The Journal of Philosophical Ideas, Special Issue, 89-120, 2017.
DOI : http://dx.doi.org/10.15750/chss.65s.201708.005

The General Concept of Species*

Yuichi Amitani**

【Keywords】 the Species Problem, Good Species, Prototype, Precisification, Semantic Indecision

【ABSTRACT】 In the species controversy, biologists and philosophers have discussed various definitions of species, like the Biological Species Concept. However, biologists often use the term 'species' without having any particular definition in mind. This suggests that many biologists have the"general," umbrella concept of species besides individual definitions. This paper describes this"general" concept and its relationship with definitions of species. I point out several features of the general concept including phenotypic similarity, being a metapopulation lineage, and good species as a prototype of species. I then argue that particular definitions are ways of precisifying the general notion of species. This leaves biologists room for semantic indecision: when biologists use the term species, they could leave

* Versions of this paper were presented at the Colloquium for Foundations of Biology (Tokyo University of Agriculture, Okhotsk, Japan), the Third Conference on Contemporary Philosophy in East Asia (Seoul National University, Korea) and NUS Workshop 'Scientific Controversy in a Complex Social World' (National University of Singapore, Singapore). I thank the participants for their questions and comments. The author would also like to thank three anonymous reviewers for their valuable comments and suggestions to improve the manuscript. This work is financially supported by JSPS KAKENHI (Grant No. 16K02137).

** Faculty of Bioindustry, Tokyo University of Agriculture, yuiami@gmail.com

its exact reference open until they precisify it. Finally, I draw some implications to some extant attempts to solve the species problem.

Ⅰ. Introduction

One prominent feature of the modern species debate is that there are many species definitions on the market. John Wilkins (2006) reported that there are 26 species definitions proposed so far and more definitions have been proposed since then. Meanwhile biologists do not always think of individual species definitions when they reason on species. Darwin attests this fact in *the Origin* (p. 44):

> No one definition [of 'species'] has as yet satisfied all naturalists; yet every naturalist *knows vaguely what he means* when he speaks of a species. (italics added)

Darwin suggests that although biologists often disagree with each other on the correct definition of species, they do have some shared understanding of *species*,[1] partly by non-definitional means (he calls this a "vague way of understanding"). In other words, there is more to biologists' understanding of *species* than individual definitions.[2] This is an important but relatively unattended aspect of the species problem, because biologists and philosophers have typically discussed one definition of species or another as if biologists understand the concept of species through those definitions.

1) Names of concepts are written in italics.
2) Of course, Darwin's suggestion alone is not enough to prove that biologists have the shared understanding of *species*. Discussion in section 2 will give more support to the hypothesis.

This paper aims to explore what Darwin observed in biologists' dealing of the concept of species------that is, various definitions and the more "general" concept of species and the relationships between them. This will include a look at the possible epistemic functions of the non-definitional mode of understanding *species* and how some extant attempts to solve the species problem will have trouble with this.

The structure of the paper is as follows. In the next section, I will describe several important features of the "general" concept of species. First is the semantic components of the general concept of species, that is, phenotypic similarity and being a metapopulational lineage. Since most of major definitions of species explicitly state or implicitly assume that a distinct species has both of those features, we take them as the components of the general concept of species. The other is a non-definitional mode of understanding *species*. A part of it is the understanding through a *prototype*. Like many other concepts, biologists do understand the category of species through its prototype. I describe this prototype by observing how biologists use the term "good species." One might wonder, then, how the "general" concept of species and individual definitions of species like the Biological Species Concept are related. In the third section, I will propose that the precisification relation, as supervaluationists claim about vague predicates, obtains between them. Individual species definitions are attempts to make the general concept of species more precise. Then we will discuss the epistemic roles of the "general" concept of species in section 4. For instance, the general concept sets a research domain and motivates further research in biological science. The general concept also helps us communicate effectively; it allows us to be *in*decisive about the referent of the term species and enables biologists to save time and energy to precisify what they mean when there is no such need and to make rough and ready generalizations about individual species. In section 5, I examine other attempts to capture the relation between the general concept and individual definitions of species in the light of our findings.

Ⅱ. The General Concept of Species

In this section, we will see the components of the general concept of species. We use two strategies to find them. The first strategy is to see what biologists and taxonomists have appealed to when they profoundly disagreed with each other on the nature and the right definition of species. We expect that they are the items at the basis of the concept of species — the components of the general concept of species. An assumption behind this is that biologists and taxonomists share something even when they have different views on the content of *species* and it is what they appeal to in such a situation. We will count phenotypic similarities, *good species* (as a prototype of species), and exemplars as such items. The other strategy is to find conceptual components common to various definitions of species. This strategy is famously employed by de Queiroz (1999, 2005a, 2005b, 2007) ------although his purposes are not the same as the ones served here------ and we will reach the similar conclusion that most, if not all, definitions of species currently proposed state or assume that a species is a lineage at a population level. We will also argue that phenotypic similarities are implied by all or almost all definitions of species.

1. Discontinuities

First we will see semantic components of the general concept of species. By "semantic" components I mean that they provide something close to sufficient conditions for an object to count as a distinct species. They include phenotypic discontinuities between species and being a population-level lineage.

