Chapter 8 Are Species Good Units for Biodiversity Studies and Conservation Efforts?



Thomas A. C. Reydon

Abstract While species have long been seen as the principal units of biodiversity, with prominent roles in biodiversity research and conservation practice, the long-standing debate on the nature of species deeply problematizes their suitability as such units. Not only do the metaphysical questions remain unresolved what kinds of things species *are*, and whether species are at all real, there also is considerable disagreement on how to define the notion of species for use in practice. Moreover, it seems that different organism groups are best classified using different definitions of 'species', such that species of organisms in very different domains of biodiversity are not generally comparable units. In this chapter I will defend and elaborate the claim that species are not good units of biodiversity, focusing in the issue of species realism. I will sketch a pragmatic notion of 'species' that can be used as an epistemic tool in the context of biodiversity studies, without however involving a view of species as basic units of biodiversity or as the focal, real entities in biodiversity conservation.

Keywords Species · Species concepts · Species problem · Units of biodiversity

8.1 Introduction

Biodiversity studies and conservation biology are rapidly growing fields of work, aimed, among other things, at mapping the diversity of life on our planet, studying its origins, assessing how humanity benefits from its presence, and achieving clarity about possible ways of preserving it (Ehrlich and Wilson 1991). The growth of both

Institute of Philosophy & Centre for Ethics and Law in the Life Sciences (CELLS),

Leibniz Universität, Hanover, Germany

e-mail: reydon@ww.uni-hannover.de; http://www.reydon.info

¹Conservation biology is a well-defined discipline with its own textbooks, journals, scientific societies, and so on. Biodiversity studies, in contrast, is a loose collection of disciplines (or perhaps

T. A. C. Reydon (⊠)

fields is fueled by a number of factors, one of which is the realization that still only a small fraction of the Earth's extant biological diversity is known, and that many organism groups — most importantly local populations and entire species — are threatened with extinction, such that there is an urgency to map out our planet's biological diversity and undertake appropriate conservation efforts before these have disappeared forever (e.g., Wheeler et al. 2012).

Studying and conserving biodiversity is not merely a matter of the disinterested acquisition of knowledge about the world we live in, though, nor is it a matter of simply wanting to preserve the world as we find it. The importance of mapping, studying and conserving biodiversity is related foremost to the availability of natural resources that are crucial to human survival and well-being, i.e., to the availability of ecosystem services (Costanza et al. 1997; Dirzo and Raven 2003; Mace 2015; Hunter and Gibbs 2007: 348–349; Mace et al. 2012). Ecosystem services include resources such as clean water, clean air, arable land, fuel, building materials, and so on, as well as natural environments that can be used for recreative and aesthetic purposes. In addition, potential resources that as yet unexplored organism groups could provide for the production of new medicinal products, better foodstuffs, etc. constitute potential ecosystem services that support the value of biodiversity studies and conservation efforts (Maclaurin and Sterelny 2008: 5–6). In sum, studying and conserving biodiversity is important because human survival and well-being depends on it.

Yet, notwithstanding the importance and rapid growth of biodiversity studies and conservation biology as academic fields as well as areas of activism and engagement, they are faced with profound challenges. As highlighted in the Introduction to this volume, while the many practical challenges (due, among other things, to political and economic interests making it difficult to achieve conservation targets) are widely recognized, conceptual challenges are much less widely discussed. As Casetta et al. rightly point out, "[w]hen biodiversity conservation is at issue, theoretical and practical matters go hand in hand, and practical challenges are intertwined with conceptual ones". This chapter addresses such a conceptual challenge concerning the notion of 'species', and aims to resolve some conceptual difficulties to obtain a notion that is better suited for application in biodiversity studies and conservation biology. Considering that these fields are practice-oriented areas of work, it is surprisingly hard to pin down the meanings of many of their core concepts – a state of affairs that makes conceptual work a crucial prerequisite for practical interventions.

rather an interdisciplinary field of work) that are in some way or other concerned with earthbound biodiversity. The term 'biodiversity studies' is common in the literature (Ehrlich and Wilson 1991; Agapow et al. 2004; Raczkowski and Wenzel 2007), but is not used to denote a well-delimited set of disciplines. Ehrlich and Wilson (1991) conceive of biodiversity studies as combining elements of evolutionary biology, ecology, applied areas of biology (such as forestry, agriculture, and medicine) and public policy, and see conservation biology as a subdiscipline of biodiversity studies. For the purposes of the present chapter, I think the term does not need to be specified in more detail beyond the meaning of "any area of work that studies biodiversity".

²Casetta, Marques da Silva & Vecchi, this volume.

Consider for instance the notion of biodiversity itself. It is notoriously hard to define and is the topic of ongoing debate among philosophers of biology as well as biologists themselves (e.g., Purvis and Hector 2000; Hamilton 2005; Colwell 2009; Santana 2014, 2018; Faith 2016; Odenbaugh 2016; Burch-Brown and Archer 2017).3 In its broadest sense, biodiversity simply means the diversity of living entities, of their parts, and of systems composed of them, at all levels of organization, from the genetic level all the way up to the ecosystem level (Hunter and Gibbs 2007: 22; Odenbaugh 2016: Section 1). A simple definition of the term 'biodiversity' thus would be "the variety of all forms of life, from genes to species, through to the broad scale of ecosystems" (Faith 2016). In addition to the various levels of organization in the living world, biodiversity is studied with respect to a number of different aspects of living systems, such as the roles organisms play as parts of ecosystems or food webs (functional diversity), the specific morphological or behavioral properties shared by organisms of particular groups (trait diversity), their lines of descent (phylogenetic diversity), and so on. Colwell (2009: 257), for example, explains the notion of biodiversity as encompassing "the variety of life, at all levels of organization, classified both by evolutionary (phylogenetic) and ecological (functional) criteria" and Dirzo and Raven (2003: 138) explain it as "the sum total of all of the plants, animals, fungi, and microorganisms on Earth; their genetic and phenotypic variation; and the communities and ecosystems of which they are a part." Accordingly, there are various ways of conceiving of biodiversity that differ from one another in regard to the specific levels of organization and the specific aspects of living systems one is interested in. Biodiversity can be thought of as the genetic diversity in a local population, the species richness of a local community or region, the diversity of functional groups (such as primary producers, herbivores, etc.) in a particular ecosystem, the diversity of habitats making up an ecosystem, and so on. As a result, researchers often focus on only one or a few aspects of biodiversity, rather than assessing the biodiversity of a particular area as such. Note that this multidimensionality of the concept is precisely the reason for which some authors are skeptical about the concept's scientific value: generally, it does not make much sense to talk about the biodiversity of a particular region or the biodiversity of planet Earth, because there are too many distinct aspects to consider and a region can be very diverse in some aspects and much less diverse in others (Santana 2014, 2018).

While 'biodiversity' thus is a multifaceted concept and the interests that guide work in biodiversity studies differ from those in conservation biology – the former being more aimed at producing scientific knowledge and the letter more oriented towards intervention and activism –,⁴ both fields use largely the same basic units to individuate groups of organisms and living systems of interest. Many studies and

³ See also, in this volume, Toepfer, Chap. 18; Sarkar, Chap. 18; and Santana, Chap. 19.

⁴Indeed, conservation biology is often conceived of as a "mission-driven discipline" and as "the applied science of maintaining the earth's biological diversity" (Hunter and Gibbs 2007: 14; see also Soulé 1985: 727; Meine et al. 2006: 631; Odenbaugh 2016). The mission of the discipline is sometimes framed in terms of "healing" an ailing patient (Casetta, Marques da Silva, and Vecchi, Chap. 1, in this volume).

interventions are aimed at a particular level of the taxonomic hierarchy, namely the species level. In the same way as species serve as the basic taxonomic units and as such constitute the basic kinds of organisms studied by biologists, they also count among the basic units of biodiversity and constitute targets of many conservation efforts. In this chapter, however, I want to argue that species are not good units of biodiversity and conservation, while at the same time trying to develop a pragmatic notion of 'species' that can be used in the context of biodiversity studies while avoiding the problems highlighted in this chapter. To do so, I will examine the main aspects of the role of species in biodiversity studies and conservation efforts from an epistemological and a metaphysical perspective. Section 8.2 sketches the central role of species in biodiversity studies and conservation efforts. In Sect. 8.3, I will look at relevant debates in the philosophy of biology as well as in biology itself to highlight epistemological and in particular metaphysical problems (connected to the reality of species) that confront the notion of species in these contexts. In Sect. 8.4, I will suggest an alternative interpretation of the notion of species based on Darwin's views that might better fit the role the notion of species plays in biodiversity studies and conservation biology. Section 8.5 concludes.

