



On species concepts, phylogenetics and the science of natural history— three current issues facing taxonomy

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Taxonomy faces some major challenges in the 21st Century (Godfray 2002). The threat to biodiversity comes largely from human overpopulation, but the impact of climate change is unprecedented (Pievani 2014) and increasingly a risk factor for many species. This makes it even more critical to rapidly catalogue our biodiversity to better protect it (Mace 2004). If you do not know what is there, it is impossible to know what we are losing, let alone protect something for which we have no name and cannot identify. Understanding diversity and the dynamics of evolution and speciation is important to discover the adaptability of species in a changing world dominated by humans (e.g. Harvey et al. 2014), but at the same time education about the natural world seems to have failed our children.

Below I address three major questions or issues that are current in taxonomy, and natural history in the broader sense, related to species concepts, classification, communication and education.

When is a species a species?

A species, be it a plant, fungus or animal, has long been argued to be fictional, a mental construct without objective, scientific existence (Burma 1949). Lines of descent exist in a four-dimensional continuum, and, to delimit species along this continuous line of descent, it has been argued that we must chop diversity into arbitrary units. It is implicit in the theory of evolution that species should change over space and time. There should be populations in a gradual evolutionary series that are on the border between an ancestral and a descendant species (unless one believes in evolution by saltation), but even such borderline populations can be good species in relation to others with which it is in contact (Mayr 1949). Therefore, applying a species concept in an evolutionary framework can be difficult, but there should be gaps even in a multidimensional, apparently continuous system when gene flow ends or there is strong selection on

particular important traits, both leaving “gaps”, genetic or morphological/ecological.

The concept of genus and species originated from the logic of Greek philosopher Aristotle, but these ideas were introduced to biology through works of Bauhin (1596), Ray (1686) and contemporaries. However, it was not before these were widely applied by Linnaeus (1736), forming the basis of the binomial nomenclatural system, that species became the biological working entity (Svenson 1953). A plethora of species concepts have been proposed in the past (Wheeler & Meier 2000; De Queiroz 1998; 2007), but none defines what a species is across all life forms. These concepts of species often fail (Blaxter 2004), and although some may work well for birds, others can only be applied to plants. Importantly, few appear to work well with micro-organisms and fungi.

The most commonly discussed and applied concept is the biological species concept (Wright 1940; Mayr 1942; Dobzhansky 1950), in which species are defined as populations that can potentially or actually interbreed to produce fertile offspring. This concept may work in some species of higher vertebrates, but certainly falls apart when looking at, for instance, cnidarians (Medina et al. 1999), tardigrades (Stec et al. 2020), plants (e.g., Mayr 1992) or fungi (Harrington & Rizzo 1999; Taylor et al. 2000). In addition, potentially interbreeding populations can be separated by oceans, deserts or mountains, effectively making them separate species, but they can still mate and produce fertile offspring if they are brought together either through natural or human-induced events. This in turn may intermingle regional variants and create novel entities/populations. On the other hand, hybridisation between species when they come into contact occurs frequently and can be a way for species to evolve, as is evident in lycopods (Taylor et al. 1985), ferns (Barrington et al. 1989) and many angiosperms (Paun et al. 2009). This also occurs in various groups of animals including insects, amphibians and fish (e.g., Abbott & Rieseberg 2012), and we can add taxa that are apomictic, hermaphroditic or asexual to list of problematic organisms. Where to draw

the line using a biological species concept is often difficult if not impossible, particularly because it is not practically viable to do breeding experiments with all known taxa.

The phylogenetic species concept (Wheeler & Meier 2000) has been widely touted as a good alternative to the biological species concept, and if the group of organisms has enough morphology to make this concept operable it should be useful in many groups of organisms. It clearly will fail in those groups with simple morphology in which the same traits evolve repeatedly in parallel, such as bryophytes, lycopods and even ferns (Christenhusz & Chase, 2014). It also is problematic in cases in which the morphology of the organism is not sufficiently understood, and good examples of this are “cryptic species”, in which on morphological grounds a species was viewed as indistinct from another (others), but genetic data demonstrates otherwise. The morphological traits that are later found to distinguish such cryptic species were omitted from the data matrix, thus leading to the failure of cladistic analyses to discover the true relationships of such species.

Several techniques have recently been developed that use molecular data to identify which populations have experienced gene flow and which do not (e.g., SNAPP coalescent analyses; Bryant et al. 2012; applied for instance in Brandrud et al. 2019), effectively showing where genetic gaps may or may not exist and making the boundary between species clear. It has to be considered that most species have had gene flow with other taxa in the past, and some restricted gene flow may still be ongoing between well-established species, so even these techniques are not one hundred percent fool proof, but at least they can aid in providing objective data to circumscribe species as genetically meaningful entities. As mentioned above, in many groups, such approaches have often been found to identify “cryptic species” of which we previously were unaware. These sometimes are morphologically ambiguous but have clear ecological differences from their congeners, but in other cases there overlooked morphological differences, which when examined in the light of genetic distinctiveness, suddenly become evident. Our perceptions are imperfect tools that in many cases fail to detect that which eventually becomes obvious through further study.

