How Are Biology Concepts Used and Transformed?

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1 Introduction

Scientific knowledge (and its transformation) is often presented in terms of models or overarching theories (Parke this volume). This chapter, in contrast, focuses on *concepts* as units and organizers of scientific knowledge. Concepts, on the one hand, are more fine-grained units in that a scientific theory contains many individual concepts. On the other hand—and this makes a look at concepts in biology particularly interesting—a concept can be used across several theories, and it can persist even when a theory has been discarded. The concept of a species continues to be used well after pre-Darwinian theories about species were abandoned, and this concept is used across all of biology, in such different theoretical context as vertebrate development and microbial ecology. The gene concept is likewise used in very different fields, and has survived despite the flaws of the original Mendelian theory of inheritance and a move toward molecular accounts.

A scientific concept is expressed in public discourse by a scientific term. But one should not identify concepts with terms, as the same term (the same word) can be used with different meanings and thus correspond to different concepts. For instance, the term ‘function’ can refer to an evolutionary adaptation, where a trait is understood to have a certain function if in the past there was selection for this function. But there are many contexts, especially in molecular biology, where the same term ‘function’ instead means (current) activity, for example, a protein binding or a gene being expressed in some tissue—a notion of function that is independent of evolutionary considerations, given that such an activity can actually be present even if it is new and in the past there was no selection for it. Conversely, different terms may all happen to express the same concept; and one may ponder which of several possible terms is best to talk about a previously established concept. For example, the way in which development generates phenotypic variation used to be referred to by the term ‘developmental constraint,’ but since this term has misleading connotation of variation always being prevented, nowadays other terms, such as ‘developmental bias’ and ‘evolvability,’ are more commonly used to express the same basic idea.

Philosophers construe a concept as the mental content associated with a term, and because of its content, the concept plays a distinctive role in reasoning, from theorizing to practical action. A concept may be explained or standardized by means of a definition, but often the content of a concept is more encompassing than a short definition. A definition permits one to *identify* an object, but some concepts (e.g., ‘allopatric speciation’) embody larger causal models, in which case they can be used to *explain* how and why a biological phenomenon occurred. It is because of its rich content that a biology concept can perform various functions in theory and practice. The following sections provide several examples of the different roles that concepts can play.

What matters especially in the present discussion is that concepts are not static objects (embodying knowledge that was obtained long ago and captured by an authoritative definition), but *dynamic* entities. Even once introduced, a biological concept can be revised and undergo transformation upon new empirical findings. Another dynamic aspect of concepts is that they guide scientific activity and investigative practice (Depew this volume; Feest and Steinle 2012). A biology concept does not just figure in abstract theorizing, but figures more general in biological *practice*, for instance, by motivating steps of experimental discovery. Given that philosophers commonly employ the term ‘epistemic’ to refer to anything related to human knowledge, including the formation of knowledge, my discussion can be said to be about the epistemic role of concepts, as long as it is made clear that this also includes biological practice and the methodological role of concepts. Overall, this chapter is not just about what the content of biological concepts is, but how concepts are *used* by biologists.

Illustrated by means of several biology concepts, the following discussion first covers one possible function of a concept—to set an explanatory agenda—a function that is of particular importance because of its forward-looking nature of motivating ongoing and future explanatory efforts. Then I discuss the gene concept as a prime case where a concept has undergone substantial transformation throughout its rich history, without ceasing to evolve. Finally, I turn to instances of conceptual diversity where a term can fruitfully be associated with different meanings, using species concepts as a case where a pluralism about concepts is warranted.

2 Setting a Research Agenda: A Forward-Looking Function of a Concept

Like all scientific concepts, biological concepts refer to scientific phenomena, be it specific entities (e.g., synapses) or complex processes (e.g., natural selection). A concept can be articulated by a definition. Such a definition not only specifies what natural objects the concept picks out, but also conveys some important characteristics of these objects (and standardizes how a scientific term is to be understood within a scientific community). But besides describing phenomena of the *natural world*, it is also important to consider how concepts are used by *scientists* and how they function in scientific practice. We particularly need to ask for what *scientific purpose(s)* a given concept is used. One biology concept may primarily be used for the purpose of classification, such as classifying organisms into different species (see also Reydon this volume). Another concept may instead serve the scientific aim of explanation, for example, by explaining the mechanism of cell-cell signaling (see also Potochnik this volume). Scientific aims are also called *epistemic aims* by philosophers, although one needs to bear in mind that scientific aims are not exclusively about intellectual understanding ('episteme' meaning knowledge), but often include practical aims (Kitcher 2001; Potochnik 2017). Relevant examples of practical aims are uncovering causes and mechanisms for the purpose of intervening in nature by means of applications (e.g., biomedical ones), or investigating species and ecosystems in order to provide guidance to conservation efforts.

