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A species definition for the Modern Synthesis

James Mallet

One hundred and thirty-six years since *On the Origin of Species...*, biologists might be expected to have an accepted theory of speciation. Instead, there is, if anything, more disagreement about speciation than ever before. Even more surprisingly, 60 years after the biological species concept, in which species were considered to be reproductive communities isolated from other such communities, we still do not all accept a common definition of what a species is. And yet, if speciation is to be any different from ordinary evolution, we must have a clear definition of species. The emerging solution to the species problem is an updated, genetic version of Darwin's own definition. This definition is useful and is already being used in taxonomy, in biodiversity studies and in evolution.

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In a recent undergraduate text, Ridley[1] discusses no fewer than seven species concepts (phenetic, biological, recognition, ecological, cladistic, pluralistic and evolutionary), and concludes that a combination of four (biological, recognition, ecological and cladistic) is ideal, making a confusing read for researchers, let alone students. King[2] ponders eight (morphological, biological, recognition, cohesion, evolutionary, cladistic, ecological and phylogenetic), eventually concluding that the biological concept is the best. I argue

that the problems of defining species and of understanding speciation stem from a single cause – a logical flaw with most current definitions of species. We must return to Darwin and add the discoveries of mendelian, molecular and biochemical genetics, in order to bring species into the Modern Synthesis in a way that reproductive definitions never did. It may seem absurd to scrap approximately 60 years of consensus that Darwin's species definition was wrong, but even the most ardent followers of Mayr and Dobzhansky must agree that the past couple of decades have seen unprecedented challenges to their views of species and speciation.

Darwin's definition

Darwin felt he had solved the 'species problem'; by 1859 he was an experienced systematist, having just finished his barnacle monograph, and had accumulated an encyclopaedic knowledge about species, both from his own travels and researches, and through prodigious correspondence with other zoologists and botanists. His private income left him free of bureaucracy and teaching; he had the time, the facts at his disposal, and the intellect to solve the problem of the nature of species. It is at least worthwhile re-examining Darwin's arguments.

Under Darwin's theory, species evolved rather than being created. Darwin's materialistic, morphological definition of species was central to his theory of natural selection[3,4]: '...varieties have the same general characters as species, for they cannot be distinguished from species, – except, firstly, by the discovery of intermediate linking forms...; and except, secondly, by a certain amount of difference,

for two forms, if differing very little, are generally ranked as varieties...'. 'Independently of blending from intercrossing, the complete absence, in a well-investigated region, of varieties linking together any two closely-allied forms, is probably the most important of all the criterions of their specific distinctness.'

To Darwin, the lack of a discrete 'reality' of species was the key to his evolutionary hypothesis of speciation[3]: 'In short, 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'. Recent authors, steeped in the more concrete biological species concept and derivatives, have criticized Darwin's position as a pragmatic strategy to wriggle out of defining species[5], or as a misunderstanding of the true nature of species[6]. Darwin was even accused of making species appear more fluid than they really are as a ('perhaps unconscious') means of gaining support for evolution[7]. In fact, as I shall show, Darwin and Wallace had carefully considered alternatives, particularly definitions based on interbreeding, and rejected them.

The biological species concept

There are undeniable difficulties with Darwin's morphological definition. Two in particular led to the formulation of the biological species concept. The first difficulty concerned what Darwin called 'varieties': discrete polymorphism and racial variation within species[8]. Morphs, including separate sexes in sexually dimorphic species as well as the polymorphic colour patterns of snails, butterflies and birds, maintain distinctness in sympatry; geographic races, like the British red grouse (*Lagopus lagopus scoticus*), which lacks the white winter phase of its continental

relative (*L. l. lagopus*), are often clearly distinguished from their neighbours, though can only doubtfully be considered separate species. Darwin, the inventor of sexual selection, obviously knew that separate sexes were conspecific and also recognized that all humans belonged to the same species[4], but nevertheless did not strictly allow for discrete morphs or races in his morphological definition. To Darwin, this problem was unimportant: evolution accounted for the difficulty of demarcating species from varieties; the blurred nature of species was a key fact rather than a difficulty with definitions.

