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The Angiosperm Terrestrial Revolution and the origins of modern biodiversity

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Summary

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Biodiversity today has the unusual property that 85% of plant and animal species live on land rather than in the sea, and half of these live in tropical rainforests. An explosive boost to terrestrial diversity occurred from c. 100–50 million years ago, the Late Cretaceous and early Palaeogene. During this interval, the Earth-life system on land was reset, and the biosphere expanded to a new level of productivity, enhancing the capacity and species diversity of terrestrial environments. This boost in terrestrial biodiversity coincided with innovations in flowering plant biology and evolutionary ecology, including their flowers and efficiencies in reproduction; coevolution with animals, especially pollinators and herbivores; photosynthetic capacities; adaptability; and ability to modify habitats. The rise of angiosperms triggered a macroecological revolution on land and drove modern biodiversity in a secular, prolonged shift to new, high levels, a series of processes we name here the Angiosperm Terrestrial Revolution.

I. Introduction

Most of life's diversity is on land. It is estimated that there are 10–15 million species of animals, plants, and fungi on Earth today (Costello *et al.*, 2012; Monastersky, 2014; Christenhusz & Byng, 2016; Stork, 2018), and some 85% of these live on land, even though the oceans cover 71% of the Earth's surface (Wiens, 2015). Macroscopic life today (i.e. excluding microbes) is dominated in numerical terms by species of insects, spiders and relatives, flowering plants and fungi, and vertebrates such as lizards, birds,

and mammals. An intriguing observation (Vermeij & Grosberg, 2010) is that biodiversity on land may have exceeded marine biodiversity since 110 million years ago (Ma); why the switchover?

Terrestrialization began by the Ordovician and Silurian, when plants and animals ventured onto land, and more complex ecosystems emerged in the Early Devonian. Although arborescence had already evolved in several lineages of vascular plants, the evolution of seeds in the Late Devonian enabled trees to colonize nearly all of Earth's surface, changing weathering and atmospheric cycles forever (Algeo & Scheckler, 1998; Morris *et al.*, 2018). The

Carboniferous–Permian deglaciation and the 252 Ma end-Permian mass extinction each reset the nature of terrestrial ecosystems substantially, and many new groups of plants and animals originated or diversified in the ensuing Triassic, 252–201 Ma (Looy *et al.*, 2001; Montañez *et al.*, 2007; Benton, 2010, 2016). Further significant changes began in the Cretaceous, 145–66 Ma, which coincided with the rise of the angiosperms, the flowering plants (Crane *et al.*, 1995; Herendeen *et al.*, 2017; Magallón *et al.*, 2019). Events of this time have been called the Cretaceous Terrestrial Revolution (KTR; Lloyd *et al.*, 2008) because many of the most species-rich living clades of terrestrial plants and animals originated then, as shown by numerous fossils and molecular phylogenetic studies of vertebrates (Alfaro *et al.*, 2009; Meredith *et al.*, 2011), insects (Peters *et al.*, 2017; Espeland *et al.*, 2018; Kawahara *et al.*, 2019; McKenna *et al.*, 2019), and plants (Wing & Boucher, 1998; Herendeen *et al.*, 2017; Magallón *et al.*, 2019; Ramírez-Barahona *et al.*, 2020). However, it has become increasingly clear that some of the most significant events in the rise of angiosperms occurred during the early Paleogene, and it is time to revise the KTR concept.

In our view, the KTR was part of a more protracted change in terrestrial ecosystems driven by angiosperms and lasting minimally from 100–50 Ma, through the Late Cretaceous and early Palaeogene (Fig. 1). This interval ranges from the appearance of highly diverse angiosperm leaf floras, when angiosperms first had more species than other plants (Crane *et al.*, 1995; Herendeen *et al.*, 2017), to the Early Eocene Climatic Optimum (EECO) when features of many modern ecosystems had emerged around the world, including angiosperm dominance, very high biodiversity, and the presence of numerous angiosperm crown lineages (Jaramillo *et al.*, 2010). This prolonged series of events can be missed because it is punctuated by the famous Cretaceous–Palaeogene mass extinction (KPME), 66 Ma, when dinosaurs and other land organisms died out along with *c.* 70% of marine species, and so triggering the explosion of modern mammals, birds, and lizards (Slater, 2013; Field *et al.*, 2019). For land plants, the KPME had devastating effects, punctuating the diversification of the angiosperms and altering the trajectory of their evolution (Nichols & Johnson, 2008; Vajda & Bercovici, 2014). This is especially clear in the development of modern-style Neotropical rainforests. The KPME caused a 45% loss of plant diversity in Colombia, followed by 6 million years (Myr) of slow recovery and the appearance of several of today's characteristic, dominant Neotropical plant families (Carvalho *et al.*, 2021); later, rapid warming at the Palaeocene–Eocene Thermal Maximum (PETM) and sustained warmth during the EECO brought originations of many more significant tropical taxa and diversification (Jaramillo *et al.*, 2010). Other warming events during the rise of angiosperms, including two Ocean Anoxic Events (OAEs) in the Early and Late Cretaceous, had major impacts on life in the sea but perhaps had smaller impacts on terrestrial ecosystems or angiosperm evolution (Crane & Lidgard, 1989; Huber *et al.*, 2018; Magallón *et al.*, 2019). Thus, the definitive emergence of biodiverse, angiosperm-dominated forests and continuing restructuring of terrestrial ecosystems occurred in the Paleogene, and the whole long-recognized (Crane *et al.*, 1995; Wing & Boucher, 1998; Wing *et al.*, 2012; Herendeen

et al., 2017; Magallón *et al.*, 2019) but often overlooked process might be better termed the Angiosperm Terrestrial Revolution (ATR), spanning both the Late Cretaceous and the early Palaeogene. This proposed term is not intended to minimize the significance of preceding or subsequent events involving angiosperms but rather to highlight the long interval from the first appearance of high angiosperm diversity (*c.* 100 Ma) to their overwhelming dominance in biodiverse terrestrial ecosystems (*c.* 50 Ma).

Questions of timing and relative impacts of these stages in angiosperm diversification are critical. Further, if angiosperms drove global biodiversity up by as much as an order of magnitude, based on the fact that global marine and terrestrial species richness were once more equal and that terrestrial biodiversity is now as much as 10 times marine biodiversity (Vermeij & Grosberg, 2010), how did that happen? The answer undoubtedly relates to unique attributes of angiosperms and how they differ from gymnosperms, ferns, and other plant groups in terms of reproductive biology, mutualisms, ability to capture energy, and adaptability (Onstein, 2020). Identifying such factors depends on the study of the physiology and ecology of modern plants and fossil evidence. The story is not always easy to construct. For example, close correlations have been identified in timing of diversification of plant hosts and their insect pollinators or herbivores in some cases (Farrell, 1998; Cardinal & Danforth, 2013; Peters *et al.*, 2017; McKenna *et al.*, 2019) and not in others (Labandeira, 2014; Condamine *et al.*, 2016). Further, ecological impacts of angiosperms emerged at different times in different parts of the world or different habitats.

Here, we explore the nature of the ATR, comparing recent multidisciplinary research on the key terrestrial groups of plants, insects, and vertebrates. We consider innovations of flowering plants and disentangle how the angiosperms might have impacted the diversification of other groups. A key question is whether it is plausible to explain the high biodiversity of life on land today as a result of the unique characteristics of the flowering plants, and when and how such changes happened. First, we should try to visualize what happened.

II. Can the Angiosperm Terrestrial Revolution be quantified?

The ATR could be visualized as a time–biodiversity plot, showing the rise and fall of relevant major clades through the past, including the ATR interval of *c.* 100–50 Ma (Fig. 1). However, in constructing this first attempt we had to make numerous assumptions. Thus, we present this image of diversification associated with the ATR (Fig. 1) as a plausible hypothesis, designed to launch the discussion and most of all to emphasize how little is known, especially in terms of how present-day data might directly compare with ancient diversity known from fossils.

There are five aspects of the geometry of this plot, of which three are reasonably certain, namely the identities of the clades, their phylogenetic relationships, and their modern species richnesses, although even those are controversial (Table 1; see Costello *et al.*, 2012; Monastersky, 2014; Christenhusz & Byng, 2016; Stork, 2018). The other two characteristics are the depth and shape of each clade. The depth is the age of origin of the crown clade, namely all

