Hybridization, ecological races and the nature of species: empirical evidence for the ease of speciation

James Mallet*

Galton Laboratory, University College London, 4 Stephenson Way, London NW1 2HE, UK

Species are generally viewed by evolutionists as 'real' distinct entities in nature, making speciation appear difficult. Charles Darwin had originally promoted a very different uniformitarian view that biological species were continuous with 'varieties' below the level of species and became distinguishable from them only when divergent natural selection led to gaps in the distribution of morphology. This Darwinian view on species came under immediate attack, and the consensus among evolutionary biologists today appears to side more with the ideas of Ernst Mayr and Theodosius Dobzhansky, who argued 70 years ago that Darwin was wrong about species. Here, I show how recent genetic studies of supposedly well-behaved animals, such as insects and vertebrates, including our own species, have supported the existence of the Darwinian continuum between varieties and species. Below the level of species, there are well-defined ecological races, while above the level of species, hybridization still occurs, and may often lead to introgression and, sometimes, hybrid speciation. This continuum is evident, not only across vast geographical regions, but also locally in sympatry. The existence of this continuum provides good evidence for gradual evolution of species from ecological races and biotypes, to hybridizing species and, ultimately, to species that no longer cross. Continuity between varieties and species not only provides an excellent argument against creationism, but also gives insight into the process of speciation. The lack of a hiatus between species and ecological races suggests that speciation may occur, perhaps frequently, in sympatry, and the abundant intermediate stages suggest that it is happening all around us. Speciation is easy!

Keywords: hybridization; speciation; species concepts

1. INTRODUCTION

(a) *A brief history of evolutionary views of species*

Charles Darwin's 'On the Origin of Species by Means of Natural Selection' (1859) was universally acclaimed as soon as it was published. Yet, perhaps the most insidious and long-lasting critique of Darwinism was contained within the very writings of its first supporters and promoters. 'Darwin's bulldog', Thomas Henry Huxley maintained that Darwin had not fully explained how infertility between species could result from natural selection: 'Mr Darwin is perfectly aware of this weak point, and brings forward a multitude of ingenious and important arguments to diminish the force of the objection' (Huxley 1860). Huxley admitted 'the value of these arguments to their fullest extent', but he nevertheless argued that this apparent problem with the Origin of Species 'is not to be disguised or overlooked'.

The always faithful Alfred Russel Wallace would have liked to rise to the occasion and explain how hybrid inviability and sterility could arise by natural selection to protect the purity of the species, but Darwin apparently persuaded him in private letters that his theory would not wash (Mallet in press c): evolution

by natural selection did not work for the good of the species. Sterility was bound to be a disadvantageous trait for individuals to have (Wallace 1889).

These arguments misunderstood Darwin's intended message. Darwin's 'multitude of ingenious and important arguments' were produced not to wriggle out of a major difficulty with his theory, but to demonstrate that sterility simply was not the point of speciation at all, so that the criticism was irrelevant. Hybrid sterility (and hybrid inviability) is often associated with crosses between species, but does not at all provide a good definition of species because there are cases of sterility and inviability in crosses within species, and, conversely, cases of species that are interfertile. For example, Darwin documented inbreeding depression and self-sterility within species, whereas hybrids between species in genera such as *Pelargonium*, *Fuchsia*, *Calceolaria*, *Petunia* and *Rhododendron* are often completely fertile; the same is true in some animal species, such as in the genera *Phasianus* and *Cervus*. Furthermore, interspecific sterility is often asymmetric: a cross between a female of one species and a male of another may be fertile, while its reciprocal is sterile (Turelli & Moyle 2007; Lowry *et al.* 2008). In Darwin's (1859) words:

'Now do these complex and singular rules indicate that species have been endowed with sterility simply to prevent their becoming confounded in nature? I think

*j.mallet@ucl.ac.uk

not. For why should sterility be so extremely different in degree, when various species are crossed, all of which we must suppose it would be equally important to keep from blending together?... To grant to species the special power of producing hybrids, and then to stop their further propagation by different degrees of sterility, not strictly related to the facility of the first union between their parents, seems to be a strange arrangement.'

To convince his readership that species have evolved from non-species (such as morphs, varieties and geographical races), Darwin needed a new and flexible definition of species. They would have to be very different from the species hitherto envisaged by biologists, many of whom agreed with the creationist Buffon that species were defined by inability to cross, or 'sterility' (in Darwin's terminology, sterility included hybrid inviability). Species, in Darwin's view, are recognized by consistent gaps in morphology (figure 1a), but they form part of a continuum with varieties within species, which do not show such gaps. The evolution of these gaps, 'speciation' as we call it today, in Darwin's view, results from divergent selection, leading to the extinction of intermediates. Darwin called this his 'principle of divergence'. Discussions on the topic of sterility were placed by Darwin in his chapter 'Hybridism', and consist of two main arguments alluded to above, i.e. sterility within species and fertility between them.

It is hard to throw out one's education and preconceptions and get to grips with what Darwin is asserting. And his readers did not. By Darwin's time, it had become ingrained that the correct definition of species was that they were intersterile. Even his chief supporter, Huxley (1860), misunderstood or was unconvinced by Darwin's uniformitarian argument, as we have seen, to the latter's evident frustration.

Later on, this discussion about hybrid sterility became even more confused. Romanes (1886), an ardent Darwin acolyte, followed Wallace in arguing for a kind of 'physiological selection' that would explain interspecies sterility via natural selection. Another staunch Darwinian, Poulton (1904), while recognizing the force of Darwin's arguments against adaptive sterility, proposed that 'asyngamy' was the true reality of species. Asyngamy meant, I think, mainly mate choice, or literally, 'lack of coming together of gametes', another form of reproductive isolation. These views were reiterated and consolidated in the period of the 'Modern Synthesis' by Dobzhansky (1937), Huxley (1942) and Mayr (1942). Among evolutionary biologists, perhaps the prevailing view today is characterized as Mayr's 'biological species concept': that species are reproductively isolated groups of populations (Coyne & Orr 2004; Futuyma 2005); hybrid sterility and inviability, among other 'isolating mechanisms', form key parts of our normal definition of species in evolutionary biology (figure 1b). Today's evolutionists are, of course, fiercely supportive of Darwinism. Yet, they ignore or reject Darwin's key argument that reproductive isolation (a trait that can only exist, by definition, at the level of species) is a bad definition of species. Instead, they argue that species are 'real' in the sense that they have an unambiguous
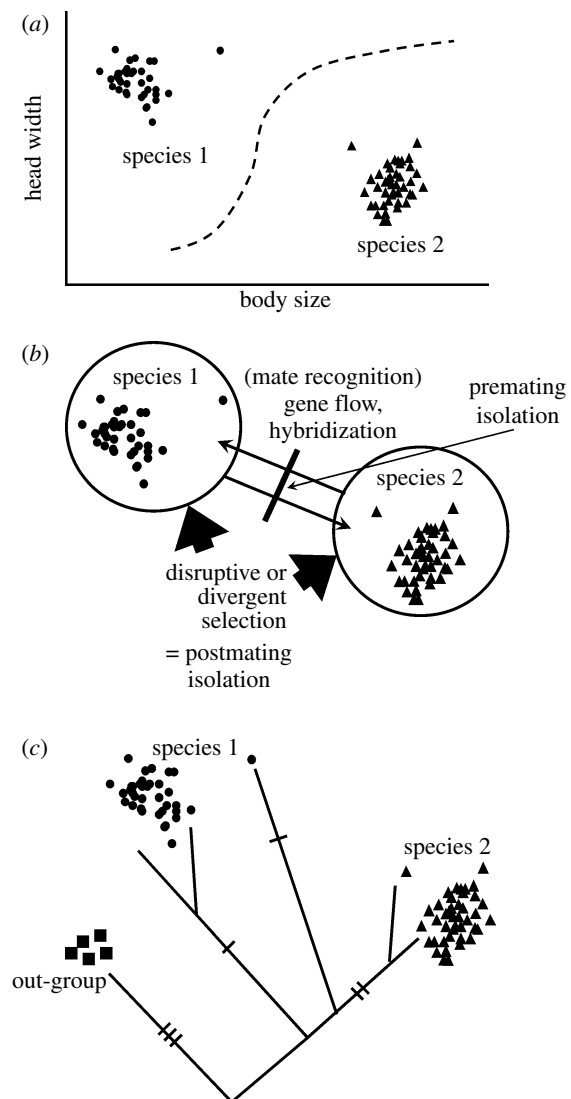

