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A Century of Evolution: Ernst Mayr (1904–2005)

Mayr's view of Darwin: was Darwin wrong about speciation?

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We commonly read or hear that Charles Darwin successfully convinced the world about evolution and natural selection, but did not answer the question posed by his most famous book, '*On the Origin of Species* . . .'. Since the 1940s, Ernst Mayr has been one of the people who argued for this point of view, claiming that Darwin was not able to answer the question of speciation because he failed to define species properly. Mayr undoubtedly had an important and largely positive influence on the study of evolution by stimulating much evolutionary work, and also by promoting a 'polytypic species concept' in which multiple, geographically separated forms may be considered as subspecies within a larger species entity. However, Mayr became seduced by the symmetry of a pair of interlocking ideas: (1) that coexistence of divergent populations was not possible without reproductive isolation and (2) reproductive isolation could not evolve in populations that coexist. These beliefs led Mayr in 1942 to reject evidence of the importance of intermediate stages in speciation, particularly introgression between hybridizing species, which demonstrates that complete reproductive isolation is not necessary, and the existence of ecological races, which shows that ecological divergence can be maintained below the level of species, in the face of gene flow. Mayr's train of thought led him to the view that Darwin misunderstood species, and that species were fundamentally different from subspecific varieties in nature. Julian Huxley, reviewing similar data at the same time, came to the opposite conclusion, and argued that these were the intermediate stages of speciation expected under Darwinism. Mayr's arguments were, however, more convincing than Huxley's, and this caused a delay in the acceptance of a more balanced view of speciation for many decades. It is only now, with new molecular evidence, that we are beginning to appreciate more fully the expected Darwinian intermediates between coexisting species.

ADDITIONAL KEYWORDS: ecological races – essentialism – history of science – interspecific hybridization – introgression – nominalism – philosophy of science – species concepts.

'And this vast, this totally unprecedented change in public opinion has been the result of the work of one man, and was brought about in the short space of twenty years! This is the answer to those who continue to maintain that "the origin of species" is not yet discovered . . .' (Wallace, 1889: 'Darwinism', p. 9)

INTRODUCTION

Today, it has become widely accepted that although Darwin (1859) wrote a great book about evolution and natural selection, he was mistaken about species and therefore did not answer the question posed in the title '*On the Origin of Species* . . .' (hereafter *The Origin*). I cannot count how many times I heard or read statements of this sort during my own education. Many of my colleagues and friends continue to use this kind of assertion in their lectures, and indeed, until the mid-1990s, I did so myself. The claim is an old one, having first been made in various forms by creationists and other critics of Darwin as soon as *The Origin* was published, even by his 'bulldog' and firm supporter, Huxley (1860), as well as by his critic Romanes (1886). Romanes and Huxley both claimed that Darwin had not explained the origin of sterility and inviability of hybrids between species. The claim was repeated by Mendelians and mutationists of the early 20th Century, and again, even when the Modern

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Synthesis of genetics and Darwinian evolution had been largely reconciled, the idea was revived by Goldschmidt (1940), who believed that species originated by major 'systemic mutations' or chromosome rearrangements leading to major developmental changes. Goldschmidt claimed that these macro-mutations were unrelated to the minor genic changes found in typical populations, although he did argue that some such macro-mutations could also be important in intraspecific evolution when shifts in developmental systems were involved, such as in butterfly mimicry (Goldschmidt, 1945). Finally, the claim was again reiterated for still other reasons, discussed below, during the late Modern Synthesis, as exemplified by Mayr (1942).

One reason for the popularity of the claim that Darwin was mistaken is undoubtedly that it is a beautiful paradox: Darwin discovered the basis of evolution by natural selection, but he could not apply it himself to the origins of species, his major focus of interest; Darwin convinced the world of evolution, but failed to explain the title of his own book. It is a wonderful 'factoid', a 'sound-bite' which has been used as an *aide-memoire* by generations of lecturers, textbook writers, and students. But is it really true?

I believe it is worth revisiting and critically evaluating the argument that Darwin was mistaken, and especially Ernst Mayr's role in this claim. It is the modern version of the claim that is so widely believed, and through his influence on the development of theories of speciation, Mayr has been perhaps its most influential proponent. What exactly is the nature of the claim about Darwin's mistaken ideas made by Mayr and others subsequently? What did Darwin actually say on the matter? What does today's knowledge of evolutionary genetics and speciation tell us, and are the claims of Darwin's mistakenness unfounded, based on today's understanding about evolution? I believe, and will try to demonstrate here, that Darwin's own arguments have been largely misunderstood from the Modern Synthesis onwards, in part because few evolutionary biologists today read his book carefully, and in part because those who do so misunderstand the nature of the arguments by attempting to interpret Darwin's writings in the light of today's viewpoints and species definitions.

There is always a danger, of course, of setting Darwin on a pedestal. When I suggested to a colleague that his writings had misrepresented Darwin's views, he replied 'Sometimes I think that Darwin, at least on speciation, is like the Bible: one can buttress any view by choosing the right quotations'. I hope I avoid this problem, and I do not believe I have had to scour *The Origin* to find shreds of textual evidence that can be used to support an extreme and unlikely argument. Darwin clearly had many imperfections. One of these is that his writing style was suitable mainly for upper middle class readers in the mid 19th Century, who had plenty of leisure, servants, and long evenings lacking distractions of television, radio, or internet. Although a book of 490 pages, *The Origin* was intended as a mere abstract for a much longer work. Even so, this abstract is famously 'one long argument' that is both complex and discursive by today's standards, and also by the standards of the war-torn 1940s during the time that Mayr was writing. Another obvious imperfection is that Darwin did not know any of the genetics or evolutionary theory needed to gain today's full understanding of speciation. His ideas about blending inheritance were simply wrong. He was also wrong to believe in the inheritance of acquired characters (one aspect of 'Lamarckian' evolution), mainly because he was too credulous of the supposedly reliable evidence his animal and plant breeder correspondents had provided.

