

The rise of birds and mammals: are microevolutionary processes sufficient for macroevolution?

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It is a basis of darwinian evolution that the microevolutionary mechanisms that can be studied in the present are sufficient to account for macroevolution. However, this idea needs to be tested explicitly, as highlighted here by the example of the superceding of dinosaurs and pterosaurs by birds and placental mammals that occurred near the Cretaceous/Tertiary boundary ~65 million years ago. A major problem for testing the sufficiency of microevolutionary processes is that independent ideas (such as the existence of an extraterrestrial impact, and the extinction of dinosaurs) were linked without the evidence for each idea being evaluated separately. Here, we suggest and discuss five testable models for the times and divergences of modern mammals and birds. Determination of the model that best represents these events will enable the role of microevolutionary mechanisms to be evaluated. The question of the sufficiency of microevolutionary processes for macroevolution is solvable, and available evidence supports an important role for biological processes in the initial decline of dinosaurs and pterosaurs.

A major question for evolutionary biology is whether the ecological, populational and genetical processes that can be studied in the present (microevolution) are sufficient to explain evolution over timescales of, say, more than 10 million years (macroevolution) [1]. Ernst Mayr interpreted the early history of evolutionary biology in two major phases [2]: in the first phase, biologists during the 1860s and 1870s were convinced that evolution had occurred; that all organisms were linked in the past through a common set of intermediates. Mayr's second phase did not occur until around the 1940s when, under the New Synthesis, biologists accepted that microevolutionary processes (i.e. mendelian genetics together with ecological and population mechanisms) were necessary for evolution. This followed the mathematical work of Chetverikov, Fisher, Haldane and Wright, as discussed in [3].

However, over the past 20–30 years, there has been increasing interest in a third phase: whether microevolutionary processes are sufficient for macroevolution [1,4]. Areas where there have been major

developments include: (i) evolutionary ecology and evolutionary psychology [5]; (ii) experimental and field studies of short-term evolution [6,7]; and (iii) molecular evolution in general. The first two are outside the scope of this article, and the question of whether standard genetic processes are sufficient for the origin of humans is discussed elsewhere [8]. Our concern here is whether ecological, population and genetic mechanisms of microevolution that can be studied in the present are sufficient to explain major radiations, such as the rapid radiation of birds and mammals during the early Tertiary, following the Cretaceous/Tertiary (K/T) boundary ~65 million years ago (Mya). Given the recent republication of Feduccia's catastrophic avian extinction model [9] (i.e. that all modern birds arose from a single avian lineage that survived the K/T boundary), it is now a suitable time to reconsider the survival of birds and mammals across the K/T boundary.

From a scientific perspective, it is important to have alternative models for any subject under investigation: hypotheses (or models) should be tools to help thought and to use to help design experiments. To aid the determining of the order of divergences, specialization and extinctions that occurred during the Late Cretaceous, we give five models (Figure 1) for modern birds and placental mammals. The models lie more or less along a continuum and each accepts the reality of the extraterrestrial impact that marks the end of the Cretaceous. However, they lead to different predictions about the timing of events and the mechanisms involved. The evidence for the extraterrestrial impact is overwhelming [10,11], but the original paper [12] provided no evidence for when modern birds and mammals began to diversify, or for when pterosaurs and dinosaurs* began to decline. By using the five models detailed in Figure 1 we can devise new tests on the observed data, and of the possible mechanisms involved. This second point is crucial as there is little point in 'explaining' the data if the models are physically and/or biologically unlikely. The five models that can be used to explain the rise of both birds and mammals need not yield the same conclusions for both groups. Discussion of this radiation has, in the past, been confused by the linkage of

* The questions that we are considering here are about ecological and microevolutionary processes rather than taxonomy; thus, we use the term 'dinosaur' in its usual (non-avian) meaning.

