The Species Concept in Nature Conservation Theory and Practice

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To Václav Petříček (1944 – 2022) who told me dragons did not exist, then led me to their lairs

It is no secret that there hardly is any other issue in biology which has been full of contradiction as the species, whether as a concept, category or taxon in systematics. The continuing debate which set of individuals could be considered the species resulted in at least 35 various concepts: although most species concepts have strong implicit similarities and they in some extent overlap each other, some of them exclude others (ZACHOS 2015, 2018b). It is necessary to mention that many of them in the fact do not define what species are or should be but rather provide differently complicated approach how to delimitate them (MAYDEN 1997, QUEIROZ 1998, 2007, STEWART 2018, REYDON & KUNZ 2019). Taking into account the extent of the debate the following reflection offers only a glimpse of the topic from a point of view of nature conservation, not an exhaustive analysis.

In addition to the well-known Rowan (*Sorbus aucuparia*) also called Mountain-ash there are other 28 species of the genus *Sorbus* in the Czech Republic. Ten of them are endemics or rather microendemics: they grow only at a few small sites and they developed themselves through hybridization or asexual reproduction. © Jan Plesník

Species is if....

Most biologists seem to agree that species are separately evolving (meta-)population lineages (QUEIROZ 2005a, 2005b, 2007, ZACHOS 2018a, 2018b). We can in a simplified way say that species is the smallest distinctive group of individual organisms. Moreover, there has been a question about differences we prefer and how we delimitate them. Of various species concepts, we present three most often applied in practice.

Based on morphological traits and more recently genetic analysis there are eight subspecies in the Tiger (*Panthera tigris*): three of them have to be considered extinct. On the contrary the opinion that according to the Phylogenetic Species Concept (PSC) there are two and even three species has not been broadly accepted. © Jan Plesník

Species can be the smallest groups that are constantly and determinedly distinctive and distinguishable by average means, *e.g.* by external traits. Thus, species are the smallest natural populations permanently separated from each other by a distinct discontinuity in the series of biotype. Therefore, we speak about the Morphological Species Concept (MSC, RAY 1686, CRONQUIST 1978). The MSC considering species to be constant, unchanging and well separated entities has been the most widely spread species concept in taxonomic practice, having had a monopoly in biology for a long time and despite its great subjectivity it dominates also in present (ZACHOS 2016). Problems raised when a certain group of individuals displayed a huge variability in some trait or traits, *e.g.* coloration, and it was necessary to decide whether this has been the single species yet. Description of species was becoming difficult also in cases if the species shows in external appearance different stages in the course of an individual development (ontogeny) or if single sex can appear in two or more morphological forms. In addition, it was found that the species called cryptic are morphologically indistinguishable: moreover, they differ, often sharply, in genetics, ecology and in animal also in behaviour. Therefore, although they were believed to be a single species they in reality comprise more than one evolutionary distinct lineage or species. It must also be added that external morphological similarity does not necessary reflect the true phylogenesis (evolutionary development of a species).

Due to continuing development in evolutionary biology and population genetics in the 1930s and 1940s biologists had turned their attention in seeking for suitable species concept to knowledge of these scientific disciplines. Thus, at the time revolutionary approach rather generally called the Biological Species Concept (BSC) appeared. It means an interbreeding natural population reproductively isolated from other such groups; all individuals produce actually or potentially fertile offspring (MAYR 1942, 1963). BSC´s clear weakness is that it cannot be, of course, applied onto asexual organisms as well as onto fossils. The question raised directly from the above definition is how to determine that individuals from a certain group can interbreed among themselves in the wild, *e.g.* if populations are spatially separated each other, live at different times or their biology or bionomics has been little, if anyhow known. Simply said it is difficult or impractical to determine whether populations are reproductive isolated: the direct testing of the reproductive compatibility by *e.g.* mating experiments in most groups of sexual organisms is logistically infeasible. When applying the BSC every clonal organism should be the separate species. From a broader point of view the BSC ignores evolutionary and ecological processes forming reproductive isolation mechanisms among groups of organisms.