Poulton[8] had studied butterflies such as *Papilio dardanus* in which females had a number of forms mimicking unpalatable species. At first it was thought that the male and each female form of *P. dardanus* were different species. Observations of structural similarities of the females, together with the absence of male-like females in most areas led to the suggestion that all of the forms belonged to a single species. The hypothesis was clinched when reports came from Africa of nonmimetic males mating with mimetic females. Poulton therefore proposed that the solution to the difficulty of discrete polymorphism was to use interbreeding as a definition of species.

The second problem with Darwin's definition is essentially the reverse of the first. Dobzhansky discovered that certain 'good species', characterized by strong hybrid inviability when crossed, were morphologically inseparable. These 'sibling' species were clearly reproductively isolated from other species, but could not be distinguished by Darwin's morphological gap criterion. Once again, Darwin was aware of, but untroubled by the problem; he knew that morphologically similar 'willow wrens' (i.e. willow-warbler and chiff-chaff, *Phylloscopus* species), distinguishable chiefly by their nests and songs[9] were 'certainly as distinct species as any in the world'. Difficulties with discrete morphs and sibling species led to Poulton's[8] and Dobzhansky's[10] interbreeding species concept.

The interbreeding species concept had its own difficulties, especially that populations found at a distance from each other could not easily be treated, since they were not in contact. Successful crossing by these forms in captivity did not prove conspecificity either, since it was known that good sympatric species, for example of orchids and ducks, frequently hybridized under artificial conditions. Mayr[11] proposed a 'multidimensional' extension to the 'non-dimensional' interbreeding definition, which he called the biological species concept, in which allopatric forms were included in biological species if they were 'potentially' able to interbreed.

Following the lead of American ornithologists in the 1880s, European systematists, led by Karl Jordan and Ernst Hartert, were, by 1910–1920, convinced that the solution to geographic variation was to propose a separate category, the subspecies[12]. Under this system, parapatric varieties were included as subspecies within widely ranging polytypic species if there were intergradation (i.e. presence of intermediate forms) at their boundaries; allopatric replacement forms were also included as subspecies if they were presumed able to intergrade. Although Mayr is usually credited with the biological species concept, his main rôle was to combine the, by then standard, taxonomists' polytypic species with the Poulton/Dobzhansky interbreeding concept.

Although the biological species concept is often claimed as a crowning achievement of the Modern Synthesis[7,13], in which mendelian genetics was proved compatible with darwinism, it owes nothing either to genetics or to darwinism. The interbreeding concept could have been adopted by Darwin himself, but was, as we shall see, rejected by him.

Difficulties with the biological species concept
Darwin's critique

According to Darwin[3]: '...neither sterility nor fertility affords any clear distinction between species or varieties'. First, there were plenty of examples of sterility, especially sterility associated with inbreeding or self-sterility within plant species. Second, many good species seemed to have little in the way of sterility barriers (e.g. dogs, pheasants and *Crinum* lilies). The explosion of data we have today confirms this: for instance, intraspecific sterility barriers caused in insects by the endosymbiont *Wolbachia* have little to do with speciation[14], and Darwin's finches hybridize regularly without amalgamation of the species[15]. Darwin, the inventor of sexual selection, discussed mate choice[4], but not in the context of reproductive isolation. However, the same problems are evident before as well as after mating: strong mate choice may exist within species, while separate species can and do hybridize in nature.

Wallace's critique

Wallace[16] presented a very clear interbreeding species definition, then immediately dismissed it in his treatise on speciation of the Papilionidae of Indonesia. 'Species are merely those strongly marked races or local forms which, when in contact, do not intermix, and when inhabiting distinct areas are...incapable of producing a fertile hybrid offspring. But as the test of hybridity cannot be applied in one

case in ten thousand, and even if it could be applied, would prove nothing, since it is founded on an assumption of the very question to be decided...it will be evident that we have no means whatever of distinguishing so-called "true species" from the several modes of [subspecific] variation here pointed out, and into which they so often pass by an insensible gradation'. Wallace is first saying that it is practically impossible to make all the necessary crosses to test genetic compatibility. Second, since theories of speciation involve a reduction in ability or tendency to interbreed, species cannot themselves be defined by interbreeding without confusing cause and effect.

