Darwin's bridge between microevolution and macroevolution

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Evolutionary biologists have long sought to understand the relationship between microevolution (adaptation), which can be observed both in nature and in the laboratory, and macroevolution (speciation and the origin of the divisions of the taxonomic hierarchy above the species level, and the development of complex organs), which cannot be witnessed because it occurs over intervals that far exceed the human lifespan. The connection between these processes is also a major source of conflict between science and religious belief. Biologists often forget that Charles Darwin offered a way of resolving this issue, and his proposal is ripe for re-evaluation in the light of recent research.

Charles Darwin and Alfred Russel Wallace based their insight that organisms evolve by natural selection on four principles[1,2]: first, that organisms have "individual variations" that are faithfully transmitted from parent to offspring; second, that all organisms produce more offspring than are required to replace themselves in the next generation; third, that limited resources create a "struggle for existence" that regulates population size, such that most offspring die without reproducing; and fourth, that the individuals that survive and reproduce are, on average, by virtue of their individual variations, better suited to their local environment than those that do not.

Given these four principles, evolution by natural selection (Darwin's 'principle of descent with modification') naturally follows. Such adaptive modifications within populations over time are now referred to as microevolution. Darwin anticipated that microevolution would be a process of continuous and gradual change.

The term macroevolution, by contrast, refers to the origin of new species and divisions of the taxonomic hierarchy above the species level, and also to the origin of complex adaptations, such as the vertebrate eye. Macroevolution posed a problem to Darwin because his principle of descent with modification predicts gradual transitions between small-scale adaptive changes in populations and these larger-scale phenomena, yet there is little evidence for such transitions in nature. Instead, the natural world is often characterized by gaps, or discontinuities. One type of gap relates to the existence of "organs of extreme perfection", such as the eye, or morphological innovations, such as wings, both of which are found fully formed in present-day organisms without leaving evidence of how they evolved. Another category is that species and higher ranks in the taxonomic hierarchy are often separated by gaps without evidence of a transition between them. These discontinuities, plus the discontinuous appearance and disappearance of taxa in the fossil record, form the modern conceptual divide between microevolution and macroevolution (Box 1).

Most evolutionary biologists think that Darwin explained macroevolution simply as microevolution writ large. In fact, Darwin had rather more to say about the relationship between microevolution and macroevolution and invoked additional principles to define it. It is these additional principles that are of interest here because they are often forgotten in discussions of the relationship between microevolution and macroevolution.

The keys to Darwin's thinking about macroevolution are the 'principle of divergence' and extinction. In this Review, we consider how these principles have fared since the publication of *On the Origin of Species*[1], and we discuss whether Darwin's concept of the relationship between microevolution and macroevolution can provide useful insight today. This relationship continues to generate controversy both within the biological sciences and in the confrontation between science and religion. On the 200th anniversary of Darwin's birth, a status report is surely in order.

Divergence and extinction in 1859

Extinction was a hot topic during Darwin's formative years. Many fossils had been found that were not identifiable as living organisms, but it was not until the early nineteenth century that Georges Cuvier argued that these fossils represented organisms that were extinct. A competing hypothesis was that these creatures lived on in the vast (at that time) unexplored regions of the globe. When US President Thomas Jefferson dispatched Meriwether Lewis and William Clark to explore the interior of North America, he expected them to find living mammoths and mastodons, which he knew about from fossils. The French biologist Jean-Baptiste Lamarck championed another alternative: that these fossil organisms, rather than being extinct, had evolved into contemporary forms. Cuvier, who did not believe in evolution, based his thesis of extinction on detailed anatomical comparisons that emphasized differences between fossil and living forms[3].

Darwin embraced Cuvier's explanation and then extended it by proposing that extinction was a by-product of evolution. Accordingly, as organisms evolve under the struggle for existence, some species acquire superior adaptations and exclude other species through competition or exploitation. In this way, extinction reflects the existence of a tipping point in the ongoing struggle for existence. An increase in the severity of any factors that regulate population size can cause populations to decline in abundance and then disappear.