Since the 1990s a variety of the Phylogenetic Species Concepts (PSC) has been more and more advanced. It is the smallest diagnosable cluster of individual organisms within which there is a parental pattern of ancestry and descent. The individuals within PSC share in both sexes a certain absolutely unique trait which occurs neither in their ancestors nor in other group. The given trait is characteristic of the particular independent evolutionary lineage maintaining its identity across space and time: these are groups of organisms with unique defined and measurable genetic similarity. The PSC and its variants define species either as the smallest cluster sharing genetically transmitted characters, such that all individuals are unequivocally diagnosable on the basis of those diagnostic characters, or as monophyletic assemblages. In these, all individuals sharing a common ancestor belong to one species, with common ancestry inferred on the basis of shared derived characters (CRACRAFT 1983, NIXON & WHEELER 1990, DAVIS & NIXON 1992, BAUM & DONOGHUE 1995). The fact that the PSC, *i.e.* two populations are listed as distinct species if they have a common ancestor but differ physically or genetically, has been more and more used in practice is significantly supported by rapid development in phylogenetics (the study of the evolutionary history and relationships among or within groups of organisms trying to reveal evolutionary relationships among biological entities – often species, individuals or genes) related to a boom in molecular genetics including genomics (an interdisciplinary field of biology focusing on the structure, function, evolution, mapping, and editing of genomes: the latter are organism's complete sets of DNA, including all of its genes as well as its hierarchical, three-dimensional structural configuration). Not all by now proposed species concepts can be applied in all species, but the PSC considering species as the results of evolution, thus according to some opinions providing the best balance of theoretical consistency with an evolutionary framework and necessary operationalism of all existing concepts, can do it (RUSSELLO & AMATO 2014). Moreover also the PSC has – after all, like anyone – its quirks. Which criteria allow to determine some organisms as diagnosable different from others? It is rarely possible to reconstruct with certainty the past evolutionary pathway; and if so, it is hardly possible to devise a satisfactory method of designation a branching pattern by

A new insight into phylogenesis and consequently classification of giraffes (*Giraffa* spp.) was supported particularly by applying molecular genetic techniques and phylogenetic methods. A recent analysis of the genome (all the genetic information of an organism) confirmed there are four species of these popular big herbivores. © Jan Plesník

Applying the Phylogenetic Species Concept increased the number of bovids from commonly referred 143 to 279 species. Instead of the original single species of the African buffalo some zoologists distinguish four. The West AFrican buffalo (*Syncerus brachyceros*), also known as the North-western or Lake Chad buffalo, inhabits African savannas from Senegal where the photo was taken to Ethiopia and Sudan. © Jan Plesník

means of a single linear sequence. Which genetic and morphological traits and how many of them we need to delineate various species if they are reproductively isolated? In addition, it has been found that various parts of genome can display different genetic history? Therefore, opinions on whether the particular group of organisms is the true species can differ according to markers (DNA sequences with a known location associated with a particular gene or trait) is used during genetic relatedness analysis. The PSC highly depends in the variability of the chosen DNA marker and in the chosen threshold of genetic divergence between two species.

Does nature conservation need its own species concept?

Together with protection, conservation and management of the selected sites/areas species conservation has been traditional approach in nature conservation. Species are one of three generally respected biological diversity levels (UN 1992, WRI/IUCN/UNEP 1992). How the persisting ambiguity of what species is impact nature conservation?

Changes in taxonomic classification of a certain groups of organisms caused by applying the particular species concept can enhance its protection, conservation and management, do not impact its conservation status or on the contrary to reduce programmes or project aiming at its conservation (MORRISON *et al.* 2009). According to the PSC particularly the populations originally considered to be subspecies (once named geographical races) often become new species. Sometimes there is a dramatic increase in the number of species not because of extensive description of new ones: the process is aptly called taxonomic inflation (ISSAC *et al.* 2004). It is the rapid accumulation of scientific names due to processes other than new discoveries of taxa. According to moderate estimation there was overall an increase in species numbers of 48.7% when a PSC replaced other concepts, although there were significant difference among various groups of animals, plants and fungi: *e.g.* there was a 50% decrease in mollusc species (AGAPOW *et al.* 2004). In this respect the record holder is the diatom *Pinnularia borealis*: it was found that in the fact there are 200 to 600 species instead the single one (PINSEEL *et al.* 2020, KOLLÁR 2022).

