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Species

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The Concept of Species and Its definition: An Historical Perspective

Species are the fundamental units of biological classifications. Understanding the concept of species is important both because species are the units of comparison across different biological disciplines including behavior, evolution, genetics, ecology, anatomy, development, and molecular biology, and because it plays an important role for the formulation of environmental law and ecological conservation. Species are also the currency by which biologists measure biodiversity. However, biologists largely disagree on the definition of "species."

Attempts to define the concept of species date back to the Greek philosophers Plato and Aristotle, who viewed the world as we know it as a flawed shadow of the eternal and immutable world of ideas. Indeed, the word "species" originates from the Latin "kinds" which is a translation of the Greek word *eidos* (idea). According to this view, the world we live in is imperfect and variable and it is only a projection of the ideas that are real and unchanging.

However, it was an English naturalist, John Ray (1628–1705) who introduced for the first time the concept of "species" in biology. In his 1686 *Historia Plantarum* he wrote:

> In order that an inventory of plants may be begun and a classification of them correctly established, we must try to discover criteria of some sort for distinguishing what are called 'species'. After a long and considerable investigation, no surer criterion for determining species has occurred to me than distinguishing features that perpetuate themselves in propagation from seed. (quoted in Briggs and Walters 2016, p. 4)

In other words, according to Ray, species are those groups of organisms that resemble their parents. Although Ray acknowledged that there can be some variants or "accidents" – as he called them – within a species, such as different heights, scents, or colors, organisms that differ by these characteristics should not be considered as different species. Ray, also, tried to reconcile the idea of "species" with the Bible account of Creation, and believed that all species were created at the same time and no new species could come into existence. While Ray is regarded as the first person who introduced the concept of species in biological terms, Carl Linnaeus (Carl von Linné, 1707–1778) is considered the true father of modern biological taxonomy and classification. In his *Systema Natura* (first edition 1735), Linnaeus formulated a system to classify organisms, by identifying five categories: kingdom, class, order, genus, and species. Before Linnaeus, the

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classification of organisms was somewhat arbitrary, and organisms were often given long names that could be easily altered, making it more difficult for different biologists to understand what species they were referring to. Linnaeus was the first one to formulate the classification based on organism similarities, and to designate the binomial system (*genus* + *species*) to classify organisms. Interestingly, in the first editions Linnaeus still considered species as fixed, a view that emerges also in other publications. In *Critica Botanica* (1737), for example, he defended the concept of fixity of species:

> All species reckon the origin of their stock in the first instance from the veritable hand of the Almighty Creator: for the Author of Nature, when He created species, imposed on his Creations an eternal law of reproduction and multiplication within the limits of their proper kinds. He did indeed in many instances allow them the power of sporting in their outward appearance, but never that of passing from one species to another. (quoted in Briggs and Walters 2016, p. 6)

Over the years, however, Linnaeus's observations led him to realize that species are not immutable entities as different species of organisms cannot always be easy to distinguish, and in his tenth edition of *Systema Natura* he acknowledged that new species of organisms can be formed through intergeneric crosses. He even wrote a document, *Plantae Hybridae* (1751), where he listed 100 plants that might have been considered as hybrids.

One of the most influential figures in human history, because of his theory of evolution by natural selection, is undoubtedly Charles Darwin (1809–1882), author of the *On the Origin of ~~the~~ Species* (first edition: 1859). There is still large debate on Darwin's concept of species, mainly because of largely contradicting statements that emerged from his book. In some cases, Darwin (1859) appears to consider the concept of "species" as a human construct: in p. 52 he wrote:

> I look at the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms.

While in a letter dated 1860, he wrote:

> How absurd that logical quibble—'if species do not exist how can they vary?' As if any one doubted their temporary existence?

