Speciation

REVIEW

The Red Queen and the Court Jester: Species Diversity and the Role of Biotic and Abiotic Factors Through Time

Michael J. Benton

Evolution may be dominated by biotic factors, as in the Red Queen model, or abiotic factors, as in the Court Jester model, or a mixture of both. The two models appear to operate predominantly over different geographic and temporal scales: Competition, predation, and other biotic factors shape ecosystems locally and over short time spans, but extrinsic factors such as climate and oceanographic and tectonic events shape larger-scale patterns regionally and globally, and through thousands and millions of years. Paleobiological studies suggest that species diversity is driven largely by abiotic factors such as climate, landscape, or food supply, and comparative phylogenetic approaches offer new insights into clade dynamics.

There are two ways of viewing evolution, through the spectacles of either the Red Queen or the Court Jester. The Red Queen model (*1*) stems from Darwin, who viewed evolution as primarily a balance of biotic pressures, most notably competition, and it was characterized by the Red Queen's statement to Alice in *Through the Looking-Glass* that "it takes all the running you can do, to keep in the same place." The Court Jester model (*2*) is that evolution, speciation, and extinction rarely happen except in response to unpredictable changes in the physical environment, recalling the capricious behavior of the licensed fool of Medieval times. Neither model was proposed as exclusive, and both Darwin and Van Valen (*1*) allowed for extrinsic influences on evolution in their primarily biotic, Red Queen views.
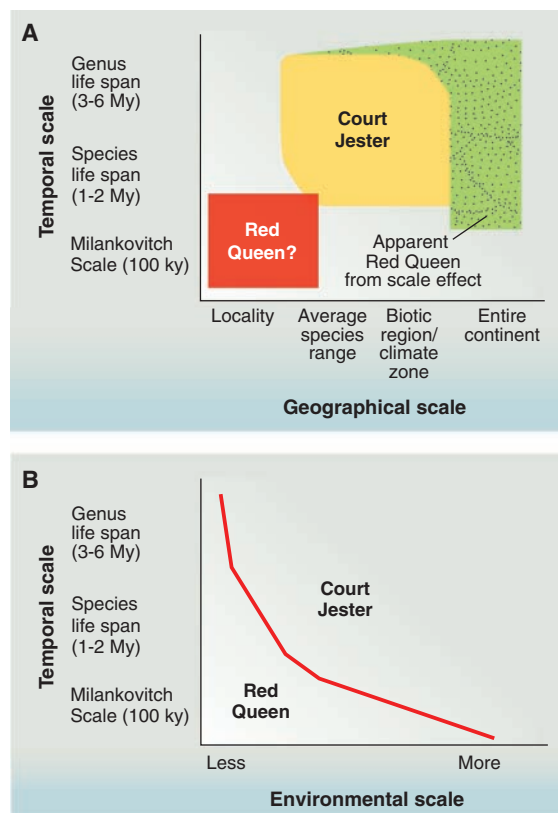
Species diversity in a Red Queen world depends primarily on intrinsic factors, such as body size, breadth of physiological tolerance, or adaptability to hard times. In a Court Jester world, species diversity depends on fluctuations in climate, landscape, and food supply. In reality, of course, both aspects might prevail in different ways and at different times, what could perhaps be called the multilevel mixed model. Traditionally, biologists have tended to think in a Red Queen, Darwinian, intrinsic, biotic factors way, and geologists in a Court Jester, extrinsic, physical factors way.

Much of the divergence between the Red Queen and Court Jester world views may depend on scale (*2*) (Fig. 1): Biotic interactions drive much of the local-scale success or failure of individuals, populations, and species (Red Queen), but perhaps these processes are overwhelmed by substantial tectonic and climatic processes at time scales above 10^5 years (Court Jester). It is im-

portant not to export organism-level processes to regional or global scales, and it is likely that evolution operates in a pluralistic way (*3*).

There are two broad methodologies for studies of species diversity through time, taxic and phylogenetic (*4*). The taxic approach involves treating species, genera, or families as independent entities and counting their occurrences against time and other factors. The phylogenetic approach uses cladograms or molecular trees to

disentangle key aspects of clade histories. Clades are monophyletic, including all descendants of an ancestor, whereas taxa may be monophyletic or paraphyletic, excluding some descendants of the ancestor. Comparative macroecological studies add rigor to analyses showing that sister clades may vary in rate of evolution, timing of increases in species richness and morphospace occupation, and distributions of evolutionary novelties across lineages and subclades. Here, I will explore the largest-scale global, taxic investigations, provide an outline of how these and other studies correspond to the predictions of the Red Queen, Court Jester, and multilevel mixed models (Table 1), and outline some phylogenetic studies of the macroevolution of species diversity.