Darwin argued that the struggle for existence was caused by interactions among organisms and was the dominant factor that shaped how organisms evolve. He considered the physical environment to be of minor importance in evolution. Through his experience as a gardener and his visits to the zoological park in London, he observed that organisms from

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Box 1 | A brief survey of macroevolution

An undercurrent of the debate about the mechanisms of macroevolution is whether natural selection (microevolution) is also the cause of macroevolution. Charles Darwin argued that, although natural selection is the sole mechanism that causes evolution, both divergence and extinction shape the larger-scale patterns that emerge from this process.

Macromutations
The initial phase of this debate focused on the expectation that change caused by natural selection will cause continuous variation. It was argued that if natural variation — such as the distinction between species or ranks above species in the taxonomic hierarchy (for example, genera and families) — is discontinuous, then the underlying mechanism that caused that change must also be discontinuous. Some championed macromutation: the origination of a new species as a result of a single large mutation[61].

Punctuated equilibrium and species sorting
Two patterns of evolution revealed in the fossil record have been argued to be inconsistent with natural selection.

First, Stephen Jay Gould and Niles Eldredge observed that the detailed history of individual lineages reveals prolonged intervals with little or no change (equilibrium or stasis) interspersed with intervals of rapid change (punctuations) that are associated with the origin of new species[62]. They proposed that natural selection could fine-tune organisms during periods of stasis but that another mechanism had to account for punctuated change. Second, the fossil record often reveals species sorting, meaning that some lineages rapidly diversify into new species whereas others decline. Gould argued for species selection as the mechanism to explain both phenomena[63]. Species selection treats species as the unit of selection in the same way that natural selection treats individuals as the unit of selection.

Megaevolution and adaptive radiation
George Gaylord Simpson's proposed mechanism of 'megaevolution'[64] was a modern synthesis (1930s–1950s) proposal for how natural selection can combine with other processes to explain species sorting.

It stands in opposition to species selection because macroevolution emerges from microevolutionary processes. Simpson combined the idea of key adaptations, or changes that would allow organisms to expand into previously underutilized environments, with Sewall Wright's theoretical models[65] to explain the sudden appearance and expansion of successful lineages.

The key feature of Wright's models is the adaptive landscape. Adaptive peaks are defined by a combination of characters that must appear together to define a well-adapted phenotype. Peaks are separated from one another by 'valleys', or character combinations that result in reduced fitness. Wright's models invoked the combination of natural selection, genetic drift, mutation and migration, in allowing shifts between peaks. Simpson adapted these models to a logical scenario for how a new lineage could be the product of accelerated peak-to-peak evolution. The fact that such evolution is accelerated and happens in a restricted geographical region means that it is unlikely to be seen in the fossil record.

Simpson later developed the concept of adaptive radiation[17], which still stands as a competing explanation for species sorting because such radiations are caused by natural selection and can account for differences among lineages in the rate of diversification (see the section 'Update on divergence').

Heterochrony
Particular types of natural selection and adaptive response have been credited with the potential to cause rapid morphological evolution. Gould[66] championed heterochrony, or changes in the rate of development of one component of an organism relative to others, as a mechanism for the rapid evolution of descendent species that are a mixture of juvenile and adult characters in their ancestors. One hypothesis for the origin of vertebrates is that they are derived from a tunicate-like ancestor that had an actively swimming larval stage with a nerve cord, but then metamorphosed into adults that lost these characters. A common ancestor of the vertebrates could evolve from such a tunicate-like ancestor with the deletion of metamorphosis and the retention of these larval characters into adulthood. The adults of such a descendent species would not be readily identifiable as being closely related to the adult life stage of its ancestor.

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a diversity of climates could survive and reproduce perfectly well when transported to England, so their natural distributions were not limited by their climate tolerance. Instead, their distributions were shaped by their ability to disperse and by the presence of other species. For Darwin, the interactions that define the struggle for existence and shape how organisms evolve were diverse, including competition, predation, parasitism, disease and pollination. This same range of interactions can therefore contribute to extinction.

