Species, Concepts of

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Abstract

What are species? We take a historical approach to demonstrate how our understanding of the nature of species has changed since Darwin's time until the current postgenomic era. If species are fundamental units of nature (like cells, or organisms, say), as some scientists believe, then their underlying basis has yet to be revealed. Instead, it seems more likely that the species rank in taxonomy is a man-made distinction; a heuristic cut-off that can perhaps be agreed upon by biologists to enable communication on issues of biodiversity, human health, agriculture, and conservation.

Keywords

Conservation, Conservation legislation, Darwin, DNA barcoding, Gene flow, Genotypic cluster, History of science, Multispecies Coalescent, Philosophy of science, Phylogeny, Species concept, Species delimitation Subspecies, Systematics, Taxonomic inflation, Taxonomy

Glossary

Cladistic A classification based entirely on monophyletic taxonomic groupings within a phylogeny; taxonomic units that are paraphyletic or polyphyletic are rejected. A cladist is one who practices cladistics, usually in the sense of using parsimony to adjudicate between data from multiple characters in the construction of a cladogram, which is an estimate of the true phylogeny.

Coalescent The coalescent is a mathematical branch of population genetics, which investigates the merging of gene sequences traced backward in time within gene genealogies.

Cohesion The sum total of forces or systems that hold a species together. The term is used especially in the interbreeding and cohesion species concepts. Cohesion mechanisms include isolating mechanisms in sexual species as well as stabilizing ecological selection, which may cause cohesion even within asexual lineages.

Disruptive selection Selection acting to preserve extreme phenotypes in a population. Speciation usually involves disruptive selection, because intermediates (hybrids between incipient species) are disfavored (*also see* Stabilizing selection).

DNA barcoding A method of delimiting species via clustering of short stretches of DNA sequence data called "barcodes," in animals usually from mitochondrial DNA.

Gene flow Movement of genes between populations, usually via immigration and mating of whole genotypes, but sometimes single genes may undergo horizontal gene transfer via transfection by microorganisms.

Gene pool The sum total of the genetic variation within a reproductively isolated species population; this term is mostly used by supporters of the interbreeding species concept.

Genomic cluster A synonym for genotypic cluster.

Genotypic cluster In a local area, a single genotypic cluster (or species) is recognized if there is a single group of individuals recognizable on the basis of multiple, unlinked inherited characters or genetic markers. A pair of such genotypic clusters (or species) is recognizable if the frequency distribution of genotypes is bimodal. Within each genotypic cluster in a local region, allele frequencies will conform to Hardy–Weinberg equilibrium, and the different unlinked loci will be in approximate linkage equilibrium. The presence of more than one species or genotypic cluster can then be inferred if the distribution of genotypes is bimodal or multimodal, and strong heterozygote deficits and linkage disequilibria are evident between the clusters.

Isolating mechanisms The sum total of all types of factors that prevent gene flow between species, including prezygotic mechanisms (mate choice, gamete recognition), and postzygotic mechanisms (hybrid sterility and inviability). Modern authors deny that these "mechanisms" have necessarily evolved to preserve the species' integrity as originally assumed, though this may sometimes be the case in reinforcement of prezygotic isolation. Isolating mechanisms are a subset of the factors that cause cohesion of species under the interbreeding and cohesion species concepts.

Monophyletic A grouping that contains all the descendants of a particular node in a phylogeny. Monophyly is the state of such groupings. Compare paraphyletic and polyphyletic. Butterflies (Rhopalocera) and birds (Aves) are the examples of two groups thought to be monophyletic.

Paraphyletic A grouping that contains some, but not all, of the descendants of a particular node in a phylogeny. Paraphyly is the state of such groupings. Compare monophyletic and polyphyletic. Moths (Lepidoptera, excluding butterflies) and reptiles (amniotes, excluding birds and mammals) are examples of two groups thought to be paraphyletic.

Phenetic A classification or grouping based purely on overall similarity. Pheneticists use matrices of overall similarity rather than parsimony to construct a “phenogram” as an estimate of the phylogeny. Examples of phenetic methods of estimation include unweighted pair group analysis (UPGMA) and neighbor joining. Cladists reject phenetic classifications on the grounds that they may result in paraphyletic or polyphyletic groupings.

Phylogenetic Pertaining to the true (i.e., evolutionary) pattern of relationship, usually expressed in the form of a binary branching tree, or phylogeny. If hybridization produces new lineages, as is common in many plants and some animals, the phylogeny is said to be reticulate. Phylogenies may be estimated using phenetics, parsimony (cladistics), or methods based on statistical likelihood.

Polyphyletic Groupings that contain taxa with more than one ancestor. "Polyphyly" is the state of such groupings. Compare paraphyletic and monophyletic. "Winged vertebrates" (including birds and bats) are examples of a polyphyletic group.

Real, reality Two tricky words found frequently in the species concept debate. Reality is typically used to support one's own species concept, as in: "The conclusions set forth above … lead to a belief in the reality of species" (Poulton, 1904); similar examples can be found in the writings of Dobzhansky, Mayr, and many phylogenetic systematists. The term reality in this sense is similar to an Aristotelian essence, a hypothetical pure, albeit obscure, truth that underlies the messy actuality; unfortunately, in everyday language real also means actual (curiously, a reality in the first sense may be unreal under the second!). By rejecting the reality of species, one can therefore send very mixed messages: some readers will understand the author to be a nominalist who merely believes useful terms require no theoretical underpinning; others assume the author is nonsensically using some definition that does not apply to the actual organisms. Here, when we discuss the reality underlying a species concept, we mean it in the first sense, a hypothesis. Many authors of species concepts and some philosophers of science argue that that definitions must be underpinned by a theoretical justification or reality. Other philosophers such as Wittgenstein and Popper agree that terms need no such definition to be useful.

Sibling species A pair of closely related, morphologically similar species (usually sister species).

Speciation The evolutionary process of the origin of a new species.

Specific mate recognition systems (SMRSs) Fertilization and mate recognition systems in the recognition concept of species, the factors leading to premating compatibility within a species. Also see cohesion, which is similar to SMRS, but includes postmating compatibility as well.

Stabilizing selection Selection which favors intermediate phenotypes.

Taxonomic inflation The process whereby the numbers of species in the checklist of a group increases due to a change in species concept rather than due to new discoveries of previously unknown taxa.

Objectives

- To document the chief characteristics that species have, and which lower and higher ranks in the Linnean hierarchy of classification (e.g. populations and genera) do not.
- To survey the main concepts of species proposed since Darwin.
- To question a prevailing belief in the fundamental nature of species as a unit in biology.
- To argue for a pragmatic approach for species delimitation to better understand biodiversity, and the many uses of taxonomy.

Introduction: What are Species Concepts for?

Individual organisms can usually be recognized, but the larger units we use to describe the diversity of life, such as populations, subspecies, species, or genera are not so readily discerned.

Taxonomists further group species into genera, families, orders, and kingdoms, whereas ecologists group species into higher structures such as communities and ecosystems. The justification for these group terms is utility, rather than intrinsic naturalness, but as far as possible we attempt to delimit groups of organisms along natural fault lines, so that approximately the same groupings can be recovered by independent observers. However, there will be a virtually infinite number of different, albeit nested, ways of classifying the same organisms, given that life has evolved more or less hierarchically.

Darwin (1859) felt that species were similar in kind to groupings at lower and higher taxonomic levels; in contrast, many recent authors suggest that species are more objectively identifiable, and thus more real than, say, populations or genera. Today, much of ecology, evolution, and biodiversity appears to assume that the species is the fundamental taxon. It has been argued that these fields could be undermined if, say, genera, or subspecies, had the same logical status as species.

