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SPECIES AND CONSERVATION

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Abstract

There is a great deal of confusion about species “concepts” in the biological literature. It is currently fashionable to say that there are no species concepts that can satisfy all fields, and that we should have a different species concept for each kind of research programme. I disagree with that view, because to me, the term species expresses something universal and practical that enables the different fields of biology to speak to each other. I here argue that species are best defined as genotypic clusters that are distinguishable from other such clusters when they overlap. This is not a new idea, and it can be traced back to Darwin's idea of species as morphological clusters. I discuss a number of potential problems with a genotypic cluster definition of species. The most apparently severe is that species and subspecies (or races) are not easy to distinguish, especially if they are not in contact. However, the biological, genealogical, phylogenetic, ecological and a whole host of species concepts flounder as well. Genotypic clusters are at least definable in parapatry, which would not necessarily be true for the others. Viewing species as genotypic clusters that coexist in sympatry, and races as allopatric or parapatric genotypic clusters, in any case stresses the important continuity between species and races; this indefiniteness between species and subspecies is a fact of life that should be incorporated into our way of thinking about these taxa, rather than avoided. How should species be incorporated into conservation decisions? On the one hand, I agree that overall levels of genetic divergence should be taken into account when deciding what to conserve.

On the other hand, I feel strongly that, as well as scientific data, political, economic, and aesthetic considerations will determine conversation decisions. Genes which affect ecology and behaviour to cause genotypic clustering in sympatry are to me more "aesthetically pleasing", and worthwhile considering in conservation than neutral genetic markers. Species distinctions as well as overall genetic distance will affect the relative values of conservation of different taxa.

Species: part of a general problem of definitions

Many different definitions and “concepts” of species now exist. The uncertainty over species is causing angst in any work involving taxonomy, biogeography, species evolution, speciation, and in applied subjects such as conservation or genetic resource management. Whole chapters of undergraduate textbooks on evolution now discuss how the many different species concepts fit together. At the same time, most evolutionists agree they can study speciation without having a clear definition of species which works in practice. Conservationists can conserve, genetic resources can be managed, and so on. How have we got ourselves into this weird pickle? Can we do anything to extricate ourselves from this philosophical ooze? Or is the “species problem” something to be lived with rather than solved? In this paper I argue that we should discard most modern species “concepts”, which require comparison of actual populations with an idealized evolutionary processes, and instead concentrate on a simple definition which works in practice.

To strip away the layers of tortuous reasoning which have led us to mystify the field of species evolution over the last sixty years or so, it may be eventually necessary to undertake a full logical and historical treatment. The problems go far deeper than mere problems with species. They are general problems about definitions in the pursuit of knowledge, problems which have been a part of epistemology since the times of Plato and Aristotle. One reason we biologists persist in using terms from ancient philosophy, like “species” and “genus”, when they are obsolete in other branches of knowledge, is that many of us subconsciously retain the vitalist notion that organisms must be studied differently from inanimate objects. The claim that biology is different from other sciences, and should therefore not be judged by the same standards, has recently been revived forcefully by Ernst Mayr (1982). This view is, I believe, quite mistaken. While living things have emergent properties that make them qualitatively different from non-living things; they are made of the same stuff, and there is no *a priori* reason why the same laws of classification (along with the same laws of physics and chemistry) should not apply.

But the reader (or listener) may be relieved to note that I am neither qualified nor inclined to do a full analysis; instead, I will argue using evidence and examples from biology rather than philosophy. Although biological classification is not so different from the hierarchical classifications of inanimate objects like library books (it is of course true that biology may *fit* a hierarchical classification better than non-living things, but the process of classification will still be similar), I do not advocate scrapping the term “species”. To do so would cause chaos in nomenclature, systematics and biodiversity databasing. In any case, the term species is usable if interpreted clearly. So I will follow Darwin (1859) by merely advocating a more theory-neutral and practical way to think about species.