The current view that tries to reconcile these apparently contradicting opinions Darwin held on the concept of species is that Darwin did believe that the specific species taxa exist, but he questioned the existence of the "species" category, given that, according to Darwin, there cannot be a clear boundary between species and variety. In other words, the variation that distinguishes each set of individuals is so continuous that setting the boundaries to attribute to these different populations the rank of species appears to be more a convention than a reality. This view sets Darwin's approach apart from earlier naturalists' idea that each species was produced in the current form by a Creator, with only little variation between individuals belonging to the same species.

Current Concepts of Species

A high number of species concepts has been developed over the years: Wilkins (2006) identified a total of 26 definitions of species, while Zachos (2016), more recently, counted 32 species concepts. According to Wilkins (2006), only seven of these concepts are really independent: *morphological*, *biological*, *evolutionary*, *genetic*, *taxonomic*, *ecological*, and *agamospecies concepts* and, as Wilkins himself pointed out, some of these concepts are not definitions of what species are, but how biologists can identify them. In other words, most of these concepts do not question whether species are concrete describable objects in nature, but how best to define this class of objects so that any other object that possesses attributes that do not belong to this class of object can be excluded. Here some main species concepts, namely the morphological, biological, evolutionary, genetic, ecological, and agamospecies, will be discussed, while a complete and recent list of all the concepts can be found in Zachos (2016).

Morphological Species Concept

Under the Morphological Species Concept, Cronquist (1978) defined the species as "the smallest groups that are consistently and persistently distinct, and distinguishable by ordinary means" (quoted in Wilkins 2009, p. 214). According to this concept, the species can be distinguished on the basis of their morphological features. This approach is also called *essentialist*, as, under this view, members of a species can be identified by their essential characteristics, or *typological* since it posits that all the diversities on earth reflect a limited number of "types." While this concept dates back to Aristotle and Plato's concept of "ideas" and was adopted by Linnaeus and other earlier naturalists to classify the organisms, this view has been largely abandoned on the ground that individuals belonging to the same species can display large intraspecific differences, because of marked sexual dimorphism, aging, or polymorphism or perfectly distinct species can be morphologically similar to each other (the-so called cryptic species).

The Biological Species Concept

The Biological Species Concept is probably one of the most cited definitions of species. It was first defined by Dobzhansky (1935) as follows:

> A species is a group of individuals fully fertile inter se, but barred from interbreeding with other similar groups by its physiological properties (producing either incompatibility of parents or sterility of the hybrids, or both)

This definition was then expanded by Mayr (1940) who originally defined species as

> A group of populations which replace each other geographically or ecologically and of which the neighboring ones inter-grade or interbreed wherever they are in contact or which are potentially capable of doing so (with one of more of the populations) in those cases where contact is prevented by geographical or ecological barriers.

In other words, species are groups of individuals who interbreed but who are reproductively isolated from other groups. Mayr (1969) defined a species as both *a reproductive unit*, in which members seek each other to reproduce, *an ecological unit*, as individuals of a species share the same environment, and *a genetic unit*, whose members share the same set of genetic information. There are two main mechanisms by which reproductive isolation can be achieved: *pre-zygotic* and *post-zygotic*. Pre-zygotic isolation includes:

- *Ecological isolation*: when different populations occupy different geographical areas or different ecological niches.
- *Behavioral isolation*: when different populations display different behaviors that prevent them from interbreeding, such as different courtship rituals, mating calls, or chemical signals.
- *Temporal isolation*: when different populations produce gametes at different times. This is particularly common in plants that exhibit different flowering periods.
- *Mechanical isolation*: when females and males have reproductive organs that are compatible only among members of their own species. This type of reproductive isolation is particularly common in insects.