Paying attention to the aims and purposes for which biological concepts are used is important, because it reveals the *forward-looking* nature of concepts. All too often concepts are merely seen as the outcome of science—a term being coined once a new biological entity has been discovered, or a mature definition being established once the relevant scientific knowledge is in. But concepts also continuously undergo transformation, and they function by *guiding ongoing scientific practice*. A biology concept can motivate *future* scientific efforts, and it can also provide a scaffold to direct the generation of new knowledge and the organization of complex knowledge.

One instance of the forward-looking functions of concepts is when a biological concept sets a research agenda. A striking case in point is the concept of *evolutionary novelty* (as it is especially used in evolutionary developmental biology). A novelty is a qualitatively new trait that arose in some biological taxon, such as the evolutionary origin of the fins of fish, or their later transformation into the limbs of tetrapods—which are quite different from fins, among other things due to the presence of digits. There are major scientific efforts devoted to understanding the evolution of particular novelties, and accounting for evolutionary novelty may well be among the major aims of evolutionary biology. Despite the scientific significance of the concept of novelty, there is in fact disagreement about how to *define* novelty. One definition may focus on a morphological trait as such, while another definition will also consider its underlying developmental or genetic basis. Many definitions focus on structure (e.g., defining a trait as novel whenever it is not homologous to any ancestral trait; Müller and Wagner 1991), while some definitions bring in functional considerations such as adaptation and selection (Hallgrímsson et al. 2012). A universally agreed upon definition would pick out exactly those biological traits that are novelties, while excluding those traits that do not qualify as novel.

However, the root of the definitional disagreement is that there may not be any principled difference between evolutionary changes that are qualitatively distinct (and thereby novel) and those that are mere quantitative variants of existing traits. Indeed, there are many morphological structures that look clearly novel, but where closer biological investigation reveals that various components of such a structure already had precursors in ancestral taxa or that the ‘novel’ structure arose from modifications of previously existing regulatory pathways (Hall and Kerney 2012). In the case the tetrapod limb, the classical example mentioned above, at the very least the digits of the limb were deemed to be completely novel. Yet *Hox* gene expression patterns also seen in the distal part of fish fins and other data have been used to suggest that even the digits of tetrapods can be homologized with structures in fish (Johanson et al. 2007).

But this disagreement of how to define ‘evolutionary novelty’ does not impugn this concept. Some scientific concepts do serve the purpose of classification (which in the present case would be classifying traits into those that are novel and those that are non-novel), in which case a precise definition is needed. But this is hardly the purpose that the concept of evolutionary novelty serves; instead, this concept fulfills a vital scientific function by setting up an *explanatory agenda* (Brigandt and Love 2012). The point is that rather than debating which particular structures are really novel, it is more fruitful to work towards explanations of the evolutionary origin of various structures.

Philosopher of biology Alan Love (2013b) has called the explanation of novelty a *problem agenda*. The label ‘agenda’ reflects that this scientific problem does not just consist in a single question, but rather in a whole set of interrelated questions and explanatory tasks. The label also highlights that there is an ongoing and forward-looking process. Some scientific concepts embody explanatory theories, and the concept of evolutionary novelty may at some point in the future do this. However, rather than delivering complete explanations, the concept of evolutionary novelty points to explanatory frameworks that yet have to be established. Indeed, evolutionary developmental biologists argue that a traditional neo-Darwinian approach, which focuses on the dynamics of genetic variants within populations, is unable (or at least woefully incomplete) to adequately explain the very origin of novelties. Instead, knowledge about developmental processes is needed in order to understand how the modification of those processes could have given rise to the novel structure. The problem agenda of evolutionary novelty entails that a host of explanatory ingredients are needed, some of which come from different biological disciplines (Love 2013a). This includes phylogenetic trees from systematics, fossil evidence about ancestral structures from paleontology, gene regulatory pathways from developmental genetics, phenomena such as phenotypic plasticity studied in developmental biology (especially ecological developmental biology), and knowledge about selection pressures implicating ecology. As a result, the concept of evolutionary novelty sets an agenda that not only motivates ongoing and future research efforts, but also prompts *interdisciplinary* research (Brigandt 2013; Love 2013b).

A related function of the concept of evolutionary novelty is that it provides intellectual identity to a biological approach. In some cases, a scientific concept can even provide identity to a scientific discipline. Accounting for novelty is certainly one of the core items on the agenda of evolutionary developmental biology. At the same time, there are different possible ways of construing evolutionary developmental biology and its relation to other fields (Brigandt and Love 2012). Some biologists prefer to construe evolutionary developmental biology as an autonomous discipline. But rather than asserting independence from other disciplines, often evolutionary developmental biology is framed as a synthesis of evolutionary biology and developmental biology (among other disciplines), so as to augment the neo-Darwinian Modern Synthesis established in the middle of the 20th century. However, the label 'synthesis' may suggest in a misleading fashion that different disciplines have been merged into one, single discipline (of evolutionary developmental biology), which is certainly not the case. Therefore, a more cautious characterization may be that evolutionary developmental biology is a field that also operates at the intersection of different fields. We fortunately do not have to settle on a unique construal of the disciplinary nature of evolutionary developmental biology. In any case, agenda-setting concepts like evolutionary novelty provide substantial *intellectual identity* to the approach of evolutionary developmental biology (and coordinate interaction with other fields).[1]