I have been unable to find a recent version of Wallace's 'circularity' criticism of the interbreeding definition, but it is arguably the most important logical difficulty with the biological species concept. Mayr and Dobzhansky quite happily used the term 'concept' (Poulton used 'conception') to emphasize that their species included ideas of self-maintenance, and they regarded this as an advance over merely taxonomic definitions. Evolutionary biology is riddled with problematic concept-definitions of this kind. For example, in this sense 'mimicry' is also a bad term because it superimposes an evolutionary explanation on a morphological description. Ideally, we should use the neutral term 'resemblance' for the similarity, and then test whether mimicry is a satisfactory explanation in each case. This logical tangle may be unimportant in mimicry because, for many cases of close visual similarity, mimicry seems virtually the only explanation. But, for the maintenance and evolution of species, various alternative hypotheses are possible and are actively debated. The use of an interbreeding concept strongly taints our view of these processes. Under interbreeding concepts, species 'cohesion' is due to interbreeding or gene flow within species and an absence of gene flow between species, by definition. Because no gene flow between species is conceptually possible under interbreeding concepts, it is extremely hard to imagine how speciation, which must often involve a gradual cessation of gene flow, can occur. An external barrier to gene flow, allopatry, becomes the easiest way to imagine speciation, to the exclusion of parapatric and sympatric speciation. To give the latter a fair chance of explaining speciation, we must define species as populations that can emerge via disruptive selection in sympatry or, perhaps, via adaptation leading to pleiotropic divergence of reproductive characters in parapatry. If we accept Wallace's critique, we need a definition that is useful, however species are maintained and however

they have come to be. We clearly do not need a bias against certain evolutionary modes.

A theory-independent definition of species that is not a concept would contradict many years of writings by Mayr and others. Mayr has repeatedly stressed that the biological concept cannot be refuted by practical difficulties in its application[17]; this means it is untestable. Sokal and Crovello's damaging criticisms[18] of the biological species concept were scornfully dismissed by Mayr because a simple definition of species was 'confused' with the 'concept' of species. But it has never been clear why we need to improve on a good taxonomist's or naturalist's definition. Viewing species as anything other than definable groups of individual organisms risks weaving hidden evolutionary constraints into the definition, just as the creationist concept of species made it hard to imagine evolution. Instead of seeing species as groups of individuals, the biological species concept and its derivatives see whole species as 'individuals', 'evolutionary units' that have internal 'cohesion', or as the only taxonomic level that is 'objectively real'[6,7,10,17,19–22]. Similarly, speciation has been proposed to occur via 'genetic revolutions', 'genetic transilience' or 'punctuated equilibria'[6,23,24]; these ideas are necessary more to circumnavigate the difficulties of a theory-laden species concept than to overcome any real barriers to gradualistic darwinian evolution. Whether species do have a greater 'objective reality' than lower or higher taxa is either wrong[3,25–29] or at least debatable; the idea that species are qualitatively different from other taxa is therefore best not included within their definition.

The genotypic cluster definition

An obvious alternative approach to the biological species concept is (1) to define species in the darwinian way as distinguishable groups of individuals that have few or no intermediates when in contact, (2) to extend the definition to cover polytypic species, and (3) to incorporate new knowledge from genetics as well as morphology. When we observe a group of individuals within an area, we intuitively recognize species by means of morphology if there are no or few intermediates between two morphological clusters, and because independent characters that distinguish these clusters are correlated with each other. Adding genetics to this definition, we see two species rather than one if there are two identifiable genotypic clusters. These clusters are recognized by a deficit of intermediates, both at single loci (heterozygote deficits) and at multiple loci (strong correlations or disequilibria between loci that are divergent between

clusters). Mendelian variation is discrete; therefore we expect quantized differences between individuals. We use the patterns of the discrete genetic differences, rather than the discreteness itself, to reveal genotypic clusters.

This definition will, of course, best apply to populations in contact. To treat polytypic species, it is obvious that we could, if we wanted, define allopatric geographic races as separate species, since they are often separate genotypic clusters. Indeed, present-day sympatric species seem frequently to have evolved from such geographical races. Darwin and Wallace realized that the precise level at which species were defined was arbitrary. But, taking the lead from the taxonomic subspecies revolution of the 1880s–1920s (see Ref. 12) epitomized by Jordan's work[30,31], we should investigate contact zones, and determine whether genotypes within these blend zones form bimodal or single clusters.