Species concepts originate in taxonomy, where the species is “the basic rank of classification” according to the International Commission of Zoological Nomenclature. The main use of species in taxonomy and derivative sciences is to order and retrieve information on individual specimens in collections or biodiversity databases. In evolutionary biology, it may also be helpful to delimit a particular kind of divergent evolution, “speciation,” which produces a result qualitatively different from within-species evolution, although it may of course involve the same processes. In ecology, the species is a group of individuals within which variation can often be ignored for the purposes of studying local populations or communities, so that species can compete, for example, whereas subspecies or genera are not usually considered in this light. For measuring biodiversity, in conservation studies, and in environmental legislation, species are potentially important units, which we would like to be able to count both regionally and globally.

It would be helpful if a single definition of species could satisfy all these uses, but a generally accepted definition has yet to be found, and indeed is believed by some to be an impossibility. Yet a unitary definition should be possible if species are more real, objectively definable and fundamental than, say, genera or subspecies, as many people apparently believe. For example, "the species category is ... one of the fundamental categories of biological existence. Other such categories are the cell and the organism" (de Queiroz, 1999). Conversely, even if species have no greater objectivity than other taxa, unitary nominalistic guidelines for delimiting species might be adopted, perhaps after much diplomacy via international agreement among biologists. After all, if we can adopt meters and kilograms, perhaps we can agree on units of biodiversity. In either case, knowledge of the full gamut of today's competing solutions to the species concept problem will probably be necessary for a universal species definition to be found. This article reviews major proposals currently on the table, and their usefulness in ecology, evolution, and conservation.

Statement of Bias

We are of Darwin's opinion that species, like genera and populations, do not have clear boundaries. In evolution and in ecological and biodiversity surveys over large areas, their reality has, in our view, been grossly overestimated (Mallet, 2008). In contrast, it is clear to any naturalist that species are usually somewhat objectively definable in local communities. It is our belief that confusion over species concepts has been caused by scientists not only attempting to extend this demonstrable local objectivity of the species over space and evolutionary time, but also arguing fruitlessly among themselves about which is the most important apparent reality (or concept) that underlies this spatiotemporal extension of local objectivity. To us, agreement on a practical, unified species-level taxonomy is possible, but will be forthcoming only if we accept that different species may often lack a unitary biological reality over their geographic ranges and across geological time. Under this view, it is more important to develop a somewhat consistent and useful method of delimitation for actual taxa we would like to recognize as species than it is to find a single "species concept" that underlies all such taxa.

Just as Marxist theory may be wrong, yet remains a useful empirical framework for studying political history, we hope our own views can provide, even for those who believe in a crisp natural boundary of species, a useful framework on which the history of proposals for species concepts can be compared. A variety of alternative outlooks can be found by Mayr (1970, 1982), Cracraft (1989), Claridge *et al*. (1997), Howard and Berlocher (1998), Hey (2001), and Coyne and Orr (2004).

Darwinian Species Criteria

Darwin's Morphological Species Criterion

Early thinkers assumed that each species had an Aristotelian form or essence, and that variation within a species was due to imperfections in the actualization of this form. Each individual species was defined by its essence, which itself was unvarying and inherently different from all other species essences. Before 1859, it was generally agreed that this essence was descent: all individuals within a species were related by descent, whereas no individuals were descended from individuals in another species. This mode of thought of course precluded transformation of one species into another and was associated with belief that each form was separately created by God.

Darwin's extensive travels and knowledge of taxonomy led to a realization that the distinction between intraspecific and interspecific variation was false. Individuals could be descended from members of other species: “descent with modification.” His abandonment of essentialist philosophy and its species concept went hand in hand with his appreciation that variation itself was among the most important characteristics of living organisms, because it was this variation that allowed species to evolve and diverge. To Darwin, species could be distinguished from divergent varieties if they showed few intermediates: “hereafter we shall be compelled to acknowledge that the only distinction between species and well-marked varieties is, that the latter are known, or believed, to be connected at the present day by intermediate gradations, whereas species were formerly thus connected” (Darwin, 1859, p. 485).

Darwin guessed (correctly) that essentialist species would be hard to give up: “… we shall have to treat species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience. This may not be a cheering prospect, but we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species” (Darwin, 1859, p. 485). He argued that species were little more than varieties that acquired their claim to a greater reality only when intermediates died out leaving a morphological gap: "… I believe that species come to be tolerably well-defined objects, and do not at any one period present an inextricable chaos of varying and intermediate links" (Darwin, 1859, p. 177). This morphological gap criterion, which seems to have been accepted by many early evolutionists (e.g., Wallace, 1865; Robson, 1928), has been called a "morphological species concept" because Darwin used the gaps in morphology to delimit species; however, it is easy to extend his species criterion to ecology, behavior, or genetics (*see* Ecological Species Concept and Genotypic Cluster Criterion and Assignment Tests).

Polytypic Species

A major revolution in zoological taxonomy occurred around 1900. As the great museum collections became more complete, it became obvious that many apparently distinct species found in different areas intergraded where they overlapped. These replacement species began to be regarded as subspecies within a polytypic species, an idea suggested for geographical varieties by early systematists and Darwinists such as Wallace (1865). The taxonomic clarification that followed, which allowed identifiable geographic varieties to be named validly below the species level as subspecies, was conceptually more or less complete by the 1920s and 1930s. At the same time, other infraspecific animal taxa such as local varieties or forms were deemed un-nameable in the Linnaean taxonomy. These changes are now incorporated into the International Code of Zoological Nomenclature. Similar ideas were promoted in botany by G.L. Stebbins (see Mayr, 1982), although in the International Botanical Code local varieties and polymorphic forms remain valid and nameable taxa.

The Rephilosophization of Species, the “Interbreeding” Concept

In January 1904, Poulton read his famous presidential address – “What is a species?” – to the Entomological Society in London (see historical analysis by Mallet, 2004). Following up on ideas raised (but immediately dismissed) by Wallace (1865), Poulton proposed “syngamy” (i.e., interbreeding) as the true meaning of species. Poulton and Wallace were both particularly knowledgeable about swallowtail butterflies (Papilionidae). In swallowtails, there exist strong sexual dimorphisms: the female color pattern often mimics unrelated unpalatable butterflies whereas the male is nonmimetic. The females themselves are sometimes polymorphic (e.g., in *Papilio memnon* and *Papilio dardanus*), each female form mimicking a different distasteful model. Under a crude morphological criterion, each divergent form could be designated as a different species, whereas mating observations in the wild showed that the forms were part of the same interbreeding group. A related idea was promoted by the botanist Lotsy, who termed the interbreeding species a “syngameon” (Lotsy, 1917). In the 1930s, Dobzhansky studied morphologically indistinguishable sibling species of *Drosophila* fruit flies and concluded that Lotsy's approach had some value (Dobzhansky, 1937). A member of a species will rarely, if ever, interbreed with a member of a sibling species; each chooses mates within its own species. Dobzhansky proposed his own interbreeding species concept, later popularized by Mayr as the “biological species concept,” so named because interbreeding within species, coupled with reproductive isolation between species, was considered the single true biological meaning or reality of the term species (reviewed by Mayr, 1970, 1982).

A short definition of the biological species concept is as follows: “species are groups of interbreeding natural populations that are reproductively isolated from other such groups” (Mayr, 1970). The biological concept of species was not so much new as a clarification of two distinct threads: (1) a local component, the Poulton/Dobzhansky interbreeding concept, and (2) a global component, which extended the interbreeding concept to cover geographically separated populations of actually or potentially interbreeding subspecies, as in the preexisting idea of polytypic species.

