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Defining 'Species,' 'Biodiversity,' and 'Conservation' by Their Transitive Relations

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1. Introduction

"...it follows that we should not regard the organism or the individual (not to speak of the species) as the ultimate element of the biological system. Rather it should be the organism or the individual at a particular point of time, or even better, during a certain, theoretically infinitely small, period of its life. We will call this element of all biological systematics... the character-bearing semaphoront."—W. Hennig [1: p6, emphasis original]

Definitions offer meanings of words by way of associations with other terms [2, 3]. Accordingly, a definition relates a concept to a name [4]. Like any field of science, precision of communication in biology is dependent upon the use of terms, while actions taken as consequences of the acceptance of those terms are constrained by definitions. The importance of the meanings of words is especially critical when actions in one subfield of biology are dependent on terms developed in other subfields. A case in point involves the terms *species*, *biodiversity*, and *conservation*. With a voluminous literature regarding what species are supposed to be, the topic has suffered from an overemphasis on 'species concepts' that are largely detached from more inclusive biological systematics principles (e.g. [5]) required to answer the question 'What is a species?' While upwards of 26 species 'concepts' are recognized [6–8], there is inconsistency among these in that they either refer to causal or acausal constructs. Causal characterizations typically present species as entities involved in past events, whereas acausal accounts refer to differentially shared features of organisms. Wilkins [8: p58, emphasis original] refers to causal-based concepts as indicating "*what species are,*" and acausal concepts as "*how we identify species.*" The implication of either perspective leans toward species being

entities that can be perceived by way of their properties, yet too often species and the organisms to which they refer are conflated (cf. [9]).

Settling the matter of what species are and the definition of the term requires a perspective that goes beyond the traditional, inordinately narrow consideration of just species. In acknowledging that species are taxa, we first must consider the formal definition of *taxon*. By extension, the definition of taxon must be consistent with the goal of biological systematics, and that goal must be accordant with that of scientific inquiry. The perspective regarding species, as with all taxa, must be reflective of scientific practice in not only systematics but also other fields in biology. For instance, we too often neglect to acknowledge that because evolutionary biology is foundational to systematics, taxa are not class constructs, but rather the products of discreet inferential actions intended to impart causal understanding, e.g. the inferences of phylogenetic hypotheses—as cladograms—from observations of differentially distributed organismal characters. Systematics deals with systematization, not classification [10–14]. As will be shown in this chapter, the scope of taxa extends to a number of types of biological phenomena involving organisms that are not routinely recognized by our formal nomenclatural systems, i.e. the *International Codes of Nomenclature* (e.g. [15]) or the *PhyloCode* [16]. The challenge is to place species into the more inclusive context of taxa. In doing so, we have an opportunity to not only formally define the term *species* such that it is concordant with the definition of *taxon*, but also acknowledge that the one term species has taken on a responsibility beyond its means in service of scientific inquiry.

In parallel with the significance and difficulties associated with the terms *species* and *taxon*, biologists have yet to settle the matter of defining *biodiversity*. Consider the following characterizations: “the collection of genomes, species, and ecosystems occurring in a geographically defined region” [17; see also 18–21; but see 22 for alternative opinions]; “the number of species observed or estimated to occur in an area (species richness)... This results from widespread recognition of the significance of the species as a biological unit...” [23: p220; see also 24–27]; “variation at all levels of biological organization” [28: p3; see also 29]; or “the variability among living organisms from all sources including... terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems” [30: p89; 31: p13, 109]. While biodiversity encompasses notions of spatial and temporal variation, the currency of that variation remains unsettled, ranging from the properties of organisms to taxa, but with species being the most popular subject [9, 32]. The definitional ambiguities regarding species and biodiversity carry with them potential negative epistemic and operational implications in fields as diverse as systematics, evolutionary biology, ecology, and conservation.

The vagaries of defining biodiversity stem in large part from the lack of consensus among systematists as to the definition of species, much less the more inclusive term taxon (e.g. [7, 33–36]). Thus, justifying actions under the guise of conservation will remain ambiguous per the largely arbitrary focus on the one taxon, species. As will be shown in this chapter, settling the matter of how to characterize biodiversity and conservation requires acknowledging the transitive relations between taxa, biodiversity, and conservation: {(taxa, biodiversity), (biodiversity, conservation), (taxa, conservation)}. These relations manifest themselves as follows:

biodiversity must be determined in the context of *taxa*; *biodiversity* determines the limits on *conservation*; *taxa* determine the realization of *conservation*. Regarding species, these relations have the added benefit of emphasizing the relevance of formal definitions of biodiversity and conservation to a formal definition of species that is consistent with biological systematics practice. These definitions follow from the fact that they reflect the inferential products of our observations of organisms. There is the added consequence of recognizing that the one term species cannot accommodate the variety of causal events to which it has been associated and also be cogently defined. The time has come to begin giving serious consideration to a more scientifically and operationally reasonable parsing of 'species' with new sets of terms that accurately convey a variety of non-comparable causal events.

Pursuant to the transitive relations outlined above, this chapter will pursue three interrelated issues. The first is to present a solution regarding the role of *taxa* when speaking of systematics, biodiversity, and conservation. This entails identifying the objects that cause our perceptual beliefs, i.e. individual organisms, and the inferential relations of objects/beliefs to the variety of explanatory hypotheses referred to as *taxa*. It is then a straightforward matter to show that species, as a taxon, is but one of the classes of hypotheses used in the pursuit of causal understanding in systematics. This offers an advance toward defining the term species as developed by Fitzhugh [12–14, 37] and recognizing the inherent limits of that definition and the need for additional terms.

If the objects from which our perceptual beliefs are derived in the biological sciences are individual organisms (more properly 'semaphoronts' *sensu* [1]; cf. quote above **Introduction**), not species or other *taxa*, then we need to assess whether or not genes, species, ecosystems, etc., can be regarded as 'units' or 'entities' to which biodiversity and conservation refer. The second goal of this chapter is to present a formal, operational definition of biodiversity that is not only consistent with conservation, but also the nature of *taxa* as explanatory hypotheses. From a systematics perspective, biodiversity cannot be construed in terms of genes, specific/phylogenetic *taxa*, or ecosystems, but rather in the context of past, proximate tokogenetic (reproductive) events related to groups of organisms that exist in the present. The restriction imposed is one directly related to the objects and events that conservation attempts to conserve: circumscribed tokogenetic events into the future – *not species, not taxa*. When referring to biodiversity, one can argue that population- or intraspecific-level variation/polymorphism, inclusive of smaller-scale heterogeneity (e.g. 'distinct population segments' [38]; 'evolutionarily significant units' [39–42]; 'designatable units' [43]) can be considered along with specific- and supraspecific-level (i.e. phylogenetic) hypotheses. The only roles population-, intraspecific-, specific-, or phylogenetic-level *taxa* have to play in this regard is in the capacity of surrogates for denoting inferred, temporally proximate systems of past tokogeny. *Taxa*, including species, are inferential products functioning to provide causal understanding of what is perceived of observed organisms, thus *taxa* are not objects to which biodiversity can directly apply. The subjects to which biodiversity refer are, instead, individual organisms that exist in the present – not species, genomes (which, while a functional term, refer to parts of organisms), or ecosystems (the interactions of organisms with their surroundings as well as other organisms). The reference to

organisms in the context of biodiversity is operational only in the sense of maintaining geographically circumscribed sets of tokogenetic events into the future, i.e. conservation.

In speaking of maintaining future tokogeny in reference to biodiversity, the third goal of this chapter will be a formal, operational definition of conservation. This will entail the view that conservation is an activity focused on future tokogeny among or between individuals, not the maintenance of taxa, including species. It is individual organisms and their potential to undergo future tokogeny that is the subject of conservation. The definition of conservation in terms of individuals and potential tokogeny imposes limits not only on the definition of biodiversity but also definitions of taxon and species. As conservation pertains to the maintenance of tokogenetic events among groups of individuals into the future, the subject of biodiversity is also those groups of individuals. But in the case of biodiversity, taxa provide the epistemic, as well as causal basis for delimiting those groups, upon which conservation has a basis for implementation.

2. The nature of taxa

As indicated in the **Introduction**, definitions of taxon, biodiversity, and conservation are interdependent by way of their transitive relations. For instance, a key element in discussions of biodiversity and conservation has been species [9, 32, 44–46], and sometimes by extension, intra- and supraspecific taxa. Addressing the matter of defining biodiversity and conservation cannot solely rely on presentation of a definition of species. The more general question, ‘what are taxa?’, must first be addressed. Answering this question has significant consequences for characterizations of biodiversity and conservation if taxa are to play any role, per their transitive relations.

Definitions of taxon have taken two general approaches: (1) taxa are class constructs: e.g. “a taxonomic group of any rank” [47: p9; 48–59]; or (2) taxa are quasi-explanatory accounts, e.g. “A taxon or taxonomic group... can mean only a group of organisms related genetically (or so related to the best of our knowledge)... It is a taxonomic group or assemblage of plants or animals, having certain characteristics in common which we take as evidence of genetic relationships, and possessed of some degree of objective reality” [60: p38; 15, 61, 62]. This class versus explanation distinction is often ambiguous. It is not uncommon to see definitions of taxon as a class construct yet also referred to in an evolutionary context, such that taxa must be interpreted as explanatory vehicles. For instance, Kardong [63: p330] states, “A taxon is simply a named group of organisms. A taxon may be a natural taxon, one that accurately depicts a group that exists in nature resulting from evolutionary events. Or a taxon may be an artificial taxon, one that does not correspond to an actual unit of evolution.” The causal connotations associated with (2) have also taken on the form of considering taxa as natural kinds, or ‘homeostatic property cluster kinds’ [64–71].

In contrast to characterizations of taxa, discussions of species *per se* tend to consider three alternatives. Species are (1) class constructs [48, 53, 72], (2) entities with the ontological status of individuals [5, 35, 36, 70, 73–90], or (3) natural kinds [64–71, 88, 91–95]. A fourth option is

the view that species are 'segments of lineages' [16, 45, 94]. Discussions of individuality and natural kinds, whether in regard to species or taxa as a whole, have degraded into little more than rhetorical devices, e.g. [71, 88, 95, 96]. Considering species in the broader context of taxa, arguments have been provided by Fitzhugh [10–14, 37, 97, 98] outlining that neither the class nor individuality thesis is appropriate to the issue (see [34] for extensive critiques), and the lineage and natural kinds concepts are incomplete characterizations relative to the treatment of taxa as explanatory hypotheses. Taxa are not mere classes, given that the goal of science is not classification but rather systematization, i.e. the placement of objects into some theoretical framework for the purpose of acquiring causal understanding [55, 99–101; *contra* 93]. Taxa, including species, cannot be conceived as individuals for the fact that there are no discernible properties by which such 'entities' could be discovered, recognized, or described [102, 103]. While the lineage and natural kinds concepts approach the necessary explanatory tone, neither has been sufficiently developed in terms of their inferential relations to the nature of other taxa and the intersections with the objects that are our interest, i.e. organisms. What was proposed by Fitzhugh [12, 13, 37; cf. 34 for a similar, independently derived perspective] is that as our perceptions are caused by individual organisms, we naturally apply a variety of explanatory hypotheses to those perceptions, and at least some of those hypotheses are formally represented by names controlled by international bodies governing nomenclatural actions (e.g. [15]; cf. [104, 105] for examples of implementation in this context). Several classes of these hypotheses are shown in Figure 1, derived from Hennig [1: fig.6; see also 12: fig.1]. Note that what are observed in the present are individual organisms (semaphoronts). Such perceptions are possible because of the particular properties instantiated by those objects. An observation statement is itself an explanatory account of one's sense perceptions, where the causes of those perceptions are the existence of objects [106]. Beyond our perceptual hypotheses are a variety of other causal accounts that are routinely invoked to answer specifiable questions regarding the properties of organisms. The relations between causal questions that might prompt explanatory hypotheses of the types shown in Figure 1 and how they are communicated by way of informal and formal names are presented in Table 1.

What is apparent is that species *sensu lato*, much less all taxa, are not the fundamental objects or entities of which we speak when referring to observations (*contra* e.g. [9]). Indeed, as outlined later, questions like "Are species real?" can be only answered by a very qualified 'yes.' Species are real to the extent that they, as well as all taxa, represent specifiable sets of past causal events involving individual organisms, not for the fact that species/taxa are entities (*fide* [9, 35, 107]). As well, the nature of inferences to species cannot entail the notion that the relation between organismal characters and species is one of 'diagnosis,' or that diagnoses are a matter of hypothesis testing (e.g. [108]).