Darwin's principle of divergence derives from what he thought to be one of the most potent components of the struggle for existence. He argued that the strongest interactions would be among individuals within a population or among closely related populations or species, because these organisms have the most similar requirements. Darwin's principle of divergence predicts that the individuals, populations or species most likely to succeed in the struggle are those that differ most from their close relatives in the way they achieve their needs for survival and reproduction.

The principle of divergence has had strong detractors. Ernst Mayr singled it out as a failed theory[4]. His reasoning paralleled his argument that *On the Origin of Species* is not about the origin of species[5]. Darwin saw each species as an arbitrary point on a continuum of populations that are diverging from one another as a consequence of evolution by natural selection. For this reason, he saw the principle of divergence as acting among individuals within a population or among populations or species. He did not distinguish between these levels of interaction. The crucial contribution of Theodosius Dobzhansky[6] and Mayr[5] to the modern synthesis was to recognize that speciation involves both divergence and the origin of discontinuity, or reproductive isolation. Mayr argued that individuals within a population cannot diverge from one another because they are part of an interbreeding gene pool[4].

If it is accepted that reproductive isolation between species is a prerequisite for divergence, then Darwin's principle must be modified so that the initial stages of diversification do not involve interactions between individuals or between closely related populations. This condition does not invalidate Darwin's principle that divergence and extinction are often a consequence of interactions among close relatives; it merely delays the action of the principle until the reproductively isolated descendants of a common ancestral lineage begin to interact.

Darwin illustrated the combined action of his principle of descent with modification, the principle of divergence, and extinction in the only figure in *On the Origin of Species* (Fig. 1). It showed the link between microevolution and macroevolution. Each branch in the evolutionary tree of life is seen as sprouting 'buds' that are emerging varieties or locally distinct populations. These buds are the consequence of the overproduction of offspring whose individual variations allow them to outcompete others or to probe the environment for open ecological space. Most of these buds go extinct, but some persist, becoming modified and improved descendants that tend to drive their close relatives to extinction, or to fill the unoccupied ecological space. According to Darwin, this combination of replacement and divergence causes cladogenesis: the splitting of one ancestral species into more than one descendant. Continued divergence of form and function between genetically isolated species causes the branches of the tree of life to grow ever farther apart, separated from one another by what seem to be unbridgeable gaps. Darwin argued that the processes of diversification and extinction can explain the gaps that are seen among living species. Divergence pushes lineages apart, and extinction erases the bridge that once joined them, creating the appearance of discontinuity.

How has Darwin's proposal for the relationship between microevolution and macroevolution fared since its publication in *On the Origin of Species*? Here we evaluate three conditions necessary for the structural integrity of Darwin's proposed bridge between microevolution and macroevolution. First, some speciation events should be associated with the divergence of ecologically relevant characteristics among descendent lineages; second, at least some extinction events should be attributed to interactions among closely related species; and third, extinction of some lineages should be linked to the diversification of closely related lineages.

Update on divergence

The principle of divergence has never been an explicit subject of analysis, but its imprint can be found in the early development of evolutionary ecology, when it was established that closely related organisms could inhabit the same environment only if they differed in morphology, habitat use or some other characteristics that reduced their ecological similarity[7]. Such observations fostered the idea that competition among close relatives had a significant role in shaping communities[8–10]. Character displacement, or the evolution of increased dissimilarity among species whose geographical ranges overlap[11], provides a natural experimental test of the hypothesis that selection favours individuals in each species that diverge further from the ecological requirements of the other species. Such displacement has now been well characterized in a variety of organisms[12–16].