Figure 1. What do we mean by species? How do the concepts relate to one another? There is little disagreement over what we mean by species in sympatry, even though species concepts appear to conflict (see text for details and appendix A for further discussion). (a) Darwin's conception of species. Species in a single region do not differ essentially from 'varieties' except that they have a morphological gap between them. The formation of the gap (or the extinction of the intermediates) by competition and divergent selection was what Darwin meant by speciation. Although he did not know about genes, Darwin's arguments are readily extended to genotypes; species would then represent multilocus genotypic or genomic clusters. (b) The reproductive isolation or 'biological' concept of species (e.g. Mayr 1942). Here, the accent is on the processes maintaining the separateness of the clusters that we call species. Hybridization and gene flow may blur the species boundary, but this is prevented by disruptive or divergent natural selection against intermediates (or 'postmating isolation') and by assortative mating ('premating isolation'). (c) Phylogenetic species concepts. Two major types of phylogenetic species concepts are generally recognized (Baum 1992). First of all, species could be defined as monophyletic groups (Papadopoulou et al. 2008), perhaps based on multiple gene genealogies (Baum & Shaw 1995). Others recommend using diagnostic characters possessed by clusters of individuals as a means to define species (Cracraft 1989); this is sometimes called the diagnostic concept of species.

definition (reproductive isolation), unlike lower or higher taxonomic ranks. Furthermore, they claim that Darwin wrote an interesting book about evolution by natural selection, but failed to explain how species arose:

> '... Darwin's book was misnamed, because it is a book on evolutionary changes in general and the factors that control them (selection, and so forth), but not a treatise on the origin of species'.
>
> (Mayr 1942)

> '...despite the title of his greatest book, Darwin did not solve, and scarcely addressed, the problem of how two different species evolve from a common ancestor'.
>
> (Futuyma 1998, p. 449)

> 'Darwin's magnum opus remains largely silent on the '*mystery of mysteries*,' and the little that it does say about this mystery is seen by most modern evolutionists as muddled or wrong'.
>
> (Coyne & Orr 2004)

Darwin has even been accused of attempting to make the evolutionary origin of species more likely than it in fact is by blurring the boundary between species and varieties. According to Mayr (1982, p. 269), Darwin treated species

> 'purely typologically as characterized by degree of difference', and also that 'there was a strong, even though perhaps unconscious, motivation for Darwin to demonstrate that species lack the constancy and distinctiveness claimed for them by the creationists. For how could they be the result of gradual change through natural selection if it were true, as Darwin's opponents continued to claim for the next hundred years, that species are sharply delimited and separated by 'bridgeless gaps'?'

The notion that Darwin was wrong about species and speciation goes hand in hand with the reproductive isolation view of species. Elsewhere, I have discussed whether the idea that Darwin was wrong can be sustained (Mallet in press *a*). But a far more important point to get ironed out is what happens in nature. If we could affirm, as did Darwin, that species are not real at all, but man-made groupings are merely useful in communication among biologists, and if we could show that what we call species and what we call populations actually blend imperceptibly into one another, with no clear natural dividing line, it seems to me that our understanding of how species form would be enhanced, because we would be able to study the entire continuum of varieties diverging into species. We would still be interested in the evolution of reproductive isolation, since the effect of reproductive isolation is to cause divergence along this continuum, but the need to invoke special mechanisms that apply only to speciation would be reduced. In addition, as Mayr implies in the quotation of the previous paragraph, if Darwin was right and species and varieties actually *did* form a continuum, we would have much more convincing arguments against creationists. Divergent evolution by natural selection and other forces commonly seen within species, which are simple to demonstrate, could then provide unproblematic modes of speciation.

Should we tailor scientific definitions to improve discussions with non-scientists? It seems to me that we should, given the problems we biologists presently have with the religious right. Surely, it is better to define terms if necessary in order to win an argument that we know to be correct than to stick blindly to principles (e.g. based on monophyly) that are not helpful in this effort. A creationist theory of species is a theory, even if not a very useful one, and definitions of terms should at least consider the possibility that any possible alternative theory is correct (i.e. that there is no true phylogeny generated by evolution). Perhaps more importantly, if Darwin's uniformitarian conception rather than Mayr's 'species reality' view were generally accepted, it could have critical implications for understanding the biological basis of speciation. The punctuated equilibrium theory to explain gaps in the fossil record was founded on the Mayrian view of species and speciation (Mayr 1963), that speciation was not possible without some kind of *deus ex machina* to help it along, in the form of allopatry, rapid founder effects, leading to genetic revolutions (Eldredge & Gould 1972; Gould 1980). By contrast, if all stages of speciation from local populations, geographical or ecological races, to full species were commonly visible in nature, there would be good evidence that continuous processes of divergence leading to speciation can often occur, even while populations are in contact. This was the purpose of Darwin's argument.

For these reasons, I feel the time is right for evolutionists and geneticists to re-examine the Darwinian views on the nature of species. I worry that this proposal may seem too radical to many. For 70 years, we have come to accept that Darwin did not write a book about the origin of species at all; that species are real facts of nature, rather than human-circumscribed entities; that speciation is difficult, or at least more difficult than ordinary within-species evolution; and that the origin of species requires special conditions not normally found in everyday populations. Yet, I hope it can be accepted that it would be worth achieving a more uniformitarian, Darwinian view of species and speciation if that is the way nature really is.

The other problem with attempting to revive a more Darwinian view of species is the reverse: that the argument is not radical enough, and it seems merely like an exercise in splitting hairs. We all in some sense know that varieties blend imperceptibly into species, and that there are many 'difficult cases'. Furthermore, we have certainly endured too many tedious arguments about species concepts, when we all really know what we mean by species anyway. My defence is that, having studied the problem and its history in some detail, I feel it could be a rather more important definitional problem than usual, and that there is something still missing from most current definitions of species. In particular, crude thought experiments and simplistic caricatures of theoretical phylogeny or reproductive isolation between species have been too widely used in this debate in the past. All too often, the many clear facts in nature have hardly been perceived through a thick idealized smokescreen of species beliefs. The Darwinian view, once seen, allows many facts to fit more simply into place, even though from the outside
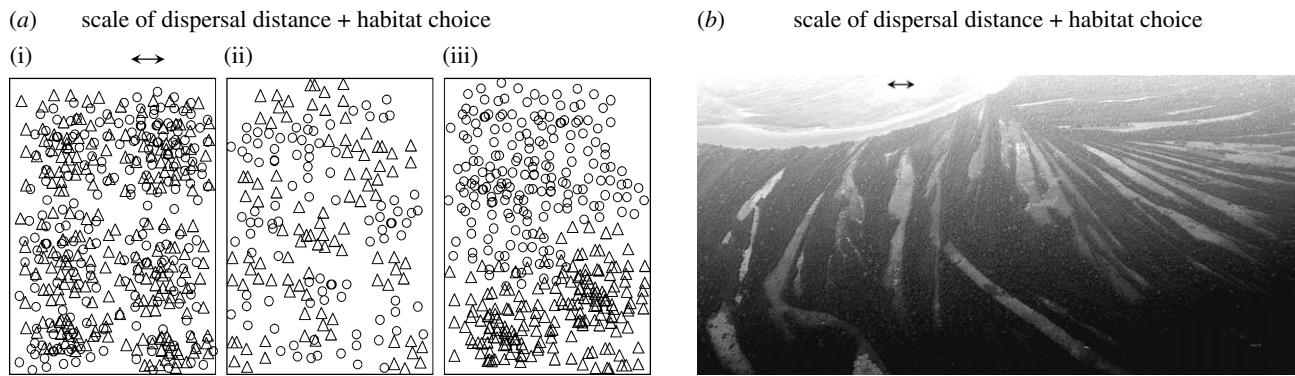
(*a*)   scale of dispersal distance + habitat choice

