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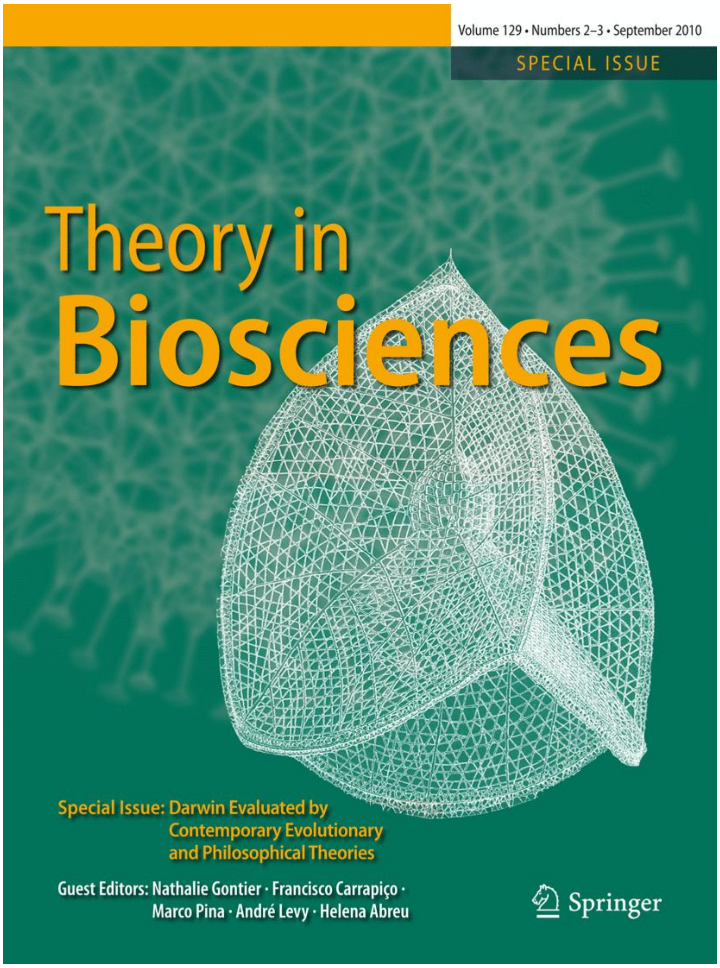

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ORIGINAL PAPER

Pattern, process and the evolution of meaning: species and units of selection

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Abstract Many of the fundamental concepts of biology lack consensual, precise definitions. Partly, this is due to a contrast between our discrete language and the continuous character of nature. Some debates over these concepts are confounded by the use of the same terms with different specific meanings, indicating a possible need for an expanded scientific lexicon. Words have their own histories, and frequently scientific terms with a vernacular origin retain associated vestigial meanings. Even terms newly coined within science have histories and changing meanings, which can lead to confusion among debaters. Debates over concepts are further confounded when the same terms are used in different fields of biology, with distinct (even conflicting) objectives, and by biologists with different approaches and perspectives. I illustrate these issues by considering the debate over the concept of *species* and the *unit of selection*.

Keywords Definition · Language · Species concept · Unit of selection

Concepts and terms as historic entities

Visual graphics (such as phylogenetic trees or distribution maps) and formal mathematics are used for conveying and clarifying scientific ideas, but verbal language is an essential medium in describing and discussing nature. Given the continuous character of natural processes and the discrete nature of our verbal language, we are immediately faced with a difficulty. It is not surprising, therefore, that the definition and usage of words is often the object of intense debate. For instance, within biology, several articles and books have been dedicated to discussing the concept of *species* (Coyne and Orr 2004; Hey 2001; Mallet 1995; Wu 2001 and accompanying commentaries). This is only one among several terms within evolutionary biology with some degree of associated ambiguity, whose precise definition is object of discussion, and whose definition varies among authors and context. Indeed, this is the case for many of the central terms of biology, for instance, *population*, *fitness*, *adaptation*, *niche*, *gene*, and *life* itself. Fortunately, these debates do not entirely hinder research: the scientific community continues to use them despite a certain degree of ambiguity. Rather, discussion—among scientists and philosophers of science—concerning the meaning of these terms can lead to further clarification of the entities and processes.

Some of these terms were originally part of the vernacular lexicon, prior to their use within a scientific context where a greater precision is required or demanded. This is certainly the case with the term *life*. In common parlance and upon consideration of quotidian cases, little doubts arise as to whether a specific entity is a living or non-living object. Yet if one is pressed to formulate a precise definition of *life* it is no easy task. Properties such as metabolism, growth, reaction to stimuli, and reproduction are frequently invoked as properties of life. But one can evoke cases that question the universality of these defining characteristics. Take the case of dormant seeds. These have the potential for metabolism, growth and eventually reproduction, but *as such* dormant seeds do none of these things. It is the recognition that they are a stage of a larger life cycle that leads one to consider them as living.