The inferential derivation of all other taxa becomes even more apparent when we acknowledge that the goal of biological systematics is (or should be, cf. [10, 12–14, 98, 109]) consistent with that of scientific inquiry [55, 110–118]: to acquire ever-increasing descriptive and, more importantly, causal understanding. Indeed, the view that systematics is not a process of classification *qua* discerning and arranging classes via acausal 'relationships' (e.g. [57]) or discovering metaphysical individuals (e.g. [85]), but instead an endeavor to pursue causal

understanding clearly extends from Darwin's [119: chapter XIII] own views. Ghiselin [61: p87] correctly notes that,

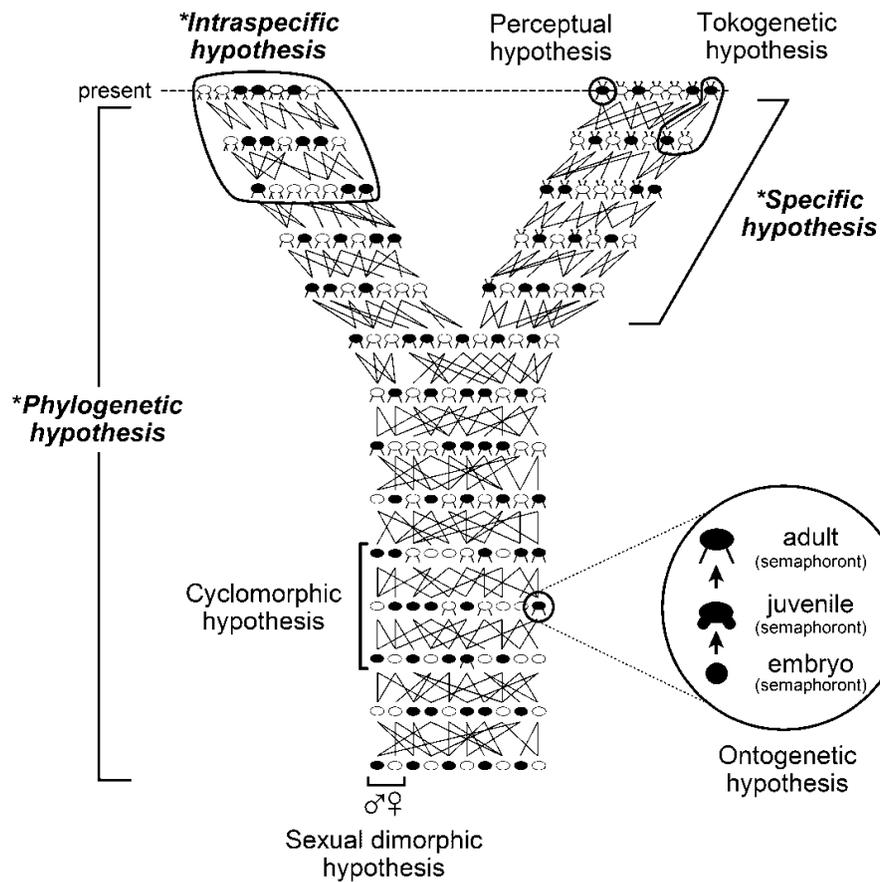


Figure 1. Relations between perceptual, ontogenetic, tokogenetic, intraspecific, specific (cf. Table 1: 'species₁,' 'species₂,' 'species₄') and phylogenetic hypotheses (adapted in part from [1: fig.6; 12: fig.1; 37: fig.1; 98: fig.1]). Those classes of taxa that might be referred to in the context of biodiversity and conservation are marked with an asterisk (*), i.e. intraspecific, specific, and phylogenetic.

"Systematics has scientific value as explanation, not as mere description. The purpose of classification is not the accurate pigeonholing or identification of enzymes or dried specimens, but the assertion of meaningful propositions about laws of nature and particular events."

If taxa are explanatory hypotheses directed at our observations of organisms, then there are two interesting consequences for biodiversity. The first is that species are not the exclusive units or entities to be considered in the determination or communication of biodiversity or conservation. It has been the pervasive conflation of individual organisms with species that has led to the misconception that species are discernible things and the principle objects of interest. The second consequence is that supraspecific hypotheses are not epistemically equivalent to specific hypotheses, thus negating the notion of taxonomic surrogacy [26, cf. references therein promoting its use; also referred to as 'taxonomic sufficiency,' e.g. 120–123; not to be confused with 'surrogacy' as applied in conservation, cf. 32]. These are distinct classes

of hypotheses inferred from different sets of theories [12–14]. Similarly, supraspecific hypotheses assigned the same rank are not epistemically equivalent relative to hypotheses of other ranks [12, 26, 120; *contra* 124]. Viewed from the perspective of cladograms, there are no objective criteria for selectively assigning some taxa formal, ranked names to the exclusion of remaining hypotheses implied by those cladograms. Lacking such equivalence is the strongest argument against the use of taxonomic surrogacy, at least with regard to supraspecific taxa serving as representations of species.

Causal questions:	Relations:	Represented by:
"Why do I have these sense perceptions?"	<i>Perceptual hypothesis</i> – An individual exists.	Observation statement
"Why does this individual have character X at time t_2 in contrast to Y at t_1 ?"	<i>Ontogenetic hypothesis</i> – This individual has character X at time t_2 because it is part of the ontogenetic trajectory.	Semaphoront names, e.g. "embryo," "larva," "adult"
"Why are these individuals observed at this location in contrast to some other location?" "Why does this individual, or individuals, have character X in contrast to Y?"	<i>Tokogenetic hypothesis</i> – Individuals are at this location because they are products of past tokogenetic events among other individuals. This individual, or individuals, has character X because the genetic capacity to exhibit the character was passed on from their parent(s).	Families, demes, populations, communities, etc.
"Why do individuals to which species hypothesis <i>x-us</i> refers have either character X or Y in contrast to only character X observed among other individuals?"	<i>"Intraspecific" hypothesis</i> – The reproductively isolated population is polymorphic because character Y originated in the population, such that observed individuals with X and Y are products of past tokogenetic events among individuals with those characters.	Polymorphism
"Why do these individuals have character X in contrast to character Y observed among individuals to which other species hypotheses have been applied?"	<i>Species₁ hypothesis</i> – <i>character origin, with subsequent fixation via tokogeny by sexual reproductive events</i> . Individuals have character X because it originated among individuals with character Y, and X eventually became fixed throughout the population, such that individuals observed in the present are products of past sexual-based tokogenetic events involving individuals with that character.	Species <i>sensu lato</i> names

Causal questions:	Relations:	Represented by:
	<p><i>Species₂ hypothesis – simultaneous character origin/fixation via tokogeny by sexual reproductive events, i.e. hybridization, polyploidy. Individuals have character X because it immediately originated as a consequence of hybridization, such that individuals observed in the present are products of past sexual-based tokogenetic events involving hybrid individuals with that character.</i></p> <p><i>Species₃ hypothesis – simultaneous character origin/fixation, with subsequent tokogeny by asexual, apomictic/ parthenogenetic, or self-fertilizing hermaphroditic reproductive events.</i></p> <p>Individuals have character X because it originated in an individual, such that individuals observed in the present are products of subsequent past asexual-, apomictic- / parthenogenetic-, or self-fertilizing-based tokogenetic events derived from that original individual.</p> <p><i>Species₄ hypothesis – character origin, with subsequent fixation via tokogeny by alternations of sexual and asexual reproductive events. Individuals have character X because it originated among individuals with character Y, and X eventually became fixed throughout the population, such that individuals observed in the present are products of past alternating sexual and asexual tokogenetic events involving individuals with that character.</i></p> <p><i>Species₅ hypothesis – immediate character origin/fixation via horizontal genetic exchange. Individuals have character X because it immediately originated in an individual from a horizontal genetic exchange event, such that individuals observed in the present are products of subsequent past asexual-based tokogenetic events derived from that original individual.</i></p>	

Causal questions:	Relations:	Represented by:
"Why do these individuals, to which species hypotheses <i>a-us</i> and <i>b-us</i> refer, have character <i>X</i> in contrast to character <i>Y</i> ?" (applicable to gonochoristic or cross-fertilizing hermaphroditic organisms)	<i>Phylogenetic hypothesis</i> – Individuals have character <i>X</i> because this character originated within a population with character <i>Y</i> , and <i>X</i> eventually became fixed throughout the population, and there was subsequent splitting of that population into two or more populations.	Supraspecific names

Table 1. Comparisons of hypotheses commonly encountered in biological systematics (modified from [12]). Note that within what has traditionally been considered the scope of species it is necessary to distinguish five different sets of causal events that account for shared features. See Figure 1 for graphic representations of each hypothesis (only 'species,' hypotheses shown).

3. Inferences of taxa

The previous section outlined the link between biological systematics hypotheses, colloquially known as taxa, and what exists in the form of observed organisms with properties explained by those hypotheses (Table 1, Fig. 1). As the principle goal in all fields of science is the acquisition of causal understanding, the inferential relations in systematics that span our observation statements and explanatory hypotheses can be summarized as follows:

[A]

- a. organisms, as objects, are perceived as a matter of the properties they instantiate;
- b. as consequences of perceptions in (a), represented by our causal questions, the focal point of biology is individual organisms (semaphoronts), or parts or remnants of organisms (Table 1);
- c. there are a variety of explanatory hypotheses that serve as answers to questions in (b) regarding perceptions of organisms; the following classes of hypotheses are common in systematics and other biological fields (Table 1; Fig. 1):
 - i. ontogenetic (via semaphoronts)
 - ii. tokogenetic
 - iii. intraspecific/polymorphic
 - iv. specific (species) *sensu lato* (cf. Table 1)
 - v. phylogenetic;
- d. the goal of inferring the hypotheses in (c) is to provide at least preliminary explanatory accounts of differentially distributed properties observed among semaphoronts.

It is from these inferential relations that implications can be identified for considerations of intraspecific/polymorphic, specific, and phylogenetic hypotheses for biodiversity and conser-

vation. Notice that each class of explanatory hypothesis in **[A](c)** has as its basis particular properties of organisms (Table 1). Each type of hypothesis serves to address a subset of the totality of properties one perceives, and as such, hypotheses inferred from different causal theories are not epistemically equivalent [12, 13]. These conditions present consequences for the view that taxa, no matter the rank, are the relevant subjects in the definitions or discussions of biodiversity and conservation.

The inferential links between our perceptions of organisms and conclusions in the form of taxa [cf. **[A](c)**] have been analyzed by Fitzhugh [10, 12–14, 37, 97, 98, 109, 125, 126], thus only briefly described here. The process of reasoning from observed effects, in this case the properties of organisms, to explanatory hypotheses (taxa) is known as abduction or abductive inference [127–154; cf. 10–13, 37, 97, 98, 109, 125, 126 for considerations of abduction in relation to biological systematics and evolutionary biology]. Abduction can be schematically represented as:

[B]

- auxiliary theory(ies)/hypotheses
- theory(ies) relevant to perceived effects
- perceived effects
- therefore, explanatory hypothesis

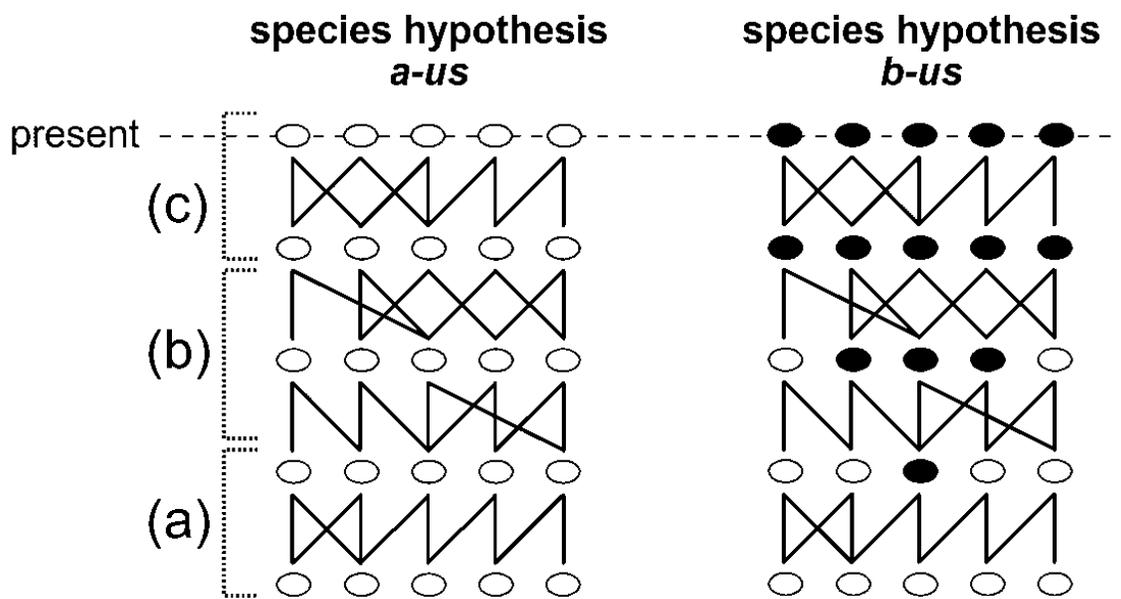


Figure 2. Diagrammatic representations of two specific hypotheses (cf. Table 1: ‘species₁,’ ‘species₂,’ ‘species₄’), indicating (a) origins and (b) fixation of the respective properties of gray and black body walls, with (c) subsequent tokogeny resulting individuals observed in the present.

While a form of non-deductive inference, abduction is distinct from induction *sensu stricto*, which entails the process of hypothesis testing, *contra* [155]. Deduction provides for stipulating potential test evidence.

Consider the example in Figure 2. Specimens are observed with the unexpected or surprising properties of either gray or black bodies. It is the nature of these observations that prompts the implicit or explicit causal questions of why these properties are present among individuals in contrast to what has been previously observed (and expected). Specific hypotheses *a-us* and *b-us*¹ provide respective explanatory accounts of the observations. The theory used for the purposes of inferring these hypotheses would have the form described by Fitzhugh [12, 13; see also 37]:

[C]

If property *Y* originates by mechanisms *a, b, c... n* among gonochoristic [*partim*] or cross-fertilizing hermaphroditic individuals of a reproductively isolated population with character *X*, and *Y* subsequently becomes fixed throughout the population during tokogeny by mechanisms *d, e, f... n*, then individuals observed in the present will exhibit *Y*.

The basis for giving the label 'species' to these hypotheses is contingent on the same theory being applied to particular features, which is consistent with the formal definition of species offered by Fitzhugh [13: p207]:

[D]

An explanatory account of the occurrences of the same character(s) among gonochoristic or cross-fertilizing hermaphroditic individuals by way of character origin and subsequent fixation during tokogeny.