Why bother?

A recurring view I have encountered in letters from other evolutionists is that we don't actually need species concepts or definitions to study evolution. To some extent, of course, this is true; changing the definition of species is not going to change the value of studies on, say, hybrid zones, or coevolution. But, as someone interested in speciation, I do think it is well worth making definitions which clarify what my field is about. A definition of species will demarcate speciation from other kinds of evolution; we can then go on to investigate the ways in which speciation happens. I agree that studies of the continuum between races and full species are worthwhile, but we would like to know if there are any crucial events which make speciation different from ordinary microevolution. In my view (see also Bengtsson, 1982) there is a critical transition in speciation which corresponds to crossing the cusp between allopatric and sympatric differentiation at multiple loci. I am less sure about the value of species definitions in conservation (see below); but we need to clarify the evolutionary arguments before applying the results to conservation.

A universal and practical definition?

It is fashionable to argue that definitions of species should be varied depending on the question being asked in a particular research program, because different species concepts give different answers (de Queiroz & Donoghue 1988, Sluys 1991). In systematics, we might have phylogenetic species (Cracraft 1989); in molecular studies, genealogical species (Baum & Shaw 1995); in the fossil record, evolutionary species (Simpson 1951); in studies of speciation, biological, recognition or cohesion species (Mayr 1942, Paterson 1981, Templeton 1989); and in ecology, ecological species (Van Valen 1976). In conservation, it is suggested, we should be more interested in "evolutionar[il]y [significant] units" than in species (Rojas 1992, Moritz 1994). But, historically, species and taxonomy have been a universal backbone which connects different branches of biology. Universality is the reason why species are useful categories, and finding general principles is the goal of science; a universal species definition should not be given up without a fight.

In addition to universality, I think we should strive for practicality; a definition that can be applied to actual organisms. In speciation research, we would like to know whether there are any general modes of evolution of *actual* new species. When a new type of organism is discovered, we would like this *particular* organism to be classified unambiguously as a morph, geographic race, species, or higher taxon. Discussion of whether species are important in conservation is hardly possible (and certainly not necessary!) without practical criteria to decide whether *particular* endangered populations are species or not.

The alternatives to a practical definition, usually called “species concepts”, require comparison of actual populations with some kind of evolutionary ideal. The “biological species concept”, in which species are groups of “actually or potentially interbreeding” populations, implies there should be a lack of gene flow between species, but does not specify what the lower cutoff point is in practice. Natural hybrids and backcrosses between many sympatric taxa that supporters of the biological concept classify as species (whales, many birds such as duck and birds of paradise, plants such as orchids, and so on) suggest that the biological species concept has some major difficulties. Interspecific hybridization occurs in about 9-12% of bird and butterfly species (Guillaumin & Descimon 1976; Grant & Grant 1992), and in a much higher proportion of plant species (Stace 1991), to say nothing of the problems among bacterial or other largely asexual taxa (Cohan 1994). Phylogeny or genealogy might seem to give us a better, more “pattern-based” concept of species, but phylogenetic concepts are plagued by the fact that genealogies of different parts of the genome are often different, suggesting reticulate evolution or horizontal gene transfer (Avise 1994), to say nothing of the problems of genealogy estimation.

In addition, these concept-definitions are circular when used in evolutionary studies, because studying evolution requires defining the things that evolve, independently of the process of evolution to be investigated. (Like de Queiroz & Donoghue, I include phylogeny as a type of evolutionary study). The various species “concepts” of Dobzhansky, Mayr and subsequent evolutionists have been stimulating and useful, but are best interpreted as hypotheses for the evolution and maintenance of distinctness of species, rather than being definitions of the evolving categories. Thus, absence of interbreeding or monophyly are two evolutionary hypotheses which can explain the gaps between species. To be testable hypotheses, these concepts must be falsifiable under certain imaginary or real circumstances. This requirement is met under the practical definition of species outlined below: actual species can and do interbreed or evolve reticulately.