Post-zygotic isolation includes:

- *Hybrid viability*: when the hybrid dies prematurely
- *Hybrid infertility*: when the offspring that is produced by the two different species is infertile

There are a number of problems with the Biological Species Concept:

1. Mayr's biological concept definition can only apply to sexual organisms but it does not work for those organisms who do not reproduce sexually, such as protozoans.
2. The biological species concept can only be applied to the species that share the same space at the same time, making the definition inapplicable to species that live at different times (i.e., fossils) or in different geographic regions. This is because it is hard to test whether two populations that live at different times or in different areas can reproduce. In

p. 121 Mayr (1940) states that: "the application of a biological species definition is possible only in well-studied taxonomic groups, since it is based on a rather exact knowledge of geographical distribution and on the certainty of the absence of interbreeding with other similar species." To address this issue, Mayr (1970) took out the word "potentially" by the Biological Species Concept and defined species "as those groups of interbreeding natural populations that are reproductively isolated from other groups" (p. 12).

3. Finally, there is a plethora of cases in which interbreeding between different species results in fertile offspring. Some *genera* are renowned for including species that have a high ability to interbreed, such as the genera *Cervus*, *Lepus, Canis,* and *Macaca*. Hybridization appears to be particularly common in birds: Grant and Grant (1992) calculated that about 1 in 10 species of birds are known to have bred in nature with another species. Mayr (1970) tried to solve the problem of hybridization by revising his definition of "isolating mechanism" to "biological properties of individuals which prevent the interbreeding [fusion] of populations" (p. 56). In other words, these isolating mechanisms would not be able to guarantee the complete lack of interbreeding between different species, but it would prevent the complete fusion between them.

The Evolutionary Species Concept

The Evolutionary Species Concept tried to solve the nondimensional nature of the Biological Species concept by defining species as "a lineage (an ancestral-descendant sequence of populations) evolving separately from others and with its own evolutionary role and tendencies" (Simpson 1961, p. 153). The second part of the definition ("own evolutionary role and tendencies") is particularly important as it implies that there should be some sort of biological relevance when assigning a group of individuals the status of species, and it precludes considering species from any ephemeral offshoot of the species, such as small captive populations. The main criticism is that this concept is not an operational definition as it does not help to identify whether a specific class of individuals belongs to a specific species. Furthermore, from the definition of Evolutionary Species Concept, it is unclear which level of lineages we should consider the species level, as lineages exist at different levels. Wiley and Mayden (2000) solved this issue by identifying evolutionary species as those tokogenetic entities "composed by parts (individual organisms) linked by reproduction and manifested by tokogeny" (p. 74) where tokogeny is defined as the biological relationship between parents and offspring or, more generally, between ancestors and descendants.

The Genetic Species Concept

Baker and Bradley (2006) defined a genetic species as a "group of genetically compatible interbreeding natural populations that is genetically isolated from other such groups." While the core aspect of the Biological Species Concept is reproductive isolation, the key element at the basis of the Genetic Species Concept is *genetic* isolation, produced by an accumulation of genetic changes. The initial criticisms against this concept is that it would be hard to accurately estimate genetic distance, especially considering our lack of knowledge of an organism's genetic information. However, recent genetic advances have made it possible to assess genetic differences between organisms. For example, an examination of the variation in mitochondrial cytochrome-*b* gene sequence across several mammalian species suggests that genetic distance values lower than 2% indicate intraspecific variation (hence the organisms belong to the same species), values >11% represent different species, while values that range between 2% and 11% deserve further investigation in order to understand whether they should be considered the same or different species (Bradley and Baker 2001). The important difference between the Genetic and Biological Species Concepts is that while the former considers populations as distinct species even if there is gene flow and their hybridization produces fertile offspring, the Biological Species Concept would recognize these two populations as the same species (and different subspecies). There are numerous examples in nature of populations that might appear to belong to the same species, but genetic analyses reveal as different species, and Baker and Bradley (2006) estimate that there are more than 2000 unrecognized species.

The Ecological Species Concept

The Ecological Species Concept was introduced by Van Valen (1976), under the idea that differences in ecological niches, more than genes, are the primary drivers of evolution and that reproductive isolation plays a minor role in the formation of the species.

