

1 ***Title***

2 **The dual role of the angiosperm radiation on insect diversification**

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13

14 **Abstract**

15 Most of the animal pollination is realized by insects, interactions between them and flowering
16 plants have been hypothesized to be important drivers of diversification. Yet, there is weak
17 support for coevolutionary diversification in plant–pollinator interactions. Macroevolutionary
18 studies on insect and plant diversities support the hypothesis that angiosperms evolved after an
19 insect diversity peak in the Early Cretaceous, suggesting that gymnosperm pollinators may have
20 been accessible for angiosperms when they evolved. We examined fossil and phylogenetic
21 evidence documenting this hypothesis and provide new clues on the impact of angiosperm
22 radiation on insect diversification. Using the family-level fossil record of insects and a Bayesian
23 process-based approach, we estimated diversification rates and the role of six different variables
24 on insect macroevolutionary history. We found that, among the six tested variables, angiosperms
25 had a dual role that has changed through time with an attenuation of insect extinction in the
26 Cretaceous and a driver of insect origination in the Cenozoic. However, increasing insect
27 diversity, spore plants and global temperature also showed strong positive correlation with both
28 origination and extinction rates of insects, suggesting that different drivers had important effect
29 on insect evolution, not just angiosperms, which would deserve further studies.

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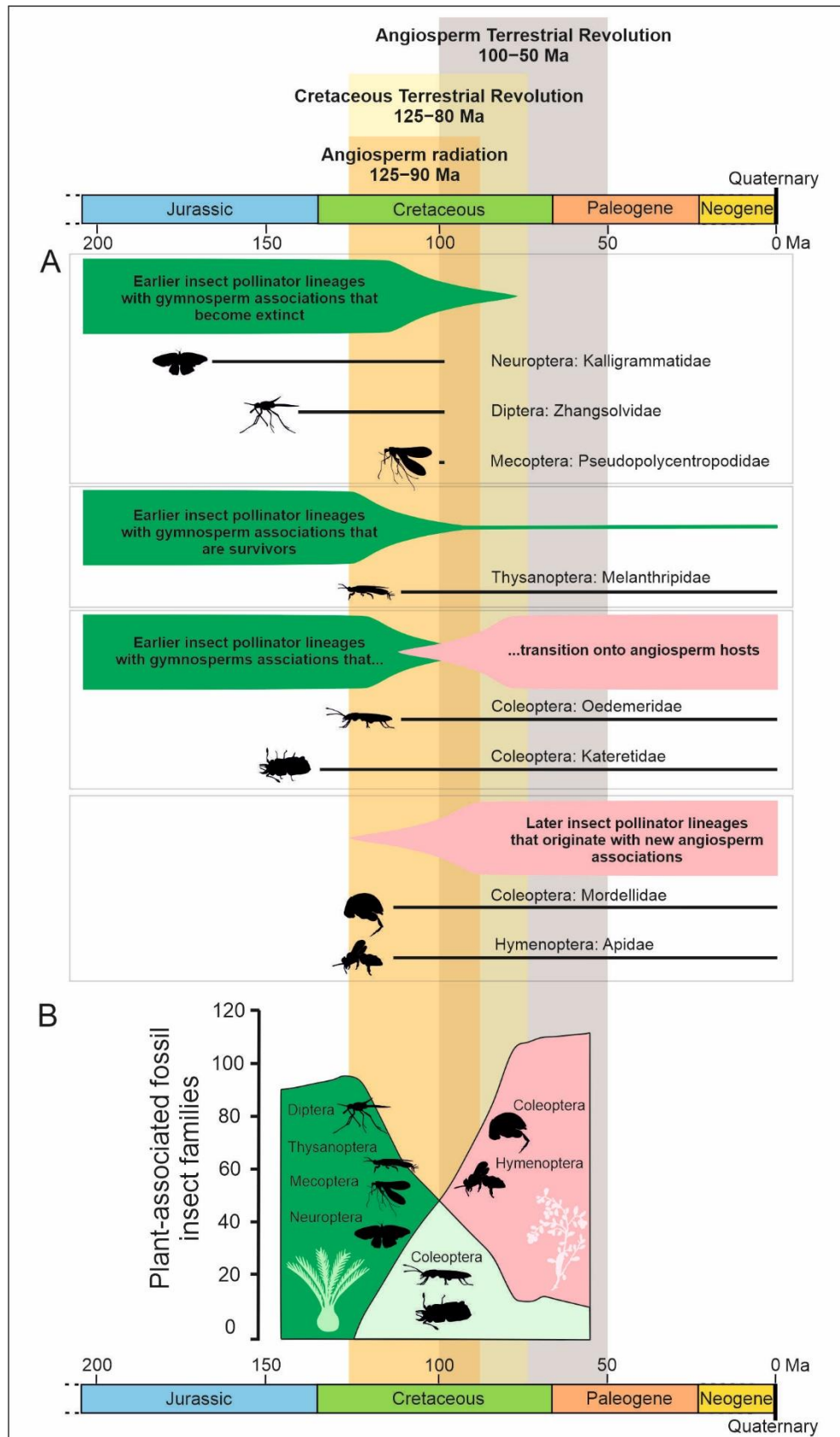
31 **Introduction**

32 Pollination is an essential activity in the sexual reproduction of many plants, particularly for plants
33 producing seeds. The difficulty of active movement in most plants makes necessary the action of
34 different pollination agents to transport their male gametes contained within pollen to ovule
35 bearing, female structures of the same species. These transport agents can be wind, water, or
36 vertebrate animals, although most plants require principally the action of invertebrate animals for
37 their reproduction (Ollerton, 2017). Most current pollinators belong to one of the four major insect
38 orders: Hymenoptera, Diptera, Lepidoptera and Coleoptera (Ollerton, 2017). Iconic pollinator
39 groups currently include bees and butterflies. However, a variety of seed plants existed and
40 possessed reproductive organs long before the evolution of these more notable pollinator groups.
41 This suggests that ancient plants were pollinated by a different spectrum of pollinator agents
42 (Labandeira, 2007; Peris et al., 2017; Khramov et al., 2020).

43 Gymnosperms dominated the land surface until their sister clade, the angiosperms,
44 experienced a rapid diversification in the Cretaceous, for some authors called the Angiosperm
45 Radiation (125–90 Ma, *e.g.*, Labandeira, 2014), the Cretaceous Terrestrial Revolution (125–80
46 Ma, Lloyd et al., 2008), but recently also known as the Angiosperm Terrestrial Revolution (ATR,
47 100–50 Ma, Benton et al., 2022) (Figure 1). This turnover likely caused a decline of conifers
48 (Condamine et al., 2020) and other plant lineages (Lidgard and Crane, 1988). First plants were
49 wind pollinated until some insects diversified and started to feed on gymnosperm ovular
50 secretions in a surface-fluid-feeding way or gymnosperm pollen (Labandeira 1998), predating
51 that of nectar-feeding insects on angiosperms (Nepi et al., 2017) (Figure 1).