Species as genotypic clusters

I have therefore proposed that species should be defined practically, as distinguishable “genotypic clusters” in sympatry (Mallet 1995a,b, 1996a,b). Within a local area, we can recognize two species instead of one if we find two peaks in a multilocus genotypic distribution instead of one. Species are clusters separated by gaps in multidimensional genotypic and phenotypic space (Fig. 1). The idea is not only mine: viewing species as genotypic clusters traces its ancestry to the morphological cluster ideas of Charles Darwin, Alfred Russel Wallace and Karl Jordan (see Mallet 1995a for a brief history). Recent evolutionists and systematists working on everything from bacteria to ants to fossil sea urchins to whales, have revived these ideas about morphology, and have added genetic information (e.g., Hutchinson 1968, Guillaumin & Descimon 1976, Avise & Ball 1990, Sbordoni 1993, Longino 1993, Cohan 1994, Patton & Smith 1994, Smith 1994). An appeal to genotypes as opposed to morphology gets around the two major problems with Darwin's morphological cluster definition of species (these problems were first raised by Poulton [1902], Dobzhansky [1937] and Mayr [1942]). The first problem is that discrete morphs within species could have been defined as separate morphological clusters, and therefore separate species, under Darwin's definition. Genetically, however, morphs in a polymorphic species differ genetically at only one locus or a tightly linked block of loci; other loci will demonstrate continuity between the two morphs. Genetic differences, as well as similarities, characterize individuals both within and between species, so it must be a particular kind of genetic divergence that characterizes the groups of individuals we call species. I argue this divergence must consist of correlated multilocus differences. Genotypic distributions at multiple, unlinked loci will therefore distinguish between species and morphs within any local area. The second problem is that certain populations almost universally agreed to be species, dubbed “sibling species” by Dobzhansky, are virtually indistinguishable morphologically. Well-known examples are found among willow warblers (*Phylloscopus*), fruitflies (*Drosophila*) and *Anopheles* mosquitoes. However, these species also have multiple genetic differences (usually including genes that cause assortative mating) which enable their clear recognition (Mallet, 1996a, b).

In palaeontology, as well as in many living organisms, we do not yet have genotypic information; however, morphology usually gives good clues to genetics, and taxonomists have developed useful morphological techniques to distinguish species from morphs within polymorphic or sexually dimorphic species (Rothschild & Jordan 1903; Longino 1993, Smith, 1994). This is achieved by investigating character differences unlikely to be correlated with morph- or sex-specific characters (Hutchinson 1968). With reduced amounts of information available to morphological systematists, it is obvious that some species will be misclassified; especially sibling species. However, this is not a serious problem because it is true of all scientific assessments that they will be improved by more data.

In the genotypic cluster definition, there is no distinction between what a species is (its definition) and how it is recognized (its use). This is extremely difficult for some people to accept. Species defined merely as a convenience for human discourse do not satisfy our urge to incorporate “underlying biological reality” into the definition. My answer to this is that the nature of this “underlying reality”, if it means anything more than clusters of organisms with gaps between them, is almost always controversial and best treated as a set of hypotheses. I believe most will find a practical species definition more useful both in evolutionary theory and in taxonomic practice.

Apparent problems with species as genotypic clusters

a) Species versus races or subspecies

A number of correspondents have complained to me that under the “genotypic cluster” definition, geographic subspecies (races) cannot be distinguished from species. My answer to this is admittedly confusing and even apparently contradictory: I argue both (1) that species are very *similar* to races, indeed they overlap in terms of genetic differences, so that mistakes do not matter much; and also (2) that, even so, genotypic cluster species are *easier* to distinguish from races than species defined under biological, phylogenetic or genealogical concepts. I will here try to defend these paradoxical views.