Taxonomically, this goes back to Jordan's definition of polytypic species[31]: 'The principal criterion of the conception "species" is that species can exist together without fusing, no other barrier keeping them apart than their own organisation'. Evolutionarily, the definition means that speciation is the formation of a genotypic cluster that can overlap without fusing with its sibling. A sample obtained from a single site plotted as a histogram along a hybrid or species index (Fig. 1) should show a single bell-shaped curve if all individuals belong to a single species, and a multiply-peaked curve if they belong to two or more sibling species. In cases where two populations are not in contact, the definition remains arbitrary, and 'the opinion of naturalists having sound judgement and wide experience seems the only guide to follow'[3]. This arbitrariness in allopatry is an inevitable consequence of evolution; it might be viewed as a weakness of the genotypic cluster definition, but the biological concept has the same problem[7]: 'the decision whether or not to call [geographical isolates] species is by necessity somewhat arbitrary'. The arbitrariness of allopatric races and species is a consequence of the lack of reality and cohesion of actual species over long distances, rather than any problem with definitions. 'Naturalists having sound judgement' will appeal to a null hypothesis: if there is no evidence for separate species from sympatric overlap, closely related allopatric forms should mostly be considered conspecific.
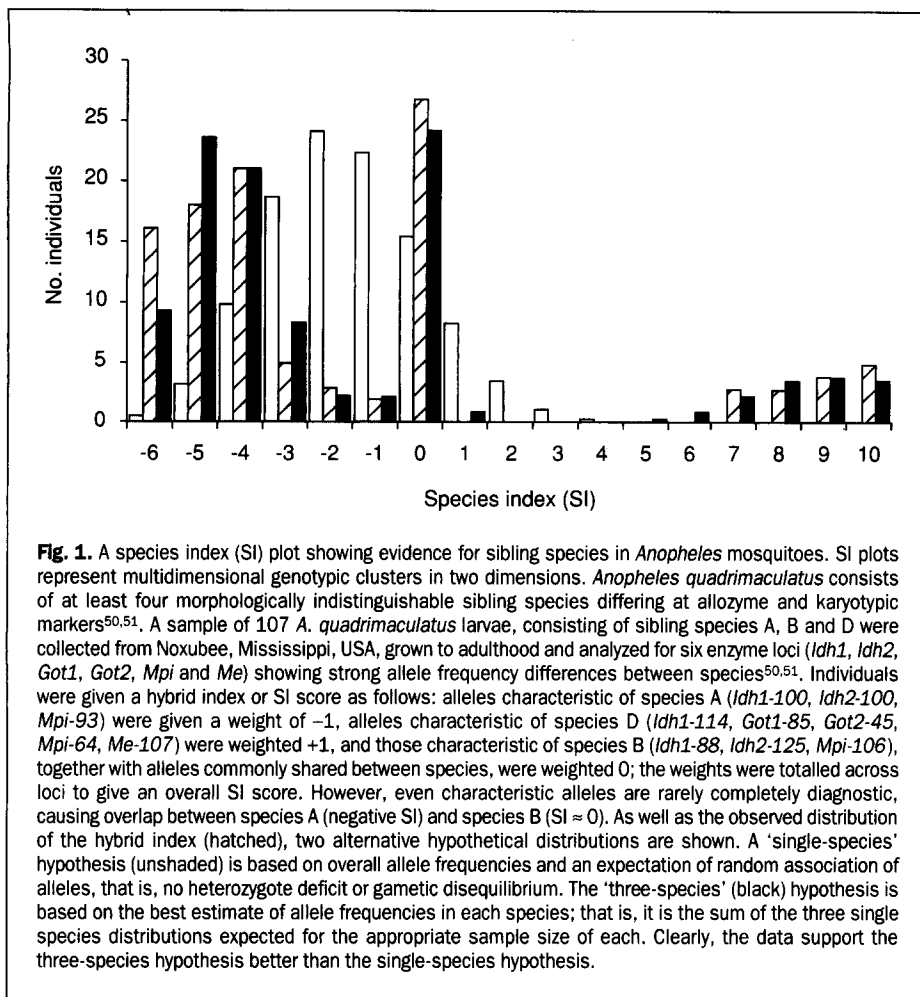
The most important feature of the genotypic cluster definition is that species can be affected by gene flow, selection and history, rather than being defined by these processes. We can then discuss