Van Valen (1976) defined species as “a lineage (or a closely related set of lineages) which occupies an adaptive zone minimally different from that of any other lineage in its range and which evolves separately from all lineages outside its range.” According to Van Valen (1976), an adaptive zone is considered the part of the environment that contains a specific set of resources along with certain levels of predation and parasitism, and can have boundaries that are either pre-existing or defined by the species that are living there. Under this concept, populations that live in separate areas can still be considered as belonging to the same species if they are under the same ecological pressures. Grant (1992) pointed out that the idea that ecological adaptations play an important role for the formation of species is not new and even the “fathers” of the Biological Species Concept acknowledged the importance of ecological factors. In the *Genetics and Origin of ~~the~~ Species* Dobzhansky (1951), for instance, highlighted how the phenotypic and genetic discontinuities between species are probably related to differences in their ecological niches, and that reproductive isolation manages to fix these phenotypic and genetic differences. The main criticism of the Ecological Species Concept, however, is that we cannot have a priori knowledge of what makes an ecological niche and, in fact, researchers often use ecological differences between species to characterize their ecological niches (Grant 1992). Furthermore, in many species, different morphs or different sexes can occupy different niches and so we cannot reliably use ecological differentiation as a diagnostic of a species.

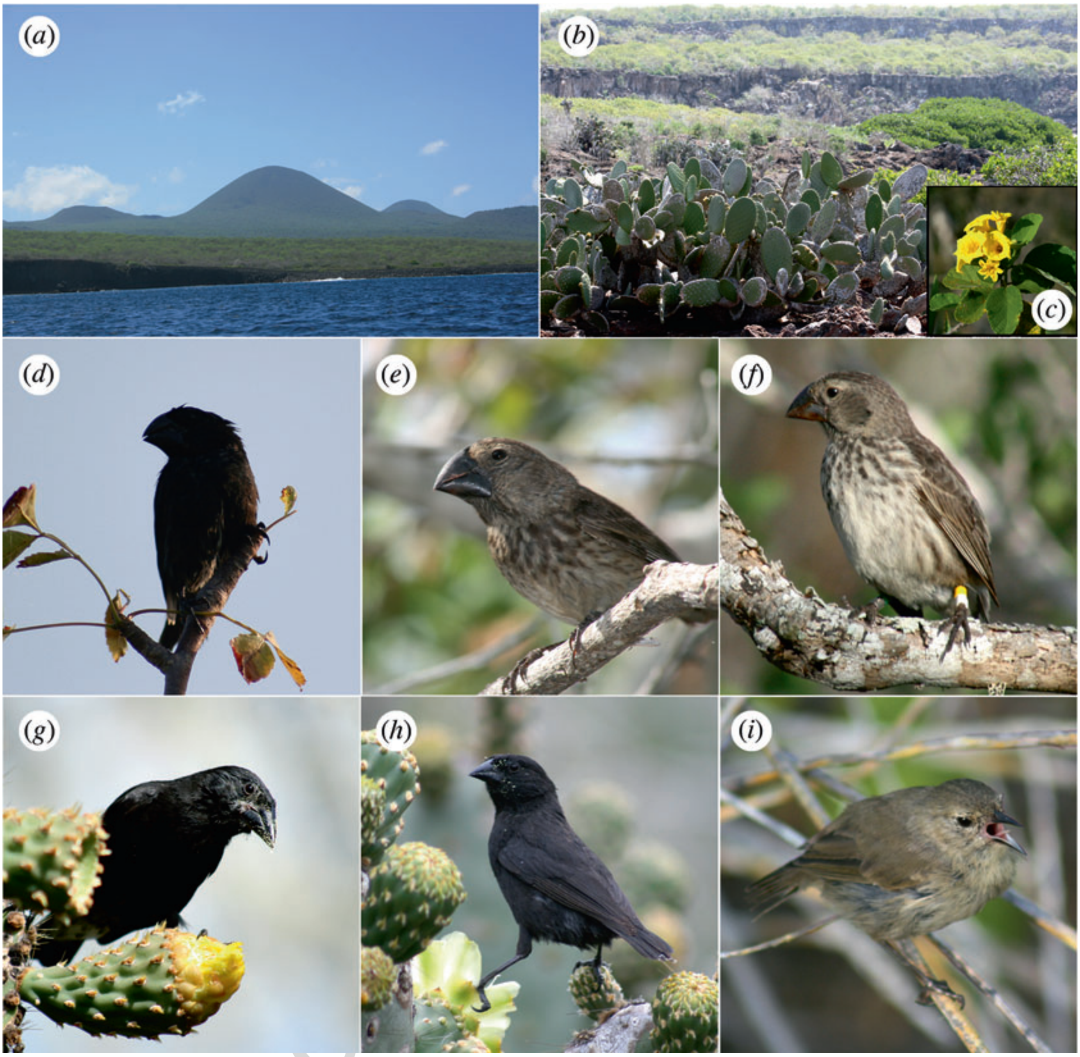
The Agamospecies Concept