52 The complex interactions between pollinators and gymnosperms seems to have been
53 persisting since, at least, the early Permian (283–273 million years ago, Ma), predating the first
54 flowering plants by more than 100 Ma (Khramov et al., 2022). There is a diverse well-documented
55 herbivore community from the Cretaceous found in sediments and ambers supporting
56 gymnosperm–insect pollination modes and host associations with ginkogaleans, cycads, conifers
57 and bennettitalean gymnosperms during the Early and the beginning of the Late Cretaceous
58 (Labandeira, 2007; Peris et al., 2017, 2020; Khramov et al., 2020) (Figure 1). By contrast,
59 evidence for angiosperm-pollen consumers or flower visitors appeared only in the Late
60 Cretaceous, around 99 Ma (Peris et al., 2020; Peña-Kaitath et al., in prep.). It is thought that
61 flowering plants have interacted with pollinating insects since their beginning (Grimaldi, 1999;
62 Labandeira, 2007), but gymnosperm-adapted insects were not using extensively angiosperms
63 resources yet until the Late Cretaceous (Labandeira, 2007; Peris et al., 2017; 2020). Elucidating
64 when, how and why the ecological transformation of ecosystems began with the coevolution
65 between insects and flowering plants has become an idea of recent interest (van der Kooi and
66 Ollerton, 2020; Benton et al., 2022; Asar et al., 2022).

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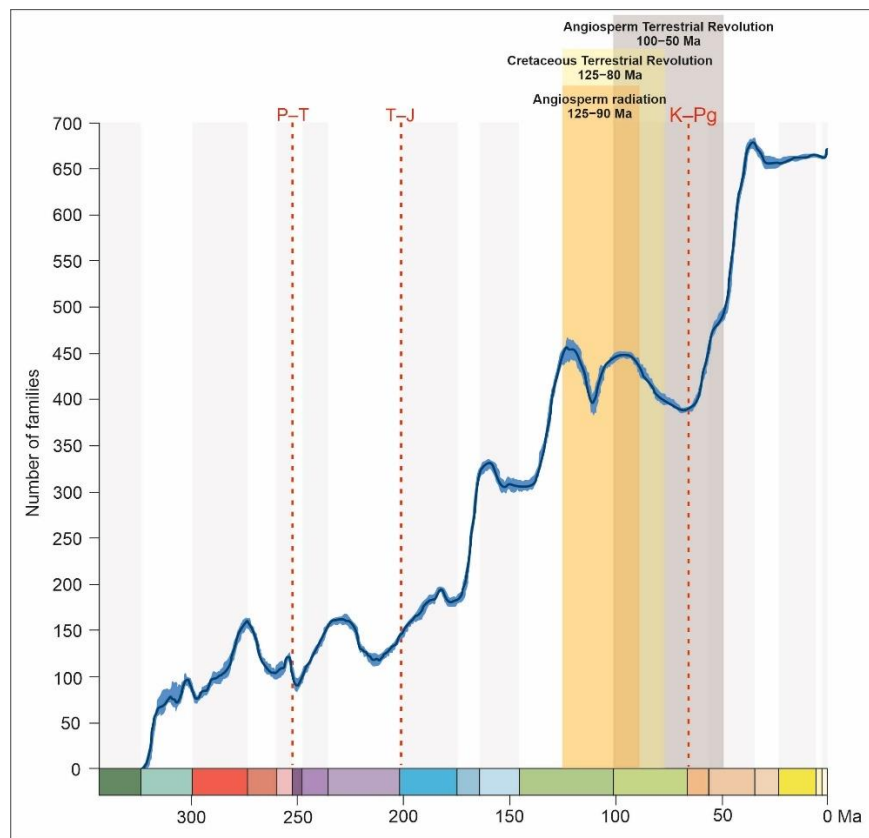
69 **Figure 1.** Different Cretaceous pollination modes described in Peris et al. (2017), showing different groups of insects
 70 under distinctive patterns of extinction, survival, and origination following the gymnosperm-angiosperm transition.
 71 The fossil pollination cases reviewed in Peris et al. (2020) and Peña-Kaitath et al. (in prep.). The period of angiosperm
 72 evolution is marked as Angiosperm Radiation (Labandeira, 2014), Cretaceous Terrestrial Revolution (Lloyd et al.,

73 2008), and Angiosperm Terrestrial Revolution (Benton et al., 2022). **A.** Diverse fossil community of Cretaceous
74 pollinators and the lifespan of these families. **B.** Representation of the transition from gymnosperm–insect pollination
75 to angiosperm–insect pollination with the transitional examples.

76

77 The great radiation of modern insect lineages started 245 Ma (Labandeira and Sepkoski,
78 1993; Rainford et al. 2014). Since the Jurassic, insect families showed low extinction rates
79 (Labandeira and Sepkoski, 1993; Jarzembowski and Ross, 1996; Condamine et al. 2016). Insect
80 family-richness peaked during the Early Cretaceous around 125 Ma, when angiosperms were still
81 rare (Claphman et al., 2016; Schachat et al., 2019). This peak occurred prior to extinctions within
82 early-diverging groups, in part linked to mid-Cretaceous floral turnover following the evolution
83 of flowering plants (Claphman et al., 2016; Condamine et al., 2020) (Figure 2). The Early
84 Cretaceous richness peak may therefore reflect a transitional period in insect evolution where
85 radiating extant families coexisted with early-diverging ones that are rare today or that became
86 extinct (Peris et al., 2014; 2020b; Nel et al., 2015; Claphman et al., 2016). The overlap between
87 insects that had specialized relationships with gymnosperms and insects that had specialized
88 relationships with angiosperms may have also contributed to the Early Cretaceous peak in insect
89 diversity (Peris et al., 2017; 2020b; Schachat et al., 2019).

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92 **Figure 2.** Insect family accumulation through time using the software PyRate and the family-level fossil dataset of
93 Condamine et al. (2016). Red dot lines indicate the Permian–Triassic (P–T), Triassic–Jurassic (T–J), and the
94 Cretaceous–Paleogene (K–Pg) mass extinction. The period of angiosperm evolution is marked as Angiosperm

95 Radiation (Labandeira, 2014), Cretaceous Terrestrial Revolution (Lloyd et al., 2008), and Angiosperm Terrestrial
96 Revolution (Benton et al., 2022).

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98 Here we reviewed the evidence on the origin of flowering plants and their related
99 pollinator insect lineages, and we tested the impact of angiosperm radiation on insect
100 diversification. We analysed the role that six different variables (diversity dependence,
101 angiosperms, gymnosperms, spore plants, continental fragmentation, and temperature) have on
102 diversification rates of insects (Figure 3).

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105 **Evolution of angiosperms**

106 Today angiosperms dominate most terrestrial ecosystems and provide an important part of the
107 food chain and niche requirements for many other organisms. Estimations indicate that flowering
108 plants represent about 90% of all land plants (embryophytes), which is around 300,000 living
109 species (Christenhusz and Byng, 2016). The present-day diversity of species and forms in
110 flowering plants have intrigued biologists for more than 150 years (Buggs, 2021). Their origin
111 was one of the most transformative events in Earth history (Figures 1–2). However, the age of
112 crown angiosperms remains highly uncertain (Sauquet et al., 2022), despite recent claims of more
113 definite answer to when exactly angiosperms originated and began to diversify (*e.g.*, Barba-
114 Montoya et al., 2018; Li et al., 2019; Silvestro et al., 2021). The stem age of angiosperms, their
115 divergence time from extant gymnosperms, is dated as 310–380 Ma depending on the study
116 (Clarke et al., 2011; Magallón et al., 2013, Silvestro et al., 2015, Nie et al., 2020). By contrast,
117 the morphological age of flowering plants, that is the age when they are morphology identifiable
118 in the fossil record, is not yet well understood, variously dated from 250–140 Ma (Sauquet and
119 Magallón, 2018).