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A precise definition of *life* is no easier for biologists, familiar with a broader spectrum of entities, particularly those that boarder and defy common definitions. As our knowledge of the diversity of the natural world increases, so does the challenge in finding an overarching definition. Take, for instance, the case of viruses. These entities are composed of a protein capsid that encloses a strand of nucleic acid. They are incapable of reproducing by themselves, independently of their host's biochemical machinery, and do not grow in size or metabolize. They are therefore at the fringe of what one might consider *living*, particularly when compared to certain chemical processes, such as crystallization. A phenomenon similar to reproduction occurs when adding a sodium chlorate crystal to a supersaturated solution of this compound: new crystals are formed, not unlike reproduction. Furthermore, if one stirs this solution vigorously, new crystals preserve the chirality of the original crystal: a phenomenon analogous to heredity (Plaxco and Gross 2006). Yet, virus require proteins to reproduce—proteins composed of the same 20 L-α-amino acids common to all known members of the Tree of Life—and nucleic acids are the basis of their heredity. Their genes can suffer mutation, generating variation, and they are thus able to evolve by natural selection and adapt.

Consider some additional fringe examples. (1) Some free RNAs are capable of auto-catalyzing their replication without additional structures, merely requiring a sufficient source of nucleic acids in their medium. They function both as hereditary units and enzymes, and raise interesting possibilities regarding the evolution of pre-cellular life. (2) Prions are mis-folded variants of regularly folded proteins, which perform a necessary function within their host. When prions come into contact with normal proteins, given the presence of host polysaccharides, they are able to transform these into new prions, i.e., reproduce. The propagation of prions within a host leads to diseases such as bovine spongiform encephalopathy (BSE, or "mad cow disease") in cattle and Creutzfeldt–Jakob disease in humans. Wickner et al. (2009) have recently shown that prions are capable of crossing host species, yet when the evolutionary distance between hosts is too wide, they can mutate and evolve producing new prion variants. Prions, however, have no nucleic acids, a characteristic common to all unambiguously recognized forms of life on earth. (3) Computer programmers use systems to evolve computer code, using the processes of mutation, recombination, reproduction and selection, i.e., a virtual process analogous to biological evolution by natural selection. All these phenomena pose a challenge when attempting to formulate a definition of life that is both precise and maintains some correspondence with the traditional conception of the term.

These examples not only illustrate some difficulties in defining *life*, but also illustrate how new challenges to our scientific definition of terms increases as our knowledge of the natural (and artificial) world expands. In the case of the term *life*, scientists are also confronted with issues that arise when they incorporate vernacular terms into their scientific vocabulary. Despite efforts to use more precise definitions within the scientific context, inevitably these terms, even among scientists, continue to be connoted with their prior, vernacular definitions, i.e., using an evolutionary analogy, they retain vestigial meaning. Charles Darwin considered the pitfalls of using existing terms, for instance, when he considered the use of the less connoted term *contrivance* rather than the term *adaptation*, one used by William Paley and others in using adaptations and complexity as demonstrations of design and divine intervention, a far cry from Darwin's meaning of the term. Darwin by and large retained the term *adaptation*, but in his book on orchids (Darwin 1862) used the term *contrivance* to refer specifically to structures that evolved by natural selection. Likewise, Darwin debated whether to use an historically more neutral term such as *natural preservation*, rather than the term *natural selection* (see for instance, Browne 2006), as this term, by analogy to *artificial selection*, can imply the existence of a natural (or supernatural) entity responsible for actively selecting individuals. In these two cases, the common and more semantically charged terms prevailed. In contrast, Darwin strived to distinguish the use in scientific contexts of the vernacular terms *development* and *evolution*, distinguishing *development* as those ontogenetic processes that occur during the life of an individual and *evolution* as those processes that occur between generations of individuals. Despite his and subsequent efforts to distinguish the two terms within the scientific community, confusion between them still persists today within common parlance.