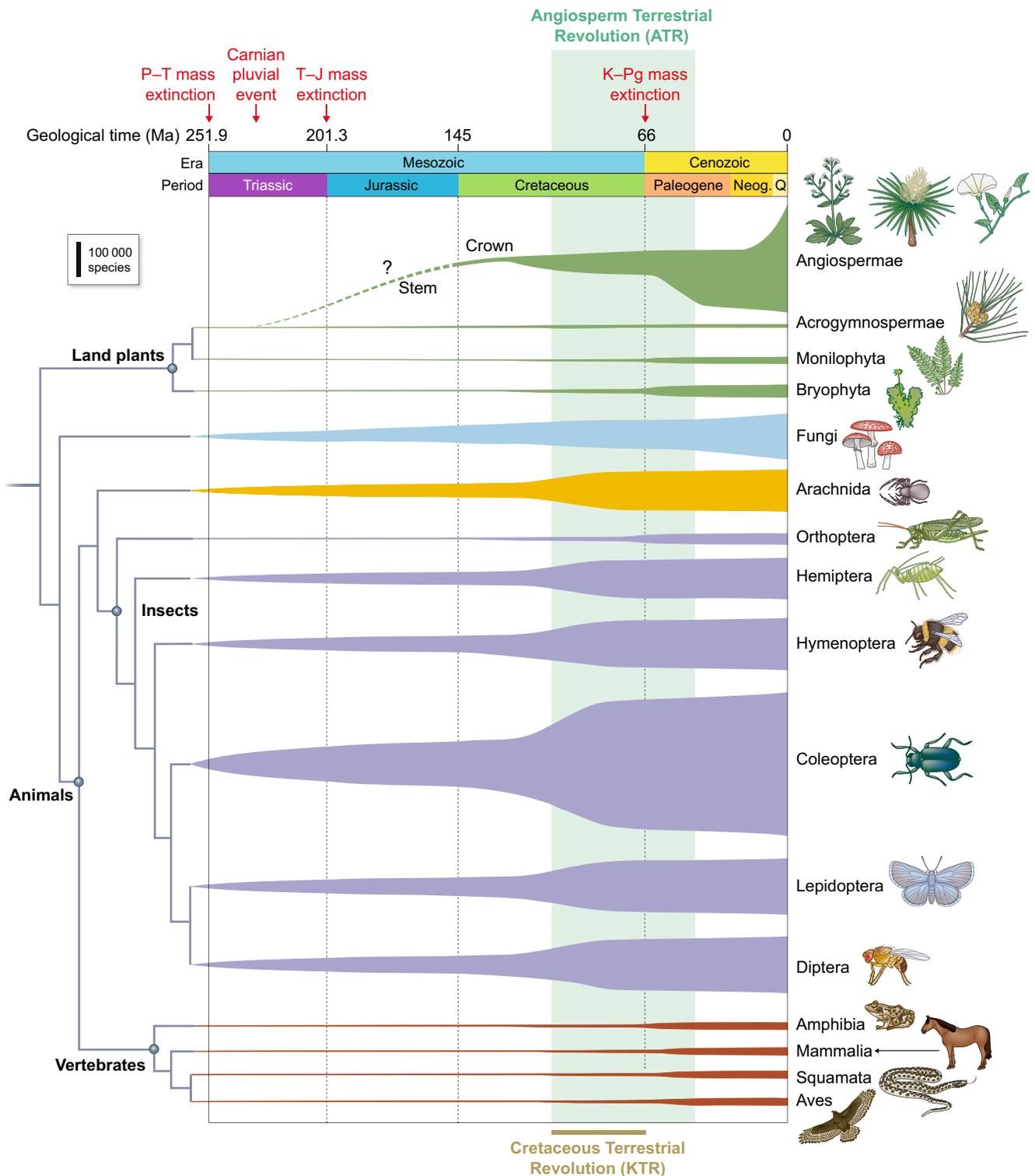


Fig. 1 Evolution of hyperdiverse terrestrial life. Many of the most diverse organisms today, including angiosperms, spiders, insects (bugs, beetles, bees and wasps, butterflies and moths, flies), and vertebrates (lizards, birds, mammals) trace their origins deep into the Mesozoic, but they showed their major diversifications in the Cretaceous and Paleogene, apparently fuelled by the Angiosperm Terrestrial Revolution (ATR). The diagram shows modern diversity (species richnesses from Table 1) in proportion on the vertical axis on the right, and key points of clade origin against the geological time scale, which also highlights significant environmental events. The shapes of the diversification curves are largely conjectural and for illustrative purposes, and should be treated with caution due to the overall limited data, but they are based on knowledge of modern biodiversity and key events represented in the fossil record; the upper segment of the angiosperm spindle includes an attempt to model the LTT curve (Fig. 2), which includes only lineages that survived to the Present, to contrast with the 'conventional' view shown on the lower spindle, which includes both extant (known) and extinct (mostly unknown) lineages. Events in order are the Permo-Triassic (P-T) mass extinction, the Carnian Pluvial Event, the Triassic-Jurassic (T-J) mass extinction, the ATR emphasized in this paper, and the Cretaceous-Paleogene mass extinction (KPME). Organism icons are from pixabay.com, except for the three angiosperm icons from Albino Luna, Instituto de Biología, UNAM.

the living and extinct species back to the last common ancestor of the living species, excluding extinct stem species that lie outside the crown clade. The depth is based on a combination of fossils and divergence date estimations, which can go further back in time than the oldest fossils because individual node dates are conditioned by all input data.

The shapes of the clades in Fig. 1 are hypothetical but based on current evidence. As an experiment, we plotted two curves for the angiosperms (Fig. 1), the upper based on lineages-through-time (LTT) plots, calculated from the most comprehensive molecular trees (Fig. 2) and the lower based on the LTT plot plus estimated fossil diversity. At present, we have no appropriate method nor sufficient data from the fossil record to reliably estimate the past diversity of these major clades. The clade shapes we show are plausible hypotheses but are subject to revision by new phylogenetic analysis or discovery of new fossils.

III. Evolutionary patterns among plants and fungi

1. Angiosperms

Flowering plants first appeared in the fossil record during the Early Cretaceous and came to dominate plant diversity by the Late Cretaceous (Niklas *et al.*, 1983; Herendeen *et al.*, 2017; Coiro *et al.*, 2019). Fossil evidence includes monoaperturate pollen grains in the Valanginian–Hauterivian, *c.* 140–130 Ma, and triaperturate pollen grains, typical of eudicots, appearing around the Barremian–Aptian boundary, 125 Ma (Herendeen *et al.*, 2017; Coiro *et al.*, 2019). By the end of the Early Cretaceous, 100 Ma, both pollen types were abundant and diverse in deposits around the world. Larger angiosperm remains, first known from the Barremian–Albian, 129–100 Ma (Friis *et al.*, 2011), include numerous mesofossil flowers, and later leaves and other organs, from several continents, eventually representing all major angiosperm clades (Amborellales, Nymphaeales, Austrobaileyales, Chloranthaceae, Ceratophyllaceae, magnoliids, monocots, and eudicots).

Putative angiosperm fossils have been reported as far back as the Triassic, but all are rejected (Herendeen *et al.*, 2017; Coiro *et al.*, 2019), even though phylogenetic data indicate that the angiosperm stem lineage had split by then from the clade containing the living gymnosperms (conifers, cycads, *Ginkgo*, and gnetophytes; the numerous extinct gymnosperm groups cannot be sampled genetically; Sauquet & Magallón, 2018). This implies a long ‘hidden record’ of angiosperm stem relatives preceding their Cretaceous first fossil appearance and explosive diversification (Fig. 1). However, the putative stem taxa are not yet recognized from fossils. The age of crown Angiospermae, variously dated from 250–140 Ma, remains controversial and a matter of intense research from both palaeobotanical and fossil-calibrated molecular dating approaches (Herendeen *et al.*, 2017; Sauquet & Magallón, 2018; Coiro *et al.*, 2019; Li *et al.*, 2019).

Recent work has highlighted at least 30 bursts of angiosperm diversification (Tank *et al.*, 2015; Magallón *et al.*, 2019), concentrated in three phases (Fig. 3): steady expansion through the Cretaceous, more complex ecological radiations in the latest Cretaceous, and origins of tropical everwet forests in the early Palaeogene. In terms of community contribution in the fossil

Table 1 Species richnesses of key terrestrial clades of fungi, plants and animals, based on the numbers of described living taxa.

Clade	Species richness	References
Fungi	100 000	Monastersky (2014)
Bryophyta	21 925	Christenhusz & Byng (2016)
Monilophyta (ferns, horsetails)	10 560	Christenhusz & Byng (2016)
Acrogymnospermae (gymnosperms)	1079	Christenhusz & Byng (2016)
Angiospermae	295 383	Christenhusz & Byng (2016)
EMBRYOPHYTA	330 237	Christenhusz & Byng (2016)
Arachnida	110 615	Stork (2018)
Blattodea	7314	Stork (2018)
Orthoptera	23 855	Stork (2018)
Hemiptera	103 590	Stork (2018)
Coleoptera	386 500	Stork (2018)
Hymenoptera	116 861	Stork (2018)
Lepidoptera	157 338	Stork (2018)
Diptera	155 477	Stork (2018)
INSECTA	1013 825	Stork (2018)
Amphibia	7340	Marin <i>et al.</i> (2018)
Mammalia	5364	Marin <i>et al.</i> (2018)
Squamata	9378	Marin <i>et al.</i> (2018)
Aves	9879	Marin <i>et al.</i> (2018)

These are indicative estimates of described species, which vary according to sources (especially for plants and insects). True numbers (including undescribed and undiscovered species) are probably much higher for some of these clades. Upper case for EMBRYOPHYTA and INSECTA, as these are totals, including the clades above each.

record, angiosperms rose from 0–5% of species lists in typical Aptian floras to > 80% by the Maastrichtian (Lidgard & Crane, 1990). This represents a rise from very few species in the Early Cretaceous to 10–150 species per flora at the end of the Cretaceous (Lidgard & Crane, 1990). In terms of extant family numbers, recent evidence from molecular phylogenies, dated using 238 fossils to calibrate 203 of 1209 nodes in the phylogeny, indicates that most angiosperm families (58–80%) also originated (stem age) in the Cretaceous (Ramírez-Barahona *et al.*, 2020), generally agreeing with fossil evidence (Wing & Boucher, 1998). Nevertheless, palaeobotanical data indicate that rising species and family numbers probably did not translate into general angiosperm ecological abundance or biomass dominance until after the KPME (Wing & Boucher, 1998; Wing *et al.*, 2009, 2012; Carvalho *et al.*, 2021), and molecular timetrees indicate that crown ages of most families (56–91%) are Cenozoic (Ramírez-Barahona *et al.*, 2020). Consistent with this idea, the earliest Cenozoic tropical rainforests identified from macrofossils are Palaeocene (Wing *et al.*, 2009; Carvalho *et al.*, 2021), and they were precursors to rapid diversifications of some insect groups, frogs, birds, and mammals as well as plants.