In spite of these deficiencies, it is remarkable how broadly acceptable many of Darwin's deductions and views about speciation are turning out to be, in view of today's knowledge about genetics, evolution, and ecology. I believe it is possible to discern a return to a more Darwinian viewpoint on speciation, after a period of approximately 40–50 years in which speciation was dominated by certain views of Mayr and his followers (Mallet, 2001b, 2005b). Herein, I argue that Mayr's influence was beneficial for systematics and for the promotion of the study of evolution and speciation in general, but also at the same time blocked adoption of a Darwinian view of species and speciation, a block which we are beginning to remove only today. I shall attempt to show that much evidence in favour of the Darwinian view was known to Darwin and used by him, and that even more was known by the time of Mayr. Therefore, Mayr could have played a very different role by integrating natural history and systematics more closely with genetics and Darwinism, rather than creating an artificial division and claiming that modern knowledge about evolution disproved Darwin's views about species.

WHAT DARWIN ACTUALLY SAID (AND MEANT)

Darwin's 'one long argument' is complex, defended with abundant empirical evidence, as well as verbal theory and thought experiments, and it runs throughout *The Origin*. It consists of long, complex sentences, embedded in long paragraphs, within long chapters that each form a key component of the overall argument. It is therefore extremely hard to summarize what Darwin was trying to say without paraphrasing the argument almost beyond recognition, within a short article as the present one. Others have attempted to use short quotations, often parts of sentences, which I shall show can obscure and even completely reverse the overall meaning Darwin intended. One might almost believe that Mayr deliberately selected unfair Darwinian text about species (e.g. in Mayr, 1982; and see below) in order to make out that Darwin was wrong-headed. But I do not accept this; if Mayr had been thinking of deliberately obfuscating Darwin's thoughts, he must also have known that he could not have got away with it. We would only have to read Darwin ourselves, and he would have been found out. Instead, I think Mayr took from Darwin's book what he genuinely thought he had read in it. I think he probably just copied out fragments of sentences or paragraphs for brevity, and then did not often check back to the original text to make sure he had not misconstrued Darwin's precise meaning. Having formed a very different interpretation of species from Darwin's, indeed one which has now become the standard today, Mayr found it hard to see the logic in these fragmentary statements about species and speciation. Although I cannot lay out Darwin's whole argument, I here attempt to avoid the problem of short quotations by quoting extensive passages from the first edition of *The Origin*. These are more extended sections of text than used by Mayr, and are those that I consider especially relevant to the argument that Darwin was confused about or did not properly deal with species and speciation.

Darwin on artificial selection and the nature of species

In Chapter I, 'Variation under Domestication', after a brief introduction explaining the history and background of evolutionary ideas, and also the scope of the book, Darwin introduces the ideas of variability within species, and of artificial selection. A major argument in this chapter is that breeds of domesticated animals are much more divergent in form than varieties of the same species in nature, and often more divergent even than separate species in nature. Darwin is not just making an argument that animal and plant breeds are similar to species, and that artificial selection by humans is analogous to natural selection; he is making a much more radical argument: that domesticated animal and plant breeds *are* in a sense separate species.

Of course, pigeon breeds such as pouters and tumblers are not reproductively isolated in the classical sense, but Darwin clearly rejects hybrid sterility and inviability as a useful species definition in the chapter on 'Hybridism' (see below). The different breeds of pigeons, dogs, or sheep remain separate because they have adapted to different ecological niches, niches which are determined by their symbiosis with humans. Their divergence into these separate niches, and their ability to maintain themselves distinct is of course due to human-aided selective breeding, but this is in practice the same as the way in which natural selection for nonhuman ecological niches can keep species separate in nature. The only difference is that the ecological niches of domesticated breeds depend on human preferences or uses, rather than on survival or ability to reproduce in natural environments. Today, we are entrained by our education, due in no small part to Mayr's own influence, to place species in nature on the one hand, and breeds of domesticated animals on the other, in separate mental boxes. We can no longer appreciate the radical vision that Darwin was outlining. In particular, we think of natural selection (and artificial selection) as an essentially within-species process that affects the whole population identically, rather than as a process which may include divergent selection into separate niches. For me, it still took several years after my initial conversion before I really understood the full power of the uniformitatian, Darwinian view of the nature of species. A simple question from an undergraduate after a lecture on species and speciation finally made the penny drop. She asked: 'if what you say about species is true, why aren't breeds of dogs considered separate species as well?' When I recovered from the question, I had to reply that breeds of dogs were indeed exactly what Darwin, and indeed I, in my lecture, had meant by separate species.

The argument then moves on to Chapter II, 'Variation in Nature'. At this point, Darwin raises the problem of a species definition, and it is his solution here that has led so many to criticise him since, and often to argue that his book was not really about speciation at all. Darwin came from a world where most people believed that species were separate, created kinds, each with a 'true' Aristotelian essence. At that time, educated and literary people in Europe had classical educations that would have encompassed Latin and Greek, and Ancient philosophy including arch-essentialists such as Aristotle and Plato. Consciously, or unconsciously, pre-Darwinian thinkers applied the essentialist terms 'genus' and 'species' to taxonomic categories in biology, as well as in other philosophical activities. Varieties within each species, on the other hand, were simply the imperfect expression of the species essence. Darwin had to overturn this view, because in any theory of evolution, varieties must evolve into species, and probably do so gradually, which means that species and varieties must be very much the same kind of thing: the boundary should be a continuum, and a clear definition of species can no longer be made. To make the argument for evolution, Darwin had to steer a fine line to show not only that species lacked an unchanging essence or, equivalently, hard-and-fast criteria for the species rank, but also that the term 'species' still meant something in the new, evolutionary sense needed to discuss their evolution.

The problem that leads to the Darwin's mistakenness claim is that many people, even today, and even some philosophers of science, feel that we need strict definitions for science to advance. You, the reader, may agree with the idea that strict definitions in science are necessary to make progress. I am not trying to say that this is in some way completely wrong (even though I do not personally believe it), but I do want to sow the seeds of doubt in your mind, and to point out that the idea that science does not require watertight definitions is a perfectly respectable viewpoint. Philosophers who write now about species often disagree, but many are rather negative about the need for hard-and-fast definitions (Wilson, 1999). We can find examples even at around the time of Mayr's first book (Popper, 1945: 19):

> 'In science, we take care that the statements we make should never depend on the meaning of our terms. Even where the terms are defined, we never try to derive any information from the definition, or to base any argument upon it. . . . This is how we avoid quarrelling about words. The view that the precision of science and of scientific language depends on the precision of its terms is certainly very plausible, but it is none the less, I believe, a mere prejudice . . .'