This extended interbreeding concept was, until about 40 years ago, almost universally adopted by evolutionists. The species concept problem appeared to have been solved; species were interbreeding communities, each of which formed a “gene pool” reproductively incompatible with other such communities. The new concept answered both perceived problems of Darwin's morphological approach: (1) That mutants and polymorphic variants within populations might be considered as separate species. (2) That sibling species might be misclassified as members of the same species. The new approach was promoted in a long series of books and articles by Dobzhansky, Mayr, and their followers. Mayr was highly influential by justifying the taxonomic application of the polytypic species criteria in terms of the new concept of “gene flow.” The new species concept was considered necessary for understanding speciation using population genetics. Darwin was hereafter deemed to have failed to solve, or even address the origin of species in his 1859 book, because he supposedly had not appreciated the fundamental importance of interbreeding (Mayr, 1970, p. 10; Mallet, 2010a).

To take this view, it was necessary to see species in a new post-Darwinian light. Instead of species being defined simply, using man-made criteria based on demonstrable characters such as gaps in morphology, species became defined by processes important in their own maintenance, that is by means of their biological function (Mayr, 1982). Significantly, the philosophical term “concept” came into vogue along with these new ideas about species, and the term “species problem,” which hitherto had referred to the problem of how species arose (Robson, 1928), became instead the problem of defining what species were. The important features of species defined by the “biological species concept” were that they were protected from gene flow by physiological isolating mechanisms (Dobzhansky, 1937) or “reproductive isolating mechanisms,” including prezygotic mechanisms (ecological, mate choice, and fertilization incompatibilities) and postzygotic mechanisms (hybrid inviability and sterility caused by genomic incompatibilities). Curiously, by going beyond simple, Darwinian character-based identification of species, the “biological concept of species” became less universally applicable in biology; for example, Dobzhansky (1937) simply concluded that asexuals (between which no interbreeding is possible) could not have species.

Poulton, Mayr, and Dobzhansky emphasized that their new concept was based on the reality that underlay species, rather than being merely a criterion useful in taxonomy. In this new philosophical approach, taxonomic criteria became separated from conceptual issues, and practical delimitation took on a secondary role. The same division between concept and criteria is still evident in most discussions of species concepts today, for example in the "general lineage concept" (de Queiroz, 1999; *see* Evolutionary and Lineage Concepts). The concept was seen to be true from first principles, and became untestable: violations of the criterion of reproductive isolation, such as hybridization, intermediates, and inapplicability to many plants and asexuals caused problems in classification, but did not disprove or even challenge the underlying truth of the concept itself. These imperfect actualizations of species' true reality were expected in nature. Mayr claimed that the biological concept would do away with "typology" (his term for species definitions based on a fixed, unvarying type or Aristotelian essence), but in many ways it can be seen that the biological concept reverts to a new kind of essentialism, where evolutionary maintenance via interbreeding is the underlying reality, or essence of species.

Alternative Species Concepts

It is interesting that exactly this kind of search for the essence of species had already been criticized by Darwin (1859), as we have seen (*see* What are Species Concepts for?). In his chapter "Hybridism," Darwin specifically argued against using postzygotic isolation (hybrid sterility and zygote inviability) as cut-and-dried characteristics of species; instead he argued that hybrid sterility was an incidental by-product of evolution, and variable in its appearance between species. In this discussion, Darwin made no mention of prezygotic isolation, another component of the reproductive isolation that characterizes species under the biological concept. However, we can infer that Darwin, the discoverer of sexual as well as of natural selection, would almost certainly have argued that mate choice, along with hybrid sterility and inviability, are all found within as well as between species, although to a lesser extent. Oddly, Mayr (1982, p. 269) claimed that Darwin treated species "purely typologically (i.e., as an essentialist) as characterized by the degree of difference,” and also that Darwin “had strong, even though perhaps unconscious, motivation … to demonstrate that species lack the constancy and distinctiveness claimed for them by the creationists.” Whether or not it is reasonable to criticize Darwin in such a contradictory way can be debated, but Mayr's proposition that interbreeding was the true essence or reality of species immediately laid itself open to debate. Although the interbreeding concept had a long run (and still does), proposals for different kinds of biological reality of species were not long in coming. By proposing a single reality for species, Poulton, Dobzhansky, and Mayr reopened Pandora's box of alternative essences deemed more important by other biologists.

Ecological Species Concept

Asexual organisms such as the bdelloid rotifers can clearly be clustered into groups recognizable as taxonomic species, very likely because competition has led to the extinction of intermediates (Hutchinson, 1968; Fontaneto *et al*., 2007). However, distinct sexual forms such as oaks (*Quercus*), between which there are high rates of hybridization, can remain recognizably distinct even where they co-occur. This suggested to van Valen (1976) that the true meaning of species was occupancy of an ecological niche or adaptive zone rather than interbreeding, yielding an ecological species concept. It became clear to Mayr by 1970 also (see Mayr, 1982) that gene flow could not unite every population in a polytypic, biological species' range, and that stabilization of phenotype might also be effected by ecologically mediated stabilizing selection (*see also* Recognition Concept of Species *and* Evolutionary and Lineage Concepts) rather than purely because of gene flow.

Recognition Concept of Species

An important attack on the biological species concept came from Hugh Paterson in the early 1980s. His claims were two-fold: First, that the Dobzhansky/Mayr term “isolating mechanisms” implied that reproductive isolation was adaptive, which Paterson felt was unlikely. Second, that the true reality underlying species was prezygotic compatibility, consisting of mating signals and fertilization signals. According to Paterson (1985), this compatibility is strongly conserved by stabilizing selection, whereas isolating mechanisms such as hybrid sterility or inviability are nonadaptive and can be argued to be a result rather than a cause of species separateness. To Paterson, the true reality of species must be adaptive, and the idea that species are held together by beneficial isolating mechanisms was a fallacious argument that relied on adaptation at the whole species level (Mallet, 2010a, b). Paterson termed his idea of species the “recognition concept” versus Mayr's “isolation concept,” and its important characteristics specific mate recognition systems (SMRSs) instead of isolating mechanisms. Species were defined as “that most inclusive population of individual biparental organisms, which share a common fertilization system” (Paterson, 1985).

The idea is generally recognized as a useful critique and has gained strong currency in some circles. However, it appears also that SMRSs are more or less the inverse of prezygotic isolating mechanisms, and that the recognition concept therefore differs practically from the biological species concept mainly by focusing on the subset of traits acting before fertilization. In addition, the interbreeding concept had always stressed a common gene pool and compatibility within a species, as well as isolation between species.

Species Concepts Based on History

Monophyly

The rise of cladistic methods revolutionized systematics by proposing that all classification should be based on the idea of "monophyly." Cladistics formalized the principle that paraphyletic and polyphyletic taxa were unnatural groupings, which should not be used in taxonomy. It was natural to attempt to apply this idea throughout systematics, all the way down to the species level, leading to a monophyly criterion of species (Hennig, 1966), a type of phylogenetic species concept (*see* Diagnostic Species Concept). Species were seen as forming when a single interbreeding population became split into two branches or lineages that did not exchange genetic material. In a somewhat different formulation, the cladistic species concept, species are branch segments in the phylogeny, with every branching event leading to a new pair of species (Ridley, 1989). Otherwise, if only one of the two branches were recognized as new, the other branch would become paraphyletic.

Perhaps the main criticism of this idea is that it could, if applied in taxonomy, cause great nomenclatural instability. Monophyly exhibits fractal self-similarity and can exist at very high or very low levels of the phylogeny, so the precise level at which species taxa exist becomes unclear. Suppose that a new monophyletic form is discovered overlapping with, but remaining distinct from, a closely related local form in the terminal branches of an existing species.

Recognition of this taxon as a species would leave the remaining subspecies branches within the original species paraphyletic. Many other branch segments might then need to be recognized at the species level, even if they interbreed and have reticulate, intermingling relationships. Many phylogenetic systematists therefore adopt a different phylogenetic concept, the Diagnostic Species Concept (below), which can allow paraphyly at the species level.