Many of the abovementioned concepts do not apply to organisms who do not reproduce sexually and who lack genetic exchange. This is because the key aspects of the Biological and Genetic Species Concepts are reproductive and genetic isolation, respectively, and Wiley and Mayden (2000) had to drop the word “population” from their definition of Evolutionary Species Concept in order to be able to include asexual organisms. The first definition of agamospecies concept was given by Turesson (1929), who defined species as “an apomict-population the constituents of which, for morphological, cytological or other reasons, are to be considered as having a common origin” (quoted in Zachos 2016, p. 98). This definition can be considered as a “Morphological Species Concept” applied to asexual organisms. Another definition was provided by Cain (1954) who defined agamospecies as “those forms to which [the biological species concept] cannot apply because they have no true sexual reproduction.” The problem with this definition is that it defines the “species” as *not being* something else. A better definition, which was originally used to define viruses, was given by Eigen (1993), who coined the term *quasispecies*, defined as “a self-sustaining population of sequences that reproduce themselves imperfectly but well enough to retain a collective identity over time.” The concept of quasispecies hinges on the observation that in a cluster of genotypes of viruses there is an optimal (or wild) type with specific mutations that make it particularly adapted to a specific environment, from which other viruses reproduce. This definition is very similar to the *Ecological Species Concept* and can be applied more generally to asexual organisms, which is why Wilkins (2009) considers *agamospecies* and *quasispecies* synonyms.

Modes of Speciation

Speciation (or *cladogenesis*) is the biological process by which species originates from the ultimately irreversible splitting of one population lineage in two or more lineages. Importantly, this evolutionary process is different from the *anagenesis* that occurs when a population lineage gradually changes over time until it reaches the point when it becomes sufficiently distinct from its ancestor. There are three main modes of speciation: *allopatric*, *sympatric*, and *parapatric*.