Darwin's principle of divergence also figures prominently in the process of adaptive radiation, as originally proposed by George Gaylord Simpson[17] and as defined by Dolph Schluter[18] as "the evolution of ecological and phenotypic diversity within a rapidly multiplying lineage. It occurs when a single ancestor diverges into a host of species that use a variety of environments and that differ in traits used to exploit those environments." Adaptive radiations are commonly associated with diversification in sparsely occupied ecological space, for example following the colonization of a remote island, the survival of a mass extinction event, or the crossing of an adaptive barrier to open new evolutionary opportunities. Competition for resources has been shown to have had a dominant role in some adaptive radiations[12,16]. Perhaps the most famous is the evolution of 13 species of geospizine finches (Darwin's finches) within the Galapagos archipelago. The birds' diverse body sizes, beak shapes and diets are all derived from a single common ancestor that colonized an almost bird-free island[12,13]. Diversification within the much larger areas of continents undoubtedly proceeds in the same way for many types of organism.

In the absence of a fossil record, the radiation of any living group of organisms can be visualized by reconstructing the evolutionary relationships among the living species in a lineage to create a phylogeny[19], usually from DNA sequence data. This approach derives from models for lineage diversification that were originally developed in the palaeontological literature[20]. As well as defining the patterns of relatedness among species, phylogenies can yield more specific information about the tempo and possible mode of evolution that underlies contemporary diversity[19,21–24]. The baseline for such analyses is the temporal distribution of branching points in the phylogeny, which allows certain inferences about rates of speciation and extinction in the past[19,25], although there are sources of uncertainty and bias in doing this[26,27].
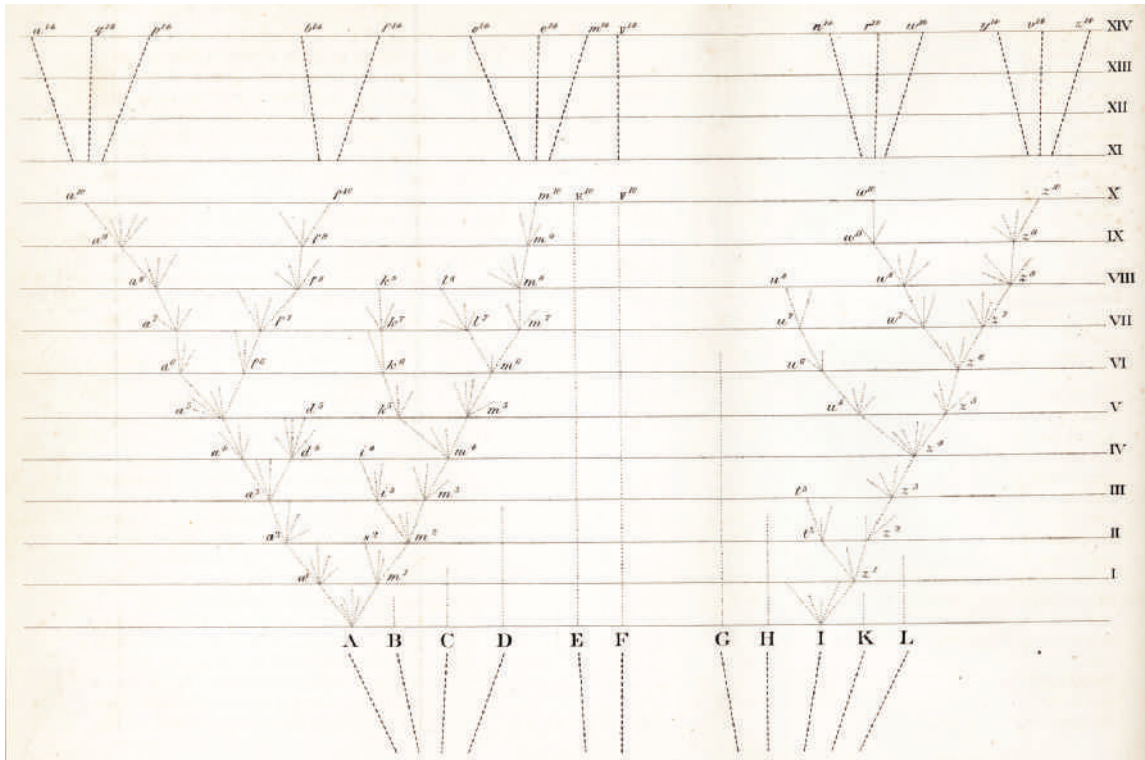