(1) Some have argued for the abolition of the category of subspecies (Wilson & Brown, 1953) on the grounds that subspecies are, in practice, not well-defined. Many systematists support this view, even today. However, while there is a continuum from single character (or gene) differences between populations to multiple gene difference, many subspecies are now realized to be meaningful in terms of multiple character differences (Wilson, 1994). For example, a large sample of pairs of taxa that meet at hybrid zones (mainly geographic races initially detected on the basis of morphology or chromosomal structure) were found to have fixed differences at 20% of their enzyme loci (Barton & Hewitt 1983). Clearly, these parapatric forms (e.g. *Bombina* - see Fig. 1a) are definable genotypic clusters that lose their identity only in narrow zones of contact; in allopatry they are easily identifiable. They belong to the same species, under my definition, because in areas of overlap there is only one genotypic cluster. But parapatric species and races are both genotypic clusters; they only differ because of a trifling (though evolutionarily important) feature in their extremely narrow zones of contact.

It is easy to imagine that, under this definition, one pair of geographic races could be more divergent genetically than another pair of species. Fig. 1 provides examples. The *Bombina* pair is more divergent genetically; yet wherever these two toads overlap, they form a single genotypic cluster (Fig. 1a; see Szymura 1993). The

Heliconius pair are less divergent genetically, but, where they overlap, the two forms remain separate (Fig 1b). Speciation is probably broadly correlated with genetic divergence, but the correlation is imperfect. In conclusion, species and races under the genotypic cluster definition form a quantitative continuum with respect to genetic divergence; the only criterion to distinguish species from races is a qualitative difference in the arrangements of genes into genotypes, expressed solely in narrow zones where two forms overlap.

(2) On the other hand, it is the distinguishability in a local area which allows a practical definition capable of being applied to actual cases. Consider the *Heliconius himera* vs. *H. erato* contact in Fig 1b. Under the biological species concept, it is unclear whether hybridization, which occurs at a rate of about 5-10%, and includes backcrosses, is sufficient to cause one to think of the two taxa as a single species. Although hybrids are quite common, the two pure taxa do not fuse in sympatry, unlike the *Bombina*. Where should one draw the line using the biological species concept? Hybridization at the rate of one in a hundred, one in a thousand? Genealogical studies in the two forms may also give poor definition. Phylogenetic analysis of mtDNA sequence information puts *H. himera* on a cladistic par with other races or groups of races within *H. erato* (Brower 1996), as expected if speciation is a normal kind of population divergence. The boundary between monophyletic species, and races or

populations which also may happen to be monophyletic, is unclear under phylogenetic or genealogical concepts of species.

In contrast, the genotypic cluster definition gives a clear cutoff. As we extrapolate between a case like that in Fig. 1a to another like that in Fig. 1b, we traverse an intermediate stage, in which the distribution of genotypes becomes just significantly bimodal. At this point that we gain evidence that two genotypic clusters are being maintained separately in sympatry, i.e. as separate species. More genetic evidence may enable us to make finer distinctions, or to overthrow shaky distinctions; but this does not invalidate the approach, that is the way science ought to be.

When two populations are allopatric, on separate islands for example, the genotypic cluster definition becomes unworkable because there is no geographical area of overlap between them. The biological species concept, of course, fails at this point as well. “Potential” interbreeding can never be assessed, except in artificial situations which might anyway lead to a breakdown of natural isolation. Phylogenetic and genealogical concepts might seem to have an advantage in this respect since there is no inclusion of geographic information. However, phylogenetic concepts have two much more severe problems: (1) monophyly may exist for small populations, or even single individuals; and, since an unambiguous rather than a hierarchically uncertain grouping is the purpose of species definitions, mere monophyly does not guarantee a reasonable answer. (2) If hybridization between monophyletic taxa is successful and some fertile backcrosses are produced, many perfectly identifiable taxa may not be monophyletic at all of their genes. Whenever there is hybridization, discordant genealogies at different genes ensure that there may often be no single true phylogeny of species on which to base species distinction. Even if hybridization ceased completely, millions of generations may elapse before allelic "sorting" gives similar genealogies at the majority of loci.