The issue of historical baggage associated with scientific terms is not restricted to terms that were part of the vernacular lexicon. Even terms newly coined within the scientific context change their meaning, for science also has its history. For example, Wilhelm Johannsen first used the term *gene* in 1909, in reference to the smallest unit of hereditary. (He also coined the terms *phenotype* and *genotype*.) The word was thus coined prior to our knowledge that *genes* are located in chromosomes, prior to our knowledge of the molecular structure of DNA and of the existence of the genetic code, and prior to our knowledge of the existence of introns, exons, and regulatory regions. As our knowledge expanded we have drifted far from the original idea of particulate, physically well defined genes, and also from the notion of a correspondence between a single gene variant and a single protein. On the one hand, regulatory regions (promoters and enhancers) are frequently not physically adjacent to the protein encoding regions of the gene (the exons). One the other hand, in eukaryotes, during transcription, different combinations of exons of a *gene* may be transcribed and translated, giving rise to different proteins (alternative splicing).[1] However, many biologists (and biology teachers) still refer to *genes* as if they were closer to the original meaning of particulate hereditary factors and we frequently encounter news referring to genes as having a simple, direct effect on phenotypes.

Thus, as our knowledge of phenomena expands and the meanings of terms evolve, so does our difficulty in precisely defining scientific terms. Furthermore, the scientific community does not adjust synchronously to newer, more complex meanings of scientific terms leading to discrepancies in the use of the terms. As Hey (2001, p. 38) recognizes: "As we learn more about something, the more our word for that something becomes ambiguous". Terms are used with somewhat different meanings depending on the context (e.g., the *fitness* of an allele vs. the *fitness* of an individual). The recognition of increasing complexity of phenomena and entities would perhaps warrant a broadening of our scientific lexicon, each with more precise definitions. New terms are indeed frequently coined, yet they are not always incorporated into the common scientific vocabulary (a topic certainly worth studying by historians of science). Despite exceptions (e.g., the adoption of several cladistics terms to distinguish among the evolutionary information content of characters), there is a tendency to use already familiar terms. Even when authors are clear about what they mean by a given term, some degree of confusion is generated among readers. This is perhaps an indication that, in research papers, most scientists are more focused on presenting results than on formulating precise, formal definitions, or that frequently the formulation of a precise definition is not a scientific problem per se, i.e., it is not due, for instance, to lack of scientific information.

We need not abandon our quest for better definitions of terms, capable of being applied in different contexts and encompassing a broad spectrum of phenomena and entities. Different definitions for the same term may coexist in different sub-fields of biology, which use different approaches to similar phenomena. This may create some confusion in the communication among these sub-fields, and between the scientific community and the general public. However, this can be surpassed if scientists are clear about framing the perspective with which they are using these terms. Eventual confusion created in such cross-disciplinary discourse should not be avoided, but engaged, as it is during such discussions that progress can be achieved in clarifying the causes of misunderstanding and in comprehending the broader complexity and richness of a phenomena or entity.

Within biology, a divide among the meaning of terms occurs frequently between those biologists studying pattern versus process. Given the continuous nature of certain biological phenomena (particularly evolutionary processes), perhaps certain terms cannot be formally defined in a precise way that satisfies both type of approaches. If the lack of evident real boundaries results from the nature of certain biological phenomena and entities, then our difficulty in formulating widely usable definitions is not a reflection of our inability to elaborate them or to agree upon a single definition, but a predictable consequence of the continuous character of our objects of study. This may lead to an impasse, which I believe is the case regarding the 'species definition problem'.

The concept of *Species*

One of the main areas of interest within the biological sciences pertains to the diversity of life (at its many levels, from biochemistry to organisms to ecosystems), and includes our ability (and compulsion) to organize and categorize diversity, and to understand the proximate and ultimate causes of this diversity. The *Systema Naturae* of Carolus Linnaeus, in the seventeenth century, with its system of hierarchical taxonomic ranks and binominal nomenclature for naming and organizing species (the basal rank), remains the hallmark of most present-day taxonomy and systematics. With the growth of our biological knowledge about taxa and of evolutionary theory—stemming largely from Darwin's groundwork—progress was made in our understanding of the causes of diversity and in our methods of classifying and organizing taxa.

One fundamental contribution of evolutionary thought was attributing importance to time and history. In this framework, taxa are viewed as being related to one another according to a branching model. For some time, the model of a bifurcating evolutionary Tree of Life appeared quite consistent with Linnaean hierarchical systematics, and thus the initial integration of systematics within the Modern Synthesis, in the 1930s–1940s, was fairly unproblematic. In subsequent decades, however, exactly whether or how systematics was to incorporate evolutionary thought turned out to be a point of intense debate. Broadly speaking, *numeral taxonomists* relied strictly on present patterns of similarity, strict *cladists* based classifications on phylogenies and required that taxa correspond to monophyletic

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[1] Exons are sections of a gene that are transcribed and translated into a protein sequence. Introns are regions of DNA that occur interspaced between exons and are not translated into protein. A gene can include several interspaced exons. Some genes can potentially produce different proteins when different combinations of exons are translated. The timing, location and pattern of exon transcription is regulated via the activation and inhibition of additional DNA sequences: the enhancers and promoters.

groups (clades[2]), and *evolutionary systematists* combined both similarity and evolutionary information. One more recent, and radical proposal, the Phylocode (de Queiroz 2006), calls for an abandonment of Linnaean taxonomic ranks altogether and the establishment of a systematics based on monophyletic groups of taxa revealed by phylogenetic information.