The first semantic component of the general concept of species is phenotypic discontinuities in the biological world: a species is different from others in some phenotypes. Those discontinuities include ecological and behavioral discontinuities as well as morphological ones. For one, major definitions of species state, imply, or assume that different species are phenotypically different. Morphological and phenetic definitions of species (Cronquist, 1978; Sneath, 1976) are based on morphological differences, and so is one version of phylogenetic definitions (Nixon and Wheeler, 1990). Reproductively isolated populations will diverge morphologically over generations due to natural selection and genetic drift (Mayr, 1942). Some versions of phylogenetic definitions (for instance, de Queiroz and Donoghue, 1988) do not mention phenotypic differences, but construction of a phylogenetic tree assumes that populations and species differ phenotypically. Furthermore, taxonomic practice indicates that taxonomists view such discontinuities as a component of the general concept of species. The nomenclature of plant species (McNeill et al., 2006) requires that a name for a new species is legitimate if the description of it is sufficiently detailed to discriminate it from other species. This means that taxonomists appeal to phenotypic discontinuities in naming a new species while they do not necessarily spell out their choice of definition.[3] Indeed, Melissa Luckow's

---

3) Since a large part of the history of the species controversy has focused eukaryotes, what I describe here is the way in which biologists and philosophers understand eukaryote species. However, as Ereshefsky (2010) suggests, this may not be the case in prokaryotes: there may be no distinct "species phenomena" in the prokaryote world, and biologists may be fully aware of it.

observation (Luckow, 1995) that taxonomists often fail to make explicit which species definition they adopt when they describe a new species reflects this requirement. It is worth noting here that this practice enables those with different definitions of species to register new species and make use of the information contained in the description of a newly- or already-registered species.

A component related to this is the postulation of causal mechanisms which are responsible for the phenotypic discontinuities between species. When biologists discover phenotypic discontinuities in nature and characterize species as entities bearing those discontinuities, they may well believe that a species has some mechanisms behind the discontinuities, even though they are not aware of what they really are. Biologists may represent this component as a placeholder for causal mechanisms: a species should have some causal mechanisms responsible for its phenomenological homogeneity. Ronald Amundson (2005) calls this stance "cautious realism" and illustrates how prevalent it has been in the history of systematics. A cautious realist believes that there are phenomenal laws and that there are common cause(s) for them. But she is cautious enough to refrain from pointing to what the cause(s) are. According to Amundson, several naturalists took this position about species and higher taxa before Darwin.4)

4) One might wonder why phenotypic discontinuities have priority over genetic discontinuities in our picture of the general concept of species. It is not true that we ignore the role of genetic information in classification of species. But in many cases taxonomists use it to construct phylogenetic trees, and this element is included in the general concept of species when we discuss a species as a matapopulation lineage (see the next section). However, recently some taxonomists began to describe a new species from the information of its DNA sequence alone (see, for example, Halt et al., 2009); we can distinguish those species only by their DNA sequence, not their morphology. Although this usage of genetic information is not popular yet, it is not covered in our picture and one day taxonomists might agree that information on DNA sequence should be mentioned when describing a new species. Then genetic

2. Population-Level Lineage

Another semantic component is to be segments of a lineage at a population-level. After Darwin proposed his theory of evolution as descent with modification (or perhaps before him; see Richards 2010), many naturalists have been attracted to the idea that the ancestor-descendant or phylogenetic relationship obtains between species. According to this conception, speciation (the event of one species becoming two) means that a lineage, one branch of the phylogenetic tree, splits into two (Figure 1). But if one looks at this relation closely, she would find that it is also a relation *between populations*, because a species is not a mere aggregate of organisms, but

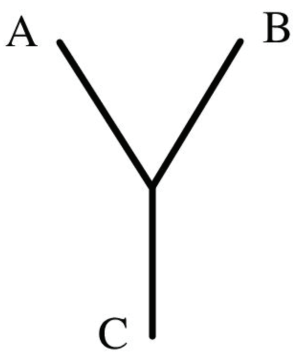

Figure 1: When one species (*C*) becomes two species (*A* and *B*), the lineage splits into two.

---

discontinuities would be at the core of the notion of species. But this would not pose any serious threat to our project. We do not claim that the general concept of species cannot change, and it has apparently changed in the past. For example, the component of a metapopulation lineage has been more emphasized since the advent of phylogenetic systematics (Hennig, 1966). Thus, if more and more taxonomists describe new species with information on its DNA sequence alone, then we can expect that the importance of phenotypic discontinuities to the general concept of species will depreciate.

is made of population(s), a place where organisms interact with each other reproductively and ecologically. From this consideration, we can infer that a species is located in a lineage at a population level.

This is what Kevin de Queiroz (1998, 1999, 2005a, 2005b, 2007) says all of the modern species definitions share. He examines a wide variety of species definitions proposed after the Evolutionary Synthesis and finds that all of them share the assumption that a species is segment(s) of population-level lineage. One can easily see this in "phylogenetic" definitions of species. This is also true of many other "non-phylogenetic" definitions of species, such as the biological species concept and the ecological species concept. Since they refer to a species as population(s) and a population is a segment of a lineage, those definitions assume that a species is a segment of a lineage. Even the conception of species by pheneticists, who have attempted to build a classification system independent of the theory of evolution, implicitly assumes that a species is a segment of a lineage. Although those definitions may differ in how to confirm whether a lineage really splits into two ------the biological species concept says it is when reproductive isolation is established, while the ecological species concept says it is when a lineage occupies an adaptive zone different from others------ those definitions at least share the above assumption.

What this means for our project is clear. Contemporary taxonomists share at least one assumption and they can return to this basis even when they are in a profound disagreement on the nature of species. In this sense, being segments of a lineage is at the basis of the concept of species.

3. *Good Species* and Exemplars of Species

In the introduction, I suggested that there is more to species than individual definitions. This is in line with what cognitive psychologists have said about concepts in general (see Laurence and Margolis (1999) for the history of discussions on the nature of concepts). One of the things they observed from 1970s is that many concepts have a prototype, a highly exemplary instance of a concept, and we often represent a concept through it. We may represent *bachelor* via its prototype besides the definition of it, for example. Now I discuss a prototype of the general concept of species and argue that the concept of 'good species' is so.[5)]

'Good species' is a rather unofficial technical term used in systematics and contemporary biology in general. One often sees it used in taxonomic description papers and scientific papers on topics related to species, such as speciation. In this section, I first describe a couple of usages of 'good species' among biologists (section 2.3.1), and I then propose that a good species is a "prototype" of species, as explicated in cognitive psychology (section 2.3.2).