8.2 Species as the Units of Biodiversity and Conservation

While biodiversity can be studied at a variety of levels of organization and with respect to a variety of aspects of living systems, one or more units of biodiversity are needed as a basis for comparisons between different areas of work and different studies. Without a common "currency", the notion of biodiversity is meaningless. A number of biodiversity measures are currently in use, many of which (including species richness, species diversity, and species evenness) focus on species as basic units of biodiversity (Purvis and Hector 2000; Faith 2016: Section 2).⁵ Hamilton (2005: 90), for example, writes:

There are currently many definitions of biodiversity and most are vague, which probably reflects the uncertainty of the concept. Some consider it to be synonymous with species richness [...], others see it as species diversity [...], whereas many propound a much broader definition such as the 'full variety of life on Earth' [...]. NRE [the Department of Natural Resources and Environment, State of Victoria, Australia] distinguish between native and introduced species, and others have put extra emphasis on threatened species [...].

Sometimes species are even considered to be the most important or the most fundamental units of biodiversity (e.g., Claridge et al. 1997; Mace et al. 2012: 20; Hohenegger 2014). Given the centrality of species as the basic taxonomic units for the whole of the life sciences as well as in the context of public representations of organismal diversity (in natural history museums, science centers, zoos, botanical gardens, etc.), putting species central seems an appropriate choice.

⁵ See also Crupi, Chap. 6, and Branquinho et al., Chap. 7, in this volume.

Closely connected to their role as units of biodiversity is the central position that species occupy in conservation efforts. Similar to biodiversity studies, conservation biology is concerned with living entities and systems on all levels of organization from the genetic level up to the ecosystem level, and conservation efforts can be directed at the genetic diversity of a particular area or taxon, at taxa themselves, at communities or ecosystems, and so on. Even though "conservation biology [...] does not yet have a general and coherent account of what should be conserved and why" (Maclaurin and Sterelny 2008: 26) and the field has since the 1990's been moving away somewhat from its earlier focus on species towards a focus on interactions between people and their environments (Mace 2015: 1558–1559), species are still among the principal entities in focus. In part this is for historical reasons. One of the main factors that contributed to both the establishment of conservation biology and the coining of the term 'biodiversity' in the 1980s was the realization that species extinction currently proceeds at a much higher rate than the natural extinction rate, and that this increased extinction rate is very probably due to the impact of the human population on the planet. Discussions of the causes of current biodiversity loss (often referred to as the "sixth mass extinction" - e.g., Barnosky et al. 2011; Ceballos et al. 2015, 2017) and of possible countermeasures tended to revolve around the extinction and conservation of local populations as representatives of a particular species in particular areas, as well as entire species (Soulé 1985; Meine et al. 2006: 637). Perhaps the best-known example of the ongoing centrality of species in conservation efforts is the IUCN Red List of Threatened Species that categorizes species according to the level at which they are threatened with extinction (Mace and Lande 1991; Mace et al. 2008; http://www.iucnredlist.org) and is widely used by researchers, NGOs, governments, politicians and the general public as a basis for conservation efforts. Another well-known example of the keystone role of species is the Convention on Biodiversity, which is aimed at facilitating biodiversity conservation and specifies that biodiversity "includes diversity within species, between species and of ecosystems" (see www.cbd.int, Article 2; emphasis added).

In addition to the historical focus on species in conservation biology, species also are sometimes highlighted in environmental ethics as morally relevant entities. In discussions on the normative aspects of human interactions with nature and the normative principles that could underwrite conservation efforts, several authors have argued that we have a moral obligation to preserve species, have attributed intrinsic value to species, or have argued that species should be counted among the entities toward which humans can have duties and obligations (e.g., Soulé 1985, and most famously Rolston 1975, 1985, 1995). Soulé (1985: 731), for example, writes: "Species have value in themselves, a value neither conferred nor revocable, but springing from a species' long evolutionary heritage and potential or even from the mere fact of its existence." Ignoring for the moment the question whether it makes sense at all to attribute intrinsic values to natural entities, such as individual organisms, species or ecosystems, it is clear that species are among the basic natural entities

(along with individual organisms) that at least sometimes are seen as bearers of value in conservation contexts.⁶

Species, then, have long been among the principal units of biodiversity studies as well as one of the principal kinds of focal entities in conservation efforts. This role entails a number of epistemological and metaphysical requirements. For one, it seems that to be able to serve as units in biodiversity estimates of a particular area or as the subjects of biodiversity conservation efforts species must be real entities – at least it seems that for species to be entities that can become extinct or can be kept in existence by human efforts, or for them to be bearers of intrinsic value, they cannot be *purely* conventional or instrumental units and a minimal level of realism with respect to species is required. But if species are real entities, what exactly are they? This is the core issue in the long-standing debate on the nature of species, and it deeply problematizes the suitability of species as units of biodiversity.

In addition, not only do the questions what kinds of things species *are* and whether species are at all real entities remain highly controversial metaphysical issues, there also is considerable epistemological disagreement on how to best define the notion of species for use in practice. For practical purposes in biodiversity inventories and conservation contexts, species should possess an unequivocal and generally agreed upon epistemic status as well-delimited and recognizable groups of organisms that, by being groups at the same level of the biological hierarchy, are comparable throughout the whole of earthbound biodiversity. A species of fruit fly should be a similar kind of unit as a species of flowering plant, or a species of fungus – they all are species, after all, and not groups at higher or lower taxonomic levels. However, it seems that different organism groups are best classified using different definitions of 'species', such that species of organisms in very different domains of biodiversity are not generally comparable units.

The preceding issues suggest that species are not good units of biodiversity, that is, units that meet the various epistemological and metaphysical requirements for performing the roles assigned to them in biodiversity research and conservation practice. In what follows, I will explore this suggestion in more detail.

8.3 Why Species Are Not Good Units of Biodiversity and Conservation

A number of aspects of the role species play in biodiversity studies and conservation efforts are philosophically controversial. In this section, I will highlight four such aspects: the reality of species (and the connected issue of the naturalness of species), the role that species play as counting units, the idea that species should be targets of conservation efforts because they are repositories of genetic information, and the relation between species and ecosystem services.

⁶I am sceptical about using notions of intrinsic value in general and in the context of environmental ethics in particular. This is an issue for another paper, though.

A first issue that needs to be addressed is the reality and naturalness of species. If species are the sort of things that can come into existence in speciation events and go extinct, that can be attributed an intrinsic value, or can be counted in biodiversity surveys of particular areas, then surely they must be real things. If species are purely conventional units without *any* basis in nature, then what exactly are we counting in biodiversity inventories? The concept of species richness, for example, is the simple idea of the number of species in a particular area or system: "[E]cosystem A is easily recognized as more diverse than B or C because it has four species instead of three. This characteristic is called species richness or just richness, and it is a simple, commonly used measure of diversity" (Hunter and Gibbs 2007: 25). For comparisons between ecosystems with respect to species richness to make sense, species counts must be counting real features of ecosystems – or at least features that are not *purely* conventional.

Accordingly, the view that species must be real entities is widespread among biologists. Cracraft, for example, writes:

Unless species concepts are used to individuate *real*, *discrete entities in nature*, they will have little or no relevance for advancing our understanding of the structure and function of biological phenomena involving those things we call species. [...] If species are not considered to be discrete real entities [...] then it implies that evolutionary and systematic biology would be based largely on *units that are fictitious*, whose boundaries, if drawn, are done so arbitrarily. It would also mean that most, if not all, of the processes that we ascribe to species are concoctions of the mind and have no objective reality. Entities of postulated processes must be real and discrete if those processes are to have much meaning. [...] Unless a species concept can be used to individuate *real-world entities*, that concept will have limited utility for systematists getting on with their task of sorting out and understanding biological diversity. (Cracraft 1997: 327–328; emphasis added).

In a similar vein, Wilson writes:

Not to have a *natural unit* such as the species would be to abandon a large part of biology into free fall, all the way from the ecosystem down to the organism. It would be to concede the idea of amorphous variation and *arbitrary limits* for such intuitively obvious entities as American elms (species: *Ulmus americana*), cabbage white butterflies (*Pieris rapae*), and human beings (*Homo sapiens*). Without natural species, ecosystems could be analyzed only in the broadest terms, using crude and shifting descriptions of the organisms that compose them. Biologists would find it difficult to *compare results* from one study to the next. How might we access, for example, the thousands of research papers on the fruit fly, which form much of the foundation of modern genetics, if no one could tell one kind of fruit fly from another? (Wilson 1992: 38; emphases added).

⁷Note that is not the case that only real things can be attributed a value. Here, however, species are thought to have *intrinsic* value, i.e., values that a species are supposed to have in and of themselves, and it is difficult to see how non-real things could be the bearers of such intrinsic values.

⁸An additional problem is the following. If there indeed are too many different aspects of biodiversity such that studying *the* biodiversity of a region does not make sense (see Sect. 8.1; Santana 2014, 2018), a question is what species as units of biodiversity are supposed to represent. They cannot represent biodiversity *as such*, but only one or a few aspects of it. So, species could not be units of biodiversity without further qualification. At most, they could be units of some aspect(s) of biodiversity.

⁹The authors make reference to a table in their book in which ecosystem A consists of four species, and ecosystems B and C three.