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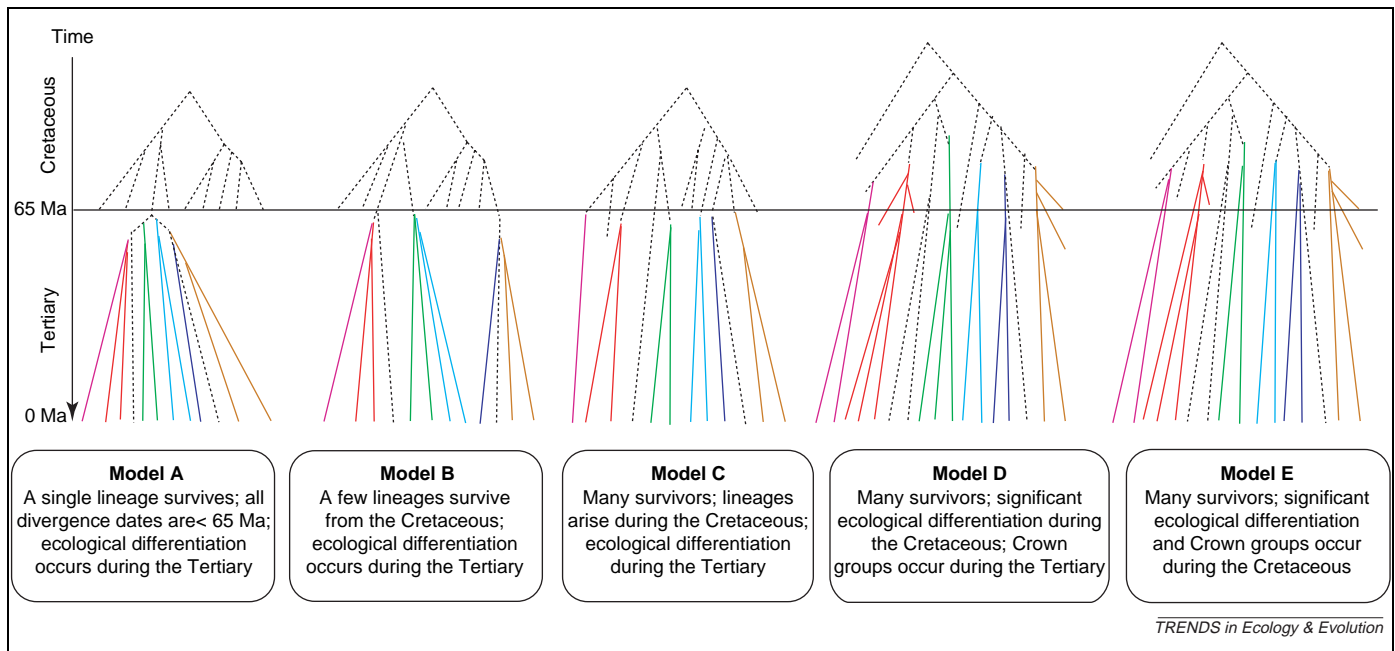


Figure 1. Five models for the divergence of birds and placental mammals. Each colored solid line represents an order of modern mammals or birds. Dotted lines represent lineages in the ancestral niche (small insectivores for mammals, and probably ground-feeders for birds). In each case, families and genera evolve during the Tertiary but the models differ in the time both for the origin of orders and infra-orders, and for the ecological transitions from the ancestral niche. The models differ markedly in their implications for the mechanisms of macroevolution. A subset of these models is given in [58]. Abbreviation: Ma, millions of years before the present.

unrelated ideas (Box 1), a point that readers should be aware of before proceeding further.

The five models of bird and mammal radiation

The purpose of the five models discussed here is to help develop ideas for testing events around the end of the Cretaceous. All we report here is that there is widespread querying among the geological and paleontological communities [13–16] of any ‘sudden and unexpected’ demise of dinosaurs at the K/T boundary. Indeed, the impact/extinction hypothesis [12] cut short a promising approach

that used ecological principles to develop models of the latter stages of the decline of the dinosaurs [17].

