

Species concepts: what for?

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Recent papers have brought to light again the problems associated with species concepts and speciation modes. Such issues are highly relevant for our understanding of biodiversity. However, it appears that many kinds of organisms are poorly taken into account (if at all) in these works. Even if microorganisms seem recently to have attracted more attention, parasitic organisms, despite their biological and numerical importance, have not been considered in recent reviews. It is important not to disregard such organisms because they can help us to perceive the futility of seeking a single, unifying species concept, and thus how speciation mode concepts become abstruse.

Species concepts and speciation modes have experienced renewed interest [1–8]. The different ways species arise and are described is crucially linked to the comprehension of biodiversity and evolution. However, it seems that most authors base their arguments on organisms (i.e. some insects and vertebrates) that do not represent the vast majority of global biodiversity. In particular, unicellular organisms are only now starting to be included in the relevant literature [7–10], and parasitic organisms (30% of described eukaryotic species [11]), which are often known to challenge classical species concepts [12,13], are completely disregarded, despite the growing evidence that they probably far exceed macroscopic and free-living organisms in terms of biological diversity [11,14–16].

What is more, it is even argued that the many attempts to challenge the Biological Species Concept (BSC, see Box 1) in recent decades were of little use: 'like barnacles on a whale, their main effect (was) to retard slightly the progress of the field' [5]. The BSC could thus be considered to have proven its robustness by resisting such attacks. However, this resistance could be caused by a quite different property: humans need to be able to classify species. We share with other authors skepticism on the relevance of developing new species concepts [5]. Nevertheless, our position is based on different arguments, and ultimately disagrees with the defenders of the BSC. We do not believe that the BSC has greatly facilitated the debate on the evolutionary biology of adaptation and divergence in living organisms [5].

BSC faced to the diversity of life

Templeton's 1989 contribution to the field of speciation and species concepts [17] is, to our point of view, too often

neglected (and not cited in the most recent reviews [5,18–21]). Even if one can argue how difficult it is to apply Templeton's 'cohesive species concept' [17] in nature, like other 'evolutionary biology' concepts (as evoked in Ref. [3], p. 163), his article is one of the first to demonstrate clearly how the BSC fails to be a useful concept. Revisiting all the arguments against the BSC and how parasites can be useful in the field of concern would be time consuming, as much has already been written on this subject [3,12,13,17]. Therefore, we will focus on a few illustrative biological examples as to why the BSC fails as a general species concept.

Box 1. The biological species concept (BSC) and its problems

Definition: a species is a population or a group of populations whose members have the potential to interbreed with one another in nature, producing viable and fertile offspring, and are reproductively isolated of other such groups and thus cannot produce viable, fertile offspring with members of other species.

This definition thus necessarily applies only to organisms exclusively reproducing through bi-parental sexual reproduction, and excludes all organisms able to crossbreed between more or less distant lineages, as it excludes clones and cannot apply to strict selfers.

Other species concepts have been designed. The definition of these concepts is easily accessible through the web or in the articles cited in this paper (e.g. in Refs [2,3]). The concepts might be less flawed than the BSC, but they all fail because they try to fit living things into fixed categories. But life is not fixed and Darwin early understood this problem (cited in Ref. [3], pp. 6–9).

Species identification and speciation cannot be disentangled as long as the BSC will be used to describe life. The BSC exactly describes how members of a group must behave to be considered as belonging to the same species (reproductive isolation) and, at the same time, how speciation occurs (evolution of reproductive isolation). Because of this, the use of the BSC is misleading in two ways: with regard to understanding evolution and describing biological diversity.

A strict application of the BSC makes the speciation process difficult because it requires the evolution of a character (reproductive isolation) that is hardly adaptive by itself. In allopatry (where the two groups of interest are geographically isolated), it is ineffective (by definition) and in sympatry (where there is no geographical barrier), it is deleterious because it requires organisms to be sexually selective (only reproduce with the alike) in comparison with those who are not selective. Here we meet another field, which is not within the scope of this paper: the evolution of sex [41]. Indeed, the major advantage of sexual reproduction lies in recombination. With the BSC, we see that speciation, because it requires that breeding only occurs between the alike, significantly weakens the advantage of sex for those species fitting in the BSC.

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In bacteria, plants and other organisms (e.g. mussels [22] or parasitic kinetoplastids [23,24]), the horizontal transfer of genes is not uncommon, even between distant lineages [23–27]. An absence or rarity of sex is found in many kinds of organisms (bacteria, protists, fungi, animals and plants) [12,17,28,29], among which many are parasitic. The ‘pork tapeworm’ *Taenia solium* is almost always found alone in the definitive host and is thus an obligate self-fertilizer. This property is shared by other cestodes, trematodes and plants [12,17]. For all of these organisms, each individual is reproductively isolated, and thus is defined as a species under the BSC. Using a strict interpretation of the BSC, *T. solium* could be cited as one of the best and irrefutable examples of multiple and recurrent sympatric speciation: it cannot be more sympatric (speciation occurs within a single individual) and new infections lead to immediate and perfect reproductive isolation. In our opinion, this is meaningless.