Although the scientific problem agenda set up by the concept of evolutionary novelty (or,

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[1] The concept and explanatory agenda of evolvability has likewise be seen as establishing intellectual or disciplinary identity for evolutionary developmental biology (Hendrikse et al. 2007). Looking at precursors in the 1980s, well before any distinct field of evolutionary developmental biology existed, the concept of developmental constraint (also setting an explanatory agenda) already provided some intellectual identity across different approaches (Brigandt 2015).

more precisely, by how this concept is *used* in biological practice) is quite complex, there is some structure to it. The different component questions of the overall problem agenda stand in systematic relations, which provide clues for how the different explanatory contributions—some coming from different biological fields—are to be coordinated so as to arrive at an explanatory framework (Love 2013a). For instance, one first needs evidence about the phylogenetic sequence of structural transformations (including which traits are homologous to precursors and which ones are new) before information about regulatory pathways and developmental processes (in different extant taxa) can be used to formulate an explanation of how changes in developmental mechanisms resulted in the novel structure under study. Thereby, in addition to motivating explanatory (and interdisciplinary) efforts—as one *forward-looking* function of a concept—the concept of evolutionary novelty also provides a scaffold for integrating new scientific findings into an emerging explanatory framework—another forward-looking aspect.

Another example is the concept of a *living fossil* (Lidgard and Love 2018). Here it is also controversial which taxa should actually count as living fossils. Various different criteria have been proposed and used: a gross similarity to an ancestral fossil or slow evolutionary change (compared to similar taxa), an unusually long geological presence (compared to similar taxa), a very low current taxonomic richness relative to the past, or a very limited geographic range compared to the taxon's past. One complaint about some criteria is that they are ill-defined. For instance, according to one criterion a living fossil is a taxon that is known from the fossil record before it is discovered alive. But this is not about the characteristics of this taxon. This criterion is about what scientists happen to have discovered first (the fossil or the extant version), which would make the living fossil status relative to the idiosyncrasies and hazards of scientific discovery. Another issue is what to do with cases of morphological stasis where molecular genetic change has occurred (which is in a sense the opposite of what we encountered in the case of evolutionary novelty, where a morphologically novel trait may be due to minor modifications of gene regulatory mechanisms). Generally, employing one rather than another of the available criteria yields a different judgement about whether a given taxon is actually a living fossil. But in this case again, the point is not (or should not be) to be able to classify taxa into living fossils and others. Rather, the concept of a living fossil can still play a fruitful role in biological practice by setting an explanatory agenda. Directing future investigative efforts, this problem agenda includes uncovering the mechanisms responsible for the retention of morphological traits over longer period of time, investigating the relative rates of change across different traits in one lineage (e.g., molecular as opposed to morphological traits) plus explaining why some traits change faster than others, and accounting for slow evolutionary change in one lineage compared to other lineages (Lidgard and Love 2018).

The main message of this section is that apart from referring to phenomena of the natural world, biology concepts also have important functions for researchers and are used for various aims and purposes in scientific practice. If the primary scientific aim is to classify objects or to precisely characterize phenomena, an accurate definition is in fact needed. But we have seen that definitions of ‘evolutionary novelty’ and ‘living fossil’ are contested, and that these concepts instead have an additional, more fruitful function—to set an explanatory agenda. In this fashion, such concepts are not just the outcome of scientific knowledge obtained in the past, but also have important implications for ongoing and future scientific practice.

3 Concept Change and Transformation

So far we have seen that concepts are not only receptacles that contain knowledge about biological phenomena, but are also used for purposes set by scientists, including explanatory and investigative agendas (see also Kindi 2012). And it is because of such scientific purposes and aims underlying the use of concepts that the latter can have a forward-looking dimension with impacts on future research, beyond storing knowledge that was previously acquired. One aspect of the forward-looking dimension of concepts we now turn to is the fact that a concept can *change* and undergo transformation. A concept may be articulated by a definition, which standardizes its meaning for biologists and facilitates communication across different biological fields. A definition may also provide focus to ongoing research in that it delineates the objects or the phenomenon to be investigated in this context, for example, what counts as 'speciation.' At the same time, the definition of a biological term is often revised (hopefully amounting to an improvement on an earlier definition). And for such a modification of a concept to be possible, it cannot be the case that scientists always adhere to the original definition—which would mean to set aside findings about biological processes that do not count as instances of speciation on some definition of 'speciation,' or to take as irrelevant for the concept of the gene all cellular structures that happen to not count as genes on some original definition of 'gene.' Therefore, biology concepts are *open-ended*, in that they permit modification and can come to encompass new and quite different phenomena.