Given the theory in [C] and definition in [D], Fitzhugh [13] pointed out that specific-level hypotheses cannot be applied to organisms with obligate asexual, parthenogenetic, or self-fertilizing hermaphroditic reproductive strategies, suggesting that causal accountings applicable to such individuals would be akin to phylogenetic hypotheses (cf. [G], [H]); not to be confused with the 'phylogenetic species concept' [6, 156, 157; cf. 158]. The situation is, however, more complex as is apparent in Table 1. At least five sets of general causal conditions are subsumed under species *sensu lato*—'species₁' through 'species₅'. Contrary to Fitzhugh's [13] suggestion, it would be more accurate to regard 'species₃' (asexual, apomictic/parthenogenetic, self-fertilizing hermaphroditic hypotheses) and 'species₅' (horizontal genetic exchange hypotheses; [159–163]) distinct from phylogenetic hypotheses since the causal events entailed by the latter involve character origin/fixation as part of tokogeny that is to some extent sexual-based interbreeding, with subsequent population splitting (cf. [H]). The remaining classes of hypotheses, 'species₁', 'species₂', and 'species₄', refer to causal events among individuals to which phylogenetic hypotheses *also* apply. While the definition of species by Fitzhugh ([13];

¹ I have intentionally avoided using the binomial arrangement of genus and specific epithet to denote specific hypotheses. As supraspecific (= phylogenetic) hypotheses are the products of inferential acts that are separate from inferences of specific hypotheses (Table 1), it can be argued that there should be no requirement that formal recognition of a specific hypothesis be made in conjunction with any phylogenetic (= genus ranked) hypothesis [12, 14, 104, 105].

cf. [D]) satisfies the requirement of limiting specific hypotheses to obligate sexual-based interbreeding ('species₁', 'species₂'), this definition can be extended to organisms with more complex life histories involving combinations of asexual and sexual reproductive events ('species₄').

Two alternative strategies might be considered for handling the five connotations of species in Table 1. Either approach might appear unorthodox, but what we save by holding to tradition comes at the expense of precisely conveying hypotheses and accurately representing biodiversity and conservation. What is apparent is that effective communication of a multitude of causal events represented in systematics hypotheses cannot be accomplished with the one term, *species*. The more radical approach would be to limit specific hypotheses to 'species₁' via the theory in [C], while referring to 'species₂₋₅' as inferential products of four additional theories:

[E]

- a. *species theory* ('species₁'): See [C]; phylogenetic hypotheses, *sensu* [H], are also applicable to individuals to which such specific hypotheses apply;
- b. *interspecific hybrid theory* ('species₂'): if property *Y* simultaneously originates and is fixed by hybridization, e.g. polyploidy, among gonochoristic or cross-fertilizing hermaphroditic individuals to which respective 'species₁' hypotheses refer, such that subsequent tokogeny is limited to individuals with *Y*, then individuals observed in the present will exhibit *Y*; phylogenetic hypotheses, *sensu* [H], are also applicable to individuals to which such specific hypotheses apply;
- c. *asexual-autogamic theory* ('species₃'): if character *X* exists among individuals with obligate reproduction that is asexual, apomictic/parthenogenetic, or self-fertilizing, and character *Y* originates by mechanisms *a, b, c... n*, during tokogeny, then individuals observed in the present exhibiting *X* and *Y* are respective tokogenetic products of individuals with those characters [13: p210]; phylogenetic hypotheses are not applicable to individuals to which such specific hypotheses apply;
- d. *asexual-sexual theory* ('species₄'): if property *Y* originates by mechanisms *a, b, c... n* among individuals with *X* during one of the alternative phases of asexual or sexual tokogenetic events, and *Y* subsequently becomes fixed throughout the population during tokogeny by mechanisms *d, e, f... n*, then individuals observed in the present will exhibit *Y*; phylogenetic hypotheses, *sensu* [H], are also applicable to individuals to which such specific hypotheses apply;
- e. *horizontal genetic exchange theory* ('species₅'): if character *X* exists among individuals and character *Y* subsequently occurs by horizontal genetic exchange mechanisms *d, e, f... n* with other individuals, then individuals observed in the present exhibiting *X* and *Y* are respective tokogenetic products of individuals with those characters.

A more conservative approach entails using the specific theory and definition in [C] and [D], respectively, to broadly accommodate 'species₁', 'species₂' and 'species₄'. 'Species₃' and 'species₅' remain classes of explanatory accounts among organisms that cannot be co-

ordinately accommodated by either specific *sensu stricto* (cf. [D]) or phylogenetic (cf. [G], [H]) hypotheses and both types of hypotheses would require new, separate formal names distinct from the rank of species. Acknowledging theories [E](c) and (e) for 'species₃' and 'species₅,' respectively, makes apparent the importance of the suggestions offered here: the applications of these theories are not necessarily mutually exclusive for obligate asexually reproducing individuals [80, 159, 163–166]. The solution to conveying both classes of events must be by way of taxon names distinct from the one term 'species.' No doubt exceptions to the theories in [E] can be pointed to. Rather than intended as an exhaustive list, the objective here is to recognize that protocols need to be pursued for accommodating a variety of classes of events to be communicated in a manner more effective than under the one heading, 'species.'

Applying the specific theory in [C] or [E](a) to the observations in Figure 2, the inference can be summarized as follows:

[F]

Theory: If property Y originates by mechanisms $a, b, c... n$ among gonochoristic or cross-fertilizing hermaphroditic individuals of a reproductively isolated population with character X , and Y subsequently becomes fixed throughout the population during tokogeny by mechanisms $d, e, f... n$, then individuals observed in the present will exhibit Y .

Observed effects: Individuals have gray bodies, in contrast to white or black.

Therefore, explanatory hypothesis (species taxon a -us, cf. Fig. 2): The gray character arose in a reproductively isolated population of white individuals, and the gray condition subsequently became fixed throughout the population during tokogeny, leading to gray individuals observed in the present.

While this inference pertains to 'species₁' hypotheses, there are several aspects that can be extended to all of the classes of hypotheses in Table 1 that are inferred from theories in [E], and will also figure prominently in the definitions of biodiversity and conservation presented later. Note that individuals observed in the present are products of proximate instances of tokogeny (Fig. 2c). Regardless of whether these tokogenetic events occurred subsequent to the origin (Fig. 2a) and fixation (Fig. 2b) of the character to which the hypothesis refers, or were contemporaneous with either of those events, observed individuals are products of tokogeny. What will be shown later regarding proximate tokogeny is that specific *sensu lato* as well as supra-specific taxa (phylogenetic hypotheses) are only tangentially relevant to biodiversity and conservation. Specific- and phylogenetic-level taxa serve as surrogates, referring to separate, hypothesized proximate systems of tokogeny (Fig. 2c) that are used to denote biodiversity. But in the case of conservation, taxa are largely irrelevant, as the scope of the act of conservation is potential processes of tokogeny into the future, not the maintenance of intraspecific, specific, or supraspecific taxa (Fig. 1, Table 1). Taxa cannot be conserved because they are not spatio-temporally restricted things – they are explanatory constructs only relevant to observed organisms.

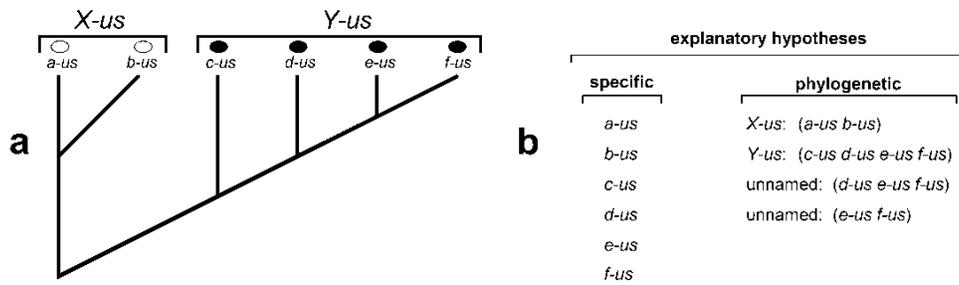


Figure 3. a) Cladogram schematically summarizing hypothesized causal events. (b) List of all hypotheses indicated in the cladogram in (a).

Consider next the example in Figure 3a. Presented as a cladogram, phylogenetic hypothesis *X-us* implies that the property gray originated and became fixed among individuals as a result of an unspecified causal event(s), subsequent to which was a population splitting event, the specifics of which are also not indicated in the diagram. *Y-us*, on the other hand, entails that the character black originated and became fixed, subsequent to which were a series of population splitting events, to which other unspecified hypotheses refer. Unlike the previous example of inferences of specific hypotheses *a-us* and *b-us* (cf. [F], Fig. 2), phylogenetic hypotheses *X-us* and *Y-us* are derived from a phylogenetic theory; somewhat different from the theory used to infer *a-us* and *b-us* (cf. Table 1: ‘species₁’, ‘species₂’, ‘species₄’, [E](a), (b), (d); [10, 12–14, 37, 98, 126]):

[G]²

If character X exists among individuals of a reproductively isolated, gonochoristic or cross-fertilizing hermaphroditic population and character Y originates by mechanisms a, b, c... n, and becomes fixed within the population by mechanisms d, e, f... n [= ancestral species hypothesis], followed by event or events g, h, i... n, wherein the population is divided into two or more reproductively isolated populations, then individuals to which descendant species hypotheses refer would exhibit Y.

The abductive inference of hypothesis *Y-us*, for instance, would have the form:

[H]

Theory: If character X exists among individuals of a reproductively isolated, gonochoristic or cross-fertilizing hermaphroditic population and character Y originates by mechanisms a, b, c... n, and becomes fixed within the population by mechanisms d, e, f... n [= ancestral species hypothesis], followed by event or events g, h, i... n, wherein the population is divided into two or more reproductively isolated populations, then individuals to which descendant species hypotheses refer would exhibit Y.

² While this ‘phylogenetic theory’ offers a common cause accounting, it actually refers to two classes of common cause events: character origin/fixation (applied to each set of shared characters) and population splitting. The implementation of the theory in [H] obviates Sober’s [167: p157] view that phylogenetic inference is a two-step process, i.e. “The first problem is... one infers a tree;... one uses an inferred tree to solve a further problem [of ancestral character transformation].”

Observed effects: Individuals to which species hypotheses *c-us*, *d-us*, *e-us*, and *f-us* refer have black bodies, in contrast to white or gray.

Therefore, explanatory hypothesis (supraspecific taxon *Y-us*, cf. Fig. 3a): The black character among individuals to which species hypotheses *c-us*, *d-us*, *e-us*, and *f-us* refer arose in a reproductively isolated population of white individuals, and the black condition subsequently became fixed throughout the population during tokogeny, followed by three events of population splitting to produce isolated populations to which descendant species hypotheses refer (*c-us*, *d-us*, *e-us*, *f-us*).

Note that the cladogram in Figure 3a refers to two classes of hypotheses – specific (*sensu stricto*; [F]) and phylogenetic. Of these, eight (six specific, two phylogenetic) are formally named, while two phylogenetic hypotheses are unnamed (Fig. 3b), i.e. (*d-us*, *e-us*, *f-us*) and (*e-us*, *f-us*). Acknowledging the presence of these latter, unnamed hypotheses highlights the erroneous view that supraspecific hypotheses can serve as 'taxonomic surrogates' for specific hypotheses. Supraspecific taxa invariably subsume any number of less general phylogenetic hypotheses, such that attempts to treat formally named hypotheses as surrogates for specific hypotheses is not only arbitrary at the level of phylogenetic hypothesis selection, but also arbitrary with regard to only focusing on the one class of systematics hypothesis called species (cf. Fig. 1, Table 1).

The inference in [H] would typically be said, albeit erroneously, to be a 'parsimony' approach (cf. [167–169]), in contrast to implementations of either maximum likelihood or Bayesianism (cf. [170–172]). Parsimony and likelihood cannot, however, be treated as separate concepts in abduction [10, 14]. So-called maximum likelihood methods require the assumption that one's observation statements regarding shared characters are inconsistent with the causal questions to be asked in relation to explaining those observations, given that a cladogram subsumes a series of incomplete explanatory hypotheses that take 'branch length' into consideration. By extension, likelihood methods utilize theories that are not necessarily common cause theories (cf. [G]) because rates of change are involved. Strictly speaking, using a rate-based theory applies to tokogenetic-, not phylogenetic-level phenomena. The consequence is that the scope of such inferences moves from being phylogenetic to either specific, polymorphic, or intra-specific/tokogenetic [10, 13, 14]. As noted by Cleland ([173: p572, emphasis original; see also 174–177]),

"The scientifically most fruitful common cause explanations appeal to *last* (proximate) common causes. A last common cause represents the causal juncture at which the items in the collection cease to share a more recent common cause. Because they maximize causal unity last common cause explanations have greater explanatory power than other common cause explanations."

Bayesianism, on the other hand, addresses changes in hypothesis belief relative to test evidence (*contra* e.g. [178–180]). Bayes' Theorem has no role to play in abductive inference for the fact that character data, as the basis for inferring phylogenetic hypotheses, cannot in turn be used to test those hypotheses [10, 14, 126].

4. Defining biodiversity and conservation

Most of the definitions of biodiversity cited in the **Introduction** make reference to three qualities: genomes, species, and ecosystems. Noss [22: p356] included an additional dimension, claiming that “Biodiversity is not simply the number of genes, species, ecosystems, or any other group of things [*sic*] in a defined area... Ecologists usually define ‘diversity’ in a way that takes into consideration the relative frequency or abundance of each species or other entity, in addition to the number of entities in the collection.” But as taxa are explanatory hypotheses rather than objects, Noss commits the common mistake (cf. [9]) of conflating species with individual organisms. As shown in Figures 1–2, [A], [F], and Table 1, individuals (represented/communicated by observation statements) and species are separate subjects produced from different inferential actions. Noss [22: p356, fig.1] further states there are “three primary attributes of ecosystems: composition, structure, and function,” and within each are interdependent, interrelated relationships (Fig. 4). Interdependence, much less hierarchical organization is at best dubious. For instance, ‘genes,’ if one assumes this to mean a discrete sequence of nucleotides, are not dependent upon ‘genetic structure’ and ‘genetic processes.’ The latter two are dependent on the presence of genes, as properties of organisms, not vice versa. Given what was discussed earlier regarding individual organisms as the focal point of observations in biology, we need only consider the compositional aspects in Figure 4, where the hierarchy includes genes, populations, and species. A key question to ask is whether or not any of these actually match what we perceive. Species *sensu lato* (Table 1, [E]) are explanatory hypotheses, not individuals, entities, or things. While a sequence of nucleotides can be indirectly discerned, they are only referred to as genes because of the functional role they play in causal processes during the life (ontogeny) of an organism. Sequences, as opposed to functional units *qua* genes, are properties of organisms. A population is a group of individuals, and speaking of that group is by way of one’s perceptions of individual organisms, and perhaps by extension past causal relations (Fig. 1, Table 1). There are no applicable emergent properties of a population one might perceive that are not manifestations of the component organisms of that population or their collective actions. The biological components that can be perceived in the more inclusive concepts shown in Figure 4, communities/ecosystems and landscape types, are individual organisms. Biodiversity could not have as its focus genes, species, or populations. The pertinent functional subjects are individual organisms. If we are to characterize a concept of biodiversity, it must be in terms of the tangible aspects of organisms, i.e. their intrinsic properties, that provide the basis for making relational statements about spatially or temporally different areas as consequences of the range of inferences in [A](c) (Table 1, Fig. 1). By their very nature, specific-level hypotheses – indeed all taxa – do not represent the totality of what is perceived of organisms. This is apparent from what is shown in Table 1, Figures 1–2, and [A](c). Different classes of biological systematics hypotheses provide answers to causal questions addressing any number of different classes of properties among organisms. To limit a conception of biodiversity to species [*sic*] would not only be to deny the explanatory relevance of other hypotheses used to account for other organismal properties, but also arbitrary. Circumventing this problem requires orienting focus away from species, to individual organisms and the properties they instantiate.