The reason that definitions are relatively unimportant, Popper explains, is that scientific theories do not flow from concepts and definitions, as might naively be believed. Instead, completely new definitions and concepts flow from scientific theories. Definitions and concepts should be made the servants of the theories and facts; otherwise, one risks impoverishing and restricting scientific progress by a too-restrictive definition. This was exactly the problem Darwin encountered with species; the facts told him that something was wrong with a non-evolutionary theory of life, he developed a theory of evolution to explain those facts, and so had to change the definition of species to fit the new theory. He could not have developed the same theories with the rigid, creationist definition used hitherto.

Having painted the backdrop, what was Darwin's new view of species, and was it coherent and fit for purpose? He made the argument that more or less everyone knew what a species was, namely that they were divergent forms between which one found morphological gaps in nature; members of the same species, in contrast, were connected by intermediates. However, with this definition, there were always going to be difficulties in deciding whether particular forms were species or varieties:

> 'Practically, when a naturalist can unite two forms together by others having intermediate characters, he treats the one as a variety of the other, ranking the most common, but sometimes the one first described, as the species, and the other as the variety. But cases of great difficulty, which I will not here enumerate, sometimes occur in deciding whether or not to rank one form as a variety of another . . . Hence, in determining whether a form should be ranked as a species or a variety, the opinion of naturalists having sound judgement and wide experience seems the only guide to follow.' (p. 47, in Chapter II, 'Variation under Nature')

Mayr (1982: 267) cites this section, but omits the entire passage, up to and including 'Hence', starting it 'In determining . . .'. By getting rid of the morphological gaps argument, Mayr changes the apparent intent of the above section from a carefully reasoned discussion into an apparently completely arbitrary species concept depending on experts.

To avoid promulgating the idea that evolutionary species are going to be clearly demarcated by a new, hard and fast definition, Darwin argues that he is what Popper and others today call a 'nominalist'.

> '. . . it will be seen that I look upon the term species, as one arbitrarily given for the sake of convenience to a set of individuals closely resembling each other, and that it does not essentially differ from the term variety, which is given to less distinct and more fluctuating forms.' (p. 52)

Species are distinct; varieties are not; but species and varieties are nonetheless very much the same kinds of things. One may not agree with Darwin's definitions, but he has, it seems to me, defined clearly what he is going to discuss.

Darwin then shows that there is a correlation among genera between the numbers of varieties within species and species diversity within that genus. Here is evidence for his belief that species within genera and varieties within species obey the same laws, and are the same kinds of things, adding further support that his nominalist view of species and varieties makes sense.

> 'Similarly, if species are only strongly-marked or well-defined varieties, we expect that species of larger genera should have greater intraspecific variability. This is not expected if each species is a special act of creation. . . . I have tested this using plants of 12 countries, and Coleoptera of two districts. Invariably, a larger proportion of the species in larger genera present varieties, and there are a larger number of varieties per species on average, than do the species in smaller genera.' (p. 55)

Darwin then sums up his definition of species. Varieties are the same kinds of things as species, except (1) that varieties have intermediate linking forms, whereas species do not and (2) that even if there are not linking forms or hybrids, many people are going to be very resistant to calling two forms separate species, unless they show at least some major diagnostic differences.

'Finally, then, varieties have the same general characters as species, for they cannot be distinguished from species, – except, firstly, by the discovery of intermediate linking forms, and the occurrence of such links cannot affect the actual characters of the forms which they connect; and except, secondly, by a certain amount of difference, for two forms, if differing very little, are generally ranked as varieties, notwithstanding that intermediate linking forms have not been discovered; but the amount of difference considered necessary to give to two forms the rank of species is quite indefinite.' (pp. 58–59)

Here again, Mayr only partially quotes Darwin and in doing so changes the apparent intent. Mayr (1982) quotes the first clause of this sentence as 'Varieties have the same general characters as species, for they cannot be distinguished from species'. By missing out the ', – except, firstly, . . ;' and 'except, secondly, . . .', Mayr again almost completely reverses the sense of Darwin's intended message. Darwin is not saying species are the same as varieties at all, he is merely saying that they are on the same continuum, but that they differ only quantitatively.

The supposed need for geographic isolation in species formation

How do species arise? One obvious idea is that species diverge because of geographic isolation or lack of contact (allopatry). Contact (sympatry) would lead (in Darwin's view, as well as today's view informed by genetics) to obliteration of differences, and could therefore impede speciation. Darwin uses the term 'isolation' to mean geographic isolation in today's terminology.

'Isolation, also, is an important element in the process of natural selection. In a confined or isolated area . . . natural selection will tend to modify all the individuals of a varying species throughout the area in the same manner in relation to the same conditions. Intercrosses also, with the individuals of the same species, which otherwise would have inhabited the surrounding and differently circumstanced districts, will be prevented. But isolation probably acts more efficiently in checking the immigration of better adapted organisms, after any physical change, such as of climate or elevation of the land, &c; and thus new places in the natural economy of the country are left open for the old inhabitants to struggle for, and become adapted to, through modification in their structure and constitution. Lastly, isolation, by checking immigration and consequently competition, will give time for any new variety to be slowly improved; and this may sometimes be of importance in the production of new species.' (pp. 104–106)

However, geographic isolation has a downside:

'If, however, an isolated area be very small, either from being surrounded by barriers, or from having very peculiar physical conditions, the total number of the individuals supported on it will necessarily be very small; and fewness of individuals will greatly retard the production of new species through natural selection, by decreasing the chance of the appearance of favourable mutations.'

Isolation may be important, but in large continental areas where there are large populations, more variation will arise via mutation. The more extensive biotic interactions, particularly competition, in such areas, will provide a better testing ground leading to greater improvement and potential for divergence, and faster evolution, and will ultimately lead to lineages that are more successful.

'Although I do not doubt that isolation is of considerable importance in the production of new species, on the whole I am inclined to believe that largeness of area is of more importance, more especially in the production of new species, which will prove capable of enduring for a long period, and of spreading widely. Throughout, a great and open area, not only will there be a better chance of favourable variations arising from the large number of individuals of the same species there supported, but the conditions of life are infinitely complex from the large number of already existing species; and if some of these many species become modified and improved, others will have to be improved in a corresponding degree or they will be exterminated. . . . the course of modification will generally have been rapid on large areas; and what is more important, that the new forms produced on large areas, which already have been victorious over many competitors, will be those that will spread most widely, will give rise to most varieties and species, and will thus play an important part in the changing history of the organic world.'