Model 1

The first model of the radiation of birds and/or mammals (Figure 1a) is based largely on Feduccia’s model of the radiation of birds [9], with a single group of survivors (of either placental mammals or birds) ‘inheriting’ the Earth following a Great Destruction of Life (traditionally by great floods). Under this model, all significant morphological, physiological and ecological changes occur during the Tertiary, following the removal of potential

Box 1. Linkage of unrelated ideas

There have been 20 years of confusion surrounding the extraterrestrial impact at the Cretaceous/Tertiary (K/T) boundary and dinosaur extinctions because two unrelated ideas were linked together.

Example A

- Idea a: the end of the Cretaceous is marked by a major extraterrestrial impact; with
- Idea b: this impact was the cause of the ‘sudden and unexpected’ extinction of the dinosaurs.

Alvarez *et al.* [12] presented substantial evidence for the physical impact (Idea a) but no evidence for the sudden and unexpected extinction of the dinosaurs ‘at the boundary’ (Idea b). Therefore, the concept of a major impact marking the end of the Cretaceous was linked, without evidence, to the extinction of dinosaurs. Unfortunately, this linkage of independent ideas is common. Other examples include:

Example B

- Idea a: if at least one dinosaur survived up to the Cretaceous/Tertiary (K/T) boundary, is linked with the unrelated
- Idea b: then all dinosaur groups must have survived at full diversity. (This has led to the search for the ‘last dinosaur’, but, as we see later, the ‘last dinosaur’ is not that important under models c–e detailed in Figure 1, main text.)

Example C

- Idea a: if the full diversity of dinosaurs survived until the K/T impact (Idea a), then:
- Idea b: so must have other groups, such as mosasaurs and pterosaurs

Example D

- Idea a: Wegener’s theory of continental drift (Idea a), was linked with the unrelated hypothesis that

• Idea b: Greenland is drifting away from Europe at 10–30 m yr⁻¹ [50]. Problems arise when only one of the ideas is well supported. The process can work either way; a bad idea might be accepted because it is linked to a good one, or vice versa (Sober calls this latter the ‘lightning rod’ effect [51]). For example, Wegener’s concept of continental drift (Idea a) was rejected because he asserted that Greenland was speeding away from Europe at a high rate (Idea b); namely 10–30 m yr⁻¹ [50]. If Wegener had taken known rates of uplift (say a few cm yr⁻¹, a thousand times slower than his suggested movement of Greenland away from Europe) and applied this to sideways motion, his idea would not have been rejected with such vigor.

A major theme of our work here is that the ideas of an asteroid impact marking the end of the Cretaceous, and the demise of dinosaurs, are independent. The evidence for or against each idea must be evaluated separately.

competitors (i.e. the dinosaurs). This model is usually linked with the concept that normal evolutionary processes are insufficient to cause major macroevolutionary changes; that is, extraordinary circumstances, such as mass extinctions, and/or unusual genetic mechanisms, are required [11,12]. Again, we must be careful not to link unrelated ideas; the sudden and unexpected extinction of dinosaurs (idea a) with the question of whether known microevolutionary processes are sufficient for macroevolution (idea b; Box 1).

Model 2

The second model (Figure 1b) is similar to Figure 1a, but several, rather than one, lineages survived the Great Destruction of Life. However, because of the increased number of survivors, the times of divergence of some pairs of lineages (of either birds or placental mammals) could date back to the mid-Cretaceous. The number of lineages that survived (be that one, two or three, etc.) does not lead to fundamental differences in outcome in terms of the mechanisms involved: the major morphological, physiological and ecological transformations that characterize most modern orders still occurred during the Tertiary as a result of lineages evolving to fill 'vacant niches'. The significance of Figure 1b is that, although it is similar to Figure 1a in being a catastrophic extinction model, it predicts that some orders will have diverged during the Cretaceous. Thus, we cannot use a few early divergences between mammalian or avian orders to eliminate catastrophic extinction models. Again, this second model can be linked with the idea that the extinction of dinosaurs and/or pterosaurs was necessary before modern birds and placentals could radiate; however, as discussed above, these are separate issues and should be considered as such.