(*b*)   scale of dispersal distance + habitat choice

(i)   ↔   (ii)   (iii)

Figure 2. (*a*) (i) Pure sympatric, (ii) mosaic sympatric and (iii) parapatric distributions. Geographical sympatry is not necessarily the same as perfect panmixia (see appendix B for further discussion). Compared with the scale of dispersal (double-headed arrow, top left), distributions of individuals of two types (triangles and circles) may be (i) sympatric (i.e. in panmixia) or (iii) parapatric. However, there is an important intermediate situation which neither corresponds to large-scale geographical parapatry, nor is it truly panmictic. We might call this 'mosaic sympatry', characterized by patchy, interdigitated distribution of the two forms and their resources, with the patch size not much larger than the scale of dispersal. (*b*) An example of mosaic sympatry from the Amazon basin. Meanders of the Río Ucayali have created repeated marshy river beds and banked-up sediment that create habitat heterogeneity. Compared with the per-generation dispersal range of many species, these habitat types allow a great deal of contact between populations inhabiting forest versus open vegetation, while at the same time preventing complete panmixia. Ecological patchiness is predicted to be frequently of this mosaic type.

the change from the Mayrian viewpoint may seem subtle. Having made this small transition against the force of the education we have all received, I can assure the reader from personal experience that it allows a much greater understanding of just how major were Darwin's discoveries about evolution. In particular, it suddenly becomes clear how and why 'On the Origin of Species…' was a book about speciation after all.

Here I outline the mounting empirical evidence from nature for a more Darwinian view of species. Some of this evidence has been known for a long time, but, writing in 1942, Mayr was able to argue, in his chapter VIII on non-geographical speciation, that most cases of ecological races, species swarms in isolated lakes, etc., could be explained either by arguing for phenotypic plasticity rather than genetic differences, or by positing that the 'races' were in fact sibling species that had undergone former periods of allopatry (geographical isolation) necessary to achieve the level of divergence seen. Similarly, Mayr (1942) insisted that hybridization between species was an unusual 'break-down of isolating mechanisms', that it was caused mainly by human-induced environmental changes, and had little importance for the understanding of species and speciation, thus adding to the impression that there was no middle ground between species and varieties. By contrast, Huxley (1942) reviewing the same kinds of evidence, argued for a much more nuanced view of species and of speciation (although still not entirely Darwinian). The title of Huxley's (1942) book introduced the term 'Modern Synthesis', which in Huxley's view represented a fusion of Darwinian evolution and Mendelian genetics. By contrast, Mayr argued that in the Modern Synthesis an important part of the Darwinian hypothesis about the nature of species and speciation needed to be overturned (Mayr 1981, 1982). As it happened, Mayr's arguments have been more persuasive––until recently, now that new genetic data begin to blur the earlier certainties.

(b) *The real advance made by the biological species concept*

Before I review the empirical information, I should point out an aspect of the Mayrian view of species that is beyond reproach, and which builds on the ideas of E. B. Poulton, D. S. Jordan, K. Jordan and others from the 1890s and early 1900s. This was to deal with the issue of spatially separated forms. To Darwin (1859), species were morphologically differentiated populations separated by gaps, which in his view were caused by competition, leading to the extinction of intermediates (figure 1*a*, appendix A). Geographical populations of a lineage with different morphologies were therefore often regarded as separate species in the mid-nineteenth century, rather than as geographical races within the more inclusive 'polytypic' species that became popular later. In the late nineteenth and early twentieth century, it became obvious that the evolution of such geographical forms was somewhat different from the evolution of forms that can overlap in sympatry (Mallet 2004). Clearly, when an isolated population evolves a new morphological or genetic trait, this is probably due to natural selection, but can it be said to be speciation? Mayr, Dobzhansky and Huxley promoted the idea that geographical divergence was not the same thing as speciation. I suspect Darwin and certainly Wallace would have agreed, but they did not express it very clearly (but see Wallace 1865). Only if the new form could overlap in sympatry (figure 2) would this kind of evolution contribute to the most interesting kind of multiplication of species, an increase of biodiversity that shows itself within one time and place as well as globally.

In the 1940s, speciation then became, correctly in my view, the evolution of differentiated forms that could coexist in sympatry. Darwin and his immediate circle probably did not fully appreciate this. When geographical forms in different areas were connected by zones of intergradation, nineteenth century Darwinians argued that this was evidence for speciation.

'This complacent attitude was distinctly associated with the old morphological species concept and it reigned supreme until the new biological species concept began to replace it. Then it was suddenly realized by the more progressive systematists that those species between which they had found intergradation were their own creations, and not biological units. As the new polytypic species concept began to assert itself, a certain pessimism seemed to be associated with it. It seemed as if each of the polytypic species (Rassenkreise) was as clearcut and as separated from other species by bridgeless gaps as if it had come into being by a separate act of creation'.

(Mayr 1942, pp. 113–114)

A practical version of what became the biological species concept (figure 1*b*), known as the polytypic concept, which involved the concept of sympatry, became important in taxonomy and evolutionary biology at the beginning of the twentieth century, and grew in influence at least until the 1980s. Today, however, consensus is changing towards a more phylogenetic approach to species classification (e.g. Papadopoulou *et al.* 2008), typified by Cracraft's (1989) phylogenetic or diagnostic species concept (figure 1*c*; for further discussion of the relationships between Darwin's morphological concept, the biological concept and the phylogenetic concept of species, see figure 1 and appendix A). These newer ideas have led to rapid taxonomic inflation, especially in some charismatic vertebrate groups. In primates, the number of taxonomic species has actually doubled since 1985 (Isaac *et al.* 2004), even though few new taxa have been discovered. Inflation resulted when formerly recognized subspecies were elevated to species level. Evidently, we are returning to a pre-Darwinian view of species as differing in a number of characters, rather than in ability to overlap in sympatry. Changes in taxonomy are a worry for biodiversity studies and conservation (Isaac *et al.* 2004), but do not concern us here, because speciation scientists generally employ the sympatry overlap argument in defining species.

Today, it is not generally realized that the original purpose and chief advantage of the biological species concept was to address the taxonomic problem of geographically divergent taxa by naming many of them as subspecies within inclusive, more broadly distributed species, rather than just to promote reproductive isolation as the only true reality or essence of species. This 1900–1940s definition of species implied that speciation consisted of the evolution of morphologically (and genetically) differentiated forms that could coexist in sympatry (Mayr 1942). Sympatric species that remain distinguishable in sympatry are generally accepted whatever the species concept adopted (Cracraft 1989; Mallet 1995; Coyne & Orr 2004), even though distinct geographical populations may be classified sometimes as species, sometimes as subspecies, depending on the concept employed.

2. THE EMPIRICAL EVIDENCE

We are here interested in whether populations in sympatry (loosely defined, to include mosaic sympatry;

figure 2, appendix B) show uniformitarian continuity between varieties and species, as Darwin argued, or whether there is evidence for some special hiatus or species reality indicating a discrete nature of species. Ecological races and forms within species, as well as hybridization between species are all well known in plants, and these are the chief reasons why the biological species concept is not generally accepted by plant biologists (Raven 1976). (This is not to say that all botanists doubt the importance of reproductive isolation in the maintenance of species in sympatry; Abbott & Comes 2007; Soltis *et al.* 2007.) I therefore concentrate on whether similar evidence exists for animals.