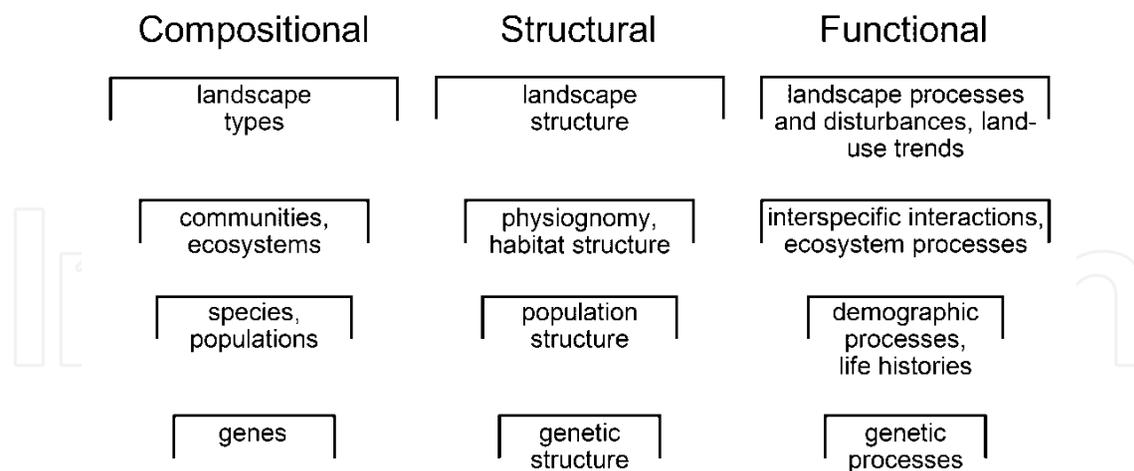


Figure 4. The three principle attributes of biodiversity according to Noss [22: fig.1], compositional, structural, and functional, and the hierarchical arrangements of components within each.

In contrast to the three-part hierarchies of Noss [22], Sarkar [32] suggested that among the entities [*sic*] considered in biodiversity and conservation, two hierarchies are used: spatial and taxonomic. The spatial hierarchy entails molecules, cell organelles, cells, individuals, populations, communities, and ecosystems. The taxonomic hierarchy contains alleles, linkage groups, genotypes, subspecies, species, genera, families, orders, classes, phyla, and kingdoms. While Sarkar's spatial hierarchy conveys part-whole relations, the taxonomic hierarchy is a mix of part-*cum*-function and explanatory hypotheses. As noted in the previous paragraph, such a 'hierarchy' fails for the fact that it does not contain entities to which biodiversity and conservation can refer.

If there is no epistemic basis for restricting a definition of biodiversity to genes, species *sensu lato*, or other taxa, and the objects of our observation statements are individual organisms, to what does biodiversity refer? Sarkar [32] is correct in pointing out that the answer is contingent upon identifying what is being conserved. If conservation is the act of conserving something, and that something is conveyed by the term biodiversity, then clearly we are not conserving specific or supraspecific taxa *sensu* [F] and [H] (Figs. 1–3, Table 1), or any taxon for that matter. Taxa are explanatory accounts, as inferential reactions to our observations of organisms, providing understanding of relevant features by way of past causal processes. Taxa are not tangible qualities existing in the present to which conservation efforts can be applied into the future. But it can be argued that there is a relation between conservation and taxa that allows for a cogent and operational definition of biodiversity – exemplifying the transitive relations between taxa, biodiversity, and conservation, and solidifying the status of species, regardless of connotation, as explanatory hypotheses. Recall the inferences of specific hypotheses in [F] (Fig. 2). It was noted that while such hypotheses have causal components that include character origin and fixation, the hypotheses also imply that individuals are products of proximate events of tokogeny (Fig. 2c). Per a given specific hypothesis, those proximate tokogenetic events would be separate from other such sets of tokogeny outlined by other specific hypoth-

eses. Similarly, since the phylogenetic inference in [H] (Fig. 3a) entails separately-inferred specific hypotheses (cf. [F], Fig. 2), the ‘terminal branches’ of the cladogram imply the same sets of proximate tokogenetic events. In point of fact, as exemplified in Figure 1 (Table 1), proximate tokogenetic events are components of not only specific and phylogenetic hypotheses but also intraspecific/polymorphic, and cyclomorphic hypotheses.

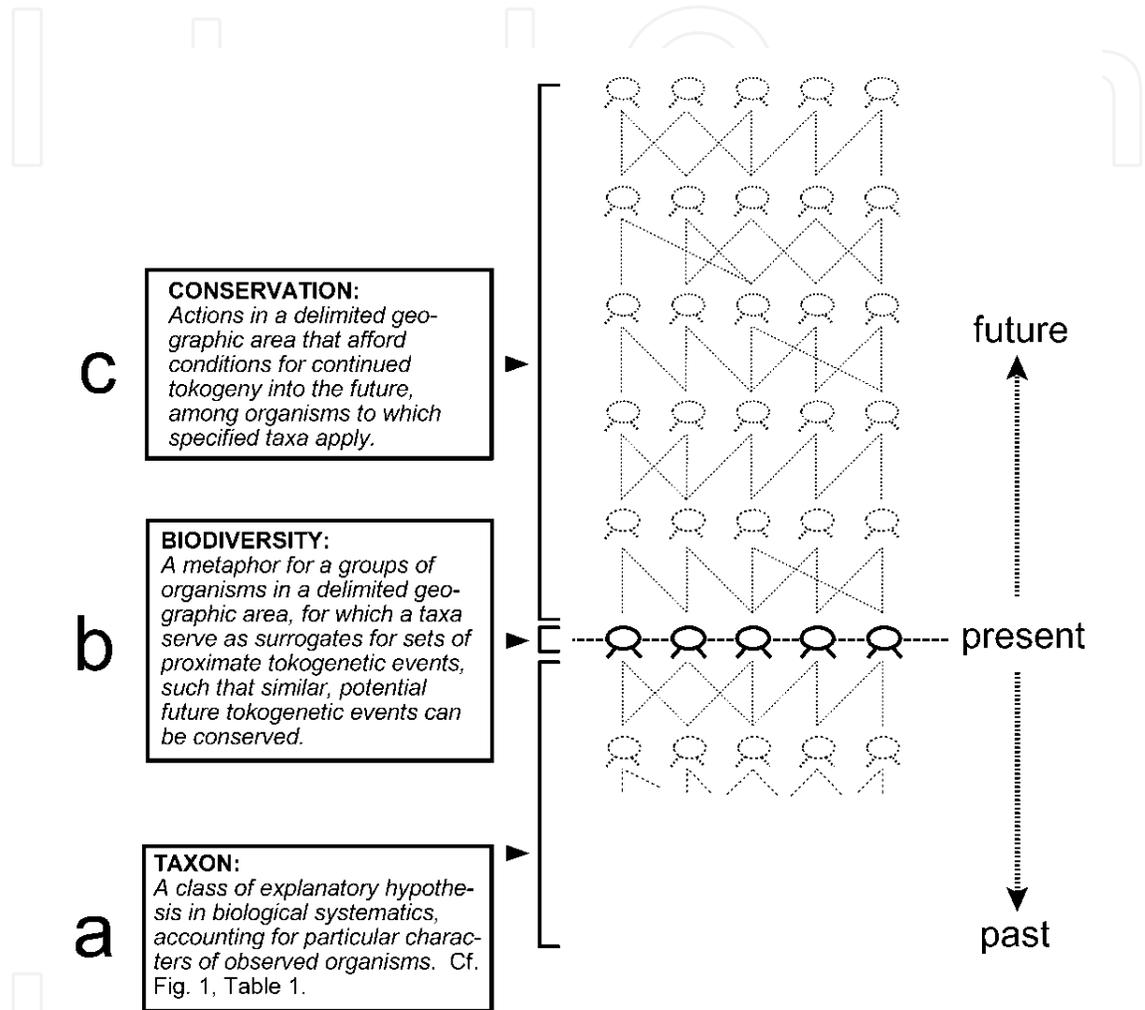


Figure 5. Schematic representation of relations between observed organisms, taxa, biodiversity, and conservation. Formal definitions of biodiversity and conservation are provided. Note that explanatory hypotheses referred to as taxa will be of different forms depending on the questions to which those hypotheses serve as answers (cf. Table 1, Figure 1). Yet, biodiversity and conservation focus on future tokogenetic events, regardless of the taxon used (cf. Figs. 3–5). Taxa serve as surrogates to denote the geographic scope of individuals to which biodiversity refers, and conservation is to be applied. Hypotheses regarding obligate asexual, apomictic/parthenogenetic, or self-fertilizing hermaphroditic tokogeny, or horizontal genetic transfer (cf. Table 1: ‘species₃,’ ‘species₅’) can be conveyed in the same type of diagram

Identifying temporally proximate tokogenetic events as components of most (ontogenetic excluded) classes of hypotheses in systematics provides not only the basis for defining biodiversity, but furnishes the relevant conceptual link to conservation – again illustrating the transitive relations between taxa, biodiversity, and conservation. Defining biodiversity can be

accomplished by illustrating the relations between taxa (*qua* sets of proximate tokogenetic events), organisms existing in the present, and conservation. These relations are schematized in Figure 5. Given our observations of organisms in the present, we abductively infer explanatory hypotheses referred to as taxa. Based on what was described earlier, a formal definition of taxon would be (cf. [12, 13]):

[I]

Taxon: A class of explanatory hypotheses in biological systematics, causally accounting for particular characters of observed organisms.

Contrary to what was suggested by Wilkins ([90: p146; see also [89]), taxa are not “phenomena that call for a theoretical explanation.” Taxa *are* the explanations. The phenomena to which they refer are organisms with differentially shared characters. Regarding intraspecific/polymorphic, specific *sensu lato*, and phylogenetic taxa, all of these hypotheses entail proximate tokogeny (Figs. 1, 5a). But taxa, inclusive of hypothesized proximate tokogenetic events, are not the actual objects of concern. Biodiversity cannot be characterized in terms of taxa *simpliciter*. Rather, biodiversity is best conceived as a metaphor, relating a circumscribed, contemporaneous group of organisms (Fig. 5b) to taxa, insofar as taxa serve as surrogates for proximate tokogeny (e.g. Fig. 2c). A formal definition of biodiversity would then be:

[J]

Biodiversity: A metaphor for groups of organisms in a delimited geographic region, for which taxa serve as surrogates for sets of proximate tokogenetic events, such that similar, potential future tokogenetic events can be conserved.

The definition allows for making rational decisions about what taxa serve as surrogates. Depending on the spatial scope of organisms under consideration, biodiversity cannot be strictly equated with just species or phylogenetic hypotheses (cf. ‘phylogenetic diversity,’ [107, 181–185]). That one speaks of biodiversity is first contingent upon observations of organisms by way of the properties they instantiate, followed by abductive inferences to hypotheses that account for certain of those properties, in part as matters of past tokogeny. Associated with reference to proximate tokogeny, itself a taxon (Fig. 1, Table 1), the definition of biodiversity in [J] has its greatest strength in providing an operational relation to conservation. The most tangible aspect of biodiversity as defined here is that it is either prompted by considerations of conservation or is the unambiguous concept to which conservation is directed, which is consistent with the perspective offered by Sarkar [32]. In terms of proceeding from the present – with observations of organisms in given areas – into the future, what are to be conserved are conditions offering the greatest potential for tokogenetic events like those referred to or implied by taxa (Fig. 5c). Regarding biodiversity as sets of tokogenetic systems is then consistent with this definition of conservation:

[K]

Conservation: Actions in a delimited geographic region that afford conditions for continued tokogeny into the future, among organisms to which specified taxa apply.

The intent of conservation is to enable future events of tokogeny among individuals, not to conserve taxa. To reiterate, taxa are inferential reactions to observations of individuals, indicating relevant past causal events accounting for particular organismal properties. It is epistemically meaningless to say conservation seeks to maintain explanatory hypotheses or taxa, especially since those hypotheses only have relevance to effects observed in the present, as individual organisms, not potential causal events among future individuals. But this error is the case when one suggests, for instance, that a habitat should be maintained as part of an effort to conserve particular species. Beyond correctly characterizing the nature and role of taxa, the utility of the definitions in [J] and [K] is that they are fully operational in relation to those taxa that would serve as relevant surrogates for biodiversity (Fig. 1, Table 1). Generalized examples of application, derived from Figure 5, are provided next.