120 The earliest fossil remains that can be assigned with high confidence to crown-group
121 angiosperms are tricolpate pollen grains from the Barremian–Aptian transition (121 Ma, Hughes,
122 1994), which states the morphological age of angiosperms. Oldest pollen exhibiting subsets of
123 definitive crown-angiosperm characters is known as far back as the Middle Triassic (237–247
124 Ma), but these are difficult to discriminate from pollen produced by stem-angiosperms or
125 gymnosperms (Doyle and Hotton, 1991; Coiro et al., 2019). Slightly younger Aptian floral
126 assemblages was followed by an explosive increase in diversity in the middle and Late Cretaceous
127 (Lidgard and Crane, 1988; Friis et al., 2011). The fossil record provides fundamental evidence on
128 the timescale and pattern of the origin and early evolution of angiosperms (Coiro et al., 2019).
129 This is what some authors interpreted as an explosive radiation from a Cretaceous crown-ancestor
130 (Benton et al., 2022). By contrast, there is a nearly universal molecular support for a pre-
131 Cretaceous origin of crown angiosperms (Barba-Montoya et al., 2018).

132 Differences between molecular results and fossil record when estimating the age of crown
133 angiosperms are not in conflict according to Sauquet et al. (2022), because both approaches rely
134 ultimately on data from the fossil record since molecular dating studies are fossil-calibrated, albeit
135 with different assumptions. Discrepancies between molecular clock and purely fossil-based
136 interpretations of angiosperm diversification may be explained by two possible causes. One
137 explanation suggests a long, cryptic evolutionary history of a non-ecologically significant group
138 of early angiosperms (Doyle, 2012). They probably lived in environments in which fossilization
139 was unlikely, resulting in an unrepresented fossil record. This idea is based on the early existence
140 of triaperturate grain, known in the eudicots, which originated much later than the angiosperm-
141 crown ancestor (Clarke et al., 2011). But this pollen character is also converging in
142 Schizandraceae (Friis and Pedersen, 1996). It means that the record of the stem-group and original
143 crown-group of angiosperms is still undiscovered, or at least unidentified. However, the
144 synchronous diversification of fossil pollen, mesofossils and macrofossils through the Early
145 Cretaceous would be difficult to explain if angiosperms had diversified cryptically for a
146 significant time interval (Herendeen et al., 2017). It seems unlikely that crown groups emerge and
147 keep an extensive period of hidden diversification. Instead, once they emerge, crown groups are
148 probed to diversify rapidly and should quickly enter the fossil record (Budd and Mann, 2020).
149 Thus, although early crown-group angiosperms may well have originated in the Jurassic (Coiro
150 et al., 2019), the radiation of core angiosperms may have begun in the Cretaceous (Budd et al.,
151 2021). An alternative explanation may be that molecular clock estimates are inaccurate with a
152 trend to overestimation (Barba-Montoya et al., 2018). Indeed, molecular dating methods are not
153 free from potential sources of bias (Beaulieu et al., 2015; Bromham et al., 2018; Budd et al., 2021;
154 Sauquet et al., 2022). However, it is technically possible to reconcile prior assumptions drawn
155 from the fossil record with fossil-calibrated molecular dating approaches, since fossil-calibrated
156 molecular dating analyses can be designed based on such prior assumptions of what crown
157 angiosperm age is (Budd et al., 2021; Sauquet et al., 2022).

158 The discussion is taking part while putative crown-angiosperm fossils from the Jurassic
159 of China (*e.g.*, Fu et al., 2018) have been consistently rejected (Herendeen et al., 2017; Bateman,
160 2020; Sokoloff et al., 2020). All these supposed crown groups of angiosperms described from
161 pre-Cretaceous time either represent other plant groups or lack features that might confidently
162 assign them to the angiosperms (Coiro et al., 2019). It is therefore likely that some seed plants
163 along the angiosperm stem-lineage from the Triassic and Jurassic possessed some, but not all, of
164 the features of crown group angiosperms. So far, however, the discrepancy remains, due to the
165 lack of undisputed pre-Cretaceous crown-angiosperm fossils (Herendeen et al., 2017).

166 Despite the uncertainty in the timing of the origin of crown-angiosperms, it seems clear
167 that the diversification of the major lineages of angiosperms occurred during the Late Cretaceous
168 (Magallón et al., 2015; Barba-Montoya et al., 2018; Li et al., 2019; Budd et al., 2021). From that

169 time, the fossil record reflects flowering plants to have risen to ecological dominance in terrestrial
170 communities up to the Paleogene (Silvestro et al., 2015; Ramírez-Barahona et al., 2020), along
171 with the origin of hyperdiverse biomes such as tropical rainforests (Carvalho et al., 2021). This
172 time does appear to coincide with a peak in the diversity of insects, including herbivores and
173 pollinators and their predators (Claphman et al., 2016; Schachat et al., 2019), corroborating the
174 hypothesis of the ATR — an explosive boost to terrestrial diversity occurred from 100–50 Ma,
175 the Late Cretaceous and early Palaeogene (Benton et al., 2022).

176

177 **Evolution of pollinators**

178 Assuming that a pollinator is an organism that moves pollen from the male anther to the female
179 stigma in flowers is simplistic. This statement faces two main problems. On one hand, insect
180 pollination (entomophily) is a process that occurs especially but not exclusively on flowering
181 plants. While around 85% of flowering plants are biotically pollinated (Ollerton et al., 2011),
182 around 40% of gymnosperms (including Cycadales and Gnetales) are also pollinated by insects
183 (Ickert-Bond and Renner, 2016; Toon et al., 2020). However, pollination requirements of most
184 gymnosperms and most wild plants are surprisingly unknown. On the other hand, if the definition
185 of a pollinator implies an active process, it would be difficult to find evidence of such a behaviour
186 from the fossil record, and when and how the pollination process evolved. The characters that a
187 fossil must meet to be considered a pollinator is still an open discussion (Peris et al., 2020; Peña-
188 Kairath et al., in prep.).

189 Organisms involved in the pollination process include iconic groups of Recent
190 pollinators, namely bees (Hymenoptera), long-proboscis butterflies (Lepidoptera), or many
191 different groups of beetles and flies (Coleoptera and Diptera, respectively). However, although
192 less significant in present times, some families in Thysanoptera, Hemiptera, Neuroptera,
193 Orthoptera and Blattodea have been proved to be pollinators of some plant groups (Ollerton et
194 al., 2017; Peña-Kairath et al., in prep.) (Figure 4). Within the extant insect orders, different extinct
195 groups in Neuroptera, Mecoptera and Diptera display long mouthparts and rostra adapted to
196 feeding on pollination drops of extinct gymnosperms and floral nectar (Khramov et al., 2020,
197 2022). It is interesting to note that all ancient representatives with long mouthparts are currently
198 extinct in Mecoptera and Neuroptera, and that Mecoptera, unlike Neuroptera, do not include
199 specialized-pollen feeders today. This indicates that any relationship with pollination in
200 Mecoptera corresponds to an ancestral behaviour. Finally, two fossil groups of insects have also
201 been cited as presumable pollinators in deep times (Peña-Kairath et al., in prep.): Permopsocida,
202 an insect order known from the early Permian but extinct during the mid-Cretaceous, for which
203 angiosperm pollen has been found in the intestines and in contact with the abdomen of a taxon
204 (Huang et al., 2016); and Alienoptera, an extinct group with described species since the Early
205 Cretaceous to the Eocene, for which a Cretaceous nymph has been described in contact with

206 gymnosperm pollen clumps (Luo et al., 2022). Fossils from the extant order Grylloblattodea and
207 the extinct orders Miomoptera and Hypoperlida have been described from early Permian
208 sediments, more than 270 Ma, with pollen grains in their guts (references in Peña-Kairath et al.,
209 in prep.), which suggests these organisms were likely consuming pollen at that time. However,
210 their pollination habit in these last cases is more dubious (Peña-Kairath et al., in prep.).