Model 3

In the third model (Figure 1c), large numbers of lineages survive from the Cretaceous to the present. With a relatively small data set, at least 22 lineages of modern birds [18] and ~22 lineages of placental mammals [19] were estimated to have survived from the Cretaceous to the present. These estimates are concordant with the results of Figure 6 in [20]; that the mass extinction that occurred around the end of the Cretaceous had less impact on terrestrial vertebrates than on marine vertebrates. Eventually, we must also include lineages that survived into the Tertiary but which then go extinct, including several lineages of early mammals (such as multituberculates).

If large numbers of lineages survived from the Cretaceous to the present, this limits the extent of the catastrophe that resulted from the K/T impact. Therefore, the asteroid impact is less useful as an explanation for linking dinosaur extinction with mammalian and avian diversification. Another consequence of Figure 1c is that ancient divergence times between lineages do not of themselves distinguish between Figures 1b, and 1c–e. For the present analysis, we are not distinguishing whether morphological and ecological diversification occurred long before the K/T boundary (long-fuse model, [18,21]), or closer to the boundary (short-fuse model, [18,21]). In Figures 1b and 1c,

all lineages surviving into the Tertiary still occupy their ancestral niches, and were probably small nocturnal insectivores and omnivores for placental mammals, and ground-feeding birds for the Neornithes (modern birds).

Model 4

Figure 1d has the same older times of divergence as Figure 1c (i.e. occurring during the Cretaceous) but, in addition, many ecological and morphological transformations also occur during the Late Cretaceous. From a taxonomic viewpoint, early diverging groups might be either on the stem-lineages of extant orders of birds or mammals rather than within current crown groups (crown groups being only extant species and their common ancestors). However, the questions that we consider here are ecological rather than taxonomic, and if birds and/or mammals [22,23] are moving into new niches then this must be at the expense of other organisms. Thus, for the model detailed in Figure 1d, we must consider that early birds and mammals might have competed with, for example, small pterosaurs and/or small dinosaurs. Although it is the largest pterosaurs and dinosaurs that get the most attention in the literature, the focus of this model (Figure 1d) is on the smaller (and juvenile) members.

Model 5

Finally, the fifth model (Figure 1e) is similar to Figure 1d except that some current crown groups arose during the Late Cretaceous. Although it is an interesting taxonomic question as to whether a fossil is a member of a crown group, it is the ecological or evolutionary question that is more important here. An animal near the end of the Cretaceous that is about to be caught and eaten by a carnivore is not concerned with whether the predator will be considered, 65+ million years later, as a member of the Carnivora crown group. Alroy [24] has established a database of North American mammalian fossils, and the timing of events in his data could argue against Figure 1e with respect to mammals in North America; however, the model depicted in Figure 1e needs to be evaluated both in other regions and for birds.

Extending the models

Figure 2 extends aspects of the models detailed in Figure 1. Figure 2a shows the dinosaurs continuing uninterrupted up to the K/T boundary, at which point a 'sudden and unexpected' extinction occurs. At the other end of the spectrum, Figure 2b shows a successive decrease in the overall taxonomic diversity (bi) of dinosaurs (or pterosaurs), followed by a decline in smaller (bii), and then in larger (biii), dinosaurs (or pterosaurs). Figure 2c indicates that placental mammals (or modern birds) could be diversifying ecologically and morphologically before (ci), simultaneously with (cii), or after (ciii), the decline of smaller dinosaurs. Again, ideas resulting from these models need testing.