As our knowledge of nature's diversity has expanded, particularly among microorganisms, and with the explosion of molecular information and methods of phylogenetic inference, systematics has faced new challenges and our view of the Tree of Life has changed. For instance, our acknowledgement of endosymbiogenesis has forced us to recognize that during the evolution of life there have been events of fusion of lineages (sometimes, widely divergent lineages) and that therefore the Tree of Life is not a simple bifurcating tree. Increasing recognition of horizontal gene transfer among lineages (for instance, via hybridization, introgression, bacterial exchange of plasmids, or viral transfer of genes), as well as phenomena like lineage sorting and recombination, have brought attention to discrepancies between population or taxon trees (phylogenies) and gene trees (genealogies). These advances have also affected how we view *species*.

Ernst Mayr's *Biological Species Concept* (BSE; Mayr 1942, 1982) emerged during the Modern Synthesis. It is based on the existence of reproductive isolation between populations. The BSE became the most widely referenced and used species definition, despite several recognized limitations, including the detection of isolation between allopatric populations that seemingly belong to the same species, the inapplicability to asexual species and fossils, and the existence of hybridization and introgression between apparently different species. Mayr's original definition of the BSE underwent minor modifications in response to some of these problems. Its success is, to some extent, due to the fact that it leads to a clear research program on speciation, namely studying the evolution of reproductive isolation (Coyne and Orr 2004). It is not, however, a very operational definition, i.e., one easily used by empirical systematists to identify species. Our advance in knowledge, the limitations of the BSE and the interest in incorporating evolutionary information within classification, led to the formulation of additional definitions of species that transcend the criteria of reproductive isolation or phenetic similarity. Recent reviews consider as many as 25 different definitions of *species*, many of which suggested within the last few decades (Coyne and Orr 2004; Mayden 1997; Wilkins 2006).

Although the BSC has fostered research on the *process* of speciation, its practical application, for many systematists, involves the present state of populations and species, i.e., their present *pattern* of reproductive isolation, as well as their current morphological similarities, their present ecology, distribution, etc. It is not fortuitous that several of the new species definitions derive from the recent field of molecular phylogenetics, which focuses rather on the evolutionary *process* and the identification and description of the history of evolutionary groups, or lineages.

Even systematists, concerned with identifying species, that resort to molecular genealogies do so, primarily, in order to identify the extent of present-day gene flow among populations or, conversely, how genetically divergent are present putative species. (Molecular systematists also use genealogies to identify relationships among species and higher order taxa in order to study higher level taxonomy, but this does not pertain to the problem of the species concept.) Naturally, ambiguities arise, given the continuous nature of the process of speciation and evolution, for instance, regarding how much genetic diversity is sufficient, when combined with other characters (e.g., morphological, biogeographical, ecological, etc.), to consider a lineage a separate species.

To achieve their field's objective, empirical systematists need to recognize discrete units and divisions among them, to identify and organize taxonomic groups, and to establish a practical and informative classification. Ambiguities and practical difficulties arise in this practice (e.g., ring species,[3] incipient species[4]), generally the more in detail one studies a system: "The ambiguity does not arise because of lack of understanding; rather, the reverse, the ambiguity is revealed by a thorough understanding" (Hey 2001, p. 37). Nonetheless, it is the job of systematists to decide how to resolve such ambiguities, given the ultimate goal of identifying meaningful lower-level taxa. What is meaningful may (and certainly does) vary among systematists. Some

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[2] A clade is a monophyletic group, i.e., a group consisting of a single common ancestor and all its descendants. It is thus based on evolutionary relationship and not strictly on similarity. It also implies the inclusion of *all* the descendents of an ancestor. Thus, according to cladists, Reptiles are not a monophyletic group as they to not include all the descendents of their common ancestor, namely the Birds.

[3] As a species expands its distribution, local populations adapt to their local environment and diverge from one another, but retain the ability to interbreed with adjacent populations. A «ring species» is used to describe a species whose distribution has expanded such that the most extreme, divergent populations secondarily contact one another and are reproductively isolated, even though they can exchange genes via the remaining intermediate populations. For instance, *Larus* gulls have a cirum-polar distribution around the North Pole. Most adjacent populations are able to hybridize, forming a chain of interbreeding. However, the Herring Gull, from Great Britain, does not hybridise with the Northwestern European Lesser Black-backed Gulls.