211 The fossil record together with phylogenetic studies show a scenario in which all the
212 extant and extinct orders of insects that include pollinators evolved well before the Early
213 Cretaceous (Figure 4). They show an origin that largely predates the diversification of crown
214 angiosperms, except for lineages of some flies, bees and long-proboscid butterflies
215 (Supplementary Information).

216

217 **Angiosperms evolved in a time of insect diversity peak**

218 A growing number of fossil insect taxa have been described pollinating different groups of plants
219 in the fossil record. All these fossil pollinators were described exclusively associated with
220 gymnosperms until the beginning of the Late Cretaceous, when a combination of both
221 gymnosperm and angiosperm hosts are found associated with the described fossils, but only
222 evidence of angiosperm host remain in more recent cases (Peris et al., 2020; Peña-Kairath et al.,
223 in prep.) (Figure 1). Entomophilous pollination is found to be common during the Cretaceous,
224 which is consistent with the diversification of the major groups of angiosperms around 100 Ma
225 (Barba-Montoya et al., 2018; Budd et al., 2021) and their rise to ecological dominance in
226 terrestrial communities in the late Cenozoic (Condamine et al. 2020; Ramírez-Barahona et al.,
227 2020).

228 Highly specialized pollination is evidenced in some groups of insects by the development
229 of suctorial feeding structures such as long-proboscid nectar-feeding mouthparts (Khramov et al.,
230 2020), described since the early Permian (Khramov et al., 2022). Such mouthparts are thought to
231 be used for feeding on pollination drops released on the micropyles of the ovules concealed inside
232 the gymnosperm strobili (Labandeira et al., 2007). It is not surprising that lineages with specific
233 adaptations were extinct together with their gymnosperm host when angiosperms turnover ancient
234 ecosystems, such as the long-proboscid Mecoptera, Neuroptera, and the zhangsolvid Diptera
235 (Figure 1). Plant diversity declined by 45% at the K/Pg boundary (Silvestro et al., 2015;
236 Condamine et al. 2020; Carvalho et al., 2021) probably exacerbated by pollinator specialization.
237 By contrast, other groups represent generalist feeding habit, such as mandibulate beetles, that
238 successfully transitioned from a gymnosperm- to angiosperm-dominated flora (Peris et al., 2017,
239 2020). With the beginning of the Cenozoic the long-proboscid Mecoptera and Neuroptera were
240 supplanted by Hymenoptera and Lepidoptera in the nectar-feeding niche (Khramov et al., 2020),
241 but already on angiosperms. All these cases correspond to different pollination modes covered in
242 Peris et al. (2017), showing different groups of insects under distinctive patterns of extinction,

243 survival, and origination following the gymnosperm-angiosperm transition (Figure 1). Wind
244 pollination probably evolved in angiosperms from insect pollination in response to pollinator
245 limitation and changes in the abiotic environment (Culley et al., 2002). Accordingly, insect
246 pollination is still considered as the initial pollination mode for angiosperms (Hu et al., 2008).

247 Growing evidence from molecular dated phylogenetics, fossil record of pollinator insects,
248 paleontological data on morphological features of plants and modelling of diversification
249 dynamics support the hypothesis that angiosperms evolved in a time of insect diversity peak
250 during the Early Cretaceous (Claphman et al., 2016; Schachat et al., 2019) (Figure 2). The
251 essential trophic machinery of insects was in place nearly 100 million years before angiosperms
252 appeared in the fossil record (Labandeira and Sepkoski, 1993). This high diversity represents a
253 true burst of origination (Schachat et al., 2019), including insect lineages with highly adapted,
254 pollination modes on gymnosperms (Peris et al., 2020; Khramov et al., 2020). That would mean
255 that gymnosperm pollinators were available for angiosperms when they evolved, predating the
256 first flowering plants (Labandeira, 2007; Peris et al., 2017, 2020; Khramov et al., 2020). However,
257 assuming that the fossil record might be biased and incomplete, flowers might have arisen earlier
258 according to molecular phylogenetics of plants. In addition, pollen and pollination-fluid-feeding
259 have evolved independently across more than a dozen of insect orders, and in hundreds of families
260 (Wardhaugh, 2015). Such an evolutionary convergence supports the hypothesis that it is relatively
261 easy for pollinivory to evolve from feeding on the spores of fungi, ferns and other spore plants
262 (Labandeira, 2000). The pre-Cretaceous diversity of insects that developed with non-angiosperm
263 plants might have constituted a supertramp by which adaptations arose when angiosperms
264 diversified and replaced gymnosperms by the end of the Cretaceous (Condamine et al. 2020).

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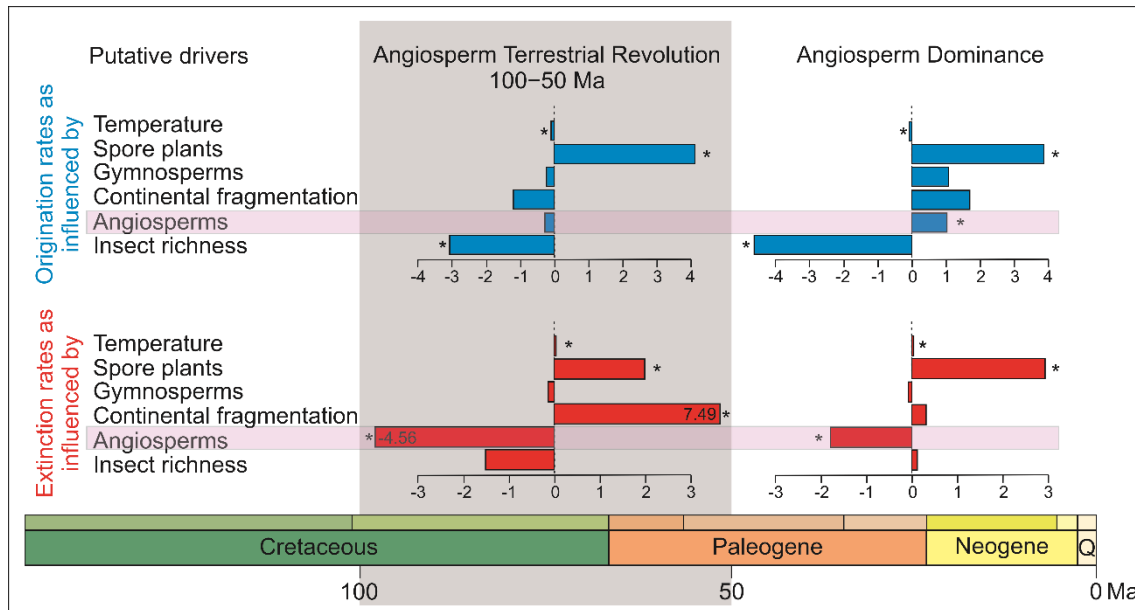
266 **Role of the Angiosperm Revolution on the insect diversification**

267 The apparent temporal gap between insect pollinators and crown angiosperms seems to question
268 the reciprocal diversification model, or coevolution between insects and flowering plants (Asar
269 et al., 2022). Relying on qualitative comparisons has limits, and there are little quantitative tests
270 to evaluate whether coevolution has spurred diversification between plants and insects. Here we
271 retrieved the family-level fossil dataset of Condamine et al. (2016) to estimate whether origination
272 and/or extinction rates varied through time and whether they could be correlated to the
273 angiosperm radiation. We relied on the Bayesian framework implemented in PyRate (Silvestro et
274 al., 2014, 2019) to simultaneously estimate correlations between diversification dynamics and
275 multiple environmental variables (Lehtonen et al., 2017). We focus on the role of angiosperms
276 but are aware that several drivers can have complementarily impacted the diversification of insects
277 (see *Methods* for details). We thus incorporated six variables: the number of insect family through
278 time (diversity dependence), the relative diversity of angiosperms, gymnosperms and spore plants

279 (Silvestro et al., 2015), the continental fragmentation (Zaffos et al., 2017), and the change in
280 temperature (Prokoph et al., 2008).