Diagnostic Species Concept

The motivation for the diagnostic concept, usually called the “phylogenetic species concept” by its adherents, was again to incorporate phylogenetic thinking (Hennig, 1966) into species-level taxonomy. There are many cases of hybridization between taxa on very different branches of species-level phylogenies, which suggests that interbreeding and phylogenetic realities conflict. Cracraft (1989) also noted that many bird taxa, normally thought of as subspecies, were far more recognizable and stable nomenclaturally than the polytypic species to which they supposedly belonged (*see* Genotypic Cluster Criterion and Assignment Tests). Cracraft therefore argued that the polytypic/interbreeding species concept should be rejected, and, in its place, we should use a diagnostic criterion in the form of fixed differences at one or more inherited characters. "A phylogenetic species is an irreducible (basal) cluster of organisms, diagnosably distinct from other such clusters, and within which there is a parental pattern of ancestry and descent." (Cracraft, 1989). According to Cracraft, species defined in this way are the proper basal, real taxa suitable for phylogenetic analysis and evolutionary studies.

Of course, if diagnostic criteria are applied strictly, rather small groups of individuals, or even single mutant specimens, might be defined as separate species, leading to potentially unbridled taxonomic inflation. Cracraft recognized this and argued that such trivial diagnosable groups would have no parental pattern of ancestry and descent, that is, they are not proper populations. However, this qualification appears similar to an interbreeding criterion of species, whereas the whole approach of using diagnostic characters was an attempt to get away from interbreeding.

Most evolutionary biologists balk at the idea of speciation being merely the acquisition of a new geographically diagnostic character, a DNA substitution or color pattern change perhaps (Harrison, 1998). Speciation is only a different, or special, kind of evolution if the new species is a distinct population that can coexist locally with its sibling or parent population without losing its integrity.

Characters used to diagnose phylogenetic species may not be shared derived characters; they may be primitive (plesiomorphic) characters, or they may have evolved several times. Therefore, phylogenetic species need not be monophyletic, and could presumably be paraphyletic and perhaps polyphyletic. Cracraft appears confused on this matter: on one hand, he claims that phylogenetic species "will never be nonmonophyletic, except through error" (Cracraft, 1989, p. 35), but on the other hand he recognizes that "their historical status may (sometimes) be unresolved because relative to their sister species they are primitive in all respects. Whether they … (are) truly paraphyletic … is probably unresolvable" (Cracraft, 1989, p. 35). It seems odd to allow a phylogenetic species even to be paraphyletic (let alone polyphyletic), because paraphyly and polyphyly contravene the basic tenets of phylogenetic systematics, and because one of the main justifications for a phylogenetic species concept is that species defined via other concepts might sometimes be paraphyletic: "the biological species concept cannot be applied to the

Thomomys umbrinus complex unless one is willing to accept paraphyletic species, and to do so would be a de facto admission that biological species are not units of evolution" (Cracraft, 1989, p. 46; also see Davis, 1997, p. 374). The phylogeneticists' resolution of that problem, using diagnostic characters, leads to the same difficulty all over again! This rather glaring logical inconsistency considerably undercuts the argument for a diagnostic species concept.

In spite of these logical problems, Cracraft highlighted genuine and important practical problems with the polytypic application of the interbreeding concept, and as a result this phylogenetic species concept has been very influential. Many molecular systematists, including botanists (Davis, 1997), took up Cracraft's suggestion and used diagnostic differences between geographic populations, in some cases at single DNA base pairs, as evidence that two forms are separate species even if they intergrade freely at the boundaries of their distribution. Ornithologists and primatologists in particular have used diagnostic characters to reassign many taxa long thought of as subspecies to the level of full species, resulting in rather severe taxonomic inflation (Isaac *et al*., 2004).

Gene Genealogy

Other phylogenetic systematists continued to be interested in monophyly-based species concepts. A problem with a monophyly concept is that a single, true phylogeny of taxa may, in a sense, rarely exist: a phylogeny of species can be seen as an abstraction of the actual genetic history, consisting of multiple organismal genealogies (Hennig, 1966), or multiple gene genealogies (Avise and Ball, 1990; Maddison, 1997) where ancestral polymorphism and gene flow may lead gene trees to be discordant with the branching pattern in the species tree. There is now good evidence that occasional horizontal gene transfer and hybridization can cause substantial genetic material to flow between species (Mallet et al., 2016). Furthermore, there are multiple gene lineages within any population, so that, if such a population were to become geographically or genetically split into distinct forms, it would take some time before each population became fixed for different, reciprocally monophyletic gene lineages at any single gene (Hudson & Turelli, 2003; Knowles & Carstens, 2007), just as it would take some time to become distinct morphologically recognizable species. The idea of monophyly for whole genomes then becomes hard to define, especially near the species boundary. However annoying, phylogenetic methods and evolutionary theory must face up to these facts (Avise and Ball, 1990; Maddison, 1997; Knowles & Carstens, 2007). Instead it was suggested that monophyletic species could be defined if they formed exclusive sets, where each member's genes were related more closely to members of its own species than to any members of another species. Species were argued to be formed at the fuzzy boundary between reticulate (within species) and divergent (between species) organismal genealogies; it was suggested that such species could be delimited when a consensus or majority of multiple gene genealogies indicated reciprocal organismal monophyly. This was called the “genealogical species concept” (Baum and Shaw, 1995).

Critics argue that this idea has many problems in common with other monophyly concepts of species (Davis, 1997; Hudson and Coyne, 2002). Geographic forms that have become isolated in small populations or on islands, say, could rapidly become fixed for most gene lineages and become viewed as separate species without any biologically important evolution taking place. Conversely, clearly distinct sister taxa such as humans and chimpanzees still share gene genealogy polymorphisms due to balancing selection at some genes such as the Major

Histocompatibility Complex (MHC) genes in humans due to selection for polymorphisms in immunological defence (Klein et al., 2007). Although balancing selection probably rare, humans and chimpanzees might therefore be classified as the same species under a strict genealogical interpretation.

Evolutionary and Lineage Concepts

Faced with the problem of studying the evolution of species through time, the paleontologist Simpson (1951) proposed his evolutionary species concept, in which a species is "a lineage (an ancestral–descendant sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies." In other words, Simpson combined the idea that species were historical lineages with the concept of their evolutionary and ecological role. The key essence here appears to be evolutionary independence. This concept appeals to phylogenetic systematists and paleontologists alike, because of its historical dimension, and to neontologists because of its acknowledgment that biological mechanisms are what make the species real. De Queiroz (1999) is one of the more recent reviewers to propose that a single concept, which he calls "the general lineage concept," under which species are segments of population-level lineages, underlies all other species concepts. According to de Queiroz, the other apparently competing species concepts merely emphasize different characters or criteria for species delimitation, but all adhere implicitly or explicitly to the notion that evolutionary separateness of lineage is the primary concept. This is a nice ideal, but vague terms like "evolutionary independence" have little logical force in their application to actual forms that hybridize or undergo genetic exchange. Furthermore, by failing to delimit where species are along the continuum of diverging lineages, de Queiroz sidesteps the whole issue of species definition rather than solving it. The main content of de Queiroz's (1999) idea seems to be that species often emerge gradually. However, this particular finding had been clarified 140 years earlier.

A somewhat similar idea was Templeton's (1998) “cohesion concept,” which combined several competing ideas of species. He accepted criticisms of the interbreeding species concept and attempted to correct it by infusing ideas from the evolutionary, ecological, recognition, and genealogical concepts. Templeton argued that a combination of ecological, reproductive and genealogical cohesion is important for maintaining a species' evolutionary unity and integrity. As well as applying to asexual taxa (too little sex), Templeton also applied his idea to species like oaks that undergo frequent hybridization and gene flow (too much sex for the interbreeding concepts).