[4] As speciation is a continuous process, «incipient species» is a term used to refer to populations that appear to be in an early stage of speciation, revealing some degree of reproductive isolation and/or phenotypic divergence, yet not having yet attained full isolation.

are considered “lumpers” or “splitters” depending on their tendency (or resistance) to establishing new species and genera. In part this reflects a conflict between having clearly defined taxa and a workable, useful classification versus accepting the natural variation within taxa and establishing a less tractable classification. Recently, taxonomists have also felt pressures to erect new taxa as biological units in order to ensure their conservation.

Underlying this discussion is also a debate regarding the ontological nature of species. Are they concrete categories, natural kinds, with an ontological status—the realist position regarding categories; are they categories, but abstract mental constructs with no real correspondence in nature, where the real entities are the category’s elements, the individual organisms—the nominalist position among 18th and 19th centuries wherein species were categories and therefore not real (see Mayr 1982); or, are species real (evolutionary) entities, not categories—the nominalist position regarding categories, e.g., Ghiselin (1997)? Hey (2001, p. 107) suggests this either/or dichotomy—species as abstract categories versus real entities—as “misleading and unnecessary.”

Given recurrent patterns among organisms, humans naturally construct mental categories. Ethnographic studies reveal that different human populations naturally establish a hierarchical classification of local species, wherein the most basal level corresponds closely to species identified by systematists (Coyne and Orr 2004). That is, our mental categories corresponding to *species*, based on similarities whose ultimate cause is their evolutionary relationship, tend to correspond to real *entities* in nature, the evolutionary lineages recognized by biologists. Do our mental categories also correspond to real *categories* in nature? At least for some taxa, this may indeed be true, as indicated by the organisms themselves. They recognize, interact and reproduce with conspecifics in very different ways than with individuals of other species. Regardless of the generality of the reality of *species* as categories in nature (a topic which would require further development), they do constitute mental categories, which serve as the basis for taxonomy. The organisms we include in such mental categories will often not correspond, however, to evolutionary entities. But they can, and should, be considered as hypotheses of evolutionary lineages.

Naturally, evolutionary systematists do not simply develop a classification based upon our mental categories. They revise these categories based on additional information, particularly evolutionary information, e.g., recognition of homologous and analogous characters. But this process still results in discrete units, bound furthermore by the use of a discrete language to describe them. Thus, a lack of correspondence between *species* as categories (real or not) and real evolutionary entities is not resolved by species concepts focused on the genealogical process and the identification of evolutionary groups. This latter perspective deals directly with processes through time, with historical processes, with indistinct and interlaced entities. The continuity and complexity of evolutionary phenomena does not pose a practical quandary for those studying the history of evolutionary groups. Indeed, it is a point of interest. Thus, perhaps, we should restrict the application of the discrete term *species* to approaches that deal with static entities, amenable to delimitations, although this may at times be difficult. This is not to say we should disregard underlying information regarding the continuous processes of speciation. Indeed, this is necessary to understand cases where delimitation is unclear or reversible. This seems preferable to applying an intrinsically discrete term to an intrinsically continuous history, such as the history of relationships between lineages, where delimitations and ranks seem arbitrary.

The debate on the definition of *species* is due not to of lack of information (Hey 2001), nor is it merely a scientific problem (Brookfield 2002). I would suggest it arises rather from a difference in perspective and object of focus. Systematics and phylogenetics, i.e., understanding and recovering the evolutionary Tree of Life, have different perspectives, somewhat different objectives, and perhaps irreconcilable differences regarding our conception of *species*. This need not constitute an epistemological problem, as long as one recognizes the difference between the fields. It does, however, muddle the discussion if the debaters do not realize and recognize their different perspectives on the same phenomena. We should perhaps reconsider whether there is a species definition *problem*, abandon the objective of agreeing upon a single overarching definition, and find terms and language applicable and adequate for different perspectives (classification of patterns vs. understanding the processes of diversity) and, also, for different groups of taxa (for instance, for asexual organisms). Systematists, by necessity, use different methods to differentiate categories. Different species conceptions may be a requirement, given the diversity of, for instance, modes of reproduction. Ambiguities and difficulties will arise and are, in fact, to be expected, given that the proximal entities that serve as objects of categorization are the result of a historical, continuous, ongoing process of diversification.