(a) *Continuity of reproductive isolation across the species boundary*

One way in which species might be more real than populations and subspecies within species would be if reproductive isolation exhibited a sudden jump up at the species boundary. Are species almost completely reproductively isolated, while populations within species are hardly isolated at all? Today, many individual studies have been performed on reproductive isolation, and have been summarized in a number of comparative analyses (figure 3). There is no evidence whatsoever for a sudden hiatus at the species boundary. Reproductive compatibility, whether based on mate choice (figure 3*f*,*g*) or other factors (figure 3*a–e*, *h–j*), appears to decline in inverse proportion to the degree of genetic divergence and time since divergence. This is not to say that the decline is smooth; compatibility among different pairs of species varies widely and noisily, within any one group, even for a given degree of genetic divergence. Both the noisy decline of compatibility and the tendency to asymmetry in reciprocal crosses suggests that relatively few genes may often be involved in major incompatibility effects (Turelli & Moyle 2007; Lexer & Widmer 2008; Gourbiere & Mallet in press).

Perhaps another surprising fact emerges from figure 3. Most of the pairs of taxa between which prezygotic isolation (i.e. assortative mating) or postzygotic isolation (i.e. laboratory expressed hybrid inviability or sterility) have been estimated are classified as separate species, yet also show considerable compatibility. Not only does complete reproductive isolation fail to evolve suddenly at speciation, but also compatibility often lingers on for many millions of years after speciation (Bolnick & Near 2005; Mallet 2005). Reproductive isolation is of course associated with species divergence, but it is hard to categorize species versus varieties or races on the basis of these data alone. A possible logical way to classify species on the basis of reproductive isolation would be to demand 100% incompatibility (Barton & Hewitt 1989; Turelli & Orr 1995); however, for taxonomy of a very large fraction of the world's biodiversity, this would be quite impractical, because we often need to recognize ecologically, behaviourally, morphologically and genetically different taxa that can and do hybridize (see below). Reproductive isolation is clearly important in the formation and maintenance of the sexual populations that we would like to call species, but
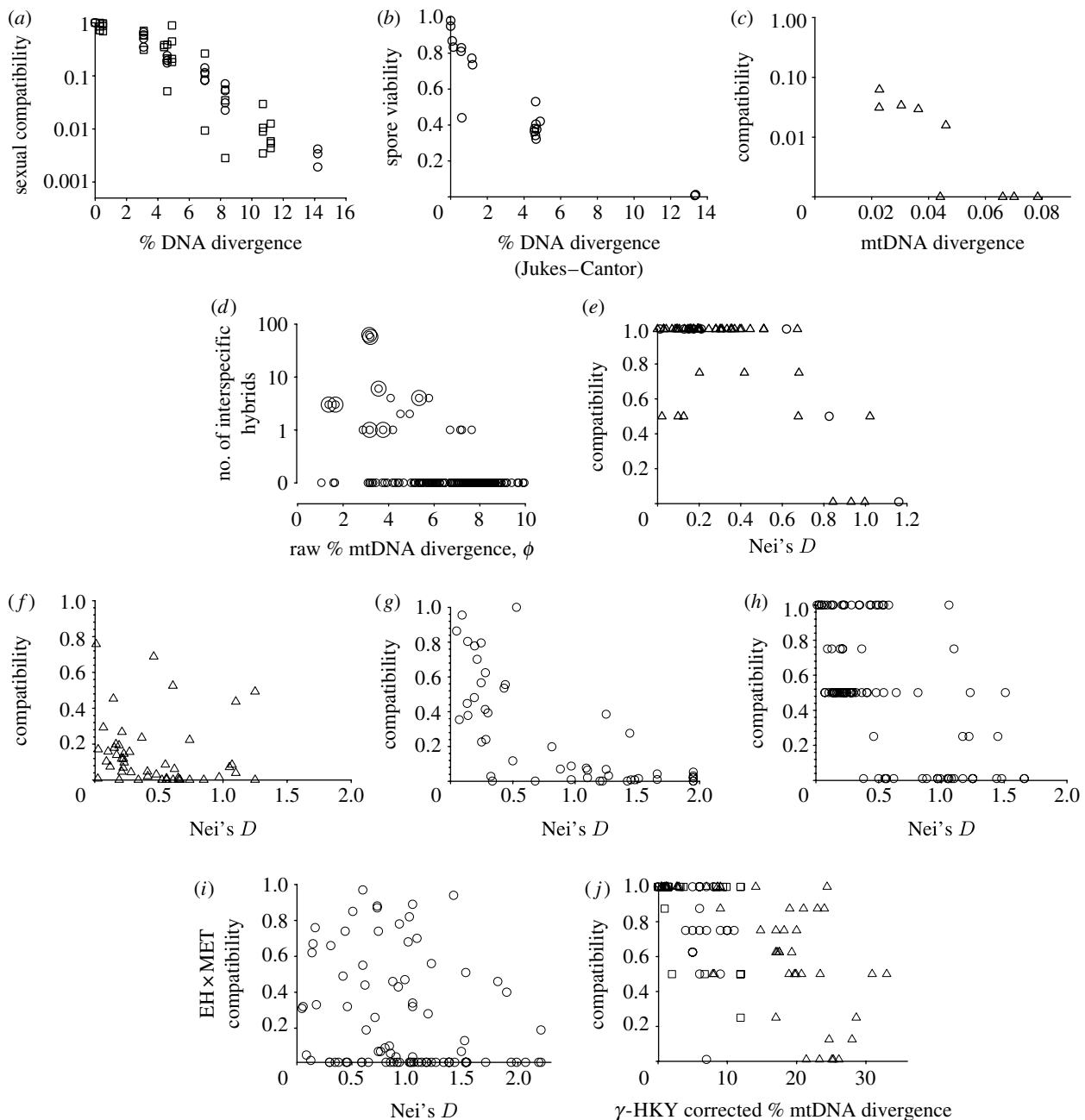
Figure 3. Plots of prezygotic and postzygotic compatibility against genetic distance. In all cases, some form of sexual compatibility of parents or their hybrids is measured between pairs of taxa, to show its relationship with genetic divergence. Very approximately, genetic divergence is proportional to the age of the split between the two taxa. (a) Transformation rate of *Bacillus* DNA, relative to within-strain transformation rate, plotted against raw DNA divergence between strains (Zawadzki *et al.* 1995). (b) Spore viability in hybrids between *Saccharomyces* species, as well as among strains of *S. cerevisiae* (Liti *et al.* 2006). (c) *Leptasterias* starfish hybridization rates (Foltz 1997). (d) The number of wild-caught hybrids between species of *Heliconius* in world collections (Mallet *et al.* 2007). Hybridizations for which backcrosses have been found are shown haloed. (e) Compatibility of Lepidoptera species measured via hybrid viability (Presgraves 2002). (f) Mating compatibility of sympatric pairs of *Drosophila* species (Coyne & Orr 1997). (g) Mating compatibility of allopatric pairs of *Drosophila* species. The more rapid loss of mating compatibility in sympatry (f), for a given genetic distance, suggests that assortative mating has evolved to prevent hybridization (Coyne & Orr 1997). (h) Compatibility of *Drosophila* species measured via a combination of F$_1$ hybrid viability and fertility (Coyne & Orr 1997). (i) Survival of eggs and larvae of hybrids between species of frogs (Sasa *et al.* 1998). (j) Compatibility of bird species measured as a combination of viability and fertility of bird hybrids (Price & Bouvier 2002).