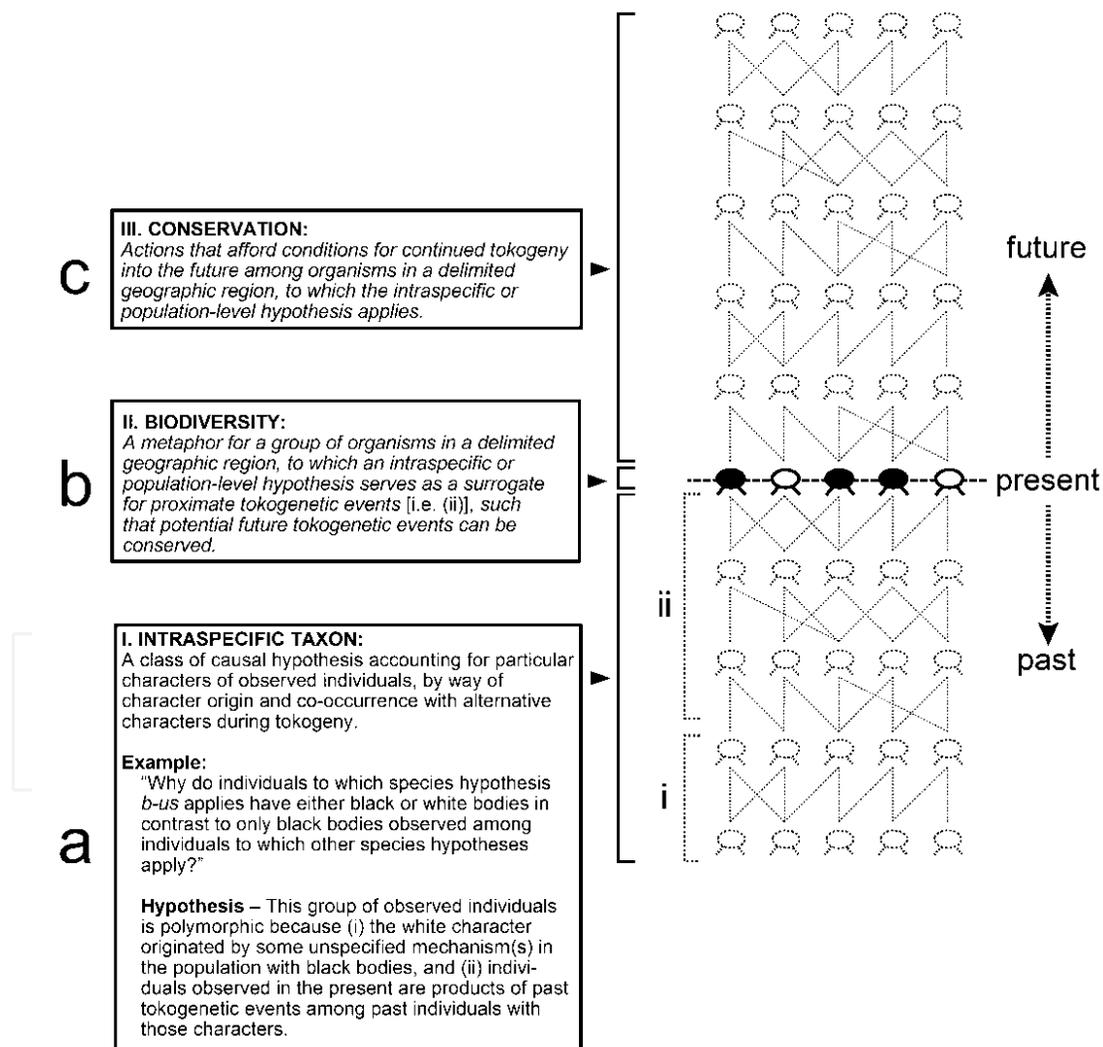


Figure 6. Example of the relations between observed individuals to which an intraspecific hypothesis is applied (cf. Figs. 1–2, Table 1), and biodiversity and conservation. See Figure 5 and text for additional explanation.

Speaking of intraspecific/polymorphic variation within a population implies past causal events of character origin [Fig. 6a(i)] and incomplete fixation [Fig. 6a(ii)] as accounting for observed conditions. Biodiversity within the present population is a matter of referring to variation or polymorphism as results of recent tokogeny (Fig. 6b). By extension, conservation involves actions that allow for continued tokogeny that might ensure the properties of individuals to which biodiversity refers (Fig. 6c). The consideration of biodiversity in terms of specific *sensu stricto* taxa as surrogates is essentially identical (Fig. 7). Biodiversity in relation to supraspecific taxa (Fig. 8), i.e. phylogenetic hypotheses, is similar to the two previous examples, once again indicating that biodiversity and conservation pertain to tokogeny, not species *sensu stricto* (i.e. 'species₁,' 'species₂,' 'species₄') or supraspecific taxa. Referring to supraspecific taxa (Fig. 8a) in the context of biodiversity necessitates considering specific hypotheses (Fig. 8b), since it is the latter that entail the relevant proximate sets of tokogenetic systems. Conservation then pertains to maintaining the continuity of those sets of tokogenetic systems into the future (Fig. 8c).

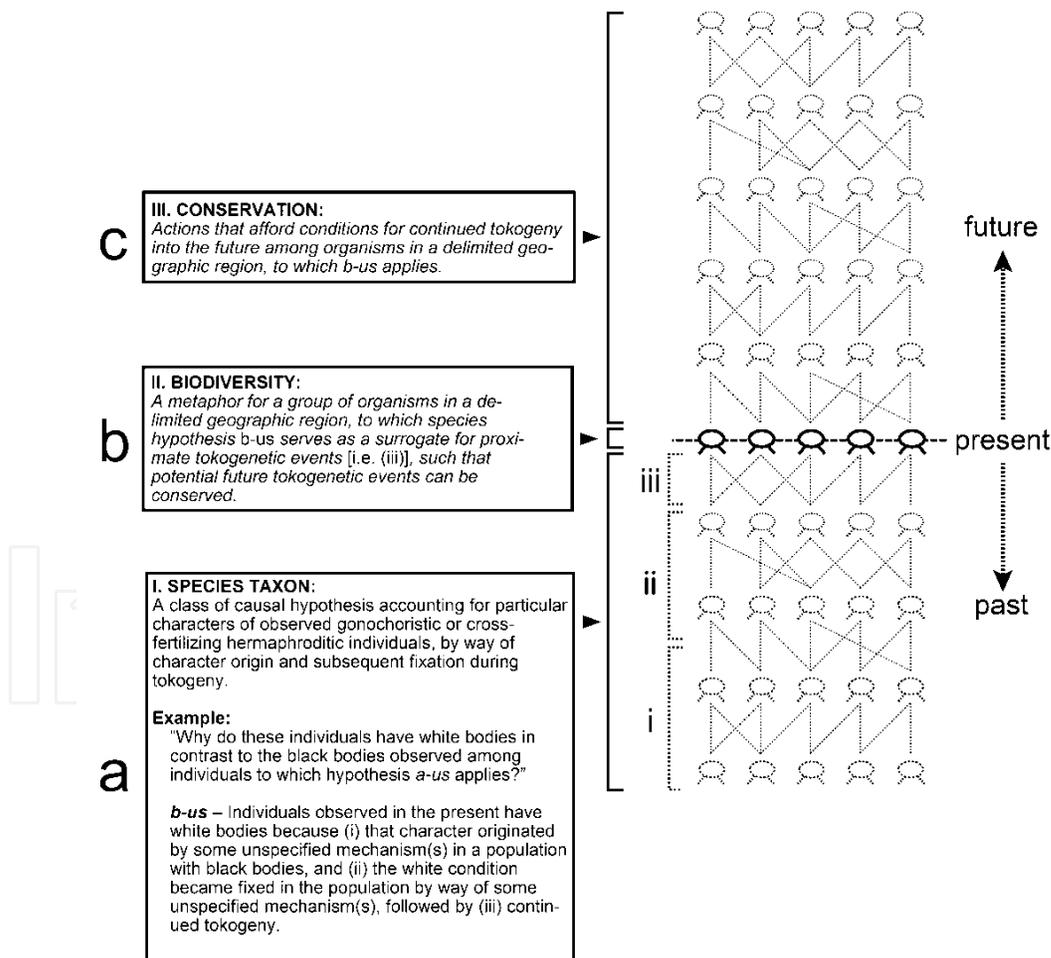


Figure 7. Example of the relations between observed individuals to which a species hypothesis is applied (cf. Figs. 1–2, Table 1), and biodiversity and conservation. See Figure 5 and text for additional explanation.

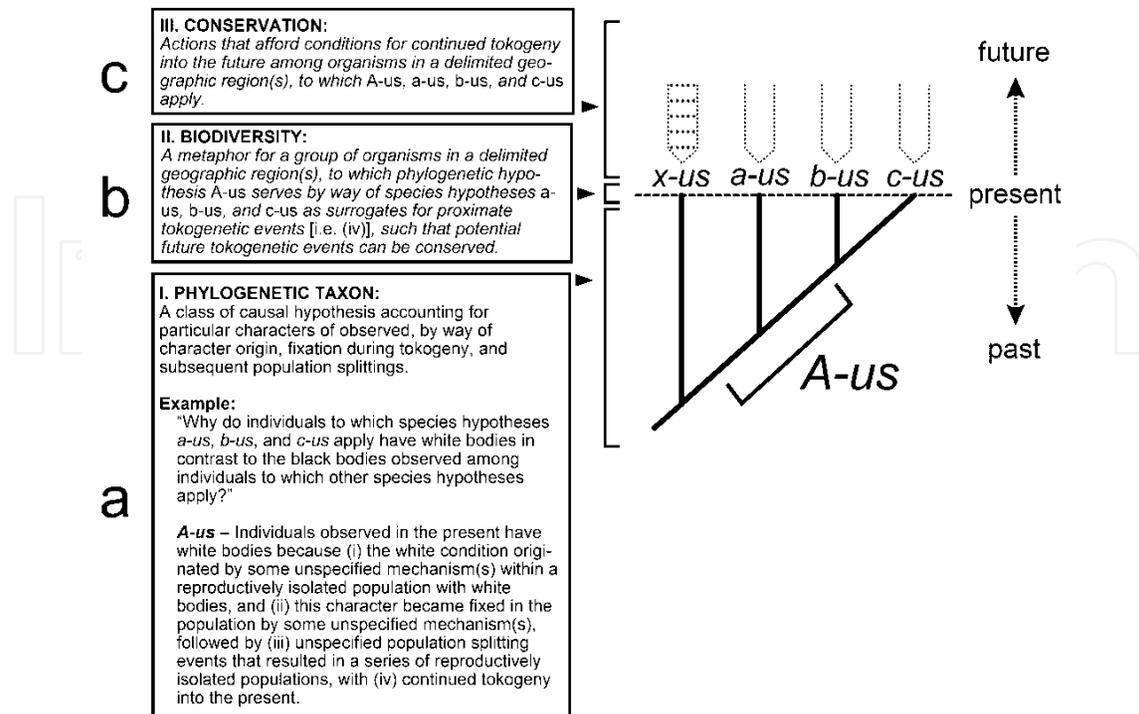


Figure 8. Example of the relations between observed individuals to which a phylogenetic hypothesis is applied (cf. Figs. 1–2, Table 1), and biodiversity and conservation. See text for additional explanation.

5. Discussion

The crux of the analysis presented in this chapter is that defining *species* (including *taxa*), *biodiversity*, and *conservation* are best approached from the perspective of the transitive relations between the concepts to which each of these terms refers. Recognizing these relations follows from the pursuit of causal understanding that is not only the goal of science in general but also the subfield known as systematics. But instead of limiting the question to “What are species?”, it has been shown that the more relevant question is, “What are taxa?” If species are taxa, then species have a standing no more and no less epistemically important than what are accorded other taxa. The consequences of answering the two questions can be summarized as follows: (1) at best, *species* [Table 1: ‘species₁’, ‘species₂’, ‘species₄’; [E](a), (b), (d)] is a class of systematics hypotheses applied to those organisms among which to some extent there is obligate genetic exchange by way of tokogenetic-based sexual reproductive events; the matter of other causal events to which species have been referred, i.e. ‘species₃’ and ‘species₅’ (Table 1, [E](c), (e)), require separate consideration; (2) *biodiversity* is a rhetorical device indicating relations between observed organisms and hypothesized sets of past sexual or asexual proximate tokogeny, not limited to species *sensu lato*, inferred from characters of organisms (cf. [J]); and (3) *conservation* is a reaction to the metaphor of *biodiversity*, in the form of actions that promote tokogeny into the future (cf. [K]).

In the context of taxa as explanatory hypotheses, as reactions to our observations of organisms, the scope of species in biology is in need of revision. Consider the insightful treatment by Wilkins [8]³. Among the 26 'species concepts' identified by Wilkins [6], Wilkins [8: p58, emphasis original] suggests there are "seven 'basic' species concepts:"

"...*agamospecies* (asexuals), *biospecies* (reproductively isolated sexual species), *ecospecies* (ecological niche occupiers), *evolutionary species* (evolving lineages), *genetic species* (common gene pool), *morphospecies* (species defined by their form, or phenotypes), and *taxonomic species* (whatever a taxonomist calls a species)."

Wilkins segregates morphospecies and taxonomic species as focusing on "how we *identify* species," whereas remaining concepts refer to "*what* species are." It is among these latter 'basic' concepts that Wilkins [8: p59] narrows the distinction to "ecospecies" and "biospecies." But he regards ecospecies and biospecies as referring not to a concept of species but rather causes of species. In other words, they are explanatory accounts. Wilkins [8: p59] (see also [89]) raises the important point that "Theory-based [species] concepts presume the universal applicability of that theory outside the groups on which it was formulated.... Discovery techniques [*sic*] that are based on explanatory concepts are hostage to empirical fortune." To that end, he suggests that species be defined as "those groups of organisms that resemble their parents." As a necessity borne out of the need to subsume asexual- and sexual-based tokogeny and horizontal genetic exchange under the one term species, this definition is reduced to being largely equivalent to tokogeny (cf. Fig. 1, Table 1). Notice also that Wilkins' definition is imbued with causal content. As all taxa refer to explanatory accounts, tokogeny already serves that role in a capacity that is more restricted relative to species. But to say "explanatory concepts are hostage to empirical fortune," cannot be regarded as a negative consequence. At best, it is nothing more than acknowledging that conclusions of all abductive inferences, from observation statements to taxa, are never theory neutral. To think that systematics should be divorced from considerations of explanation is contrary to the very objective of scientific inquiry. Rather than attempting to reduce the definition of species to that of tokogeny, we need to face the issue that the one term species has been given the unrealistic task of encompassing a spectrum of causal conditions intended to account for select properties of organisms ([E], Table 1). Since it is our observations of properties of organisms that compel our inferential actions leading to the explanatory conclusions we call taxa, the challenge with respect to species is straightforward. We need to limit the scope of specific hypotheses to the explanatory realm of character origin/fixation within reproductively isolated populations of organisms with obligate, albeit not exclusive, sexual reproduction (i.e. [C]; Table 1: 'species₁,' 'species₂,' 'species₄'), and recognize other classes of hypotheses-as-taxa when speaking of organisms that are strictly asexual, apomictic/parthenogenetic, self-fertilizing hermaphroditic, or engage in horizontal genetic exchange ([E], Table 1: 'species₃,' 'species₅'). With respect to obligate asexual,

³ It should be noted that Wilkins (pers. comm.) does not subscribe to the view that species are explanatory hypotheses.

apomictic/parthenogenetic, or self-fertilizing hermaphroditic organisms, or events of horizontal genetic exchange, neither specific *sensu stricto* nor phylogenetic hypotheses apply in the capacity required for sexually-reproducing organisms.