Units of selection

I do not intend to review the extensive debate on the unit of selection (e.g., Dawkins 1982; Gliddon and Gouyon 1989; Hull 1988; Lewontin 1970; Shanahan 1997), simply to make some observations, following the previous lines of thought. One consideration, which I think is noteworthy, concerns the coinage of new terms as this debate has progressed. This allowed a specification of the aspects authors were focusing on and which they considered most relevant regarding the debate. Dawkins (1976) introduced the distinction between *replicator* and *vehicle*. His point was that the organism is a mere vehicle for replicators, the only entities to persist across generations. This, organisms would be best thought as the means through which there is selection among replicators.

The term *interactor*, a less passive term than vehicle, was introduced by Hull (1988); and Lloyd (2000) introduced additional terms to distinguish among levels: *beneficiaries* and *manifestors*. Using these more specific terms one can distinguish more precisely and clearly which functional roles authors attribute to each hierarchical level of organization and their relation to a key concept in this debate: *adaptation*. The discussion about which level selection acts upon is also a discussion about which unit manifests and benefits from an adaptation, and at what level does the adaptive interaction occur.

These distinct terms prove useful, for instance, in order to distinguish among different models of group selection. George William's (1966) attack on group selection was focused on criticizing the interpretation of Wynne-Edwards (1962) and others when group selection was proposed as the cause of adaptations "for the good of the species". Using the above terminology, Wynne-Edwards viewed the group as the interactor, manifestor and beneficiary of the adaptation. More recent models of group selection, such as Wilson's (1983), consider the group as the interactor, but not as the manifestor or beneficiary, i.e., selection occurs as a result of group interaction, but the adaptive characters are not properties of the groups (they are not the manifestors), and groups benefit only indirectly as adaptive characters are not selected for "the good of the group" (group members are the direct and ultimate beneficiaries of adaptive characters). Although Williams (1966) admitted group selection under very stringent conditions, the models developed by Wilson, together with the clarification about what is meant by adaptation, has led to a broader acceptance of group selection as a valid perspective.

If one accepts a model of origin of life with a pre-cellular stage, for instance, with selection among self-replicating RNAs, with no distinction among genotype and phenotype, "genes" could be considered both replicators and interactors. But the vast majority of known life forms are cellular, thus genes are rarely interactors. Genes are recognized as the quintessential unit of replication, despite the fact that, as referred above, molecular biology has revealed that their structure is more complex that the term *unit* may imply, i.e., it is not only the "organism [that] is so difficult to define satisfactorily" (Dawkins 1982, p. 253). There are also clearly cases where genes should be considered the beneficiaries of selection, e.g., meiotic drive and spacer, or junk, DNA which Dawkins (1982) refers to as outlaws, e.g., meiotic drive[5] and its suppression in diopsid flies (Wilkinson et al. 1998). But are genes the only valid replicators? Many individuals modify their environment, through processes such as "niche construction", thus modifying the process of natural selection that acts upon those individuals. Dawkins (1982) would consider such aspects as components of the extended phenotype, which transcend the more cohesive organism. But such modifications of the environment can be transmitted across generations, via a process of ecological inheritance (Odling-Smee et al. 2003). Additionally, when considering certain social species, e.g., humans, there is also cultural transmission. One need not consider Dawkin's (1976) model of memes, to recognize that in these species there is cultural inheritance among individuals, across and within generations, including among individuals that are not genetically related. Therefore, a comprehensive understanding of certain evolutionary processes may require the simultaneous consideration of all three forms of inheritance (or replication)—genetic, ecological, and cultural—and the interactions among them (Durham 1991; Odling-Smee et al. 2003).

Are genes the only benefactors of adaptation? In order to address this question one must delve further into a parallel discussion of another fundamental term within evolutionary biology: the meaning of adaptation. [A discussion which has also led to additional, more specific and clarifying terms, such as exaptation, disaptation, maladaptation and aptation[6] (Gould and Vrba 1982; Lauder et al. 1993).] Within the biological literature one encounters the term *adaptation* with somewhat distinct meanings: (1) adaptation as a *process*, which ultimately benefits the propagation of the unit of selection through time; and (2) adaptation as a *condition*, whereby a given character is an adaptation to a certain function or an aspect of the environment. From a historic, evolutionary perspective, i.e., adaptation as a process, the replicator may warrant being categorized as

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[5] During regular meiosis of a diploid cell, each copy of the two homologous chromosomes is present in half of the descendent haploid cells (e.g., sperm). Under meiotic drive, this ratio is biased in favour of one of the chromosomes.