Darwin's idea that it is better to classify species taxa via whether they remain distinct, i.e. the results of these processes, seems at least eminently sensible. This is, *de facto*, what most evolutionary biologists do today, even if they argue that species are defined by reproductive isolation. Most would now agree that populations differing at a number of morphological, ecological or genetic traits occurring in sympatry should be classified as separate species, even given evidence for gene flow between them (Harrison 1998; Coyne & Orr 2004); in a sense, they are not assessing reproductive isolation at all, but instead the ability to coexist without fusion in sympatry, which is an effect rather than a cause of separate species.

Table 1. Examples of sympatric races and ecotypes within species. (Only cases backed by good genetic, behavioural and/or morphological evidence for stable differentiation are shown here. Many additional cases of sympatric forms normally too weakly reproductively isolated to be recognized by evolutionary biologists as 'good species' are known (Huxley 1942; Mayr 1942; Kondrashov & Mina 1986; Skulason & Smith 1995; Berlocher & Feder 2002; Drès & Mallet 2002; Bolnick & Fitzpatrick 2007).)

taxon	references
ecological morphs of *Actinia* and other sea anemones	Quicke *et al.* (1983), Solecava & Thorpe (1992), Dalby (1997) and Watts & Thorpe (1998)
pig- versus human-infecting *Ascaris* races (Nematoda)	Anderson *et al.* (1995)
shore snails, upshore and downshore; exposed versus unexposed forms (e.g. *Littorina*)	Johannesson *et al.* (1993), Wilding *et al.* (2001) and Cruz *et al.* (2004)
host races of plant-feeding insects and their parasitoids	Berlocher & Feder (2002), Drès & Mallet (2002) and Abrahamson & Blair (2007)
pheromone morphs in European corn borer moths (*Ostrinia*)	Dopman *et al.* (2005) and Malausa *et al.* (2006)
head louse versus body louse on humans, *Pediculus*	Leo *et al.* (2002), Kittler *et al.* (2003) and Reed *et al.* (2004)
Anopheles gambiae sensu stricto, M and S races	Tripet *et al.* (2001) and Turner *et al.* (2005)
Drosophila melanogaster morphs in Zimbabwe and Kronenbourg brewery, Congo	Wu *et al.* (1995), Hollocher *et al.* (1997), Capy *et al.* (2000), Alipaz *et al.* (2001), Kauer & Schlotterer (2004) and Haerty *et al.* (2005)
fish benthic versus limnetic morphs (stickleback, whitefish, salmonids, etc.)	Bell & Foster (1994), Schluter & Nagel (1995), Skulason & Smith (1995), Lu & Bernatchez (1999), Jonsson & Jonsson (2001) and Knudsen *et al.* (2006)
Crossbill (*Loxia*) biotypes coevolving with pines (*Pinus*)	Benkman (2003) and Smith & Benkman (2007)
Darwin's finch 'species' (*Geospiza*) on the Galapagos Islands	Grant & Grant (1992, 1996, 2008) and Price (2008)
bottlenose dolphin sympatric morphotypes (*Tursiops*)	Wang *et al.* (1999) and Natoli *et al.* (2004)
Resident versus transient killer whales (*Orca*) off British Columbia and elsewhere	Ford *et al.* (1998) and Hoelzel *et al.* (2007)
pygmy hunter-gatherers and Bantu-speaking agriculturalists in Central and West Africa	Jakobsson *et al.* (2008) and Quintana-Murci *et al.* (2008)

(b) *Ecotypes, ecological and host races*

Apart from laboratory studies of hybridization, recent years have seen an explosion of genetic and ecological studies of forms generally classified as infraspecific, but which show some characteristics of species, such as distinct morphological, ecological and/or genetic differences in sympatry, and a degree of reproductive isolation. Some such biotypes may be created by phenotypic plasticity or single-locus polymorphisms. However, we are here interested only in sympatric populations that can be inferred to show 'dumbell' or 'bimodal' distributions of genotypes at multiple loci, but which nonetheless are considered members of the same species (Kondrashov & Mina 1986; Jiggins & Mallet 2000; Drès & Mallet 2002).

Such forms might be called ecological or genetic races if they form 'genetically differentiated, sympatric populations between which there is appreciable gene flow'. The rate of hybridization and gene flow should be greater than approximately 1% per generation when the races are sympatric, or we might be tempted to classify them instead as separate species (Drès & Mallet 2002). The 1% stipulation is not meant to be a hard and fast rule, and it indeed highlights the lack of any obvious distinction along a gene flow continuum between species and sympatric intraspecific races and ecotypes. The main problem with classifying all such ecological races as separate species is that we would not find it very convenient, owing to their inconstancy and extensive gene flow.

It is now clear that many animal species contain divergent sympatric forms (table 1). Among invertebrates, there are habitat-associated, genetically differentiated colour morphs in sea anemones (Quicke *et al.* 1983; Solecava & Thorpe 1992; Dalby 1997; Watts & Thorpe 1998), distinct *Ascaris* roundworms parasitizing humans and pigs (Anderson *et al.* 1995), *Littorina* shore snails differing in shell shape and thickness (Johannesson *et al.* 1993; Wilding *et al.* 2001; Cruz *et al.* 2004; Butlin *et al.* 2008), and head- and body-infesting forms of human lice (*Pediculus*; Leo *et al.* 2002; Kittler *et al.* 2003; Reed *et al.* 2004). Phytophagous insects also produce well-known examples of host races feeding on different plant species (Kondrashov & Mina 1986; Berlocher & Feder 2002; Drès & Mallet 2002). Surprisingly few cases of phytophagous host races have been studied genetically in much detail, but in the case of the apple and hawthorn races of *Rhagoletis pomonella*, the larch and pine races of *Zeiraphera diniana* and the goldenrod gallfly *Eurosta solidaginis*, there is good evidence for assortatively mating, genetically differentiated host races between which there is still gene flow (Drès & Mallet 2002). In many other cases, host-associated forms have very low gene flow and might better be characterized as sibling species, such as the *Enchenopa* treehoppers and certain other species allied closely to *Rhagoletis pomonella* (Berlocher & Feder 2002; Drès & Mallet 2002). Recent evidence has shown that natural enemies of many of these host races, which often use plant chemistry cues to locate their phytophagous hosts, have themselves formed matching host races in turn; a process of 'sequential radiation' in higher trophic levels (Abrahamson & Blair 2007).

In the African malaria-carrying mosquito, *Anopheles gambiae sensu stricto*, there are sympatric M and S forms, detectable only via certain nucleotide polymorphisms which deviate from Hardy–Weinberg, indicating that the forms are sympatric races. The

ecological significance of these forms, if any, is not clear, but the hybridization rate in sympatry appears to be approximately 1% (Tripet *et al.* 2001). There is evidence for genetic divergence only at a few genomic regions, or 'speciation islands': all such regions combined contain only 67 genes. The rest of the genome shows little differentiation (Turner *et al.* 2005). There are also examples of ecologically differentiated forms in the African *Drosophila melanogaster*. Flies collected in the Kronenbourg brewery in Brazzaville, Congo were differentiated from other African flies, presumably owing to ecological specialization on brewery products (Capy *et al.* 2000; Haerty *et al.* 2005). In Zimbabwe, flies with strongly assortative mating behaviour and divergent genetics have been identified; the assortative mating behaviour appears to be polymorphic in the population, with some forms showing intermediate levels of assortative mating (Wu *et al.* 1995; Hollocher *et al.* 1997; Alipaz *et al.* 2001; Kauer & Schlotterer 2004).

