

S23-3 The ultrataxon and its use in pure and applied biology

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Abstract The basic units of avian biodiversity are arguably panmictic regional taxa that are genetically distinct from sister taxa in the same or different regions. Historically, the “species” has been used as their taxonomic surrogate. The role of the species as such a standard, however, is confounded by its use under the biological species concept, and by the introduction of other species concepts to replace it, e.g. phylogenetic species concept. In practice, the first commonly lumps sister allopatric units under a single species; and the second, which does single out regional units, nevertheless employs the term “species” for taxa with quite different properties, thereby creating confusion in the meaning of the term for the rest of the biological and administrative world outside systematics. To keep the “species” in its traditional biological context, to avoid confusion over its meaning and to provide a simple, neutral reference point for identifying biodiversity units, new terms such as “ultrataxon” are needed. Meaning far end taxon, “ultrataxon” may be used for any terminal taxon at any taxonomic rank on the phylogenetic tree; and it has already been applied at the level of “biological subspecies” (= regional biodiversity units) for Australian passerines. Such a term overcomes the stigma attached to subspecies in conservation biology, and averts reclassifying the world’s bird fauna under alternative species concepts.

Key words Biological species, Phylogenetic species, Concept applications, Ultrataxon

1 Introduction

In birds, as in all bisexually reproducing organisms, the basic units of biodiversity are panmictic regional populations that are genetically separated from sister populations in the same or different regions. They are, in the context of evolution, at once the products of the past and the potential building blocks of the future. Knowledge of them is the first step in piecing together knowledge of the whole of biodiversity, information that is essential for using, managing and conserving the earth’s bio-resources sustainably. Only after the units have been quantified in the first place is it logical to go about qualifying them, in terms of genetic distinctness, for prioritizing resource management.

By tradition, it is the taxonomic (or classificatory) arm of systematics that has had the job of identifying the units of biodiversity for biology and the community at large. This places an enormous responsibility on that discipline to “get it right”, and highlights a core functional question: what is the taxonomic category appropriate for the purpose? Traditionally, the “species” category has been used as the surrogate for the units. How well does it serve this role? Judged by its use today in conservation biology, in other biological disciplines outside systematics, in sciences outside biology, and in industry and public sectors outside science, it is generally considered satisfactory. Thus for ecologists working on the birds of a small region, the geographic frame for most ecological studies, that region will normally possess a suite of clearly differentiated populations of birds that equate with species in any current taxo-

nomical classification. Species in such situations have tangible reality, each occupying its own niche separate from others.

2 Species concepts and problems in their application

Yet populations of any one of these “species” in widely separated regions, such as the east and west coast forests of temperate north America, or the eucalypt woodlands in different corners of Australia, are often quite different from one another in appearance or behavior or ecology, or all three (Fig. 1). Even though not necessarily as differentiated as sympatric species, they have, over time, diverged genetically from one another through isolation past and present to become units of biodiversity. Despite this, they are still commonly treated as forms of one and the same species because they fulfil, or are presumed to fulfil, the criteria of the species concept with greatest currency in biology at present. That concept is the biological species concept (BSC) of Dobzhansky (1935, 1937), Mayr (1942, 1963), Bock (1986, 1995), and Johnson et al. (2000); and the criteria that such populations are presumed to fulfil are those of genetic miscibility were they to come naturally into contact.

Such a taxonomy may well contribute to the understanding of adaptive and evolutionary processes, and serve other ecological and biological ends as well. But for the basic inventoring of biodiversity units, it commonly lumps — sweeps “under the carpet” — genetically-differentiated

sister populations that replace one another geographically or which hybridize introgressively where they meet. The BSC does distinguish them as subspecies, but, perhaps because they are perceived as less than species and because of conflicting and often trivialising definition (Ford, 1974; cf. Mayr, 1942, 1969), subspecies are viewed pejoratively and widely ignored outside systematics. Over the last 50 years or more, species-level taxonomy in birds, and resulting handbooks and most checklists apart from Peters', have focused far more on assessing whether allopatric or parapatric populations qualify as species than in inventoring subspecies. So biologists, administrators and others outside systematics who rely on such sources for their information on biodiversity are denied access to the fundamental units that they need. The biological species is simply too coarse a measure of biodiversity for taxa that are polytypic and differentiated allopatrically.

As the essential unit of biodiversity, the "species" has problems on another front as well. They are encapsulated in the question: "What is a species?" Through much of the 20th century, that question meant finding out whether the characteristics of a population or group of populations met the criteria for a species under the BSC. Today it means instead: "What is the species concept used". Since the time of Darwin, numerous species concepts have been advanced for circumscribing "species" in nature (Claridge et al., 1997), many of them put forward in the later 20th century as understanding of genetic and evolutionary processes has grown. Haffer (1992) groups them into three categories:

(i) first, the pre-Dobzansky-Mayr morphological concepts of the 19th and early 20th centuries, then underpinning what is now understood as alpha-taxonomy;

(ii) secondly, the biological species concepts, based on the panmictic or inter-fertile breeding population and its genetic isolation from others; and



Fig. 1 Three regional taxa (biodiversity units) of the Australian magpie (*Gymnorhina tibicen*) in situ
In each pair, the bird on the right is male.

(iii) thirdly, the historic time concepts, based on unique phylogenetic lineages termed clades in cladistic theory (after Hennig, 1966).