Four questions that arise from Figure 1 are discussed in Box 2. Sometimes, a crown group is a proxy for an ecological or morphological transition but, in other cases, fossils that are diagnosable to a stem lineage have already

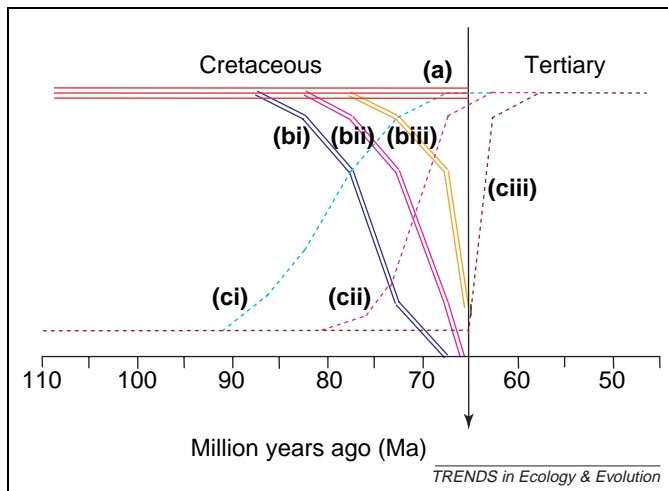


Figure 2. Alternatives for the decline of dinosaurs (or pterosaurs) and the radiation of modern mammals (or birds) with respect to the Cretaceous/Tertiary (K/T) boundary. Alternative (a) (triple line): no reduction in dinosaur diversity right up to the K/T boundary (a sudden and unexpected extinction). Alternative (b) (double lines): decline of dinosaurs (pterosaurs) starting from around the mid-Cretaceous with: (bi) decline in new families being identified (a proxy for continuing diversification); (bii) decline of smallest dinosaurs (pterosaurs), and (biii) later decline of large dinosaurs (pterosaurs). Alternative (c) (dashed lines): models for the diversification of modern mammals and/or birds; (ci) before, (cii) simultaneously with, or (ciii) after the decline of dinosaurs and/or pterosaurs. Mechanisms involved will differ markedly depending on the relative timing of the decline and diversification of dinosaurs and mammals (or birds), respectively. Based on the models detailed in Figure 1; many variants on these alternatives are possible.

made major morphological or ecological transformations. It is such ecological and/or functional changes that are important for testing and differentiating between Figures 1c and 1d, with different implications for the faunal turnover that occurred near the K/T boundary. A strictly taxonomic use of terms can obscure underlying scientific questions. In this case, classifying a range of animals from the Triassic to the Late Cretaceous as 'dinosaurs', or phrases such as 'dinosaurs ruled for 150 million years', emphasizes stasis and masks the expectation that plants and animals are continually evolving and redistributing around the world. Indeed, there was continued turnover of major dinosaur groups during their existence [25]. With a dynamic view, there is no *a priori* expectation that dinosaurs will, or will not, always be the dominant group of land vertebrates.

Inverting the questions

Another way of examining the questions in Box 2 is to ask them from alternative viewpoints. One example has already been mentioned.

Box 2. Questions from the five models for bird and mammal radiation

From the five models detailed in Figure 1 (main text), we can derive four questions for both birds and placental mammals. Answering these will aid hypotheses that can be tested for the mechanisms involved in dinosaur and pterosaur extinctions, and the placental and bird radiations.

- What were the times of divergence for extant lineages?
- How many lineages survived across the Cretaceous into the Tertiary (including those not surviving to the present)?
- When did birds and mammals make the important ecological transformations from their ancestral niches (and, could increasingly compete with smaller dinosaurs and pterosaurs)?
- During the Late Cretaceous, what happened to dinosaurs and

'How many land vertebrate lineages survived into the Tertiary' inverts the question 'how many went extinct?' (If the answer to this inverted question is only 'one lineage surviving for each of birds and mammals', then it is equivalent to Figure 1a.) The number of surviving lineages is important for inferring the mechanisms involved.

The second question to invert is as follows: 'when did mammals and birds start replacing small dinosaurs and small pterosaurs?' This replaces the question 'when did the last dinosaur, or the last pterosaur, perish?' This latter question has received much attention in the literature, but the inverted question is more fundamental and requires consideration of the mechanisms that might have been involved.