Can we create a stable nomenclature for phylogenetic classification?

Naming is important for communication, legal status and protection, but the wrong application of names can be problematic, so naming has to be done with care and diligence. Biological nomenclature should be standardised to have the most stable names for organisms possible. Long-established names have large amounts of literature

associated with them, and thus it is important that names only change in extraordinary circumstances. Conservatism is therefore important. Taxonomic ranks are useful for classification and ease of identification in the field. For communication purposes in most groups of organisms, the ranks of family, genus and species are the most widely used outside the field of taxonomy. Therefore, when these names change, there are often some disgruntled comments from people that are used the ‘old’ name and do not wish to change (Grey-Wilson 2019; Lidén 2019). This of course is generational: the next generation of students will pick up the new names and slowly these will become the standard. However, if change was not a necessity, the old names would have been just as good. Needless splitting has come to light where authors decide to split because they want names for each clade so that they can discuss these in a paper, but when this is done, these authors forget the user of the names and the associated literature, and ignore the connection between the clades, and shared characters and evolutionary history.

A good botanical example is the genus *Nothofagus*, which was separated in its own family Nothofagaceae (APG 2009; 2016), but included a single genus with a long fossil history. It has an extensive literature associated with the name, particularly when it was used in biogeographical studies (e.g., Linder & Crisp 1995; Swenson et al. 2001; Cook & Crisp 2005). A phylogeny-based classification of extant members divided this clade into four genera (Heenan & Smitsen 2013), which resulted in name confusion and orphaned fossil taxa, which due to their incompleteness often must continue to be known as *Nothofagus*. Such name changes for the sake of changing the names should thus be discouraged and not forced upon the public.

A zoological example can be found in the kangaroo and wallabi clade of Macropodidae. Most kangaroos and wallabies were traditionally placed in *Macropus*, with wallaroos and wallabies often placed in separate subgenera. However, this clade includes the deeply embedded *Wallabia bicolor* Desmarest, 1804, the swamp wallabi (Meredith et al. 2008; Dodt et al. 2017), which hops a little crouched and has a different karyotype, but to the general natural historian looks otherwise like a wallabi. *Wallabia* was sunk in *Macropus* by Meredith et al. (2008), but this was not generally followed and resulted in the split of *Macropus* into four genera (Jackson & Groves 2015; Celik et al. 2019) or merger of just the wallabi clade, *Macropus* subgenus *Notamacropus* with the genus *Wallabia* (Nilsson et al. 2017). There are thus three options and because generic delimitation is an arbitrary, personal choice without scientific basis, this has caused destabilisation of the names used for wallabies in Australia. It unfortunately generated a great deal of confusion among scientists, the public and online and in popular and scientific literature.

There are many such examples, and these unnecessary name changes have given taxonomy a bad name among the other biological disciplines and the public, who therefore tend to avoid scientific names rather than embrace them. The solution is to be conservative when changing names, placing them into historical context and changing them only once if absolutely unavoidable. A good example of such conservatism is the recent lumping of *Rosmarinus* in *Salvia*, rather than the splitting of *Salvia* into several genera in order to retain *Rosmarinus* (Paton, 2019).

Darwin (1857) stated that “it is good to have hair-splitters & lumpers”, because splitters remind lumpers that variability should not be ignored, while lumpers remind splitters that variability should not be overinterpreted. The disagreement between these two camps is on-going and sometimes counter-productive to the advancement of biodiversity science. With the advent of molecular systematics, classification is moving away from subjectively chosen characters that may or may not have a genetic basis (based solely on morphology and thus not always accounting for convergence of characters or environmentally induced variability) to more objective characters (based on, admittedly selected, sequences and chemistry), but even when objective characters are used, delimitation of higher categories is arbitrary (Blaxter 2004). One can decide that a clade represents a species, genus or family. This often depends on how names were applied in the past. A historical concept is inevitable in taxonomy, partially because of nomenclatural priority and partly because of the volume of data and literature attached to a name, which makes changing the name a destabilising action. Changes should therefore only be made when absolutely necessary, but in the field of molecular taxonomy, there is a tendency to name newly discovered clades to acknowledge our prior neglect of these entities, regardless of their historical concepts. In many groups this destabilises the classification: with every new tree, a new classification is proposed, often resulting in the need for a phylogenetic analysis before a specimen can be correctly assigned. A broader concept of higher ranks is more stable because large families and genera are less likely to need to be changed to maintain monophyly. Of course, it is important to have morphological characters that are shared by all members of the group for ease of recognition in the field. Therefore, in general, higher taxonomic ranks should focus on similarities rather than differences, whereas differences are important at the ranks of species and below. This should not be taken as an argument to recognize paraphyletic groups, to which we remain opposed. We should, for example, look for the shared features of reptiles and birds to emphasize their similarities rather than focusing on the differences and splitting the reptiles into a multitude of higher taxa in order to maintain birds as a major taxonomic group.