This seems to me a balanced argument about the role of geographic isolation in speciation, which incorporates an extraordinary understanding of the relevant information, based on Darwin's own travels on 'The Beagle', as well as his reading. It almost could have been written today. The breadth of topics and knowledge covered here is extraordinary, and include island biogeography (the Galapagos, and Galapagos finches must surely be at the back of his mind here (Sulloway, 1979), knowledge of species diversity on islands versus mainlands (the Galapagos and South America, for example), and invasion biology of continental species on islands.

Darwin's mechanism of speciation: the principle of divergence

But what actually causes speciation? According to Darwin's earlier definition of species, speciation is the production of divergent forms that lack intermediates. In Darwin's view, the causes of speciation are a combination of two principles: the principle of divergence, and the principle of extinction (Kohn, 2008).

'How do the lesser differences between varieties evolve into the greater differences between species? Firstly, mere chance may allow some divergence, but this seems unlikely to account for such a habitual and large amount of difference.' (p. 111, para 1)

Although Darwin did not know about genetic drift, he seems to have intuited it, presumably from information which suggested that not all differences between populations made adaptive sense.

A more important cause of speciation is, in Darwin's view, competition leading to divergent natural selection, for which artificial selection by humans on domestic animals is a useful and relatively uncontroversial analogue.

'Again, we may suppose that at an early period one man preferred swifter horses; another stronger and more bulky horses. The early differences would be very slight; in the course of time, from the continued selection of swifter horses by some breeders, and of stronger ones by others, the differences would become greater, and would be noted as forming two sub-breeds; finally, after the lapse of centuries, the sub-breeds would become converted into two well-established and distinct breeds. As the differences slowly become greater, the inferior animals with intermediate characters, being neither very swift nor very strong, will have been neglected, and will have tended to disappear. Here, then, we see in man's productions the action of what may be called the principle of divergence, causing differences, at first barely appreciable, steadily to increase, and the breeds to diverge in character both from each other and from their common parent.'

'But how, it may be asked, can any analogous principle apply in nature? I believe it can and does apply most efficiently, from the simple circumstance that the more diversified the descendants from any one species become in structure, constitution, and habits, by so much will they be better enabled to seize on many and widely diversified places in the polity of nature, and so be enabled to increase in numbers.' . . . 'We can clearly see this in the case of animals with simple habits. Take the case of a carnivorous quadruped, of which the number that can be supported in any country has long ago arrived at its full average. If its natural powers of increase be allowed to act, it can succeed in increasing (the country not undergoing any change in its conditions) only by its varying descendants seizing on places at present occupied by other animals.' (p. 112, para 2)

Of course, this principle of divergence applies as much to plants as to animals:

'It has been experimentally proved, that if a plot of ground be sown with several distinct genera of grasses, a greater number of plants and a greater weight of dry herbage can thus be raised. The same has been found to hold good when first one variety and then several mixed varieties of wheat have been sown on equal spaces of ground.'

'The truth of the principle, that the greatest amount of life can be supported by great diversification of structure, is seen under many natural circumstances. . . . For instance, I found that a piece of turf, three feet by four in size, which had been exposed for many years to exactly the same conditions, supported twenty species of plants, and these belonged to eighteen genera and to eight orders, which shows how much these plants differed from each other.' (p. 114, para 1)

It is possible to interpret Darwin's principle of divergence as an argument for sympatric speciation (Kohn, 2008), as Mayr and others have done. But the argument for and against geographic isolation has been dealt with earlier in *The Origin*. Perhaps Darwin was not entirely clear, but I think it fairly self-evident that he was here discussing the ecology of available niches for populations that have already become somewhat divergent, rather than arguing that the whole process of speciation is necessarily sympatric. Having diverged, these forms would not go extinct because they could 'seize on many and widely diversified places in the polity of nature'. Darwin did not clearly specify a proximate cause for the initial divergence, but was arguing that, however divergence came about, it could be stabilized in separate niches, and that this would lead to an increase of surviving divergent forms. The ultimate cause of diversity was that only diverse forms can coexist. The argument about multiple species having greater productivity than a single species is, it seems to me, prescient: in the 1970s and 1980s, ecologists began to realize that high productivity was associated with diversity of compatible species in both natural and agricultural systems (Vandermeer, 1981). More recent studies have shown similar productivity gains in higher diversity ecosystems (Tilman *et al.*, 2002).

'The accompanying diagram will aid us in understanding this rather perplexing subject'. This famous tree diagram, inserted between pp. 116–117, is the only figure in 'T*he Origin*.' In Darwin's view, the figure was not so important as a phylogenetic theory of evolution, as some have suggested, but as an explanation of how gaps in the distribution of phenotypes appeared as a result of the principles of divergence and extinction. The section describing the figure is 3000 words long, explaining in detail how divergence might come about, and how each particular node and branch had parallels in the origins and extinctions of real varieties, species, genera and families.

WHY DO WE NOT SEE MORE INTERMEDIATES?

In Chapter VI, 'Difficulties on Theory', Darwin attempts to answer doubts that he expects his readers will have about the continuous nature of evolution.

For example, if evolution is a continuous process, why do we not see more intermediates between species? His answer is that the evolutionary process quickly obliterates the intermediates (his principle of extinction) and become distinct in nature:

'To sum up, I believe that species come to be tolerably well-defined objects, and do not at any one period present an inextricable chaos of varying and intermediate links: firstly, because new varieties are very slowly formed, for variation is a very slow process, and natural selection can do nothing until favourable variations chance to occur, and until a place in the natural polity of the country can be better filled by some modification of some one or more of its inhabitants. . . .'

'Secondly, areas now continuous must often have existed within the recent period in isolated portions, in which many forms . . . may have separately been rendered sufficiently distinct to rank as representative species. In this case, intermediate varieties . . . must formerly have existed in each broken portion of the land, but these links will have been supplanted and exterminated during the process of natural selection, so that they will no longer exist in a living state.'

'Thirdly, when two or more varieties have been formed in different portions of a strictly continuous area, intermediate varieties will, it is probable, at first have been formed in the intermediate zones, but they will generally have had a short duration.'