The concerns expressed above regarding parsing the various classes of hypotheses we call taxa brings to light significant consequences for considerations of biodiversity and conservation. That biodiversity is a metaphor is a consequence of our reliance on intraspecific/polymorphic, specific, and phylogenetic hypotheses serving as surrogates for hypotheses of proximate tokogeny (Fig. 5). It is the continuation of tokogenetic events, asexual or sexual, that conservation seeks to preserve. The inherent constraints imposed by the nature of taxa as explanatory hypotheses determine these characterizations. The most notable outcome is that the relevance of species to biodiversity and conservation is both diminished and placed in proper perspective with all other taxa. The definition of biodiversity in [J] is thus at odds with the more standard view that biodiversity is a hierarchy of 'things,' e.g. genes, species/taxa, ecosystems, in need of conservation. For instance, Margules et al. [19: p310] state that,

"The concept of biodiversity encompasses the entire biological hierarchy from molecules to ecosystems. It includes entities [sic] recognisable at each level (genes, taxa, communities, etc.) and the interactions between them (nutrient and energy cycling, predation, competition, mutation, and adaptation, etc.). These entities are heterogeneous, meaning that all members at each level can be distinguished from one another; they form a hierarchy of nested individuals... The complete description of each level requires the inclusion of all members. The number of viable entities at all levels is phenomenally large and in practice unknown. Yet sustaining this variety, unknown and unmeasured, the variety of life on earth, is the goal of biodiversity conservation. To achieve this goal it will be necessary to retain the complex hierarchical biological organization that sustains characters within taxa, taxa within communities or assemblages, and assemblages within ecosystems."

Biodiversity purportedly encompasses a hierarchy of individuals, e.g. nucleotides, organisms, taxa, communities, ecosystems, etc, and conservation is the attempt to preserve some semblance of the variety of individuals at each level. The assumption that the individuality thesis is ontologically appropriate to taxa, communities, and ecosystems cannot be defended. Consider the variety of hypotheses in Figure 1 (see also Table 1, Figs. 2–3, 5–8). What are graphically depicted is past causal events relative to specimens observed in the present. The totality of events entailed by any of these hypotheses does not connote individuals, things, or 'historical entities.' The illustrated events involved past individuals *qua* organisms, but the events themselves are not individuals [12–14, 37, 126]. None of these hypotheses present emergent properties that would allow one the opportunity to perceive more inclusive individuals beyond the specimens upon which the hypotheses have been inferred. The inferential path from observation statements regarding organisms, which is contingent upon our perceptions of the properties of those organisms, does not lead to observation statements regarding taxa, communities, or ecosystems as individuals or entities (cf. [F], [H]). This chapter has echoed what was recognized by Fitzhugh [10, 12–14, 37, 97, 98, 126], that taxa are consequences of our inferential actions, prompted by perceptions of individual organisms.

With taxa acknowledged as representations of our explanatory hypotheses, it becomes immediately apparent that we are not speaking of a hierarchy of ever-inclusive individuals [*contra* 32, 186–191]. What is critical to correctly speaking of biodiversity is that we identify the subjects to which we are referring (Figs. 5–8). The present analysis has provided arguments intended to reorient the focus of biodiversity and conservation away from genes, taxa, communities, or ecosystems as ontological individuals, to the subjects that are perceived by biologists, i.e. organisms, and the relations of organisms to past proximate tokogeny (biodiversity) and potential future tokogeny (conservation). The subjects of biodiversity and conservation can be conceived as intersections between a multitude of fields of research, including ecology, systematics, developmental biology, paleontology, biogeography, and population genetics. But in each instance, taxa are not the ontologically or biologically relevant units of interest. Our interest is in individual organisms per our inferential reactions to the properties they instantiate, e.g. [F], [H]. Some of those reactions are communicated under the rubric of taxa, and conveyed in the context of biodiversity. Via biodiversity, our selective endeavors to ensure tokogeny among organisms are the acts of conservation.

Recall the quote from Noss [22: p356] given in **Defining Biodiversity and Conservation**, that biodiversity is not typically considered only in terms of the number of groups of things, “the number of genes, species, ecosystems, or any other group of things [*sic*] in a defined area,” but also “the relative frequency or abundance of each species or other entity, in addition to the number of entities in the collection.” It was noted that Noss’ characterization conflates species with the individuals to whom those hypotheses refer. The relative abundance of hypothesized sets of tokogenetic systems between given areas, indicated by taxa as surrogates, is not the same as the number of individuals in those areas. The correct relation is between abundance of individuals in an area relative to particular systematics hypotheses. But that relation would be one predicated on biodiversity, not part of it. There is the alternative view that species richness is an index of biodiversity. Maclaurin and Sterelny [46: p173] suggest that “Species richness, supplemented in various ways, is a good multipurpose measure of biodiversity, because many processes affect richness...and it is causally relevant to many outputs.” The problem is that species richness is limited to relations with specific hypotheses, and do not subsume explanations of observed properties of individuals denoted by other classes of taxa. There is no epistemic basis for restricting biodiversity to species, just as conservation is not the act of maintaining species or other taxa. Rather, biodiversity encompasses our hypotheses of past causal events that give us at least tentative understanding of what we observe in the present, with conservation a concerted effort to maintain opportunities for specified organisms, not species or other taxa, to continue to engage in tokogenetic events into the future. And just as specific *sensu stricto* (Table 1: ‘species₁’, ‘species₂’, ‘species₄’) and phylogenetic hypotheses (cf. [H]) applied to sexually reproducing organisms serve as proxies for tokogeny in both the context of biodiversity and conservation, the taxa employed to account for properties among obligate asexual, apomictic/parthenogenetic, or self-fertilizing hermaphroditic organisms (Table 1: ‘species₃’) and horizontal genetic exchange (Table 1: ‘species₅’) also connote surrogates for tokogeny when speaking of the biodiversity or conservation of those organisms.

The misconception that species are the units to which biodiversity refers and conservation seek to maintain also extends to phrases such as ‘species extinction’ or ‘endangered species.’ Extinction is not the transition from existence to non-existence of species or taxa, but rather the cessation of reproductive events among a group of organisms. What is endangered is not a species, but rather the opportunities for tokogeny conveyed in intraspecific/polymorphic, specific *sensu lato*, or phylogenetic hypotheses, among others (cf. Table 1, Fig. 1). Orienting focus away from the ontologically specious view that taxa are spatio-temporally restricted things or individuals, to the relevant representations of our select, biased explanatory accounts of what we observe of organisms provides the most effective route to ensuring the integration of biological disciplines that go into ‘biodiversity studies’ and conservation efforts.

A final observation is in order. In conjunction with establishing that taxa are explanatory hypotheses for particular features of organisms, and species are taxa, this chapter set out to define the terms *species/taxa*, *biodiversity*, and *conservation* by acknowledging their transitive relations, {(taxa, biodiversity), (biodiversity, conservation), (taxa, conservation)}. Pursuant to these definitions, it is evident that these relations are not representative of our actions in various fields of biological study. We observe individual organisms, and infer classes of hypotheses referred to as taxa. On the basis of particular taxa, we attempt to conserve organisms and their opportunities for tokogeny into the future. Notice that it is taxa, *not biodiversity*, that serves as the conceptual link. What is apparent is that *biodiversity* offers no tangible contributions to our characterizations of organisms, references to taxa, or implementations of conservation. At best *biodiversity* is redundant relative to *taxa*, at worst gratuitous for *conservation* (cf. Figs. 5–8). The transitive relations that in fact exist are, {(individuals, taxa), (taxa, conservation), (individuals, conservation)}. These revised relations manifest themselves as follows: *taxa* must be determined in the context of *individuals*; *taxa* establish the limits on *conservation*; *individuals* determine the realization of *conservation*. *Biodiversity* is an unnecessary concept—a contrivance of unbridled reification, along the same lines of excess that have befallen *species*.

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References

- [1] Hennig W. *Phylogenetic Systematics*. Urbana: University of Illinois Press; 1966.
- [2] Hanson NR. *Perception and Discovery: an Introduction to Scientific Inquiry*. San Francisco: Freeman, Cooper & Company; 1969.
- [3] Psillos S. *Philosophy of Science A–Z*. Edinburgh: Edinburgh University Press; 2007.
- [4] Hempel CG. *Fundamentals of Concept Formation in Empirical Science*. Chicago: The University of Chicago Press; 1952.
- [5] Agapow P-M, Bininda-Emonds ORP, Crandall KA, Gittleman JL, Mace GM, Marshall JC, Purvis A. The Impact of Species Concept on Biodiversity Studies. *Quarterly Review of Biology* 2004; 79(2): 161–179.
- [6] Wilkins JS. *Defining Species: a Sourcebook from Antiquity to Today*. New York: Peter Land; 2009.
- [7] Wilkins JS. *Species: a History of the Idea*. Berkeley: University of California Press; 2009.
- [8] Wilkins JS. Philosophically Speaking, How Many Species Concepts are There? *Zootaxa* 2011; 2765: 58-60.
- [9] Wheeler QD, Knapp S, Stevenson DW, Stevenson J, Blum SD, Boom BM, Borisy GG, Buizer JL, De Carvalho MR, Cibrian A, Donoghue MJ, Doyle V, Gerson EM, Graham CH, Graves P, Graves SJ, Guralnick RP, Hamilton AL, Hanken J, Law W, Lipscomb DL, Lovejoy TE, Miller H, Miller JS, Naeem S, Novacek MJ, Page, LM, Platnick NI, Porter-Morgan H, Raven PH, Solis MA, Valdecasas AG, Van Der Leeuw S, Vasco A, Vermeulen N, Vogel J, Walls, RL, Wilson EO, Woolley JB. *Mapping the Biosphere: Exploring Species to Understand the Origin, Organization and Sustainability of Biodiversity*. *Systematics and Biodiversity* 2012; 10(1): 1–20.
- [10] Fitzhugh K. The Abduction of Phylogenetic Hypotheses. *Zootaxa* 2006; 1145: 1–110.
- [11] Fitzhugh K. The Philosophical Basis of Character Coding for the Inference of Phylogenetic Hypotheses. *Zoologica Scripta* 2006; 35(3): 261–286.
- [12] Fitzhugh K. Abductive Inference: Implications for 'Linnean' and 'Phylogenetic' Approaches for Representing Biological Systematization. *Evolutionary Biology* 2008; 35(1): 52–82.
- [13] Fitzhugh K. Species as Explanatory Hypotheses: Refinements and Implications. *Acta Biotheoretica* 2009; 57(1–2): 201–248.
- [14] Fitzhugh K. The Limits of Understanding in Biological Systematics. *Zootaxa* 2012; 3435: 40–67.

- [15] International Commission on Zoological Nomenclature. *International Code of Zoological Nomenclature*. London: The International Trust for Zoological Nomenclature; 1999.
- [16] Cantino PD, de Queiroz K. *PhyloCode: International Code of Phylogenetic Nomenclature, Version 4c*. The International Society for Phylogenetic Nomenclature; 2010. <http://www.ohio.edu/phylocode/> (accessed 27 March 2012).
- [17] Committee on Biological Diversity in Marine Systems. *Understanding Marine Biodiversity: a Research Agenda for the Nation*. Washington DC: National Academy Press; 1995.
- [18] Solbrig O. The IUBS-SCOPE-UNESCO Program of Research in Biodiversity. In: Solbrig OT. (ed.) *From Genes to Ecosystems: A Research Agenda for Biodiversity*. Cambridge: The International Union of Biological Sciences (IUBS); 1991. p5–14.
- [19] Margules CR, Pressey RL, Williams PH. Representing Biodiversity: Data and Procedures for Identifying Priority Areas for Conservation. *Journal of Biosciences* 2002; 27(4): 309–326.
- [20] Koricheva J, Siipi H. The Phenomenon of Biodiversity. In: Oksanen M, Pietarinen J. (eds.) *Philosophy and Biodiversity*. New York: Cambridge University Press; 2004. p27–53.
- [21] Rawles K. Biological Diversity and Conservation Policy. In: Oksanen M, Pietarinen J. (eds.) *Philosophy and Biodiversity*. New York: Cambridge University Press; 2004. p199–216.
- [22] Noss RF. Indicators for Monitoring Biodiversity: a Hierarchical Approach. *Conservation Biology* 1990; 4(4): 355–364.
- [23] Gaston KJ. Global Patterns in Biodiversity. *Nature* 2000; 405(11 May): 220–227.
- [24] Agapow P-M. Species: Demarcation and Diversity. In: Purvis A, Gittleman JL, Brooks T. (eds.) *Phylogeny and Conservation*. New York: Cambridge University Press; 2005. p57–75.
- [25] Ricotta C. A Semantic Taxonomy for Diversity Measures. *Acta Biotheoretica* 2007; 55(1): 23–33.
- [26] Bertrand Y, Pleijel F, Rouse G. Taxonomic Surrogacy in Biodiversity Assessments, and the Meaning of Linnean Ranks. *Systematics and Biodiversity* 2006; 4(2): 149–159.
- [27] Barraclough TG, Fontaneto D, Herniou EA, Ricci C. The Evolutionary Nature of Diversification in Sexuals and Asexuals. In: Butlin RK, Bridle JR, Schluter D. (eds.) *Speciation and Patterns of Diversity*. New York: Cambridge University Press; 2009. p29–45.
- [28] Gaston KJ, Spicer JL. *Biodiversity: an Introduction*. Malden: Blackwell Publishing; 2004.