- *Allopatric (or geographic) speciation* is the most common form of speciation and occurs when different populations from the same species become isolated and no genetic exchange occurs between them. These isolated populations undergo genetic changes over time due to mutations, migration, or other evolutionary forces, to the extent that they become reproductively isolated from each other. There are two main forms of allopatric speciation: *dichopatric* and *peripatric*. Dichopatric speciation arises when populations inhabiting a specific geographic area become isolated due to the development of a new geographic barrier that splits the original population into two or more groups. Peripatric speciation occurs when a single gravid female or few individuals of a species colonize a new geographic area. This, in turn, results in *genetic drift* and *bottleneck effects* that lead to genetic changes and reproductive isolation from the original species. Classic examples of allopatric speciation are Darwin's Galapagos finches: these are 15 species of birds inhabiting different islands on the Galapagos archipelagos, located in the Pacific Ocean off South America. Over millions of years, these bird species have evolved different types of beaks of different size and shape that are particularly adapted to the type of food they eat (Abzhanov 2010). For example, ground finches, like *Geospiza magnirostris*, *G. fortis*, and *G. fuliginosa,* have stout beaks for eating seeds, while cactus finches, such as *G. conirostris*, have longer more pointed beaks to feed on nectar or getting seeds from cacti (Fig. 1).
- *Sympatric speciation* occurs when a new species originates in the same geographic area of the parental population. It is less common than allopatric speciation and can occur, for instance, when part of the population starts using a new niche, and is more likely to occur in herbivorous insects that display a particularly specialized relationship with their host plants. A textbook example of sympatric speciation is the apple maggot *Rhagoletis pomonella*: apple maggots used to lay their eggs exclusively in hawthorns, which are native to America. However, 200 years ago, they started using also domestic apples, which were introduced to America by immigrants. Since males generally look for mates on the type of fruit they grew up in and females lay their eggs on the type of fruit they grew up in, hawthorn flies generally mate with hawthorn flies and apple flies mate with apple flies preventing gene flow between the two types of flies and providing the first step for sympatric speciation.
- *Parapatric speciation* occurs when individuals from a continuous population tend to mate with geographic neighbors more often than with individuals belonging to other areas of the population's range due to differences in the same environment. These local populations are called *demes*. Different demes of a population are not isolated from each other, as individuals can move from a deme to the other but given that individuals tend to mate only with members of their own demes, they might be subject to specific selective pressures that can lead them to become a whole new species. A species who might be undergoing parapatric speciation is *Anthoxanthum odoratum*. This plant species grows in mining zones, whose soil is contaminated with high levels of heavy metals, and members of this species have developed a high tolerance for heavy metal. Although these tolerant individuals live close to the same species of plants that do not grow in contaminated ground, tolerant and nontolerant plants have ~~evolved~~ ~~during~~ different flowering times. This temporal isolation indicates that tolerant individuals would breed only with tolerant individuals and nontolerant individuals would reproduce only with nontolerant individuals, providing the first step for (parapatric) speciation.



Species, Fig. 1 (**a**) Galápagos Islands, such as Isla Floreana, are volcanic islands visited by Charles Darwin in 1835; (**b**) bushes of the prickly pear cactuses (*Opuntia helleri*) on Isla Genovesa (Tower Island); (**c**) flowers of the yellow geiger (*Cordia lutea*); (**d**) male of the large ground finch (*Geospiza magnirostris*) singing during the rainy season; (**e**) female of the large ground finch (*G. magnirostris*) on Isla Genovesa; (**f**) female of the medium ground finch (*G. fortis*) on Isla Santa Cruz; (**g**) male large cactus finch (*G. conirostris*); (**h**) male sharp-beaked finch (*G. difficilis*) feeding on cactus flowers on Isla Genovesa; (**i**) male warbler finch (*Certhidea fusca*) singing next to its nest (Abzhanov 2010; © 2010 The Royal Society)