In vertebrates, there are also many ecologically differentiated forms. Among the best studied are fish with benthic, limnetic and sometimes other morphs, which appear in a variety of salmonids, whitefish, cichlids and sticklebacks (*Gasterosteus*). These forms may differ in feeding habits, spawning, behaviour and tend to mate assortatively (Bell & Foster 1994; Schluter & Nagel 1995; Skulason & Smith 1995; Lu & Bernatchez 1999; Jonsson & Jonsson 2001; Knudsen *et al.* 2006). There is very strong evidence that the same evolutionary transitions have taken place repeatedly in different lakes, resulting in a form of parallel ecotype (or species) formation (Schluter & Nagel 1995). Among birds, crossbills (*Loxia*) coevolve with different lodgepole pine populations, and diverge in beak morphology and song type, and may breed in different seasons. This can result in very strong assortative mating, sometimes leading to less than 1% hybridization. However, the rate of gene flow is probably greater in other parts of the range (Benkman 2003; Smith & Benkman 2007). It has been argued that birds rarely show any evidence of ecological or sympatric speciation, though there are a few cases that seem to provide cast-iron evidence of the theory (Price 2008). However, in one of the best long-term studies of any bird group, Darwin's finch (Geospizinae) 'species' may hybridize at rates of 1% or more, e.g. among the small, medium and large ground finches (Grant & Grant 2008). Molecular data, both mitochondrial and nuclear, fail to find fixed differences among these taxa, suggesting that speciation has taken place only within the last few thousand years, so that coalescence of gene genealogies within species has failed to occur (Price 2008), or that gene flow and extensive introgression is ongoing, which is supported by the good breeding success of hybrids and backcrosses (Grant & Grant 1996, 2008). In any case, the ground finch lineage seems to represent, on at least some islands and at least some times, ecological races rather than species (Zink 2002).

The bottlenose dolphin (*Tursiops truncatus*) exists in coastal (*aduncus*) and offshore (*truncatus*) forms in certain parts of the globe. These morphologically differentiated forms can have fixed differences at mtDNA and it is unclear how much gene flow still occurs between them; in some areas (off the coast of China and in the western Atlantic) they may represent locally distinct species. In other parts of the world, only one form may exist, and mitochondrial and microsatellite alleles are found mixed or in the 'incorrect' form, suggesting gene flow. There is genetic evidence that the different coastal forms are not closely related to one another. Instead, each coastal form around the world seems to be related to nearby pelagic *truncatus* forms, again suggesting parallel evolution (Wang *et al.* 1999; Natoli *et al.* 2004).

In killer whales (*Orcinus orca*) the situation is similar. In coastal populations of the eastern North Pacific, two weakly morphologically differentiated types are known that feed mostly on fish ('resident' type) or mammals such as seals ('transient' type). Similar distinctions are known from the Antarctic, where sampling has been very full because orcas are hunted extensively. Individuals swim separately in 'pods' with other adults and offspring of their own type, and the types also differ in song repertoire, suggesting assortative mating. Although much genetic variation is shared, there is clear evidence from Bayesian population structure analyses of microsatellites for differentiation among pods of different types (Ford *et al.* 1998; Hoelzel *et al.* 2007).

Overall, there is now plenty of evidence, not just for geographical variation among populations, but for subdivision of populations in sympatry or mosaic sympatry. Many and perhaps all of these forms are also ecologically segregated to some extent, suggesting that specialization has led to divergence in phenotype and genotype. There is evidence for sympatric genetic differentiation even in our own species. For example, there are genetic differences between pygmy hunter-gatherers and sympatric Bantu agriculturalists in Central and West Africa (Jakobsson *et al.* 2008; Quintana-Murci *et al.* 2008). It is tempting to suggest that we shall find examples of ecological races whenever we investigate a species in detail. Although I have concentrated here on the evidence from some of the best known invertebrate and vertebrate groups, analogous ecological and reproductive differentiation is found in essentially all life, including bacteria, protists and plants.

We usually do not class these ecotypes or races as species, but they clearly have many of the same characteristics, including ecological and genetic differences, and assortative mating. These are therefore clear forerunners of species, but high rates of gene flow and likely sensitivity to ecological conditions (well understood in the case of Darwin's finches, see Grant & Grant 1996, 2008) probably means that the fate of many ecological races is extinction. For instance, almost all the many forms of sticklebacks in Canadian lakes will go extinct during the next Ice Age (Bell & Foster 1994). Nonetheless, while most actual ecological races probably never reach the status of species, some ecological races are likely to speciate as they already maintain the linkage disequilibria needed to evolve further speciation-related traits (Felsenstein 1981), such as divergently selected genes that cause hybrid inviability as a by-product, or reinforcement

Table 2. Hybridization between species in major taxonomic assemblages in the wild.

taxon	location	fraction of species with hybrids (%)	references
vascular plants	Great Britain	25	Stace (1997) and Mallet (2005)
butterflies	Europe	16	Descimon & Mallet (2008)
birds	worldwide	9	Grant & Grant (1992)
mammals	Europe	6	MacDonald & Barrett (1995) and Mallet (2005)

leading to assortative mating. It does not seem unlikely that speciation via this route is the source of most new and successful species.

(c) Hybridization between species in nature
The lack of clarity of ecotypes and species is mirrored, above the species level, by hybridization and introgression, or 'successful' gene flow between species (Arnold 1997; Coyne & Orr 2004). In truth, hybridization between species has always been well known, since Mayr's (1942) excellent review. However, it is only recently that we are beginning to understand its extent and genetic importance across substantial fractions of biodiversity.

Hybridization is usually rare in nature between sympatric species, but this is hardly surprising because the statement is implicit in many definitions of species. Following from our earlier definition of an ecological race, a reasonable definition of species is that they should represent differentiated clusters of genotypes between which hybridization is very rare, say less than approximately 1% per generation. Typical rates of hybridization between forms considered good species are usually much lower, say 0.1 or 0.01% per generation.

Recently, a number of surveys have been made of hybridization in the wild. Although hybridization is rare on a per individual basis, many species do hybridize (table 2). Plant hybridization is notorious, but, although some have suggested it is less important than generally supposed (Mayr 1992), most botanists accept that hybridization is common, widespread and leads to frequent introgression in vascular plants (Stace 1975; Raven 1976; Ellstrand *et al.* 1996; Arnold 1997). However, I could find few studies that explicitly estimated its importance in terms of the fraction of biodiversity involved in a widespread flora (but see Ellstrand *et al.* 1996). On the basis of Stace's work, I estimate that approximately 25% of the British native vascular plant species are involved (Stace 1997; Mallet 2005). Given that species in low-diversity Britain will be more distantly related on average than in higher diversity regions, and given that families such as the Orchidaceae which are renowned hybridizers also are particularly diverse in the tropics, this is probably an underestimate of the global importance of plant hybridization.

Since the 1930–1940s revival of the biological species concept, hybridization has often been considered unimportant for the biology of many species. This is partly for the good reason that many hybrids are inviable or sterile (figure 3b). Yet, the overall extent of hybridization had rarely been estimated for any group of animals. Hybridization appears rarer in animals than plants, hovering at approximately 10% of species in major faunal groups (table 2), but these overall figures hide much higher rates in some of the most rapidly diversifying subgroups, as in plants (Ellstrand *et al.* 1996). For example, birds of paradise (43% of 42 species of Paradiseidae), grouse (100% of four British species of Tetraoninae) and ducks (76% of 21 British species of Anatidae) are renowned hybridizers among birds. Many groups, such as Parulidae (New World warblers, 24% of 116 species) and Paridae (tits, 29% of 70 species), hybridize as readily as vascular plants (Mallet 2005). Insects are similar. Approximately 16% of European butterfly species hybridize (Descimon & Mallet 2008), but the rapidly evolving *Heliconius* of tropical America have higher rates (35% of 46 species). Overall among the subtribe Heliconiina, which includes a number of more distantly related genera, 29% of 73 species hybridize (Mallet *et al.* 2007).

Although mammals are argued to be better behaved, and to hybridize rarely (Grant & Grant 1992), many hybrids are known. A recent newsworthy case was the shooting of a 'pizzly', or polar bear × grizzly hybrid by a hunter in the Canadian Arctic (Roach 2006). From a variety of sources, I was able to collate evidence for natural hybridization in approximately 6% of the 200 European mammal species (Mallet 2005).