why a species is maintained as a single genotypic cluster. One of the reasons, of course, will be reproductive continuity and gene flow; but, with the biological concept, such a question and answer is logically impossible since reproductive continuity is used in the definition. In any case, gene flow is not the only factor maintaining a cluster; stabilizing selection will also be involved[7,22], as well as the historical inertia of the set of populations belonging to the cluster.

We can also ask, now, what keeps sympatric species separate. Part of the answer is a low level of gene flow, but distinctness also depends on the strength of selection, mutation and drift keeping the populations apart. Clusters can remain distinct under relatively high levels of gene flow provided there is strong selection against intermediates; species will be maintained when selection balances gene flow. Thus, species defined as genotypic clusters can hybridize, as in many plants like Darwin's cowslip and primrose, and as in ducks, orchids and birds-of-paradise. The maintenance of sympatric species is not just due to reproductive traits, but also due to ordinary within-species, stabilizing, ecological adaptations that select disruptively against intermediates or hybrids. By concentrating on genotypic clusters as opposed to an interbreeding concept, we are able to separate the causes of species distinctness from the observable distinctness itself.

The genotypic cluster definition of species is already in use. Avise and Ball[32] have tackled how modern genetic information can be used to define species. They arrive at a 'genealogical concordance' method, whereby species are recognized if there are correlated molecular character sets that do not form intermediates when in contact. In the bluegill sunfish (Lepomis macrochirus) allozyme and mtDNA characters, although highly divergent between races, are found in near-random combinations in the centre of a zone of overlap. Their method, therefore, showed a single genotypic cluster at the site of contact, which led to the conclusion of a single species. The method did not depend explicitly on assumptions of genealogical divergence of the markers used (though the existence of separate species will ultimately result in genealogical concordance for different markers), or on particular levels of interbreeding; instead the method simplifies to a pattern-based definition, identical to that used by Jordan for morphologically defined species and subspecies more than 80 years earlier[31].

Many other scientists use essentially the same definitions. Studies of sibling species have always relied on genetic evidence for separate sympatric clusters to

Fig. 1. A species index (SI) plot showing evidence for sibling species in *Anopheles* mosquitoes. SI plots represent multidimensional genotypic clusters in two dimensions. *Anopheles quadrimaculatus* consists of at least four morphologically indistinguishable sibling species differing at allozyme and karyotypic markers[50,51]. A sample of 107 *A. quadrimaculatus* larvae, consisting of sibling species A, B and D were collected from Noxubee, Mississippi, USA, grown to adulthood and analyzed for six enzyme loci (*Idh1, Idh2, Got1, Got2, Mpi* and *Me*) showing strong allele frequency differences between species[50,51]. Individuals were given a hybrid index or SI score as follows: alleles characteristic of species A (*Idh1-100, Idh2-100, Mpi-93*) were given a weight of –1, alleles characteristic of species D (*Idh1-114, Got1-85, Got2-45, Mpi-64, Me-107*) were weighted +1, and those characteristic of species B (*Idh1-88, Idh2-125, Mpi-106*), together with alleles commonly shared between species, were weighted 0; the weights were totalled across loci to give an overall SI score. However, even characteristic alleles are rarely completely diagnostic, causing overlap between species A (negative SI) and species B (SI ≈ 0). As well as the observed distribution of the hybrid index (hatched), two alternative hypothetical distributions are shown. A 'single-species' hypothesis (unshaded) is based on overall allele frequencies and an expectation of random association of alleles, that is, no heterozygote deficit or gametic disequilibrium. The 'three-species' (black) hypothesis is based on the best estimate of allele frequencies in each species; that is, it is the sum of the three single species distributions expected for the appropriate sample size of each. Clearly, the data support the three-species hypothesis better than the single-species hypothesis.