So, what should we do in practical situations of allopatric differentiation? The answer is bound to be disputed since many isolates have been defined as separate species already. My own preference is that of a "lumper", to use a single species as a null hypothesis. Suppose there are a series of mainland races (which sometimes abut, and always produce single genotypic clusters in areas of overlap), and mainland species (which, where they overlap, do not fuse into single genotypic clusters). An isolated population which does not contact its congeners should be included as a member of the most similar species unless the nature of its differences are equivalent to those which characterize species on the mainland.

Mistakes about allopatric populations will inevitably be made, since the only good test is where two forms overlap. But, provided one agrees that names should be practical rather than represent evolutionary ideals, I don't think these mistakes matter as much as might be imagined. Perhaps the most bitter pill to swallow by naturalists who know the taxa is that I am advocating that *Bombina bombina* and *B. variegata*, for example, should be considered only as subspecies rather than full species (Fig. 1a). But very little information is lost if people continue to refer to the two forms as separate species on the grounds of their great ecological, behavioural, and genetic differences in allopatry (Szymura 1993). Although I do not know of detailed studies in zones of contact, gray wolves (*Canis lupus*) and coyotes (*C. latrans*) may also be conspecific under a genotypic cluster definition because mtDNA horizontal transfer into wolves is so widespread (Lehman et al. 1991). Again, the names are obviously useful and informative about behaviour, ecology, genetics and morphology, at whatever level they are accepted.

The strong genetic, ecological and behavioural differences between some pairs of parapatric subspecies argue that subspecies and species are very much the same kinds of things. Provided easily recognized allopatric taxa can continue to be named (either as subspecies or species), studies in phylogeny, evolution, ecology and biodiversity can be performed without worrying about exact taxonomic levels. Accurate species counts will only be possible in small areas, such as small nature reserves or single small islands, rather than over large regions, such as continents or major archipelagos, where allopatric species are hard to distinguish from races. But local species counts are usually the most important. In ecology, species packing in different areas is affected by the behaviour and feeding habits of ecological replacement forms, independently of whether these forms are races or species. In conservation, comparison of the biodiversity of two continents (e.g. South America vs. Papua New Guinea) is normally unnecessary. One will be more interested in comparing the biodiversity of two local areas within the same continent or even between continents, and making conservation decisions on the basis of this comparison.

b) Effective gene flow

Various correspondents have pointed out to me that genotypic clusters correspond closely to a gene flow concept of species like the biological concept, provided that one means, by “gene flow”, “genes that get through”, or “effective gene flow”. The idea is that interbreeding or hybridization is not the same as gene flow. If we assess whether genes are moving between taxa and then staying, instead of assessing interbreeding, then we can distinguish races from species under this definition: there are two species if genes are not getting through, and only one if they are. “Effective gene flow” has two major problems. First, like the term “reproductive isolation” (see Mallet 1995a), “effective gene flow” incorporates not just gene flow itself, but also selection against the genes which flow. These are opposing forces which, in my view at least, are best kept completely separate. Second, “effective gene flow” is extremely difficult to detect. We cannot just look at F1 hybrids; we must look at F2s, backcrosses and beyond, for many generations, to see if any genes in any hybrids make it through to other taxa. Short of following in detail all consequences of all hybridizations (I do know of one such study - see Grant 1993), the only way to detect “effective gene flow” is indirect, i.e. by studying the genotypes of hybridizing taxa. The existence of two genotypic clusters would imply that “effective gene flow”, as defined above, is not happening, at least at some loci. In other words, the genotypic cluster definition of species is the practical application of the “effective gene flow” concept. If this is the intent of supporters of the “biological species concept”, then I agree with it, although I prefer terminology to reflect practice rather than evolutionary ideals. However, I have not yet seen any printed attempt to make the biological species concept practical in terms either of genotypes or of morphological characters.

