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Title

Fossil and phylogenetic analyses reveal recurrent periods of diversification and extinction in dictyopteran insects

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Short running title

Extinction events in cockroaches and allies

25 ***Abstract***

26 Variations of speciation and extinction rates determine the fate of clades through time.
27 Periods of high diversification and extinction (possibly mass extinction events) can punctuate
28 the evolutionary history of various clades, but they remain loosely defined for many
29 biological groups, especially non-marine invertebrates like insects. Here, we examine
30 whether the cockroaches, mantises and termites (altogether included in Dictyoptera) have
31 experienced episodic pulses of speciation or extinction and how these pulses may be
32 associated with environmental fluctuations or mass extinctions. We relied on molecular
33 phylogeny and fossil data to shed light on the times and rates at which dictyopterans
34 diversified. The diversification of Dictyoptera has alternated between (1) periods of high
35 diversification in the Late Carboniferous, Early-Middle Triassic, Early Cretaceous, and
36 middle Paleogene, and (2) periods of high extinction rates particularly at the Permian-Triassic
37 boundary, but not necessarily correlated with the major global biodiversity crises as in the
38 mid-Cretaceous. This study advocates on the importance of analyzing, when possible, both
39 molecular phylogeny and fossil data to unveil diversification and extinction periods for a
40 given group. The causes and consequences of extinction must be studied beyond mass
41 extinction events alone to gain a broader understanding of how clades wax and wane.

42

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66 **Introduction**

67 The death of species, also known as species extinction, is a natural process, but today human-
68 driven decline of global biodiversity is dramatic and is eventually leading us to the sixth mass
69 extinction (Barnosky et al., 2011; Pimm et al., 2014; Ceballos et al., 2017). Yet, how lineages
70 face extinction and recover from it or not remains elusive. Mass extinction events draw much
71 attention because they resulted in dramatic species losses over very short times (Raup and
72 Sepkoski, 1982). Nevertheless, if more than 99% of all species that ever lived are now extinct
73 (Raup, 1992), these losses cannot be related to mass extinctions (Jablonski, 2002). Beyond
74 astronomic or anthropogenic events responsible for these biological crises, species extinction
75 is more commonly driven by interspecific competition, environmental changes, and
76 stochastic factors (Benton, 2009). These account for ‘background’ extinction, but we also
77 need to look at contrasts between mass extinctions to understand better the dynamics of
78 species extinction (Blois and Hadly, 2009; Harnik et al., 2012; Condamine et al., 2013).

79 Mass extinctions have punctuated the history of life, eliminating whole groups of
80 organisms while fostering the subsequent diversification of others (Raup and Sepkoski, 1982;
81 Alroy, 2010). These events caused, in less than one million years (Myrs), more than 75%
82 species loss (Raup and Sepkoski, 1982; Barnosky et al., 2011; Culshaw et al., 2019). Five
83 mass extinction events over the past 542 Myrs, often referred to as the ‘Big Five’, have been
84 identified (Raup and Sepkoski, 1982; Alroy, 2010): the Ordovician–Silurian extinction event
85 (~443 Myrs ago, ~86% species loss), the Late Devonian extinction event (~376–359 Myrs
86 ago, ~75% species loss), the Permian–Triassic (P-T) extinction event (~252 Myrs ago, ~96%
87 species loss), the Triassic–Jurassic (T-J) extinction event (~201 Myrs ago, ~80% species loss)
88 and the Cretaceous–Paleogene (K-Pg) extinction event (~66 Myrs ago, ~76% species loss).
89 However, those percentages of species lost are to be taken with caution because they do not
90 include some of the most diverse clades since the Late Carboniferous, and in particular

insects (Nel et al., 2010). For instance the T-J extinction event does not correspond to any visible mass extinction among this already hyper-diverse clade.