2. Other land plants

Fossil-dated molecular phylogenies suggest that extant lineages of liverworts, mosses, ferns, and some gymnosperms also diversified in the Cretaceous (Schneider *et al.*, 2004; Magallón *et al.*, 2013; Feldberg *et al.*, 2014; Morris *et al.*, 2018). Among these, key groups (Fig. 1) were epiphytic liverworts (Porellales) and polypod ferns,

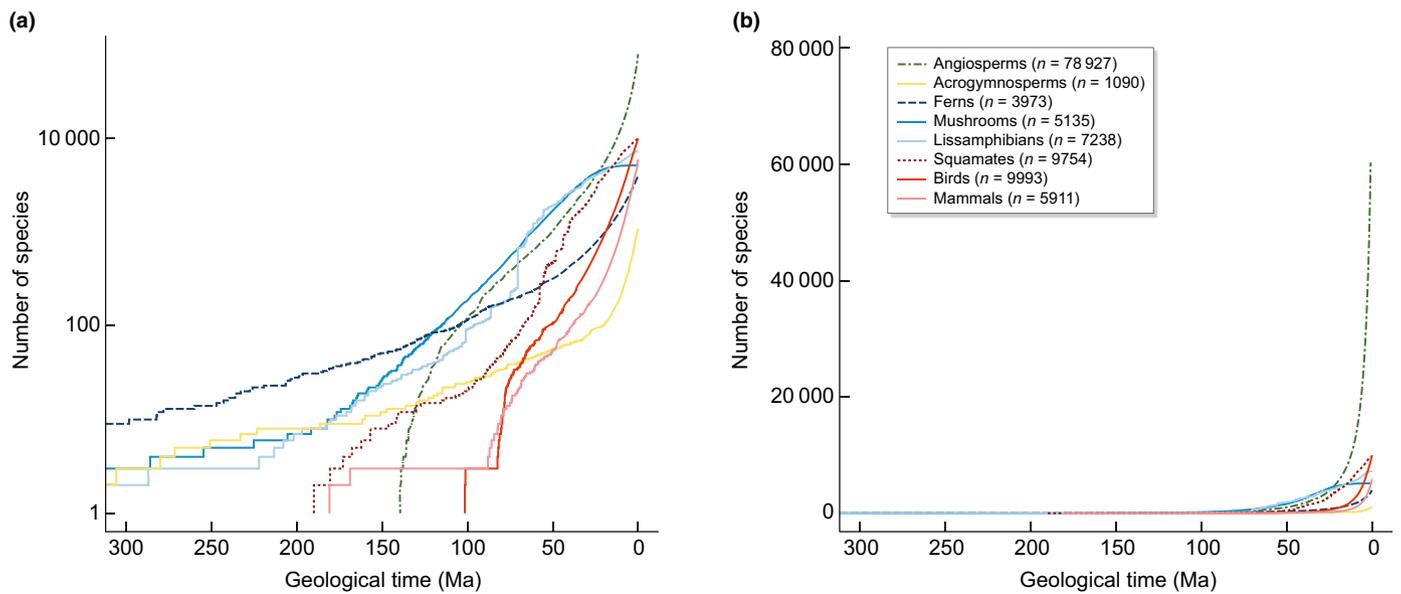


Fig. 2 Lineages-through-time plots for modern biodiverse terrestrial clades. (a) Logarithmic scale; (b) linear scale. These plots represent the number of lineages that survived to the Present against geological time (in millions of years), based on the latest, most complete dated phylogenies available. These phylogenies include all currently known species for acrogymnosperms, lissamphibians, squamates, birds, and mammals, based on combinations of molecular data for most species and taxonomic constraints for the remaining species. The remaining phylogenies represent the most densely sampled dated trees to date but remain incompletely sampled (angiosperms, 26%; ferns, 36%; mushrooms, 24%). Other key terrestrial lineages depicted in Fig. 1 (bryophytes, arachnids, and insect orders) are not plotted here for lack of sufficiently well-sampled dated phylogenies. These lineage-through-time (LTT) plots should be interpreted with great caution, for a number of reasons: each represents a single tree sampled from large posterior tree sets; divergence times remain uncertain and for some clades are a matter of ongoing debate (e.g. angiosperms); each LTT curve is consistent with an infinity of diversification scenarios (Louca & Pennell, 2020); and extinct diversity (e.g. fossils) is not counted here. Nevertheless, they provide an interesting visualization of the relative trajectories of the surviving lineages of major biodiverse terrestrial clades through the last 300 million years. The number of extant species sampled in each source phylogeny is given in the inset legend. Data sources for the lineages through time plots are as follows: angiosperms (Angiospermae), Smith & Brown (2018); acrogymnosperms (Acrogymnospermae), Forest *et al.* (2018); ferns (Monilophyta), Testo & Sundue (2016); mushrooms (Agaricomycetes), Varga *et al.* (2019); lissamphibians (Lissamphibia), Jetz & Pyron (2018); squamates (Squamata), Tonini *et al.* (2016); birds (Aves), Claramunt & Cracraft (2015); mammals (Mammalia), Upham *et al.* (2019).

which represent > 80% of living species, both benefiting from the increase in everwet angiosperm-dominated forests in the Palaeogene (Magallón *et al.*, 2013). In these scenarios, the expansion of leafy liverwort diversity occurred in the Cretaceous, but epiphytic polypod ferns diversified in parallel with angiosperms, beginning in the Early Cretaceous, and continuing through the Palaeogene (Feldberg *et al.*, 2014; Du *et al.*, 2021). Fossil data remain too limited to test these specific patterns.

Bayesian modelling of speciation dynamics of living vascular plant genera identifies transformations during the Cretaceous in terms of both increased origination and extinction rates for spore-bearing plants and accelerated extinction rates for nonflowering seed plants (Silvestro *et al.*, 2015). In those models, spore-bearing plants were hit hard by the KPME, and angiosperms showed increased origination rates in the Palaeogene (Magallón *et al.*, 2019). However, the success of ferns and other free-sporing plants in comparison with angiosperms in KPME sections is well documented palynologically around the world (Nichols & Johnson, 2008; Vajda & Bercovici, 2014).

3. Fungi

Changes in fungal diversity also appear to be closely linked to the ATR, based on dated molecular phylogenies and the host specificity

of many extant mutualisms (Brundrett & Tedersoo, 2018; Lutzoni *et al.*, 2018). New mutualisms with angiosperms enabled saprophytic fungi to diversify, which in turn provided water and mineral nutrients to the plants through mutualistic mycorrhizal root systems. Although direct fossil evidence is limited, fossil-calibrated phylogenies indicate that the rise of the angiosperms enabled the expansion of ectomycorrhizal fungal genera during the Cretaceous (Brundrett & Tedersoo, 2018), further enabling angiosperm diversification (Lutzoni *et al.*, 2018).

IV. Evolutionary patterns among animals

1. Insects

The timing of insect diversification is debated. Many fossil-calibrated molecular phylogenetic analyses conclude that 80% of modern species are in families that first appeared in the Cretaceous (Fig. 1). This is usually explained by the rise of mutualistic relationships (pollination, herbivory) between angiosperms and insects (Farrell, 1998; Espeland *et al.*, 2018; Kawahara *et al.*, 2019; McKenna *et al.*, 2019).

On the other hand, some quantitative palaeontological studies suggest that nothing much happened among insects at family level

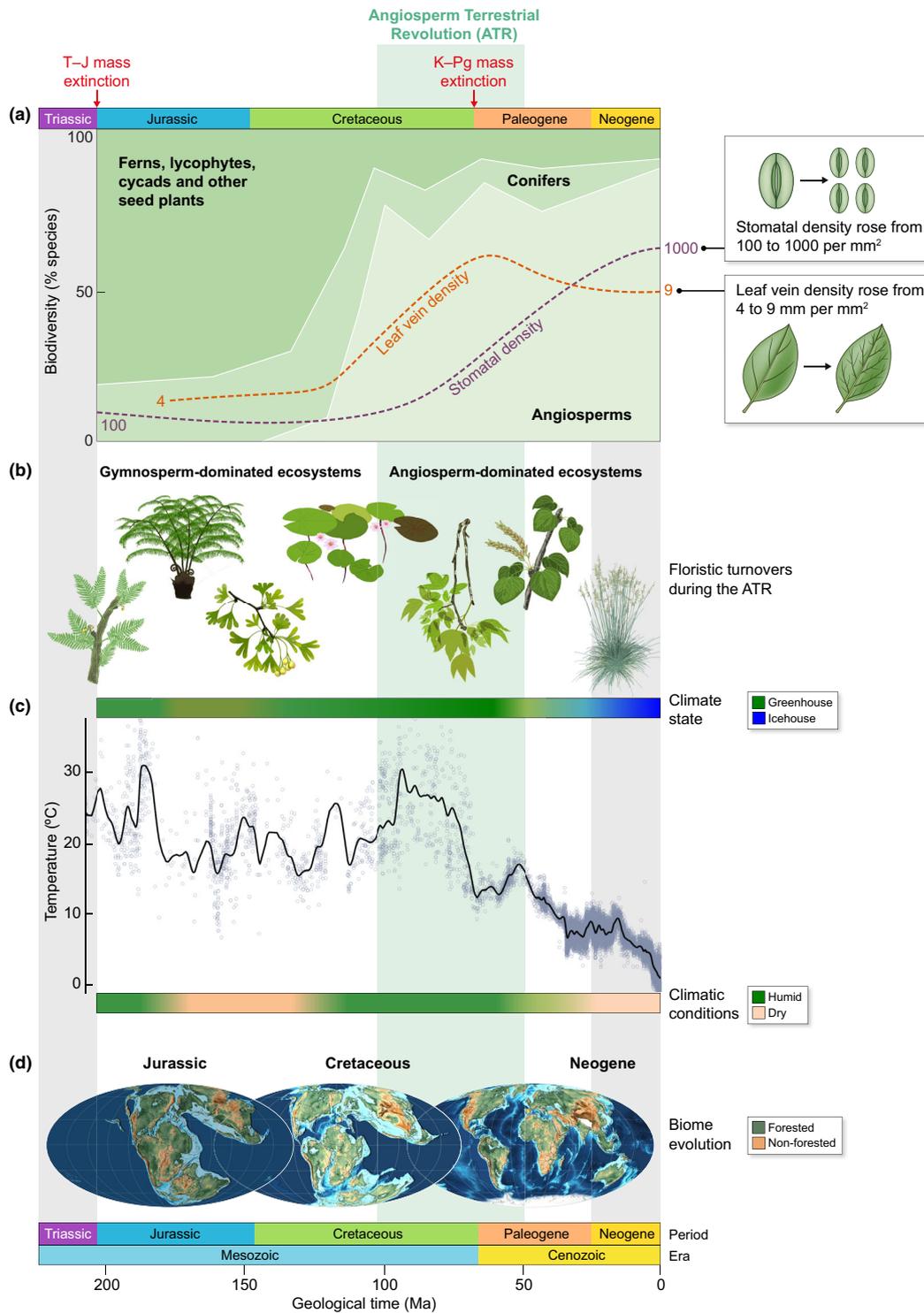


Fig. 3 Some key stages in Earth history and angiosperm evolution through the Angiosperm Terrestrial Revolution. (a) Relative importance of angiosperms, gymnosperms, and other vascular plants through the Mesozoic, measured as proportions of total species counts in fossil assemblages. Overlain are simple curves representing two key indices relating to leaf function, the stomatal density and leaf vein density. (b) Pictorial summary of some well-known fossil plants broadly representing the switch from gymnosperm-dominated to angiosperm-dominated floras, from left to right, including *Umkomasia uniramia*, *Marattiopsis patagonica*, *Ginkgo yimaensis*, *Nymphaeaceae*, *Erlingdorfia montana*, *Joffrea speirsii*, and grasses. (c) Marine temperatures inferred from oxygen isotopes, showing ranges of values and the moving average values, together with global-scale climate states and climatic conditions through time. (d) Continental distributions through time, with forested vs nonforested biomes highlighted. Based on data and images from studies by Kergoat *et al.* (2014); Boyce & Lee (2017), and Shin *et al.* (2018) and palaeomaps by Christopher Scotese. Palaeobotanical icons in (b) by Rebecca Horwitt, available at full size and open access from <https://sites.psu.edu/rhorwitt/>; authorities and references for the taxa, from left to right, are: *U. uniramia*, Axsmith *et al.* (2000); *M. patagonica*, Escapa *et al.* (2014); *G. yimaensis*, Zhou & Zhang (1989); *E. montana*, (R.W. Brown) Johnson (1996); *J. speirsii*, Crane & Stockey (1985). Data for the oxygen curve (c) are from Zachos *et al.* (2008).