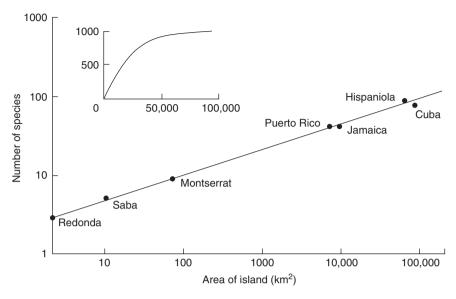


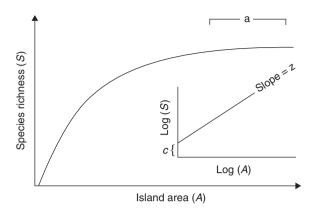
Fig. 8.1 The number of species of reptiles and amphibians of the West Indies. (From Lomolino et al. 2017, *Biodiversity (Fifth Edition)*, Fig. 13.5; reproduced by permission of Oxford University Press, USA)

And, as a final example, Mace expresses a strong view of the reality of species that involves the idea of objectivity: "the species rank is unique in the taxonomic hierarchy in that it has claim to *objective reality*, since gene flow is largely restricted within species [...]. Almost all of the many variants on a species definition agree at least that *species are real and distinct entities in nature* [...]" (Mace 2004: 711; emphasis added).

And there are empirical patterns that support this view. For example, the generality of the species-area curve, that plots species richness against area size, strengthens the suggestion that species are real things. The number of species in a particular area or ecosystem tends to be larger for larger areas or ecosystems. However, the number of species does not simply rise proportionally to the area, habitat or ecosystem size, but flattens out in a way that in island biogeography (and other contexts in which the areas are clearly delimited) is described by the equation $S = cA^z$ or $\log_{10}(S) = \log_{10}(c) + z\log_{10}(A)$, where S is the number of species and A the area. The corresponding species-area curve has the general form pictured in Fig. 8.1 and Fig. 8.2: it is a curve that for S plotted against A rises sharply near the intersection of both axes and smoothly flattens out with increasing area, and a straight line for $\log S$ plotted against $\log A$. This is a semi-universal pattern – not one that holds up without exception and as a strict law of nature, but a pattern that

¹⁰The equation was first developed by Arrhenius (1921) and modified by Gleason (1922). See Connor and McCoy (1979: 794).

Fig. 8.2 The characteristic general species-area curve. (From Lomolino et al. 2017, *Biodiversity (Fifth Edition)*, Fig. 13.8; reproduced by permission of Oxford University Press, USA)



holds up pretty well nonetheless.¹¹ The species-area relationship "is often referred to as the closest thing to a rule in ecology" (Lomolino 2000: 17), and "one of the most general, best-documented patterns in nature" (Lomolino et al. 2017: 449). Some authors even call it "one of community ecology's few genuine laws" (Schoener, cited in McGuinness 1984: 423; Lomolino et al. 2017: 449).

For a pattern such as this to hold up so well, an epistemological requirement is that species must be uniquely countable (it must be possible to obtain clear species counts for areas and ecosystems) and comparable (species counts of different areas and ecosystems must have the same meaning). 12 Metaphysically this implies a minimal realism about species. With 'minimal realism' I mean the view that species are not completely artificial units, that is, units constructed by us without having any grounding in nature. Examples of such completely artificial units that are often mentioned in philosophical discussions are the group of all items that happen to be on my desk as I am writing this, or, for a biological example, the grouping of whales and fish together in one kind because they look very similar and live in water. Nothing prevents us from grouping things in this way or from referring to these groups in everyday or even scientific contexts if we feel this serves some purpose. But we cannot think of them as real groupings in nature – we could just as easily have grouped things differently (taking all items on the left half of my desk as one group and all items on the right half as another, or grouping whales with fish larger than a particular size and taking smaller fish as a distinct group), and in the case of whales and fish there are clear scientific reasons to deny the reality of the grouping.

¹¹Although the pattern is strong, depending on sampling methods (e.g., how the sampling area is determined) and the model used to produce a species-area relationship on the basis of the data, different types of curves exist (see Scheiner 2003; Tjørve 2003, 2009).

¹² Note that this does not necessarily entail that species counts must be comparable for *all* species throughout the living world and for *all* kinds of areas, habitats and ecosystems. But at the very least, comparability must be guaranteed for counts of, say, mammalian species in forests or avian species on islands. Comparability is affected greatly by sampling methods and the possibility of uniquely delimiting the areas in which species are sampled (see footnote 5), but here I will only address the issue of species.

They are groups *by convention*, not because they represent some aspect of a natural order. For species-area curves to have scientific meaning, species cannot be artificial or conventional units in this sense, but must have at least *some* reality in nature.¹³

Indeed, the reality of species has long been a topic of discussion among philosophers of biology as well as biologists (e.g., Rolston 1995; Cracraft 1997; Mishler 1999, 2010; Bachmann 2001; Wilkins 2009; Claridge 2010; Richards 2010: Chapters 1 & 4; Kunz 2012; Slater 2013). As remarked above, there is a strong motivation for considering species to be real entities. Since the origins of biology as a science, species of organisms have been among the focal entities of research. They play an important role in nature conservation efforts. They are the basic constituents of the tree (or bush, or network) of life, as it is often presented in natural history museums. Species come into being in speciation events, participate in evolutionary processes, and go extinct. How could species not be real? But notwithstanding these strong motivations for assuming the reality of species, there are good reasons to doubt their reality. Perhaps the most important such reason is the persistent failure of biologists and philosophers of biology to agree what, exactly, species are. This is the metaphysical question at the heart of what has come to be known as "the species problem" (e.g., Mayr 1957; Stamos 2003; Reydon 2004, 2005; Wilkins 2009; Richards 2010). The problem has been a topic of debate at least since the publication of Darwin's Origin of Species, and Darwin himself addressed it in the book (Ereshefsky 2010, 2011, 2014).

The problem has turned out surprisingly difficult and at present there exists a massive volume of literature on the topic, most of which is concerned with the plurality of species concepts that have been proposed over the years and are currently used in biological science. There are around two dozen competing explanatory definitions of the term 'species' (so-called species concepts) available in the literature (Mayden 1997, 1999; Wilkins 2009; Mallet 2013). ¹⁴ Metaphysically, these definitions provide different views of what kind of things species are – populations or metapopulations, lineages, monophyletic groups of lineage segments, groups of morphologically and behaviorally similar organisms, groups of genetically similar organisms, groups of organisms that inhabit the same niche, or some combination of these characterizations – that roughly fall into the two main metaphysical categories of kinds and individuals. But none of the available definitions has gained acceptance as the one, correct definition and the nature of species remains elusive.

¹³ This brings us to the highly difficult metaphysical issue of what it means for something to be real. For reasons of space, I have tried to avoid delving into this discussion and I am assuming that it is intuitively clear what it means for something to be minimally real in the sense discussed here: to be minimally real means to have some foundation in the world as it is independently of us.

¹⁴The exact number of species concepts (or definitions) proposed in the literature is unclear, and much depends on how one counts. Wilkins (2011) counts seven definitions and 27 variations and mixtures of those seven definitions, Mayden (1997, 1999) lists 22 definitions, and Lherminer and Solignac (2000) list 92 definitions. In the end, though, what matters is that there are multiple distinct and mutually incompatible definitions of the concept of species that are used side by side in biological science and yield mutually incompatible groupings of organisms into species (Reydon 2005).

The question thus remains what biodiversity inventories are counting and what conservation efforts – when successful – are preserving.

At present, the debate (that has been going on for more than 150 years) seems to have reached something of an impasse and it looks like we have run out of unexplored options that could break the deadlock between the available definitions. As a better metaphysical understanding of the nature of species as real entities in nature does not seem to be on the horizon, the suspicion is growing that the starting point of the guest – the assumption that species are real entities in nature – was wrongheaded all along and species should be considered conventional, instrumental units after all. This latter view - species antirealism - can take two forms. One is the denial that species names such as Drosophila melanogaster or Quercus rubra refer to real entities – they refer to artificial groupings made by us for particular purposes but do not represent real groupings in nature (for an overview of this position, see Stamos 2003: Chapter 2; Wilkins 2009: 221ff.). This version of species antirealism entails that in nature there is no such things as a species – species are our inventions. The other form is the denial that the species *category* is a real category, while taking species names such as Drosophila melanogaster or Quercus rubra as referring to real entities. ¹⁵ On this latter view, the entities referred to by means of species names may be real, but they are not members of one ontological category and thus are not comparable entities or units. Accordingly, there is nothing special about species: Drosophila melanogaster or Quercus rubra may be real entities in nature that are of interest in the sciences or in conservation efforts, but not because they are species.

The view that species are artificial groupings and in particular the view that the species category is not a real category (while species are real) may well strike many as odd. For the purposes of the present chapter, however, the precise ways in which one can be a species antirealist are less important than the point that realism about species is far from straightforward. The plurality of mutually incompatible explanatory definitions of the concept of species and the persistent problem of identifying one definition as the correct characterization of species strongly suggest that species are not real entities in nature (see Richards 2010: 10ff.). But the central role of species in biological science and the existence of patterns such as the species-area curve suggest otherwise. What can be made of this situation? At the very least, the doubts raised here regarding the reality of species should raise doubts regarding the suitability of species as focal units in biodiversity studies and conservation efforts.