Insects have undergone multiple and contemporary ecological and evolutionary radiations as well as extinction events (Engel, 2015; Footit and Adler, 2018), resulting in at least one million species worldwide (Stork, 2018) and in a rich fossil record extending back to more than ~410 Myrs ago (Grimaldi and Engel, 2005; Garrouste et al., 2012). During their history, they have survived the most severe mass extinctions and evolved against the backdrop of radical alterations in terrestrial floras, continental rearrangements, and changes in key environmental parameters such as average global temperatures (Labandeira and Sepkoski, 1993; Mayhew, 2007; Rainford et al., 2014; Condamine et al., 2016). Yet, today, insect diversity tumbles: for example, between 1989 and 2016 in Germany, flying insect biomass has dropped in average by 76% (Hallmann et al., 2017). There is a consensus that insect diversity is strongly affected in many ecosystems (Sánchez-Bayo and Wyckhuys, 2019; Seibold et al., 2019; Simmons et al., 2019) and those population declines bring the question of how insects coped with preceding extinction events like mass extinctions.

Insects are thought to be resilient to mass extinctions. Except for the P-T event, the history of insect diversification reveals no clear evidence of mass extinction (Labandeira and Sepkoski, 1993; Condamine et al., 2016). At best, evidence is conflicting or equivocal. For instance, most fossil-based studies discovered a drop in diversity during the P-T mass extinction, but phylogenetic studies did not (Labandeira and Sepkoski, 1993; Condamine et al., 2016). The impact of other mass extinctions, such as the T-J or the K-Pg events, is even less obvious or not detectable at the family-level or above. Similarly, other clues, such as those drawn from morphological changes, also failed to identify an impact of the main biodiversity crises on insects (Nel et al., 2010; Rainford et al., 2016; Nel et al., 2018). To refine these results, different lines of evidence like phylogenies and fossils should be studied

together (Mayhew, 2007; Ksepka et al., 2014; Condamine et al., 2016). They provide two complementary windows for understanding the temporal variations in biodiversity and investigating what lies behind the dynamics of insect diversification.

Among insects, the Dictyoptera (mantises, cockroaches and termites; **Fig. 1**) is an ideal group to contrast background and mass extinction. The current knowledge on Dictyoptera allows investigating extinction, the most critical and controversial component of net diversification rates, for two main reasons (Rabosky, 2010; Beaulieu and O'Meara, 2015; Hagen et al., 2018). First, dictyopteran fossils and molecular phylogenies indicate these insects originated during the earliest Late Carboniferous (~310 Myrs ago, Zhang et al., 2013; Legendre et al., 2015), suggesting they experienced at least three known mass extinctions (i.e. 252, 201 and 66 Myrs ago) without disappearing, but the extent of the clades' extinction remains unknown. In other words, studying Dictyoptera allows investigating multiple mass extinction events to contrast with background extinction. Second, although not devoid of gaps and taxonomic issues (Nel et al., 2018), a large fossil record of dictyopterans is available (Grimaldi and Engel, 2005; Bechly, 2007). This should allow inferring a global diversification pattern across the evolutionary history of Dictyoptera. Finally, phylogenetic-based and fossil-based analyses can be confronted to identify their limits and complementarities (Sanmartín and Meseguer, 2016), as it has been done for insects as a whole (Condamine et al., 2016).

In this study we asked how extinction events influenced the diversification of Dictyoptera. Did dictyopteran insects suffer declines of diversity during periods of dramatic environmental changes or instead experienced pulses of speciation, for instance when other clades disappeared or new niches opened? To investigate these diversification dynamics, we relied on a molecular phylogeny to shed light on the time and rate at which modern dictyopterans attained their diversity. Molecular phylogenetic analyses of Dictyoptera have

resulted in a taxonomically well-sampled time-calibrated tree suited for examining their diversification dynamics until the early Cenozoic (Legendre et al., 2015). Time-calibrated trees inform us on historical extinction rates as they retain signatures of shifts in diversification (Nee et al., 1994; Harvey et al., 1994). Teasing apart speciation and extinction from phylogenies remains, however, challenging (Rabosky, 2010, 2016; but see Morlon et al., 2011; Beaulieu and O'Meara, 2015). To address this caveat, we also relied on the dictyopteran fossil record. We studied both types of data with Bayesian and maximum-likelihood birth-death models to estimate the past dynamics of speciation and extinction rates. We aimed at proposing a scenario for the macroevolutionary history of dictyopterans by examining whether the clade has experienced episodic pulses of speciation or extinction and how these pulses may be associated with environmental fluctuations or mass extinctions.