c) Evolutionary independence

Others feel strongly that species should ideally be “evolutionarily independent” (e.g. Bush 1994, Baum & Shaw 1995). To my mind, the trouble with this is that the evolutionarily independent category is likely to be too broad. The abundance of interspecific, and even intergeneric hybrid birds of paradise (Mayr 1942; Fuller 1995) or Darwin's finches (Grant 1993) implies that advantageous, and perhaps even neutral genes, could very likely pass between currently defined species. Actually, different genes will behave differently. In two sympatric genetic clusters, the first genes to diverge will be those under disruptive selection. Next, genes that are neutral will start to diverge. Finally, if isolation becomes extremely strong, even globally advantageous genes will be prevented from crossing between taxa. There is some evidence for differential gene flow between species: Yang & Patton (1981) showed that different Darwin's finch species on the same island may share more enzyme alleles than conspecifics from different islands; this would also fit with knowledge of hybridization (Grant 1993). Of course, it might be quite sensible to call all birds of paradise, or all Darwin's finches, members of the same species. But we would still be left with the need to discuss sympatric forms with different genetics, morphology, behaviour and ecology; we would probably want to name them as some new kind of sympatric subspecies. In fact, evolutionary independence, when (or if) it does finally arise, has as an initial trigger this kind of genetic divergence that can be maintained in sympatry (Cohan 1994). My personal taste is for species to be defined at a lower level than complete evolutionary independence, or completely effective genetic isolation. To me the most interesting part of speciation is the production of genetic divergence at multiple loci that can be maintained in sympatry, not the final demise of a trickle of ineffective gene flow. Sympatric genotypic clusters are already partly evolutionarily independent since they can evolve genetic, ecological and behavioural differences. However, they may not become completely evolutionarily independent for many millions more generations, if at all.

Should species status enter into conservation decisions?

I have already pointed out that pairs of species may be more similar genetically than pairs of races in different taxa. Races, except for trivial differences in areas of overlap, are very much the same kinds of things as species. If we equate conservation value with genetic distance (Crozier 1992), whether two populations are species or races may be irrelevant to conservation. Species are usually more divergent than races, but this is only a general tendency (see Ayala et al. 1974, Emelianov et al. 1995). I have already put forward the view that, all other things being equal, I would probably agree with Crozier, and conserve a pair of strongly divergent races rather than a pair of only slightly divergent species (Mallet 1995a).

I would now like to draw back somewhat from this view, and give an argument for the alternative view, that separate species might be more valuable than races, at least when genetic differences between races and species are similar. Speciation into separate genotypic clusters occurs when populations become partially independent of one another in sympatry. These species must diverge at important genes affecting ecology and behaviour, and, eventually, they may diverge even at genes that have little effect on survival. Races also diverge, but species differ in that they can coexist in sympatry; their ecology and behaviour must be sufficiently divergent to allow stable coexistence (Bengtsson 1982). Arguably, genes causing such ecological and behavioural change are more valuable in conservation than genes which permit divergence only in allopatry.

Is conservation an art or a science?

While scientists are the best people to advise on conservation, conservationists have to compare the values of different actions. For example, Great Britain, consisting of a group of small and species-poor islands close to a more diverse mainland, has few endemics worth conserving. Arguably, we British should spend all our conservation money on European habitats in the Alps, in Mediterranean habitats, or even on tropical rainforests. These habitats have orders of magnitude more species, and far more endangered ones than in our blighted and overpopulated country. In fact, many charity and government organizations spend a great deal of money conserving expensive land in Britain. Mostly, this benefits species with highly restricted distributions in semi-natural habitats on our islands, but which are common in larger areas of less degraded biotopes on the continent. I doubt an internationally ideal solution will be very popular with local British conservationists, and I don't think I entirely disagree with them. I am very keen on conserving the rainforest, but let me have my home patch of sheep-grazed chalk downland as well! The political and economic will for conservation is not on a purely scientific basis of global biodiversity (see Tisdell, this volume), but will have to take into account social factors like the proximity of conservation areas to the homes of influential taxpayers and contributors.