To illustrate this second question, consider the analogy: when did the last sphenodontid perish? The answer is that they have not because one or two closely related tuatara *Sphenodon* species survive on islands off the coast of New Zealand [26]. However, this observation does not alter the fact that, although relatively common 200 Mya, the fossils of sphenodontids become rare from ~140 Mya, and no fossil remains have been found for this group from the last 65 million years [27] (see also [28]). Determining which factors led to their decline, (presumably initial replacement by lizards and eventually competition from *Rattus exulans* [29]) is a more ecologically significant point than the precise time of the 'last sphenodontid'. The implications of this conclusion for dinosaurs and pterosaurs will be considered next.

The time of the 'last dinosaur' or the 'last pterosaur' is not a crucial question for models 1c–e because it does not identify whether dinosaurs and pterosaurs (just as for sphenodontids) also declined over many millions of years. Under models 1d,e, modern mammals and birds diversify during the Late Cretaceous at the expense of other groups, potentially competing with the smallest dinosaurs and pterosaurs. Effects of the competition could vary with taxonomic group and/or ecological niche. One useful approach would be to place dinosaur and pterosaur fossils into size categories, perhaps adult length for dinosaurs and wingspan for pterosaurs. For example, we could classify adult dinosaur body lengths into <1.5m, 1.5–2.5m, 2.5–4m, >4m to test whether origination and extinction rates of these groups correlated with the body lengths of land vertebrates that are potential competitors. As a first step towards this, we have data from 1485 fossil records

pterosaurs with respect to taxonomic divergence (e.g. new families appearing), adult body size, and the ecological niches that they occupied?

The first question has been well studied [18,52], although further research, more taxa, longer sequences and improved fossil calibration points are required. The second (how many lineages survived into the Tertiary) is important because it places limits on the biological consequences of the asteroid impact at the end of the Cretaceous. Following on from this, ecological shifts from ancestral to new niches are crucial for our understanding of the possible biological interactions between the diversifying mammals and birds on the one hand, and with the smaller dinosaurs and pterosaurs on the other.

(Figure 3, see Supplementary Information, which is available online) that, on the surface, indicates a decline in the abundance of small dinosaurs ($<2\text{m}$ long as adults) over the last 20 million years of the Cretaceous. In Figure 1d and 1e, this is the time period over which modern birds and mammals diversified.

The main limitation of the results in Figure 3 could come from differences between fossil sites in their potential for fossilization. Such an ‘ascertainment bias’ can arise in addition to normal stochastic effects (including local fossilization conditions). Larger dinosaurs are more likely to leave fossils, and to be discovered, studied and published. Nevertheless, the trend in Figure 3 requires explanation and is presented as a stimulus to further research. In a review of modern (neornithine) birds from the Late Cretaceous [30], Hope points out that, in the Lance formation (Maastrichtian, the most recent part of the Cretaceous) there are 25 records of modern birds (Neornithes) but only five from an older radiation of birds (enantiornithine birds). Thus the fossil record appears to support the idea that the transition to modern birds largely occurred before the end of the Cretaceous. Some research groups [21,31] have already made good progress in developing databases of fossil occurrences. An analysis of fossil footprints [32] is also important for estimating the distribution of size classes through time, and for reducing ascertainment bias from fossils alone. Thus, the five models of Figure 1 should enable a range of hypotheses to be tested, provide new questions for