Multispecies Coalescent and the Species Tree

The General Lineage and Diagnostic Concepts of species pay little attention to the gene genealogical discordance that make definitions of monophyly and lineage so difficult. Recently, the theory of the coalescent, which views gene genealogical processes backwards in time, has enabled new approaches to estimating phylogeny and discovery of the original species tree. This backward in time approach differs from classical forward population genetics in that a population sample (usually of gene sequences) allows inferences of the demographic state of the populations or species in the past. The coalescent framework provides huge computational advantages because inference is based on statistical modelling only of sampled sequences and their ancestors, rather than requiring modelling the entire unsampled population currently extant.

One may conceive of a species taxon that joins backwards in time with a sister lineage as two branches in coalescent-based species tree, even though ancestral polymorphisms may remain in one or both gene lineages. By statistically accounting for shared variation due to incomplete lineage sorting of ancestral polymorphism, methods underpinning the Multi-Species Coalescent (MSC) relax the assumption of reciprocal monophyly of genes when estimating a species tree (Knowles & Carstens 2007). Furthermore, unlike the Genealogical Species Concept, which ignores gene tree estimation errors, a statistical model can accommodate uncertainties in gene trees probabilistically.

An estimated species tree suggests a method of delimitation of species. In the simplest case, delimitation of species can be seen as a test between two competing models: a one-species model which assumes that the gene trees for different loci fluctuate according to the standard neutral (coalescent) theory within a single population, and the two-species model which assumes two species populations that diverged some time ago, so that there will be greater concordance among the gene trees across loci within than between species (Yang and Rannala, 2010). This basic method can be extended to Multi-Species Coalescent (MSC) analysis of larger species trees, and there are now various implementations (Grummer et al., 2014; Yang & Rannala, 2014; Pei et al. 2018; Smith & Carstens, 2019). In a justification of the idea, the two-species model without gene flow was argued to correspond to the Biological Species Concept because of the assumption of strict branching of the species tree, which assumes that gene flow ceased at some time in the past (Yang and Rannala, 2010, 2014). This delimitation method can also be viewed as uniting the Biological Species Concept with a Phylogenetic/Evolutionary Concept of species, by requiring a separate lineage concept of species based on splits in the species tree.

However, the "species tree" exhibits the same fractal self-similarity of all phylogenetic trees. It is arguable that the MSC alone is poorly suited to delimiting species, because many local populations that have some genealogical concordance might be thereby delimited as separate species, even if there is considerable gene flow between them (Sukumaran and Knowles, 2017; Jackson et al., 2017; Barley et al., 2018; Chambers and Hillis, 2020). Different extant human populations (Americans, Asians, Europeans, Africans) can readily be delimited into separate species using the Yang & Rannala (2014) method (Jackson et al., 2017). The method therefore seems to suffer from the same problem of over-splitting and taxonomic inflation as the phylogenetic species concept. The utility of the estimated "species tree" is not in doubt, but this tree delimits any distinguishable populations, rather than just those populations that biologists think of as species.

Species Delimitation via a Heuristic

These criticisms led the authors of one of the MSC species delimitation methods to agree that the MSC is really a method for delimitation of populations, and to argue that the use of the MSC in species delimitation would require in addition some divergence heuristic (Leaché et al., 2019). Such heuristics could be simple, for example cut-offs based on genetic divergence of sequences between species. For example, a rule of thumb widely employed in bacteriology is to use > 97% similarity of the 16S rRNA sequence (Edgar, 2018), while a rule proposed for eukaryotic species is based on >97% similarity at the mitochondrial "barcode" locus (a fragment of the cytochrome

C oxidase I gene) (Hebert et al., 2003). These have the drawback that they are not based on the whole genome, and therefore may display the history only of that gene, and not of the whole genome. A more complex suggestion for the whole genome was to use a "genealogical divergence index" to ensure that coalescence within each species is considerably more recent than between sister species (Jackson et al., 2017; Leaché et al., 2019).

Dissent: Maybe Species Are Not Real

Throughout the history of the species debate, starting with Darwin, there have been some who argue that species are not individual real objects, but should instead be considered man-made constructs, merely useful in understanding biodiversity and its evolution. These people are not necessarily nihilists, who deny that species exist: they simply argue that morphological and genetic gaps between actual populations would be more useful for delimiting species than inferred processes underlying evolution or maintenance of these gaps. By their refusal to unite these ideas under a single named concept, this silent majority has rarely found a common voice.

Taxonomic Practice

Taxonomists are on the front line of the species battle, because it is they who ultimately decide whether to lump or split taxa, and at what level to name them as species. If the objectivity and individuality of species as the primary taxon exists, taxonomists' activities do not seem to have been made any easier. Many taxonomists have simply ignored or denied belief in the evolutionary reality of species. In any group, it is probably true to say that at least 10% of taxonomic species are subject to revision because of the practical difficulties in delimitation.

For this reason, since the rise of the polytypic/interbreeding species concept, there has been little impact of the postwar species concepts on practicing taxonomists, even while the debate raged around them, at least up until the 1980s. Procedure, at least in zoology, was more or less as follows: geographic variants, which blended (or were thought to be able to blend) together at their boundaries were united within a single, polytypic species, unless morphological or genetic differences were so great that it seemed necessary to recognize two species. However, whenever two divergent forms differing at several unrelated traits overlapped spatially, they were recognized as separate species even if a few intermediates suggested some hybridization or gene flow. Some taxonomists regarded subspecies as artificial taxa to be avoided, and may either have ignored geographic variation, or elevated subspecies of formerly polytypic species to the rank of full species. But good taxonomic practice on species remained broadly similar across most branches of systematics, and involved careful analysis of multiple, chiefly morphological character sets tested in large samples of specimens collected from as many geographic regions as possible.

This view on species and subspecies had led to a steady reduction in the numbers of recognized species in zoology, as more and more dubiously separated taxa, previously ranked as species, became inserted as subspecies or local populations into larger and larger polytypic species. Recently, however, the diagnostic version of the phylogenetic species concept (*see* Diagnostic Species Concept) has been making strong inroads into zoological nomenclature, with the result that counts of species on continents are again climbing as former subspecies are re-elevated to the species level, in spite of intergradation at their boundaries (Isaac *et al*., 2004).

However, the situation could get much worse; many *Heliconius* butterflies, for example, have over 30 geographic subspecies per species, all of which can be diagnosed easily. The numbers of bird and butterfly species could easily increase 2–10 times in some groups if the diagnostic criteria were generally adopted, and indeed in some well-known groups, for example primates, a doubling of species numbers has already been observed. Most of these increases have come from reclassification of known subspecies or populations, rather than from discovery of new populations (Isaac *et al*., 2004). The one reality that is clear in species-level taxonomy is that the species is not real enough to remain at the same taxonomic rank while fashions in species concept change. This provides evidence that actual species taxa have been and still are man-made groupings that do not employ objective biological or evolutionary essences, even if such essences exist.

Populations Are Evolutionary Units, Not Species

Botanists deal with geographically variable organisms with low powers of dispersal, and have tended not to be as happy with the polytypic/interbreeding concept applied with such apparent success in zoology. Meanwhile, the strong surge in experimental population genetics and evolutionary studies that followed the books by Dobzhansky, Mayr, and Stebbins has led to a greatly improved understanding of gene flow in natural populations. Gene flow, even in quite mobile animals such as birds or butterflies, may not unite distant populations into a common gene pool. If such populations only rarely exchange genes, then gene flow across the range of a continental species is clearly insufficient to explain species integrity, because it would be outweighed easily by weak local patterns of adaptation or genetic drift (Endler, 1977).

This increasing input of population biology into systematics and evolution led to the proposal by Ehrlich and Raven (1969), Levin (1979), and others that species are not real biological units at all; instead, local populations are the only real groupings united by gene flow within a common gene pool, and which adapt to local conditions, compete, and so on. Any homogeneity of ecological niche or genetics over the range of a species might be owing either to recent spread and simple evolutionary inertia or to similar stabilizing selection everywhere. To these authors, species exist and are real in local communities, but it is fallacious to treat distant populations in the same way (*see* Genotypic Cluster or Genomic Cluster Criterion).