These doubts are deepened when looking at practices of species counts. A number of recent studies have shown that species counts are strongly dependent on the definition of 'species' that is used, and that large discrepancies can exist between species counts based on different species concepts. The number of endemic bird species in Mexico, for example, was found to vary between 101 when using the Biological Species Concept and 249 when using a version of the Phylogenetic Species Concept (Peterson and Navarro-Sigüenza 1999). Similarly, depending on the species concept that is used, the whitefly species complex *Bemisia tabaci* can be seen as a single species (using the Morphological Species Concept) or as a complex

¹⁵Ereshefsky (2010, 2011, 2014) suggested that this was Darwin's view.

of 24–28 species when species are identified according to reproductive isolation and phylogeny (Liu et al. 2012). In a meta-analysis of 89 studies, Agapow et al. (2004) found that using versions of the Phylogenetic Species Concept on average led to an increase of more than 48% in species counts as compared to counts based on non-phylogenetic species definitions, such as the Biological Species Concept. These increases in species counts were accompanied by decreases in population sizes and ranges, thus not only yielding more species, but also resulting in those species being threatened to a higher degree. Mace summarizes the problem as follows:

Without doubt, species need to be named and identified formally if they are to benefit from the conservationists' sets of legislative and planning tools. Unfortunately, all lists of species, and species richness measures generally, are extremely vulnerable to changes in species definitions. As the species concept becomes narrower, or species are split for whatever reason, the length of the list increases. The units making up the list can also alter radically. (Mace 2004: 713).

In the face of such practical difficulties we should be cautious when attributing reality to species in biodiversity studies and conservation contexts. It is crucial to ask what species counts mean, and why certain entities rather than others should be in focus of conservation efforts.

The problem is intensified by the fact that not only can different species definitions be used to partition organisms of one group into species, but it seems that different organism groups are best classified using different species concepts. In addition, microbes (which constitute the largest part of biomass on Earth) are currently classified into species on the basis of a pragmatic definition of 'species' based on a number of conventions guided by the availability of analytic technologies (such as a level of genetic similarity above which organisms should be counted as members of the same species), while it remains unclear to what extent (if at all) microbial species represent real groups in nature (Roselló-Mora and Amann (2001; Gevers et al. 2005; Doolittle and Zhaxybayeva 2009). This means that it is very difficult, if not impossible, to compare species groupings, species counts and the conservation status of species throughout the whole of biodiversity. If the same group of organisms can be classified into species in different ways, and species of birds are very different kinds of groupings from species of, say, flowering plants, then how can we be sure that we have assessed the conservation status of species correctly and how can we make good decisions on conservation priorities (which involve the comparison of species with respect to their conservation status, after all)? Moreover, how can we attribute – intrinsic or extrinsic – values to species and use these valuations as the basis for conservation efforts, if the species we pick out depend strongly on the definition we use and thus seem to lack reality as natural entities? While the practical consequences of using different species definitions for biodiversity studies and conservation efforts are widely acknowledged in the biological literature, authors have proposed diverging view of how the problem should be dealt with (e.g., Cracraft 1997; Agapow et al. 2004; Mace 2004; Dillon et al. 2005; George and Mayden 2005; Garnett and Christidis 2007; Frankham et al. 2012; Groves et al. 2017).

Taking a closer look at some of the reasons for which conservation value is attributed to natural entities is illuminating in this respect. One such reason is the view that species are repositories of genetic information, such that conserving species would be a way to conserve valuable genes and genotypes. For example, in the proceedings volume of the 1986 National Forum on BioDiversity, where the term 'biodiversity' was coined, E.O. Wilson asserted: "Each species is the repository of an immense amount of genetic information. The number of genes range from about 1,000 in bacteria and 10,000 in some fungi to 400,000 or more in many flowering plants and a few animals [...]. A typical mammal such as the house mouse (Mus musculus) has about 100,000 genes." (Wilson 1988: 7). For a number of reasons, this is a problematic basis for attributing value to species. For one, the view of species as genetic repositories involves the assumption that species are real entities in which a certain amount of genetic information is stored. Moreover, it involves the assumption that the genetic information stored in a species is specific for that species – i.e., that each species can be associated with a combination of genes that characterizes that species and distinguishes it from other species, such that in order to conserve specific genetic information we would need to conserve a particular species.

The quotation from Wilson suggests a comparatively simple view of a species' genome as consisting of a countable number of well-individuated units – genes – that together constitute the genetic information contained in the species. Recent developments in the philosophy of biology as well as in biology itself, however, have shown the picture to be much more complex. One aspect of the problem is the current debate on what, exactly, genes are. While the notion of 'gene' was explicitly introduced as a technical term in biology in 1909 by the Danish geneticist Wilhelm Johannsen, originally it was a term without any concrete material referent and the concept's meaning has been undergoing considerable change. Weber (2005: 227), for example, considered the notion of 'gene' a case of what he calls 'freely floating reference': biologists repeatedly began to use the term to refer to different kinds of DNA-segments as new molecular biological techniques became available, such that which entities were individuated as genes depended strongly on the investigative methods and techniques available, as well as on the specific interests of researchers. At present, it remains unclear what, exactly, genes are and how the notion of the gene is best conceptualized (Dietrich 2000; Griffiths and Stotz 2006, 2013). Thinking of the genetic information stored in a species in terms of the genes contained in the species' genome, then, is problematic. Thinking of genetic information in terms of whole-genome sequences does not constitute a better option. Even though colloquially references are often made to the human genome (International Human Genome Sequencing Consortium 2001; Venter et al. 2001) or the Arabidopsis thaliana genome (The Arabidopsis Genome Initiative 2000), it is clear that there is no unique, species-specific amount of genetic information stored in a species' genome. It is a fundamental fact of evolution that the organisms within a species always exhibit genetic variation, which is often considerable, while at the same time there are widespread genetic similarities between distinct species. This makes it unclear to what extent one can think of a species (or "its" genome) as a repository

of genetic information. A better view might be to think of genetic information as not stored in species as such, but in small local populations in which genetic diversity is limited (but for the fundamental reason of intra-populational genetic variation this is problematic too).

Similarly problematic is a view of species as providers of ecosystem services – one other important reason to value natural entities. Ecosystem services, such as clean water, arable land, or recreational landscapes, are provided by entities located at higher levels of organization than species. Moreover, the ecosystems providing us with ecosystem services are not composed of species as such, but of local populations that are allocated to species. Local populations, then, seem better suited than species as units of biodiversity studies and conservation efforts. For a number of reasons, species – either conceived as real entities in nature or as conventional groupings – are not well suited as focal units in these contexts.

8.4 What to Do with the Species Concept?

How can the notion of species continue to play a role in biodiversity studies and conservation efforts in the face of the problems highlighted in the preceding section? To answer this question, I want to go back to early stages of the debate on the concept and draw clues from Darwin's work.

In the *Origin of Species*, Darwin seemed to defend a view of species as artificial units that did not represent natural groupings. As he famously writes:

In short, we shall have to treat species in the same manner as those naturalists treat genera, who admit that genera are *merely artificial combinations made for convenience*. This may not be a cheering prospect; but we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species. (Darwin 1859: 485; emphasis added).

While Darwin indeed seems to propose that species are not real, Ereshefsky (2010, 2011, 2014) recently suggested that Darwin's view only was that the species *category* was not real while individual species could be thought of as real entities (see also the discussion above). But if this is correct, what should we make of Darwin's use of the term 'species' – why did he even use 'species' in the title of his book?

Ereshefsky (2010: 409; 2011: 71; 2014: 83) suggested that Darwin used the term for mere pragmatic reasons without attributing theoretical meaning to it. In contrast, but without entering into detailed Darwin exegesis, I want to suggest that for Darwin the notion of species did have a theoretical meaning. In the *Origin*, about 60 pages before the above quotation and in a part of the text in which he refers to the only figure in the book (the famous tree or bush of life in Chapter IV of the *Origin*, depicted here in Fig. 8.3), Darwin writes the following:

I believe that the *arrangement* of the groups within each class [...] must be strictly genealogical in order to be natural; but that the *amount* of difference in the several branches or groups [...] may differ greatly, being due to the different degrees of modification which they have undergone; and this is expressed by the forms being ranked under different

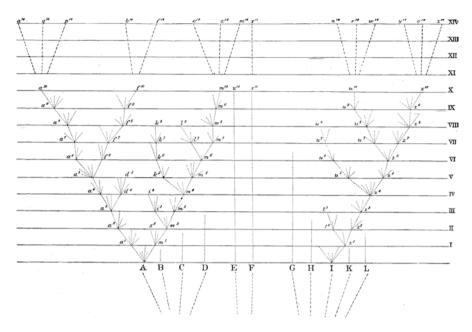


Fig. 8.3 The descent-with-modification diagram from the *Origin of Species*. (Darwin 1859)

genera, families, sections, or orders. [...] [T]he natural system is genealogical in its arrangement, like a pedigree; but the degrees of modification which the different groups have undergone, have to be expressed by ranking them under different so-called genera, sub-families, families, sections, orders, and classes. (Darwin 1859: 420 & 422; emphasis in original).