Materials and Methods

Time-calibrated phylogeny and fossil data for Dictyoptera

We used a recently published time-calibrated phylogeny of Dictyoptera including 762 extant species of the ~10,000 living dictyopteran species (Legendre et al., 2015; Stork, 2018). This phylogeny is built based on a molecular dataset comprising four mitochondrial genes (12S rRNA, 16S rRNA, and cytochrome c oxidase subunits I and II) and two nuclear markers (18S rRNA and 28S rRNA). Divergence times were estimated using a relaxed-clock approach, with the penalized likelihood method, coupled with 17 fossils, which were used as minimum age constraints on different nodes and a maximum age for the tree root (Legendre et al., 2015).

We studied the fossil record of dictyopterans using the data available in *Paleobiology Database* via the *FossilWorks* application (accessed on February 24, 2017; Clapham et al., 2016) and supplemented the matrix with recent fossil findings (e.g. Schubnel and Nel, 2019;

Zhao et al., 2019). We checked for fossil occurrences using the name ‘Dictyoptera’, and we specified the taxonomic criteria to look for family and genus names. Relying only on family names would be fraught with danger because some extinct families, supposedly related to Dictyoptera, are ill-defined and need to be investigated further. At the species level, the fossil record is equivocal because of a poor spatio-temporal distribution of fossil species and of numerous Paleozoic species unclearly described and/or based on very incomplete fossils. Combining family and genus level analyses limit these issues. We also used the geological stages and epochs as time unit.

Because phylogenetic affinities with stem Dictyoptera have been disputed (Prokop et al., 2014; Guan et al., 2016; Aristov, 2017a,b), we generated an additional dataset including Dictyoptera fossil occurrences as described above and the fossil occurrences of the putative sister lineage Paoliida. However, we did not include the previously thought sister lineage, Eoblattida, because *Eoblatta*, the type genus of the family Eoblattidae and the superorder Eoblattida, is considered as an Archaeorthoptera without any affinity to Dictyoptera (Schubnel et al., 2019). The fossil dataset is available in Appendix S1.

Bayesian analyses of the fossil record

We analyzed the dictyopteran fossil record using a Bayesian model to simultaneously infer (1) the times of speciation and of extinction for each taxon in the dataset, (2) the temporal dynamics of origination and extinction rates, and (3) the preservation of fossil taxa as implemented in PyRate (Silvestro et al., 2014). The preservation process infers the individual origination and extinction times of each taxon based on all fossil occurrences and on an estimated preservation rate, denoted q , and expressed as expected occurrences per taxon per Myrs. This approach uses as input data all fossil occurrences that can be assigned to a taxon, in our case fossil genera and families.

We followed the PyRate approach as developed in Silvestro et al. (2015) to study the long evolutionary history of vascular plants. This approach includes several modifications appropriate for the type of data and the aims of our study, which is mainly focused on variation in origination and extinction on a global scale and large temporal ranges. We used a homogeneous Poisson process (*-mHPP* option) of preservation (Silvestro et al., 2014). We also accounted for varying preservation rates across taxa using the Gamma model (*-mG* option), that is, with gamma-distributed rate heterogeneity (Silvestro et al., 2014). Because of the large number of occurrences analyzed and of the vast timescale considered, we used eight rate categories to discretize the gamma distribution (*-ncat 8* option) and accommodate the potential for more variability of preservation rates across taxa.