One important example of how a concept has continuously undergone change, and in fact major transformation, is the *gene concept* (Kampourakis 2017; Rheinberger and Müller-Wille 2017; Weber 2005). Based on studies of heredity in the second half of the 19th century, the gene concept was established in the early 20th century during the period sometimes called Mendelian genetics, which from 1920 onwards gave rise to the more mature classical genetics. In classical genetics, genes were also often called *alleles*. What could actually be observed in breeding studies and mutation experiments were phenotypic traits (more specifically, phenotypic differences between individuals and patterns of phenotypic inheritance across generations), where alleles had to be inferred as the entities that were physically passed on to the next generation and had an effect on these phenotypic traits. Consequently, the classical gene concept construed genes in terms of their function, more precisely, their *phenotypic function*. This was obviously not a definition of genes that would specify the internal structure of genes.

Our knowledge about the structure (as well as function) of genes has changed considerably (Carlson 1966). Around 1900, many biologists still maintained that the hereditary material resides in the cytoplasm (as opposed to the nucleus). In contrast, the chromosome theory of inheritance maintained that genes are part of or in any case carried by the chromosomes. It was not until 1920, based on the *Drosophila* studies by the Morgan school, that the chromosome theory was widely accepted. For instance, the inheritance of some phenotypic traits was shown to be linked to a specific sex chromosome. And the crossing-over of chromosomes that could be observed with microscopes explained why the inheritance of some alleles (those on the same chromosome) was linked, but only with a certain probability (that declines the farther apart the alleles are on the chromosome). While alleles were structurally seen to be parts of chromosomes, a definition in terms of phenotypic function still prevailed (and phenotypic impact was the only way to experimentally distinguish different genes and locate them on a chromosome).

Classical geneticists were well aware of the fact the functional relation between genes and phenotypic traits is a *many–many one* relation (Morgan et al. 1915). Not only has a gene an influence on several phenotypic traits, but a phenotype is produced by the interaction of many genes. An allele is gene ‘for’ a phenotype (e.g., a specific eye colour as one of the many mutant traits studied in *Drosophila*) only in the sense that relative to an otherwise identical genetic background, this allele results in this phenotype (e.g., the mutant eye colour), whereas other alleles at this chromosomal locus (e.g., the wildtype allele) yield a different phenotypic trait.[2] Therefore, a classical gene as such does not produce a phenotypic trait in an individual; rather, a *difference* in classical genes between individuals accounts for different phenotypes.

Later on, biochemical studies in the fungus *Neurospora* suggested that the proximate effect of an allele is the production of a specific enzyme, leading to the one gene–one enzyme hypothesis (Beadle and Tatum 1941), which was later refined to the one gene–one polypeptide hypothesis. The discovery of the molecular structure of DNA and studies with bacteria and bacteriophage viruses (which permitted much more fine-grained genetic studies) led to the advent of molecular genetics and the molecular gene concept. Roughly speaking, the molecular gene concept construes a gene as a linear, continuous segment of DNA, which (because it is preceded by a promoter) is transcribed to RNA and subsequently translated in accordance with the genetic code to a linear sequence of amino acids (a polypeptide). Note that this is more of a *structural* definition: a gene is a specific sequence of nucleotides. Moreover, the function of interest is the coding for a molecular product (a polypeptide). By now focussing on the more proximate function of molecular genes, the traditional many–many relation between classical genes and gross phenotypes was replaced by a *one–one* relation between genes and their molecular products (Griffiths and Stotz 2013).

This was clearly significant scientific advance. But in the context of *concept* transformation

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[2] "Although there is little that we can say as to the nature of Mendelian genes, we do know that they are not 'determinants' in the Weismannian sense. … All that we mean when we speak of a gene for pink eyes is a gene which differentiates a pink eyed fly from a normal one—not a gene which produces pink eyes *per se*, for the character pink eyes is dependent upon the action of many other genes." (Sturtevant 1915, p. 265)

we also need to ask why the very definition of ‘gene’ changed.[3] Why not take onboard the new knowledge from molecular genetics (e.g., that genes are strands of DNA and code for a polypeptide before having an impact on development and an organism’s phenotype) while still consistently defining genes in the classical way, as something leading to a difference in a specific phenotypic trait between individuals? To appreciate the motivations for the change of gene concept, we yet again have to look at the *scientific aims* for which concepts are used in scientific practice (Brigandt 2010). Whereas the very origin of the gene concept was the study of patterns of inheritance between generations, molecular genetics is hardly concerned with this and instead focuses on processes going on within individual organisms, typically within single cells. The purpose for which the gene concept was primarily used gradually changed during the history of genetics, which explains why the manner in which this concept was defined changed (once empirical information relevant to the new purpose became available). The molecular gene concept is used for the purpose of explaining the molecular mechanisms by which genes code for their molecular products, i.e., RNA and polypeptides. The classical gene concept (linking genes with phenotypes) does not provide this mechanistic explanation, whereas the molecular gene concept serves this purpose by means of construing a gene as a DNA segment with a specific nucleotide sequence (resulting in corresponding RNA and polypeptide sequences). Thus, the focus on a new scientific aim had the forward-looking impact on the gene concept of motivating