1) Meanings of 'Good Species'

Among the several usages of 'good species,' our focus is on a case in which it is used to refer to (i) a species which is distinctive or well-defined by multiple species criteria ------criteria typically mentioned in extant species definitions, such as reproductive isolation or being monophyletic, or (ii) a taxon that an author assumes is generally classified as a species. We will see them in turn.

First, a taxonomist sometimes implies that multiple alternative species

---

5) A more detailed analysis of this concept is given in Amitani (2015). This analysis is based on a survey of papers published in academic journals and a online mailing list. See Amitani (2011) for the details.

criteria are satisfied by a good species. The papers in which this usage occurs make the fact that their judgment is based on multiple criteria explicit. One example is the following:

> Polytene chromosomes of four members of the *Simulium perflavum* species group in Brazil are described,…Chromosomal, morphological and ecological evidence indicates that *S. maroniense* Floch & Abonnenc, previously considered synonymous with *S. rorotaense*, is a good species. (Hamada and Adler, 1999)

In this case the authors cite three kinds of evidence (chromosomal, morphological, and ecological evidence) when they call the taxon "good species."

From this usage, one can see that an interesting feature of good species is their *distinctness*. According to this usage, good species are often supposed to meet multiple criteria of specieshood. In such a case, the taxon probably looks distinct from other species to many taxonomists, because taxonomists from opposing perspectives would, nonetheless, agree that it is a species. One may find some support from cognitive psychology in this regard. Cognitive psychologists point out that human beings are particularly keen to multiple interrelational associations among objects. In other words, humans tend more quickly to learn how to tell one category from another when two categories are different in multiple properties, than a single property (Rosch and Mervis, 1975). This would encourage many taxonomists to accept it as a legitimate species taxon.

Another, related usage is the one in which it is used to refer to a taxon that an author assumes is generally classified as a species without following one particular criterion of species classification. Under this usage, biologists often use a good species as a *reference point*. The authors assume that good species *are* species and try to discover novel characters of them in order to infer something significant about the nature of species in general. Kai Chan and Simon Levin seem to use 'good species' in this way. From their observation of a good species, they attribute some properties (exchanging genetic material with each other) to species in general.

> It is commonly assumed that "good" species are sufficiently isolated genetically that gene genealogies represent accurate phylogenies. However, it is increasingly clear that good species may continue to exchange genetic material through hybridization (introgression)... (Chan and Levin, 2005)

In cases like this, the authors do not always cite any paper to support that the relevant "good species" are, indeed, actually recognized as species; it is implied that they are so recognized.

To repeat, among other things, the phrase 'good species' refers to (i) an alleged species that satisfies more than one species criterion, and (ii) a taxon generally recognized as a species. Although the two meanings are different, they overlaps significantly, in that if a taxon is a good species in the first sense, it is likely to be one in the second sense, and vice versa. The more species criteria ------such as reproductive isolation and phylogenetic properties------ a taxon satisfies, the stronger the expectation that other taxonomists would also classify it as a legitimate species will be. The reverse relation also holds: if *Xus bus* is generally judged to be a species by the taxonomic community, then *Xus bus* is judged to be a species according to many criteria.

2) Good Species is a Prototype of Species

Now I argue that *good species* is a prototype of *species*, as explicated in cognitive psychology. Over the last few decades, cognitive psychologists have discovered that different instances of a concept are represented differently in our mind, and that some exemplary instances function as prototypes of the concept and have several characteristic features (they are called the prototype effects; see, for example Laurence and Margolis, 1999). For instance, subjects require less time to identify a typical member of a category (e.g., a dog for *pet*), than an atypical member (e.g., a snake). In this section I briefly show that *good species* exhibits the same linguistic features as other prototypes do.[6)]

First, quite literally, "good *X*" is quite often used by psychologists to refer to prototypical instances of a concept. When psychologists attempt to find prototypes of a concept operationally, they almost always ask subjects to pick "good" instances of a concept. Psychologists themselves also commonly refer to a prototype by "good *X*." For example,

> "...The top half of the table contains the data for instances that were "good" members of their corresponding conjunctions …" Smith et al (1988).

Notice that Smith et al. add quotation marks to "good members." The use of quotation marks even coincides with taxonomists' use of them. Many biologists add quotation marks to "good" in "good species," as Chan & Levin do. The use of quotation marks reflects that the judgment that a taxon is a good species is unofficial. The use of scare quotes by psychologists probably reflects that prototypes have the same unofficial character. This coincidence indicates that taxonomists and psychologists

6) A more extensive discussion on this point is given in Amitani 2015.

do not just use the same phrase; "good X" has similar linguistic functions for both psychologists and taxonomists.

Another linguistic evidence comes from hedges. Although "A robin [a prototypical bird] is a bird" and "A penguin is a bird" are both true, adding some hedges (qualifying terms such as "virtually" and "technically") could change their truth values: "A penguin is technically a bird" is judged to be true while "A robin is technically a bird" is not (Lakoff, 1973; Rosch, 1978). The same thing is true of "good species": sentences such as, "*Xus bus* is a good species and technically a species", sound false. In contrast, "*Xus bus* is not a good species, but technically a species" sounds true. In other words, a good species and a prototype will never be borderline cases. Indeed, taxonomists use "*Xus bus* is a good species" to claim that the taxon is not a borderline case.