in the Cretaceous and Palaeogene. For example, compilations of fossil data show an irregular rise in insect familial diversity through the past 350 Myr, with no acceleration in the Cretaceous (Labandeira & Sepkoski, 1993; Labandeira, 2014). Fossil-insect familial diversity peaked at 125 Ma, then zig-zagged towards the present day to end up only 1.5–3 times the level in the late Palaeozoic (Clapham *et al.*, 2016), thus not changing much during the radiation of angiosperms. Similar results were reported for a major insect clade, the beetles, whose fossil record, though sporadic, appears to show no increase in family diversity since the Early Cretaceous (Smith & Marcot, 2015). A reanalysis of the fossil data using mark–recapture methodology shows an Early Cretaceous peak in insect familial diversity (Schachat *et al.*, 2019), preceding the ATR and linked to the evolution of parasitic and parasitoid clades.

The reliability of the insect fossil record comes into question because it is episodic, with rich entomofaunas known from individual locations and time periods but many gaps (Grimaldi & Engel, 2005; Schachat & Labandeira, 2021). This incompleteness of the record is confirmed by the fact that new fossils can sometimes extend dates of origin of clades and key adaptations by considerable increments (Montagna *et al.*, 2019). Can this discrepancy be resolved? Dated phylogenomic trees of major insect groups argue both ways, but the majority support substantial diversification during the ATR, especially for the key clades Hemiptera, Hymenoptera, Coleoptera, and Lepidoptera. However, counts of lineages through time based on modern taxa tail off rapidly in older time intervals, cannot show how many fossil taxa are missing, and thus cannot reliably recover the true palaeodiversity curves (Louca & Pennell, 2020). On the other hand, it is well understood that fossil data at family level mask diversifications of species within families: some insect families contain a handful of species, whereas others have hundreds or thousands of species per family, the highest being over 85 000 species in family Curculionidae, the weevils, and over 64 000 species in family Staphylinidae, the rove beetles. Constant numbers of families would mask exponential rises in species numbers at various times, and this needs further investigation. Because of the huge biodiversity of insects today, representing as much as 50% of all macroscopic life (Costello *et al.*, 2012; Monastersky, 2014; Christenhusz & Byng, 2016; Stork, 2018), it is worth considering the key clades.

Diversification bursts are reconstructed from genetic data in both Blattodea, cockroaches and termites (Bourguignon *et al.*, 2018; Evangelista *et al.*, 2019), and Orthoptera, grasshoppers, locusts and crickets (Song *et al.*, 2015). The general rise in nitrogen levels in soils arising from angiosperm productivity may have provided new opportunities for cockroaches in the Cretaceous and termites in the Palaeogene (Evangelista *et al.*, 2019).

Phylogenetic work on flies (Wiegmann *et al.*, 2011) and fleas (Zhu *et al.*, 2015) suggests that key bursts of diversification happened earlier than the ATR, concluding that flies diversified three times, in the Permian, Jurassic, and Palaeogene, whereas modern-type fleas belonging to one clade of the Siphonaptera *sensu lato* diversified after the KPME, possibly in association with the diversification of mammals and birds, their main extant hosts. Older lineages of fleas from the Jurassic and Cretaceous were larger but did not survive the KPME (Huang *et al.*, 2013).

Palaeontological studies (Grimaldi and Cumming, 1999) show substantial Cretaceous diversifications of some fly groups, for example the Brachycera, which comprise some 100 000 species of living flies. This pattern is supported by direct evidence of Cretaceous angiosperm–fly mutualism – remains of angiosperm pollen grains in their guts as well as nectar-feeding mouthparts, consistent with their modern representatives (Grimaldi & Engel, 2005). Phylogenomic data suggest that Bombyliidae, over 5000 species of bee flies, show accelerated evolution in the Late Cretaceous linked to warmer climates and the diversification of angiosperms, which provided expanded resources for their parasitoid larvae and nectar-feeding adults (Li *et al.*, 2021).

Many bugs (Hemiptera) diversified in the Cretaceous, and they show a wide variety of attachment devices adapted to diverse modes of life associated with angiosperms (Beutel *et al.*, 2017). Phylogenetic studies suggest that assassin bugs (Johnson *et al.*, 2018) radiated in the Cretaceous, but that scale insects originated earlier, presumably switching their principal host allegiance from gymnosperms to angiosperms in the Cretaceous (Vea & Grimaldi, 2016). The Auchenorrhyncha (40 000 species of cicadas, planthoppers, leafhoppers, treehoppers, and spittlebugs) are almost exclusively phytophagous and accelerated their diversification with that of the angiosperms (Shcherbakov, 2002). Study of morphological trait evolution in a phylogenomic tree of bugs suggests that the success of true bugs (Heteroptera; 40 000 species) probably relates to mutualisms with angiosperms, but key feeding innovations emerged both during the ATR and later.

Hymenoptera (ants, bees, sawflies, wasps) originated *c.* 280 Ma, in the Permian, with the oldest definitive fossil being a sawfly from the Late Triassic, 235 Ma, and they diversified in the Triassic and Jurassic, but most modern clades trace back to the Cretaceous, according to fossil-dated genomic phylogenies (Peters *et al.*, 2017). Similarly, genetic inference and fossils suggest that ants diversified dramatically *c.* 100 Ma, and this might indicate that they were taking advantage of extensive new resources of leaf litter on forest floors, as well as feeding on other expanding insect groups or building honeydew harvesting relationships with diversifying herbivorous bugs (Moreau *et al.*, 2006). Also, there is fossil evidence for diversification of wasps and bees in the Cretaceous (124–11 Ma), linked to pollination and nectarivory (Cardinal & Danforth, 2013; Peters *et al.*, 2017), but the main diversifications took place in the Palaeogene (Wappler *et al.*, 2015). Biological explanations for these diversity bursts are that the new angiosperms opened new niches in the leaf litter, on the trunks and leaves of the bushes and trees, and in coevolutionary pollen and nectar-feeding relationships. Indeed, the species specificity of such co-evolutionary relationships could generate rapid speciation as angiosperm–insect pairs became increasingly specialized (Beutel *et al.*, 2017).

Beetles are central to understanding insect evolution because they are the most diverse living clade (Fig. 1; Table 1). Phylogenetic studies (Farrell, 1998; McKenna *et al.*, 2015, 2019) suggest that most families of Coleoptera have Cretaceous origins, with for example nine of 15 diversification rate increases taking place in the Cretaceous (Zhang *et al.*, 2018). These mark the origins of family-level clades of foliage-eating beetles of the clade Polyphaga, whose diversification is associated with the rise of the angiosperms (Farrell,

1998). Some individual beetle clades, such as scarabs (Ahrens *et al.*, 2014) and weevils (Shin *et al.*, 2018), might have been part of the ATR, whereas others such as darkling beetles (Kergoat *et al.*, 2014) and rove beetles (Lü *et al.*, 2020) were not.

Lepidoptera is a key clade that diversified with the ATR (Fig. 1) because of close mutualistic relationships with angiosperms in feeding on their foliage as caterpillars and exudates such as nectar as adults (Wiens *et al.*, 2015; Mitter *et al.*, 2017). Butterflies and moths are often intricately adapted to particular plant species in terms of detecting scents and colours, and shapes of mouthparts are finetuned for nectar and occasionally pollen. Phylogenetic analyses suggest that Lepidoptera originated in the Carboniferous, 300 Ma, evolved their tubular feeding probosces in the Triassic, 241 Ma, when many modern clades emerged, diversified enormously through the Cretaceous, with the emergence of day-flying lineages 98 Ma (Mitter *et al.*, 2017; Chazot *et al.*, 2019; Kawahara *et al.*, 2019; Espeland *et al.*, 2018), and further expanded after the KPME. Although the limited fossil record of this group (Eldijk, 2018) cannot confirm these detailed patterns, lepidopteran rates of evolution appear to be the fastest among all insects, possibly even faster than among beetles (Lü *et al.*, 2020), and the link to the ATR in terms of co-adaptation with angiosperms is clear (Kawahara *et al.*, 2019).

2. Arachnids

The second-largest clade of terrestrial animals (Table 1) includes spiders, scorpions and ticks (Stork, 2018). Spiders as predators on insects have often been cited as beneficiaries of the ATR, and this is supported by recent phylogenomic analyses (Garrison *et al.*, 2016; Shao & Li, 2018): the hyperdiverse RTA spider clade, comprising 30 000 species of ground-dwelling, webless, hunting spiders, diversified 125–100 Ma in response to expansions of insect numbers, especially nonflying forms that lived in leaf litter and provided their food. The fossil record of spiders mainly comprises finds from sites of exceptional preservation, including ancient ambers, and these show that three modern families arose in the Triassic and Jurassic, 21 in the Cretaceous, and a further 40 in the Palaeogene (Selden & Penney, 2010).

Herbivorous mites, members of Prostigmata (Acari, Trombidiformes), have interacted with land plants since the Devonian, and today they are associated with numerous gymnosperms and angiosperms, especially Rosales, Fagales and Saxifragales (Ward *et al.*, 2003); however, a close linkage to the ATR is untested. New mutualisms in which diverse mites lived in acarodomatia, protective dwellings located beneath leaves, and fed on fungi and prey animals, providing some protection for the plant, emerged in the Late Cretaceous (Maccracken *et al.*, 2019). They may have evolved *c.* 100 Ma in connection with the diversification of some woody lineages of magnoliid angiosperms, and while providing secure dwelling places for mites, may also have contributed to the success of angiosperms by protecting them from fungal and herbivore attack.