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[3] Despite the advent of the molecular gene concept, the classical gene concept continues to be used in some biological contexts, as Section 4 discusses. So rather than one definition of ‘gene’ being fully replaced by another one, this conceptual change consists in the addition of a novel definition of the term ‘gene’. But we still have to understand why this new, molecular definition originated in the first place and became the most prominent one for most areas of biology.

the subsequent widespread adoption of a molecular definition.

In its early stages, the molecular gene concept basically construed a gene as an open reading frame, as a continuous segment of DNA delimited by a start codon and a stop codon and preceded by a promoter sequence. To the extent that all molecular genes fit this structural definition and any such DNA structure codes for one molecular product, this definition avoided the many–many relation between classical genes and phenotypes and seemed to yield a stable resting place for the hitherto changing gene concept (Griffiths and Stotz 2013). However, the concept transformation did not stop upon the very advent of the molecular gene concept, and the molecular gene concept has kept changing ever since the complexities of gene structure and function in eukaryotic cells were revealed (Keller 2000; Portin 1993), which underscores the open-ended nature of many concepts. In fact, already in the 1980s there were signs that a fairly unified conception of molecular genes had been replaced with diverse conceptions, where the meaning of ‘gene’ employed in a specific situation could only be gathered from the context (Falk 1986).

Here I can mention only some of the complexities that kept driving the change of the gene concept. Most prominently, the relation between continuous DNA segments and polypeptide products is often *many–many*, after all. Because of the mechanism of RNA splicing, a DNA segment is transcribed to a pre-mRNA, but then some chunks of the pre-mRNA (the introns) are spliced out, i.e., removed, before this mature mRNA (now consisting of exons only) is translated to a polypeptide. In the case of alternative splicing, a DNA segment is repeatedly transcribed to identical pre-mRNAs, but these pre-mRNAs may be spliced differently, resulting in different exon combinations and different polypeptide products. Consequently, one cell can produce chemically diverse proteins from one and the same DNA segment. There is also trans-splicing, where two or more DNA segments (possibly located on different chromosomes) are independently transcribed to pre-mRNAs, and chunks of these pre-mRNAs are spliced together to one mature mRNA, resulting in one polypeptide product. Are two such DNA segments two independent genes (which have to collaborate to generate one product at all)? Or do the two rather make up one gene (which simply consists of disjoint nucleotide sequences)? But what to say for those cases where a DNA segment engages in trans-splicing involving another DNA segment, as well as codes for its own product? Generally, the many–many relation between DNA segments and gene products raises difficult questions for how to annotate genes, for how to decide where a gene begins and ends, how many different genes there are in a certain genomic region, and for formulating an account of what genes really are.

Some further complications related to the gene concept are that not only segments of the sense strand of the double-stranded DNA (which used to be called the coding strand) are transcribed, but also that some segments of the antisense strand (‘non-coding strand’) can be transcribed so as to qualify as a coding gene. There are also many cases of overlapping genes, for example, a gene that codes for a product being situated within the intron of another, larger gene. Finally, due to the processes of RNA editing (modification of individual nucleotides of the mRNA before translation) and translational recoding, the final amino acid sequence may not be fully determined by the DNA nucleotide sequence. As a result, the central dogma of molecular biology that DNA sequence determines RNA sequence which in turn determines the protein’s amino acid sequence is not accurate (as other sources of information can be involved in specifying the amino acid sequence), and the genetic code as the mapping from nucleotide to amino acid sequence does not always tell the complete story (Griffiths and Stotz 2013).

Overall, while at the beginning of molecular biology a structural construal of genes seemed possible, the subsequent history has shown that considerations about gene *function* are vital. Ultimately, deciding what genes are and whether some structural entity counts as a gene depends on its functional behaviour, in particular whether it is transcribed and whether it codes for some product. This also depends on the larger genomic and even the cellular context, which then provides a more meaningful context for assessing gene function than simply looking at a DNA nucleotide sequence as one structure. The advent of the ‘postgenomic era,’ including functional genomics and transcriptomics, has certainly increased the focus on gene function, and keeps providing findings that continue to modify our conceptions of genes. Textbooks may still provide stereotypical characterizations of genes (a molecular gene as an open reading frame coding for a protein); and researchers may use such stereotypical visions as a general starting point, but then immediately employ a more sophisticated account that is geared to a particular genomic case and investigative context, overall resulting in a context-dependent use of the gene concept across the molecular biology community (Griffiths and Stotz 2013; Keller 2000).[4]

