Subspecies, Semispecies, Superspecies

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Abstract

Distinct populations that replace each other geographically were recognized either as full species or as lower-level varieties or forms under the original Linnaean taxonomy. In zoology, a practical resolution of this ambiguity took place largely between about 1880 and 1920, with the recognition of a single additional taxonomic rank below the species, the geographic subspecies. In botany, many infraspecific ranks remain valid. Since the 1980s, the fashion has changed once more. Some systematists are again recognizing geographical replacement forms as full species, even when they blend together freely at their boundaries.

Keywords

Artenkreis, Botanical and zoological nomenclature, Conservation, Conservation legislation, Contact zone, Formenkreis, History of science, Hybrid zone, Lumpers and splitters, Polytypic species, Rassenkreis, Species concept, Syngameon, Systematics and Taxonomy

Key points

- It is generally agreed today that evolution is continuous across the species boundary.
- Below the level of species, there may be varieties, ecotypes, ecological races, and geographical races or "subspecies."

- Above the level of species there are a variety of groups, including genera, families, and phyla. The term "superspecies" is used at the lowest of these levels for a collection of "semi-species" that replace one another geographically.
- A historical approach is adopted to outline past and current usages of these terms.

Introduction

Since the realization that evolution allowed continuity between varieties, species and genera, a variety of ranks in the hierarchy of the diversity of life have been recognized. These include recognition of Linnean species, as well as stable groupings below the level of species, and groupings of species.

A Brief History of Subspecific Taxonomy

Variation Below the Level of Species

Since the invention of binominal nomenclature by Linnaeus, there has been a conflict between “splitters” who named more or less well-defined local populations as separate species, and “lumpers” who ignored geographic variation, and united local variants into a single species. The problem was compounded by early systematists' belief that species had an Aristotelian essence, each fundamentally different from similar essences underlying other species. To Linnaeus' followers, it seemed important to decide, which level of variation was fundamental. The terms “genus” and “species” both result from Aristotelian philosophy, and although Linnaeus is usually credited with establishing the species as the basal taxonomic unit, he confused matters, after recognizing that some plant species were of hybrid origin, by suggesting that genera were a more important taxonomic level (i.e., a separately created kind) than species.

Once evolution was accepted, it became clear that variation at all levels in the taxonomic hierarchy was due to more or less similar causes; the only difference between variation above the level of genus or species and below was one of degree. Darwin realized that species could evolve from intraspecific varieties, and he used the term "species" in a new and nonessentialist sense: "… the complete absence, in a well-investigated region, of varieties linking together two closely allied forms, is probably the most important of all the criterions of their specific distinctness … Geographical distribution is often brought into play unconsciously and sometimes consciously; so that forms living in two widely separated areas, in which most of the other inhabitants are specifically distinct, are themselves usually looked at as distinct; but in truth this affords no aid in distinguishing geographical races from the so-called good or true species" (Darwin, 1874). Using this criterion, Darwin classified all human races as members of the same species. Darwin showed convincingly that there was no essential difference between species and varieties; species were simply varieties, which had diverged more, and which could coexist without intermediates being common. However, with his term "varieties" Darwin did not clearly distinguish between polymorphic variants within populations and the identifiable geographic populations normally today considered as geographic races or subspecies. To Darwin the distinction was unimportant, because polymorphic variants, clinal variation, geographic races or subspecies, and good species formed a continuum. Darwin demonstrated that this continuum was excellent evidence for an evolutionary origin of the taxa we call species.