Whales provide some particularly interesting cases of hybridization (Sylvestre & Tasaka 1985), and I summarize them here. Some of the most iconic and best known species, such as narwhal (*Monodon monoceros*) and beluga (*Delphinapterus leucas*; Heide-Jorgensen & Reeves 1993), bottle-nosed dolphin (*Tursiops truncatus*) and Risso's dolphin (*Grampus griseus*; Sylvestre & Tasaka 1985), and Dall's (*Phocoenoides dalli*) and harbour porpoises (*Phocoenoides phocoena*; Willis *et al.* 2004), are involved in hybridization in nature. The largest animal on the planet today, and indeed the largest ever to have occurred on the planet, is the blue whale (*Balaenoptera musculus*). It weighs 120 metric tonnes or more, at least three times the mass of the largest dinosaur known (*Brachiosaurus*). But even this Leviathan is involved in regular natural hybridization with its closest relative, the fin whale (*B. physalus*), at a rate of approximately 0.1–0.2% of harpooned specimens of the fin whale. Hybrids are probably underreported due to prohibitions against hunting the blue whale (Bérubé & Aguilar 1998). It seems probable that male hybrids have reduced fertility, but female blue/fin hybrids seem less affected; one female hybrid was found to be in its second pregnancy with a 20 cm backcross foetus fathered by a blue whale (Spilliaert *et al.* 1991).

Most estimates of the extent of hybridization among animal species are based on morphological identification of hybrids in hunted or museum specimens. Thus, it is possible that some hybrids are erroneously recorded. However, it is also not unlikely that the frequency of hybridization has been underestimated. Groups with high recorded rates of hybridization tend to contain brightly coloured or otherwise morphologically rather distinct species. Hybridization may be strongly underestimated when we consider that many pairs of species are only weakly diagnosable using morphology. Probably, many rare hybrids are simply lumped with one of the parents in such groups (Mallet 2005). For example, a recent review has recorded no certain hybrids among the normally drab warblers (Sylviidae) of the western Palaearctic (Parmenter & Byers 1991; Mallet 2005), yet Serge Dumont's bird hybrid database lists 20 species (32%) of western Palaearctic sylviids involved in hybridization (www.bird-hybrids.com, accessed 1 Mar 2007). It seems probable that Parmenter and Byers did not believe the evidence from subtle plumage differences, whereas Dumont's more up-to-date list included many data with recent photographic evidence. However, it is hard to judge reliability without genetic data (Spilliaert *et al.* 1991; Bérubé & Aguilar 1998; Roach 2006; Dasmahapatra *et al.* 2007), and, as far as I know, there has been no concerted genetic study to verify interspecific hybrids across a large faunal group.

Discussing the genetic importance of hybridization is not the main purpose of this paper, so a more detailed discussion has been placed in appendix C. It has often been argued that, although hybridization occurs, it is mainly caused by unusual biological situations, such as disturbance of the environment by humans (Mayr 1942, 1963). While it is undeniably sometimes the case that hybridization results from unusual conditions, it is by no means universally true (Mallet 2005; Mallet *et al.* 2007). Furthermore, it is argued that hybridization has little biological importance as it rarely leads to introgression. However, introgression is now well established via high-resolution molecular markers (Arnold 1997; Coyne & Orr 2004; Mallet 2005). Hybrid speciation also seems to be a regular feature of hybridizing lineages, even if not common (Mallet 2007; Hegarty *et al.* 2008; Jiggins *et al.* 2008; appendix C).

3. CONCLUSION

Darwin and other Darwinians, who considered that species and 'varieties' formed a continuum, missed the opportunity to clarify an important aspect of speciation. As they defined the origin of species, it could be interpreted as equivalent to mere evolution of geographical divergence. However, I here argue that a Darwinian continuum of infraspecific entities and full species is evident also in sympatry. Pairs of species differ continuously in terms of both assortative mating and tendency to produce inviable or sterile hybrids. Many subspecific forms are known that are sympatric over extensive parts of their range. These hybridize more freely than would generally allow them to be classified as species, and yet typically show assortative mating similar to although less strong than that in 'true' species. On the other side of the species boundary,

hybrids between many pairs of animal species (as well as plant species) are also known. These hybrids are often (though by no means always) fertile enough to backcross to the parents. Genetic studies have shown that hybridization can be evolutionarily important, leading to limited gene flow or introgression among species, and sometimes to hybrid speciation.

In conclusion, Darwin's conception of a relatively continuous species boundary with no major hiatus now seems well supported, not just across vast geographical distances, but also locally, between taxa that overlap extensively. The processes of evolution within and between species should be similar (although, of course, the relative emphasis on different processes may change along the continuum), and this provides support for Darwin's uniformitarian vision of species and speciation. Although the very pro-Darwinian view of species that I attempt to sustain in this article runs counter to many current literature statements about the 'reality' of species and Darwin's lack of understanding of species and speciation, it does seem to me that most will agree on the empirical examples now available, and that we should now forge more of a synthesis between opposing Darwinian and Mayrian viewpoints. Adopting a more uniformitarian view of the species boundary will make it easier to refute creationists, and should also help us to understand more clearly the process of speciation itself. For example, given there are many sympatric ecological races within species, does this mean that speciation can occur readily in sympatry? If allopatry is required, where is the break, or hiatus, along the continuum that natural selection alone cannot transcend without interruption of gene flow? We do not know, but we do now have abundant material in which to find it. Speciation appears to be easy; the intermediate stages are all around us.

APPENDIX A

(a) *What do we mean by species?*

Many learned papers, chapters and indeed whole books have been published about species concepts, and I will not go into all the possible definitions and concepts here. Instead, I show how three main strands of thought on species relate to one another. The simple Darwinian definition (figure 1a) uses morphological characteristics (and, updated, it could also use characteristics of individual genotypes) to separate clusters of sexual individuals into species. Gaps in the distributions of characters or genotypes, involving multiple loci in linkage disequilibrium, or multiple, correlated morphological characters, are used to specify the dividing lines between actual taxa. Although many evolutionists now argue for biological and phylogenetic concepts of species (see below), character-based or genotype-based arguments for Darwinian species are still widely cited today (Sokal & Crovello 1970; Mallet 1995; Feder 1998; Coyne & Orr 2004).

The clusters of individuals in figure 1*a* are associated with a number of processes that affect their integrity and perceived separateness (figure 1*b*). If the populations are sexual, hybridization and gene flow may occur. This process will tend to break down the genetic and phenotypic differences between the clusters. If it continues for multiple generations, the process will result in a single cluster, which may be referred to as a hybrid swarm. However, the process of fusion may be resisted by disruptive or divergent natural selection, consisting of classical hybrid sterility and inviability, i.e. genomic incompatibility. Alternatively, if each parental cluster is adapted to a different ecological niche, hybrids and intermediates between the two may be well adapted to either niche, and they will be out-competed. If divergent selection is strong enough, the two clusters will not fuse.

So far, this discussion has succeeded using only Darwinian terms such as 'divergent selection' relevant within species. Genomic incompatibilities may be due to interactions of a few polymorphic genes and ecological differences may be similarly generated by a few loci that differ in the kind of niche that can be exploited. However, the terms 'physiological selection', 'syngamy' and 'asyngamy', 'reproductive isolation' and 'isolating mechanisms' all make a transition to regarding some processes as special traits found only at the species level. Thus, Dobzhansky (1937) and Mayr (1942) collated a list of traits involved with natural selection and mating behaviour as isolating mechanisms whose very function was supposedly to keep species apart. Mate choice, well known to exist and cause sexual selection within species, thus becomes, at the species level, a 'prezygotic isolating mechanism', and disruptive or divergent selection becomes a 'postmating isolating mechanism'. Fundamentally, of course, the same processes are operating both within and between species. Clusterhood is maintained only if, very approximately, divergent selection is stronger than gene flow (Haldane 1932). This means that the various constituents of reproductive isolation may be quite variable and yet still maintain genetic differentiation. In one species pair, there may be a lot of hybridization, but very strong selection against hybrids; in a second species pair, low levels of hybridization may be counteracted by weak selection. Yet, both pairs of species can maintain the same level of genotypic differentiation.