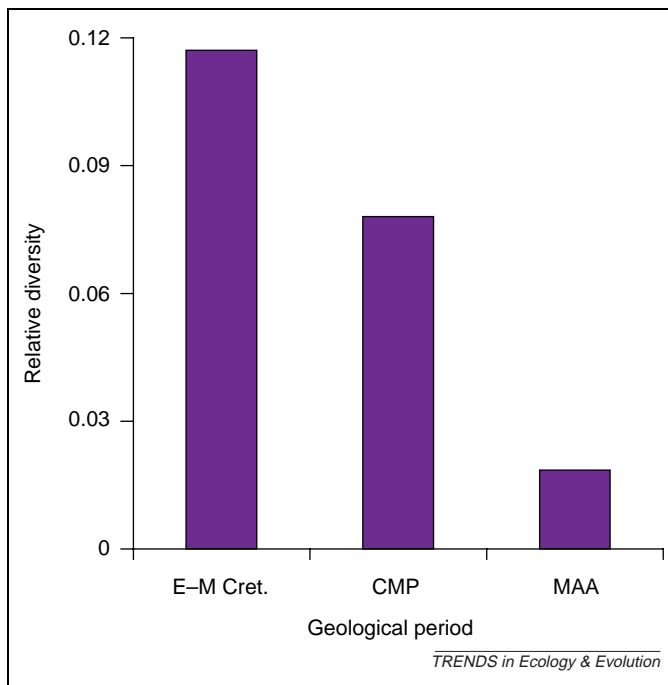


Figure 3. The decline of small dinosaurs ($\leq 2.0\text{m}$ long as adults) as a proportion of overall dinosaur species diversity. At face value, there is a decline in smaller dinosaurs during the Late Cretaceous. The data are preliminary because there might be an ‘ascertainment bias’. For several reasons, smaller dinosaurs are less likely to be fossilized, discovered, prepared, displayed and/or published. For some of the models presented here (a–e in Figure 1), it is essential to gather information about relative size or taxonomic distributions of dinosaur groups (theropods, etc.) through time. Sources of data are provided in Supplementary Information available online. Abbreviations: CMP, Campanian; E–M Cret., Early and mid-Cretaceous from ~140–83 Mya; MAA, Maastrichtian, ~74–65 Mya; Mya, million years ago.

paleontologists to address and stimulate further data collection.

Ideally, hypotheses or theories are tools or implements that can be used to develop further work. This is preferable to defending an extravagant hypothesis that goes against all new data. For example, if either Figure 1a or 1b is the best description, then we are in the interesting position of searching for new genetic mechanisms that lead to many major phenotypic changes that occur over (geologically) short timescales. Macroevolution would not be just normal microevolution over long timescales [33]. By contrast, if either Figure 1d or 1e is the most accurate for either birds or mammals, then it is expected that the normal ecological and genetic (microevolutionary) processes are sufficient for macroevolution [34].

Searching for mechanisms: physical and biological

Once we have good evidence for excluding some of the models in Figure 1 (for birds or mammals), it is necessary to consider explanatory mechanisms. Again, we run into the problem of the linkage of unrelated ideas, or of underlying assumptions about driving forces for macroevolution. Perhaps the most difficult for evolutionists is the common belief that major physical factors drive macroevolution. With respect to the last example in Box 3, there is not a single biological event from the past two million years that could not be attributed to ‘climate change’. We need not even consider evidence; whatever the biological change, we can always ‘explain’ it by climate change. Such *post hoc* explanations have no role in science. Unfortunately, it is not only climate change arguments that can be used indiscriminately.

From biological advantage, to invasive species

In light of the models detailed in Figure 1, it is important to also consider mechanisms that could have affected faunal change during the Late Cretaceous. There is a large body of earlier work about the potential competitive advantages of mammals and/or birds over earlier reptilian groups. For example, Pond [35] and Farmer [36] give details of how lactation leads to many developmental and ecological advantages for mammals; birds also feed their offspring until they can survive in their adult niche. By contrast, most large reptiles occupy different ecological niches as they mature. For example, the tuatara *S. punctatus* occupies a different niche when young compared with when it is an adult, and juveniles are particularly susceptible [37] to competition from the introduced *Rattus exulans* (although they are unaffected as adults). Similarly, the Komodo dragon [38] moves through a series of niches as it matures.