Discovery of New Species

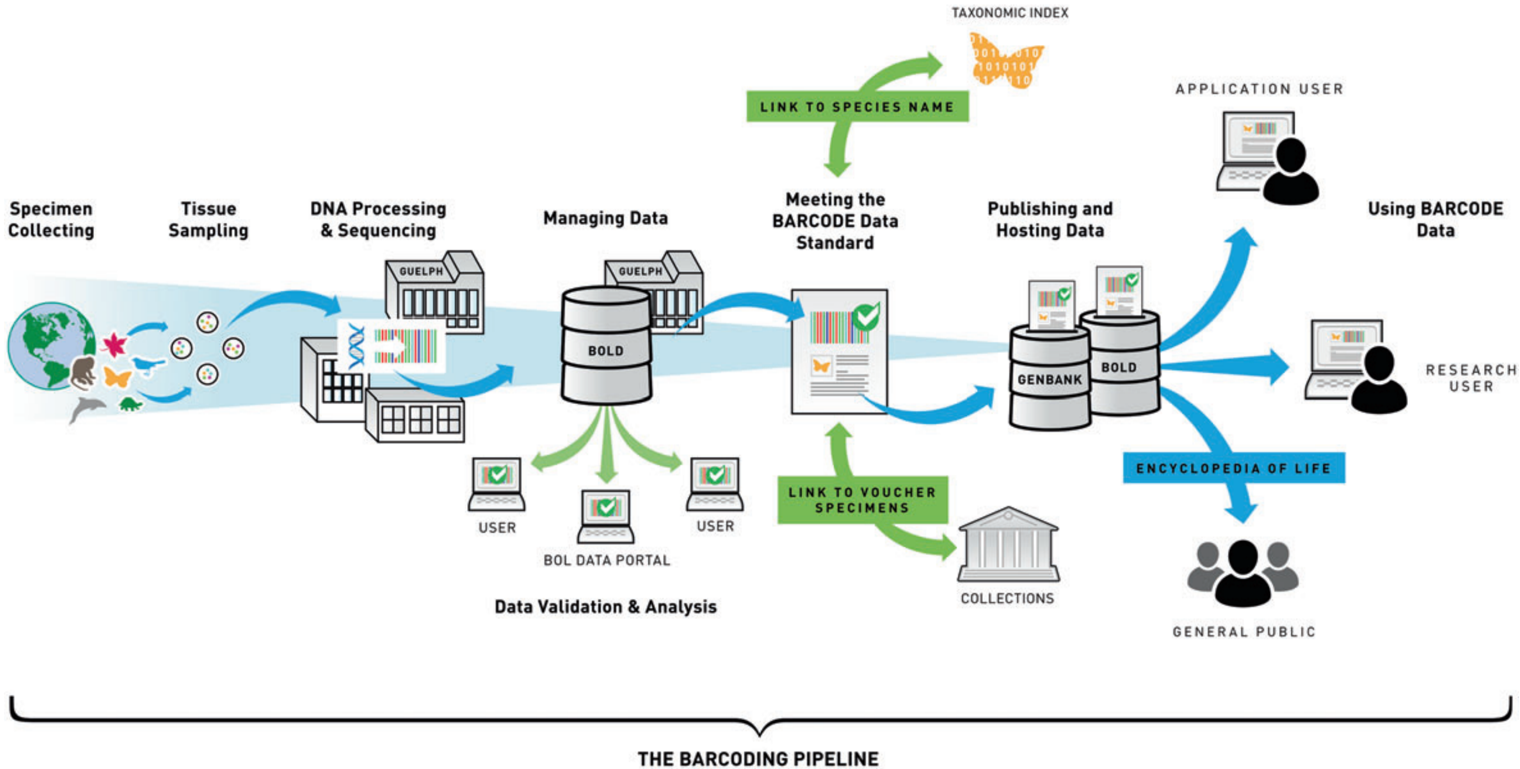
It is generally estimated that 15,000–18,000 new species are discovered every year, of which half are insects. This list includes also correction in the taxonomy or species that are moved from a family to another. Since 2008, the SUNY College of Environmental Science and Forestry releases on May 23rd (which corresponds to Carl Linnaeus' birthday) the list of the top 10 new species discovered the previous year (http://www.esf.edu/top10/).