3) Exemplars

We have seen that our representation of *good species* has the same properties as prototypical members of other categories. An observation related to this is that taxonomists have relied upon the commonality of *exemplars* of species when facing disagreement on the nature of species, even though they do not explicitly refer to them as good species. Thus the exemplars of species commonly recognized by competent naturalists may well be at the basis of the concept of species. The case of a 19th century naturalist in England called Hugh Strickland, as described by a historian Gordon McOuat's study (McOuat, 1996), illustrates this point.

McOuat's paper focuses on Strickland's "solution" to the species problem as a founding member of the British Association for the Advancement of Science (BAAS) Committee on Zoological Nomenclature. To put his effort in a context, we need to start with the debate between "conservative" and "reformist" naturalists on classification in the 19th century England. In the early 19th century, many conservative naturalists in the Linnaean Society largely followed the Linnaean hierarchical system of classification and the Lockean view on naming. On this view, names need not to represent the properties of the bearers; rather, names are directly connected to the object and tell us nothing about the essence of the things. However, beginning in the 1830s, “reformist” naturalists began to react against them. Some reformist naturalists such as Neville Wood and Charles T. Wood argued that names should reflect the essence of the objects named: it should convey some information about the object in virtue of the name itself.

While Strickland admitted a need for reform, as a conservative he supported the Lockean account of names and attempted to institutionalize his philosophy on naming species widely shared among conservative naturalists, as the official rules of nomenclature. He wrote a proposal for “Rules for Zoological Nomenclature” in 1837 (Strickland, 1837) and in 1842 proposed that BAAS establish a special committee to discuss his draft in order to make a recommendation to the society with respect to its adoption as a law for zoological nomenclature. Although the proposal was rejected due to fierce opposition by the reformists, Strickland was able to print the rules in the official 1842 BAAS report, giving “the impression that it was an official document of the BAAS” (McOuat, 1996, p. 509). This in turn led to acceptance of similar rules in United States and Italy.

This is part of the story of how conservative naturalists gained the upper hand in this controversy over nomenclature. But what is striking about this report for our purposes is that it does not specify either the ontological status or essential properties of species. For example, the first draft says that species are “tangible objects” (“Rules, Second Draught,” Strickland Papers, Cambridge University, Museum of Zoology, cited in

McOuat 1996, p. 511). However, Strickland faced E. H. Bunbery’s objection that species are an abstraction and that only individuals can be tangible. As a result, he did not put any definition of species into the Rules. According to McOuat, the significance of this is that it offers a “solution” to the species problem without any definitive definition of it by mutual understanding of “competent” naturalists. “For the Rules, species were just what competent (read: institutional, published, gentlemanly, conservative) naturalists said they were.” (512). McOuat suggests that there may have been a way of understanding species without the use of definition when he says,

> The “Rules of Nomenclature” were rules governing behavior, of proper etiquette for membership within that elite body. Yet, there was, there could be, no agreement on exactly what a species was, *definitionally*. (McOuat 1996, 515. Italics added)

That is, it is suggested that naturalists understood species in some non-definitional way.

We have good reason to think that those exemplars of species upon which Strickland eventually relied and the instances of *good species* overlap in their extension, although he did not emphasize the concept of good species. This is because both of them are likely to be classified as species by competent naturalists of their time. We have seen this in the last section on *good species*. In the case of Strickland, McOuat thinks that one of the factors supporting this mutual understanding is that naturalist contemporaries of him, including Darwin ------Darwin was a member of Strickland’s BAAS committee------ shared the same or similar set of examples of species with each other (personal communication). Therefore, we can conclude that those exemplars of species are at the basis of the concept of species.[7)]

Ⅲ. Precisification

The general concept of species has two semantic components ------discontinuities in nature and being a lineage at a population level------ and its prototype is the concept of good species. Then what is the relationship between the concept of species and individual species definitions?[8] I argue that individual species definitions *precisify* the meaning of the general concept of species.

To unpack the concept of precisification, let me give an analogy from discussion on vague predicates. According to supervaluationism, many sentences containing vague predicates, such as 'tall' and 'rich,' are neither true nor false until those predicates are under appropriate precisification (Keefe and Smith, 1999; Fine, 1975; Lewis, 1993). A statement "Betty is tall," for example, may be neither true nor false in this form. But if one gives appropriate specification to the statement, e.g. "Betty is tall for a 6th-grade girl," then one can figure out what this sentence means more precisely and whether or not it is true: Betty is 6 feet tall, so she is tall for a 6th-grade girl. But some person may be tall

7) Please note that I do not claim here that *good species* are exemplars of *species* (I thank an anonymous reviewer for bringing my attention to this point). This distinction is important because in cognitive science the prototype view (prototypes are the nature of a concept) and the exemplar view (one's concept of *X* is a set of her memory of *X*'s) are in competition. My point is that nevertheless *good species* and examplars of *species* extensionally overlap.

8) One might wonder: we may not need to consider the relationship between the general concept of species and individual definitions, given that the former has "semantic" components, conditions for a species to satisfy (I thank an anonymous reviewer for bringing my attention to it). However, this overlooks the hierarchical structure of those conditions. The semantic components specify the conditions for an object to be a species, just like those specified by individual definitions of species. But those conditions provided by individual definitions are more specific. Meanwhile I intend the semantic components of the general concept to list the most general conditions any definition explicitly or implicitly sets.

under any precification: Sultan Kosen, the world's tallest man, who is 8 feet 1 inches tall, may be tall in whatever way we precisify the predicate 'tall.' Then "Mr. Kosen *is* tall" is true, even though 'being tall' is a vague predicate (A supervaluationist calls propositions like this 'supertrue').[9)]