Pond [35] points out that changing requirements during growth make it harder, for example, to develop specialized teeth. By contrast, a mammal can evolve specialized teeth for just one niche. Similarly, brain size is considered to be important in human evolution and has been invoked as an advantage in evolutionary and behavioral flexibility in both mammals and birds [39]. For small animals, endothermy is especially advantageous [40] and this is partly why we looked at preliminary data for small dinosaurs (Figure 3). Perhaps related to

Box 3. Overuse of physical causes for macroevolution

A common assumption is that 'physical factors drive macroevolution', be they climate change, major volcanism, or extraterrestrial impacts. Or, if you prefer, 'biology is passive, physical causes drive macroevolution'. Biology is considered to be secondary, perhaps coming into force when there are 'vacant niches' caused by physical factors. (What we call physical and biological, others call extrinsic and intrinsic [53].) Four examples are given here.

Extraterrestrial impacts

The original Alvarez [12] paper did not consider any biological evidence. This continues up to the present day, with an overview article [54] that concentrates only on possible physical causes and does not refer to possible biological mechanisms.

Extinction of megafauna over the past few tens of thousand years

Until recently, the main explanation for the recent extinction of megafauna was 'climate change' that occurred around the end of the last Ice Age (a physical cause). The arrival of humans at about the same time had nothing to do with these extinctions (a biological cause). We recently summarized the competing (climate versus biological) models with respect to the Pacific region [29], where extinctions occur anywhere from 50 000 to 800 years ago. In this case, times of extinction are correlated with the arrival of humans.

endothermy is the ability to regulate rapid increases in body reserves (including fat reserves) and the rate of food assimilation [41]. Only if we disregard mammalian and avian physiology, morphology and ecology could we maintain that there were no potential advantages of mammals over, for example, the smallest dinosaurs.

Another active field is the ecology of invasive species [42] of both plants [43,44] and animals [45]; such information must also be considered when explaining past events. There is increasing evidence for mechanisms that can lead to long-term stability in some ecosystems, including game theory [46] and evolutionarily stable niche-discontinuity [47] models. However, these models of stability are still susceptible to invasive species, with a potential cascade of effects. Faunal exchange has been observed in the fossil record, for example in Africa [48], and it is interesting that the apparent influx of placental mammals into North America during the Late Cretaceous [49] is a potential explanation for the relative decline of marsupials and/or small dinosaurs in that region. We have to be careful here as concepts such as invasive species could, just like climate-change, be used to explain 'everything'. We must avoid setting up 'invasive species' as an alternative panacea; checking the evidence is crucial.

Conclusions

To conclude, it is a basis of darwinian evolution that the mechanisms that we can study in the present are sufficient [8] to account for past evolution. We need to test this explicitly, and the five models presented here are a start to explaining the rise of birds and mammals, and the decline of dinosaurs and pterosaurs. Hypotheses must be considered from different viewpoints ('inverted' in the terminology used here) and good hypotheses lead to additional data collection as well as new tests on existing data. Both biological and physical mechanisms must be evaluated, and testing these ideas requires an integration

Vicariance biogeography

One form of vicariance biogeography is that plants and animals stay put while continents move them around. By contrast, mainstream evolutionary theory assumes that there are biological processes favoring dispersal and tests this with experiments. One of the simplest examples is the legume *Sophora*, which is dispersed around the South Pacific [55] oceans (and as far as the South Atlantic). A small increase in air spaces between cells in the endosperm lowers the density of seedpods, which then float in seawater [56]. In its extreme form, vicariance is an example of 'biology is passive, physical factors drive evolution'.

Increase in human intelligence

One of the most extreme examples is the suggestion that the (apparent) increase in human intelligence is attributable to our surviving ~12 000 years ago an '8 °C change over 50 years' (measured from ice-core data) [57]. Following the same line of reasoning, oak trees, which survived the same climate change, should also be as intelligent. Of course, we are not limited to the particular climate change indicated in [57]; there are dozens of other abrupt changes during the last Ice Age, as well as during the whole series of Ice Ages, and so the intelligence argument could be extended to all organisms that survived such changes.

of information from paleontology, ecology, life cycles, physiology and molecules.

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Supplementary data

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