The Global Pattern of Diversification Through Time

A key question about the origin of modern biodiversity is how today's 10 million species arose from a single ultimate species of microbial life 3500 million years ago (Ma) (Fig. 1). Two models for global diversification are termed the saturation/equilibrium model (*5–7*) and the expansion model (*8–11*). The equilibrium model has prevailed, among marine paleobiologists at least, for a long time, and represents a classic Red Queen viewpoint because it implies primarily biotic controls (density dependence) on global diversity.

There are two versions of the equilibrium model, differing in the time when the global

Fig. 1. Operation of Red Queen (biotic causation) and Court Jester (abiotic causation) models at different geographic and temporal scales (**A**). The Red Queen may prevail at organismic and species level on short time scales, whereas the Court Jester holds his own on larger scales. The stippled green shape shows an area where Red Queen effects might be identified erroneously, but these are likely the result of spatial averaging of regional responses to climate change and other complex physical perturbations that may be in opposite directions, and so cancel each other, suggesting no controlling effect of the physical environment on evolution. Physical-environmental disruptions may elicit biotic responses along the red line separating Red Queen and Court Jester outcomes (**B**). The usage here is the microevolutionary Red Queen, as opposed to the macroevolutionary Red Queen that posits constant extinction risk, a view that has been largely rejected (*31*). Illustration based on (*2*).

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marine ecosystem became saturated. Sepkoski's coupled logistic model (*5*) identified three equilibria, in the Cambrian, most of the Paleozoic, and perhaps a third, beginning in the Pliocene and continuing to the present (Fig. 2A). These three equilibrium levels correspond to three sets of phyla, the Cambrian, Paleozoic, and Modern, that interacted and successively replaced each other through the Cambrian-Ordovician and Permo-Triassic intervals, reaching higher equilibrium levels after each long-term replacement event. The second model (*6, 7*) identifies a single equilibrium level from the early Paleozoic, perhaps 400 Ma, to the present (Fig. 2B). In both models, the equilibria correspond to biodiversity saturation in which new taxa could become established only by driving others to extinction. Key evidence is that both origination and extinction rates appear to have been density-dependent (*5–7*), limiting rises in diversity and promoting rapid recovery after extinction events.

Alternative models for global diversification are expansionist, allowing global species diversity to rise, with damping, but without a predictable limit (*8–11*). Density dependence of origination and extinction rates does not preclude expansionist models because they may be dampened by limiting factors such as shortage of food or space, or active predation, as well as by climate and other physical factors. Further, it seems that the coupled logistic model may be
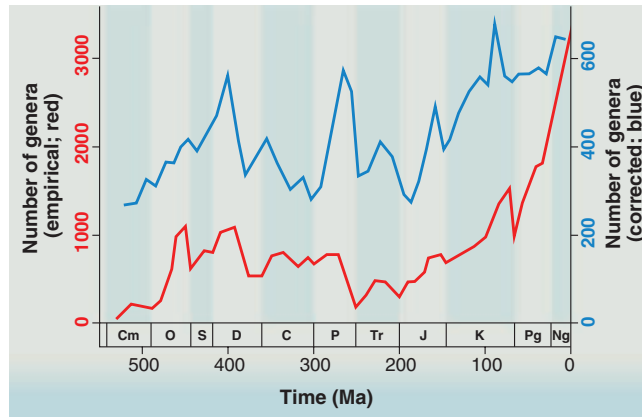

Fig. 2. Patterns of marine animal genus diversification through the past 530 My, the Phanerozoic. The two lines compare current estimates from the empirical (uncorrected) Sepkoski database (red line) and sampling-standardized (corrected) analysis of the Paleobiology Database (blue line). The empirical curve (red line) suggests that global marine diversity reached a possible plateau through the Paleozoic (450 to 250 Ma) and has risen, apparently exponentially, ever since. The sampling-standardized curve (blue line) suggests that global marine diversity reached near-modern levels some 400 Ma and there has been only modest increase since then. Cm, Cambrian; C, Carboniferous; D, Devonian; J, Jurassic; K, Cretaceous; Ng, Neogene; O, Ordovician; P, Permian; Pg, Paleogene; S, Silurian; Tr, Triassic. Based on (*6*).

partly an artifact of taxonomic scale (Fig. 2, red curve); it was worked out at ordinal and familial levels but does not work convincingly at generic or specific levels (*10, 11*), there are problems with key numerical assumptions (*11, 12*), and the background assumption of a global carrying capacity is doubtful (*8, 10, 11*). Further, it has proved hard to export the logistic model to the much more speciose terrestrial realm, whether one considers

plants, insects, or vertebrates, because these groups seem to have radiated explosively, without diversity plateaus, particularly in the past 100 million years (My) (*10*).