Finally, a key passage suggesting how the early stages of speciation should appear, and why the process eventually leads to distinct, and discrete species:

'Lastly, looking not to any one time, but to all time, if my theory be true, numberless intermediate varieties, linking most closely all the species of the same group together, must assuredly have existed; but the very process of natural selection constantly tends . . . to exterminate the parent-forms and the intermediate links.' (p. 179)

HYBRID STERILITY AND THE NATURE OF SPECIES

Chapter VIII, on 'Hybridism', is often misunderstood. This is the chapter that deals with an important and hitherto unexplained characteristic of species, that hybrids between them are often sterile or inviable. Darwin argues this is an important and common characteristic of species, but also that it is neither a necessary nor a sufficient condition for the origin and maintenance of separate species.

'Pure species have of course their organs of reproduction in a perfect condition, yet when intercrossed they produce either few or no offspring. Hybrids, on the other hand have their reproductive organs functionally impotent, . . . The fertility of varieties, that is of the forms known or believed to have descended from common parents, when intercrossed, and likewise the fertility of their mongrel offspring, is, on my theory, of equal importance with the sterility of species; for it seems to make a broad and clear distinction between varieties and species.' (p. 246)

Disagreement between experts is good reason to doubt the universality of a sterility criterion for species, but another argument is that there is evidence of hybrid sterility among populations of the same species, and evidence of gene flow among populations of different species:

'. . . for all practical purposes it is most difficult to say where perfect fertility ends and sterility begins. I think no better evidence of this can be required than that the two most experienced observers who have ever lived, namely, Kölreuter and Gärtner, should have arrived at diametrically opposite conclusions in regard to the very same species.' (p. 248)

'I have as yet spoken as if the varieties of the same species were invariably fertile when intercrossed. But it seems to me impossible to resist the evidence of a certain amount of sterility in the few following cases, which I will briefly abstract. The evidence is at least as good as that from which we believe in the sterility of a multitude of species.' (p. 269)

'Finally, then, the facts briefly given in this chapter do not seem to me opposed to, but even rather to support the view, that there is no fundamental distinction between species and varieties.' (p. 278; final summary of the chapter on hybridism)

Thus it is clear that Darwin carefully considered a species definition that depended on reproductive isolation, but rejected it on the basis of his knowledge of empirical evidence on 'post-mating' isolation. Reproductive isolation is certainly a characteristic of species, and indeed an important one, but it is not an infallible one. Darwin did not present a parallel argument against 'pre-mating' or 'behavioural' isolation (as it was later termed by Theodosius Dobzhansky and Ernst Mayr), that is, assortative mating, as defining characteristics of species. This was left to Wallace (1889: 152–186) to clarify after Darwin's death. However, as the inventor of the theory of sexual selection (in Chapter IV, 'Natural Selection; or the Survival of the Fittest'), one imagines that Darwin would quickly dismiss any idea that there was a special kind of assortative mating found only between species, and which therefore formed any part of a useful definition of species.

One might disagree with Darwin's rejection of the idea of reproductive isolation as a definition of species, but one cannot say that he had not carefully weighed it up, before deciding against it. Darwin made a clear definition of species in his terms, while rejecting reproductive isolation as a definition, and then used this definition in his argument for speciation; in view of the diversity of views about species today, I do not think one can any longer fault him on this in 1859. One should certainly treat his views more seriously than to argue glibly that he did not solve the question proposed by *The Origin*.

Another important point in 'Hybridism', which I mention in passing, is Darwin's argument that since hybrid inviability and sterility is so variable in its appearance between species, it was very unlikely to have been selected for directly, or to be necessary for speciation. In this argument, he is dealing with the possible criticism, later leveled at him particularly by Romanes (1886), who claimed that sterility and inviability must have come about by some sort of 'physiological selection'. Instead, Darwin argued that sterility of hybrids must be a by-product of natural selection or random forces in evolution, very much in line with what we believe today (Orr & Turelli, 2001).

Finally, the summary of the whole long argument:

'When the views entertained in this volume on the origin of species, or when analogous views are generally admitted, we can dimly foresee that there will be a considerable revolution in natural history. Systematists will be able to pursue their labours as at present; but they will not be incessantly haunted by the shadowy doubt whether this or that form be in essence a species. . . . The endless disputes whether or not some fifty species of British brambles are true species will cease. Systematists will have only to decide (not that this will be easy) whether any form be sufficiently constant and distinct from other forms, to be capable of definition; and if definable, whether the differences be sufficiently important to deserve a specific name. . . . Hereafter, we shall be compelled to acknowledge that the only distinction between species and well-marked varieties is, that the latter are known, or believed, to be connected at the present day by intermediate gradations, whereas species were formerly thus connected. . . . In short, we shall have to treat species in the same manner as those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience. This may not be a cheering prospect; but we shall at least be freed from the vain search for the undiscovered and undiscoverable essence of the term species.' (pp. 484–485, in Chapter XIV, 'Recapitulation and conclusion')

Darwin recognizes the difficulties we are going to have accepting his radical new view of species and speciation, but he feels it is the correct view, and it will cause fewer problems than the essentialist view that it replaces. Again Mayr (1982) quotes only the sentence 'In short . . .', thereby maximizing the seeming arbitrariness of Darwin's view of species. Darwin is really, here, arguing for a pragmatic and useful definition of species based on gaps in variation, because he feels he has proved the lack of a clear biological distinction based on reproductive isolation. He claims that we will be freed from being 'incessantly haunted by the shadowy doubt whether this or that form be in essence a species', and from 'the endless disputes' about species, because we can give up, once and for all, belief in 'the undiscovered and undiscoverable essence of the term species.' I do not believe that the word 'essence' is an idle form of words. Darwin is attacking the whole of essentialist philosophy as applied to species and speciation, both implicit and explicit. Darwin was classically educated, as all men of his class were at that time. When Darwin went up to Cambridge after giving up his medical studies in Scotland, there were no courses in science at any University south of the Scottish border in England; all one could learn at Cambridge or Oxford were the classics and theology. Among the most inflential of these creationist, essentialist ideas about reproductive isolation Darwin was trying to disprove were those of Buffon:

'We should regard two animals as belonging to the same species if, by means of copulation, they can perpetuate themselves and preserve the likeness of the species; and we should regard them as belonging to different species if they are incapable of producing progeny by the same means.' (Buffon, 1749: vol. 2, p. 14)

How right Darwin was about the 'revolution in natural history', but how wrong he was about the end of 'the endless disputes' about species! They would go on and on, and they still are.