This precisification model can be applied to the relation between the general concept of species and individual species definitions: individual definitions can be taken to be attempts to precisify the general concept of species under some interests, and the term species (before precisification) refers to the general concept of species, just as the predicate 'tall-for-a-6-grade-girl' is a precification of 'tall' and 'tall' (without any precification) refers to the general concept of tallness. Take the BSC for an example: a species is a population (or a group of populations) which is reproductively isolated from other such entities (Mayr, 1942). According to the precification model, the supporters of the BSC, who has an interest of explaining the coexistence of different taxa in a single habitat (Coyne and Orr, 2004), aim to precisify the conditions under which a taxon becomes a distinctive species. When one utters "*Aux bus* is a distinct species," we may not be sure what she means and whether or not this statement is true, because this general concept of species has a placeholder for possible causal mechanisms and the truth value of this statement may depend on what mechanism fills in it. If she tells us that she follows the BSC, then we can find what she means and whether the statement is true, because the placeholder is now filled in. This example, however, should not be taken to suggest that there is no other way to precisify the above statement. Indeed, if she adopts the monophyletic species concept (de Queiroz and Donoghue, 1988, for example), she would mean something different------that is, that *Aux bus* is the least

9) That is, it is supertrue that *Fa* if and only if '*Fa*' is true under any precisification of *Fx* where *F* is a predicate and *a* is a constant referring to a particular object.

inclusive monophyletic group, not a reproductively isolated population.[10)]

■ Support for the Model

There are reasons to believe that this is a correct description of the relationship between the general concept of species and individual species definitions.

Firstly, this model captures the ways in which biologists use the general concept of species in their research. For example, biologists frequently use the word ‘species’ in an unarticulated way first. One example is observed by a geneticist Jody Hey (2001). Hey reports that biologists uses the word “species” in the conversation casually, as if the word has one single common meaning and they fully understand it, only to realize they do not when pressed on what it is.

> It has been my experience ------and I am guessing that it is a typical one------ that when talking with biologists, one hears [the term ‘species’] tossed about regularly in a manner that supposes there is one single common meaning. If pressed on that common meaning, biologists are stuck, but they persist in using the word in a casual way much as laypersons do, as if it has a well-known meaning. (Hey, 2001, p. 11)

Just as we often use the predicate ‘tall’ rather in an unarticulated way until we are asked to clarify what we mean, biologists use the term ‘species’ in an unarticulated way on many occasions until they are asked

---

10) A couple of authors have drawn attention to this point without appealing to discussion on vague predicates. Pigliucci and Kaplan (2006) make the same point. Brigandt (2003) expresses an idea similar to this from epistemological viewpoint when he says that different species definitions are instantiations of the same broad research program, i.e., an explanation of phenomenal discontinuities in terms of hidden causal mechanisms. It is also worth noting that the idea of supervaluationism has originated in Henry Mehlberg’s attempt to analyze scientific theoretical terms (Mehlberg, 1958), although precification is supposed to obtain between a theoretical term and observational terms (Williamson, 1994).

to articulate its meaning.

Furthermore, some philosophers claim that the term species is sometimes used as a substitute for individual species concepts (Reydon, 2005). For example, in their book on speciation, Jerry Coyne and H. Allen Orr largely use the term species to refer to a taxon reproductively isolated from other such entities, because they adopt the biological species concept (Coyne and Orr, 2004). In cases like this, ‘species’ can be replaced with an appropriate phrase, such as “reproductively isolated population(s).” According to the precisification model, this means that the term ‘species’ is precisified to mean a reproductively isolated population(s).

The model also explains phenomenological features of the concept of good species. According to one usage of it, ‘good species’ refers to a taxon judged to be a species by more than one criterion (§2.3). In supervaluationist’s term, this means that *Xus bus*, a good species, is a species under several (or most) precifications and thereby it is nearly supertrue that *Xus bus* is a species. This explains that most biologists would agree that *Xus bus* is a species and take it for granted that a good species *is* a species. It also makes sense of the fact that good species is a prototype *of species* but not any of individual definitions of species, because good species is directly tied to the term ‘species’ before any precisification.

Third, this model can make sense of the fact that biologists continue to propose new definitions *of* species. Under this model a new definition of species is a new way of precisifying the general concept of species. This is why they still use the term ‘species’ for their new definition; what they propose is a new definition *of* ‘species,’ i.e., a new attempt to make the notion of species precise, but not a proposal of a new term.[11)]

---

11) Discussion in this section does not assume that supervaluationism is the right view

Ⅳ. Epistemological Roles of the General Concept

In the last section we provided an overview of the features of the general concept of species and its relationship with individual definitions of species. In this section, I will sketch epistemological roles of the general concept plays in biological researches.

1. Motivating Roles

■ Agenda-Setting

The general concept plays a motivating role in the research. First, the general concept sets the domain for research. The general concept of species is associated with phenomenal saliency in nature. One could find phenomenological discontinuities in any given biota, and assume that different entities bear those discontinuities and have causal mechanisms behind them. If we manage to identify causal mechanisms, we can explain the discontinuities in terms of the mechanisms: the discontinuities are an object of explanation. In this sense, the general concept of species sets an explanatory agenda for biologists (Brigandt, 2003). In other words, the general concept of species indicates what we do know (the phenomenology of species) and we do not know about species in general (e.g., causal mechanisms behind it), and thus provide explanandum, a research goal, to the researchers.[12] One thing to notice here is that the

---

for vague predicates in general (See Williamson, 1994, for criticisms of supervaluationism). Nor do I mean that vagueness about ‘species’ is all linguistic, which is what is often taken as an implication of supervaluationism. What I want to say here is that precisification captures the important aspects of the relationship between the general concept of species and individual species definitions, and that explication espoused by supervaluationism to vague predicates helps us understand the precisification relation between them.

12) Maclaurin and Sterelny (2008) assigns similar epistemological role to the

general concept of species in this case is characterized by phenomenological characters. It does not identify any causal mechanism.