This viewpoint is generally understood and respected by population biologists, but curiously has not been incorporated explicitly into current thinking on species in systematics and evolution. Perhaps there is a sneaking suspicion that even very low levels of gene flow may explain species integrity over wide areas, even though it is clear from delimitation using the Multispecies Coalescent (see above) and Assignment Tests (see below) that distinguishable populations can be detected within species.

Hybridization and Introgression

A major problem with the reality of species is that gene flow is often found between species. In Mayr's time (1970), hybridization among species was deemed rare and a relatively unimportant threat to the integrity and reality of biological species, but recent genomic data shows abundant evidence of horizontal gene transfer and admixture among species (Mallet et al., 2016). Probably, in most cases, there is less gene flow per generation between nominal species than among ecological races or hybridizing nominal geographic subspecies, but the differences between species and populations are clearly a matter of degree rather than of kind, as far as gene flow is concerned. This is a major reason why delimitation under the multispecies coalescent requires a heuristic cut-off in addition to a test of distinctness (*see* Species Delimitation via a Heuristic).

Perhaps the most important heuristic of all is sympatry (Mayr, 1970; Chambers & Hillis, 2020): if two genomically distinct populations are found in sympatry, most would want to call these populations separate species, even if there is evidence for ongoing gene flow and genealogical reticulation. However, even here there are problems. Many organisms have ecological races or ecotypes, for example stable populations of phytophagous insects feeding on different hosts; these are often interfertile and may hybridize where they meet in sympatry (Mallet, 2008; Lowry, 2012). Although ecological races have the character of separate species, systematists on the whole do not regard them as species, and most have not been named by taxonomists. To deal with this, one might classify sympatric taxa as species via an additional heuristic; that hybridization leading to gene flow between such genomically distinguishable taxa is less than about 1% per generation in nature (Mallet, 2008).

Phenetic Species Concept

In the 1960s and 1970s, a major systematics movement proposed numerical methods in taxonomy now usually referred to as "phenetics." Pheneticists, as they were called, argued that taxonomy and systematics should be based on multivariate statistical analysis of characters rather than on underlying evolutionary or biological process information. If taxa were defined by non-evolutionary criteria, studies of evolution would be freed from the tautology of testing hypotheses about processes, when those same processes are used as assumptions in the definitions of the taxa under study. Species, like other taxa, would be defined in numerical taxonomy on the basis of multivariate statistics, as clusters in phenotypic space (Sokal and Crovello, 1970).

Phenetics was reviled by those who believed that classifications should be phylogenetic. However, for species the approach is closely similar to the intuitive methods adopted by most taxonomists, who use multiple morphological or genetic characteristics to sort individual specimens into discrete groups between which there are few intermediates (*see* Ecological Species Concept). Some large areas of practical taxonomy are based purely on this phenetic approach. For instance, hospitals often use a battery of biochemical tests to assign microbes to species taxa (Claridge *et al*., 1997), although in some cases today by DNA sequence-based tesst. The usefulness of this taxonomic method is attested by its continued success in public health for predicting pathogeneticity and antibiotic sensitivity.

Phenetic classifications based on morphology introduce the danger that, if convergent characters are used as data, one may group unrelated forms into polyphyletic taxa. In addition, single gene polymorphisms and sexual dimorphism can affect multiple morphological characters. This could lead to a recognition of multiple species within polymorphic populations. Sibling species, however, could be lumped into the same species using a phenetic approach, unless a set of highly diagnostic characters could be found. Nonetheless, these problems are mainly due to the lack of characters found in morphological datasets. Phenetic methods have proved much more successful in distinguishing unrelated, although cryptic, taxa from polymorphic forms when coupled with molecular genetics techniques developed since the 1960s, including allozymes and DNA-based methods (Avise, 1994).

Genotypic Cluster Criterion and Assignment Tests

For morphological or genetic gaps to exist between species, gene flow (if any) between species must be balanced by an opposing force of disruptive selection. In his own work, the first author had studied hybrid zones between geographic forms of butterflies, and attempted to show that a practical statistical definition of species versus geographic races could be constructed using morphological and genetic gaps alone, rather than employing the phylogenetic or evolutionary processes that caused the gaps to exist.

However, to define species by means of the gaps between them requires consideration of the nature of the gaps to avoid falling into the trap of defining polymorphic forms as separate species, or of lumping sibling species. Rather than merely using external morphology, in difficult cases we could consider genetics as well. DNA has a digital, rather than analog code, so there are genetic gaps between virtually any pair of individuals. Clearly, then, we cannot use just any discreteness at the genetic level to define species. Separate sexes and polymorphic female forms of mimetic *Papilio* butterflies also have gaps between them in exactly this way. A genetic element, which may be a single base pair, an allele at a gene, the entire mitochondrial genome, a chromosomal rearrangement, or perhaps a sex chromosome, may determine the genetic or morphological differences between such polymorphic forms.

To be considered part of a single local population, and therefore part of the same local species, we expect that polymorphic genetic elements like mimicry genes and sex chromosomes will be approximately randomly combined with polymorphisms at genetic elements found on other chromosomes or extrachromosomal DNA. Each individual may be a distinct multilocus genotype, but we recognize a single grouping of genotypes because polymorphisms at one genetic element are independent of polymorphisms at others. Conversely, if alleles at one locus are strongly associated with alleles at other, unlinked elements (i.e., linkage disequilibrium or gametic disequilibrium), we have evidence for more than one separate population; if these two populations overlap spatially, the groupings are probably also separate species.