MAYR ON DARWIN'S FAILURE TO UNDERSTAND THE NATURE OF SPECIES

Here are a few of the examples in Mayr's writings of the claim that Darwin was not only mistaken, but also did not really deal with speciation at all.

'It is thus quite true, as several recent authors have indicated, that 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: 146)

'Darwin succeeded in convincing the world of the occurrence of evolution and . . . he found (in natural selection) the mechanism that is responsible for evolutionary change and adaptation. It is not nearly so widely recognized that Darwin failed to solve the problem indicated by the title of his work. Although he demonstrated the modification of species in the time dimension, he never seriously attempted a rigorous analysis of the problem of the multiplication of species, the splitting of one species into two. I have examined the reasons for this failure (Mayr, 1959) and found that among them Darwin's lack of understanding of the nature of species was foremost.' (Mayr, 1963: 12)

Mayr (1982: 269) claimed both that Darwin treated species 'purely typologically [i.e. as an essentialist] as characterized by degree of difference', and also that Darwin 'had strong, even though perhaps unconscious, motivation . . . to demonstrate that species lack the constancy and distinctiveness claimed for them by the creationists.' It seems to me particularly unfair to make this implication that Darwin was bending the evidence in a 'perhaps unconscious' bid to claim that species were more variable than they really were, in order to support his argument that they had evolved from varieties. Also, in view of Darwin's extremely negative views about the essence of species quoted above, it also seems very odd to argue that Darwin was a typologist.

Mayr's views are echoed by many other reviews of the evidence on speciation. For example:

> 'One of the ironies of the history of biology is that Darwin did not really explain the origin of new species in *The Origin of Species*, because he didn't know how to define a species.' (Futuyma, 1983: 152:)

> 'In fact, 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.' p. 481: '. . . Darwin thought of species as merely well-marked "varieties;" that is, as populations defined by their degree of difference in morphological features. Thus for Darwin, as for his contemporaries, explaining the origin of species was the same as explaining the evolution of morphological and other phenotypic characters . . .' (Futuyma, 1998: 449)

> 'Yet [Darwin's] magnum opus remains largely silent on the "mystery of mysteries" [i.e. speciation], and the little it does say about this mystery is seen by most modern evolutionists as muddled or wrong.' (Coyne & Orr, 2004: 9)

Mayr's important contribution

There was one good reason why Mayr felt that Darwin was wrong and this was to do with the differences between geographic varieties and species. Mayr is famous for clearly enunciating the 'biological species concept' (BSC) based on reproductive isolation (Mayr, 1940), and then elaborating it in 1942 and later works. But Mayr's BSC itself was a synthesis of two major related ideas.

The first idea was that of reproductive isolation, and in this his ideas agreed with Dobzhansky (1937). In fact, the idea of species being defined by reproductive isolation had arisen much earlier, in pre-Darwinian times, including Buffon (see above) and was an argument that both Darwin and Wallace were attempting to disprove.

In its post-Darwinian phase, the idea was probably passed to Dobzhansky via entomologists and geneticists in his native Russia (Krementsov, 1994), who had been long discussing 'physiological selection.' From Dobzhansky, it spread to today's evolutionary geneticists. These ideas are traceable to an early critique of Darwin (Romanes, 1886), through to Edward Bagnall Poulton and Karl Jordan's ideas on reproductively incompatible species (Poulton, 1904; Jordan, 1905). See Rothschild (1983); Krementsov (1994), and Mallet (2004) for documentation of this history. Yet as we have seen, his chapter 'Hybridism' shows that Darwin knew a lot about the importance of 'physiological barriers', and had argued carefully that they were a side issue in speciation.

However, it was I believe with regard to a second, systematics-based strand of his BSC formulation that Mayr had a better argument against Darwin. This second idea was that of the polytypic species. Mayr had been trained in a German taxonomy background, where he encountered the evolutionary ideas of Otto Kleinschmidt, Bernhard Rensch, and especially Erwin Stresemann. As a bird taxonomist, he had read David Starr Jordan and the 19th Century American ornithologists. He had worked as a collector in New Guinea for Walter Rothschild who together with his curators Ernst Hartert and Karl Jordan (no relation to D. S. Jordan) was amassing the largest collection of butterflies and birds in the world, at Tring, Hertfordshire. By an extraordinary coincidence, and due to a blackmailing 'smiling peeress', Walter Rothschild had been forced to sell his bird collection to the American Museum of Natural History, which was where Mayr happened to have taken his first permanent post as curator of birds (Rothschild, 1983). These scientists and collectors in the USA, Germany and England were busy promoting a new kind of species criterion in taxonomy, one in which geographic populations could be greatly different in morphology, but would not be called separate species unless they overlapped spatially without (or with few) intermediates (Stresemann, 1975; Mayr, 1982; Rothschild, 1983). This new 'polytypic species concept' originated in the 1880s in the USA and Germany, and was accepted by Rothschild, his curators, and many European ornithologists and entomologists by about 1910. These scientists promoted the idea that geographically separated varieties were often 'subspecies', rather than true species. Geographically divergent forms were only considered separate species if they overlapped without intergrading. If related, 'replacement' forms did not overlap, or overlapped only at narrow zones of intergradation, then they were considered subspecies, rather than 'true' species. The Linnean nomenclature at this time came to be formalized so that monomorphic geographic subspecies became a valid taxonomic rank, whereas most other 'sports', 'varieties' or 'var.' (of animals, at least) were relegated to synonymy. The species thus became 'polytypic', meaning that there were often a number of named, morphologically divergent, geographic subspecies within each widely-distributed species (Stresemann, 1975; Mayr, 1982; Rothschild, 1983; Mallet, 2001a, 2004).