Here, Darwin talks about higher taxa and explains that the ordering of species into higher taxa represents degrees of modification that distinguish species of different higher taxa from each other. While Darwin does not say that the grouping of organisms into species can in a similar way be seen as representing degrees of modification, I want to suggest that such an interpretation fits Darwin's views and more generally would constitute a plausible way of treating the term 'species'.

In the figure in the *Origin*, to which Darwin is referring (Fig. 8.3 here), descent with modification is represented by dotted lines fanning out from common origins (common ancestor species) indicated with A, B, C, The span between two horizontal lines, indicated with Roman numerals, represents a distance of 1000 generations. Darwin explains:

After a thousand generations, species (A) is supposed to have produced two fairly well-marked varieties, namely a^1 and m^1 . [...] After ten thousand generations, species (A) is supposed to have produced three forms, a^{10} , f^{10} , and m^{10} , which, from having diverged in character during the successive generations, will have come to differ largely, but perhaps unequally, from each other and from their common parent. If we suppose the amount of change between each horizontal line in our diagram to be excessively small, these three forms may still be only well-marked varieties; or they may have arrived at the doubtful category of sub-species; but we have only to suppose the steps in the process of modification

to be more numerous or greater in amount, to convert these three forms into well-defined species: thus the diagram illustrates the steps by which the small differences distinguishing varieties are increased into the larger differences distinguishing species. (Darwin 1859: 117 & 120).

As is well known, Darwin did not make a fundamental distinction between species and varieties. As he stated in a famous passage in the *Origin*:

I look at the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms. The term variety, again, in comparison with mere individual differences, is also applied arbitrarily, and for mere convenience sake. (Darwin 1859: 52).

So, Fig. 8.3 can be interpreted as showing very gradual divergence of forms, where smaller divergences are given the status of varieties, larger divergences the status of species, still larger divergences that status of genera, and so on. Being attributed the status of species, then, means that a group of organisms has achieved a particular level of modification in comparison to its ancestor group and to other groups in the same time-slice – a level of modification larger than that of a variety but smaller than that of a genus. This view of species – as a *status* that is attributed to a group of organisms on the basis of how far it has "evolved away" from its ancestor – fits the interpretation that Darwin thought the species category is not real. Species do not constitute a separate kind of things that are part of the furniture of the world, as for instance electrons or gold atoms, but rather the notion of species refers to a level of evolution that groups of organisms can achieve.

While this may be seen as a somewhat peculiar view of what the notion of species means – and as a view that is in conflict with much of what biologists say species are, as well as with both of the main metaphysical views of species as being either natural kinds or individuals – it is a view that can also be found in early work in the Modern Synthesis. Dobzhansky, in an early issue of the journal *Philosophy of Science*, puts it thus:

Considered dynamically, the species represents that *stage of evolutionary divergence*, at which the once actually or potentially interbreeding array of forms becomes segregated into two or more separate arrays which are physiologically incapable of interbreeding. The fundamental importance of this stage is due to the fact that it is only the development of the isolating mechanisms that makes possible the coexistence in the same geographic area of different discrete groups of organisms. [...] [D]evelopment of isolating mechanisms renders the differences between groups relatively fixed and irreversible, and permits them to dwell side by side without losing their differentiating characteristics. This, in turn, opens the possibility for the organisms dwelling together to become adapted to different places in the general economy of nature. *The usage of the term "species" can and should be made to reflect the attainment by a group of organisms of this evolutionary stage*. (Dobzhansky 1935: 354; emphasis added).

As Dobzhansky explains in his book, *Genetics and the Origin of Species*: "[I]n the light of the evolution theories [...] such concepts as race, species, genus, family, etc., have come to be understood as connoting *nothing more than degrees of separation* in the process of a gradual phylogenetic divergence." (Dobzhansky 1937: 309; emphasis added). According to Dobzhansky, however, this does not mean that

species are arbitrary or purely conventional units, that is, arbitrary divisions of a continuum into discrete units: as long as real discontinuities exist in the array of living forms, these can be interpreted as the natural boundaries of species as natural units (Dobzhansky 1937: 306–307).

The basic idea is that wherever we find stable discontinuities between groups of organisms, these natural boundaries can be taken to delimit species. Because in sexually reproducing organisms discontinuities between morphological groups are supported by reproductive isolation between populations, Dobzhansky suggested to define the notion of species in such a way as to link species status to the presence of isolating mechanisms. But the main idea is that the term 'species' indicates the achievement of a particular degree of separation by an evolving group, no matter by means of which mechanisms or other causal factors this is achieved. The development of reproductive isolating mechanisms by a group of organisms in Dobzhansky's view underlies the achievement of a level of evolutionary independence that allows us to individuate species by means of their natural boundaries: "The stage of the evolutionary process at which this fixation [of the discontinuity] takes place is fundamentally important, and the attainment of this stage by a group of organisms signifies the advent of species distinction" (Dobzhansky 1937: 312). 16 Note that achievement of this stage of evolution is not a yes-or-no matter, but a matter of degree: groups of organisms gradually develop isolating mechanisms, and may be more or less isolated from other groups. The term 'species' for Dobzhansky refers to this process stage and not to an ontological category of entities. As he emphasizes, his definition "lays emphasis on the dynamic nature of the species concept. Species is a stage in a process, not a static unit." (Dobzhansky 1937: 312).

Drawing inspiration from Darwin and Dobzhansky, I want to suggest to take Dobzhansky literally and interpret the term 'species' as signifying a particular *stage* of the evolutionary process that evolving groups of organisms can achieve. The species stage is characterized by comparative evolutionary independence: attributing species status to a population or other group of organisms means that it has reached a stage at which it has become sufficiently independent from other parts of the system in which it exists for novel traits (or at least clearly different traits from those of other

¹⁶While Dobzhansky's definition of 'species' may seem the same as Mayr's widely used Biological Species Concept, there is an important difference between them. On the Biological Species Concept, species are a particular kind of breeding populations. That is, on this concept species are entities of a particular ontological category, i.e., the species category is a subcategory of the more general category of populations. On Dobzhansky's definition, however, 'species' denotes a status that may be attributed to populations that have achieved a particular stage in the evolutionary process: populations undergo a gradual process of modification in which at some point they may (or may not) achieve an evolutionary stage at which they exist as discrete groups next to other groups, marked by morphological and genetic discontinuities that are supported by reproductive isolation mechanisms. Accordingly, asexually reproducing and obligatory self-fertilizing organisms that do not develop reproductive isolating mechanisms also do not form species (Dobzhansky 1937: 321). But note that Dobzhansky did not define species as a kind of populations: any sort of group of organisms that reaches an evolutionary stage in which it exists as a discrete group can in principle be attributed species status (but Dobzhansky did emphasize reproductive isolating mechanisms of populations in this context).

groups) to emerge and to become fixated in the population. As such evolutionary independence is a matter of degree and independence never is *complete* independence, the corresponding attribution of species status is a matter of degree too.¹⁷

How exactly is this a different view of species from the ones reflected by available species concepts? While I do not have sufficient space in the present chapter to fully articulate the suggestion that a species is a stage in the evolutionary process, I want to point to some philosophical aspects of this suggestion by way of clarification. Being a species is an accidental property, i.e., a property that a group of organisms can come to have or lose without losing its identity. As was discussed above, the view of species as process stages involves a denial that the species category is a real category of entities. Much of the debate on the species problem has been fueled by the metaphysical question what species are – natural kinds, individuals, or something else (e.g., Ruse 1987). Accordingly, available species concepts tend to be explicative definitions of the metaphysics of species – they tell us what kind of entities species are, i.e., what kinds of entities constitute the ontological category of species. The two principal options in the debate are conceptions of species as a particular kind of natural kinds or a particular kind of individuals, but other options have been suggested too (for example, that species are processes – cf. Rieppel 2009). While one could perhaps think of process stages as real in some way, this would at least not be realism about entities of a particular kind. The *entities* that one would be a realist about, after all, are populations, metapopulations, lineages, clades, and other sorts of organism groups, i.e., entities of a number of different ontological categories. I would go further, though, and say that the attribution of species status to a group is an epistemological as well as normative attribution, and not a metaphysical one. To say that a group of organisms is a species is to say that it is a group – whatever its precise metaphysical nature – that has achieved a stage of evolution that is of importance to us in the light of evolutionary theory – it is a stage we highlight, because of its explanatory importance – and that we can value accordingly. The claim that a group of organisms is a species thus does not entail anything regarding its metaphysics; in particular, it does not entail that it is a natural kind, an individual, a historical entity, and so on.