3. Tetrapods

Several modern vertebrate groups diversified in the Cretaceous, including some with plausible connections to the ATR (Fig. 1). For

example, in a molecular study of all vertebrates (Alfaro *et al.*, 2009), six accelerations in evolutionary rate were identified, each at the base of a clade, and these all occurred in the Cretaceous. These six clades (teleosts, Ostariophysi, Percomorpha, nongekkonid lizards, boreoeutherian mammals, neoavian birds) account for 85% of modern vertebrate diversity (Table 1), so exploring their roots is significant. Fossils show that lizards diversified from the Middle Jurassic onwards, but especially in the Cretaceous, and boreoeutherian mammals and neoavian birds both originated in the Late Cretaceous, then diversified mainly after the KPME (Alfaro *et al.*, 2009).

The extant lineages of amphibians (Lissamphibia) had a long and complex history. The three major clades, the caecilians, salamanders, and frogs, diverged in the Palaeozoic. All clades show deep splits in the evolutionary tree that have been linked to continental separations in the Cretaceous (Jetz & Pyron, 2018; Hime *et al.*, 2021), but molecular phylogenies indicate that the modern groups diversified in the Palaeogene. Most amphibians today live in angiosperm-dominated rainforests, where many are adapted to breeding in the canopy, occasionally on epiphytes, and they feed on insects, spiders, snails, slugs and earthworms. The Palaeogene diversifications of lissamphibians, many of which are reliant on respiration through mouth and skin, might well relate to expansion of angiosperm-dominated humid tropical forests.

Squamates, the lizards and snakes, show deep divergence events in the mid-Cretaceous that might have been initiated by continental splitting, especially the opening of the South Atlantic (Vidal & Hedges, 2009). Based on the fossil record, squamate species richness did not increase greatly in the Cretaceous, but the major lineages had already diversified in the Jurassic and, importantly, all modern feeding modes were acquired in the mid-Cretaceous, coincident with the initial diversification of angiosperms (Herrera-Flores *et al.*, 2021). The fossil record and phylogenomic studies show that lizard species richness increased at two points, 84 Ma in the Late Cretaceous, and after 66 Ma in the Palaeogene (Pyron, 2017; Herrera-Flores *et al.*, 2021). Similarly, snakes diversified from the mid-Cretaceous onwards, but they show particularly high diversification rates after the KPME, when *Titanoboa* became huge in the oldest Neotropical rainforests (Head *et al.*, 2009; Hsiang *et al.*, 2015). These macroevolutionary patterns may prove to be general, suggesting that the major divergence of squamates took place after the KPME.

Birds show a three-step diversification, with a first radiation of enantiornithines and other clades known from the mid-Cretaceous of China (Brusatte *et al.*, 2015). Then, with the extinction of these clades apparently occurring at the KPME, the modern orders of birds diversified in the Palaeogene (Claramunt & Cracraft, 2015; Field *et al.*, 2018, 2019), and the most diverse avian clade, the Passeriformes, in the Neogene (Oliveros *et al.*, 2019). Therefore, there is no clear link between the ATR and the diversifications of modern birds, but some Cretaceous birds show evidence that they fed on angiosperms from fossil seeds in their crops, which were adapted for processing this food source (Zheng *et al.*, 2011).

The rich and well documented fossil record of mammals as well as the most recent fossil-calibrated dated molecular trees confirm that modern ordinal-level clades diversified in the early Palaeogene,

especially just before and during the global biome shifts of the PETM (Gingerich, 1989; Meredith *et al.*, 2011; dos Reis *et al.*, 2012; Halliday *et al.*, 2019); however, two lines of evidence point to important earlier pulses of evolution. First, phylogenetic studies suggest that supraordinal-level modern mammal clades had already become established before the KPME and showed continuously high evolutionary rates through the KPME (Meredith *et al.*, 2011; Liu *et al.*, 2017; Halliday *et al.*, 2019). Second, fossils show widespread extinctions of mammals in the mid-Cretaceous, followed by a rebound in diversity in the Late Cretaceous, identified as part of the KTR (Grossnickle *et al.*, 2019; Halliday *et al.*, 2019) and thus the ATR. Fossil ancestral groups of modern marsupials and placentals showed diversification of functional modes, as did multituberculates, a major group of extinct mammals that survived the KPME (Luo, 2007). The Cretaceous angiosperm radiation is identified as a driver for these bursts of mammalian adaptive radiation (Grossnickle *et al.*, 2019) by providing novel food resources, stimulating the diversification of insects that became food for insectivores and, particularly in the Palaeogene, producing large seeds and fruits that triggered further dietary diversification (Wing & Boucher, 1998; Kreft & Jetz, 2007). Indeed, the overall increase in complexity of Palaeogene angiosperm-dominated ecosystems allowed diverse groups of mammals to increase niche partitioning (Wing & Tiffney, 1987; Grossnickle *et al.*, 2019).

V. Angiosperms are unique among land plants

1. Overview of angiosperm innovations

It appears that the rise of angiosperms drove an explosion of life on land. Today, there are few terrestrial locations where flowering plants do not make up at least 90% of the local vascular plant species diversity, even in coniferous forests (Kreft & Jetz, 2007). The huge diversity of angiosperms has been discussed since before the days of Darwin, and in classic essays it has been ascribed to innovations such as insect pollination, flexibility in seed production and dispersal, greater genetic and phenotypic flexibility in cell and shoot elongation, more complex mechanisms for activating and repressing the genes, and greater complexity of the flower (e.g. Burger, 1981; Stebbins, 1981).

These core adaptations (Table 2) enabled angiosperms to overcome constraints that limited species diversity and ecological niche space for other land plants such as gymnosperms and ferns. Bayesian modelling of speciation dynamics suggests that the rise of angiosperms through the Cretaceous drove the decline in conifer diversity (Condamine *et al.*, 2020) and caused conifers then and ever since to have high extinction rates. Note that the comparison is possibly biased by the fact that angiosperms are very diverse today, whereas many gymnosperm lineages are extinct, so we might be missing the full range of characteristics of the latter. The stepwise diversification of angiosperms (Fig. 3a,b) took place against a backdrop of fluctuating but overall declining global temperatures (Fig. 3c) and separating continents (Fig. 3d), and the consequent climatic and palaeogeographic changes drove their biogeography and many aspects of angiosperm evolution.

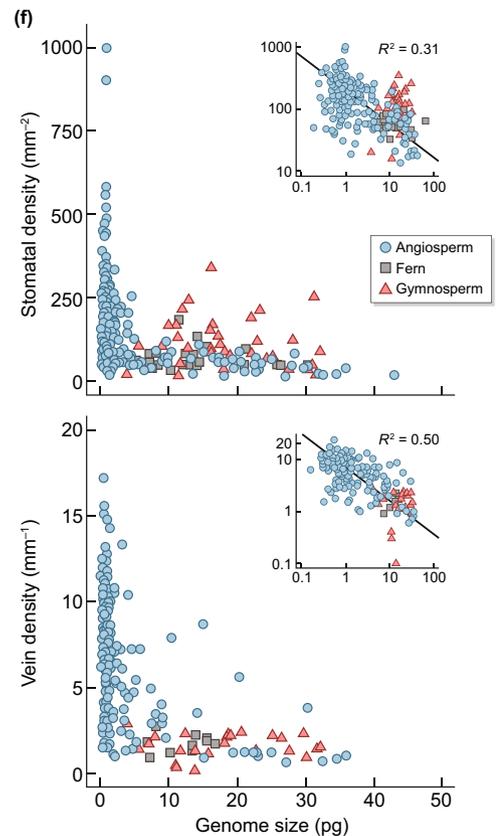
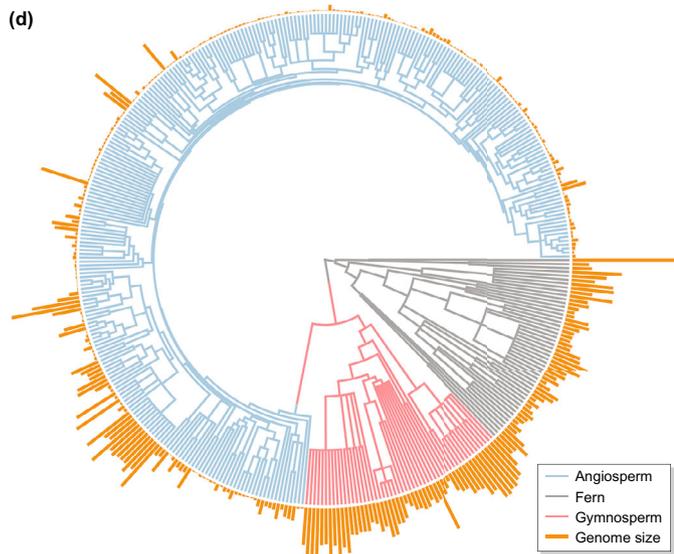
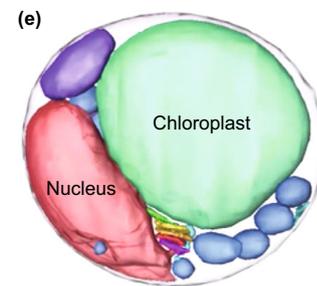
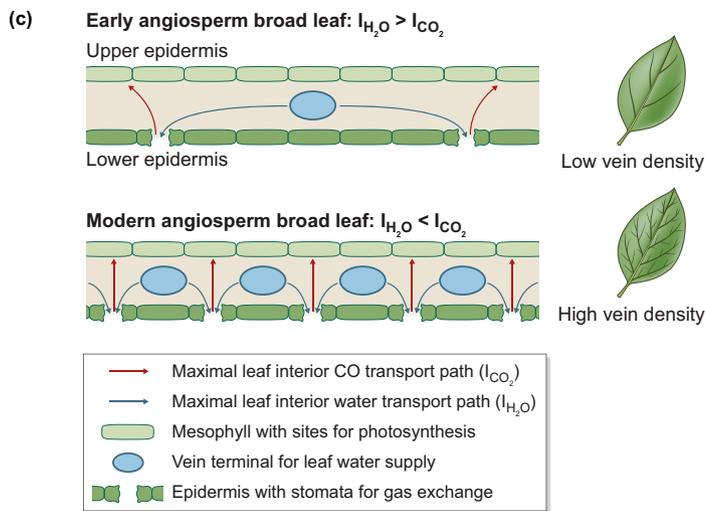
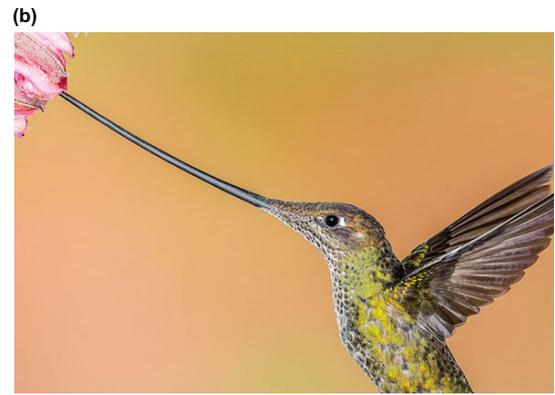
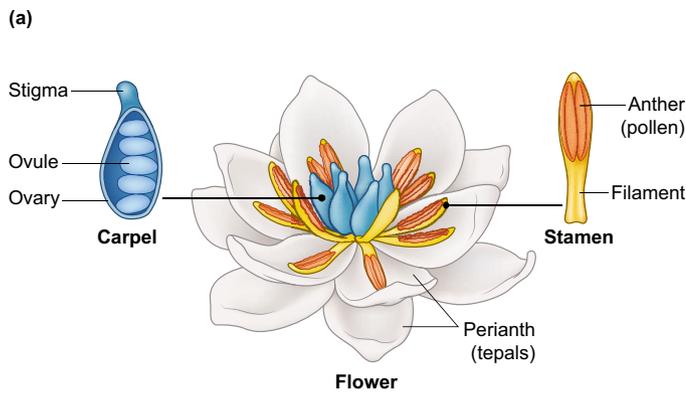
Table 2 List of angiosperm key innovations, which presumably played a central role in their extraordinary diversification and rise to ecological dominance (see also Fig. 4).