Should we resurrect natural history as a modern scientific discipline?

Why are the fundamental sciences so poorly funded? With the exception of theoretical physics and astronomy, financial support to science flows significantly more towards the applied disciplines (Salter & Martin 2001; and see overview for taxonomy in Agnarsson & Kuntner 2007), to studies that have direct application. At the same time these applied disciplines depend on knowledge of natural underpinnings. This is an inverted pyramid: a vast, top-heavy well-supported structure balanced on a small, poorly funded base.

Like taxonomy, the discipline of natural history is one of the fundamental disciplines that has suffered from a lack of funding. It is generally associated with the study of furry beasts in a far-flung forest, with dinosaurs in a landscape of exploding volcanoes, or with stuffed animals in display cabinets in a museum, but observing and describing nature – its processes and diversity – is a fundamental science (crossing the boundaries of biology, physics, geography, geology, chemistry, social sciences and art), that provided major insights into the functioning of the planet, climate, forests, mountains, oceans. Darwin and Wallace are our foremost “naturalists”. Biology, geography, geology, chemistry, physics, arts and social science all have their foundations in natural history, but yet as a discipline it is nearly forgotten. The term persists in the name of grand museums and documentaries on television, but modern scientists spend more time in laboratories and running analyses on previously collected data than on observing organisms in the field. Taxonomy (and systematics that aims to incorporate more observational data) is often slightly different, as it is usually still based on field-collected data, but even in this fundamental discipline, the focus has shifted towards lab-based and analytical techniques rather than field observation. Too many taxonomists do not spend much time in the field (usually thanks to a lack of funding), and if they can go to the field, they often do not take time to watch their species in action.

Charles Darwin based his evolution theory on observing and studying biological experiments and the natural history and geology on his voyage (Darwin 1845; Darwin & Wallace 1858). Alexander von Humboldt (1849) defined nature through observation and gave first hints to the human impact on nature that he observed in Venezuela and Cuba (Humboldt 1828; Wulf 2015), and Isaac Newton (1687) observed how an apple fell from a tree. All great science starts with observation of natural phenomena, with natural history, but can we resurrect natural history as a scientific discipline, or is it a thing of the past?

We treasure documentaries and books on natural history, and they are a large industry, but often the observations are presented as a known fact, giving the viewer a feeling of having learned something new, but also that all of nature is known and there is little new to discover. The contrary is true, of course, but the connection between the makers of these documentaries and the promotion of the science behind it is not always evident.

The interdisciplinary field of natural history would, in my opinion, be worth reviving as a discipline, perhaps not in the traditional sense of ‘learned gentlemen writing about what they saw on a stroll through the forest’, but more like a field-experiment based discipline, involving researchers from different disciplines, varying from taxonomy to economics, and involving local or even international communities. When disciplines are combined to achieve the common goal in observing and describing the natural phenomena of the world, it should be easier to fund and to train people in observation, a discipline greatly needed in a world where people are spending more and more time in a virtual world on their mobile devices rather than seeing what lives around them.

Of course, this virtual world is not all bad. It can also help people get in touch with what they are seeing in their natural surroundings. Ironically, it is taxonomy that is needed in the virtual world for people to make sense of what they see. Identification apps of plants and animals are common, but often these do not offer much for taxonomists that contribute their knowledge. Good examples from the online world of taxonomy are iNaturalist (<https://www.inaturalist.org>), where the community identifies photos online, producing data that can be used for further study on the distribution of organisms. Plant snap (<https://www.plantsnap.com>) also works well, with people sending in photos and receiving an identification. In the latter case, the identifier is financially compensated for the effort. An excellent way of introducing people to their natural world is ‘bioblitz’ events where people meet at a designated site and make checklists of all living things they find, sometimes with specialists from local natural history museums at hand.

Can we teach our young people to recognise the biodiversity that surrounds them? There have been reports where school children could not identify any common bird or animal in their area. A 2013 survey by the British Nutrition Foundation showed that few school children knew how the origin of basic foods, believing that cheese was made from plants and fish fingers (despite the name) from chicken, whereas potatoes were believed to grow on trees. It is clear that a fundamental change is needed.

One of the best new initiatives to address this is the creation of a General Certificate of Secondary Education (GCSE) in Natural History in the UK school system. This

will expose teenagers to nature, help them understand the importance of being able to identify the life around them and how it is linked to other disciplines, language and culture (Colwell 2019).

Such initiatives should perhaps be made more structured, rolled out internationally and disciplinarily inclusive. When they gather observations and data are discussed and analysed properly, it could result in publications involving large groups of people from different backgrounds, bringing science to the public and the public into science, the so-called “citizen science”. When more people are involved, the more likely it is that the studies get noticed, valued, cited and funded.

In short natural history could once again become one of the most important scientific disciplines: the fundamental exploration of the natural beauty of our planet in all its facets.

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