineage by lineage. In contrast, the Biological, Phylogenetic, Genealogical, and operationalist concepts are more *closed*, attempting to set criteria for grouping that are necessary, sufficient, and invariant.

The lack of details in our RRCC definition highlights a tension between two approaches to species. Are we deciding in advance on a precise abstract concept that we then apply as a tool, or do we see species as enigmatic objects in Nature that we stumble upon and try to understand? The former satisfies the urge for certainty and control over meaning. It is thus an approach of prescription, of telling (at least as a proposal, if not a demand). The latter cedes control to Nature, which thereby leaves us in perpetual ambivalence. It is an approach of description, of listening. Biologists must take both approaches in the dialog between ideas and Nature, but we must begin and end with listening, looking outward to the natural world, never letting ourselves believe we have tamed it.⁴⁴

It might appear we are claiming that a retrospective view of reproductive communities provides a resolution to the “species problem”. In fact, it is only the barest start in understanding what species are. Their true richness is in the myriad of interacting cohesive processes and the intricate patterns they produce. Taxonomists, having immersed themselves among thousands of organisms, touch biodiversity’s texture to feel the boundaries of reproductive communities emerging from the past into their natural history collections. Evolutionary biologists, decades after the Modern Synthesis began, continue to probe the mechanisms by which those boundaries formed and acted, and by which identities were borne. Although philosophy can help us reason, the problem of species belongs to biology. We must

⁴⁴ We capitalize “Nature” not to suggest that the natural world is a deity, but to emphasize that it exists and acts apart from us, that we must hold our abstract ideas in deference to it. This is a point not of metaphysics, but of attitude.

listen to biological diversity. If we do so, carefully, then species — or whatever there is — will reveal their natures.

Acknowledgments

The literature on species concepts is large, diverse, and intricate (de Queiroz, 2007; Harrison, 1998; Mayden, 1997; Wilkins, 2018; Zachos, 2016). Even though we recommend a single “species” concept for general use, this paper owes debts across the spectrum, and from across the decades. Our attention to the paramount value of historical explanation comes from phylogenetic systematics (e.g., Mishler & Donoghue, 1982; Rosen, 1978). Our primary focus on the reproductive community descends from speciation biology and the Modern Synthesis (e.g., Dobzhansky, 1935; Mayr, 1942). Authors embracing a comprehensive view of cohesive processes (e.g., Barraclough, 2019; Baum, 1998; Coyne & Orr, 2004; de Queiroz, 2007; Mayden, 1997; Templeton, 1989; Wiley, 1978; Wilkins, 2007) helped guide us to a concept that might be criticized as vague, but which thereby allows it to defer to Nature’s mechanisms. Our reference to time frames, pivotal to the argument, was aided by the clarity of Gannett (2003), Baum (1998), and Millstein (2009). Phenetics emphasized to us the role of taxa as predictive information organizers (e.g., Sneath & Sokal, 1973). Operationalist authors (Mallet, 1995; Nixon & Wheeler, 1990; Sokal & Crovello, 1970) reminded us to maintain caution about assumptions. Our views on the importance of balancing of history and process, and of maintaining multiple perspectives, have been heavily informed by synthesizers (e.g., de Queiroz, 1998, 2007; Donoghue, 1985; Mayden, 1997; Mishler & Brandon, 1987; Mishler & Donoghue, 1982) who have sought to bring together multiple schools of thought. Mishler, Wilkins, Zachos, and others have also encouraged us to see the species rank as secondary to the concepts that provide groups. A separate thread of synthesis, that of coalescent species inference (e.g., Degnan & Rosenberg, 2009; Knowles & Carstens, 2007; Sukumaran & Knowles, 2017; Yang & Rannala, 2010) arrived to a destination close to ours. Alongside all of this discussion, thousands of practicing taxonomists have continued to make their discover-

ies, which we value, and which challenged us to understand precisely why we value them. In writing this paper we have sought to respond to, and where apt to amplify, all of these voices, old and new.⁴⁵

Despite our acknowledgement of these debts, we have not made extensive attempts to trace ideas back to their first authors, because of the size of such a scholarly undertaking. Some or all of our ideas may have been stated before, in which case we hope that our reiteration and emphasis may serve to focus attention to them. We beg forgiveness for any failures to give credit, and for the sparsity of citations throughout, a choice that follows the tradition of philosophy to give the reader a greater density and better flow of ideas.

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⁴⁵ Hence the paper’s length!

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