The Trinominal Revolution in Zoology

Many systematists wished to preserve the purity of the simple genus–species binominal nomenclature, but by the 1850s, there were enormous stresses. It began to be realized that identifiable geographic replacement forms were an important intermediate stage between

insignificant local variants and good species. Some lumped these replacement forms as varieties within species, whereas others continued describing these replacement forms as separate species: practices varied widely, leading to considerable confusion. Although some Europeans had long advocated naming marked geographic forms as subspecies, the accumulation of major North American museum collections during the great push of colonization and railway construction westwards was probably the most important catalyst of a revolutionary new systematics. In this new approach, nomenclature consisted of a trinominal: genus–species–subspecies, which is still the dominant taxonomic practice today. The maxim was: "intergradation (at the boundary between two geographic replacement forms) is the touchstone of trinominalism." Examples from commonly observed birds, which intergrade are, in North America, the eastern rufous-sided towhee (*Pipilo erythrophthalmus erythrophthalmus*) replaced in the west by the spotted towhee (*Pipilo erythrophthalmus maculatus*), and in Europe the carrion crow (*Corvus corone corone*) found in the south and west, replaced by the hooded crow (*Corvus corone cornix*) in Italy, and the north and east of Europe. Among the ornithologists responsible for this revolution in North America was Elliott Coues, who published a catalog of American birds in 1872 incorporating an early version of this trinominal nomenclature, in which subspecies were prefixed by "var." and Robert Ridgway, who finally dropped the "var." in his own 1881 summary of North American bird nomenclature.

The American Ornithologists' Union soon adopted this policy, and the idea then spread to Europe, particularly England where Walter Rothschild began amassing his vast collection of birds and butterflies, and had hired excellent and productive staff, the ornithologist Ernst Hartert and the entomologist Karl Jordan, to curate and describe the new material. Jordan was particularly important in spreading the idea of trinominal nomenclature to entomologists, and in

promoting the abandonment of other subspecific nomenclature. He was regarded by the Rothschilds as the clever member of the staff (Rothschild, 1983), and published enormous systematic treatises as well as papers on the theory of systematics, justifying trinominal nomenclature and the recognition of the subspecies as a valid, identifiable taxon in its own right. Both Jordan and Hartert were Germans who contributed to and read European as well as English journals, and in Germany a similar revolution was taking place. Thus, these systematic ideas were able to spread to the rest of Europe in the time when science was often highly parochial. The standard trinominal nomenclature for subspecies, and the abandonment of other named ranks, such as semispecies and superspecies, soon became established in the International Code of Zoological Nomenclature, and has remained there ever since.

Meanwhile, botany, Linnaeus' major expertise, remained much less prescriptive. Many infraspecific ranks are still considered valid taxa under the International Code of Botanical Nomenclature. For instance, *Saxifraga aizoon* var. *aizoon* subvar. *brevifolia* f. *multicaulis* subf. *surculosa* is a valid scientific name in botany, with names for variety, subvariety, form, and subform as well as genus and species ranks. Cultivated strains, hybrids, subspecies, are also considered valid nomenclatural ranks in botany, whereas subspecies do not necessarily refer specifically to geographic populations, as is the case in zoology. The remainder of this article is concerned largely with zoological terminology. It is important to realize, however, that neither botanical nor zoological codes confront controversy by specifying how to decide whether a particular group of specimens is a species or infraspecific taxon. The goal of these codes is to merely regulate nomenclature once a decision of rank has been reached.

Theories of Divergence: Superspecies, Semispecies, and Subspecies

It is hard to imagine the diversity of ideas by which the systematists of 100 years ago explained geographic variation. At that time, evolution by natural selection was far from generally accepted, in fact many believed that it had been disproved. One of the most influential ornithologists of the time was Otto Kleinschmidt, who believed that all species suddenly came into being long ago, and since then had remained completely separate. Replacement forms or subspecies had diverged from the main species but, in Kleinschmidt's view, subspecies could never evolve into new species as the Darwinians supposed. To distinguish his new species concept from the older one in which geographical replacements might be named as separate species, Kleinschmidt called his theory of variation the *Formenkreis* (ring of forms) theory. The *Formenkreis* theory fitted neatly with, and indeed promoted the new practices of naming subspecies and trinominal nomenclature.