- [29] Reyers B, Polasky S, Tallis H, Mooney HA, Larigauderie A. Finding Common Ground for Biodiversity and Ecosystems Services. *Bioscience* 2012; 62(5): 503-507.
- [30] Secretariat of the Convention on Biological Diversity. Handbook of the Convention on Biological Diversity Including its Cartagena Protocol on Biosafety, 3rd Edition. Montreal: Friesen; 2005.
- [31] Expert Panel on Biodiversity Science. Canadian Taxonomy: Exploring Biodiversity, Creating Opportunity. Ottawa: The Council of Canadian Academies; 2010. http://www.scienceadvice.ca/uploads/eng/assessments%20and%20publications%20and%20news%20releases/biodiversity/biodiversity_report_final_e.pdf (accessed 5 April 2012).
- [32] Sarkar S. Defining "Biodiversity"; Assessing Biodiversity. *The Monist* 2002; 85(1): 131-155.
- [33] Mayden RL. A Hierarchy of Species Concepts: the Denouement in the Saga of the Species Problem. In: Claridge MF, Dawah HA, Wilson MR. (eds.) *Species: The Units of Biodiversity*. New York: Chapman & Hall; 1997. p381-424.
- [34] Stamos DN. *The Species Problem: Biological Species, Ontology, and the Metaphysics of Biology*. New York: Lexington Books; 2003.
- [35] Claridge MF. Species are Real Biological Entities. In: Ayala FJ, Arp R. (eds.) *Contemporary Debates in Philosophy of Biology*. Chichester: Wiley-Blackwell; 2010. p91-09.
- [36] Richards RA. *The Species Problem: a Philosophical Analysis*. New York: Cambridge University Press; 2010.
- [37] Fitzhugh K. The Inferential Basis of Species Hypotheses: the Solution to Defining the Term 'Species.' *Marine Ecology* 2005; 26(3-4): 155-165.
- [38] Anonymous. 2002 Endangered Species Act of 1973 [amended 2002]. Public Law 93-205, 87 Stat. 884, 16 U.S.C. 1531-1544; 2002. <http://www.nmfs.noaa.gov/pr/pdfs/laws/esa.pdf> (accessed 5 April 2012).
- [39] Ryder, OA. Species Conservation and Systematics: the Dilemma of Subspecies. *Trends in Ecology and Evolution* 1986; 1(1): 9-10.
- [40] Moritz C. Defining "Evolutionarily Significant Units" for Conservation. *Trends in Ecology and Evolution* 1994; 9(10): 373-375.
- [41] Moritz C. Strategies to Protect Biological Diversity and the Evolutionary Processes that Sustain It. *Systematic Biology* 2002; 51(2): 238-254.
- [42] Fraser DJ, Bernatchez L. Adaptive Evolutionary Conservation: Towards a Unified Concept for Defining Conservation Units. *Molecular Ecology* 2001; 10(12): 2741-2752.
- [43] Green DM. Designatable Units for Status Assessment of Endangered Species. *Conservation Biology* 2005; 19(6): 1813-1820.

- [44] Wilson EO. Introductory Essay: Systematics and the Future of Biology. In: Hey J, Fitch WM, Ayala FJ. (eds.) *Systematics and the Origin of Species: on Ernst Mayr's 100th Anniversary*. Washington DC: The National Academies Press; 2005. p1–7.
- [45] de Queiroz K. Ernst Mayr and the Modern Concept of Species. In: Hey J, Fitch WM, Ayala FJ. (eds.) *Systematics and the Origin of Species: on Ernst Mayr's 100th Anniversary*. Washington DC: The National Academies Press; 2005. p243–263.
- [46] Maclaurin J, Sterelny K. *What is Biodiversity?* Chicago: University of Chicago Press; 2008.
- [47] Camp WH, Rickett HW, Weatherby CA. Proposed Changes in the International Rules of Botanical Nomenclature. *Brittonia* 1949; 7(1): 1-51.
- [48] Gregg JR. *The Language of Taxonomy: an Application of Symbolic Logic to the Study of Classificatory Systems*. New York: Columbia University Press; 1954.
- [49] Simpson GG. *Principles of Animal Taxonomy*. New York: Columbia University Press; 1961.
- [50] Blackwelder RE. *Taxonomy: a Text and Reference Book*. New York: John Wiley & Sons; 1967.
- [51] Mayr E. *Principles of Systematic Zoology*. New York: McGraw-Hill Book Company; 1969.
- [52] Mayr E. *The Growth of Biological Thought: Diversity, Evolution, and Inheritance*. Cambridge: Harvard University Press; 1982.
- [53] Jardín N, Sibson R. *Mathematical Taxonomy*. New York: John Wiley & Sons, Ltd.; 1971.
- [54] Abbott LA, Bisby FA, Rogers DJ. *Taxonomic Analysis in Biology: Computers, Models, and Databases*. New York: Columbia University Press; 1985.
- [55] Mahner M, Bunge M. *Foundations of Biophilosophy*. New York: Springer; 1997.
- [56] Futuyma DJ. *Evolution*. Sunderland: Sinauer Associates, Inc.; 2005.
- [57] Williams DM, Ebach MC. *Foundations of Systematics and Biogeography*. New York: Springer; 2008.
- [58] Schuh RT, Brower AVZ. *Biological Systematics: Principles and Applications*. Ithaca: Cornell University Press; 2009.
- [59] Wiley EO, Lieberman BS. *Phylogenetics: Theory and Practice of Phylogenetic Systematics*. Hoboken: John Wiley & Sons, Inc.; 2011.
- [60] Rickett HW. So What is a Taxon? *Taxon* 1958; 7(2): 37–38.
- [61] Ghiselin M. *The Triumph of the Darwinian Method*. Berkeley: University of California Press; 1969.

- [62] Wägele J-W. *Foundations of Phylogenetic Systematics*. München: Verlag Dr. Friedrich Pfeil; 2005.
- [63] Kardong KV. *An Introduction to Biological Evolution*. New York: McGraw-Hill; 2008.
- [64] Boyd R. Homeostasis, Species, and Higher Taxa. In: Wilson RA. (ed.) *Species: New Interdisciplinary Essays*. Cambridge: MIT Press; 1999. p141–185.
- [65] Keller RA, Boyd RN, Wheeler QD. The Illogical Basis of Phylogenetic Nomenclature. *The Botanical Review* 2003; 69(1): 93–110.
- [66] Franz NM. Outline of an Explanatory Account of Cladistic Practice. *Biology and Philosophy* 2005; 20(2–3): 489–515.
- [67] Rieppel O. Monophyly, Paraphyly, and Natural Kinds. *Biology and Philosophy* 2005; 20(2): 465–487.
- [68] Rieppel O. Modules, Kinds, and Homology. *Journal of Experimental Zoology, Part B* 2005; 304(1): 18–27.
- [69] Rieppel O. The PhyloCode: a Critical Discussion of its Theoretical Foundation. *Cladistics* 2006; 22(2): 186–197.
- [70] Rieppel O. Species: Kinds of Individuals or Individuals of a Kind. *Cladistics* 2007; 23(4): 373–384.
- [71] Assis, LCS, Brigandt I. Homology: Homeostatic Property Cluster Kinds in Systematics and Evolution. *Evolutionary Biology* 2009; 36(2): 248–255.
- [72] Sneath PHA, Sokal RR. *Numerical Taxonomy: the Principles and Practice of Numerical Classification*. San Francisco: W.H. Freeman and Company; 1973.
- [73] Ghiselin MT. A Radical Solution to the Species Problem. *Systematic Zoology* 1974; 23(4): 536–544.
- [74] Ghiselin MT. Ostensive Definitions of the Names of Species and Clades. *Biology and Philosophy* 1995; 10(2): 219–222.
- [75] Ghiselin MT. *Metaphysics and the Origin of Species*. Albany: SUNY Press; 1997.
- [76] Hull DL. Are Species Really Individuals? *Systematic Zoology* 1976; 25(2) 174–191.
- [77] Hull DL. A Matter of Individuality. *Philosophy of Science* 1978; 45(3): 335–360.
- [78] Wiley EO. *Phylogenetics: the Theory and Practice of Phylogenetic Systematics*. New York: John Wiley & Sons; 1981.
- [79] Wiley EO. Kinds, Individuals, and Theories. In: Ruse M. (ed.) *What the Philosophy of Biology Is*. Dordrecht: Kluwer; 1989. p289–300.
- [80] Cohan FM. Bacterial Species and Speciation. *Systematic Biology* 2001; 50(4): 513–524.

- [81] Brogaard B. Species as Individuals. *Biology and Philosophy* 2004; 19(2): 223–242.
- [82] Härlin M, Pleijel F. Phylogenetic Nomenclature is Compatible with Diverse Philosophical Perspectives. *Zoologica Scripta* 2004; 33(6): 587–591.
- [83] Colless DH. Taxa, Individuals, Clusters and a Few Other Things. *Biology and Philosophy* 2006; 21(3): 353–367.
- [84] Ereshefsky M. Species and Linnaean Hierarchy. In: Wilson RA. (ed.) *Species: New Interdisciplinary Essays*. Cambridge: MIT Press; 1999. p285–305.
- [85] Ereshefsky M. *The Poverty of the Linnaean Hierarchy: a Philosophical Study of Biological Taxonomy*. New York: Cambridge University Press; 2001.
- [86] Ereshefsky M. Foundational Issues Concerning Taxa and Taxon Names. *Systematic Biology* 2007; 56(2): 295–301.
- [87] Ereshefsky M, Matthen M. Taxonomy, Polymorphism, and History: an Introduction to Population Structure Theory. *Philosophy of Science* 2005; 72(1): 1–21.
- [88] Rieppel O. Monophyly and the Two Hierarchies. In: Williams DM, Knapp S. (eds.) *Cladistics: the Branching of a Paradigm*. Berkeley: University of California Press; 2010. p147–167.
- [89] Wilkins JS. How to be a Chaste Species Pluralist-Realist: the Origins of Species Modes and the Synapomorphic Species Concept. *Biology and Philosophy* 2003; 18(5): 621–638.
- [90] Wilkins JS. What is a Species? Essences and Generation. *Theory in Biosciences* 2010; 129(2–3): 141–148.
- [91] Griffiths PE. Squaring the Circle: Natural Kinds with Historical Essences. In: Wilson RA. (ed.) *Species: New Interdisciplinary Essays*. Cambridge: MIT Press; 1999. p209–228.
- [92] Wilson RA. Realism, Essence, and Kind: Resuscitating Species Essentialism? In: Wilson RA. (ed.) *Species: New Interdisciplinary Essays*. Cambridge: MIT Press; 1999. p187–207.
- [93] Reydon TAC. Classifying Life, Reconstructing History and Teaching Diversity: Philosophical Issues in the Teaching of Biological Systematics and Biodiversity. *Science & Education* 2011; doi: 10.1007/s11191-011-9366-z.
- [94] de Queiroz K. The General Lineage Concept of Species and the Defining Properties of the Species Category. In: Wilson RA. (ed.) *Species: New Interdisciplinary Essays*. Cambridge: MIT Press; 1999. p49–89.
- [95] Assis LCS. Individuals, Kinds, Phylogeny and Taxonomy. *Cladistics* 2011; 27(1): 1–3.
- [96] Assis LCS. Species, Reality and Evidence: a Reply to Reydon. *Cladistics* 2011; 27(1): 6–8.

- [97] Fitzhugh K. Les Bases Philosophiques de l'Inférence Phylogénétique: Une vue d'Ensemble. *Biosystema* 2005; 24: 83–105.
- [98] Fitzhugh K. The 'Requirement of Total Evidence' and its Role in Phylogenetic Systematics. *Biology and Philosophy* 2006; 21(3): 309–351.
- [99] Griffiths GCD. On the Foundations of Biological Systematics. *Acta Biotheoretica* 1974; 23(3–4): 85–131.
- [100] O'Hara RJ. Systematic Generalization, Historical Fate, and The Species Problem. *Systematic Biology* 1993; 42(3): 231–246.
- [101] Bunge M. *Philosophy of Science, Volume 1, From Problem to Theory*. New Brunswick: Transaction Publishers; 1998.
- [102] Strawson PF. *Individuals: An Essay in Descriptive Metaphysics*. London: Methuen; 1959.
- [103] Gracia JJE. *Individuality: an Essay on the Foundations of Metaphysics*. Albany: State University of New York Press; 1988.
- [104] Nogueira JMM, Fitzhugh K, Rossi MCS. A New Genus and New Species of Fan Worms (Polychaeta: Sabellidae) from Atlantic and Pacific Oceans—the Formal Treatment of Taxon Names as Explanatory Hypotheses. *Zootaxa* 2010; 2603: 1–52.
- [105] Fitzhugh K. Revised Systematics of *Fabricia oregonica* Banse, 1956 (Polychaeta: Sabellidae: Fabriciinae): an Example of the Need for a Uninomial Nomenclatural System. *Zootaxa* 2010; 2647: 35–50.
- [106] Haack S, Kolenda K. Two Fallibilists in Search of the Truth. *Proceedings of the Aristotelian Society, Supplementary Volume* 1977; 51: 63–104.
- [107] Mishler BD. Species are not Uniquely Real Biological Entities. In: Ayala FJ, Arp R. (eds.) *Contemporary Debates in Philosophy of Biology*. Chichester: Wiley-Blackwell; 2010. p110–122.
- [108] Hey J. On the Arbitrary Identification of Real Species. In: Butlin RK, Bridle JR, Schluter, D. (eds). *Speciation and Patterns of Diversity*. New York: Cambridge University Press; 2009. p15–28.
- [109] Fitzhugh K. Fact, Theory, Test and Evolution. *Zoologica Scripta* 2008; 37(1): 109–113.
- [110] Hempel CG. *Aspects of Scientific Explanation and Other Essays in the Philosophy of Science*. New York: The Free Press; 1965.
- [111] Rescher N. *Scientific Explanation*. New York: The Free Press; 1970.
- [112] Popper KR. *Objective Knowledge: an Evolutionary Approach*. New York: Oxford University Press; 1983.
- [113] Popper KR. *Realism and the Aim of Science*. New York: Routledge; 1992.