What I believe is Mayr's novel, and maybe most important insight about Darwin's view of species most clearly is expressed thus:

'Many of Darwin's followers, including most of the taxonomists of the old school, thought that the problem of species was solved when they found that intermediate forms connect what were formerly considered two perfectly distinct species. They concluded that species are transformed into new species as they spread into new areas. 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. And this is exactly the conclusion drawn by men such as Kleinschmidt or Goldschmidt. They claim that all the evidence for intergradation between species in the past was actually based on cases of infraspecific variation, and, in all honesty, it must be admitted that this claim is largely justified.' (Mayr, 1942: 113–114)

Darwin, by not clearly distinguishing geographic from local or sympatric varieties, had thus unwittingly made speciation appear too easy. For speciation to be different from ordinary within-species evolution, speciation could not just be a problem of simple morphological and genetic divergence; it must involve the ability to overlap without fusion, which was a qualitatively different effect than mere geographic or varietal divergence. I do not think there is any doubt that the early Darwinians, including Darwin himself (especially in his 'principle of divergence', see above), Henry Walter Bates and especially Alfred Russel Wallace (Wallace, 1865, 1889), had this idea of sympatric overlap in mind, but it was not clearly expressed in *The Origin*.

This was perhaps the most important omission from Darwin's argument, and was the key reason why Mayr felt justified in promoting the biological species concept as an alternative to Darwin's view of species. Mayr's taxonomic views and influence led to a decades-long period of stability of the taxonomy of polytypic species in taxa such as birds and butterflies, and to a degree of consensus that studying speciation involved studying the evolution of reproductive isolation so that separate species could overlap. The period of stability lasted approximately from 1940 till the mid-1980s, when the phylogenetic species concept began to be adopted and taxonomic inflation had a renewed effect on species lists, in birds and mammals in particular (Isaac, Mallet & Mace, 2004; Meiri & Mace, 2007). Mayr's understanding in this area was a major advance, had far-reaching effects, and, at the same time, led to the acquisition of much useful data about speciation which informs today's understanding of the topic.

Mayr went too far

In the idea of polytypic species, then, I believe that Mayr clarified an important advance over the Darwinian evolutionary theories of the 1850s and 1860s. But there I part company with him. As we have seen, Darwin, and especially other Darwinists such as Alfred Russel Wallace and Henry Walter Bates (Mallet, 2004, 2008a, b) had thought carefully about the geographic nature of species as well. Mayr's promotion of the new polytypic, biological species concept and the 'modern synthesis' was not so much a major revolution as a fine-tuning adjustment that could have been grafted onto the main theory with more care. In important ways, I believe that Mayr missed the mark, even though he had the data at his disposal. These problems have caused delays in the understanding of speciation ever since.

First, Mayr used and promoted Dobzhansky's idea of 'isolating mechanisms.' I have discussed the group-selectionist nature of these ideas elsewhere (Mallet, 1995, 2005b, 2006). It is sufficent to say here that we now know that a great deal of the evolution of reproductive isolation has nothing to do with speciation; instead it occurs long after speciation has occurred. A good example is given by the centrarchid fish: in this family, speciation between pairs of sister taxa (in the sense of ability to overlap) is often achieved in approximately 2 million years, although some hybridization between species in nature persists until approximately 15 million years after divergence. Sterility and inviability of hybrids remains largely incomplete (as judged by laboratory crosses) until approximately 30 million years after initial divergence (Bolnick & Near, 2005). Similar observations have been made in a comparative survey of hybrid inviability and sterility in birds (Price & Bouvier, 2002). Furthermore, in hybrid zones, hybrid inviability and sterility are extremely variable and do not predict whether phenotypes or genotypes will form a bimodal distribution (which can be regarded as the cusp of speciation because hybrids or intermediates are rare; Jiggins & Mallet, 2000). By contrast, ecological divergence can often promote extremely rapid divergence in overlap by means of an indirect, pleiotropic (by-product) effect on mating behaviour (Feder, Berlocher & Opp, 1998; Jiggins, Emelianov & Mallet, 2005). The 'principle of divergence' is in this sense a valid idea, although Darwin lacked the detailed mathematical and genetic models required, and today's data to back it up with evidence.

Second, Mayr was seduced by a beautifully symmetrical pair of ideas that dovetailed in apparently perfect Yin–Yang harmony: (1) species cannot coexist unless they are reproductively isolated and (2) a lack of coexistence (allopatry), is necessary for the origin of new species. See Mayr (1942: 226), especially the last two sentences:

'. . . isolating factors can be classified, broadly speaking, into two large groups, i.e. geographic and reproductive barriers. The latter are frequently referred to as biological or physiological isolating mechanisms. There is a fundamental difference between the two classes of isolating mechanisms, and they are largely complementary. Geographic isolation alone cannot lead to the formation of new species, unless it is accompanied by the development of biological isolating mechanisms which are able to function when the geographic isolation breaks down. On the other hand, biological isolating mechanisms cannot be perfected, in general, unless panmixia is prevented by at least temporary establishment of geographic barriers.'

Having attained this clear and dichotomous view it was hard to shake. Mayr was a master of the data. By then, it was known that hybridization between species occurred regularly, albeit very rarely on a per-individual basis in natural populations. Mayr styled all such hybridization as an unnatural consequence of secondary contact between formerly isolated entities; hybridization became a pathological 'breakdown of isolating mechanisms' in his chapter 'The Biology of Speciation' (Mayr, 1942: 258). He rejected any idea that hybridization might contribute to adaptive evolution, especially hybrid speciation. Furthermore, because in 1942 he was concerned only with animal speciation, and animal chromosomes were still poorly known, he was able to argue that speciation by any sort of polyploidy was in essence absent.

What about evidence for nongeographic (sympatric) speciation? Mayr (1942) devotes a whole chapter to this topic and rejects all the evidence for sympatric ecological races and incipient species that were in contact and yet remained stably coexisting below the level normally considered species. Huxley (1942) in the same year considered such cases as excellent evidence for sympatric coexistence of incompletely reproductively isolated entities, which demonstrated a Darwinian continuity between varieties and species. The evidence included rodents like *Peromyscus* in different habitats, altitudinal races in birds, seasonal races in insects, host-related race formation in parasites, and explosive fish speciation in the African rift-valley lakes and Lake Baikal. Mayr (1942: 199) dismisses all this in terms such as:

'No evidence exists for most so-called ecological races that would indicate whether they are merely phenotypical or whether their morphological differences have a genetic basis; . . . No process is known which would permit the development and perfecting of biological isolating mechanisms in "ecological races"; Whenever two neighboring . . . subspecies are distinguished by strong ecological differences, it can nearly always be shown that these differences were acquired prior to the period of geographic contact and that the present contact is a secondary condition; There is, at the present time, no well-substantiated evidence that would prove . . . the development of interspecific gaps through habitat specialization. The cases recorded as such have all the characteristics of secondary intergradation.'