[6] The different terms allow one to distinguish different evolutionary histories of a character and its relation to its present function. Thus, *adaptation* is reserved for a character that evolved specifically for its present function. A character which originally evolved for a function distinct from its present function is considered an *exaptation*. For instance, the bird wing originally evolved for thermal regulation and only subsequently for flight. Gould suggested that when uncertain about the original function of a character one should refer to it simply as an *aptation*. *Disaptation* is a formerly adaptive character that has lost its function. If it is presently dysfunctional or detrimental, it is referred to as a *maladaptation*.

the *ultimate* benefactor of an adaptation. Yet, from the perspective of adaptation as a condition, regarding a character, this is clearly an unsatisfactory explanation. Certainly, organisms benefit from the manifestation of an adaptive character, and transmit this character (via some form of inheritance) to their descendents. We return, therefore, to the importance of perspective of an author's approach to a problem.

Dawkins (1982) considers the gene perspective more useful and comprehensive: "adaptations as being 'for the benefit' of something, that something is best not seen as the individual organism [but the] smaller unit which I call the active, germ-line replicator" (p. 4); or, "Adaptations benefit the genetic replicators responsible for them, and only incidentally the individual organism involved" (p. 249). However, in the beginning of "The Extended Phenotype" he uses the image of a Necker Cube to illustrate how selection at the level of the gene and of the organism are equally valid descriptions of the same phenomena, simply from different perspectives (Fig. 1). A gene-centered perspective and an organism-centered perspective (with its phenotypic extensions) are simply "different way[s] of saying the same thing. (…) Readers must decide for themselves" (p. 232).

Contrary to the context of species, explored in the previous section, in this debate differences in perspective are not due to differences between the objectives of different fields of biology, although some partition may be found between geneticists and organismal biologists. The division is perhaps more philosophical than scientific, in particular, whether a scientist has a more reductionist, determinist versus a more integrative, interactionist thinking.

We also re-encounter, in this debate, problems of delimitation. Firstly, regarding the delimitation of the *unit* of selection, there are ambiguities at several hierarchical levels: gene and organism/phenotype (as well as at higher levels not considered here, such as group/population and species/clade). Second, regarding the benefactor of selection, the different perspectives place the focus on different parts of a continuous process: the life cycle.

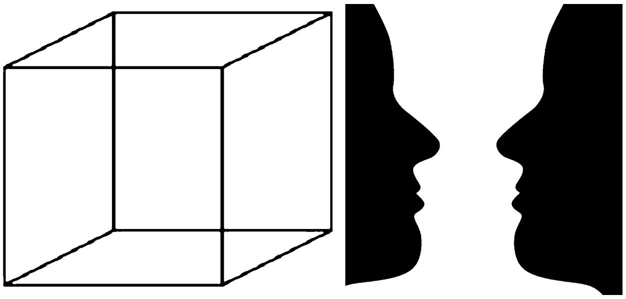

Fig. 1 Reversible figures which can be perceived as different images depending on the viewer's perspective. In the Necker Cube (*left*) one sees either a downward or upward tilted cube. In the right-hand image, one sees either a vase or two people facing one another

Two attempts have been suggested as alternatives to considering a single valid perspective. Gould (2002, p. 677), for instance, considers a system of hierarchical levels of causality. Sterenly and Kitcher (1988) proposed a view they refer to as pluralism, i.e., no single adequate representation, but several equally adequate representations for some processes, each perspective offering a partial representation of the causal structure of the selection process. They further suggest, however, that by considering the interactions and causal connections among different levels, one would obtain a *single* maximally adequate representation of the phenomena, which if considered at face value is a far cry from a pluralist view (Shanahan 2009). A different approach, derived from a developmental viewpoint, has been suggested that regards developmental systems as the units of selection, i.e., the complete life cycle, including its various components and causal contributors (the genotype, phenotype, and the environment) (Oyama et al. 2001). This holistic approach, however, entails problems of tractability and also delimitation: where does a life cycle begin and end? And, if considering an extended phenotype involving biotic interactions, should we consider the whole intervening biological system, with different symbiotic species, as the proper unit of selection? Thus once again the complex and continuous character of natural entities and processes derails our thirst for clear, clean cut explanations.

Final comment

My purpose was not to reach a conclusion regarding the 'species concept problem' or the debate on 'units of selection', simply to use these two cases to illustrate how certain debates over fundamental concepts can be confounded by differences in perspective of the same phenomena, by use of similar words used with different meanings and a lack of sufficiently precise terms, or by differences in the objectives of different fields. Ultimately, biologists face the difficulty of leading with complex systems, with multiple interacting factors, and continuous processes, all of which create a demand for further analysis and discussion, both scientific and philosophical. A discussion that should avoid rigid bi-polarizations and consider forms of integrating different perspectives.