confirm species distinctions proposed initially on the basis of crossing studies. Lack of mating, sterility or inviability in inter-strain crosses has never been taken on its own as good evidence of separate species[33], including even Dobzhansky's own studies of sibling *Drosophila* species[10]. In spite of high levels of hybridization, Grant[15] regards Darwin's finches (*Geospiza*) on Isla Daphne Major as separate species on the grounds of morphological clusters based especially on beak shape, a trait that Grant himself has shown to be controlled by selection. Sbordoni[34] produces a genotypic cluster definition based on his allozyme work of a large variety of hybridizing taxa. Patton and Smith[35] define species of pocket gopher (*Thomomys*) genotypically on the basis of few or no intermediates in sympatry, and then show genetically how *T. townsendii* must be derived from a particular chromosomal race of *T. bottae*. This forces the conclusion that the parent species, *T. bottae*, is paraphyletic. Finally, recent theoretical and genetic work on low levels of gene transfer and disequilibrium in bacteria[36] show that genotypic clusters make better-defined groups of predominantly clonal organisms than definitions based on gene flow and recombination[37,38]: 'Defining bacterial species as strains which form

distinct sequence clusters would then give prokaryotic and eukaryotic species the shared property of permanent neutral divergence'. Clearly, the definition could apply to eukaryotes as well as to prokaryotes. If we all adopted a genotypic cluster method, we would have a unified species definition for eukaryotes and prokaryotes, as well as the common property that species must differ at a number of neutral (and/or selected) genetic traits to be detectable.

Space prevents a detailed discussion here of a variety of potential problems in using a genotypic cluster approach. Problem characters include genes found in different proportions in different individuals (e.g. sex-linked genes), genes on chromosomal inversions, polyploidy and other cases where heterozygous deficit or linkage disequilibrium are important in natural populations. Broadly, these problems are solved as follows.

• In examining any set of morphological or genetic data, one should use a single species as a null hypothesis, and only accept the more complex hypothesis of two or more species if it fits the data better (Fig. 1). Typically, most problems of heterozygote deficit and gametic disequilibrium at particular loci within populations

will not lead to the recognition of separate species when the whole data set is examined (in Fig. 1, *Mpi* is sex-linked, giving pronounced apparent heterozygote deficits in males, but has been analyzed as though autosomal).
• Obviously, the pattern of inheritance is a constraint; if, as in the case of a sex-linked marker, inheritance is non-mendelian, one should incorporate knowledge of the hereditary system into a test for cluster status; likewise for inversions, polyploidy and other distortions of mendelian heredity.

Many biologists would like to define species as populations that have become permanently separate (e.g. Refs 30,38). If a genotypic cluster definition is accepted, evolutionary permanence is no longer guaranteed because the future is unpredictable. Suppose environmentally induced selection is keeping apart two sympatric, diverging genotypic clusters that continue to hybridize: if the environment changes, the two clusters may again fuse; if the selection remains the same, divergence may continue and become permanent. Permanent evolutionary separateness is therefore useless in defining species whenever there is interspecific hybridization. We all agree that species are lost by extinction; it seems not unreasonable to have a definition under which species may be lost by hybridization as well. Once again, it is better to have species that are free to evolve in a variety of ways than to restrict their evolutionary potential in a concept-definition.

'Isolating mechanism' is a useless term

The term 'isolating mechanism'[10] contains two strong implications: (1) that isolation is an adaptive 'mechanism'[21], and (2) that 'isolation' is different from other genetic traits of populations or species, neither of which are necessarily true. This term was a product of Dobzhansky's[10] holistic, strongly group-selectionist view of species cohesion, at a time when group selection and individual selection had not been clearly distinguished. Some modern evolutionists find themselves unconfused by these potential implications[39], but it is perhaps worth considering just what 'isolating mechanisms' are purported to be.

As currently formulated[6,7], 'isolating mechanisms' consist of all heritable and environmentally-determined traits that prevent fusion between the populations we call species. To say that biological species are characterized by 'isolating mechanisms' is therefore an empty statement. To include such an enormous number of different effects under a single label must be one of the most extraordinary pieces of philosophical trickery ever foisted

successfully on a community of intelligent human beings. We would be far better off thinking about levels of gene flow (so-called 'prezygotic isolation') and stabilizing or disruptive selection (so-called 'postzygotic isolation') separately[22], rather than attempting to cope with a grab-bag term that incorporates both. The more recent terms 'specific mate recognition system'[21] and 'cohesion mechanism'[22], in attempting to rectify the difficulties, have similar problems themselves: the traits to which these terms refer may explain the existence of species, but cannot also be thought of as traits that species must have in order to exist. Textbooks and undergraduate courses using the terms 'isolating mechanism' or derivatives are anachronistic; few researchers on speciation or hybrid zones seriously now use these terms[40,41].