Mayr can perhaps be defended in that his own and Huxley's cited examples of species *in statu nascendi* were by today's standards not well characterized, and, with no molecular markers available, there was no possibility of verifying multilocus genetic divergence. But, in the absence of proof, was it fair that Mayr rejected so strongly the idea of sympatric divergence, and also that ecological selection could sometimes be stronger than gene flow? I think not – there were too many niggling pieces of circumstantial evidence against Mayr's views. At the end of his chapter on nongeographic speciation, he perhaps realizes that he is 'pushing the envelope' too far on the basis of existing data:

'Certainty as to the relative importance of sympatric speciation in animal evolution cannot be expected until a much greater body of facts is available than at present.' (Mayr, 1942: 215)

But this statement of doubt did not prevent much firmer claims in later works in 1963 and 1970. It seems clear that Mayr took the view he did on the basis of that beautiful symmetry, rather than on the basis of data. Unfortunately, he knew the data well, and described its inconclusiveness extremely convincingly. Generations of evolutionary biologists for decades afterwards were brought up on Mayr's textbooks, and this, I argue, was to cause a catastrophic delay in the progress of understanding speciation.

I use the word 'unfortunately' because it is turning out that Mayr was wrong about this. Mayr himself eventually agreed that some examples of sympatric speciation, such as cichlids in African crater lakes, were likely, although still arguing that allopatric speciation was by far the most common mode (Mayr, 1999: xxx–xxxi). Ecological forms can and do coexist in nature in spite of gene flow (Jiggins & Mallet, 2000; Berlocher & Feder, 2002; Drès & Mallet, 2002; Mallet, 2008a); hybridization and introgression between species is common, and can contribute to speciation, even in nonpolyploids (Arnold, 1997; Buerkle *et al.*, 2000; Coyne & Orr, 2004; Mallet, 2005a, 2007); explosive speciation of fish in single lakes now seems most likely to involve at least some important processes in sympatry (Schluter & Nagel, 1995; Seehausen, 2004); sympatric speciation and 'reinforcement' are today viewed as likely and indeed confirmed processes, although we still do not know how common they are (Butlin, 1995; Noor, 1995; Coyne & Orr, 1997, 2004; Via, 2001; Berlocher & Feder, 2002).

WHAT IF?

It is given mainly to naive amateur historians to speculate what might have been. However, as I have few credentials to lose in the history of science, I feel free to argue that Mayr made a mistake, and to suggest that a different approach would have been better. He could have framed his new ideas and syntheses as arguments which bolstered, rather than attempting to revolutionize and in part overturn Darwinism. Mayr could easily have gone along with the Darwinian idea that species were continuous with subspecific varieties, and that varieties only had to develop quantitative differences which could lead ultimately to gaps between them. Instead, Mayr chose to support the idea that species were fundamentally different from varieties with special characteristics (reproductive isolation), and that they required special evolutionary conditions (e.g. geographic isolation, genetic revolutions) for their divergence, which subspecific evolution did not require. Speciation became more difficult than could be achieved by simple adaptation and character evolution, which Darwin believed was the key to diversification. This supposed difficulty of speciation then directly led to the view that Darwin misunderstood the topic of his own book.

Fundamental differences between species (as sources of the supposed 'reality' of species) were stressed by Mayr and his followers, in contrast to the presumed unreality of subspecific varieties. There are a number of problems with adopting Mayr's views in today's most pressing debates in the evolutionary arena. Evolutionary biology, especially in the USA and the Muslim world, is under unprecedented threat from the anti-science community, particularly the self-styled 'Intelligent Design' supporters of modified creationism. If species are viewed as fundamentally distinct from subspecies and 'varieties', the evolution of new species appears more mysterious and difficult than otherwise. Speciation then supposedly is hard to achieve, as opposed to being a natural consequence of ordinary divergent evolution occurring within species, as Darwin argued. Would not evolutionists be better off in their dispute with creationists if it could be argued that subspecies and varieties are very much the same kinds of thing, differing only quantitatively? To claim that there are clear boundaries or fundamental differences between varieties and species seems to invalidate the most important of Darwin's uniformitarian arguments for evolution.

The Mayr view of species seems to argue that the only populations with any future are 'pure' species, rather than hybrid populations. Hybrids, according to Mayr, are caused by 'breakdowns in isolating mechanisms', and are therefore of little importance. Mayr promoted the view that the diversification of life would be impossible without reproductive isolation (Mayr, 1963). These ideas of Mayr led to conservation policy: the Endangered Species Act in the USA had a notorious 'hybrid policy', in which evidence of hybridization could invalidate arguments for conservation of groups of rare organisms. Mayr himself helped to argue that this policy was too strict (O'Brien & Mayr, 1991). Viewed from today's biological and ethical standpoints, the hybrid policy seems unfairly to favour genetic purity. Given that hybrid species might sometimes arise and spread out as successful new lineages, it seems sensible to avoid value judgments on groups of organisms solely on the basis of a concept such as the Mayrian view of species purity. Today, the hybrid policy has been rescinded, and increasing numbers of biologists adopt a biodiversity viewpoint in which biological diversity at all levels is considered important in conservation, including hybrids, subspecies, and 'evolutionarily significant units'. Imagine now that Mayr had convinced us all of a less rigid, more Darwinian view of species and their value; would we not have avoided all this bother about the over-reliance on species in conservation policy?

Ernst Mayr was hugely influential force in promoting a modern view of evolution as a scientific discipline from 1940 onwards. In addition, he promoted a biological system to explain and justify wide-ranging polytypic species (i.e. species with multiple subspecies), which had a salutary effect on the history of classification and nomenclature of organisms, and led to a period of taxonomic stability. By contrast, the rise of the phylogenetic species concept has led to unprecedented levels of taxonomic inflation, especially in well-known groups like mammals and birds, causing problems for the understanding of biodiversity and in conservation (Isaac *et al.*, 2004; Meiri & Mace, 2007). On the other hand, the rigidity of Mayr's species conception, and his firm rejection of the existence of intermediate stages in speciation have led to problems in the understanding of speciation as well as practical problems in conservation and biodiversity. His legacy will always be mixed.

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