281 First, we estimated origination and extinction rates across the whole evolutionary history
282 of insects (*i.e.*, mid-Carboniferous to present), for which angiosperms were absent until the Early
283 Cretaceous. Our modelling results shows that, among the six tested variables, angiosperms
284 promoted a faster diversification of insects once they coevolved since the Cretaceous (Table 1a).
285 This remarkable link between insect origination with angiosperm radiation was most probably the
286 cause that drove the radiation of different groups of herbivores such as beetles (McKenna et al.,
287 2009; Ahrens et al., 2014; Doorenweerd et al., 2017) and pollinators such as bees and long-
288 proboscid butterflies since the mid-Cretaceous onwards (Cardinal and Danforth, 2013; Chazot et
289 al., 2019). In addition, we found that the rise of flowering plants generally not only drove the
290 origination of insect families, but they also buffer them against extinction (Table 1a). We then
291 performed the same diversification analyses but with rates only estimated for the time interval
292 covering the ATR (*sensu* Benton et al., 2022, from 100 to 50 Ma) and another set of analyses with
293 rates only estimated in the aftermath of the ATR (from 50 Ma to present). The ATR-centred
294 analyses indicated that the rise of angiosperms strongly decreased insect extinction rates during
295 the ATR but did not affect insect origination rates (Table 1b, Figure 3). The post-ATR analyses
296 indicated that the rise of angiosperms strongly increased insect origination rates and decreased
297 insect extinction rates, but lesser than during the ATR (Table 1c, Figure 3). Therefore,
298 angiosperms had a dual role that has changed through time with an attenuation of the extinction
299 in the Cretaceous and beginning of the Cenozoic and a driver of origination in the Cenozoic, from
300 50 Ma onwards.

301 It is also important to highlight, nevertheless, that the rise of angiosperms is not the only
302 driver with significant identified effect on insect evolution (Table 1, Figure 3). The analyses also
303 indicate that increasing insect diversity has slowed down origination rates in insects, which is line
304 with the role of diversity dependence. Spore plants are also found as a strong positive correlation
305 with both origination and extinction rates of insects, suggesting that higher spore plant diversity
306 spurred insect turnover; a result that would deserve further studies given the important effect in
307 our analyses (Table 1). Gymnosperms are never recovered as a significant driver in our analyses.
308 We also unveil that global temperature correlates negatively with origination and positively with
309 extinction, such that warmer climate led to lower origination and higher extinction in insects,
310 which partly corroborates previous results for invertebrates (Mayhew et al., 2008). Different
311 alternative hypotheses are also cited in the literature (*eg.* in Labandeira, 2014) but not covered in
312 this analysis, which is focused eminently on the angiosperm-insect pollinators coevolution.



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322 Triggers for the angiosperm success

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Figure 3. Correlation trends of different analysed drivers for origination (in blue) and extinction (in red) rates on insect diversity for the Angiosperm Terrestrial Revolution timeframe (100–50 Ma, Benton et al., 2022) and for the Angiosperm Dominance period (50–0 Ma). Data used in this representation is offered in the Table 1. Drivers from top to bottom are Global mean temperature (Temperature), Spore plant relative diversity (Spore plants), Gymnosperm relative diversity (Gymnosperms), Continental fragmentation, Angiosperm relative diversity (Angiosperms), and Insect family richness (Insect richness). Asterisks indicate significant correlations recovered with the MBD model (shrinkage weight >0.5 and 95% CI not overlapping with zero).

The vast current diversity of angiosperms has been ascribed to different innovations in their reproductive, vegetative and genomic biology, which presumably played a central role in their diversification and rise to ecological dominance (Vamosi and Vamosi, 2011; Sauquet and Magallón, 2018; Vamosi et al., 2018; Benton et al., 2022). These attributes were considered to provide reproductive superiority over non-angiosperm seed plants, favouring their evolution after their origin (Soltis et al., 2019). Although diversification rate shifts are caused by changes in both speciation and extinction rates, it is not trivial to find the causes of rate shifts in such a biological radiation.

Many of the morphological features thought to represent key innovations in angiosperms may not be the only, or even the primary, cause of diversification rate shifts. The trait and ecological shifts driving higher rates of diversification have not generally been the synapomorphies used by systematists to define the major clades of angiosperms, such as flowers, double fertilization, endosperm development, and seeds encased in fruits (Vamosi et al., 2018). Instead, intrinsic key innovations, extrinsic factors such as geography and environment, or trait–environment combinations are important drivers of diversification rates (Vamosi and Vamosi, 2011; Chaboureau et al., 2014; Bouchenak-Khelladi et al., 2015; Lagomarsino et al., 2016; O’Meara et al., 2016; reviewed in Vamosi et al., 2018; Simonin and Roddy, 2018; Roddy et al.,

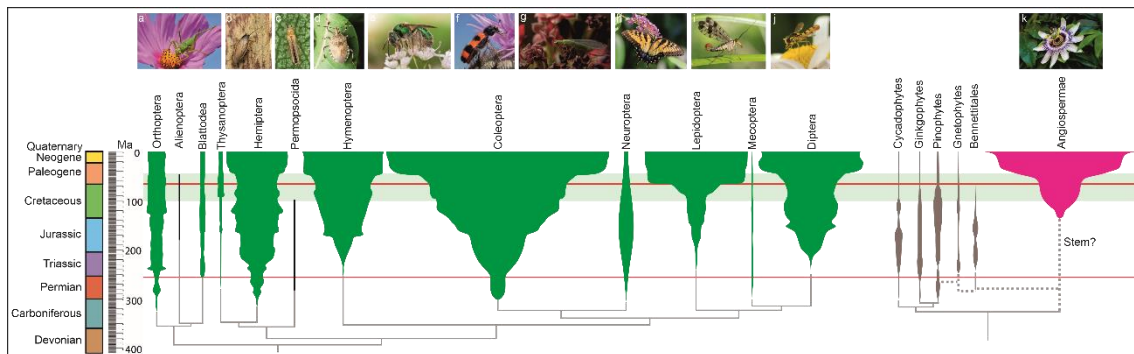
340 2020). Intrinsic key innovations include the whole-genome duplications event, named polyploidy,
341 shared by all living angiosperms; the ability to reduce genome size, that enabled the reduction of
342 the cell sizes; the herbaceousness, that is short generation time; maximizing photosynthetic
343 efficiency by the increase of venation and stomatal density into their leaves since ~100 Ma (see
344 references from above). Extrinsic factors can include patchy habitats, with habitat generalization
345 leading to decreased extinction, open habitats favouring diversification of lineages adapted to
346 such conditions, and island-like regions (including mountainous regions) increasing rates of
347 allopatric speciation.