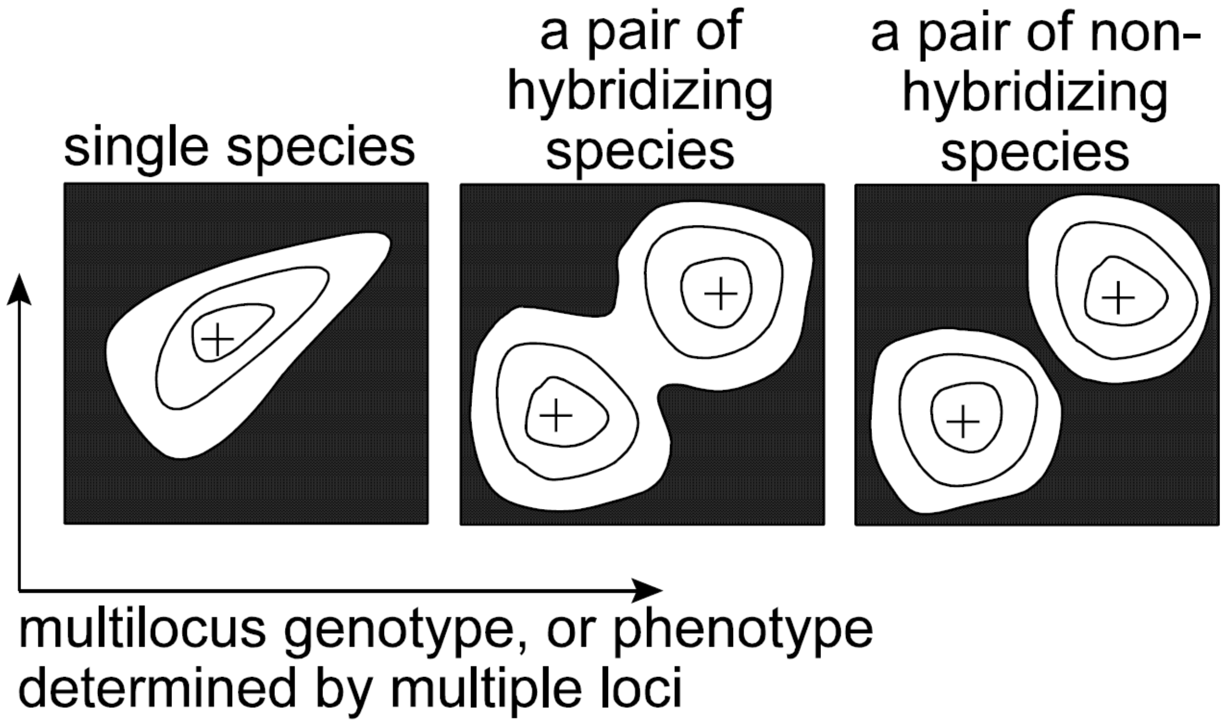

Figure 1. Heuristic for species delimitation: genotypic clusters identifiable in sympatry. A sample of individuals is made at a single place and time. Numbers of individuals are represented by the contours in multidimensional genotypic space. Peaks in the abundance are represented by "+." Two species are detected if there are two peaks in the genotypic distribution (right, bimodal distribution; also see Jiggins and Mallet, 2000). Otherwise the null hypothesis of a single species is not rejected (left, unimodal distribution). This method is agnostic to species concept: it depends on the pattern of genotypes only. Note: the axes represent multidimensional morphological/genotypic space, not geographic space.

Many of us therefore proposed a "genotypic cluster criterion" for species (Mallet, 1995; Feder, 1998). Avise & Ball (1990) pioneered the basic idea using the frequencies of allozyme loci and gene sequences of mitochondrial DNA, but called the method "genealogical concordance." The term “genomic cluster” would perhaps be a more appropriate synonym in today's postgenomic age. Species are recognized by morphological and genetic gaps between populations in a local area rather than by means of the phylogeny, cohesion, or reproductive isolation that are responsible for these gaps (Mallet, 1995). In a local area, separate species are recognized if there are several clusters separated by multilocus phenotypic or genotypic gaps. A single species (the null hypothesis) is recognized if there is only a single cluster in the frequency distribution of multilocus phenotypes and genotypes. The genotypic gaps may be entirely vacant, or they may contain low frequencies of intermediate genotypes, or hybrids (Figure 1). The definition is useful because one avoids tautological thinking: hypotheses about speciation or phylogeny of taxa become independent of assumptions about the nature of reproductive isolation or phylogeny underlying the taxa studied.

Statistical procedures, “assignment tests” based on multilocus allelic data are today regularly used to estimate the numbers of genotypic clusters from individual multilocus genotype data (Pritchard *et al*., 2000; Falush *et al*., 2003; Huelsenbeck and Andolfatto, 2007): if such genetic clusters are statistically distinguishable in sympatry, most would agree that separate species are detected. Similarly, species delimitation by means of the multi-species coalescent (MSC; see The Multispecies Coalescent and the Species Tree, above) in sympatry would similarly provide a test for the existence of sympatric genotypic clusters.

Genotypic clusters are neither profound nor original; the idea traces the earliest use of the method to Darwin's (1859) morphological gap criterion of species (*see* Darwin's Morphological

Species Criterion), although earlier sources probably employ similar ideas since acceptance of evolution is not required to identify species on the basis of character distribution. Many similar proposals have been made (Simpson, 1937; Hutchinson, 1968; Sokal and Crovello, 1970; Avise and Ball, 1990; Cohan, 1994; Smith, 1994). The approach is essentially the same in most taxonomic decisions (*see* Taxonomic Practice), in the phenetic concept (*see* Phenetic Species Concept), and in a practical application of the biological species concept (see below). Multilocus genotypic clusters are almost universally applied as a criterion of speciation in theoretical models of sympatric speciation (e.g., Dieckmann and Doebeli, 1999; Gavrilets and Waxman, 2002; Kondrashov and Mina, 1986; Kondrashov and Kondrashov, 1999): in these models, a bimodal genotypic distribution evolves via reproductive isolation, but it is the demonstration that a pair of genetically divergent groups of individuals emerge from a single population, rather than the mere existence of hybrid inviability or mate choice, that is required for evidence of speciation.

Asexual forms, unclassifiable under the interbreeding concept, and arbitrarily definable at any level under concepts depending on phylogeny, can be clustered and classified as genotypic clusters in exactly the same way as sexual species. The precise taxonomic level of species clustering for asexuals is somewhat arbitrary, as in the phylogenetic concepts, but at least the method acknowledges this arbitrariness rather than purporting to use some higher evolutionary principle. Many asexual forms such as bdelloid rotifers have clearly distinguishable species taxa (Hutchinson, 1968; Fontaneto *et al*., 2007), probably due to ecological selection for distinct characteristics. In bacteria, competition is thought to structure largely asexual populations with occasional promiscuous horizontal gene transfer into recognizable genetic clusters (Cohan, 1994, *also see* Ecological Species Concept). Thus, reproductive isolation may help but is not required to be complete for the existence of a genotypic cluster.

Critics have argued that the genotypic cluster criterion in sexual species is nothing other than a gene flow concept of species under a different guise. This is true for one specialized interpretation of gene flow in sexual populations. If we label gene flow as successful or effective, as opposed to treating gene flow as the per generation rate of hybridization and backcrossing, we can see that a gene flow criterion becomes similar to the genotypic cluster criterion. To find whether a hybridization or gene flow event is successful, we must either follow the fate of every gene through all possible descendants for all time, or we may examine the genotypic state of a population and determine if genes from one form are mixed randomly with genes from another form. Looking for random associations of genes within genotypes in the genotypic cluster approach will be methodologically the same as a genotypic analysis to determine whether a population is interbreeding, but the latter requires additional assumptions. The genotypic cluster criterion in sexual species could thus be looked upon simply as a practical application of the biological species concept. However, one may prefer the genotypic cluster criterion to the interbreeding concept, if only because its name emphasizes that the definition is character-based, rather than actually based on interbreeding, and is thus applicable to asexuals as well as sexual species.

If a single geographic race, which previously intergraded at all its boundaries with other geographic races, were to split into two forms that coexist as separate genotypic clusters, we could have a situation where the original polytypic species became paraphyletic. The new species has been derived from only one of the component subspecies. Thus, paraphyly of species would be permitted under this definition, as in both interbreeding and diagnostic concepts.

The Unreality of Species in Space and Time: Races Versus Species

Geographic races often form clusters differing at multiple loci from other races in the same species. The interbreeding concept or genotypic cluster criterion can be used to justify a classical polytypic species if the various geographic races meet at contact zones that contain abundant intermediates (hybrid zones). We sample multilocus genotypes or phenotypes in local areas of overlap and determine whether a single peak (one species, i.e., abundant hybrids) or two peaks (two different species, i.e., rare hybrids) are evident in the local genotypic distribution (Figure 1). Hybridization may occur, but if it is so rare that character and genotypic distributions remain distinctly bimodal in zones of overlap, we usually classify them as separate species, even under the interbreeding concept.

Although this spatial extension of the local species is practical to apply to any pair of forms in contact, it is unlikely to lead to general agreement. The problem is that hybrid zones can be very narrow and may have separate forms that are highly distinct at multiple characters or loci, in spite of complete unimodal blending in local areas of overlap. Even adherents of the interbreeding concept are reluctant to lump such geographic forms within the same species. Examples include North American swallowtail butterflies (*Papilio glaucus*/*Papilio canadensis*;

see Hagen *et al*., 1991) and European toads (*Bombina bombina*/*Bombina variegata*; see Szymura, 1993).