Figure 1 | Darwin's view of the link between microevolution and macroevolution. This figure appears in chapter 4 of Darwin's *On the Origin of Species*. The *x* axis represents a hypothetical ecological variable. The *y* axis represents time. Each horizontal line, associated with roman numerals I to XIV, represents a long but unspecified interval of time. A to L are 11 species in a hypothetical genus. Two of these species (A and I) diversify over time, whereas eight become extinct. One species (F) does not diversify but has surviving descendants, and it represents what Darwin described as "living fossils" — slowly evolving lineages that survived in marginal habitats where they were shielded from interactions with more rapidly diversifying lineages. At each intersection between the diversifying lineages and the divisions in time, the lineage is represented by diverging dashed lines, which are varieties that differ from one another in characteristics and habitat use. Most of these become extinct. Some, labelled with lower-case letters and numerical superscripts, represent distinct descendent subspecies or species. The descendants seen at each time horizon are not simply modified versions of their immediate ancestor but new and improved organisms that outcompeted their parental lineage and drove it to extinction. Thus a^2 is not just a^1 1,000 generations later; it is a daughter lineage that outcompeted a^1. If there is more than one surviving lineage at a node, the survivors tend to be the ones most different from one another. For example, a^1 and m^1 are the most divergent populations derived from A at the end of the first time interval, and these are the ones that survive. As each lineage diversifies, its descendants fan out along the *x* axis, occupying progressively more ecological space. They do so at the expense of the species that lie closest to them on the *x* axis, which become extinct, presumably because they lost out in competition for resources. (Figure reproduced from ref. 1.)
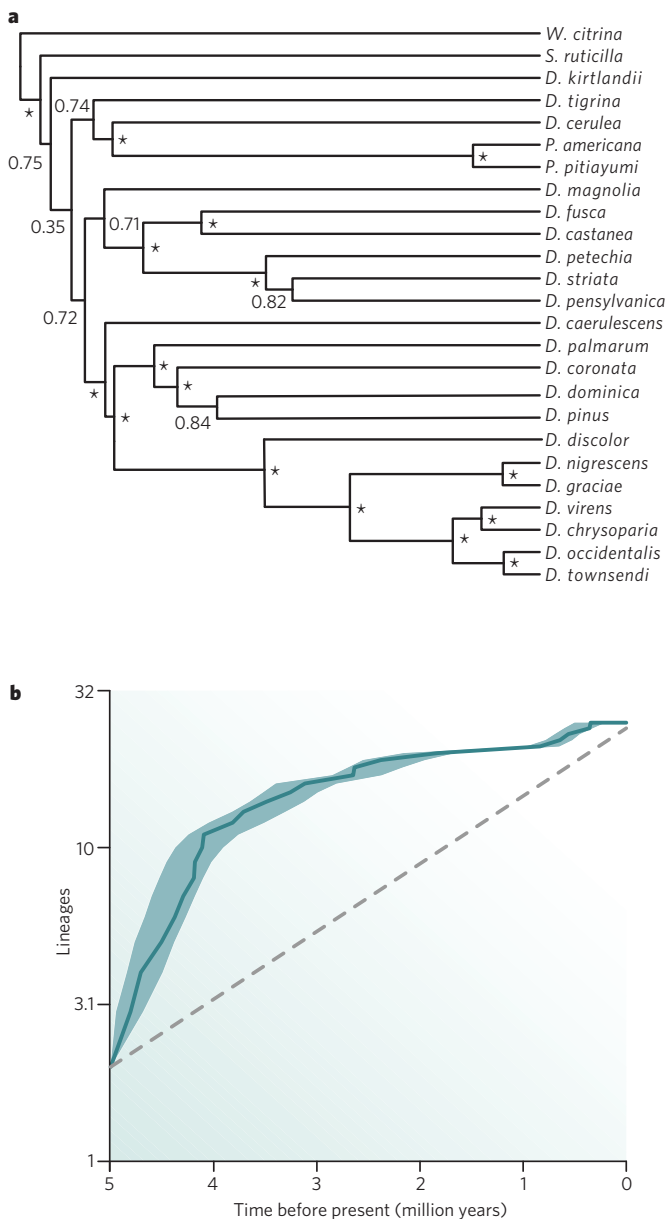
Figure 2 | A plot of lineage through time. This 'lineage through time' (LTT) plot is based on the temporal distribution of branch points in a phylogenetic tree. **a**, Phylogenetic tree for North American wood warblers based on more than 9 kb of mitochondrial and nuclear intron DNA sequence. Species are mainly *Dendroica* spp. but are also from the genera *Parula*, *Wilsonia* and *Setophaga*. The branch lengths are proportional to absolute time. Branch points marked with asterisks are supported by a posterior probability (Bayes' theorem) of >0.95. Numbers at the other branch points are exact probabilities. **b**, The LTT plot derived from this phylogeny. The *y* axis shows the number of lineages; the *x* axis shows the estimated time before present. The solid line represents the absolute value of the log of the number of ancestral lineages (different branches) present at each time interval. The shading is the 95% confidence interval for the number of lineages. The dashed line is what would be seen if the existing species were the product of a constant rate of diversification with no extinction. Note that the rate of accumulation of new lineages is initially high and then levels off. The slope of the lineage-accumulation curve represents the net rate of diversification, which is the rate of formation of new lineages minus the rate of loss of lineages by extinction. Dan Rabosky and Irby Lovette show that this pattern can be explained only by a high initial speciation rate followed by a deceleration in the rate of diversification[60]. This pattern is consistent with density-dependent speciation, or the early diversification of the lineage as it filled the available ecological space before being constrained by resource limitation. (Figure reproduced, with permission, from ref. 30.)