Similar suggestions have been advanced in the recent philosophical literature on species and natural kinds. As philosophers of science have increasingly begun to examine scientific practices (in the context of what has been called the "practice turn" in the philosophy of science – Kendig 2016a: 3ff.), focus is increasingly placed on the question how scientific concepts are used in investigative practices, rather than on questions of what in nature these concepts represent. Kendig (2014, 2016a, b), for example, has proposed that classificatory notions, such as 'species', 'natural kind', and 'homologue', are best understood as denoting practices of

¹⁷Organisms always live interdependently in ecosystems, and often populations of organisms coevolve. In cases in which two populations coevolve – for instance a particular kind of plant and its specific pollinator – the two populations can be treated as independent in the sense of the present discussion, as they each evolve their own novelties. Still, as coevolving populations they of course are dependent on each other. The notion of evolutionary independence that is in play here simply means for a population to have the ability to evolve its own novelties, and should not be read in too strong a manner.

species-making and kind-making, that is, of the grouping of organisms into species, and of things more generally into natural kinds, on the basis of various epistemological and practical considerations. Accordingly, there are multiple ways of grouping organisms into species depending on which aspects of speciation, lineage-forming processes, inheritance processes, etc. one is interested in (Kendig 2014). Being a species, then, means being used by scientists in a particular context as a species. Similarly, the notion of natural kind can be understood as consisting principally in the making use of certain groups in investigative practices (Kendig 2016a: 6). And in a historical study of the notion of homology, Kendig (2016b) showed how the notion of homology is best understood as referring to a set of practices of comparing organisms and their traits, and how different biologists highlighted certain traits as homologous on the basis of different theoretical grounds and investigative interests. What happens, in sum, is that scientists make groups of entities, organisms, and traits, and attribute some of those groups the status of natural kind, species, or homologue on the basis of a variety of theoretical and practical grounds. Different grounds yield different, oftentimes incompatible groupings of the same entities, while no particular grouping can be said to yield the natural kinds, the species, or the homologues in a particular domain of nature.

In a similar fashion, Slater (2013, 2015) recently suggested that we should not try to develop a philosophical account of what natural kinds are, but rather should think of "natural kindness" as a kind of status that things can have on epistemological grounds (Slater 2013: 150; 2015: 378). On Slater's view, rather than thinking of natural kinds as an ontological category of entities, we should think of "being a natural kind as a sort of status that things or pluralities of things (from various ontological categories) can have" (Slater 2015: 407), where the degree to which something can be attributed the status of natural kind corresponds to the degree to which it supports inferential practices in a particular context. The status of natural kindness, Slater emphasizes, is domain dependent: something may have that status in one domain of work but not (or to a lesser degree) in another (Slater 2013: 172). Slater thus takes the problem of natural kinds out of the domain of metaphysics and puts it squarely into the domain of epistemology: saying that something is a natural kind is attributing a particular epistemic status to it to a particular degree. In this case the epistemic status is that of being useful as a basis for inferences (where groups that are better suitable as bases for inferences have this status to a higher degree). The precise metaphysics underlying this status is secondary, and can take very different forms in different cases. Some things that we attribute the status of natural kind to belong to the ontological category of individuals, while others belong to other categories.19

¹⁸ Slater (2013: 107 & 150) says that his account is a characterization of natural kindness as an adjective rather than of the nature of natural kinds as an ontological category.

¹⁹Note that here I am not endorsing Slater's account of natural kindness, nor am I claiming that it is an adequate interpretation of species as natural kinds. All I want to do is to highlight the similarity between Slater's approach to the notion of natural kinds and my approach to the notion of species.

The view of species proposed here fits taxonomic practice. Take for example the recent discovery of a new species of orangutan (Nater et al. 2017; Reese 2017). In the 1930s, explorers reported the existence of a small, isolated population of orangutans in the Tapanuli district in North Sumatra. Only after reading the reports in the mid-1990s did scientists start to look for the population again and eventually managed to find nests, the remains of a female orangutan and finally in 2013 one male that was killed by local inhabitants. On the basis of comparisons of the skull of the male specimen with 33 museum specimens of the two already described species of orangutans, Pongo pygmaeus (the Bornean orangutan) and Pongo abelii (the Sumatran orangutan), as well as genetic comparisons of 37 orangutan specimens, biologists identified the population as a new species, *Pongo tapanuliensis*. As the authors write, the species "encompasses a geographically and genetically isolated population found in the Batang Toru area at the southernmost range limit of extant Sumatran orangutans" (Nater et al. 2017: 3488). The central factor in the individuation of the local population as a new species, rather than a mere morphological variety of one of the extant species of the genus *Pongo* was its evolutionary independence from the other groups, as evidenced by morphology and genetics. As the authors write: "P. tapanuliensis and P. abelii have been on independent evolutionary trajectories at least since the late Pleistocene / early Holocene" (Nater et al. 2017: 3491–3492). While the researchers found morphological differences with the Sumatran orangutan, they also found that P. tapanuliensis is genetically more closely related to *P. pygmaeus*, from which it diverged much later, than to *P. abelii*. P. tapanuliensis thus has its own evolutionary identity in distinction of the group of orangutans living on the same island, Sumatra, and due to the geographical separation of the group of orangutans living on Borneo, it had its own evolutionary identity in distinction of that group too.²⁰

How does the view of species as evolutionary process stages, and of the attribution of species status to groups as epistemological and normative attributions rather than metaphysical statements, affect biodiversity studies and conservation efforts? First, on the view of species suggested here species counts cannot be seen as counts of the real entities of a particular kind that exist in that area or ecosystem. Still, species counts are meaningful when thinking of them as counts of groups of organisms that share an important property, namely comparative evolutionary independence. When it comes to counting species in the context of making inventories of an area's or ecosystem's biodiversity it is crucial to count things that are comparable, and while on the view proposed here species cannot be seen as entities of the same kind, they still are comparable as entities that we highlight for the same epistemological reasons as the units in which evolutionary novelties can arise. For the same reason, evolutionary independence is an important basis for attributing conservation value

²⁰The newly discovered species has immediately come in focus in conservation efforts. Because of its small population size of less than 800 individuals, biologists have expressed concerns for the survival of the population, implying an urgent need for conservation measures (Nater et al. 2017: 3493; Reese 2017).

to groups of organisms: conserving groups that have a comparative evolutionary independence means conserving evolutionary potential.²¹

In conservation biology, these ideas are sometimes embodied in the – ill-defined – concept of Evolutionarily Significant Unit (ESU). An ESU is a population or other group of organisms that stands at the focus of conservation efforts because of its evolutionary significance, where evolutionary significance is fleshed out in terms of evolutionary heritage (e.g., significant divergence from other groups, or representing an important aspect of a species' evolutionary legacy) and evolutionary potential (Moritz 1994; Crandall et al. 2000; Casacci et al. 2013). Waples (1995: 9) perhaps expressed the idea of evolutionary sugnificance most clearly in specifying that "[t]he evolutionary legacy of a species is the genetic variability that is a product of past evolutionary events and that represents the reservoir upon which future evolutionary potential depends." As usually conceived, ESUs are units below the species level, even though several authors have pointed out that in principle an ESU can coincide with a species (Moritz 1994: 374; Casacci et al. 2013: 183). Ryder, who introduced the ESU concept in the literature, for example suggested that rather than attempting to conserve all subspecies and varieties of a threatened species conservation focus in zoos should be placed on subspecies that represent significant adaptive variation and "zoos ought properly to address the conservation of evolutionarily significant units (ESUs) within species" (Ryder 1986: 9-10). Ryder noted that an alternative for the ESU concept could be the concept of evolutionarily significant population (ESP), thus highlighting that ESUs are not themselves species, but smaller units. Accordingly, conservation biologists may find that a species encompasses multiple ESUs that each should stand at the focus of conservation efforts. An example is the case of White Sands pupfish (Cyprinidon tularosa), where researchers have argued that two populations constitute distinct ESUs, where "[1]oss of either of the two ESUs of White Sands pupfish would result in a substantial loss of the evolutionary legacy of this species" (Stockwell et al. 1998: 219).

Dobzhansky's view of species as groups of organisms that have achieved a particular stage in the evolutionary process and the ESU concept express similar views of why some groups of organisms are highlighted as being of particular interest to us. First, species and ESUs do not exist independently of our interests, but rather the status of species or ESU is attributed by us to certain groups of organisms on the basis of theoretical considerations. Second, these considerations are fundamentally connected to evolutionary theory: species and ESUs are of particular importance because they represent important aspects of the evolutionary process. And third, both Dobzhansky's view and the ESU concept highlight that species and ESUs are important because of their evolutionary (that is, adaptive) potential. Dobzhansky's view and the ESU concept differ, however, by focusing on different taxonomic levels.

²¹ Note that I am not suggesting that this is the only or even the most important basis for attributing a conservation value to a group of organisms. It merely is one such basis among many, as we may attach value to a group of organisms for a plethora of reasons.

On the view of species suggested here, then, populations and other groups of organisms should not be targets of conservation efforts because they would *represent* or *instantiate* a species that we want to retain in existence.²² Nor should their species status be thought of as what we would want to conserve: in general, we do not want to retain the species in the evolutionary state in which it happens to be, but we want to conserve its potential for future evolution. Summarizing, on the view of the meaning of 'species' proposed here, what we count in species counts and focus on in conservation efforts are entities to which we attribute the same epistemological and normative status – the status of species –, even though that status may be underwritten metaphysically in very different ways for different kinds of organisms.