Multiplying number of species changes the species richness (the number of species within a defined region in a defined time), one of the most common proxy of and insight into biological diversity, and related approaches, *e.g.* identifying biodiversity hotspots. Newly delineated species usually show both smaller population sizes, and narrower distribution range so they are at increased risk of extinction: nature conservation should add new species to threatened ones and provide them with appropriate protection, conservation and management. Different distribution range of a subspecies or a local population (demotope) elevated to the rank of species influences also protected area designation. In practice the process also involves necessary changes in legislation, both national and international as well as an urgency to allocate for new species the relevant capacities including financial. Therefore, species splits may amplify the number and proportion of endangered species thus reshuffling conservation priority and policy for each new split (COLLAR 1997, ISSAC *et al. l.c.*, ZACHOS *et al.* 2013a, 2013b, ZACHOS & LOVARI 2013, ZACHOS 2015, 2016, GALINDO-CRUZ *et al.* 2022). FRANKHAM *et al.* (2012) suggest that the PSC is not appropriate for nature conservation because it considers small isolated populations suffering inbreeding as the distinct species. If the BSC is consistently applied such populations can be enhanced by individuals from related populations belonging to the same species and interbreeding with individuals from the population to be rescued. According to the PSC it would be interspecies hybridization, *i.e.* crosses between species, with consequent legal and regulatory ramifications that could preclude actions to prevent extinction. Moreover, neither in birds nor in primates the increase in the number of species was followed with elevated risks of extinction within the taxa (SIMKINS *et al.* 2020, CREIGHTON *et al.* 2022, *cf.* LESLIE 2014).

On the contrary, other authors see the taxonomic inflation as the much-needed incorporation of phylogenetics into taxonomy (KNAPP *et al.* 2005). Supporters of PSC also argue that splitting the original species into more species can reveal from a point of view of nature conservation significant populations having been overlooked or ignored, and thus providing them with appropriate protection, conservation and management: those often are (micro)endemics (GUTIÉRREZ & HELGEN 2013, GROVES *et al.* 2017, GIPPOLITI 2020).

The BSC immediately implies that there should be no hybrid species, *i.e.* the stabilized species caused by hybridization between various species. Quite the opposite is true and some hybrid species, *e.g.* the European bison or Wisent (*Bison bonasus*) and Père David´s deer (*Elaphurus david-*

NATURE CONSERVATION AND WITHIN-SPECIES UNITS

Formally named subspecies or other intraspecific categories which can significantly differ in extinction risk have often been described based upon rather superficial and broadly changing characters, *e.g.* coloration or body size. In some cases because of lack of finances, staff, knowledge or time it is not feasible to protect, conserve or manage the species as a whole. Therefore, conservation biologists have independently on the debate on the species concept introduced some proposals how to delineate within a certain species priority non-taxonomic units to be specially managed.

The most important of these approaches is the Evolutionarily Significant Unit (ESU) proposed in the mid1980s (RYDER 1986). In short, it is a population, or group of closely connected populations considered due to its or their genetic, ecological or evolutionary extraordinariness worthy of particular conservation and the targeted management.

For purposes of the United States Endangered Species Act of 1973 WARPLES (1991) defined ESU as a population that is substantially reproductively isolated from other conspecific population units, and represents an important component in the evolutionary legacy of the species. MORITZ (1994) recommended specific methods to delineate ESUs. Since that time, the ESU concept has been debated, criticised, worshiped and specified (*e.g.* CRANDALL *et al.* 2000, FRASER & BERTNATCHEZ 2001, HEY *et al.* 2003, WINKER *et al.* 2007, CASACCI *et al.* 2014, BURBRINK *et al.* 2022). Moreover, an ESU meets at least one of three criteria: (i) current geographic and thus reproductive separation; (ii) past restriction of gene flow; or (iii) locally adapted phenotypic traits caused by differences in selection.

While BARROWCLOUGH & FLESNESS (1996) considered species delineated according to the PSC to be ESU, RIDDLE & HAFNER (1999) recommended to use ESUs directly just instead of species. If proposing new ESU concepts resembles the reader an early stage of the way the species concepts itself has been trudging for two centuries he is not too far from the truth.

ianus) are among the indisputable nature conservation icons (ROBOVSKÝ 2007, ZRZAVÝ 2019).