Resolution between the equilibrium models, and between these and expansionist models, might seem straightforward, but the solution depends on adequate assessment of the quality of the fossil record. The long-term saturation model for global diversification (Fig. 2, blue curve) arises from extensive attempts to correct data sets for sampling error (*6, 7*), whereas the multiple-equilibria and expansion models originally used raw data, without correction (*5, 8–11*), although more recent analyses return a somewhat dampened but congruent signal when corrections are imposed. Correction for sampling is clearly essential (*6, 7*), and future investigation must determine appropriate independent proxies for preservation and human error; some current proxies (such as number of fossiliferous localities) are themselves dependent on diversity, and other correction regimes may be so complex as to produce data in which geologic and biologic signals are not obviously separated.

Life on land today may be as much as 25 times as diverse as life in the sea, so it may be wrong to generalize from marine paleontological studies to all life. Perhaps land and sea show similar patterns of exponential increase in species numbers (*8, 9, 11*), or perhaps they

Table 1. Macroevolutionary phenomena and their support for either the Red Queen (biotic, intrinsic) or Court Jester (physical, extrinsic) models. Many could fit either worldview, and so are noted as "multilevel mixed."

Red Queen	Court Jester	Multilevel mixed
Interspecific competition	Waxing and waning of clades in association with tectonic and oceanographic events (*2, 17*)	Vicariance and dispersal in major phylogenetic splits (*17*)
Character displacement	Mass extinctions and smaller extinction events triggered by extrinsic causes such as eruptions, climate change, anoxia, impact (*10, 11*)	Latitudinal diversity gradient (*22–24*)
Evolutionary arms races (*1*)	Coordinated turnovers, originations, and extinctions in response to physical perturbations— termed "coordinated stasis" or "turnover pulse" hypothesis (*2, 29, 30*)	Occupation of new ecospace (*25*)
Constancy of ecological guilds through time (*25*)	Nonconstant probability of extinction (*3, 11*)	Subdivision of niches/specialization (*10, 25*)
Incumbency advantage (*3, 24*)	Lack of evidence for a global carrying capacity and equilibrium levels (*8, 10*)	Declining global extinction rates through time (*1, 5*)
	Lack of cohesiveness of the great "evolutionary faunas" (*12*)	Onshore-offshore patterns and disturbance (*3*)
	Species richness—energy relationship (*18, 19*)	Resource use: stenotopes are more speciose than eurytopes (*29, 30*)
	Inverse relationship between global temperature and biodiversity (*21*)	
	Lack of clear correlation of species richness with body size or other biotic factors (*16*)	

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differ in their key rules (*13*, *14*), with the sea acting as a giant Gaussian petri dish, where species diversity is equilibrial and density-dependent, and the land witnessing continuing (dampened) exponential rise in diversity as ever new sectors of ecospace are conquered (*9*, *14*). Any model for global diversification must encompass the independent evidence for increasing complexity of organisms, increases in the occupation of novel ecospace, explosive evolution within particular clades, and addition of novel clades without the loss of precursors (*9*, *11*, *15*), all of which have happened many times in the past 500 My.

Large-Scale Controls on Species Diversity

Taxic paleobiological studies have provided a great deal of evidence about controls, mainly abiotic, on species diversity. Biotic factors, such as body size, diet, colonizing ability or ecological specialization, appear to have little effect on the diversity of modern organisms, although abundance and r-selected life-history characteristics (short gestation period, large litter size, and short interbirth intervals) sometimes correlate with high species richness (*16*).