Conservation is not only political and scientific, it is also aesthetic. Science has proved very useful at solving technical “how-to” problems, but has proved useless in solving aesthetic or moral “whether-to” problems. Science is successful because it is falsifiable, and therefore may be disproved; we cannot expect science to do any more than feed data into ethical or political decisions (Packham, 1996). Consider aesthetics: we value the way works of art are put together, not just the amount of paint or the number of pages that makes a painting or book. Similarly, organisms can be valuable in conservation because of the way their genetic diversity is arranged; in this sense, species may be more interesting than races. On the other hand, the quantity of genetic differentiation, as with the quantity of output by an artist, should not be ignored. Two Darwin's finch species may differ genetically only at a handful of genes affecting beak morphology and a few song characteristics that are transmitted culturally. However, our strong aesthetic preoccupation with the important and highly selected phenotypes generated by these slight differences will bias us towards conservation of the Darwin's finches as separate species. We are not just interested in genetic distance at neutral markers. We would like to conserve genes that do more important jobs like forming appearance, determining ecology and behaviour, and especially, perhaps, making species.

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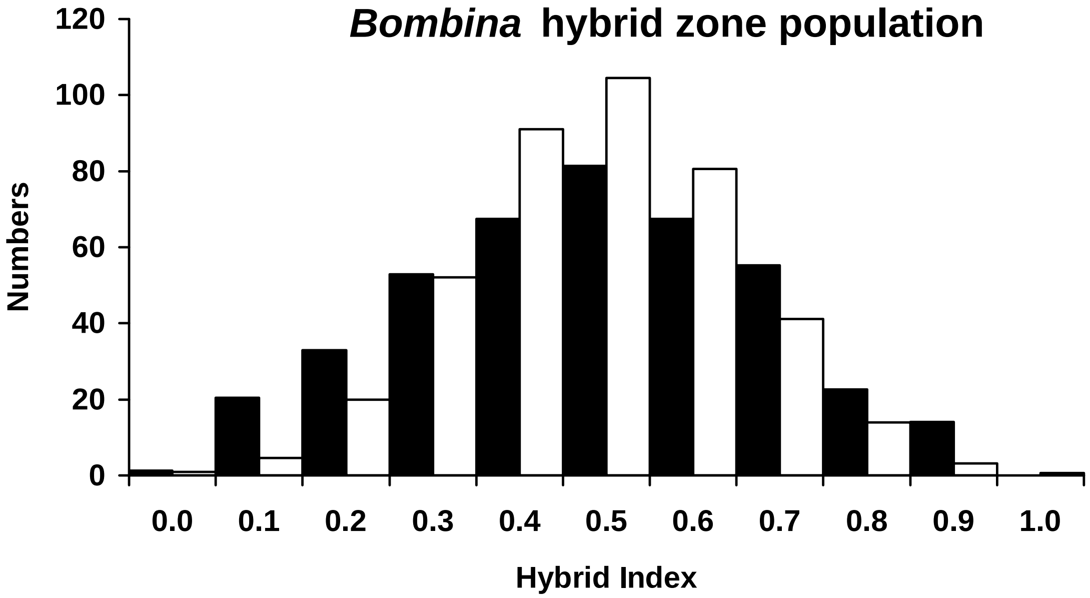
Figure legend