Responding to troubles in seeking for a consensus what should be considered the species, nature conservation has been, *inter alia*, aiming at the level below the species, *i.e.* at intraspecific conservation units – see Box on page xx.

Species mirrored by time

Ideally, species should be well delineated and captured, naturally perceived entities the result of two processes: (1) the evolutionary processes that have caused biological diversity; and (2) the human mental apparatus that recognizes and gives names to patterns of recurrence, in this case efforts to classify living elements of the world – and just the fact causes their splendours and miseries (HEY 2001, HAUSDORF 2011, KOLLÁR *et al.* 2022).

It was Charles Darwin who highlighted that no one definition of species has as yet satisfied all naturalists; yet every naturalist knows vaguely what he means when he speaks of a species (DARWIN 1859). None of the successively proposed approach has been currently generally accepted and it does not fully satisfy nature conservation needs. In addition it does not seem that the issue shall change in the future (MISHLER 2021, PYRON & MOOERS 2022, WILKINS *et al.* 2022). Therefore, not only national nature conservation legislation except Australia but also multilateral biodiversity-related agreements except the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) carefully avoid defining "species" in any way that takes sides in the scientific debate (GARNETT & CHRISTIDIS 2007). Just as biology, either nature conservation simply does without species. After all, more attention is generally paid to species protection, conservation and management, *e.g.* reintroductions, restocking or releasing recovered animals into the wild than to the ecosystem approach or enhancing the landscape connectivity. Although the main unit of field species protection has been a population, both decision-makers as well as lawmakers and the general public consider the species as a key nature conservation term. Moreover, there are two possibilities for nature conservation how to respond to the above facts.

In practice a very simple solution has currently been applied that species are whatever a component taxonomist chooses to call a species. The approach is called the Taxonomic Species Concept or rather ironically the Cynical Species Concept (KIRSCHER 1984, MAYDEN *l.c.*, WILKINS 2018). Nevertheless it implies the necessity, based on the current taxonomic knowledge, to regularly reassess priorities in species protection, conservation and management (ROBUCHON *et al.* 2019). It is worth mentioning that nature conservation legislation fails to keep pace with changes to how organisms are classified, in some cases it even does not try to do it (MACE 2004, GARNETT & CHRISTIDIS 2017).

Given that biologists have spent decades trying to find a universal definition of species and have not achieved it, it has become obvious that there is no single correct universal definition. The idea that due to a huge diversity in biota it is not quite well possible for all organisms, from viruses to humans to make do only with the single species concept and that in different groups of organisms different species conceptions that are most adequate to their biological properties responsible for their diversity should be applied has not been in any way totally new. Proposals for pluralism are motivated also by the fact that particular criteria for identifying species are not applicable in all situations and the observation that multiple concepts can give conflicting results when they are applied ((MISHLER & DONOGHUE 1982, KITCHER *l.c.*, ERESHEFSKY 1992, DUPRÉ 1999, HEY 2006). Such pluralism could terminate endless fruitless debates about appropriateness of one or another particular species concept to all groups of living beings (PAVLINOV 2021). In that case nature conservation could commonly said has an axe to grind. From a pragmatic point of view of nature conservation, a species is a group of individuals varying in numbers which is important from natural heritage management: therefore it should be reasonably protected, conserved or managed. Because the individuals share an evolutionary and ecological history they display common trait(s).

The longstanding disagreement should not become an impediment to responsible conservation and wildlife management. Moreover it has been repeatedly confirmed that populations valued by humans, for whatever reason – charisma, beauty, rarity, or economic worth – are protected regardless of their taxonomic rank (MORRISON *et al. l.c.*). Really, whether the Mountain gorilla (*Gorilla gorilla beringei*) is classified as a species, subspecies, evolutionary significant unit or local population makes little difference for its conservation in the field (UCHIDA 1996). Nevertheless we should consider also others, particularly endangered biota. This is species protection, conservation and management is or should be about. ■

The list of references is attached to the online version of the article at
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