Furthermore, we dissected the birth–death process into time intervals (*-fixShift* option), which are defined either by the geological periods of the stratigraphic timescale (Gradstein et al., 2012) resulting in 18 time intervals, or by 10-Myrs bins resulting in 32 time intervals. We estimated origination and extinction rates within these intervals (*-A 0* option). We adopted this solution as an alternative to the algorithms implemented in the original PyRate that jointly estimates the number of rate shifts and the times at which origination and extinction undergo a shift (*-A 2* option, Silvestro et al., 2014). The estimation of origination and extinction rates within fixed time intervals improved the mixing of the MCMC and allowed us to obtain an overview of the general trends of rate variation throughout a long timescale (Silvestro et al., 2015). Both the preservation and the birth–death processes are modeled in continuous time and are not based on boundary crossings. Thus, the origination and extinction rates are measured as the expected number of origination and extinction events per lineage per Myrs. One potential problem in fixing *a priori* the number of rate shifts is over-parameterization. We overcame this issue by assuming that the rates of origination and

extinction are part of two families of parameters following a common prior distribution, with parameters estimated from the data using hyper-priors (Gelman, 2004).

We ran PyRate for 10 million MCMC generations on 10 randomly replicated datasets using the *extract.ages* function, which resamples the age of fossil occurrences randomly within their respective temporal ranges (Silvestro et al., 2014; e.g. a fossil from the Sinemurian stage would have an age fixed randomly between 190.8 and 199.3 Myrs for each replicate). After excluding the first 10% of the samples as a burn-in period, we combined the posterior estimates of the origination and extinction rates across all replicates to generate rates-through-time plots. Rates of two adjacent intervals were considered significantly different when the mean of one lay outside of the 95% highest posterior density (HPD) of the other, and conversely. We looked at the marginal posterior distributions of origination and extinction rates through the largest extinction events documented in geological history. In particular, we examined the diversification dynamics at three of the Big Five events: the P-T, the T-J, and the K-Pg boundaries (*sensu* Raup and Sepkoski, 1982). We focused on the magnitude of rate changes, their statistical significance and the uncertainty around those estimates.

Episodic process of phylogeny-based diversification

We investigated whether diversification dynamics correlate with dramatic changes in tectonic or climatic settings (e.g. Pangea break-up) or environmental changes (e.g. the Cretaceous rise of Angiosperms) or rapid mass extinction events (e.g. the Cretaceous-Paleogene event) using episodic birth-death models implemented in the R-packages *TreePar* 3.3 (Stadler, 2011) and *TESS* 2.1 (CoMET model, Höhna et al., 2016b; May et al., 2016). These methods relax the assumption of constant rates and can detect discrete changes in speciation (denoted as λ) and extinction (denoted as μ) rates concurrently affecting all lineages in a tree. Both approaches

estimate changes in diversification rates at discrete points in time, but can also infer mass extinction events, defined as sampling events in the past in which the diversity is reduced to a percentage of the pre-extinction diversity. Speciation and extinction rates can change at those points but remain constant within time intervals. The underlying likelihood function is identical in the two methods (Stadler, 2011; Höhna, 2015), but TreePar and TESS differ in the inference framework (maximum likelihood vs. Bayesian) and the method used for model comparison (corrected Akaike information criterion [AICc] vs. Bayes factors [BF]). In addition, TESS uses independent compound Poisson prior (CPP) to simultaneously detect mass extinction events and discrete changes in speciation and extinction rates, while TreePar estimates the magnitude and timing of speciation and extinction changes independently to the occurrence of mass extinctions (i.e. the three parameters cannot be estimated simultaneously due to parameter identifiability issues; Stadler, 2011).

TreePar analyses were performed using the '*bd.shifts.optim*' function that allows for estimating discrete changes in speciation and extinction rates and extinction events in under-sampled phylogenies (Stadler, 2011). Going backward in time, it estimates the maximum likelihood speciation and extinction rates together with the rate shift times $t = (t_1, t_2, \dots, t_n)$ in a phylogeny. At each time t , the rates are allowed to change and the phylogeny may undergo a sudden extinction event (when the option mass extinction [ME] is set to TRUE). TreePar analyses were run with the following settings: *start* set to 60 Myrs ago (to include the K-Pg event), *end* set to the group's crown age estimated by the dating analyses, *grid* set to 1 Myrs (evaluating a possible shift every Myrs), and *posdiv* set to FALSE to allow the diversification rate to be negative (i.e. allows for periods of declining diversity).