Key innovation	Function
Reproductive biology	
Flowers: determinate, compressed, bisexual reproductive axes composed of carpels, stamens, and a sterile perianth	Improvement of pollination efficiency and success, especially by animal vectors; increased specialization and local-scale biodiversity through adaptation to precise ecogeographic situations
Double fertilization	Deferral of endosperm investment until after pollination is assured
Extreme reduction of female gametophyte (in ovule) and male gametophyte (pollen grain)	Greatest degree of protection of haploid phases, in turn freeing structural adaptation and diversity in the sporophyte
Seeds and fruits	Enhanced size range adaptive for wide range of germination conditions and novel animal dispersal, driving animal diversification
Vegetative biology	
Xylem with vessels	Increased transpiration and photosynthesis
High vein density	Improve rates of transpiration and photosynthesis
Densely packed stomata	Improve rates of transpiration and photosynthesis
Secondary chemistry/metabolites	Enables plant defences, driving diversification of numerous animal groups that interact with angiosperms
High productivity through enhanced photosynthesis	Generates opportunities for other plant and animal groups, but also for angiosperms
Genome biology	
Whole genome duplication	May (or may not) have triggered bursts of evolution
Post-polyploidization diploidization	Reduces genome size by deleting duplicated and nonfunctioning genes, and may enable angiosperms to provide new genotypes rapidly
Small genome size	Enables small cell sizes in general, and is connected with the densely packed veins and stomata in leaves

2. Reproductive biology

Flowers have been considered the foundation of angiosperm hyperdiversity because of their double fertilization followed by endosperm formation and because of intimate coevolution with animal pollinators (Endress, 2011). Although flowering plants are also remarkably diverse in other ways, such as in their vegetative growth forms and secondary chemistry, their flowers most consistently distinguish the many angiosperm species and higher taxa. Hence, it is plausible that the success of angiosperms lies not only in their possession of flowers (Fig. 4a) but also in the fact that many angiosperm groups have diversified their reproductive structures to an extent unseen in any other clade of land plants.

The origins of flower characters are widely debated (Sauquet *et al.*, 2022). Bisexual reproductive structures superficially similar to flowers evolved independently in Bennettitales, as did a form of



double fertilization in Gnetales, but angiosperms have both, giving them huge advantages. Phylogenetic analysis of trait evolution (Sauquet *et al.*, 2017) concluded that the flower of the most recent

common ancestor of extant angiosperms supported bisexuality and the perianth, but the timing and order of assembly of these and other key reproductive and vegetative angiosperm traits is uncertain

Fig. 4 Some of the winning characteristics of angiosperms. The flower (a), with female carpel and male stamen, surrounded by the perianth (often differentiated into sepals and petals) which may be brightly coloured. Depicted here is a hypothetical model for the reconstructed ancestral flower (Sauquet *et al.*, 2017); however, considerable variation exists among angiosperms in the number, arrangement, fusion, shape, size, and colour of floral parts. Double fertilization of the embryo and its nutritive endosperm ensures that investment in the food supply only occurs if fertilization is successful. The shape and colour of the flower structures are often intimately adapted to specific pollinating animals, such as this sword-billed hummingbird and passionflower (b). (c) Angiosperms also evolved key changes in their leaves, with a 10-fold increase in leaf veins and stomata, so enabling enhanced transport of water and gases. (d) In a phylogeny of plants, angiosperms (blue) commonly show lower genome sizes (orange bars) than ferns (grey) or gymnosperms (pink). (e) A consequence of small genome size is that angiosperm cells can be very small, with tightly-packed internal structures. (f) Comparisons show that stomatal density (upper graph) and leaf vein density (lower graph) are correlated with genome size (measured in petagrams, pt) for both gymnosperms (blue) and angiosperms (pink). The image in (a) is redrawn from Sauquet *et al.* (2017), CC BY <https://creativecommons.org/licenses/by/4.0/>, credit: Catherine Wardrop. (b) Credit: Andy Morffew (Wikimedia, CC by 2.0). (c) Modified from Boyce & Lee (2017). The images in (d)–(f) are based on those in a study by Simonin & Roddy (2018); CC BY <https://creativecommons.org/licenses/by/4.0/>.

(Sauquet & Magallón, 2018). Insect pollination may have been widespread in Mesozoic seed plants based on diverse evidence such as fossil insects with long probosces (Labandeira, 2010) and is seen in modern cycads and Gnetales (Ickert-Bond & Renner, 2016; Peris *et al.*, 2017; Toon *et al.*, 2020), but not in other living gymnosperms. Insect-pollinated putative ancestors of angiosperms likely possessed flowerless, possibly unisexual reproductive structures with recessed or protected ovules as seen in diverse extinct seed-plant orders (Labandeira, 2010), whereas it is the evolution of flowers that enabled angiosperms to develop varied interactions with animal pollinators (e.g. Xiao *et al.*, 2021). Further, with the deferral of seed investment until after pollination was assured, the double fertilization and nutritious endosperm of angiosperms (Fig. 4a) reduced the cost of failed reproductive efforts.

Angiosperms are noted for their intimate associations with coevolving pollinators, especially insects, bats, and birds (Fig. 4b), and the close matching of flower shape to animal mouthparts or body shapes can be extreme. Wind pollination characterizes only 24 000 (8%) of all angiosperm species (where it is often correlated with reduction of the perianth), but there is little doubt that abiotic pollination arose secondarily as many as 65 times from biotically pollinated ancestors (Linder, 1998; Hu *et al.*, 2008). Yet, many questions remain about the putative pollinators of the earliest flowers, whether these flowers could also self-pollinate or use abiotic vectors for pollination, and to what extent particular angiosperm–pollinator associations drove the diversification of particular clades.

The close association of flowering plants with host-specific animal pollinators is one of the reasons that many angiosperm species are geographically restricted in distribution and exist in small populations. By the late Early Cretaceous, the pollinator fauna shows evidence of specialization by flower morphotype and regional geography in terms of insect damage to flowers (Xiao *et al.*, 2021). These specialized associations can support the diversification of rare plants and animals with patchy distributions, low population densities, and meagre overall biomass. Specialized pollination modes promote not only reproductive isolation and arguably heterozygosity in the angiosperms, but they also drive the diversification of the animal partners that depend on flower products such as nectar, oils, and pollen for food and mating sites associated with thermogenesis (Vamosi *et al.*, 2018). These are only some of the much-discussed (Ehrlich & Raven, 1964; Janzen, 1970; Hubbell, 2001; Boyce & Lee, 2010) reasons why an angiosperm forest may contain hundreds or thousands of species,

especially in the tropics, when compared with species-poor conifer-dominated forests. Tropical rainforests are the most diverse biome on Earth (Carvalho *et al.*, 2021), supporting at least two-thirds of the world's species, even though they cover only 7% of the Earth's surface (Lewis *et al.*, 2015).

3. Vegetative biology

Angiosperms have unique innovations that enhance their photosynthetic rates. These have worked in concert to increase the diversity of leaf morphology to adapt to a wide range of environments and to increase the number of veins and the number of stomata (the openings in leaf surfaces that facilitate gas exchange). The xylem with vessels in most angiosperms that transports water from roots to leaves is more efficient than the vessel-less xylem of gymnosperms (Sperry *et al.*, 2006). Equally important are innovations leading to denser leaf venation (Fig. 4c), up to four times the level in gymnosperms (Feild *et al.*, 2011). In all vascular plants, the veins supply water across the photosynthetic surface and allow increased access to atmospheric CO₂ as transpiration occurs through the stomata. However, the density of the leaf veins in angiosperms brings fine veins closer to the stomata, allowing more efficient CO₂ uptake through intensive transpiration and thus higher photosynthetic capacity. Angiosperms can thus maintain the optimal balance of vein density, water use, and photosynthetic rate for a wide range of leaf thicknesses and habitats (de Boer *et al.*, 2012; McElwain *et al.*, 2016). This enables them to be more productive (McElwain *et al.*, 2016), to occupy more niches than other plants, and to adopt a wide range of growth architectures, promoting structural complexity and terrestrial diversity. Thus, a forest or patch of angiosperms can usually capture more energy from the Sun and turn it into organic matter faster per unit time than a forest of gymnosperms, some of which have evolved broad leaves to better compete with angiosperms, as supported by evidence from both fossils and molecular analyses (Biffin *et al.*, 2012). Extra biomass at the producer level then feeds more herbivorous animals, which in turn feed more carnivorous animals. Food webs expand.

Fossil leaf-venation density increased in two steps, one at *c.* 100 Ma, the other around the Cretaceous–Paleogene boundary, including in Palaeocene fossil-rainforest leaves from the Neotropics (Feild *et al.*, 2011). These increases in leaf-venation density were presumably enabled by the unique angiosperm ability to reduce cell

sizes to maximize photosynthetic efficiency, and these small cell sizes depend on small genome sizes (Simonin and Roddy, 2018; Roddy *et al.*, 2020).