One common pattern is for a lineage to diversify rapidly early in its history, followed by a progressive slowing in the rate of diversification[21,28–30] (Fig. 2). Such a density-dependent cladogenesis[21,24] stems from an initial rapid adaptive radiation that fills the ecological space left open by a mass extinction, for example, or from a spread into a new adaptive zone facilitated by the evolution of some trait that makes the zone more accessible[17,31]. The resultant decline in available ecological space constrains further diversification.

As Darwin envisaged in his principle of divergence, rapid diversification often ensues when a lineage evolves adaptations that enable it to breach an ecological barrier[32]. Examples include the repeated invasion of brackish water environments by the ancestors of the different lineages of mangrove plants[33], the invasion of temperate environments by lineages of trees that evolved freezing tolerance[34–36], and the radiation of skinks that occupied the expanding deserts of Australia as the climate became more arid[37]. Timothy Barraclough and colleagues summarize other radiations that have been associated with the evolution of key innovations[38]. Such radiations also occur on a much grander scale: for example, bats diversified from a single ancestor that evolved flight into the largest order of mammals with more than 1,100 species[39].

Analyses of diversification sometimes reveal other details that are consistent with Darwin's macroevolution theory. For example, the passerine birds include many depauperate lineages that occupy ecologically or geographically marginal habitats[40,41]. These lineages seem to have diversification and extinction rates that are an order of magnitude lower than those of more species-rich clades of passerines, and thus correspond to Darwin's lineage F (Fig. 1), a slowly diversifying lineage isolated from interactions with more rapidly diversifying lineages.

Certainly, Darwin's principle of divergence has been supported by a range of what are now well-characterized and generally accepted evolutionary phenomena.

Update on extinction

Analyses of extinction in the fossil record have been dominated by the discovery of mass extinction events and the later realization that the mass extinctions represent the tail of a distribution of mostly smaller events. Mass extinctions have external causes, including bolide (large crater-forming projectile) impacts, major tectonic events and global climate change[42,43]. These extinctions appear as discrete events involving multiple species and are unrelated to Darwin's proposed mechanism of extinction. Indeed, Darwin's interactive extinctions lie hidden in the background of these events. Modern analyses also almost invariably deal with the appearance and disappearance of genera or families in the fossil record, as species can rarely be distinguished among fossils, although it is the extinction of populations or species that is most relevant to Darwin's principle of divergence. However, even though the fossil record may not be fertile ground for evaluating Darwin's proposed mechanism, species-level originations and extinctions can be identified for some periods and some taxa, such as the recent fossil record for marine bivalves[44], and inferences can be drawn about Darwin's proposed mechanism of extinction.