8.5 Concluding Remarks

I have started out this chapter by noting that species are usually seen as core units in biodiversity studies and conservation biology, and asking whether species indeed are good units in these contexts. My answer has been negative: the philosophical problems regarding the species concept are such that we cannot safely assume that species are real entities (entities existing independently of us in nature) or natural units. But the notion of species can still be used as a basis for biodiversity inventories and value attributions in conservation biology if the notion of species is interpreted differently.

I have suggested an interpretation of the species concept that would fit biodiversity studies and conservation biology better than views of species as constituting a particular category of real entities in nature. Contrary to recently advanced views but in line with Darwin's and Dobzhansky's views of species, I have suggested that the species concept does have theoretical significance, even though metaphysically one cannot say that the species category is real. Species as such are not real entities in nature, but grouping organisms into species is not a matter of mere convention either. The meaning of the species concept is connected to evolutionary reality in that attributions of species status to evolving populations reflects the achievement of populations of a degree of evolutionary independence that allows them to evolve their own adaptations and maintain their identity in distinction of other populations.

 $^{^{22}}$ Let me try to clarify this point. Often, local populations or other local groups of organisms are said to represent species ("Species x is represented in five countries by twelve populations.") or to instantiate species ("Species x is instantiated in twelve populations spread over five countries."). To be sure, this is an imprecise way of speaking. The point, though, is that usually species and populations are seen as two distinct entities between which there can be a relation such as representation, instantiation, etc. The species is seen as a larger entity (an abstract kind, a lineage, a collection of populations, or something else) than the population "out there" in the field. On the account proposed here, however, 'species' is a status attributed to a group of organisms such as a population, so there cannot be a relation of representation, instantiation, or otherwise between the group of organisms to which we attribute that status and "its" species.

Whether or not this can be seen as a (weak) realism about species is a question I want to leave open here, as my aim is not to defend a particular metaphysical position in the species debate. Also, it should be noted that my aim was not to devise an overall account of the species concept for the whole of the life sciences: my focus was on the meaning of 'species' for the purposes of biodiversity studies and conservation biology, and I leave open whether the view proposed here would be applicable throughout the whole of biology. And I have largely ignored core topics in the philosophy of biology regarding species, such as the monism-pluralism debate, the kinds-individuals debate, and other issues.

Suffice it to say that although there is no category of species as entities in the way there is a category of electrons or a category of cells, there are real entities (groups of organisms of various metaphysical categories) that can be attributed an epistemological and normative status on the basis of their having achieved evolutionary independence (that is, their having achieved some degree of "speciesness"). Putting those entities at the focus of biodiversity studies and conservation efforts (in a similar way as is suggested by the Evolutionary Significant Unit concept) means putting local populations and other groups of organisms as parts of landscapes and ecosystems in the foreground, moving away from the conservation of species as an aim of conservation efforts, but retaining the notion of species as a theoretically meaningful notion in biodiversity studies and conservation biology.²³

References

Agapow, P. M., Bininda-Emonds, O. R. P., Crandall, K. A., et al. (2004). The impact of species concept on biodiversity studies. *The Quarterly Review of Biology*, 79, 161–179.

Arrhenius, O. (1921). Species and area. Journal of Ecology, 9, 95–99.

Bachmann, K. (2001). Species concepts: The continuing debate. *The New Phytologist*, 149, 367–368.

Barnosky, A. D., Matzke, N., Tomiya, S., et al. (2011). Has the Earth's sixth mass extinction already arrived? *Nature*, 471, 51–57.

Burch-Brown, J., & Archer, A. (2017). In defence of biodiversity. *Biology and Philosophy*, 32, 969–997.

Casacci, L. P., Barbero, F., & Balletto, E. (2013). The "evolutionarily significant unit" concept and its applicability in biological conservation. *The Italian Journal of Zoology*, 81, 182–193.

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., et al. (2015). Accelerated modern human-induced species losses: Entering the sixth mass extinction. *Science Advances*, 1, e1400253.

Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences of the United States of America*, 114, E6089–E6096.

Claridge, M. F. (2010). Species are real biological entities. In F. J. Ayala & R. Arp (Eds.), Contemporary debates in philosophy of biology (pp. 110–122). Chichester: Wiley.

Claridge, M. F., Dawah, H. A., & Wilson, M. R. (Eds.). (1997). Species: The units of biodiversity. London: Chapman & Hall.

²³ I am indebted to Philippe Huneman, Werner Kunz and an anonymous reviewer for helpful comments on earlier versions of this chapter.

Colwell, R. K. (2009). Biodiversity: Concepts, patterns, and measurement. In S. A. Levin (Ed.), *The Princeton guide to ecology* (pp. 257–263). Princeton: Princeton University Press.

- Connor, E. F., & McCoy, E. D. (1979). The statistics and biology of the species-area relationship. *The American Naturalist*, 113, 791–833.
- Costanza, R., d'Arge, R., de Groot, R., et al. (1997). The value of the world's ecosystem services and natural capital. *Nature*, 387, 253–260.
- Cracraft, J. (1997). Species concepts in systematics and conservation biology An ornithological viewpoint. In M. F. Claridge, H. A. Dawah, & M. R. Wilson (Eds.), *Species: The units of biodiversity* (pp. 325–339). London: Chapman & Hall.
- Crandall, K. A., Bininda-Emonds, O. R. P., Mace, G. M., & Wayne, R. K. (2000). Considering evolutionary processes in conservation biology. *Trends in Ecology & Evolution*, 15, 290–295.
- Darwin, C. R. (1859). On the origin of species by means of natural selection, or, the preservation of favoured races in the struggle for life. London: John Murray.
- Dietrich, M. R. (2000). The problem of the gene. Comptes Rendus de l'Académie des Sciences de Paris, Sciences de la Vie, 323, 1139–1146.
- Dillon, S., Fjeldså, J., & Kelt, D. (2005). The implications of different species concepts for describing biodiversity patterns and assessing conservation needs for African birds. *Ecography*, 28, 682–692.
- Dirzo, R., & Raven, P. H. (2003). Global state of biodiversity and loss. *Annual Review of Environment and Resources*, 28, 137–167.
- Dobzhansky, T. (1935). A critique of the species concept in biology. *Philosophy in Science*, 2, 344–355.
- Dobzhansky, T. (1937). Genetics and the origin of species. New York: Columbia University Press. Doolittle, W. F., & Zhaxybayeva, O. (2009). On the origin of prokaryotic species. Genome Research, 19, 744–756.
- Ehrlich, P. R., & Wilson, E. O. (1991). Biodiversity studies: Science and policy. *Science*, 253, 758–762.
- Ereshefsky, M. (2010). Darwin's solution to the species problem. Synthese, 175, 405–425.
- Ereshefsky, M. (2011). Mystery of mysteries: Darwin and the species problem. *Cladistics*, 27, 67–79.
- Ereshefsky, M. (2014). Consilience, historicity, and the species problem. In R. P. Thompson & D. M. Walsh (Eds.), *Evolutionary biology: Conceptual, ethical, and religious issues* (pp. 65–86). Cambridge: Cambridge University Press.
- Faith, D. P. (2016). Biodiversity. In E. N. Zalta, (Eds.), The Stanford Encyclopedia of philosophy (Summer 2016 Edition), https://plato.stanford.edu/archives/sum2016/entries/biodiversity/
- Frankham, R., Ballou, J. D., Dudash, M. R., et al. (2012). Implications of different species concepts for conserving biodiversity. *Biological Conservation*, 153, 25–31.
- Garnett, S. T., & Christidis, L. (2007). Implications of changing species definitions for conservation purposes. *Bird Conservation International*, 17, 187–195.
- George, A. L., & Mayden, R. L. (2005). Species concepts and the endangered species act: How a valid biological definition of species enhances the legal protection of biodiversity. *Natural Resources Journal*, 45, 369–407.
- Gevers, D., Cohan, F. M., Lawrence, J. G., et al. (2005). Re-evaluating prokaryotic species. *Nature Reviews. Microbiology*, *3*, 733–739.
- Gleason, H. A. (1922). On the relation between species and area. Ecology, 3, 158–162.
- Griffiths, P. E., & Stotz, K. (2006). Genes in the postgenomic era. Theoretical Medicine and Bioethics, 27, 499–521.
- Griffiths, P. E., & Stotz, K. (2013). Genetics and philosophy: An introduction. Cambridge: Cambridge University Press.
- Groves, C. P., Cotterill, F. P. D., Gippoliti, S., et al. (2017). Species definitions and conservation: A review and case studies from African mammals. *Conservation Genetics*, 18, 1247–1256.
- Hamilton, A. J. (2005). Species diversity or biodiversity? *Journal of Environmental Management*, 75, 82–92.