4. Genome evolution

One explanation for the success of angiosperms was that they and their ancestors underwent many whole genome duplications (WGD) and that this repeatedly stimulated their evolution (Schrantz *et al.*, 2012; Tank *et al.*, 2015). For example, a study of 106 WGDs across the phylogeny of angiosperms (Landis *et al.*, 2018) showed that 61 were associated with changes in rates of species diversification, and it has been suggested that WGDs in angiosperms might cluster around times of major environmental crisis such as the KPME (Wu *et al.*, 2020). However, the suggestion that the WGDs drove angiosperm evolution is debated (Vamosi *et al.*, 2018; Leebens-Mack *et al.*, 2019); it can be difficult to place WGD events precisely on phylogenetic trees, a necessary first step in linking a WGD event to a particular evolutionary outcome, and it is hard to show mechanisms stimulated by a WGD that drive morphological innovation (Clark & Donoghue, 2017).

More important in understanding angiosperm success may be the fact that they have smaller genomes on average than other plants. Ferns and gymnosperms have genomes that are on average 10 times larger than those of angiosperms (Dodsworth *et al.*, 2016; Simonin & Roddy, 2018). This is evident in comparisons across the plant evolutionary tree (Fig. 4d). The small genome size in angiosperms is associated with low numbers of chromosomes ($2n = 14\text{--}72$) and small average length of chromosomes, and a recent study indicated that the ancestral haploid chromosome number in angiosperms was $n = 7$ (Carta *et al.*, 2020). In contrast to angiosperms, ferns retain a major part of their duplicated genomes, as indicated by the accumulation of large chromosome numbers (Wu *et al.*, 2020), whereas gymnosperms accumulate large genomes together with large average chromosome length (Leitch & Leitch, 2012). Only angiosperms show a logistic distribution of these three parameters describing their genome structure (genome size, chromosome number, chromosome length), evidence of their unusual genomic plasticity compared to other plant groups.

The balance between WGD and small genomes in angiosperms is achieved by means of a collection of processes collectively termed post-polyploidization diploidization (PPD), meaning that they reduce extra copies of genes by repetitive DNA loss, chromosome rearrangements (including fusions and fissions), and complex patterns of gene loss (Dodsworth *et al.*, 2016; Simonin & Roddy, 2018). Post-polyploidization diploidization acts extensively to reduce genome sizes in angiosperms, despite past WGD. The fate of duplicated genomes appears to be different in angiosperms from other land plants, as new pathways enable rapid genome restructuring, including genome size reductions (Dodsworth *et al.*, 2016). Post-polyploidization diploidization may be one of the key properties of angiosperms that enables them to provide new genotypes rapidly (Leitch & Leitch, 2012) and so to drive their diversification by specialization into ecological roles other plants cannot occupy, perhaps by means of pulsed or stepwise diversification events (Tank *et al.*, 2015; Clark & Donoghue, 2017).

Small genomes lead to small cell sizes in angiosperms, sometimes so small that the nucleus, chloroplasts and other structures are very snugly packed (Fig. 4e). In comparisons across many plants (Ramos & Schiestl, 2019), both vein density and stomatal density are directly related to genome size (Fig. 4f).

Drawing all these innovations together, angiosperms show many unusual qualities in comparison with other plants, which can be viewed in terms of reinvention and trait flexibility (Ricklefs & Renner, 2000; Onstein, 2020). Reinvention is the ability angiosperms showed to enter new adaptive zones at many times through their history, confirmed by evidence for multiple bursts of evolution (Vamosi *et al.*, 2018; Magallón *et al.*, 2019) and their continuing adaptability to climate changes and plate movements. Trait flexibility is the ability to evolve physiological and ecological adaptations rapidly, as evidenced by multiple origins of particular traits (Onstein, 2020); angiosperms show considerably higher reinvention and trait flexibility than gymnosperms (Onstein, 2020), and rates are highest in notably species-rich clades of angiosperms such as Fabales (legumes) and Lamiales (lavender, ash, mint). If angiosperms have an underlying genetic propensity to speciate, and their anatomy and physiology give them higher productivity than gymnosperms, what effects did they have on ecosystems?

VI. Impacts of angiosperms

1. Impacts of angiosperms on modern biodiversity

As described earlier, angiosperms have a great propensity to adapt and evolve, and their physiology and anatomy allow them to capture energy and carbon faster than other plants, helping to drive their elevated species richness today. Could the stunning diversity of terrestrial life, especially in tropical rainforests and seen in fossil examples such as Palaeogene mid-latitude rainforests, also be explained this way, namely that angiosperms provided opportunities for novel forest structure and coevolution of pollination, herbivory, and dispersal strategies and many insect clades boomed, which together stimulated the diversification of other clades such as spiders, lizards, birds and mammals?

Along with the abundant fossil evidence, studies of modern ecology confirm this idea. As examples, angiosperms today support the great diversity of herbivorous beetles, primarily Phytophaga, some 130 000 species (Farrell, 1998; McKenna *et al.*, 2019), as well as Hymenoptera, > 117 000 species of wasps and bees that are closely associated with one or more angiosperm species (Peters *et al.*, 2017). These in turn have their predators, including other insects such as the hyperdiverse parasitoid wasps (Labandeira & Li, 2021), a key element in structuring the ATR, along with reptiles, birds and mammals. Specialized insect–angiosperm pollination associations are known from fossils in the Cretaceous (Grimaldi & Engel, 2005; Hu *et al.*, 2008; Bao *et al.*, 2019; Tihelka *et al.*, 2021; Xiao *et al.*, 2021), confirming phylogenetic studies, including that insect pollination might have been present in ancestors of angiosperms (van der Niet & Johnson, 2012; Gervasi & Schiestl, 2017) as strongly suggested by fossil evidence from extinct gymnosperms (Labandeira, 2010). Indeed, experiments with angiosperms, pollinators, and herbivores show how these

mutualisms stimulate rapid evolutionary change and diversification (Ramos & Schiestl, 2019).

How much does modern biodiversity depend on angiosperms? First, there are some 300 000 species of angiosperms (Christenhusz & Byng, 2016), but their coevolutionary dependents amount to many more. For example, among insects, we can count 795 500 species of Blattodea, Orthoptera, Hemiptera, Hymenoptera, Coleoptera, and Lepidoptera (Table 1) as depending substantially or entirely on angiosperms for their existence (Stork, 2018). These species comprise *c.* 78.4% of the 1014 000 or so named species of living insects. In addition to these insects, there are 110 000 species of arachnids and perhaps 15 000 species of lizards, birds and mammals that depend on angiosperms in one way or another. To these can be added the 29 000 species of nonangiosperm epiphytes that live attached to angiosperms in the Neotropics alone (Gentry & Dodson, 1987). Understory ferns and other herbs comprise 72 families (Cicuzza *et al.*, 2013), and numerous fungi are dependent on angiosperms for their habitats. In fact, the species richness of Fungi is huge, perhaps counting 1.5–3 million, and species likely occur in the tropics at a ratio of 1.8 : 1 in proportion to plants (Hawksworth, 2012). Therefore, the proportion of Fungi, plants, and animals that depend on, or are, angiosperms, especially in tropical rain forests, could in fact be > 50% of all living species, especially if poorly documented taxa such as fungi and soil meiofauna are also considered.

2. Environmental change

The dominance of angiosperms has strongly altered climate and water cycles, and this relates to their high capacities to increase bedrock weathering, thus drawing down $p\text{CO}_2$, and to transpire water drawn from the soil and pass it to the atmosphere. The effects are felt most in tropical rainforests, where, for example, modelling shows that if the angiosperms in South America were replaced by gymnosperms, the Amazon rainforest would reduce to 20% of its modern size (Boyce & Lee, 2010). The high transpiration rates of angiosperms massively affect the landscape and regional climate, which likely stimulates further diversification of the angiosperms themselves, together with the other plants and animals that depend on them, a positive feedback loop. This suggests why angiosperm-dominated everwet tropical forests are so diverse in species when compared to gymnosperm-dominated habitats and links to the observation that regional plant and animal diversity, in the absence of frost, are both correlated with precipitation (Kreft & Jetz, 2007).

Angiosperms did not achieve ecological dominance in a single step. The first angiosperms showed venation densities on their leaves similar to those of gymnosperms (Fig. 3a); venation and stomatal density increased *c.* 100 Ma, as indicated by the fossil record of leaves and by phylogeny (Boyce *et al.*, 2010; Simonin & Roddy, 2018). In the Palaeogene, these adaptations probably impacted world climate, as increased output of water by angiosperms might have driven a shift in equatorial climates from hot, dry and seasonal to wetter in the form of tropical rainforests (Boyce *et al.*, 2010). Angiosperms were rare or low-biomass components of most Cretaceous floras (Wing & Boucher, 1998; Wing *et al.*, 2012) and only achieved ecological dominance following the KPME (Carvalho *et al.*, 2021; Fig. 3a); an

uptick in leaf venation and stomatal density is seen in the oldest definite macrofossil examples of Neotropical rainforest floras (Wing *et al.*, 2009; Feild *et al.*, 2011) and, interestingly, molecular estimates indicate a proliferation of crown angiosperm families at this time (Ramírez-Barahona *et al.*, 2020). The diversity and dominance of crown-group angiosperm families and genera continued to rise, and thus, the sequential effects of the KPME, recovery, PETM, and EECO are linked to elevated impacts of angiosperms on ecosystems and climates and ‘modernization’ of the world flora. The Palaeogene angiosperm radiations are also associated with a massive increase in fruit and seed size (Wing & Tiffney, 1987; Wing & Boucher, 1998), a driver for expansion of fruit-eating animals (Fig. 5).

3. Productivity

Angiosperms are twice as productive as gymnosperms and other land plants (Boyce and Lee, 2017), in no small part because of their high transpiration rates (Lusk *et al.*, 2003; Feild *et al.*, 2011). These increase water loss but also CO_2 intake, and this high carbon uptake drives high productivity. In mixed forests, angiosperm seedlings tend to grow faster than conifer seedlings, and so they can quickly dominate. This is one reason why conifers are often pushed to marginal habitats such as high latitudes or high altitudes as well as infertile or poorly drained soils and frequently burned areas. Current work suggests that terrestrial productivity may have remained low through most of the Phanerozoic, despite considerable fluctuations in atmospheric carbon dioxide (McElwain *et al.*, 2016; but see Wilson *et al.*, 2020), and only increased markedly with the expansion of angiosperms, with their tightly packed stomata, high vein density, high conductivity vessels, and other relevant traits (Boyce & Lee, 2017).