■ **Reference Point**

The original domain-setting by the general concept typically occurs when a particular research program emerges. However, the general concept could also play an epistemological role in later stages of research; the general notion of species offers a *reference point* with the help of good species. Good species are almost certainly species, thus if one finds an interesting feature in them, this can be extrapolated to other instances of species. Chan and Levin make use of the concept of good species this way in the quote above (p. 99): since some good species hybridize and exchange genetic material, species in general could do so. This use of good species as a reference point could occur at later as well as early stages of research. This is suggested by the fact that scientists may reveal novel features of a species by looking at interesting features of good species. In Chan & Levin's case, we were not aware that many species frequently exchange genetic materials by hybridization (or, more species do so than we have thought). This kind of revelation often occur in later stages of research.

2. Talking About Species in a Loose Way

There is another epistemological role the general concept of species plays in research. Implication of the precisification model as described in section 3 is that the general notion of species allows what David Lewis (1986, 1993) calls *semantic indecision*------referring to something with

---

phenomenological description of ecological community. Keller (2000) points out that 'gene' plays a similar guiding role in molecular biology.

precise details being left open so that it is indeterminate what the term exactly refers to. Supervaluationists would say that ‘Fa’ is indeterminate when there are more than one way of precisifying the proposition and its truth value varies from one precisification to another. Lewis applies this to the problem of the many. Suppose there is a cat on the mat. Call her Tibbles. Suppose Tibbles has 1,000 hairs: h_1, h_2, ..., h_{1000}. Let us call Tibbles with all the hairs *c*, Tibbles with all the hairs except h_1 c_1. If one continues the same procedure, it results in 1001 objects: c, c_1, ..., c_{1000}. Question: which cat do we point to, when we say, “There is a cat on the mat”? Lewis’ answer is that we have not decided yet, and this does not matter in most cases: when we say “That cat is called Tibbles,” for example, this is true whichever object we eventually choose as a ‘cat.’

We can tell the same story about species. When biologists talk about species in a loose way, they may leave what they exactly refer to for further specification. This is particularly true when they talk of good species, a prototype of *species*. A good species will be a species according to many (or most, or all) of definitions a naturalist happens to hold. Thus when one talks about a good species, she may be able to talk about the species with leaving specifics open. This kind of indecision has some cost and benefit. Cost: it makes unclear what biologists really refer to. It may make it appear that biologists talk about the same thing when they do not. If they actually talk about radically different things under the rubric of ‘species,’ it could be an obstacle to have effective communication. But there are some benefits in using ‘species’ loosely. It takes time and energy to precisify what you mean. If we were asked to make explicit what we refer to each time we utter ‘New York’ (the state of New York or the city of New York), we would not be able to communicate effectively. We can save time and energy by leaving open which we really refer to by ‘New York’ when it does not matter. Leaving what we really mean open saves our time and energy and helps quick but sufficiently effective communication. When we know what we are talking about, we do not have to say everything, even though we cannot rule out the possibility that it is an illusion.

Another, related benefit of semantic indecision is that this leads us to make rough and ready generalizations about the biological world. We have seen Hey observes that biologists toss about the term species rather casually in conversation. Suppose biologists hold a conversation of a similar kind. Imagine a biologist claims that species S_1 is a predator of another species S_2 in such a conversation. What exactly she means by this statement partly depends on what 'species' means to her------a reproductively isolated group, or the least monophyletic group or something else. Thus we do not know exactly what she conveys with this statement until she offers further explications. However, this is not to say that this statement tells nothing at all to us. Indeed, this statement does make some rough and ready generalizations about ecological relationship between two "species," whatever S_1 and S_2 are. And there are certainly a number of situations in biological research where rough and ready generalizations like this will do, because drawing a picture at the macroscopic level will increase our understanding of the biological world. This is similar to a reason researchers use simple mathematical models to explain how a complex system, such as human behavior, works. For example, Richerson and Boyd (2005) suggest that one of the reasons they use simple mathematical models to explicate complex human behavior, such as cultural evolution, is that simple models lead us to reach "useful generalization in spite of the complexity and diversity of human behavior" (Richerson and Boyd, 2005, p. 96). Simple models, even when successful, provides at best rough and ready generalizations about complex system. However, there are certainly situations in which simple models facilitate our understanding of the subject matter and motivate us to do further research. To talk about a species is to talk about the biological world in a loose way, and there are a number of situations where talking about things loosely fosters scientific research.[13)]

Ⅴ. Implications

We have seen possible features of the general concept of species and its relation to individual definitions of species. From those findings, we can say several things about current attempts to capture how the general concept of species and individual species definitions are related. Here we will briefly review two such attempts. They are the family-resemblance view of species by Massimo Pigliucci and the general lineage concept of species endorsed by Kevin de Queiroz.

1. Family Resemblance Plays No Epistemological Role

Massimo Pigliucci (2003, 2005; Pigliucci and Kaplan 2006) do pay attention to the general concept of species, but not to its epistemological roles. Pigliucci claims that *species* is a family-resemblance concept, like *game*: it is defined by a cluster of characteristics but lacks essential properties. Those characteristics are typically the properties mentioned by major species definitions, such as phylogenetic relationships, reproductive

13) Keller (2000) makes a similar point on the concept of gene. Biologists in different experimental contexts refer to different, but extensionally overlapping objects by the same term ‘gene.’ But Keller notes that there is a sense in which this very ambiguity of the concept helps biologists communicate efficiently; if biologists assign completely different terms to refer to the “gene-like” phenomena from one experimental context to another, they would have much more trouble communicating.

isolation, ecological characteristics, and morphological similarity. Thus just as *game* is defined by a cluster of properties none of which is a necessary or sufficient condition for something to be an instance of game, *species* is defined by a cluster of properties which contains no necessary or sufficient condition in the cluster of characteristics for something to be a species.