Geographic and tectonic history has generated patterns of species diversity through time. The slow dance of the continents as Pangaea broke up during the past 200 My has affected modern distribution patterns. Unique terrestrial faunas and floras, notably those of Australia and South America, arose because those continents were islands for much of the past 100 My. Further, major geologic events such as the formation of the Isthmus of Panama have permitted the dispersal of terrestrial organisms and have split the distributions of marine organisms. A classic example of vicariance is the fundamental division of placental mammals into three clades, Edentata in South America, Afrotheria in Africa, and Boreoeutheria in the northern hemisphere, presumably triggered by the split of those continents 100 Ma (*17*). Other splits in species trees may relate to dispersal events, or there may be no geographic component at all.

Species richness through time may correlate with energy. The species richness–energy relationship (*18*) posits correlations with evapotranspiration, temperature, or productivity, and studies of terrestrial and marine ecosystems have shown that these factors may explain as much as 90% of current diversity, although relationships between species diversity and productivity change with spatial scale (*19*). Over long time spans, there are strong correlations between plankton morphology and diversity and water temperature: Cooling sea temperatures through the past 70 My, and consequent increasing ocean stratification, drove a major radiation of Foraminifera, associated with increasing body size (*20*). More widely, there is close tracking between temperature and biodiversity on the global scale for both marine and terrestrial organisms (*21*), where generic and familial richness were relatively low during warm "greenhouse" phases of Earth history, coinciding with relatively high origination and extinction rates.

A much-studied manifestation of energy and temperature gradients is the latitudinal diversity gradient (LDG), namely the greater diversity of life in the tropics than in temperate or polar regions, both on land and in the sea. There are two explanations (*22*): (i) the time and area hypothesis, that the tropical belt is older and larger than temperate and polar zones, and so tropical clades have had longer to speciate, or (ii) the diversification rate hypothesis, that there are higher rates of speciation and lower rates of extinction in the tropics than elsewhere. There is geological and paleontological evidence for a mixture of both hypotheses (*23*, *24*).

Species diversity may increase by the occupation of new ecospace. The number of occupied guilds, that is, broad ecological groupings of organisms with shared habits, has increased in several steps through time, from 20 in the early Paleozoic to 62 in post-Paleozoic marine faunas (*25*). Further, marine animals have shown several step increases in tiering, the ability to occupy and exploit different levels in the habitat: At times, burrowers have burrowed deeper, and reef-builders have built taller and more complex reefs. Analogous, if even more dramatic, expansions of ecospace have occurred on land, with numerous stepwise additions of new habitats, from the water-margin plants and arthropods of the early Paleozoic to the forests and upland habitats of the later Paleozoic when land animals first burrowed, climbed, and flew, through the introduction of herbivory, giant size, endothermy, and intelligence among vertebrates, and the great blossoming of flowering plants (with associated vast expansions in diversity of plant-eating and social insects and modern vertebrates) during the Cretaceous Terrestrial Revolution 100 Ma (*26*).

The other mode of species increase globally or regionally is by niche subdivision, or increasing specialization. This is hard to document because of the number of other factors that vary between ecosystems through time. However, mean species number in communities (alpha diversity) has increased through time in both marine (*15*, *25*) and terrestrial (*10*) systems, even though niche subdivision may be less important than occupation of new ecospace in increasing biodiversity. Further, morphological complexity may be quantified, and a comparative study of crustaceans shows, for example, that complexity has increased many times in parallel in separate lineages (*27*).

Phylogenetic Studies of Clade Histories

Species are not randomly distributed; they have an evolutionary history, and so occur as twigs on a great phylogenetic tree. Studying species as members of clades is a fruitful approach to understanding the drivers and controls on speciation. Key questions include (i) Do species diversify early in a clade's history? (ii) How do diversity and disparity (variance in characters or morphology) covary? (iii) Do major lineages within a clade follow similar, or different, patterns, and if different, why? (iv) Do evolutionary radiations follow the acquisition of new characters or emptying of ecospace? (v) How do major clades of apparent competitors interact over long spans of geologic time? and (vi) How do sister clades vary in species diversity and why?

For such analyses, the ideal is a complete species tree, a phylogenetic tree that contains all species living and extinct, plotted accurately against geologic time (*4*). Simple to say; hard to achieve. More commonly, incomplete trees have been used, with the risk of error in calculations of evolutionary rates or comparisons of subclades. In paleontology, it has proven much easier to work with higher taxa such as genera or families because species fossil records are less complete than those of higher taxa, and yet it is not clear how higher-level patterns relate to those at species level. Many key questions can be tackled by comparing a real tree to a hypothetical tree that follows an equal-rate Markov (ERM) model, equivalent to tree growth after a random walk, where equal chances of speciation and of extinction are shared by all species (*4*).