In those times many somewhat peculiar explanations competed to explain geographic variation and speciation, including Kleinschmidt's “nonspeciation” theory, Lotsy's hybridization theory, saltational evolution via mutation, inheritance of acquired characters, as well as natural selection. In Britain, Jordan and Rothschild argued eloquently and influentially against any new terminology (including *Formenkreis*) that had theoretical implications and proposed incorporating as little evolutionary theory into taxonomy as possible, in view of the lack of agreement among scientists at the time. Rothschild and Jordan (1895, 1903), supported by Hartert, agreed both with the nomenclatural practice of naming subspecies, and that subspecies were valid real taxa which could evolve into full species. They argued that the Linnaean term “species” should be retained for the whole group of races, and that the geographic races were not true species, they were simply subspecies or incipient species.

Others felt that the term species was too emotive to be used in the new, multiple-subspecies sense. Some scientists continued following the *Formenkreis* doctrine, and had begun to name quite distinct taxa, which did not intergrade at their boundaries, as subspecies. This situation led in the 1920s and 1930s to the neo-Darwinian ornithologist Bernhard Rensch scrapping the term *Formenkreis* because of its theoretical limitations, and instead substituting two new terms, *Rassenkreis* (circle of races) and *Artenkreis* (circle of species). *Rassenkreise* were again considered to be equivalent to species, composed of races or subspecies. However, now there was an additional layer in the taxonomy, of groups of *Rassenkreise* that replaced one another geographically, the *Artenkreise*. Thus an *Artenkreis* could consist of multiple *Rassenkreise*. Rensch and many others believed that the subspecies was an incipient species, of which the geographic replacement species, *Artenkreise* were a further development, until finally divergence was sufficient to allow complete geographic overlap, whereupon new *Rassenkreise* could again be formed.

These terms did not catch on, and most scientists came to the conclusion that the *Rassenkreise* were equivalent to the species taxa used by Linnaeus and Darwin. Probably a major reason that we do not use these multiple taxonomic terms in zoology is due to the prolific work published in English by another German, Ernst Mayr. Mayr had worked for Walter Rothschild and knew Hartert. After Walter Rothschild was blackmailed by a lover, his enormous bird collection of 280,000 skins was sold in 1932 to the American Museum of Natural History, where Mayr happened to have been hired as a curator. Mayr's experience of ornithology, contact with the European literature, and burgeoning friendship with the geneticist Theodosius Dobzhansky (who convinced him of the lack of evidence for inheritance of acquired characters), lent a unique opportunity to influence the course of systematics and evolutionary biology. Mayr did not waste

this opportunity. Mayr used ideas underlying Rensch's terms but renamed them in English. The *Rassenkreis* became simply the species or polytypic species, with its geographic races being subspecies, whereas the *Artenkreis* became the superspecies, and its component parts semispecies, that is, replacement species, not very divergent but which may hybridize occasionally where they overlap. Mayr successfully blended the local species concept of Poulton and Dobzhansky based on interbreeding with the geographic *Rassenkreis* idea of species, incorporating Jordan and Rothschild's ideas about subspecies. He renamed this combination of ideas "the biological species concept," a term, which has since remained strongly associated with Mayr's name. His many influential articles and books promoted a new program of species study, a science of the species that is still with us today. Central to Mayr's system was the belief that discrete taxa such as species or subspecies would normally diverge in "allopatry," that is, in complete geographic isolation.

The Subspecies Today

Modern Views of Subspecies and Semispecies

The views of Darwin, Wallace, Rensch, and Mayr that geographic replacement forms, subspecies and semispecies, are in fact incipient species, has few critics today. Most geographic replacement species (i.e., semispecies, which intergrade only rarely when they meet) must indeed have evolved from previously interbreeding subspecies. Modern genetic data have done nothing to cast doubt on this idea. Meanwhile, superspecies became a specialized term reserved for groups of semispecies that intergraded little at their boundaries. Because neither of these are valid ranks in the zoological or botanical codes, taxonomists normally name such replacement semispecies at the species rank.