348 Close associations of flowering plants with pollinator insects are particularly supposed to
349 have played an early role in angiosperm diversification (Crepet 1984; Grimaldi 1999; Hu et al.
350 2008; Van der Niet et al., 2014). This co-diversification seemed to be the result from a pollinator
351 transition of generalist pollen-feeding insects from gymnosperms to angiosperms (Labandeira et
352 al., 2007; Peris et al., 2017, 2020). However, this hypothesis was called into question because the
353 advantages offered by the gymnosperm pollinators did not prevent them from a decline (Crisp
354 and Cook, 2011; Condamine et al., 2020; Gorelick, 2001; Khramov et al., 2020) and no plants
355 other than angiosperms are diverse nowadays. Thus, it would be necessary to analyse the drivers
356 of diversification in angiosperms (O'Meara et al., 2016) using a similar approach that we applied
357 for insects here. While insect diversification was driven faster thanks to the coadaptation to
358 angiosperms, our analysis shows that the gymnosperms are not recovered as a significant factor
359 for the insect diversification (Table 1, Figure 3).

360 The rise of flowering plants through the Cretaceous, twice as productive as gymnosperms
361 (Boyce and Lee, 2017), was followed by new systems of chemical defense, tolerance to climatic
362 stress, and the (genetic) ability of certain angiosperm lineages to repeatedly evolve adaptive traits
363 (Onstein, 2020). Those facts, together with climate changes, breakup of Pangea, increase of humid
364 conditions during the Late Cretaceous (Chaboureau et al., 2014) and the global cooling at the end
365 of the Paleogene, have been linked to the decline in conifer diversity from the Cretaceous (the
366 last 110 Ma) and extended through the Cenozoic (Crisp and Cook, 2011; Condamine et al., 2020).
367 The rise of angiosperms induced an active displacement by outcompeting conifers (Condamine
368 et al., 2020), and caused conifers to have high extinction rates ever since (Crisp and Cook, 2011).
369 Faced with this situation, gymnosperm pollinators likely had little options, adapt or go extinct
370 depending on how specialized they were. The once diverse Cheirolepidiaceae and Bennettitales
371 went extinct around the K/Pg boundary, as did some highly specialized long-proboscid flies,
372 scorpionflies and lacewings related to these plants (Rothwell et al., 2009; Khramov et al., 2020).

373 Angiosperms did not achieve ecological dominance in a single step (Davies et al., 2004;
374 Magallón and Castillo, 2009; Onstein, 2020). They were still low-biomass components of most
375 Cretaceous floras (Carvalho et al., 2021). Rather, the appearance of various traits, the ability of
376 certain angiosperm lineages to repeatedly evolve them, clade-specific radiations (Sauquet et al.,

377 2017; Onstein, 2020; Ramírez-Barahona et al., 2020), and their link with insect diversification
378 likely spurred diversity in different groups following the K/Pg event (Carvalho et al., 2021). It
379 was in the aftermath of the K/Pg event that the diversification of angiosperms and of insects had
380 explosive impacts on each other through their species interactions (Asar et al., 2022), and only
381 then angiosperms achieved ecological dominance (Carvalho et al., 2021). The diversity and
382 dominance of crown-group angiosperm families and genera continued to rise in the Cenozoic,
383 accelerating insect-angiosperm co-diversification (Allio et al., 2021), evolving multiple lineages
384 of pollinating insects (Wiegmann et al., 2011; Sann et al., 2018; Chazot et al., 2019; Song et al.,
385 2020; Cai et al., 2022), driving to the ‘modernization’ of Earth ecosystems.
386



387
388 **Figure 4.** Evolution of the insect orders with extant and/or extinct pollinator representatives, gymnosperms and
389 angiosperms (flowering plants). Figure based on the “Tree of life” from the Museum of Natural History at the Oxford
390 University, courtesy from Dr. Ricardo Pérez de la Fuente. Each of the lineages shown in the tree is scaled to the
391 described number of extant species. Species’ recounts taken from the CoL (<https://www.catalogueoflife.org/>). Recent
392 groups spindles of insects extracted from Labandeira and Eble (2000) and of plants from Benton et al. (2022). As
393 Nicholson et al. (2015) showed, since 2000 the curve of insect diversity -based on families- through time has not
394 substantially changed. Smaller lineages are namely represented as a line. Phylogenetic relationships of insects extracted
395 from Misof et al. (2014), Beutel et al. (2017), and Giribet and Edgecombe (2019). Phylogenetic relationships of plants
396 extracted from Novikov and Barabasz-Krasny (2015). Divergence times obtained using the TimeTree website
397 <http://www.timetree.org/> except for the fossil insect orders Permopsocida (Huang et al., 2016) and Alienoptera (Luo et
398 al., 2022). The origin of the Gnetophytes and the extinct Bennettitalean plants is controversial. The TimeTree website
399 collates multiples papers dealing with divergence times and obtains an average. Red lines represent significant mass
400 extinctions. Green zone represents the Angiosperm Terrestrial Revolution after Benton et al. (2022). Royalty-free
401 images of insects and angiosperm on the top of the figure obtained from the website www.freepick.es: a. Orthoptera;
402 b. Blattodea; c. Thysanoptera; d. Hemiptera; e. Hymenoptera; f. Coleoptera; g. Neuroptera; h. Lepidoptera; i. Mecoptera;
403 j. Diptera; k. Angiospermae.

404

405 **Future considerations**

406 We still know little about the origins of entomophily and how it evolved, but theories regarding
407 pollination-plant coevolution always predict an increased probability of radiation of both plants
408 and the pollinating animals because of the mutualistic nature of the interaction (Gorelick, 2001).
409 However, it does not always hold. Coevolutionary processes should not be considered the only

410 major drivers of diversification in plants and insects (Suchan and Alvarez, 2015), which is
411 confirmed by our analyses indicating that global temperature, spore plants, and diversity
412 dependence are additional drivers to study for explaining insect diversity. For instance, warmer
413 global temperature drove higher origination and extinction in insects (Currano et al., 2016). Insect
414 pollination is not a guarantee of higher success. For example, cycads are insect pollinated and
415 have never been a diverse lineage (Condamine et al., 2015; Toon et al., 2020). By getting more
416 specialized, it also increases the pollination efficiency, providing a mechanism to explain the
417 boost in speciation rates (Citerne et al., 2010). However, specialization also increases the risk of
418 extinction rate with environmental upheavals. Under fluctuating conditions, plants that are
419 pollinated by specific animals will be more adversely affected than plants that are generally
420 pollinated by several species. Most of current biotically pollinated plants and their pollinating
421 animals are generalists (Waser et al., 1996), although insect pollinators that feed from and
422 pollinate a single plant species do exist (Gorelick, 2001; Toon et al., 2020). The angiosperm
423 extinction rates decreased after the K/Pg boundary in parallel to an increased speciation (Silvestro
424 et al., 2015), while the contrary is observed with the conifer diversity (Condamine et al., 2020).