Major biotic replacements, where one clade replaces another, have been a focus of debate about the roles of competition and progress in macroevolution, and dinosaurs provide a classic example. The standard view was that dinosaurs originated in the Late Triassic, some 230 Ma, by a process of competition in which they prevailed over their precursors, the crocodile-like crurotarsans and others, because of superior adaptations. A comparative phylogenetic study (*28*) shows, however (Fig. 3), that the Dinosauria expanded in two steps, one after an extinction event 225 Ma that removed dominant herbivores, and the second following the end-Triassic extinction 200 Ma that removed most of the crurotarsans. Dinosauria remained at moderate diversity and low disparity, and at lower disparity than the crurotarsans they supposedly outcompeted, during the 25 My between the events, suggesting that there was no insistent competition driving other groups to extinction but rather that the dinosaurs occupied new ecospace opportunistically, after it had been vacated.

A further study on Dinosauria explored the subsequent evolution of the clade (*26*). Classic views that the dinosaurs arose with a flourish, and then finally gave way in the Cretaceous to the superior mammals, or that they dwindled to extinction because of "racial senility," had long been abandoned. The dinosaurs seemed to be radiating actively in the Cretaceous, with many new clades appearing through their last 55 My, and especially in their final 15 My. The new study (*26*) shows that most diversification shifts (departures from ERM assumptions) fall in the

first one-third of the history of the clade and that their continuing diversification in the Late Jurassic and Cretaceous was mainly indistinguishable from a random walk. In particular, dinosaurs did not participate in the Cretaceous Terrestrial Revolution, some 130 to 100 Ma, when flowering plants, leaf-eating insects, social insects, squamates, and many other modern groups radiated substantially.

There is no geometric reason that diversification shifts should mainly occur low in a clade's history: Clade shapes vary from bottom-heavy to top-heavy, and diversification shifts may be concentrated low (dinosaurs and bats) or high (insects and ants) in a clade (*26*).

In the future, the identification of diversification shifts across numerous taxa may provide evidence for the relative importance of the Red Queen and Court Jester worldviews. If the majority of diversification shifts are coordinated, and associated with particular climatic, tectonic, and geographic drivers, then the Court Jester model of macroevolution would prevail. This would link most increases in species diversity to particular large-scale radiation events, such as the Cretaceous Terrestrial Revolution (*26*), or recoveries after mass extinctions. If, on the other hand, the majority of diversification shifts are unique to particular clades, and not coordinated temporally with others, then the Red Queen worldview might be considered.

Comparing Sister Taxa

A powerful element of the comparative phylogenetic approach to species diversity through time is the opportunity to compare sister taxa. Sisters arose from a single ancestor, and so their trajectories occupy the same amount of time, and they started with the same genotype and phenotype. Any similarities in their subsequent evolution probably reflect this phylogenetic signal of a common origin, but differences reflect independent aspects of their separate histories.

Comparisons of sister taxa have allowed tests of the resource-use hypothesis (*29*), that generalists are less speciose and have longer species durations than specialists. Specialists divide the physical environment into small patches, each occupied by a species, and each probably more subject to environmental crises than their generalist relatives. Classic examples in support of the resource-use hypothesis come from studies of Neogene mammals (*29*). For example, two antelope subgroups, the tribes Alcelaphini and Aepycerotini, diverged 6 to 8 Ma. The former is now highly speciose, with some 7 living and 25 extinct species, and the latter is represented by two species, only one, the impala *Aepyceros*, surviving. The slowly evolving Aepycerotini consists of few species at any time, and each of those is long lived, whereas the speciose Alcelaphini consists of many short-lived species. The ecological habits of both clades differ: The impala has a broad, generalist diet, whereas the speciose alcelaphines show more dietary specialization. In wider studies of many clades of Neogene African and South American mammals (*30*), the resource-use hypothesis was supported, and some subsidiary predictions confirmed: Specialists are more common than generalists, carnivores include more generalists than herbivores, and there are more specialists in habitats that underwent recent environmental change (tropical rain forests and deserts). The resource-use model then stresses the role of climate and tectonic movements in determining species diversity rather than biological controls such as competition and predation.