The highly productive angiosperms tend to have other significant functional traits in a wide variety of adaptive combinations (Coley & Barone, 1996; Wright *et al.*, 2017), including their leaf area, leaf lifespan, and chemical defences, all of which in turn affect herbivores. Leaf area is generally constrained by temperature and water availability (Wright *et al.*, 2017). Rapidly growing leaves tend to have short lifespans, thus increasing leaf turnover, but without necessarily increasing total angiosperm biomass (Wright *et al.*, 2004; Boyce & Lee, 2017). However, short lifespans correlate with higher nitrogen levels in leaves and hence palatability to herbivores (Wright *et al.*, 2004), and angiosperms such as grasses and forbs can yield energy at twice the level of conifers and cycads (Hümmel *et al.*, 2008). By contrast, slower growing, less palatable angiosperm species often have increased chemical and structural defences, but these also drive diversification of herbivores as they adapt and specialize (Coley & Barone, 1996; Furstenberg-Hagg *et al.*, 2013; Kariñho-Betancourt, 2018). Productivity, palatability, and defence of angiosperm leaves presumably were all significant factors promoting the overall uptick in biodiversity associated with the ATR.

VII. Physical drivers of the Angiosperm Terrestrial Revolution

The relative importance of intrinsic and extrinsic drivers of diversification in angiosperms remains unclear, and there appears

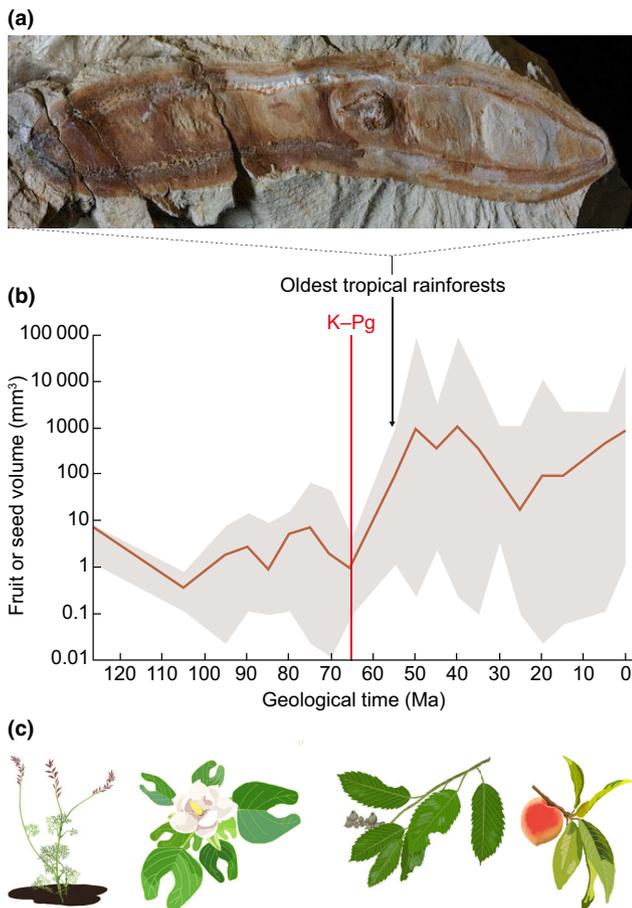


Fig. 5 Fruit and seed size from Cretaceous to Paleogene and the expansion of tropical rainforests. (a) Giant fossil legume (Fabaceae), measuring *c.* 7.9 cm long, from the Palaeocene Bogotá Formation of Colombia, marking the uptick in fruit sizes associated with the Palaeogene and the first tropical rainforests, which were recently linked directly to the KPME (Carvalho *et al.*, 2021). (b) Evolution of seed/fruit size, plotted on a logarithmic scale, showing the increase in mean size by four orders of magnitude in the Paleogene; range of values, grey; mean, brown. (c) Representative angiosperms through time, from the left: *Archaeofructus sinensis*, *Archaeanthus linnenbergeri*, the fossil chinkapin *Castanopsis rothwellii*, and the fossil peach *Prunus kunmingensis*. The image in (a) is courtesy of Fabiany Herrera; the plot in (b) is based on data from Wing & Boucher (1998); and the palaeobotany icons in (c) are all by Rebecca Horwitt (available at full size and open access from <https://sites.psu.edu/rhorwitt/>). Full authorities and references for the described species of fossil plants illustrated, from left to right, are as follows: *A. sinensis* Sun *et al.* (2002), *A. linnenbergeri* Dilcher and Crane (1984), *C. rothwellii* Wilf *et al.* (2019), and *P. kunmingensis* Su *et al.* (2015). The fossil legume shown in (a) is a specimen described in a study by Herrera *et al.* (2019).

to be growing consensus that synergistic combinations of traits and the environment may have been more significant than abiotic drivers alone (Bouchenak-Khelladi *et al.*, 2015; Sauquet & Magallón, 2018). The breakup of Gondwana promoted massive range shifts and allopatry, whose effects on angiosperm diversity, while clearly significant, have proven difficult to quantify (Sanmartín & Ronquist, 2004). Otherwise, the most notable physical change throughout the ATR, and extending to the present day, was the long-term decline in temperature since *c.* 100 Ma (Huber *et al.*,

2018), which also appears to have benefited angiosperms. Palynological evidence shows that angiosperms prospered at the expense of other lineages during Late Cretaceous cooling in Antarctica (Barreda *et al.*, 2019).

The interplay of long-term and short-term cooling and warming episodes in angiosperm evolution is hard to disentangle. For example, climatic events in the Cretaceous, such as the OAEs, and the terminal Maastrichtian warming apparently did not cause any significant changes within angiosperm clades or terrestrial ecosystem structure (Magallón *et al.*, 2019). It may be hard to detect the impact of such events on the apparently relentless increase in angiosperm diversity through the Late Cretaceous, but more subtle changes, for example favouring certain clades or differentiation between high and low latitudes, are worth considering. Further, it might be expected that events in terrestrial and marine systems were coupled in some way, and the massive decline in the abundance of *Classopollis* pollen *c.* 94 Ma, broadly matching a decline in diversity and abundance of ephedroid pollen (Crane & Lidgard, 1989), might suggest a link to the Cenomanian–Turonian marine extinctions. A large palynological and macrofossil dataset clearly shows that a single global, nonclimatic event, the KPME, caused a major extinction and set in motion a novel trajectory for angiosperm evolution in the Neotropics, leading to the present day (Carvalho *et al.*, 2021). Global temperatures warmed gradually through the late Palaeocene and early Eocene, and transiently during the PETM, which are times of substantial vegetation turnover and diversification world-wide (Wing & Currano, 2013), including in tropical rainforests (Schuettelpelz & Pryer, 2009; Jaramillo *et al.*, 2010; Carvalho *et al.*, 2021). In sum, despite several outstanding and data-rich examples such as the PETM, the data are far from comprehensive enough to generalize that all changes in temperature and the carbon cycle trigger world-wide evolutionary changes among angiosperms and terrestrial ecosystems.

Fire had a role in reshaping ecosystems through the ATR. Forest fires spread in the Late Cretaceous, perhaps fuelled by the accumulation of flammable biomass arising from increased productivity of terrestrial habitats comprising angiosperms (Bond & Scott, 2010), which in turn may have created a positive feedback loop, assisting the spread of angiosperms (Belcher & Hudspeth, 2017). Changes in the fire regime may have been further assisted by the coincident expansion of several conifer lineages. Biogeochemical modelling suggests that angiosperm-driven changes to fire feedbacks lowered atmospheric oxygen levels by 25% or more by the end of the Cretaceous (Belcher *et al.*, 2021).

VIII. Future directions

Angiosperm evolution from the Early Cretaceous onward seems to have driven the diversification of life on land in four ways: ongoing evolutionary radiations of hugely diverse lineages with a dizzying variety of structural, chemical, vegetative, and reproductive novelties providing niche opportunities; creation of pollinator and herbivore opportunities, often through intricate plant–animal mutualistic relationships, with cascading biodiversity effects through the food web; increased productivity allowing for a greater flux of energy into the fauna; and increasing the geographic extent

of wet tropical biomes through their hydrological effects. Therefore, many insect groups owed their biodiversity boost to eating plant parts, pollinating flowers, or preying on the insects that did so. Others, such as fungi, liverworts, ferns, frogs, and angiosperms themselves benefited from new habitats in expanding angiosperm-dominated everwet tropical forests. Angiosperm innovations continue to the present day with ongoing evolutionary radiations, as shown by the Neogene expansion of important biomes such as seasonal tropical forests, temperate forests, and grasslands.

Preceding and underlying all these physiological and ecological changes, angiosperms underwent genomic revolutions that enabled them to diversify and evolve in different ways from other plants, as a consequence of new pathways through WGD and PPD. It is not just that angiosperms are species-rich, but many individual angiosperm families show more morphological variety than all other seed plants combined, a distinction that reflects the dynamics of their genomes.

Key questions emerge from our efforts to document what happened as a result of the ATR (Fig. 1) and why (Figs 3, 4). First, what is the shape of the palaeodiversity curve of life on land from the beginning of the ATR to the present day? This has been difficult to establish because we are uncertain about the biodiversity of species-rich groups of plants and insects today and especially in the past, and not only because of the incomplete fossil record. Densely sampled trees are still missing for most terrestrial plant and invertebrate clades, as we observed in our effort to produce the LTTs (Fig. 2). This emphasizes the perennial need for more, and better, palaeobiological data, as well as the importance of further integration of phylogenies and fossils. Second, what is the ecological impact of angiosperms at local and regional levels through time? To what extent have angiosperms enhanced biodiversity today and in the past? How do the increases map onto the biogeographic and climatic distributions of species? Third, how have the unique reproductive, vegetative, and genomic traits of angiosperms impacted their own biodiversity and abundance? Did repeated genomic rearrangements, including WGD, play a critical role in accelerating phenotypic evolution in angiosperms? Fourth, how can we best elaborate the roles of KPME extinction and early Paleogene warming, as well as more minor abiotic events, in angiosperm evolution? And fifth, how have angiosperms triggered diversification and extinction in animals and non-flowering plants throughout their history?

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