425

426 **Conclusions**

427 The origin of angiosperms and their coevolution with potential pollinators remains enigmatic, but
428 significant progresses have been made in the last decade with fossil-based and phylogenetic
429 studies. Early diversification of angiosperms and their insect pollinators were largely decoupled
430 (van der Kooi and Ollerton, 2020; Asar et al., 2022). Pollinator insect lineages predated flowers
431 (Labandeira et al., 2007; Peris et al., 2020; Asar et al., 2022) (Figure 4). We also know that insect
432 family-richness peaked 125 Ma (Claphman et al., 2016; Schachat et al., 2019) (Figure 2), which
433 coincides with numerous pollinator lineages that were adapted to pollinate gymnosperms
434 (Labandeira et al., 2007; Peris et al., 2017; Peris et al., 2020). By contrast, most angiosperm
435 families (58–80%) originated between ~100 and 90 Ma, during the warmest phases of the
436 Cretaceous (Ramírez-Barahona et al., 2020). This is also the exact time when first angiosperm
437 pollinators are found in the fossil record (Peris et al., 2020; Peña-Kairath et al., in prep.).

438 Despite their time of origin, the rise to ecological dominance of modern-day angiosperms
439 was geographically heterogeneous and took place after a prolonged period, lasting until the
440 Palaeocene, concomitant with the onset of crown diversification in most families (Crisp and Cook,
441 2011; Ramírez-Barahona et al., 2020), and pushing different gymnosperm lineages to decline
442 (Condamine et al. 2020; Mazet et al., 2022). We have found that the flowering plant evolution
443 promoted a faster diversification of insects, not only driving the origination of insect families but
444 also buffering them against extinction since the mid-Cretaceous (Table 1, Figures 2–3).

445 Reducing the idea of angiosperm-pollinator co-evolution to a single period under the
446 analysis of being cause or consequence of each other (e.g., Khramov et al., 2020) may be an

447 excessive simplification. On one hand, there was a significant pool of gymnosperm pollinators
448 that might have been available for angiosperms since their beginning (Labandeira et al., 2007;
449 Peris et al., 2017; Peris et al., 2020). On the other hand, we found a link between the diversification
450 of angiosperms and insects, including the evolution of Late Cretaceous pollinator lineages such
451 as bees and butterflies (Sann et al., 2018; Chazot et al., 2019). Pollination is a very complex
452 system of mutualistic relationships that is necessary to be analysed in time, space and morphology
453 case by case (eg., Lavaut et al., 2022). Focusing on a single driver of increased diversification
454 seems to be a reductionist approach that will lead to incomplete explanations (O'Meara et al.
455 2016; Sauquet and Magallón, 2018). More likely, trait–environment combinations may spur
456 diversification affecting speciation and/or extinction rates (Bouchenak-Khelladi et al., 2015;
457 Lagomarsino et al., 2016; O'Meara et al., 2016; Freyman and Höhna, 2019).

458

459 **Methods**

460 *Fossil data and multivariate birth-death analyses*

461 We retrieved the times of origination and times of extinction for 1,527 families of which 671
462 extant and 856 extinct families, which have been estimated from 38,000+ fossil occurrences at
463 the family level (Condamine et al., 2016). To examine variations of insect family diversity
464 through time, we reconstructed the lineages-through-time using PyRate 3 (Silvestro et al., 2019)
465 and the input file of origination and extinction times of all insect families (*-lft 1* option).

466 PyRate has developed and implemented this birth-death model to test for a correlation
467 between speciation and extinction rates and changes in environmental variables (Lehtonen et al.,
468 2017). We used the Multivariate Birth-Death model (MBD) to assess to what extent biotic and
469 abiotic factors can explain temporal variation in speciation and extinction rates. Under the MBD
470 model, speciation and extinction rates can change through time, but equally across all lineages,
471 through correlations with multiple time-continuous variables, and the strengths and signs (positive
472 or negative) of the correlations are jointly estimated for each variable (Lehtonen et al., 2017). The
473 MBD model includes temporal fluctuations of environmental variables, so that the speciation and
474 extinction rates can depend on the variations of each factor. The correlation parameters can take
475 negative values indicating negative correlation, or positive values for positive correlations. When
476 their value is estimated to be approximately zero, no correlation is estimated. A Markov chain
477 Monte Carlo (MCMC) algorithm jointly estimates the baseline speciation (λ_0) and extinction (μ_0)
478 rates and all correlation parameters ($G\lambda$ and $G\mu$) using a horseshoe prior to control for over-
479 parameterization and for the potential effects of multiple testing. The horseshoe prior provides an
480 efficient approach to distinguishing correlation parameters that should be treated as noise (and
481 therefore shrunk around 0) from those that are significantly different from 0 and represent true
482 signal. We ran the MBD model using 50 million MCMC iterations and sampling every 50,000 to
483 approximate the posterior distribution of all parameters (λ_0 , μ_0 , ten $G\lambda$, ten $G\mu$, and the shrinkage

484 weights of each correlation parameter, ωG). We summarized the results of the MBD analyses by
485 calculating the posterior mean and 95% credibility interval of all correlation parameters and the
486 mean of the respective shrinkage weights (across ten replicates), as well as the mean and 95%
487 credibility interval of the baseline speciation and extinction rates.

488 The MBD model assumes that diversification rates vary continuously through time with
489 a given variable. However, it is possible that rates vary positively during a given time interval and
490 then negatively in another time interval (Neubauer et al., 2022). In other words, drivers of
491 diversification can vary over time. We thus tested whether the impact of angiosperm diversity
492 was similar over time, during the ATR (100-50 Ma, *sensu* Benton et al. 2022) and post-ATR (50-
493 0 Ma). The MBD analyses were thus performed with time constraints to estimate rates within this
494 time interval by setting up the *-maxT 100 minT 50* or *-maxT 50 minT 0* option to represent the
495 ATR timeframe and the post-ATR period, respectively.

496

497 ***Paleoenvironmental variables***

498 To identify putative mechanisms of insect diversification, we examined the correlation between
499 a series of past environmental variables and origination/extinction rates over their entire history.
500 We focused on the role of four paleoenvironmental variables, also called proxies, which have
501 been linked to biodiversity change. These proxies were classified as either abiotic or biotic
502 controls as follows: (i) *Abiotic controls*. Climate change (variations from warming to cooling
503 periods) is one of the most probable drivers of diversification changes throughout the history of
504 life (Erwin, 2009; Condamine et al., 2019). Major trends in global climate change through time
505 are typically estimated from relative proportions of different oxygen isotopes ($\delta^{18}\text{O}$) in samples
506 of benthic foraminifer shells. We merged $\delta^{18}\text{O}$ global temperature data from different sources
507 (Westerhold et al., 2020 for the Cenozoic; Veizer and Prokoph, 2015 for the rest of the
508 Phanerozoic) to provide $\delta^{18}\text{O}$ data spanning the full time-range over which insect families
509 originated. Second, global continental fragmentation, as approximated by plate tectonic change
510 over time, has also been proposed as a driver of diversity dynamics (Zaffos et al., 2017). We
511 retrieved the index of continental fragmentation developed by Zaffos et al. (2017) using
512 paleogeographic reconstructions for 1-million-year time intervals. This index approaches 1 when
513 all plates are not connected (complete plate fragmentation) and approaches 0 when there is
514 maximum aggregation. (ii) *Biotic controls*. Ecological interactions with rapidly expanding clades
515 are increasingly recognized as important macroevolutionary drivers (Condamine et al., 2020).
516 Insects experienced drastic floristic changes throughout their evolutionary history with the origin
517 and rapid radiation of angiosperms at the expense of a decline in diversity of gymnosperms and
518 ferns. The rise and dominance of angiosperms may have contributed to altering the dietary
519 regimes of herbivorous insects, which could in turn have affected insects that depend on
520 herbivores by a cascading effect. We thus compiled the relative diversity trajectories of

521 angiosperms, gymnosperms, and spore plants (mostly composed of ferns) based on previous
522 estimates of plant diversity (Silvestro et al., 2015). (iii) *Insect diversity*. Biotic interactions within
523 insects could also have influenced their diversification. For instance, we could draw hypotheses
524 of diversity dependence such that insects could either impact or be impacted by their own
525 diversity. In other words, the change in their diversity can affect their diversification as proposed
526 in diversity-dependent hypotheses. We thus included the paleodiversity of all insect families to
527 account for diversity dependence within insects as an independent variable.