Outlook

Paleontologists and evolutionary ecologists have debated species diversity largely independently.
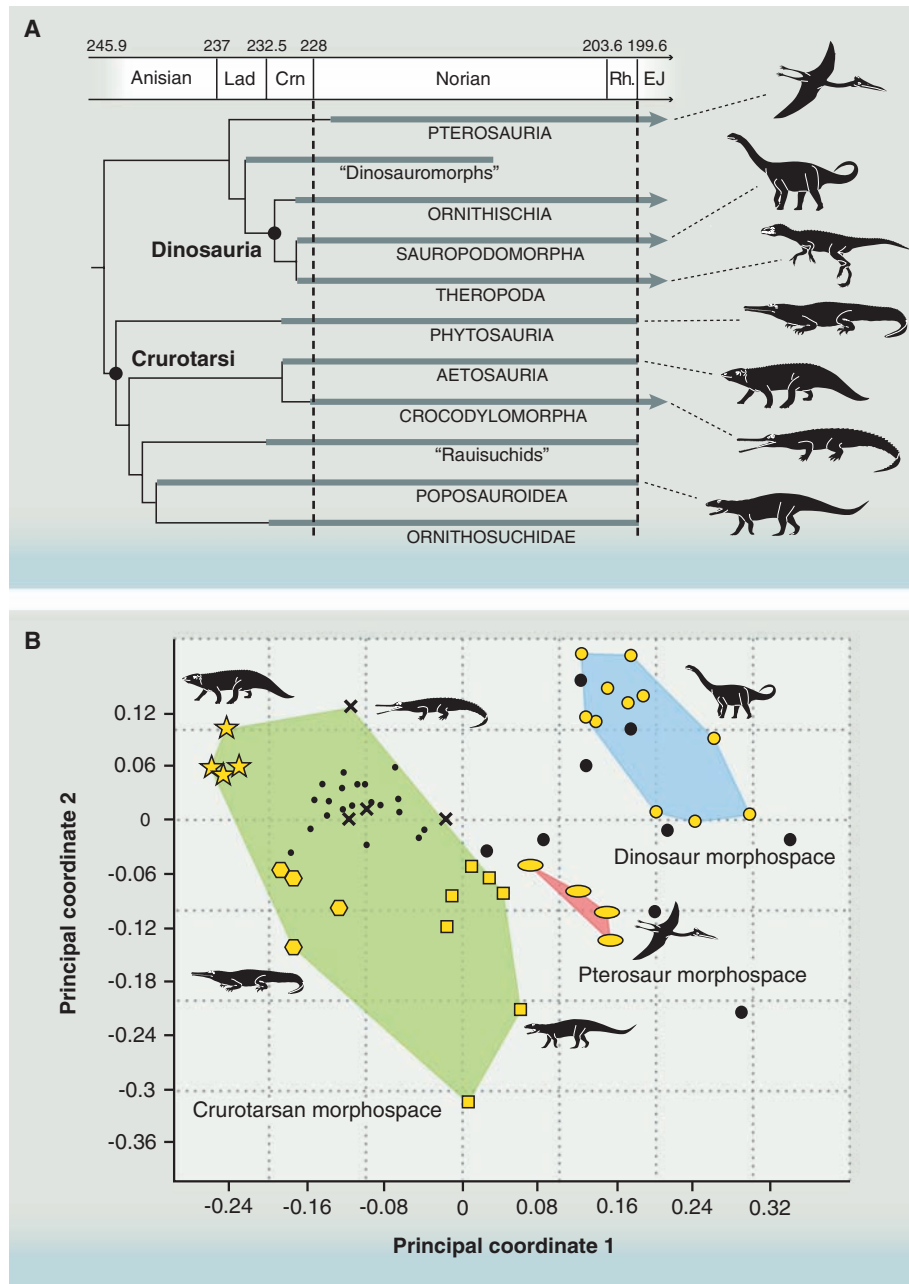

Fig. 3. Phylogenetic relationships and morphospace occupation for Triassic archosaurs. (**A**) Framework phylogeny for Triassic crurotarsans scaled to the Triassic time scale. Numbers at top refer to millions of years before the present; gray bars represent the observed durations of major lineages; vertical dashed lines denote two extinction events, at the Carnian-Norian and Triassic-Jurassic boundaries; arrowheads indicate lineages that survived the latter event. Lad, Ladinian; Crn, Carnian; Rh, Rhaetian; EJ, Early Jurassic. (**B**) Empirical morphospace for Late Triassic archosaurs, based on the first two principal coordinates. Large circles, dinosaurs; ovals, pterosaurs; squares, poposauroids; hexagons, phytosaurs; stars, aetosaurs; crosses, crocodylomorphs; smaller black dots, "rauisuchids"; larger black dots, nondinosaurian dinosauromorphs, *Scleromochlus*. Based on (*28*).