4 Pluralism and Conceptual Diversity

The previous section has emphasized that not only does the gene concept continue to change, but also that the molecular gene concept exhibits significant variation. There is no unified construal of what genes are, and biologists use the concept depending on their specific research context. One reason for this is the structure of the natural world: the complexity of gene structure and

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[4] This can also mean that apart from consistently using a stereotypical or simplistic construal, a textbook may contain different definitions of genes, without necessarily clarifying the reasons for this (Kampourakis and Stern 2018).

function. Another reason for this conceptual diversity is epistemic: the various scientific considerations and interests that scientists bring to the task. The philosophers Karola Stotz and Paul Griffiths (2004) have adopted the label *conceptual ecology* for the project of understanding the reasons for the diversification and transformation of the gene concept. Rather than endorsing proposals that a unified gene concept behind the diversity can still be recovered (e.g., Waters 2000) or that the gene concept had better be eliminated in favour of other terms (e.g., Keller 2000), the agenda of Stotz and Griffiths is to map out the empirical pressures that move the gene concept in a novel direction and the scientific agendas that diversify the use of the gene concept across different biological communities. Scientific aims matter here again; for instance, some researchers may focus on RNA as the gene product of interest, whereas others on the polypeptides produced (given their biochemical roles as enzymes). Since the relation between DNA segments and RNAs is one–one, whereas from DNA segments to polypeptides there are often many–many relations, focusing on polypeptide rather than RNA as the gene product of interest may result in a different account of whether separate DNA segments each count as an independent gene.[5]

The discussion on conceptual change in Section 3 was framed in terms of a move from the

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[5] Another example of the impact of different scientific aims is how the homology concept diversified once it came to be used in newly formed biological fields, such as evolutionary developmental biology. I have described this as the homology concept undergoing an 'adaptive radiation'—borrowing the metaphor from evolutionary biology (Brigandt 2003). Biologist nowadays talk about a phylogenetic as opposed to a developmental concept of homology. It is less important to adjudicate whether these are really distinct concepts or whether they are different variants of one concept. Instead, the philosophically interesting task ('conceptual ecology') is to understand the reasons for this diversity upon the homology concept coming to occupy new conceptual niches, among other things by the concept being used for different specific biological purposes in different fields.

classical to the molecular gene concept. However, the classical gene concept is still used nowadays, routinely in population genetics and in some contexts of medical and behavioural genetics (Griffiths and Stotz 2013). The coexistence of the classical gene concept and the molecular gene concept means that the conceptual plurality is in fact much more pronounced than just the diverse ways in which the molecular gene concept is used. Scientific aims yet again have an impact on why it is better to use a certain gene concept in a given context. The molecular gene concept construes a gene as a specific sequence of nucleotides, which is important for understanding how it codes for molecular products—even in cases where many different polypeptides are being produced from this molecular gene (and the connection to a particular phenotype is unclear). In contrast, population genetics accounts for the dynamics of genes within populations in terms of (more abstract) genes having phenotypic effects—regardless of what the molecular basis of this phenotype may be—and models how the fitness of such a phenotype results in gene frequency changes in the population. Likewise, in medical genetics (in addition to the molecular gene concept) one can also find talk about a gene 'for' breast cancer, understood as anything that has this phenotypic effect of a clear breast cancer risk (Moss 2003). This can be of interest even if several different nucleotide sequences lead to this phenotype under study.

Another prominent example of conceptual diversity is the existence of several different *species concepts*. Despite ongoing developments, the basic situation has existed for several decades: taxonomist Richard Mayden (1997, 2002) has provided a list of 22 different species concepts, and philosopher of biology John Wilkins (2018) has given a detailed update that also includes a thorough discussion of views on species in the history of biology, especially how the species problem arose in the 19th century. Some species concepts may be related or are different versions of a basic approach, for instance, there are several concepts focusing on reproductive isolation between species, just like there are several evolutionary species concepts as well as several phylogenetic species concepts. Still, the plurality of concepts is hard to do away with. In what follows, I can only present a few examples of species concepts, while my main aim is to give a sense of why it is important for biologists to have several such concepts at their disposal.

One reason for this conceptual diversity is *ontological*, in that nature is too complex that one single account would capture all of it. More precisely, there are different processes that shape biodiversity and provide cohesion within populations and differentiation into different lineages, where different concepts are needed to cover different aspects of this overall biodiversity (Ereshefsky 1992). But another reason for the conceptual diversity is *epistemic*—in line with this chapter's focus on how concepts are used and for what purposes they are used. In a nutshell, the right conceptual tool is needed for each job. One species concept may work well for one biological task, but be unsuitable for other legitimate purposes (Kitcher 1984).