- Hohenegger, J. (2014). Species as the basic units in evolution and biodiversity: Recognition of species in the recent and geological past as exemplified by larger foraminifera. *Gondwana Research*, 25, 707–728.
- Hunter, M. L., & Gibbs, J. P. (2007). Fundamentals of conservation biology (3rd ed.). Malden: Blackwell.
- International Human Genome Sequencing Consortium. (2001). Initial sequencing and analysis of the human genome. *Nature*, 409, 860–921.
- Kendig, C. E. (2014). Towards a multidimensional metaconception of species. *Ratio*, 27, 155–172.
- Kendig, C. E. (2016a). S introduction: Activities of *kinding* in scientific practice. In C. E. Kendig (Ed.), *Natural kinds and classification in scientific practice* (pp. 1–13). Abingdon/New York: Routledge.
- Kendig, C. E. (2016b). Homologizing as kinding. In C. E. Kendig (Ed.), Natural kinds and classification in scientific practice (pp. 106–125). Abingdon/New York: Routledge.
- Kunz, W. (2012). Do species exist? Principles of taxonomic classification. Weinheim: Wiley-Blackwell.
- Lherminer, P., & Solignac, M. (2000). L'espèce: Définitions d'auteurs. Comptes Rendus de l' Académie des Sciences de Paris, Sciences de la Vie, 323, 153–165.
- Lomolino, M. V. (2000). Ecology's most general, yet protean pattern: The species-area relationship. *Journal of Biogeography*, 27, 17–26.
- Lomolino, M. V., Riddle, B. R., & Brown, J. H. (2017). *Biogeography* (5th ed.). Sunderland: Sinauer Associates.
- Liu, S.-S., Colvin, J., & De Barro, P. J. (2012). Species concepts as applied to the whitefly *Bemisia tabaci* systematics: How many species are there? *Journal of Integrative Agriculture*, 11, 176–186.
- Mace, G. M. (2004). The role of taxonomy in species conservation. *Philosophical Transactions of the Royal Society of London B*, 359, 711–719.
- Mace, G. M. (2015). Whose conservation? Science, 345, 1558–1560.
- Mace, G. M., & Lande, R. (1991). Assessing extinction threats: Toward a reevaluation of IUCN threatened species categories. *Conservation Biology*, 5, 148–157.
- Mace, G. M., Collar, N. J., Gaston, K. J., et al. (2008). Quantification of extinction risk: IUCN's system for classifying threatened species. *Conservation Biology*, 22, 1424–1442.
- Mace, G. M., Norris, K., & Fitter, A. H. (2012). Biodiversity and ecosystem services: A multilayered relationship. *Trends in Ecology & Evolution*, 27, 19–26.
- Maclaurin, J., & Sterelny, K. (2008). What is biodiversity? Chicago/London: University of Chicago Press.
- Mallet, J. (2013). Species, concepts of. In S. A. Levin (Ed.), Encyclopedia of biodiversity (Vol. 6, 2nd ed., pp. 679–691). Amsterdam: Academic.
- Mayden, R. L. (1997). A hierarchy of species concepts: The denouement in the saga of the species problem. In M. F. Claridge, H. A. Dawah, & M. R. Wilson (Eds.), *Species: The units* of biodiversity (pp. 381–424). London: Chapman & Hall.
- Mayden, R. L. (1999). Consilience and a hierarchy of species concepts: Advances toward closure on the species puzzle. *Journal of Nematology*, *31*, 95–116.
- Mayr, E. (Ed.). (1957). *The species problem*. Washington, DC: American Association for the Advancement of Science.
- McGuinness, K. A. (1984). Equations and explanations in the study of species-area curves. *Biological Reviews*, 59, 423–440.
- Meine, C., Soulé, M., & Noss, R. F. (2006). "A mission-driven discipline": The growth of conservation biology. *Conservation Biology*, 20, 631–651.
- Mishler, B. D. (1999). Getting rid of species? In R. A. Wilson (Ed.), *Species: New interdisciplinary essays* (pp. 307–315). Cambridge, MA: MIT Press.
- Mishler, B. D. (2010). Species are not uniquely real biological entities. In F. J. Ayala & R. Arp (Eds.), *Contemporary debates in philosophy of biology* (pp. 91–109). Chichester: Wiley.

Moritz, C. (1994). Defining 'evolutionarily significant units' for conservation. *Trends in Ecology & Evolution*, 9, 373–375.

- Nater, A., Mattle-Greminger, M. P., Nurcahyo, A., et al. (2017). Morphometric, behavioral, and genomic evidence for a new orangutan species. *Current Biology*, 27, 3487–3498. e10.
- Odenbaugh, J. (2016). Conservation biology. In E. N. Zalta, (Ed.), *The Stanford Encyclopedia of philosophy* (Winter 2016 Edition), https://plato.stanford.edu/archives/win2016/entries/conservation-biology/
- Peterson, A. T., & Navarro-Sigüenza, A. G. (1999). Alternate species concepts as bases for determining priority conservation areas. *Conservation Biology*, 13, 427–431.
- Purvis, A., & Hector, A. (2000). Getting the measure of biodiversity. *Nature*, 405, 212–219.
- Raczkowski, J. M., & Wenzel, J. W. (2007). Biodiversity studies and their foundation in taxonomic scholarship. *BioScience*, 57, 974–979.
- Reese, A. (2017). New orangutan species identified. Nature, 551, 151.
- Reydon, T. A. C. (2004). Why does the species problem still persist? *BioEssays*, 26, 300–305.
- Reydon, T. A. C. (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, R. A. (2010). *The species problem: A philosophical analysis*. Cambridge University Press.
- Rieppel, O. (2009). Species as a process. Acta Biotheoretica, 57, 33–49.
- Rolston, H. (1975). Is there an ecological ethic? *Ethics*, 85, 93–109.
- Rolston, H. (1985). Duties to endangered species. BioScience, 35, 718-726.
- Rolston, H. (1995). Duties to endangered species. In W. A. Nierenberg (Ed.), Encyclopedia of environmental biology (Vol. 1, pp. 517–528). San Diego: Academic.
- Roselló-Mora, R., & Amann, R. (2001). The species concept for prokaryotes. FEMS Microbiology Reviews, 25, 39–67.
- Ruse, M. (1987). Biological species: Natural kinds, individuals, or what? The British Journal for the Philosophy of Science, 38, 225–242.
- Ryder, O. A. (1986). Species conservation and systematics: The dilemma of subspecies. *Trends in Ecology & Evolution*, 1, 9–10.
- Santana, C. (2014). Save the planet: Eliminate biodiversity. *Biology and Philosophy*, 29, 761–780.
- Santana, C. (2018). Biodiversity is a chimera, and chimeras aren't real. *Biology and Philosophy*, 33, 15.
- Scheiner, S. M. (2003). Six types of species-area curves. *Global Ecology and Biogeography*, 12, 441–447.
- Slater, M. H. (2013). Are species real? An essay on the metaphysics of species. Basingstoke: Palgrave Macmillan.
- Slater, M. H. (2015). Natural kindness. The British Journal for the Philosophy of Science, 66, 375–411.
- Soulé, M. E. (1985). What is conservation biology? BioScience, 35, 727-734.
- Stamos, D. N. (2003). The species problem: Biological species, ontology, and the metaphysics of biology. Lanham: Lexington Books.
- Stockwell, C. A., Mulvey, M., & Jones, A. G. (1998). Genetic evidence for two evolutionarily significant units of White Sands pupfish. *Animal Conservation*, 1, 213–225.
- The Arabidopsis Genome Initiative. (2000). Analysis of the genome sequence of the flowering plant *Arabidopsis thaliana*. *Nature*, 408, 796–815.
- Tjørve, E. (2003). Shapes and functions of species-area curves: A review of possible models. *Journal of Biogeography, 30*, 827–835.
- Tjørve, E. (2009). Shapes and functions of species-area curves (II): A review of new models and parametrizations. *Journal of Biogeography*, 36, 1435–1445.
- Venter, J. C., Adams, M. D., Myers, E. W., et al. (2001). The sequence of the human genome. Science, 291, 1304–1351.
- Waples, R. S. (1995). Evolutionarily significant units and the conservation of biological diversity under the endangered species act. *American Fisheries Society Symposium*, 17, 8–27.

Weber, M. (2005). Philosophy of experimental biology. Cambridge: Cambridge University Press.

Wheeler, Q. D., Knapp, S., Stevenson, D. W., et al. (2012). Mapping the biosphere: Exploring species to understand the origin, organization and sustainability of biodiversity. *Systematics and Biodiversity*, 10, 1–20.

Wilkins, J. S. (2009). Species: A history of the idea. Berkeley: University of California Press.

Wilkins, J. S. (2011). Philosophically speaking, how many species concepts are there? *Zootaxa*, 2765, 58–60.

Wilson, E. O. (1988). The current state of biological diversity. In E. O. Wilson (Ed.), *Biodiversity* (pp. 3–18). Washington, DC: National Academy Press.

Wilson, E. O. (1992). The diversity of life. Cambridge, MA: Harvard University Press.

Open Access This chapter is licensed under the terms of the Creative Commons Attribution 4.0 International License (http://creativecommons.org/licenses/by/4.0/), which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence and indicate if changes were made.

The images or other third party material in this chapter are included in the chapter's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the chapter's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder.