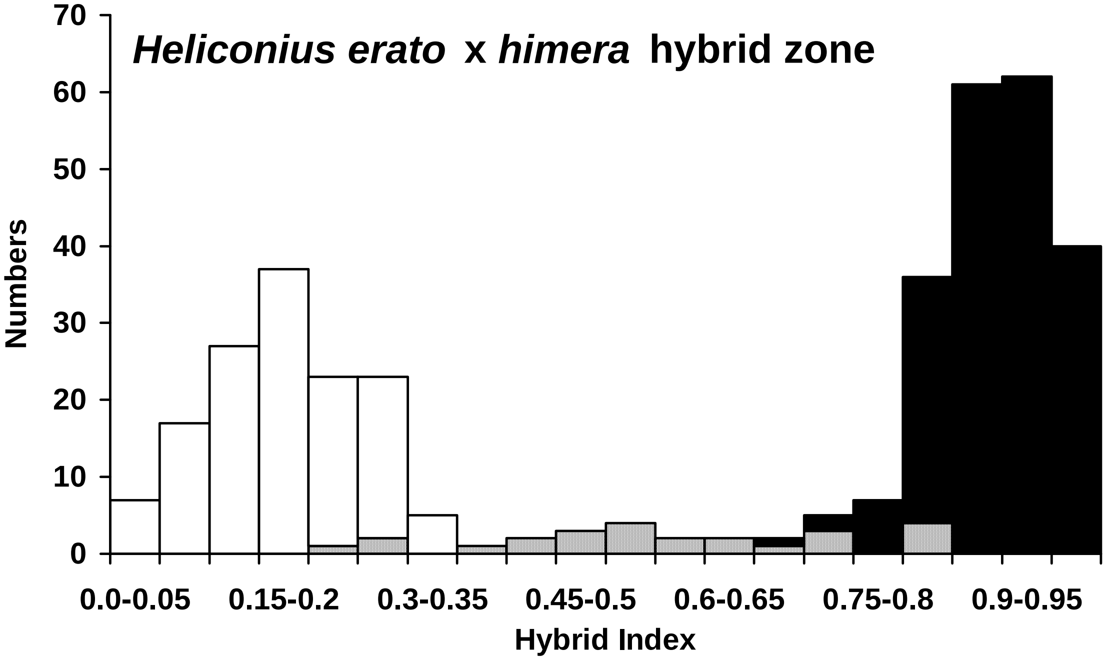
Figure 1. The distributions of hybrid index scores in two hybrid zones.

A. *Bombina bombina* x *B. variegata.* The observed distribution of scores at a single locality, Kopanka 2, in the centre of the hybrid zone in S. Poland (solid bars) is compared with the expected binomial distribution under random association of alleles (hollow bars). The hybrid index for each individual is calculated as the fraction of *variegata* alleles at five unlinked loci showing fixed differences between the two taxa. There are strong linkage disequilibria or gametic correlations between these allozyme loci (the correlation coefficient, $r \approx 0.15$), which cause the observed distribution to have a higher variance than expected under random association. However, the figure shows that even these strong gametic correlations do not result in separate genotypic clusters to be maintained (redrawn with PERMISSION (TO BE OBTAINED) from Barton & Gale [1993]).

B. Distribution of scores of hybrid index of *Heliconius himera* x *H. erato cyrbia* in the centre of a hybrid zone near Guayquichuma, Ecuador. The individuals were classified using colour pattern into three groups: *himera* (hollow), hybrids (stippled), and *cyrbia* (solid). The hybrid index is calculated as the fraction of *erato* alleles, and is based on 11 loci showing frequency differences between the species. Here disequilibria are so strong that almost all individuals fall into one or other pure species (data from Jiggins et al. 1996).


Bombina hybrid zone population
Numbers
120
100
80
60
40
20
0
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1.0
Hybrid Index

1


Heliconius erato x *himera* hybrid zone
Numbers
70
60
50
40
30
20
10
0
0.0-0.05
0.15-0.2
0.3-0.35
0.45-0.5
0.6-0.65
0.75-0.8
0.9-0.95
Hybrid Index

2