One prominent species concept is the so-called *biological species concept* championed by Ernst Mayr (who used a clever label for his favoured concept). It states that a species is a group of potentially interbreeding natural populations which are reproductively isolated from other such groups (i.e., from other species).[6] This species concept is theoretically interesting because it ties into some models explaining speciation. If two populations of what is still one (interbreeding) species become geographically isolated, due to the strongly reduced gene flow between them they may diverge genetically and phenotypically. Thus, they may eventually lose the ability to interbreed, and will then be two distinct species according to the biological species concept. Another advantageous aspect of this concept is that when it was applied to the

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[6] To illustrate that even within the approach focusing on reproductive isolation there are different concepts, another species concept is Templeton's mate recognition concept.

Anopheles mosquito genus, it succeeded in distinguishing two populations as different interbreeding species so as to shed light on the distribution of malaria in Europe—given the importance for human health a scientific use of a species concept for clearly practical purposes (Ludwig 2016).[7]

At the same time, the biological species concept has clear drawbacks. One is practical, in that the concept (relying on the ability to interbreed) cannot be used to classify extinct species that are only known as fossils, which matters for the discipline of paleontology. In this domain, instead the *morphological species concept* may be used, which construes species as the smallest groups that are consistently and persistently distinct, and distinguishable by morphological traits. But there also exist significant theoretical problems for the biological species concept. Hybridization among even distantly related lineages is widespread among plants and animals. Even proponents of a biological species concept agree that what they consider distinct species can undergo hybridization, so that they are able to interbreed after all. Conversely, geographically distant populations from the same species may not even be able to potentially interbreed. (In the case of a so-called ring species, geographically adjacent populations A and B do interbreed, as do B and C, etc., but A and F cannot potentially interbreed.) Moreover, a fundamental trouble with the biological species concept is that only sexual species interbreed, so that this species concept cannot even be theoretically employed for most microbial species. Instead, microbiologists may use a sort of morphological species concept (applied to cellular

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[7] More recently, however, it has been argued that adequately fighting malaria requires the use of the phylogenetic species concept, which offers a yet more fine-grained and detailed classification than the biological species concept by splitting certain interbreeding populations into different species (Attenborough 2015).

structures), the *genetic species concept* (which views organisms to belong to different species if their genetic similarity crosses a threshold), the ecological species concept, or a phylogenetic species concept—all of which are also used for sexually reproducing species (Bzovy 2017; Wilkins 2018).

To briefly convey more of this conceptual diversity, according to the *evolutionary species concept,* a species is a lineage evolving separately from others and with its own unitary evolutionary role and tendencies of evolutionary change, in particular long-term phenotypic change. This account is theoretically appealing, but not very useful for (putative) species that have originated recently and that do not yet have a clear evolutionary tendency or fate. And even though this concept was introduced by the paleontologist G. G. Simpson, it is not practically applicable in paleontological cases where a species to be classified (or other related species) are only known from a limited number of fossils. The *ecological species concept* (introduced by Leigh van Valen) assumes that a species is a lineage or a closely related set of lineages which occupies an adaptive zone minimally different from any other lineage in its range (and which evolves separately from all lineages outside its range). This concept focuses on ecological competition and natural selection as factors creating differences between different species. Two populations that interbreed (and are thus one species on the biological species concept) may well occupy different ecological niches, and thus exhibit relevant phenotypic (including behavioural) differences and therefore qualify as two separate species on the ecological concept. Finally, *phylogenetic species concepts* (of which there also are different variants) arose with the advent of phylogenetic systematics (cladistics). They generally conceive of species as the smallest group of organisms forming a phylogenetic lineage that are diagnosable by a unique combination of characters, which can for instance be articulated by a definition that requires the presence of a synapomorphy (i.e., a derived and thus phylogenetically new trait that is shared among these organisms). A phylogenetic species concept will consider two distinguishable phylogenetic lineages as two distinct species, even if the organisms from these two population can interbreed (Mayden 1997; Wilkins 2018).

It is easy to note that different species concepts happen to be used, but the question is: how should one evaluate this diversity? A few decades ago some biologists insisted that their favoured species concept is the only legitimate one (or the most fundamental one), and that the diversity of different species concept will go away (Ghiselin 1987; Mayr 1987; Simpson 1961). But the dominant view these days is that several species concepts are legitimate and needed for biological practice. Philosophers use the label *pluralism* for a stance that endorses a plurality of species concepts. Apart from the ontological complexity of the processes generating biodiversity (Ereshefsky 1992), we have already encountered an epistemic argument for pluralism: different species concepts fulfill *different legitimate biological purposes*, such as the explanation of speciation, or the classification of fossil taxa (Kitcher 1984). It is certainly true that there are cases where using one rather than another species concept yields a different account of the boundaries and the number of species, so as to result in classifications that cross-cut each other (Conix 2018). This clearly matters in the context of conservation biology. If a population that is likely to become extinct is classified as a distinct species, it is indeed considered as an endangered species; but this is not the case if it is deemed to merely be a population of a larger species (which as a whole is not endangered). Polar bears and Alaskan brown bears can interbreed with each other, but many will argue that the conservation status of polar bears should not be contingent on Alaskan brown bears, which are then to count as a separate species. Likewise, the eventual recognition of the Alabama sturgeon as an independent species resulted in its being listed as a critically endangered species, which was preceded by scientific, political, and legal debates (Scharpf 2000). The fact that a particular species concept can be favoured due to conservation biology considerations highlights that a scientific concept can fulfill practical purposes that have socio-political ramifications.[8]