More recently, phylogeneticists have rejected the biological species concept, on the grounds that species may arise from a single geographical race of a widespread polytypic species, and so lead to paraphyly of the ancestor. They argue that reproductive continuity within species is a primitive trait, and therefore may not be used as a synapomorphic character delimiting any groups (in this case species). Instead, they seek in some cases to define species via monophyly, and, in other cases, via diagnostic characters (Hennig 1968; Cracraft 1989; Baum & Shaw 1995; Papadopoulou *et al.* 2008; see also figure 1*c*).

Biological and phylogenetic species concepts, then, are two post-Darwinian definitions of species that focus on processes and patterns of origin, and the maintenance of the clusters which Darwin called species. Darwin as well as the supporters of the biological and phylogenetic concepts of species would all probably have agreed on the status of sympatric clusters, like those in figure 1, as separate species, but in Darwin's case, species were defined by distributions of the characters themselves rather than via processes that maintain the distinction (reproductive isolation) or the history of their pattern of branching (phylogeny). Given these close links between process and pattern, it seems to me that Darwin's character-based idea of species should be at least understandable to today's evolutionists.

However, because geographical populations or subspecies may also show multiple correlated differences and yet blend together in areas of overlap, and are no longer considered separate species in modern taxonomy, this gap definition can only really apply (and only needs to apply) in sympatry. This is what Mayr (1982) calls a 'non-dimensional' definition of species. The polytypic geographical extension of the idea of species is more controversial, and indeed is resisted by today's phylogenetic systematists. But even Mayr (1963, pp. 29–30), who highlights 'the importance of a non-arbitrary definition of species', admits that arbitrariness is unavoidable for forms that are geographically separated: 'It cannot be denied that an objective delimitation of species in a multidimensional system [i.e. over large expanses of space or time] is an impossibility' (Mayr 1963, p. 13). Thus, although actual or assumed reproductive compatibility between such geographical populations might give some evidence for the ability to overlap locally without fusing, it by no means provides an unambiguous resolution to what is a species spread over a wide geographical area.

In any case, whatever the species concept we prefer, in speciation research we are chiefly interested in the evolution of the ability to overlap in sympatry.

APPENDIX B

(a) *What do we mean by sympatry?*

The term 'sympatry' was invented by Poulton (1904): it means a geographical range that overlaps so that individuals are 'within cruising range' of one another. Mathematical models of sympatric speciation (Maynard Smith 1966; Dieckmann & Doebeli 1999; Kondrashov & Kondrashov 1999; Gavrilets 2003) have generally been predicated on initial panmixia, or complete random mating (figure 2*a*(i)), in which individuals of different types (circles and triangles) are almost always near and can readily mate with members of another type. Today, anything less than random mating is viewed as a kind of 'parapatry' (figure 2*a*(iii); see for example Gavrilets (2003, p. 2198) and Coyne & Orr (2004, p. 86)). However, if species specialize on different resources or niches, they may coexist in a different kind of sympatry, 'mosaic sympatry' (figure 2*a*(ii)). Ecological resources, including other species that act as niches, tend to be distributed patchily, so populations using these resources will be patchy too. If these patches are similar in size or sometimes greater than the typical range of dispersal of individuals, populations exploiting such resources may not be in perfect panmixia, even though

they overlap in overall distribution. An example is in Amazonian rainforests (figure 2b). Although the climate is very wet and homogeneous across the whole of the Amazon, there are many different kinds of habitats available. In figure 2b, the meanders of the Río Ucayali near Pucallpa, Peru, have left multiple striations of marshy low vegetation among patches of closed canopy forest in a region tens of kilometres on either side of the main river course. Each patch is a few hundreds of metres to kilometres across, of the same order as or greater than dispersal distances of many birds and butterflies, to say nothing of those of plant seeds and flightless invertebrates.

APPENDIX C

(a) *The importance of hybridization in nature*

It is evident from today's molecular marker studies that hybridization can often lead to introgression and sometimes to hybrid speciation (Arnold 1997; Rieseberg *et al.* 2003; Coyne & Orr 2004; Mallet 2005, 2007). Introgression takes place due to backcrossing. Although viable F$_1$ hybrids between pairs of species are often rare, once formed they backcross much more readily with one or more parent species, provided they are fertile enough. The ability to backcross is especially common among recently diverged pairs of species (Bolnick & Near 2005). In *Heliconius*, it occurs in approximately 60% of cases of hybridization between species whose mitochondrial *CoI/CoII* gene sequences differ by less than 6% (Mallet *et al.* 2007). There are few estimates of the extent of gene flow, but there are now so many plant examples of introgression (Arnold 1997) that it almost certainly occurs in an appreciable proportion of those hybridizing. In animals, it is probably rarer, mainly because hybridization itself is less common, but again it is mainly likely to occur in recently diverged species. A combination of genealogy-based and population structure studies has shown that selective introgression is occurring among some typical hybridizing species, e.g. in *Drosophila* (Noor *et al.* 2000; Machado *et al.* 2002) and butterflies (Aubert *et al.* 1997; Cianchi *et al.* 2003; Bull *et al.* 2006; Kronforst *et al.* 2006).

Furthermore, hybridization can sometimes lead to speciation. Perhaps 40–80% of the diversity of vascular plants is known to be derived from chromosome-doubled, polyploid ancestors (Stebbins 1950). It is thought that the majority of major polyploid lineages are allopolyploid (i.e. polyploidy occurring in hybrids between two species) (Stebbins 1959; Grant 1981; Coyne & Orr 2004; Soltis *et al.* 2004; Mallet 2007) as opposed to autopolyploid (chromosome doubling of a single species' genome), though this has recently been disputed (Ramsey & Schemske 2002). Even if it is not certain that allopolyploidy is most prevalent, there is no doubt that it is common; we know this because in many cases the parents can be identified through chromosomal morphology or other genetic markers (Coyne & Orr 2004; Soltis *et al.* 2004). If recent polyploidy caused a substantial fraction of today's species, even chromosome counts should outnumber odd counts. The predicted bias is significant in plants, suggesting that 2–7% of species of vascular

plants do indeed originate from polyploid speciation; in animals, no such bias is evident, and it seems probable that speciation via polyploidy is rare (Otto & Whitton 2000).

Polyploidy is thus rarer in animals, especially in the vertebrates and insects that have most often been studied. However, it does occur, and it is then often associated with parthenogenesis. The problem may be that a newly formed polyploid individual will be intersterile when mated with a diploid parent, and will suffer a frequency-dependent 'minority cytotype disadvantage'. The bias towards polyploidy in plants can be explained in various ways, but the greater prevalence of hermaphroditism and selfing, and so reproduction of rare polyploids than in the 'higher' animals, must rank among the more likely reasons.

There should be comparatively less of a problem for homoploid speciation in animals (i.e. without chromosome doubling), compared with plants. Homoploid hybrid speciation is thought to be rare (Rieseberg 1997), but there are growing numbers of putative cases even in animals, e.g. in fish (Nolte *et al.* 2005) and butterflies (Mavárez *et al.* 2006; Gompert *et al.* 2006). It is hard to prove homoploid hybrid speciation, in part because it is hard to define. Selective introgression may sometimes provide genetic variation, which could boost the possibility of speciation; this is rather distinct from the simple idea of a 50 : 50 mix of the two genomes. Given that hybridization and introgression are more prevalent in recently diverged species, homoploid hybrid speciation seems especially likely in rapidly evolving adaptive radiations, e.g. in cichlid fish and *Heliconius* butterflies (Seehausen 2004; Mavárez *et al.* 2006; Mallet in press *b*).

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