In our opinion (see also Ref. [30]), the most interesting consequence of the use of the BSC might have been to limit the description of new species, whose number would have exploded without it (but see below). The BSC was defined by the well-known ornithologist E. Mayr [31], and it seems to fit for birds (but see Refs [32–34]). Interestingly, the fit is quickly lost outside of this clade. The fact that more avian than bacteria species are presently described (9672 versus 9280) [35] reflects the clear limitation of the BSC for assessing biological diversity. It is indeed accepted that the microbial biosphere is greatly more extensive than that of macroorganisms ([36], p. 616), whether we consider bacteria alone [16] or only unicellular eukaryotes [9]. The fact that only 30% of described eukaryotic species are parasites is further evidence of description biases [11]. For example, for gregarine parasites, which can be considered to be host specific and infect over one million host species, only 2000 species are currently described [11].

One might ask what evolutionary meaning can the BSC have if the majority of organisms constitute ‘glaring exceptions’ [5], i.e. reproduce differently than do birds? As nicely explained by Hey [2,3], species are taxonomical categories and any attempt to reconcile this with functional and evolutionary concepts will always tend to fail. Species are entities that can be discriminated from one another, following criteria that seem the most appropriate at one place in time and space, and for one class of organisms (see also Ref. [3]). We could not work without using these categories. Nevertheless, nature hardly conforms to human-made definitions, and even the most operational species definition, in terms of classifying life, will never be able to appropriately describe the process of life (see also Box 1). Considering the permeability of many genomes and the large proportions of parasitic (selfish) DNA (i.e. noncoding DNA, satellite DNA and transposons) that make them up (from 15% to 95% [37,38]), we are tempted to follow Dawkins [39] and view living organisms as collections of portions of DNA that are more or less linked, and collaborate more or less well for the constitution of the organism that we aspire to classify using a species concept.

Conclusion

Trying to determine how species appear (sympatrically, allopatrically or otherwise) becomes very difficult when one cannot really tell what is meant by a species in the first place or what sympatry or allopatry really mean (see Ref. [40] for a discussion on the problems these terms pose for parasites, and Box 1 for more general problems). After all, is not the universal speciation mode when a systematician, specialist of one group, splits one recognized species into several new ones?

Microorganisms and, particularly, parasites, despite their overwhelming importance and relevance (numerically, ecologically, economically and medically), are still largely disregarded in discussions of species concepts and modes of speciation. Perhaps it is time for evolutionary ecologists to acknowledge how diverse life can be, in particular how parasites and pathogens can be informative in that perspective. This might then make it clear that, rather than continuing the countless discussions on what constitutes a species and how speciation takes place, it could be more productive to focus efforts on the mechanisms responsible for diversity maintenance, adaptation, specialization and divergence. Are not such topics, to the evolutionary biologist point of view, what it is all about? Because they are everywhere, because they are highly diversified and because they continuously shape biodiversity, parasites can tell much about it.

Acknowledgements

We thank Christine Chevillon, Karen McCoy and Philip Agnew for a critical reading of our article. We would also like to thank the five referees who did tremendous work that considerably helped to improve this article. We thank the CNRS and the IRD for their financial support.

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doi:10.1016/S1471-4922(03)00195-8

Tick ‘talk’: protein release by tick salivary cells

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Tick salivary gland proteins involved in exocytosis via soluble N-ethylmaleimide sensitive factor attachment proteins (SNAPs) and their receptor proteins (SNAREs) were recently identified. This new line of research looks at protein trafficking in the salivary glands. How do tick cells ‘talk’ in order to move important proteins out of the granular acini and into the saliva?

The biological success of ectoparasitic ticks stems from their unique physiology. During blood feeding, the tick becomes a continuous extension of the host. Specialized salivary glands are vital to the ixodid tick and are key to the transmission of bacteria, viruses and protozoans. The salivary glands function to excrete surplus fluid (blood-meal concentration) during blood feeding, and to secrete bioactive proteins and lipid molecules that defend against host responses to tick attachment [1]. Ticks have a system of differential gene expression where the activity in the cells goes from undetectable to highly expressed levels in only a few minutes. Reports of proteins induced by tick

feeding are common and it appears that blood feeding can induce the expression of many tick genes. An example of this type of induction is that of calreticulin, which is not detectable in the unfed salivary glands, but is strongly present in the salivary gland tissues three days after feeding [2]. The *in vitro* translation of enriched poly A + RNA isolated from salivary glands of feeding female ticks has demonstrated *de novo* gene expression [3]. Although the number of cells in the glands does not increase, mass and protein content of the salivary glands increase during feeding [1]. Ticks ingest over a hundred times their own weight in blood in a few days and, in this process, defeat their hosts’ mechanisms to prevent blood loss from injured vessels. This chemical communication must continue for the adult hard tick for >6–10 days and, after an initial phase of slow feeding, a rapid feeding phase ensues when the tick takes in the bulk of the bloodmeal [4]. This is accomplished by the salivary secretion of anti-hemostatic, anti-inflammatory and immunoregulatory molecules into the feeding lesion [5]. It is not known what regulates and controls many of the aspects of blood feeding including that of protein secretion events. A lot is known about the

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