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The realization that the Red Queen and Court Jester models may be scale-dependent, and that evolution may be pluralistic (*3*), opens opportunities for dialog. Taxic studies in paleontology continue to have great value in highlighting correlations between species richness and other factors, but comparative phylogenetic methods will illuminate questions about clade dynamics, species richness, and the origin of novelties. Further, methods are shared by paleontologists and neontologists, and this allows direct communication on the patterns and processes of macroevolution. Viewed close up, evolution is all about biotic interactions in ecosystems (Red Queen model), but from further away, the large patterns of biodiversity are driven by the physical environment (Court Jester model).

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REVIEW

Adaptive Radiation: Contrasting Theory with Data

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Biologists have long been fascinated by the exceptionally high diversity displayed by some evolutionary groups. Adaptive radiation in such clades is not only spectacular, but is also an extremely complex process influenced by a variety of ecological, genetic, and developmental factors and strongly dependent on historical contingencies. Using modeling approaches, we identify 10 general patterns concerning the temporal, spatial, and genetic/morphological properties of adaptive radiation. Some of these are strongly supported by empirical work, whereas for others, empirical support is more tentative. In almost all cases, more data are needed. Future progress in our understanding of adaptive radiation will be most successful if theoretical and empirical approaches are integrated, as has happened in other areas of evolutionary biology.

The spectacular diversity of life on Earth that Darwin sought to explain in *On the Origin of Species* emerged through a variety of intricate biological processes. One of these is adaptive radiation, which some consider of foremost importance and potentially responsible for much of the ecological and phenotypic diversity of life (*1*, *2*). "Adaptive radiation" refers to those evolutionary groups that have exhibited an exceptional extent of adaptive diversification into a variety of ecological niches (*2*–*4*), with such divergence often occurring extremely rapidly (*5*). Classic examples of adaptive radiation include Darwin's finches on the Galápagos islands, *Anolis* lizards on Caribbean islands (Fig. 1), Hawaiian silverswords, and cichlids of the East African Great Lakes (Fig. 2), among many others (*1*, *2*, *6*).

Adaptive radiation has two components: the production of new species (speciation) and the adaptation of constituent species to a diversity of ecological niches. Although many classic adaptive radiations are both species rich and adaptively disparate (*7*), this correlation is far from perfect: Some adaptive radiations have relatively low species richness (e.g., Darwin's finches, Australian pygopodid lizards); alternatively, some speciose clades contain little adaptive disparity and thus would not qualify as adaptive radiations (*3*, *8*).

The classic view of adaptive radiation focuses on ecological opportunity, in which an ancestral species finds itself in an environment in which resources are abundant and underutilized. Such resource availability may result from colonization of an underpopulated area (e. g., island or lake), extinction of previously ecologically dominant groups, or evolution of a character—sometimes termed a "key innovation"—that allows the lineage to interact with the environment in novel ways (*1*, *2*). Different evolutionary factors allowing the populations to take advantage of new ecological opportunity have been emphasized, including genetic drift in small founder or peripheral populations (*9*), relaxed (*9*) or strong selection (*2*, *10*), and hybridization (*11*, *12*).

Empirical Approaches for Studying Adaptive Radiation

Four main empirical approaches have been used:

Fossils. Methods based on fossil data allow one to infer the history of the clade through time and to use information from extinct taxa. The disadvantages of this approach are incompleteness of the fossil record, difficulty in assessing the adaptive significance of phenotypic variation among taxa, and the absence of ecological, behavioral, physiological, and other types of data.

Phylogenetic comparative methods. Phylogenetic approaches take advantage of increasingly complete phylogenies for many important groups and have the ability to integrate studies of the evolution of organismal function and ecology. The main disadvantage of these methods is that extinct taxa are often not represented so that there is no way, for example, to detect whether a clade has been more species-rich in the past. Moreover, phylogenetic inferences about character states in the past can be unreliable (*13*, *14*).

Microevolutionary studies of extant taxa. Studies focusing on traits of and processes affecting extant taxa—e.g., phenotypic characters, ecological niches, spatial structure, genetics, local adaptation, competition, and sexual selection—can elucidate much about the processes driving

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