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References

Brookfield J (2002) Review of genes, categories, and species by Jody Hey. Genet Res 79:107–108. doi:10.1017/S0016672302215608

Browne J (2006) Darwin's origin of the species a biography. Atlantic Books, London

Coyne JA, Orr HA (2004) Speciation. Sinauer Associates, Sunderland

Darwin CR (1862) On the various contrivances by which British and foreign orchids are fertilised by insects, and on the good effects of intercrossing. John Murray, London

Dawkins R (1976) The selfish gene. Oxford University Press, Oxford

Dawkins R (1982) The extended phenotype. Oxford University Press, Oxford

de Queiroz K (2006) The PhyloCode and the distinction between taxonomy and nomenclature. Syst Biol 55:160–162. doi:10.1080/10635150500431221

Durham WH (1991) Coevolution: genes, culture and human diversity. Stanford University Press, Stanford

Ghiselin MT (1997) Metaphysics and the origin of species. State University of New York Press, Albany

Gliddon CJ, Gouyon PH (1989) The units of selection. TREE 4:204–208

Gould SJ (2002) The structure of evolutionary theory. Harvard University Press, Cambridge

Gould SJ, Vrba E (1982) Exaptation: a missing term in the science of form. Paleobiology 8:4–15

Hey J (2001) Genes, categories and species. Oxford University Press, Oxford

Hull DL (1988) Science as a process: an evolutionary account of the social and conceptual development of science. University Chigago Press, Chicago

Lauder GV, Leroi AM, Rose MR (1993) Adaptations and history. TREE 8:294–297. doi:10.1016/0169-5347(93)90258-Q

Lewontin RC (1970) The units of selection. Annu Rev Ecol Syst 1:1–18. doi:10.1146/annurev.es.01.110170.000245

Lloyd E (2000) Units and levels of selection: an anatomy of the units of selection debates. In: Singh R, Krimbas C, Paul D, Beatty J (eds) Thinking about evolution: historical, philosophical, and political perspectives. Cambridge University Press, Cambridge, pp 267–291

Mallet J (1995) A species definition for the modern synthesis. TREE 10:294–299. doi:10.1016/0169-5347(95)90031-4

Mayden RL (1997) A hierarchy of species concepts: the denouement in the saga of the species problem. In: Claridge MF, Dawah HA, Wilson MR (eds) Species: the units of diversity. Chapman and Hall, London, pp 381–423

Mayr E (1942) Systematics and the origin of species. Cambridge University Press, Cambridge

Mayr E (1982) The growth of biological thought. Harvard University Press, Cambridge

Odling-Smee FJ, Laland KN, Feldman MW (2003) Niche construction: the neglected process in evolution. Princeton University Press, Princeton

Oyama S, Gray R, Griffiths P (eds) (2001) Cycles of contingency: developmental systems and evolution. MIT Press, Cambridge

Plaxco KW, Gross M (2006) Astrobiology. A brief introduction. Johns Hopkins University Press, Baltimore

Shanahan T (1997) Pluralism, antirealism and the units of selection. Acta Biotheor 45:117–126. doi:10.1086/289544

Shanahan T (2009) Unidades de selecção. In: Levy A, Carrapiço F, Abreu H, Pina M (eds) Evolução: conceitos e debates. Esfera do Caos, Lisbon

Sterenly K, Kitcher P (1988) The return of the gene. J Philos 85:339–361

Wickner RB, Edskes HK, Shewmaker F, Kryndushkin D, Nemecek J (2009) Prion variants, species barriers, generation and propagation. J Biol 8:47. doi:10.1186/jbiol148

Wilkins J (2006) A list of 26 species "Concepts". Available via EVOLVING THOUGHTS. http://scienceblogs.com/evolvingthoughts/2006/10/a_list_of_26_species_concepts.php. Accessed 1 Aug 2009

Wilkinson GS, Presgraves DC, Crymes L (1998) Male eye span in stalk-eyed flies indicates genetic quality by meiotic drive suppression. Nature 391:276–279. doi:10.1038/34640

Williams G (1966) Adaptation and natural selection. Princeton University Press, Princeton, New Jersey

Wilson DS (1983) The group selection controversy: history and current status. Annu Rev Ecol Syst 14:159–188. doi:10.1146/annurev.es.14.110183.001111

Wu C-I (2001) The genic view of the process of speciation. J Evol Biol 14:851–865. doi:10.1046/j.1420-9101.2001.00335.x

Wynne-Edwards VC (1962) Animal dispersion in relation to social behaviour. Oliver and Boyd, Edinburgh