Analyses of extinction in living organisms fall almost exclusively in the province of conservation biology. Primary causes of extinction in this context include introduced predators and competitors, climate change, and habitat destruction, with the consequent subdivision of once-widespread populations into small isolates. Current research focuses on defining those properties of species that can predict susceptibility to extinction, such as geographical range, population density, life history and trophic level[45–47]. Many of the causes and correlates of contemporary extinctions have the signature of Darwin's emphasis on biotic interactions and the tipping of the balance of factors that regulate population size. For example, small geographical range, low population density and occupation of a high trophic level often figure as significant correlates of a high risk of extinction. Small changes in the factors that normally regulate population size can tip the balance towards extinction for species that are already less abundant or have restricted distributions. Many of these factors involve interactions with other species. Although the causes of current extinctions often lie outside the natural processes envisaged

by Darwin, many of them, such as the impact of invasive species, are enhanced versions of natural processes.

Recent work on West Indian birds provides an unusual opportunity to observe progressive stages of ecological and geographical contraction leading to extinction, using inferences from current geographical ranges and DNA-based phylogenies. Birds that colonize islands embark on sequential phases of range expansion and contraction, referred to as a taxon cycle[48,49]. Recent colonists are genetically indistinguishable from their mainland source populations, occupy wide geographical distributions and live mainly in lowland habitats[50]. Older, genetically differentiated, populations occur on one or a few islands, often restricted to forested environments at higher elevations. Each species provides a snapshot of this process, leading from the initial occupation of open, lowland habitats, to expansion into forested montane environments and exclusion from lowland habitats by new colonists. As they adapt to island interiors, older taxa also become isolated into small populations that are susceptible to local extinction. This process of cycling, with a consequent increase in the probability of extinction, fits well with Darwin's concept of extinction being driven by biotic interactions. Such support from the study of contemporary extinctions is understandably limited, but evidence should begin to accumulate more rapidly with the recent availability of molecular tools for investigating population history.

Darwin's proposal for the cause of extinction has yet to be fairly evaluated. He suggested that many taxa are driven to extinction by competition from ecologically similar but adaptively superior groups undergoing diversification. This core assumption of Darwin's explanation for macroevolution has little empirical support, mainly because the search for appropriate evidence has fallen through the gap between evolution and ecology; of course, pertinent evidence would strongly resist discovery under any circumstance.

Bringing divergence and extinction together

Central to Darwin's explanation for macroevolution is that the success of one group is gained at the expense of another. Palaeontological studies often reveal replacements in the fossil record, but their temporal, spatial and taxonomic resolution is generally limited. Research on faunal replacements tends to focus on biotic changes associated with major changes in the Earth's environment, such as the mid-Tertiary temperature decrease and the increasing aridity at temperate latitudes. For example, Christine Janis and co-workers documented the Miocene replacement of browsing mammals by grazers in North America and attributed it to replacement of forest by grasslands[51]. Jin Meng and Malcolm McKenna documented a similar Eocene–Oligocene replacement on the Mongolian plateau — where a perissodactyl-dominated mammalian fauna occupying a forested landscape was replaced by a rodent- and lagomorph-dominated grassland fauna — in association with the uplift of the Himalayas and the Tibetan plateau[52].