An even worse problem is found in ring species, which form a continuous band of intergrading subspecies, but whose terminal taxa may be incompatible, and overlap without intergrading. Commonly cited examples are the herring gulls and lesser black-backed gulls (*Larus argentatus* complex) and the Ensatina (Mayr, 1970; Irwin et al., 2001). Similarly, although most hybrid zones between European *Bombina* are unimodal, the same pair of taxa may have bimodal genotypic distributions in other zones of overlap (Szymura, 1993). Thus, geographic forms may be apparently conspecific in some areas, but overlap as separate species in other areas. Finally, if distinct populations are geographically isolated and there is no area of overlap, one cannot disprove the null hypothesis of same species under interbreeding or genotypic cluster criteria, but biologists are reluctant to unite such populations if they are very divergent. Laboratory hybridization could be tried, but many overlapping species are known to hybridize freely in captivity, while remaining separate in nature. There are good examples even in our closest relatives, the great apes, for instance the bonobo (*Pan paniscus*) versus the chimpanzee (*Pan troglodytes*), and among the gorillas (Uchida, 1996), but similar decisions must be made in almost any animal or plant group.

The problem of extending local species criteria spatially is due to the way in which spatially separated lineages diverge: time since population divergence is usually somewhat correlated with geographic distance. Paleontologists face a similar temporal problem when classifying fossils in different strata. Evolutionary rates may vary, but all lineages must ultimately be continuous, so there may be no very logical place to put a species boundary in time any more than there is in space. Paleontologists, like neontologists, use operational species on the basis of morphological gaps between taxa from the same and different time periods (Simpson, 1937; Smith, 1994).

These difficulties show why there is no easy way to tell whether related geographic or temporal forms belong to the same or different species. Species gaps can be verified only locally and at a single point in time. One is forced to admit that Darwin's insight is correct: any local reality or integrity of species is greatly reduced over large geographic ranges and time periods (*see* Mayr (1970) *and* Biodiversity in Space and Time).

The Importance of Species Concepts for Biodiversity and Conservation

Traditional: Species as Real Entities

Different species concepts seek to define species in mutually incompatible ways. Thus, a monophyletic species concept seems not very useful to evolutionary biologists because of difficulties with multiple gene genealogies and paraphyletic remnants. In contrast, the interbreeding concept and other concepts incorporating biological processes of species maintenance (e.g., recognition, ecological, evolutionary, and cohesion concepts) suffer in the eyes of phylogenetic systematists because they lack phylogenetic coherence and produce paraphyletic taxa, or worse. If we were to allow the basal unit of our taxonomy to incorporate paraphyly, it would be harder to justify a strict adherence to monophyly at other taxonomic levels. It is beyond the scope of this article to resolve these difficult issues, but these conceptual conflicts fuel the continued debate, and also highlight the fact that if species are indeed real, objective biological units, their unifying reality has been extremely difficult to verify.

Many ecological and biodiversity studies of actual organisms ignore these difficulties and assume that species are objectively real basal units. Thus, in ecology, we have theories of global species diversity. In conservation, we have the Endangered Species Act in the US, which prescribes the conservation of threatened taxa we call species. Populations not viewed as species, particularly putative hybrid taxa (like the red wolf, *Canis rufus*, of the southeast US), became seen as less valuable, even if rare. How do we recognize that a taxon is hybridized? Obviously, to be a hybrid, it must be a mere intergrade between two, real, objectively identifiable entities. The Endangered Species Act had a tendency to view species as important real conservation units and hybrids as unimportant. It did this because it incorporated the species concept in vogue at the time of its enactment, that is the biological species concept, in which hybridization is seen as an unnatural breakdown in isolating mechanisms (Mayr, 1970).

Alternatives: Genetic Differences More Valuable than Species Status

Increasingly, as we have seen, hybridization and gene flow among species became recognized as important in many groups, and in 1990 the hybrid policy of the Endangered Species Act was rescinded. Today, although some hybrid populations are eligible to be viewed as valuable in conservation, others, especially hybrids with invasive taxa can be a problem for conservation. Despite much discussion, no replacement policy about hybrids has been forthcoming. There is undoubtedly a new acceptance that other levels in the taxonomic hierarchy are important elements of biodiversity. The diagnostic concept of species, while claiming to support the basal, objective nature of species, may be useful in that it encourages recognition of important biodiversity at level lower than the interbreeding concept, for example subspecies within polytypic species. Conservation geneticists today often advocate the conservation importance of "evolutionary significant units," "management units," or "stocks" (a fisheries term) defined below the species level by means of various criteria along the continuum of genetic differentiation at molecular markers (Moritz, 1994). But the reality of spatiotemporally extended species continues to elude us, and biodiversity in terms of numbers of species, including endangered species, remains difficult to measure. We argue that this will always be the case. Because populations evolve, cohesion over large regions of space and time will continue to break down. If this is so, then it might seem best to adopt some other measure of conservation value that relies purely on genetic differentiation, for instance, at molecular genetic markers.

Species Differences as Ecologically Important Markers

However, there are many who would oppose just using molecular divergence as a measure of biodiversity. Species of sexual macroorganisms within a local area such as a nature reserve are, for the most part, easily and objectively identifiable using morphology, behavior, genetics, or phylogeny. A pair of similar species normally must be ecologically distinct to coexist. Sexual species will need some prezygotic isolation, so their mating behavior must also be different. Thus, counting species in a local area makes considerable ecological sense, and conserving species diversity in a local area would conserve actual ecological and behavioral diversity. Behavioral and morphological differences that differ among species seem more valuable evolutionarily, as well as having more interest to conservationists, than the probably mainly neutral differences at molecular genetic markers.

Conclusion: Biodiversity in Space and Time

As we have seen, the relative local objectivity of species delimitation breaks down when we try to apply the term "species" over large areas or geological timescales. In some cases, there is an excellent homogeneity over large areas; for example, the painted lady butterfly (*Vanessa cardui*) and the barn owl (*Tyto alba*) have virtually worldwide distributions and look similar everywhere. Other species are not so homogeneous: the familiar mallard (*Anas platyrhynchos*) group of ducks is as widespread, but has become highly differentiated into some 18 or so forms in far-flung outposts of the world. Exactly how many mallard populations are good species, and how many are races, or indeed, how many races there are in total, is a matter of taste. Current authorities recognize about 10 species, but there might easily be five or 15 in alternative treatments. One of the forms, the Mexican duck, *A. platyrhynchos diazi*, is threatened with hybridization by the true mallard, *A. platyrhynchos platyrhynchos*, which has been expanding from the north, and the American black duck (*Anas rubripes*) also hybridizes with the mallard, but appears to resist hybridization somewhat better than the Mexican form – hence its species status.

Faced with these difficulties, should we worry about whether or not we have a real species when conserving endangered taxa over large areas? In our view, probably not, and criteria of distinctiveness, or ecological role should be more important on a case-by-case basis. Whatever one's answer to this question, it does not seem sensible to rely on a unitary spatiotemporal reality of species as a guide. We might conform to the current trend for taxonomic inflation, and upgrade the Mexican duck to a separate species instead of a subspecies, but this should ideally have little effect on our view of its conservation value since it led to no actual change in our knowledge of biological characteristics that affect conservation value. Most conservationists now agree that the former fetish for species-level legislation was a mistake. Conservation and legislation now generally recognize that living, evolving populations form fractal continua with species and genera over time and space, rather than attempting to rely on spurious fundamental units.

Species can still be fundamental units of local biodiversity, but they have this clarity only in a small zone of time and space, and so species counts become less and less meaningful as larger and larger areas are covered. Taxonomists might come to nominalistic agreements on a case-by-case basis, but even this shows little sign of happening yet. Ecological theory, as well as conservation and biodiversity studies must however recognize that species counts over large expanses of space and time represent only a sketchy measure of biodiversity, a measure that owes more to taxonomic and metaphysical fashion than to science. Yet conservation still depends on lists of endangered species at both local and global levels. It might seem more sensible to have either a better way than species lists to estimate conservation value, or at the very least a more stable species criterion less prone to taxonomic inflation. However, it is the bleak truth that agreement on this matter has not yet been achieved.

See also

Differentiation.

Speciation, Process of.

Subspecies, Semispecies, Superspecies

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