Potential effects of adopting the genotypic cluster definition

In taxonomy

As already emphasized, many, perhaps most, systematists are currently using the genotypic (or morphological) cluster definition. A recent approach that differs from this is the phylogenetic species concept. Cracraft argues that species should be defined by apomorphies[42]: any apomorphies characterizing a group of individuals may be used to recognize a separate species. But with detailed morphology or modern molecular techniques, one can find apomorphies for almost every individual[30,32]. The phylogenetic species concept is refreshingly sensible in that, by treating races as potential species, it agrees with Darwin's idea that geographic races and species are quantitatively rather than qualitatively different. However, the phylogenetic species concept is less sensible in practice since there can be no clear guidelines as to where in the taxonomic hierarchy to separate species. 'Speciation' would come to mean merely the evolution of a uniquely derived trait, rather than the production of divergent populations that can coexist in sympatry. As a final argument, I question the validity – possibility, even – of using phylogeny to determine species, when these same species are then used as terminal taxa in estimating a phylogeny. Phylogenetic systematics may be the best way to organize terminal taxa, but it cannot be used also to define the terminal taxa that are to be organized.

In practice, most phylogenetic taxonomists (with a few notorious exceptions) stop short of defining species using Cracraft's and related definitions. But there is an opposite extreme. Many systematists feel that subspecies are not objectively definable, whereas species are[20]; a movement now exists to rid zoology of the sub-

species category. This would be a pity, since there are certainly many races that intergrade freely at their boundaries, but that are strongly differentiated and relatively constant in morphology, genetics and ecology[41,43,44] – for example, Bombina toads[45] and Lepomis sunfish[32].

Under the genotypic cluster definition, subspecies are not very different in kind from species, differing only in their tendency to produce intermediates when they overlap. Except in zones of overlap, subspecies are often as objectively definable as some species. Successive taxonomists have shuffled well-defined bird and butterfly subspecies between species, showing that in these cases species are less easily defined than their component races[42,46]. To avoid the twin dangers of oversubdivision via the phylogenetic species concept, and of lumping obviously distinct infraspecific variation via an over-strict application of the biological species concept, we need subspecies as well as species categories[30,31].

In speciation studies

Under the genotypic cluster definition, the interesting part of speciation is divergence into genetic clusters that can coexist, not the final demise of gene transfer. To understand speciation, we need to understand when disruptive selection can outweigh gene flow between populations. Disruptive selection will dominate when gene flow is low, but it is unlikely that gene flow must be reduced to zero, as in the allopatric model.

While 'hybridization' may sometimes be caused by unusual circumstances like climatic change or human intervention[7], it should also be a common feature of ongoing parapatric or sympatric divergence. There is little reason why speciation cannot occur via something similar to Darwin's and Wallace's mechanism[3,47], whereby divergent selection favours extremes at the expense of intermediates. A relictual hybrid zone would be left between the forms during intermediate stages of divergence in parapatry. Gene flow only weakly inhibits adaptation in parapatric populations[48]. Whenever divergent adaptation has pleiotropic effects on gene flow, population divergence and speciation could result simply as part of the normal process of evolution by natural selection[3], rather than requiring special conditions, such as founder events or complete allopatry.

In conservation

Are species more important in conservation than races or hybrids[44,49]? Clearly, there is no simple solution, but it seems obvious that we should not ignore the huge amount of genetic biodiversity found

in infraspecific taxa[33,49]. 'Hybrids', such as the 'red wolf' might be relicts of formerly widely distributed forms; there seems little reason to discriminate against such populations in conservation decisions provided that they are not suffering outbreeding depression. Hybrid zones are natural morphological and genetic phenomena[41,43], intrinsically worth preserving regardless of taxonomic status. Similarly, subspecies such as Bombina toads[45] and Lepomis sunfish[32] can be genetically more different than sibling species in other groups. As a member of a genetically heterogeneous species that values its own genetic diversity, I can think of no logical reason for preferring species over equally divergent races, subspecies or hybrid swarms. We are much more interested in conserving actual morphological, ecological and genetic diversity than in structuring conservation around a nebulous taxonomic level about which, in the past, there has been so much disagreement.