Under the trinominal approach, taxonomists were now required to describe subspecies, which has been never seen as a particularly noble activity in comparison to the description of species, especially recently. A strong attack on the zoological subspecies was mounted by Wilson and Brown (1953). Both were systematists working on ants, a group particularly riddled with poorly conceived trinominals and other named varieties at the time. Wilson and Brown argued that subspecies rarely, if ever, could be justified on the basis of multiple characters, and that therefore they were not real taxa. The only real taxa were species, which in a sense were self-defining because interbreeding prevented divergent genes from flowing from one species to another. Subspecies that interbred at their boundaries, however, were not so endowed, so that genes and morphological characters could flow between them. Wilson and Brown put forward examples of subspecies that undoubtedly would be hard to justify on multiple character grounds. This single paper was enormously influential on systematics in the US, and generations of insect systematists trained at Harvard and Cornell, where Wilson and Brown worked, together with their own many intellectual descendants, and their students' students in turn, have eschewed the practice of naming subspecies.

However, recent work shows that many subspecies separated by hybrid zones do in fact differ at multiple morphological, behavioral, and genetic characters (Barton and Hewitt, 1985). For instance, the toad *Bombina bombina* meets its relative *Bombina variegata* across a broad front in Europe. The two forms hybridize freely in the contact zone – although the hybrids can be shown to suffer some inviability – and so should really be classified as members of the same species under polytypic or biological species concepts. However, it has always seemed natural to place such well-defined forms in separate species in spite of the fact they have not truly speciated in the sense of failing to form hybrid swarms whenever they meet. The two taxa differ strongly

in call, morphology, skin thickness, the sizes of water bodies used for breeding, and egg size, as well as in mitochondrial DNA and protein sequences. The levels of differentiation suggest that the *Bombina* taxa have evolved separately for many millions of years. This situation of multiple character changes has now been shown to be true across many examples of subspecies as well as (semi-) species separated by hybrid zones. Effective gene flow can be shown to be almost completely blocked by hybrid zones such as these, even if hybridization is frequent (Barton and Hewitt, 1985). Thus, although some named subspecies undoubtedly merited Wilson and Brown's scorn, genetic evidence shows that there are plenty of local replacement forms, which hybridize at their boundaries but which do form real identifiable taxa that are not reproductively isolated, and are therefore valid subspecies under the Wilson and Brown criteria.

Conclusion: Subspecies, Species, and Conservation

This opposition among modern taxonomists to subspecies taxa can be traced as one catalyst of the recent diagnostic version of the phylogenetic species concept. The adherents of this view of species, led by the ornithologist Cracraft (1989), proposed a radical species concept so that even a single fixed character difference may define a geographic form as a separate species. Multiple character justification is not considered necessary, even at the species level. The practical result of this new concept is that many local forms, having been downgraded to subspecies in polytypic species, are again being recognized as species, leading to taxonomic inflation (Isaac *et al*., 2004). In birds and butterflies, which often have many morphologically or genetically distinct subspecies, this could easily result in a 2 to 10-fold increase in the number of species.

It is probable that the revision of geographic forms upward to the level of species is being driven not only by theoretical considerations, but also by existing conservation legislation, which proposes that endangered species are the valuable units to be conserved. If a reserve contains a

taxon recognized as a species rather than just as a local subspecies, it may be seen as more valuable for conservation purposes. The potential consequences for biodiversity and conservation of the continued instability of the term “species” are detailed in the article Species, Concepts of. Today's conservationists are reducing emphasis on species conservation, and are becoming increasingly aware of biodiversity at all the levels of the hierarchy of life, including well-marked subspecies. Thus, the legislative need for differentiating local races as species may ultimately become less important provided that future legislation falls more into line with the prevailing biological thought.

Further Reading

Much of the historical overview in this article is covered by the excellent reviews of Stresemann (1936, 1975), Mayr (1982), and Rothschild (1983), as well as by other sources already cited. For plants, a useful historical summary of variation below the species level is given by Lowry (2012). A recent biography of Karl Jordan (Johnson, 2012) and work on the connections between the species concepts of Darwin, Wallace, Poulton, Karl Jordan, and Ernst Mayr (Mallet, 2004a,b, 2008, 2009) may also be of interest.

See also

Speciation, Process of.

Species, Concepts of

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