The diversity of species concepts and the possibility of cross-cutting classifications sounds certainly challenging. But taxonomists use various local decisions about the aims of classification to arrive at the most legitimate taxonomic account (Conix 2018). Moreover, the fact that different species concepts can serve different specific purposes should not be misunderstood to mean that in one scientific context only one species concept is of relevance (while other species concepts will be used by other researchers). Instead, several species concepts can be jointly used during a research project. A case in point is how yeast taxonomists use the morphological, the ecological, the biological, the genetic, and the phylogenetic species concept to supplement one another so as to arrive at a solid classification (Bzovy 2017). The morphological species concept may be used early on in a study of a new strain of yeast, but then additional concepts provide more fine-grained information, such as the ecological species concept or the biological species concept for sexual yeast taxa. This interplay among different species concepts illustrates again that concepts are relatively fine-grained units of knowledge whose use is subject to change and that dynamically interact, guided by local scientific purposes.

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[8] Conservation concerns may often favour the splitting of populations into distinct species (so-called ‘taxonomic splitting’), but considerations about habitat fragmentation (likewise a conservation concern) can work in the opposite direction, i.e., they favour the viewing of several populations as forming one species (Frankham et al. 2012).

5 Concluding Remarks

Science is often described in terms of scientific theories and scientific disciplines, as relevant units of knowledge and knowledge organization. But this discussion has shown that concepts are also epistemic units of interest. On the one hand, concepts can have a longer reach insofar as a concept (e.g., ‘species’) can be used across different disciplines, and can persist even if an older theory has been abandoned (the classical gene concept continuing to be used despite the original Mendelian theory of genetics having become obsolete). One the other hand, concepts can be more fine-grained and dynamic than disciplines and theories, in that many different concepts are used by a discipline or figure in a theory, where these individual concepts interact and the use of one such concept can be sensitive to and change across scientific contexts. Indeed, beyond the traditional focus on scientific theory, philosophers of science have come to study scientific *practice*. Rachel Ankeny and Sabina Leonelli (2016) have adopted the notion of ‘repertoires’ to analyze the organization of scientific practice—repertoires do not just contain scientific ideas, but also such things as experimental tools, databases, and model organisms. Yet in addition to such material entities, this chapter has made plain that intellectual entities like concepts are also an important player in scientific practice, at least if one is mindful of how biology concepts are being *used*.

Such a focus on the practice of science also aligns with current trends in science education, which beyond the content of science—encapsulated in learning outcomes—also endeavours to teach students about the process of scientific investigation (e.g., NGSS Lead States 2013). In the case of biological concepts, we have seen that concepts not only embody scientific knowledge that was obtained in the past, but also actively *guide* ongoing and future scientific practice. One reason for this is that biology concepts are used for specific *purposes* (which are often a combination of intellectual and practical purposes). Such concept use can generate diversity in science. A plurality of species concepts is needed as one species concept may be more suitable for a concrete biological task then another one; and a researcher may first employ one and then another species concept depending on the particular biological aim at hand. Biological concepts are also open-ended, in that definitions once adopted are revised and concepts keep undergoing transformation. In the case of the gene concept, we have seen that the advent of the molecular gene concept (and its ongoing modification) was guided by the concept coming to be used for the purpose of explaining the molecular processes of gene function. A concept such as evolutionary novelty or living fossil may not embody explanatory models (at least not yet), while still significantly influencing biological practice by setting an explanatory agenda. The problem agenda of accounting for the evolutionary origin of evolutionary novelty even motivates interdisciplinary research, and the concept of evolutionary novelty provides an epistemic scaffold that guides how new findings and explanatory contributions are to be integrated in an emerging, future scientific account.[9] Teaching about scientific investigation, including how open-ended concepts motivate and diversify research, matters for science education not only because of the need to convey how science works (beyond what scientific theories say). It is also impossible to cover the ever increasing and changing body of current knowledge in secondary education, while teaching in the classroom about how concepts can scaffold students' and scientists' problem solving provides a lasting lesson.

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[9] Beyond biology and in the case of scientific concepts in general, philosopher of science Nancy Nersessian (2008) discusses how problem situations (and concomitant model-based reasoning) influence the creation and modification of concepts.

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