From our point of view, Pigliucci's account sheds little light on the epistemological roles the general concept plays. Since the *species-as-a-family-resemblance* is defined by a cluster of characteristics associated to different species definitions, it says little about how biologists began their study regarding species. Before the first (or second) definition of species was proposed, *species* was not a family-resemblance concept in a straightforward sense, because no cluster of properties was associated with *species* in biologists' minds. Then one would suspect that a family-resemblance concept played no role when biologists or naturalists decided on what the domain of their research is and what they should seek for.

2. the General Lineage Concept of Species

Recently Kevin de Queiroz (1999, 2005a, 2005b, 2007, see also Richards 2010) proposed what he calls *the general lineage concept of species* and he claims that it is a species concept unifying other individual definitions. His basic strategy consists of two steps. The first step is to find something in common among various individual species definitions, and define 'species' by this common part as a "unified" species concept. This is the general lineage concept of species as seen in an earlier section (§2.2). The second step is to take the residual criteria unique to individual definitions ------such as reproductive isolation and being monophyletic------ as providing *evidence* of the separate evolution of each lineage. Thus, under this conception, one successfully solves the conceptual problem of species by saying that a species *is* a separately evolving population-level lineage while, in practice, she uses (say) reproductive isolation to see whether or not a taxon at hand does evolve separately from other such lineages: if the taxon is reproductively isolated from others, she has a piece of evidence for the existence of a legitimate species. Thus, according to de Queiroz, the concept of species has a two-tier structure: the general lineage concept as the unified concept, which describes the metaphysical nature of species, and more epistemic criteria, partly borrowed from extant species definitions, which have little to do with the nature of species, but help biologists discern whether or not a particular group of organisms is really a species taxon.

de Queiroz's proposal is compatible with ours in several respects. For example, although de Queiroz says little about *good species*, it could nicely mesh with his picture of speciation. In his picture, two taxa satisfying all or most of the extant species definitions will certainly be different species, because there is overwhelming evidence that they are separately evolving lineages: that is, they are good species. It also explains the fact that the extant definitions of species are really *of* species, because they provide evidence that a lineage is actually a species. Nevertheless, de Queiroz's picture does not fit with what we have seen in biologists' practice in important ways. First, although de Queiroz's proposal is concerned with the relationship between the general concept of species and individual definitions, it is by and large silent on semantic relationship between them. For example, as we have seen, philosophers and biologists often use 'species' as a substitute for their favorite definition. de Queiroz would not explain this; he would rather view this as an illegitimate use of individual species definitions, because a reproductively-isolated species is not species *per se* for him. Second, although the general lineage concept has some resources to accommodate the notion of good species, it does not explain its epistemological role as a reference point. Biologists study good species to find the *nature* of species in general. But within de Queiroz's account, we already know the nature of species (i.e., a metapopulation lineage). So his account makes little sense of the fact that biologists often study good species to find what the nature of species is. Thus one can conclude that de Queiroz's proposal does not offer correct description of the relationship between the general concept of species and individual species definitions.[14]

Ⅵ. Conclusions

In this paper we have described the components of the general concept of species and its relationship with individual definitions of species, such as the biological species concept and versions of the phylogenetic species concept. According to our description, the general concept of species refers to discontinuities at some level in the biological world and a lineage at a population-level, and has *good species* as its prototype and exemplars. Individual definitions of species are precisifications of this general concept of species. While the general concept of species often leaves the causal

14) Another implication is criticism of a common assumption among various attempts to solve the species problem, i.e., the assumption that biologists represent the notion of species through one definition or another (or they should) and that reconciling conflicting definitions in one way or another is necessary for the resolution of the species problem (Mayden, 1997; Hull, 1999; Ereshefsky, 1992; Reydon, 2005). But limitations of space prevent us from exploring this point in more detail. See Amitani (2015) for further discussion.

details of a species open, restricting contexts gets us close to individual species definition, such as the ecological species concept.

The general concept of species plays epistemological roles in biologists' research. It is an agenda-setter in that it designates the domain for research or explanandum (similarities in the biological world) and what the researchers should seek for. *Good species*, a prototype of *species*, also offers a reference point: if a good species has *f*, we can infer that a species in general has *f*. The general concept allows us to be indecisive about the semantic content of the term species. This also enable biologists to save time and energy to precisify what they mean when there is no such need and to make rough and ready generalizations.

If this picture is on the right track, then several extant attempts to describe the relationship between the general concept and individual definitions has problems. The view endorsed by Pigliucci does not account for the epistemological roles the general concept plays. de Queiroz's picture of the unified concept and individual definitions of species does not fit with what we have seen in biologists' practice in important ways. In those respects, we provide a clearer picture of what biologists really do with *species*.

Submitted: 2017. 02. 25
Reviewed: 2017. 08. 02
Confirmed for Publication: 2017. 08. 02

References

Amitani Y (2011) The Persistence Question of the Species Problem. Ph.D. Thesis, Submitted to the University of British Columbia.

Amitani Y (2015) Prototypical reasoning about species and the species problem. Biological Theory 10:289–300.

Amundson R (2005) The Changing Role of the Embryo in Evolutionary Thought: Roots of Evo-Devo. Cambridge University Press, Cambridge.

Brigandt I (2003) Species pluralism does not imply species eliminativism. Philosophy of Science 70:1305–1316.

Chan K, Levin S (2005) Leaky prezygotic isolation and porous genomes: Rapid introgression of maternally inherited DNA. Evolution 59:720–729.

Coyne J, Orr H (2004) Speciation. Sinauer Association Inc, Sunderland MA.

Cronquist A (1978) Once again, what is a species? In: Biosystematics in agriculture, Rombergered Allanheld & Osmun: Montclair, NJ, pp 3-20.

Ereshefsky M (1992) Eliminative pluralism. Philosophy of Science 59:671–90.