More direct evidence of continual background replacement of species comes from long fossil sequences with reasonable taxonomic resolution, such as the 40-million-year Palaeocene-to-Miocene record of pollen morphotypes from northwestern South America documented by Carlos Jaramillo and colleagues[53]. Although environment and overall diversity both varied over this period, the morphospecies composition of the flora turned over continually, even during periods of relative climate stability. More marked examples of such changes in the fossil record include the low-latitude replacement of gymnosperms by angiosperms during the mid-Cretaceous[54,55], and the post-Eocene replacement of non-passerine birds by passerines in Europe[56]. In both cases, older groups were replaced almost completely by more modern groups, leaving only sporadic relicts of the biotas — the Podocarpaceae and *Gnetum* in the case of gymnosperms, and swifts and woodpeckers, among others, in the case of European birds.

Additional indirect evidence for Darwin's theory of diversification and extinction comes from the observation that, following recovery from mass extinction events, species richness remains relatively stable. This pattern appears in the fossil record[57] and is evident in the absence of a correlation between clade age and contemporary diversity in several taxa[27,58]. This pattern suggests an underlying equilibrium between speciation and extinction during these intervals[24,29]. Perhaps speciation and extinction are random, unconnected events that balance out over time. However, models of random speciation and extinction processes suggest that the average time required for the complete replacement of species is approximately the product of the number of species and the average duration of individual species. The duration of species can be estimated directly from the fossil record[31] and, more recently, from the analysis of phylogenies[24,26]. These estimates, which typically fall between 1 million and 10 million years, are far too long for random speciation and extinction to account for observed species turnover rates[27]. Instead, more rapid turnover of species can be reconciled only when some lineages exhibit an excess of speciation and others an excess of extinction. Only a direct link between the two is needed to support Darwin's mechanism of macroevolution.

Conclusions

Although Darwin might have erred in some of the details of his principle of divergence, particularly the generally agreed starting point of reproductively isolated species, his basic idea has merit. The fundamental truth of his principle of divergence has emerged in different facets of evolutionary ecology, a field in which the same principle, in the form of character displacement or some models of sympatric speciation, was discovered independently in different contexts over a century after the publication of *On the Origin of Species*. Darwin's linking of extinction to diversification did not re-emerge as the study of extinction rose to prominence in conservation biology. Competitive replacement leading to extinction was once generally and uncritically accepted by palaeontologists before fading into the background after the discovery of mass extinctions. There is compelling evidence, however, of a role for biotic interactions in at least some extinction events, and a complementary relationship between divergence and extinction finds enough support for Darwin's proposal to merit further consideration as a viable link between microevolution and macroevolution.

Darwin's proposal carries a more general message for contemporary discussions of macroevolution, namely that microevolution alone cannot explain macroevolution. Understanding macroevolution requires the integration of ecology, evolution and the role of history in shaping the diversification or decline of lineages. Other investigators, most recently David Jablonski[59], have conveyed similar messages. Jablonski's vision is more complex than Darwin's and reflects the growth of ecology, evolution and palaeontology as disciplines since 1859, but it retains Darwin's emphasis on the presence of a biological filter that lies between microevolution and macroevolution and shapes the long-term consequences of evolutionary change. Jablonski concludes by calling for increased integration between fields to build a bridge between microevolution and macroevolution, and we concur with him. Mass extinctions and the large-scale expansions and contractions of clades in the fossil record are captivating but are only part of the story. Background extinctions are more elusive, but they must be considered in order to understand Darwin's mechanism of the turnover of species resulting from their evolution and interactions. Studies of extant populations — including mechanisms of population regulation, the contemporary causes of extinction and the causes of adaptive radiations — can yield important clues to factors that shape the history of life. Finally, information about the historical patterns of diversification of lineages can now be mined from molecular phylogenies, shedding light on the underlying causes of these patterns. It is the integration of information from the fossil record, the population and evolutionary dynamics of extant organisms, and phylogenetics that will provide the ultimate test of Darwin's bridge between microevolution and macroevolution.

Many people see *On the Origin of Species* as a beautiful fossil, but we view it as a living document that continues to offer insights and to enlighten modern research. It contains a wealth of ideas that have slipped through the cracks of the modern synthesis and, when appropriately updated, can provide inspiration for addressing some of the major unanswered questions in evolutionary biology. ∎

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