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Species diversity or biological diversity?

Biological Diversity: The Coexistence of Species on Changing Landscapes

by Michael A. Huston

Cambridge University Press, 1994. £60.00/$100.00 hbk, £24.95/$34.95 pbk (xix + 681 pages) ISBN 0 521 36093 5

Throughout the 1960s and 1970s, a centerpiece of ecology was the search for comprehensive explanations of patterns in 'species diversity'. By 1980, the term 'biological diversity' had entered both technical and popular writings, partly in response to rising concern about a contemporary global extinction crisis[1]. And while basic and theoretical ecologists sought to explain patterns of species diversity, conservation biologists strove to protect biological diversity.

Given this usage, the title of Huston's book *Biological Diversity* does not accurately reflect its content or the author's goal – 'to explain the regulation of species diversity and why the number of co-occurring species varies under different conditions'. Only a short concluding chapter deals with the broader connotations of biological diversity. This disconnection between title and text is evident throughout the book, starting in the table of contents: 'biological diversity' appears twice, 'species diversity' a dozen times.

Huston begins with a comprehensive overview of patterns of species diversity and factors (productivity, sample area, spatial heterogeneity) correlated with pattern for

many taxa and environments. He notes, and I agree, that attention to statistical methods for quantifying diversity 'has contributed virtually nothing to the ecological understanding of species diversity' (p. 64).

General theories are essential for qualitative predictions about patterns of species diversity. Huston's general theory sees species diversity as a reflection of a dynamic equilibrium between competitive displacement and disturbance at a site; stochastic events prevent simple competitive equilibrium in small populations. Across heterogeneous landscapes, equilibrium properties emerge as an asymptotic limit of increasing area – the ecological equivalent of the law of large numbers – rather than the result of competitive equilibrium.

Quantitative predictions about species diversity require well-defined mechanisms. Huston's mechanistic approach is based on the premise that understanding ecological phenomena must begin with a focus on individual organisms – their growth, survival and reproduction, their responses to physical environments, their interactions with other individuals and their responses to environmental gradients, disturbance regimes and successional processes.

In Huston's view, plants are the key group because they play a predominant role in structuring most terrestrial and some aquatic and marine environments. [Structural species (e.g. trees, corals, kelp) create or provide the physical structure of the environment; interstitial species (e.g. birds, arthropods) live within that structure.] As an animal ecologist, I would prefer a better balance among taxa, especially, as Huston himself notes in a discussion of genetic diversity, because hypotheses are 'likely to

apply only to a subset of communities in which the diversity is regulated by mechanisms compatible with the assumptions of the hypothesis'.

For plants, disturbance frequency and nutrient limitation are dominant gradients. Huston contrasts the influence of 'resource gradients', which can be depleted by organisms, with 'regulator gradients' (e.g. temperature), along which a principle variable regulates the rate of physiological processes in organisms. From this synthesis, he reveals, counterintuitively, that the highest species diversities are found in areas of reduced nutrient availability and low productivity, such as tropical rain forests.

Huston measures the success of his synthesis with four detailed case studies (Part 4): endemism and invasions (42 pages), marine ecosystems (70 pages), fire-influenced ecosystems (70 pages) and tropical rain forests (72 pages). These explorations are more satisfying to me than the plant-dominated synthesis of Part 3, although I expect that readers will find points for debate in the chapters dealing with their areas of expertise. Huston's text sometimes is not successful in distinguishing inferences from empirical observations, theory or predictions based on theory.

In the last chapter, Huston goes astray with a short and entirely too superficial analysis of the connections among low agricultural productivity, low primary productivity in natural ecosystems, and high species diversity in plants and low trophic levels. Because, Huston argues, land with high plant species diversity, such as tropical rain forest, rarely can sustain profitable agriculture or even productive forestry, 'there is no inherent conflict between the preservation of