- [114] Salmon WC. *Scientific Explanation and the Causal Structure of the World*. Princeton: Princeton University Press; 1984.
- [115] Van Fraassen BC. *The Scientific Image*. Oxford: Clarendon Press; 1990.
- [116] Strahler AN. *Understanding Science: an Introduction to Concepts and Issues*. Buffalo: Prometheus Books; 1992.
- [117] Hausman DM. *Causal Asymmetries*. New York: Cambridge University Press; 1998.
- [118] de Regt HW, Leonelli S, Eigner K., editors. *Scientific Understanding: Philosophical Perspectives*. Pittsburgh: University of Pittsburgh Press; 2009.
- [119] Darwin C. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. London: John Murray; 1859.
- [120] Maurer D. The Dark Side of Taxonomic Sufficiency (TS). *Marine Pollution Bulletin* 2000; 40(2): 98–101.
- [121] Terlizzi A, Bevilacqua S, Frascchetti S, Boero F. Taxonomic Sufficiency and the Increasing Insufficiency of Taxonomic Expertise. *Marine Pollution Bulletin* 2003; 46(5): 556–561.
- [122] Domínguez-Castanedo N, Rojas-López R, Solís-Weiss V, Hernández-Alcántara P, Granados-Barba A. The Use of Higher Taxa to Assess the Benthic Conditions in the Southern Gulf of Mexico. *Marine Ecology* 2007; 28 (Supplement 1): 161–168.
- [123] Musco L, Mikac B, Tataranni M, Giangrande A, Terlizzi A. The Use of Coarser Taxonomy in the Detection of Long-Term Changes in Polychaete Assemblages. *Marine Environmental Research* 2011; 71(2): 131–138.
- [124] Hedges SB, Kumar S., editors. *The Timetree of Life*. New York: Oxford University Press; 2009.
- [125] Fitzhugh K. Clarifying the Role of Character Loss in Phylogenetic Inference. *Zoologica Scripta* 2008; 37(5): 561–569.
- [126] Fitzhugh K. Evidence for Evolution versus Evidence for Intelligent Design: Parallel Confusions. *Evolutionary Biology* 2010; 37(2–3): 68–92.
- [127] Peirce CS. *Illustrations of the Logic of Science. Sixth Paper – Deduction, Induction, and Hypothesis*. *Popular Science Monthly* 1878; 13(August): 470–482.
- [128] Peirce CS. *Collected Papers of Charles Sanders Peirce, Volume 1, Principles of Philosophy*. In: Hartshorne C, Weiss P, Burks A. (eds.). Harvard University Press, Cambridge; 1931.
- [129] Peirce CS. *Collected Papers of Charles Sanders Peirce, Volume 2, Elements of Logic*. In: Hartshorne C, Weiss P, Burks A. (eds.). Harvard University Press, Cambridge; 1932.

- [130] Peirce CS. *Collected Papers of Charles Sanders Peirce, Volume 3, Exact Logic*. In: Hartshorne C, Weiss P, Burks A. (eds.). Harvard University Press, Cambridge; 1933.
- [131] Peirce CS. *Collected Papers of Charles Sanders Peirce, Volume 4, The Simplest Mathematics*. In: Hartshorne C, Weiss P, Burks A. (eds.). Harvard University Press, Cambridge; 1933.
- [132] Peirce CS. *Collected Papers of Charles Sanders Peirce, Volume 5, Pragmatism and Pragmaticism*. In: Hartshorne C, Weiss P, Burks A. (eds.). Harvard University Press, Cambridge; 1934.
- [133] Peirce CS. *Collected Papers of Charles Sanders Peirce, Volume 6, Scientific Metaphysics*. In: Hartshorne C, Weiss P, Burks A. (eds.). Harvard University Press, Cambridge; 1935.
- [134] Peirce CS. *Collected Papers of Charles Sanders Peirce, Volume 7, Science and Philosophy*. In: Hartshorne C, Weiss P, Burks A. (eds.). Harvard University Press, Cambridge; 1958.
- [135] Peirce CS. *Collected Papers of Charles Sanders Peirce, Volume 8, Correspondence and Bibliography*. In: Burks A. (ed.). Harvard University Press, Cambridge; 1958.
- [136] Hanson NR. *Patterns of Discovery: an Inquiry into the Conceptual Foundations of Science*. New York: Cambridge University Press; 1958.
- [137] Harman G. The Inference to the Best Explanation. *Philosophical Review* 1965; 74(1): 88–95.
- [138] Achinstein P. Inference to Scientific Laws. In: Stuewer RH. (ed.) *Volume V: Historical and Philosophical Perspectives of Science, Minnesota Studies in the Philosophy of Science*. Minneapolis: University of Minnesota Press; 1970. p87–111.
- [139] Fann KT. *Peirce's Theory of Abduction*. The Hague: Martinus Nijhoff; 1970.
- [140] Reilly FE. *Charles Peirce's Theory of Scientific Method*. New York: Fordham University Press; 1970.
- [141] Curd MV. The Logic of Discovery: an Analysis of Three Approaches. In: Nickles T. (ed.) *Scientific Discovery, Logic and Rationality*. Dordrecht: D. Reidel Publishing Company; 1980. p201–219.
- [142] Nickles T. Introductory Essay: Scientific Discovery and the Future of Philosophy of Science. In: Nickles T. (ed.) *Scientific Discovery, Logic and Rationality*. Dordrecht: D. Reidel; 1980. p1–59.
- [143] Thagard P. *Computational Philosophy of Science*. Cambridge: The MIT Press; 1988.
- [144] Ben-Menahem Y. The Inference to the Best Explanation. *Erkenntnis* 1990; 33(3): 319–344.
- [145] Lipton P. *Inference to the Best Explanation*. New York: Routledge; 2004.

- [146] Josephson JR, Josephson SG., editors. *Abductive Inference: Computation, Philosophy, Technology*. New York: Cambridge University Press; 1994.
- [147] McMullen E. *The Inference That Makes Science*. Milwaukee: Marquette University Press; 1995.
- [148] Hacking I. *An Introduction to Probability and Inductive Logic*. New York: Cambridge University Press; 2001.
- [149] Magnani L. *Abduction, Reason, and Science: Processes of Discovery and Explanation*. New York: Kluwer Academic; 2001.
- [150] Douven I. Testing Inference to the Best Explanation. *Synthese* 2002; 130(3): 355–377.
- [151] Psillos S. Simply the Best: a Case for Abduction. In: Kakas AC, Sadri F. (eds) *Computational Logic: Logic Programming and Beyond*. Springer: New York; 2002. p605–625.
- [152] Godfrey-Smith P. *Theory and Reality: an Introduction to the Philosophy of Science*. Chicago: University of Chicago Press; 2003.
- [153] Walton D. *Abductive Reasoning*. Tuscaloosa: The University of Alabama Press; 2004.
- [154] Aliseda A. *Abductive Reasoning: Logical Investigations into Discovery and Explanation*. Dordrecht: Springer; 2006.
- [155] Nichols, JD, Cooch, EG, Nichols, JM, Sauer, JR. Studying Biodiversity: Is a New Paradigm Really Needed? *BioScience* 2012; 62(5): 497–502.
- [156] Nixon KC, Wheeler QD. An Amplification of the Phylogenetic Species Concept. *Cladistics* 1990; 6(3): 211–223.
- [157] Wheeler QD, Meier R., editors. *Species Concepts and Phylogenetic Theory*. New York: Columbia University Press; 2000.
- [158] Staley JT. The Bacterial Species Dilemma and the Genomic–Phylogenetic Species Concept. *Philosophical Transactions of the Royal Society, Series B* 2006; 361(1475): 1899–1909.
- [159] Koonin EV, Makarova KS, Aravind L. Horizontal Gene Transfer in Prokaryotes: Quantification and Classification. *Annual Review of Microbiology* 2001; 55: 709–742.
- [160] Lawrence JG. Catalyzing Bacterial Speciation: Correlating Lateral Transfer with Genetic Headroom. *Systematic Biology* 2001; 50(4): 479–496.
- [161] Papke RT, Gogarten JP. How Bacterial Lineages Emerge. *Science* 2012; 336(6077): 45–46.
- [162] Shapiro BJ, Friedman J, Cordero OX, Preheim SP, Timberlake SC, Szabó G, Polz MF, Alm EJ. Population Genomics of Early Events in the Ecological Differentiation of Bacteria. *Science* 2012; 336(6077): 48–51.

- [163] Ochman H, Lerat E, Daubin V. Examining Bacterial Species Under the Specter of Gene Transfer and Exchange. *Proceedings of the National Academy of Science of the United States of America* 2005; 102(Supplement 1): 6595–6599.
- [164] Cohan FM. What are Bacterial Species? *Annual Review of Microbiology* 2002; 56: 457–487.
- [165] Konstantinidis K, Ramette A, Tiedje JM. The Bacterial Species Definition in the Genomic Era. *Philosophical Transactions of the Royal Society, Series B* 2006; 361(1475): 1929–1940.
- [166] Wilkins JS. The Concept and Causes of Microbial Species. *History and Philosophy of the Life Sciences* 2006; 28(3): 389–408.
- [167] Sober E. Reconstructing the Character States of Ancestors: a Likelihood Perspective on Cladistic Parsimony. *The Monist* 2002; 85(1): 156–176.
- [168] Sober E. *Reconstructing the Past: Parsimony, Evolution, and Inference*. Cambridge: MIT Press; 1988.
- [169] Sober E. *Evidence and Evolution: the Logic Behind the Science*. New York: Cambridge University Press; 2008.
- [170] Felsenstein J. Evolutionary Trees from DNA Sequences: a Maximum Likelihood Approach. *Journal of Molecular Evolution* 1981; 17(6): 368–376.
- [171] Felsenstein J. *Inferring Phylogenies*. Sunderland: Sinauer Associates, Inc; 2004.
- [172] Swofford DL, Olsen GJ, Waddell PJ, Hillis DM. Phylogenetic Inference. In: Hillis DM, Moritz C, Mable BK. (eds) *Molecular Systematics*. Sunderland: Sinauer Associates; 1996. p407–514.
- [173] Cleland CE. Prediction and Explanation in Historical Natural Science. *The British Journal for the Philosophy of Science* 2011; 62(3): 551–582.
- [174] Cleland CE. Historical Science, Experimental Science, and the Scientific Method. *Geology* 2001; 29(11): 987–90.
- [175] Cleland CE. Methodological and Epistemic Differences between Historical Science and Experimental Science. *Philosophy of Science* 2002; 69(3): 474–96.
- [176] Cleland CE. Philosophical Issues in Natural History and its Historiography. In: Tucker A. (ed.) *A Companion to the Philosophy of History and Historiography*. Oxford: Wiley-Blackwell; 2009. p44–62.
- [177] Tucker A. Historical Science, Over- and Underdetermined: a Study of Darwin's Inference of Origins. *The British Journal for the Philosophy of Science* 2011; 62(4): 805–829.
- [178] Huelsenbeck JP, Ronquist F. MrBayes: Bayesian Inference of Phylogeny. *Bioinformatics* 2001; 17(8): 754–755.

- [179] Huelsenbeck JP, Ronquist F, Nielsen R, Bollback JP. Bayesian Inference of Phylogeny and its Impact on Evolutionary Biology. *Science* 2001; 294(5550): 2310–2314.
- [180] Ronquist F, Mark PVD, Huelsenbeck JP. Bayesian Phylogenetic Analysis using MrBayes. In: Lemey P, Salemi M, Vandamme A-M. (eds.) *The Phylogenetic Handbook: a Practical Approach to Phylogenetic Analysis and Hypothesis Testing*. New York: Cambridge University Press; 2009. p210–266.
- [181] Faith DP. Conservation Evaluation and Phylogenetic Diversity. *Biological Conservation* 1992; 61(1): 1–10.
- [182] Faith DP. Phylogenetic Pattern and the Quantification of Organismal Biodiversity. *Philosophical Transactions of the Royal Society of London, Series B Biological Sciences* 1994; 345(1311): 45–58.
- [183] Faith DP. Quantifying Biodiversity: a Phylogenetic Perspective. *Conservation Biology* 2004; 16(1): 248–252.
- [184] Vane-Wright RI, Humphries CJ, Williams PH. What to Protect? – Systematics and the Agony of Choice. *Biological Conservation* 1991; 55(3): 235–254.
- [185] Barker GM. Phylogenetic Diversity: A Quantitative Framework for Measurement of Priority and Achievement in Biodiversity Conservation. *Biological Journal of the Linnean Society* 2002; 76(2): 165–194.
- [186] Vrba E, Eldredge N. Individuals, Hierarchies and Processes: Towards a More Complete Evolutionary Theory. *Paleobiology* 1983; 10(2): 146–171.
- [187] Eldredge N. *Unfinished Synthesis: Biological Hierarchies and Modern Evolutionary Thought*. New York: Oxford University Press; 1985.
- [188] Eldredge N. *Macroevolutionary Dynamics: Species, Niches, and Adaptive Peaks*. New York: McGraw-Hill Publishing Company; 1989.
- [189] Eldredge N, Salthe SN. *Hierarchy and Evolution*. Oxford Surveys in Evolutionary Biology 1984; 1: 184–208.
- [190] Salthe SN. *Evolving Hierarchical Systems: Their Structure and Representation*. New York: Columbia University Press; 1985.
- [191] Miller III W. What's in a Name? Ecologic Entities and the Marine Paleoecologic Record. In: Allmon WD, Bottjer DJ. (eds.) *Evolutionary Paleoecology: The Ecological Context of Macroevolutionary Change*. New York: Columbia University Press; 2001. p15–33.