528

529 **Figures**

530 Figures were created using CorelDRAW Graphics Suite software, version 19.0.
531 (www.coreldraw.com). Figure 2 was designed based on the results obtained after the data analysis
532 with the software R. Figure 4 was designed based on the “Tree of life” from the Museum of
533 Natural History at the Oxford University, courtesy from Dr. Ricardo Pérez de la Fuente.

534

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544

545 **Competing interests**

546 Authors declare that they have no competing interests.

547

548 **Data and materials availability**

549 All data are available in the main text or the supplementary information.

550

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853 **Table 1.** Results of the multivariate birth-death model applied to insects in three set of analyses. The table reports the mean and median posterior parameter estimates (and 95% credibility
854 interval, CI) for the parameters of the MBD model: baseline speciation (λ_0), extinction rates (μ_0) and correlation parameters ($G\lambda$ and $G\mu$) for each of the environmental drivers. Shrinkage
855 weights (ω) greater than 0.5 (highlighted in bold) indicating significant evidence for correlation (positive or negative depending on the respective $G\lambda$ or $G\mu$ value).
856

Parameters	a) Global insect diversification			b) Diversification during the ATR (100 to 50 Ma)			c) Diversification after the ATR (50 Ma to present)		
	Mean	Median	95% CI	Mean	Median	95% CI	Mean	Median	95% CI
Baseline origination rate λ_0	0.4907	0.3092	[0.1419, 1.196]	0.8383	0.3012	[0.0754, 3.278]	0.4248	0.1669	[0.0206, 1.0825]
Baseline extinction rate μ_0	4.8284E-3	4.5032E-3	[1.9721E-3, 8.4722E-3]	7.542E-3	6.6918E-3	[2.2163E-3, 0.0149]	4.7067E-3	4.4166E-3	[1.9018E-3, 7.9883E-3]
G λ Insect diversity	-5.0235	-4.9936	[-5.9243, -4.1341]	-3.0585	-3.0844	[-5.1351, -0.8334]	-4.6166	-4.6026	[-5.9835, -2.983]
G λ Angiosperms	0.8165	0.8283	[0.1442, 1.4328]	-0.3412	-0.2878	[-1.3542, 0.5499]	1.0401	1.0524	[0.1234, 1.9712]
G λ Continental frag.	2.1159	2.1251	[0.7511, 3.453]	-1.3638	-1.216	[-5.057, 2.2001]	1.695	1.7441	[-0.1398, 3.392]
G λ Gymnosperms	0.7459	0.7819	[-0.0773, 1.5622]	-0.3112	-0.2339	[-1.29, 0.4962]	1.0731	1.1089	[-0.0532, 2.3286]
G λ Spore plants	3.6681	3.6892	[2.9137, 4.3556]	4.0704	4.108	[3.0406, 4.9928]	3.8781	3.8383	[3.0373, 4.7885]
G λ Temperature	-0.0822	-0.0807	[-0.1097, -0.0564]	-0.0935	-0.0925	[-0.1368, -0.0469]	-0.0683	-0.0643	[-0.1125, -0.0159]
G μ Insect diversity	0.1455	0.0932	[-0.524, 0.9017]	-1.4949	-1.5064	[-3.1339, 0.2498]	0.164	0.1091	[-0.5198, 0.9159]
G μ Angiosperms	-1.8155	-1.7999	[-2.4776, -1.1818]	-4.5855	-4.5552	[-6.4712, -2.7859]	-1.8073	-1.7907	[-2.4664, -1.1584]
G μ Continental frag.	0.4273	0.3555	[-0.8756, 2.0666]	7.4912	7.486	[2.1141, 12.8511]	0.4049	0.313	[-0.8913, 2.0322]
G μ Gymnosperms	-0.1271	-0.0763	[-0.805, 0.5246]	-0.1786	-0.1251	[-0.9781, 0.4926]	-0.117	-0.0729	[-0.8323, 0.4772]
G μ Spore plants	2.887	2.8952	[2.1342, 3.6284]	1.9783	1.9942	[0.9419, 2.9952]	2.9128	2.921	[2.2031, 3.6651]
G μ Temperature	0.0335	0.0337	[0.0179, 0.0489]	0.0315	0.0318	[0.0144, 0.049]	0.0338	0.0339	[0.0183, 0.0487]
ω λ Insect diversity	0.9381	0.9551	[0.8172, 1]	0.8511	0.9029	[0.5166, 1]	0.9248	0.9472	[0.773, 1]
ω λ Angiosperms	0.5585	0.5763	[0.0881, 0.9999]	0.4305	0.392	[2.9613E-8, 0.9566]	0.6025	0.6449	[0.0957, 0.9997]
ω λ Continental frag.	0.4579	0.4197	[0.0435, 0.9816]	0.4203	0.3781	[1.0981E-7, 0.9498]	0.4007	0.3402	[3.0291E-7, 0.9413]

ω λ Gymnosperms	0.4432	0.405	[2.4415E-7, 0.9547]	0.3536	0.2545	[2.7701E-8, 0.941]	0.4942	0.507	[1.1021E-8, 0.9625]
ω λ Spore plants	0.861	0.8913	[0.6245, 1]	0.8851	0.9139	[0.6791, 1]	0.8712	0.9	[0.6482, 1]
ω λ Temperature	0.8783	0.9098	[0.6531, 1]	0.8978	0.9309	[0.6817, 1]	0.801	0.8729	[0.315, 1]
ω μ Insect diversity	0.3319	0.2344	[3.4958E-9, 0.9201]	0.6806	0.7705	[0.0725, 1]	0.3418	0.2428	[1.183E-7, 0.9353]
ω μ Angiosperms	0.7614	0.8017	[0.4099, 0.9999]	0.9264	0.9502	[0.7781, 1]	0.7592	0.7968	[0.4084, 1]
ω μ Continental frag.	0.2669	0.136	[1.7915E-8, 0.8964]	0.7439	0.8034	[0.2966, 1]	0.2667	0.1316	[7.8828E-12, 0.8947]
ω μ Gymnosperms	0.2797	0.1553	[3.1608E-8, 0.9049]	0.3161	0.1968	[2.8001E-10, 0.9324]	0.2744	0.1524	[5.2828E-8, 0.8987]
ω μ Spore plants	0.8145	0.851	[0.5176, 1]	0.7404	0.7845	[0.348, 1]	0.8195	0.8563	[0.5299, 1]
ω μ Temperature	0.6892	0.7259	[0.2751, 1]	0.6926	0.7342	[0.2646, 0.9998]	0.6846	0.7215	[0.2798, 0.9998]

857

858 **The following Supporting Information is available for this article:**

859 Supplementary Information – Origination of the insect pollinator lineages