There are different ways in which a new species can be discovered:

- *Expedition in remote areas*. There are many areas on earth that have not been explored yet, and can be home to species that have never been described. In December 2005, for instance, an international team of 11 scientists from Australia, the United States, and Indonesia travelled to the, until then, unexplored areas of Foja Mountains and discovered numerous new species (http://news.bbc.co.uk/2/hi/science/nature/4688000.stm). These included: 40 new species of mammals, many new plant species, including five new species of palms, four new species of butterflies, twenty new species of frogs, and numerous new bird species. In some cases, researchers identify new species on the basis of the vocalizations they produce. Recently, Svensson et al. (2017) described a new species of dwarf bush-baby inhabiting Angola's Kumbira Forest which produces a different type of call from the other 18 known bush-baby species.
- *Examination of museum specimens*. New species can also be discovered in museum collections, where they were collected 50 or 100 years ago but their taxonomic classification was overlooked or specimens were often mislabeled. Recently, for example, Helgen et al. (2013) have described a new species of carnivorous mammal, the olinguito (*Bassaricyon neblina*), that lives in the forests of Andes, Ecuador, and Colombia. Helgen and colleagues analyzed the fur and bones of the specimens that were stored in several museum collections and, through DNA testing, found out that this was a new species. Several zoos in the USA probably exhibited an olinguito between 1967 and 1976, but keepers mistook it for its close relative, olinga, and could not understand why the olinguito could not breed. The olinguito eventually died without being properly identified.
- *Genetic analyses*. The advancement of DNA techniques has offered researchers the opportunity to identify new species even when they are morphologically similar to another species and live in the same area. These species are also called cryptic species. DNA barcoding has become the most common technique to detect new species (Hebert et al. 2003). Through this technique, DNA is extracted from specimens that can be collected from the field, from museums, zoos, or other sources. A region of this DNA is then isolated. This region is commonly a 648 base-pair region in the mitochondrial cytochrome c oxidase 1 gene ("CO1"), located in the mitochondrial DNA, which has a mutation rate that is slow enough to be identical within the same species but fast enough to be different between species. The use of this DNA region to identify new species has been shown to be effective for many animal groups, such as birds, fish, butterflies, but not for plants, for which two DNA regions in the chloroplast are used instead. Once this region is isolated, its copies are replicated and sequenced. The sequence is then compared to the sequences of known species contained in the Barcode of Life Data Systems (BOLD) to understand whether the species is already known or is a new species (Fig. 2). Recently, barcode analysis has be used to identify a new gibbon species *Hoolock tianxing* (common name: skywalker hoolock gibbon), which is distributed on the east of Irrawaddy-Nmai Hka Rivers in China and had been previously considered to be the same species as *H. leuconedys* (Fan et al. 2017). Although researchers had suspected that the two species were different, due to differences in morphology and vocalization patterns, only genetic analyses confirmed that the two were actually distinct species.

Conclusion: The Importance of Taxonomy for Conservation

Taxonomy provides an important tool for the conservation of the species. The International Union for the Conservation of Nature (IUCN) is an organization that monitors the conservation status of the organisms, and in its Red List of Threatened Species, it classifies the species extinction risk into (1) Least Concern, (2) Near-Threatened,



Species, Fig. 2 Basic workflow for generating DNA barcodes (Image courtesy: Kris Jett; © International Barcode of Life)

(3) Threatened (divided into Vulnerable, Endangered, and Critically Endangered), and (4) Extinct. By March 2014, among the 71,576 terrestrial and freshwater species assessed, 860 were classified as extinct or extinct in the wild, 21,286 were categorized as threatened, and 4286 were deemed critically endangered. Of the 6041 marine species for which we have enough data to assess their extinction risk, 16% were classified as threatened and 9% as near-threatened. Although the extinction of a species is a natural phenomenon that occurs at a rate of one to five species per year, the most recent estimates suggest that the current rate of extinction is 1000–10000 times higher and is largely human-driven (Pimm et al. 2014). Out of an estimated 8.7 (± 1.3) million of eukaryotic species, only about 1.2 million species have been catalogued, leaving a total of 86% species on Earth and 91% of species in the ocean still undiscovered (Mora et al. 2011). With the high extinction rate that species face, many species disappear before they are discovered. In this context, identifying new species is key for their protection before they become extinct. Assigning the rank of "species" to a population is, thus, important both because it gives them legal protection and because it increases the awareness that the population is indeed unique (Zachos 2016).

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