The historical time concepts are the newcomers, embedded within which are the Evolutionary Species Concept of Simpson (1961) and Wiley (1978), and the Phylogenetic Species Concept (PSC) of Cracraft (1983, 1989, 1992), McKittrick and Zink (1988), Zink (1996a) and others. However healthy this is for evolutionary and taxonomic debate, it can be confusing for biology outside systematics, especially as the properties of species circumscribed under the different concepts are quite different (see Bock, this symposium). Under the BSC, genetic isolation from sister populations, from whatever cause, is the defining point of speciation, the point where speciated populations travel separate evolutionary paths into the future. Retracing its steps leads to a top-down approach to mapping biology's evolutionary tree, beginning with population interaction. The outer nodes of that tree are real populations of organisms in space at one time, the present; and the criterion of species-level nodes is, as stressed above, one of genetic miscibility.

Under historical time concepts such as the PSC, species taxa are essentially the ultimate tips on the evolutionary tree, the present result of past evolution along a lineage or clade. Such concepts conceive the evolutionary tree from the bottom up. The outer as well as inner nodes of the tree are divergence events rather than populations or taxa themselves; and the criterion of species is, quite simply, diagnosability at the terminal level. In this scheme, the issues of genetic miscibility and reproductive isolation are irrelevant. It should be immediately obvious that the application of historical time concepts will consistently identify, as species, the units of biodiversity so often hidden within polytypic biological species. So too do the old morpho-species concepts, upon which much of invertebrate and plant taxonomy is still based in practice. This is perhaps the cardinal reason why the "species", whatever its conceptual base, has served so long and so well as the basic taxonomic unit for biology.

Is this sufficient reason to discard the biological species in systematics? Of course not. The BSC, encompassed in its wider sense by the Comprehensive Biological Species Concept of Johnson et al. (2000), is far too deeply embedded in biological theory and thinking outside systematics, far more so than the historic time concepts. Born of biological processes in space as well as time, it places animal species in *both* those dimensional frames, and is involved integrally in the ideas of niche partitioning, character displacement, ecological interaction, adaptation, founder populations, genetic bottlenecks and exchange, selection pressure and rates of genetic change. Wedded to Linnaean binominal nomenclature, it provides a ready reference to sister and geographical replacement taxa, vital for a range of applied disciplines such as bioprospecting.

Overtuning the BSC would bring considerable prac-

tical problems to applied as well as pure biology, precipitating wholesale change in species-level taxonomy and nomenclature in birds. If, for example, it was replaced by terminal taxa under the PSC, the principles for circumscribing species, and so the species taxa themselves, would shift, the latter roughly doubling in number (Zink, 1996b). Not only would an enormous amount of biological information and theory, the outcome of the last 100 years of developmental thinking in ornithology, become confounded because the concepts and identities of species had changed, but all existing field guides, manuals, monographs and handbooks would become largely redundant. Prescriptions for bio-resource conservation would have to be extensively redrafted and relevant law rewritten. Extending this situation to the rest of the better-known groups in the living world brings the magnitude of the problem into even clearer focus.

3 Towards resolution — the ultrataxon concept

If the biological species is kept, what then are the options for bringing the real units of biodiversity into public knowledge? One approach, given that the units represent differentiated gene pools, is to introduce genetic concepts such as the Evolutionary Significant Unit of Moritz (1994a,b). Such units can nest within biological species, like subspecies. Moritz's (*ll.cc.*) criteria for such units are reciprocal monophyly for DNA alleles and significant frequency differences at nuclear loci; thus they introduce exclusively molecular yardsticks. Ultimately it may be the course to follow, but at this stage it raises once more the question of practicality. Whatever the units of biodiversity are called, they must be identifiable by the biologists who study them, by the managers and administrators who deal with them, and by the general community that is concerned with them. It may be that in the 25th century, a Buck Rogers civilization will find a way to beam on to animals with portable ray DNA decoders to read out their identities in the field; but that technology is still far off. This does not mean that we should dismiss the approach or stop building DNA libraries. It does mean, however, that we cannot yet discard the external signal traits — color, shape, structure, behavior, voice and even smell — that have served systematics well for two and a half centuries, and are accessible and familiar to almost everyone.

This throws the problem back into the lap of taxonomy for an answer. The most obvious solution is to find a naming concept that will single out biodiversity units within the context of the biological species, without the stigma attached to subspecies. One such offering is the term *ultrataxon*. It is defined as any terminal taxon on a lineage of organisms, an idea readily understood in biology (Schodde and Mason 1999: 2). Why the term *terminal taxon* itself was not used was because the reaction to it that was tapped in Australia suggested that its reception would have been terminal. The advantages of the term *ultrataxon* are that it is a single

word encapsulating a simple concept that can be readily assimilated and applied not just within systematics but, importantly, in biology, and bioresource management and conservation as well. Unlike the phylogenetic species, moreover, it is a neutral term that does not compete conflictingly with the biological species in biology. Its principal disadvantage is that it is yet another new term in a discipline already overloaded with terminology.

In practice, terminal taxa at all ranks, such as monotypic species, genera and families, are *ultrataxa*, as are terminal biodiversity units within species. For purposes of bioresource management and conservation, Schodde and Mason (1999) used the term to replace subspecies, employing the familiar Linnaean trinomial nomenclature for them. Only perceived genetically discrete populations, whether isolated geographically or secondarily intergradient, were treated as *ultrataxa* however. The end points of what were considered to be primary clines, also often recognized as subspecies, were not distinguished.

In the end, the idea of the “species” itself may be too ingrained in the human psyche to be completely replaced as the taxonomic unit for bioresource management and conservation. If that is so, and the biological species remains the standard, its conceptual modification by such genetic and cultural variants as have been put forward by Paterson (1985), Templeton (1989), Avise and Ball (1990), Bock (1995) and Grant and Grant (1997) may be needed to shift the criteria of speciation to earlier stages in the process if the catch of biodiversity units is to improve. Even so, this will never, in practice, catch all the *ultrataxa*; indeed, as much as 70% or more may fall through. Concepts such as *ultrataxa* — and subspecies — need to be kept if all biodiversity units in the Aves are to be found, identified and rated.

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