Ereshefsky M (2010) Microbiology and the species problem. Biology and Philosophy 25:553–568.

Fine K (1975) Vagueness, truth and logic. Synthese 30:265–300.

Halt MN, Kupriyanova EK, Cooper SJ, Rouse GW (2009) Naming species with no morphological indicators: species status of *Galeolaria caespitosa* (Annelida: Serpulidae) inferred from nuclear and mitochondrial gene sequences and morphology. Invertebrate Systematics 23:205–222.

Hamada N, Adler P (1999) Cytotaxonomy of four species in the *Simulium* *perflavum* species group (Diptera: Simuliidae) from Brazilian Amazonia. Systematic Entomology 24:273–288.

Hennig W (1966) Phylogenetic Systematics. Urbana, University of Illinois Press, translated by Davis, D.D. and R. Zangerl.

Hey J (2001) Genes, Categories, and Species. Oxford University Press, Oxford.

Hull D (1999) On the plurality of species: Questioning the party line. In: Wilson R (ed) Species New Interdisciplinary Essays, The MIT Press, Cambridge MA.

Keefe R, Smith P (1999) Introduction: Theories of vagueness. In: Keefe P R; Smith (ed) Vagueness: A Reader, The MIT Press, Cambridge, MA, pp 1–57.

Keller EF (2000) The Century of the Gene. Harvard University Press.

Lakoff G (1973) Hedges: A study in meaning criteria and the logic of fuzzy concepts. Journal of Philosophical Logic 2:458–508.

Laurence S, Margolis E (1999) Concepts and cognitive science. In: Margolis E, Laurence S (eds) Concepts: Core Readings, The MIT Press, Cambridge MA, pp 3–81.

Lewis D (1986) On the Plurality of Worlds. Basil Blackwell, Oxford.

Lewis D (1993) Many, but almost one. In: Cambell JRL Keith; Bacon (ed) Ontology, Causality, and Mind: Essays on the Philosophy of D. M. Armstrong, Cambridge UP, Cambridge, pp 23–38.

Luckow M (1995) Species concepts: Assumptions, methods, and applications. Systematic Botany 20:589–605.

Maclaurin J, Sterelny K (2008) What Is Biodiversity? University of Chicago Press, Chicago.

Mayden R (1997) A hierarchy of species concepts the document in the saga of the species problem. In: Claridge M, Dewah H, Wilson M (eds) Species: the Units of Biodiversity, Chapman and Hall, London, pp 381–424.

Mayr E (1942) Systematics and the Origin of Species from the Viewpoint of a Zoologist. Columbia University Press, New York.

McNeill J, Barrie F, Burdet H, Demoulin V, Hawksworth D, Marhold K, Nicolson D, Prado J, Silva P, Skog J (2006) International Code of Botanical Nomenclature (Vienna code).

McOuat G (1996) Species, rules and meaning: The politics of language and the ends of definitions in 19th century natural history. Studies in History and Philosophy of Science Part A 27:473–519.

Mehlberg H (1958) The Reach of Science. University of Toronto Press, Toronto.

Nixon K, Wheeler Q (1990) An amplification of the phylogenetic species concept. Cladistics 6:211–223.

Pigliucci M (2003) Species as family resemblance concepts: the (dis-)solution of the species problem? Bioessays 25(6):596–602.

Pigliucci M (2005) Wittgenstein solves (posthumously) the species problem. Philosophy Now 50:51, [http://www.philosophynow.org/issue50/50pigliucci.htm (Jun. 11, 2005 retrieved)]

Pigliucci M, Kaplan J (2006) Making Sense of Evolution. University of Chicago Press, Chicago.

de Queiroz K (1998) The general lineage concept of species, species criteria, and the process of speciation: A conceptual unifivation and terminological recommendations, Oxford: Oxford University Press, pp 57–75.

de Queiroz K (1999) The general lineage concept of species and the defining properties of the species category. In: Wilson R (ed) Species: New Interdisciplinary Essays, MIT Press, Cambridge MA, pp 49–89.

de Queiroz K (2005a) Ernst Mayr and the modern species concept. In: Hey J, Fitch W, Ayala F (eds) Systematics And the Origin of

Species: On Ernst Mayr's 100th Anniversary, National Academic Press, Washington DC, pp 243–263.

de Queiroz K (2005b) A unified concept of species and its consequences for the future of taxonomy. Proceedings of the California Academy of Science 56:196–215.

de Queiroz K (2007) Species concepts and species delimitation. Systematic Biology 56:879–886.

de Queiroz K, Donoghue M (1988) Phylogenetic systematics and the species problem. Cladistics 4:317–38.

Reydon T (2005) On the nature of the species problem and the four meanings of 'species'. Studies in History and Philosophy of Biological and Biomedical Sciences 36:135–158.

Richards RA (2010) Species Problem—A Philosophical Analysis. Cambridge University Press.

Richerson P, Boyd R (2005) Not by Genes Alone. University of Chicago Press, Chicago.

Rosch E (1978) Principles of categorization. In: Rosch E, Lloyd B (eds) Cognition and Categorization, Erlbaum, Hillsdale NJ, pp 27–48.

Rosch E, Mervis C (1975) Family resemblances: Studies in the internal structure of categories. Cognitive psychology 7:573–605.

Smith E, Osherson D, Rips L, Keane M (1988) Combining prototypes: A selective modification model. Cognitive Science 12:485–527.

Sneath P (1976) Phenetic taxonomy at the species level and above. Taxon 25:437–450.

Strickland H (1837) Rules for zoological nomenclature. Magazine of Natural History 1:173–176.

Wilkins J (2006) Species, kinds, and evolution. Reports of the National Center for Science Education 26:36–45.

Williamson T (1994) Vagueness. Routledge, London/New York.