Contrary to studies that examined the diversification rates of groups from their origin to the present, we focused our study on investigating macroevolutionary rates from the clade origin to a given point in time following Meredith et al. (2011) and Kergoat et al. (2014).

Potential biases in diversification rate analyses are known for incomplete phylogenies (e.g. Cusimano and Renner, 2010; Brock et al., 2011), therefore our aim is to reveal a global diversification pattern and its dynamic over deep timescales, where we assume the tree is fully sampled and all the higher-level lineages are included in the tree (Legendre et al., 2015). Indeed the tree lacks most of the extant diversity of the group, and we thus have preferred to not study the Cenozoic diversification (pending more complete phylogenetic trees for Dictyoptera). Here we studied the whole diversification history of the Dictyoptera from the origin of the clade (*ca.* 325 Myrs ago) to 60 Myrs ago. Hence, we did not use a correction for incomplete sampling since it is virtually impossible to know how many lineages were alive 60 Ma.

We fitted the constant-rate birth-death model as the reference for further model comparison. We also applied five different diversification scenarios (containing one to five shift times) to the consensus time-calibrated tree and computed the log-likelihood (logL), the corrected Akaike information criterion (AICc) and Akaike weights (AIC ω) corresponding to each scenario. We performed a model selection based on the lowest AICc and highest AIC ω , but also using the likelihood ratio test (LRT, at $P < 0.05$) since TreePar models are nested. If the model with lowest/highest AICc/AIC ω was supported by LRT, it was considered the best. If it was not supported by LRT, the simpler model — with fewer parameters — was considered the best. Given the maximum likelihood estimates of the net diversification rate ($r = \lambda - \mu$) and turnover rate ($\epsilon = \frac{\mu}{\lambda}$), we can infer the speciation and extinction rates. We investigate the robustness of our results to the effect of phylogenetic and dating uncertainties by fitting the TreePar models over 100 time-calibrated trees (Legendre et al., 2015).

CoMET uses a reversible jump Markov Chain Monte Carlo (MCMC) algorithm to test the probability of rate shifts in speciation and extinction through time, comparing the probability of temporal rate shifts to no rate shifts using BF (May et al., 2016). We specified

initial speciation and extinction rates and estimated the number of rate changes and extinction events empirically as in TreePar. Contrary to TreePar, CoMET cannot be applied over a specific temporal range, and we thus fitted CoMET throughout the dictyopteran tree. We set a correction for incomplete sampling ($p=0.1$) but we only interpreted the results prior to 60 Ma. The initial rate shift prior and number of extinction rates prior were drawn from a CPP, and the new rates drawn from a lognormal distribution with the mean and standard deviation of the distribution based on empirically estimated hyperpriors. Hyperpriors were estimated based on initial MCMC runs under constant-rate models to center the priors of the rate shift parameters with those means and standard deviations. The number of expected rate changes and mass extinction events were drawn from a CPP with a mean of $\log(2)$ to constrain the complexity of the model and avoid inferring overly complex scenarios, and expected mass-extinction time set to 3, corresponding to the P-T boundary, T-J boundary and the K-Pg boundary. We condition on the survival of the lineage to the present. We set the initial extinction probability to 0.5, and the β distributed prior on survival probability had shape values of 2 and 10, which put most of the prior distribution over low values of survival (~ 0.15) while being wide enough to allow for less strict probabilities (up to 0.70). Independent MCMC analyses were run using a minimum effective sample size (ESS) of 200 as the stopping criterion. We used the diagnostics tools to assess the convergence of MCMC using Gelman-Rubin statistics.

To compare inferences between CoMET and TreePar, we performed another series of TreePar analyses allowing for mass extinction events (argument ME=TRUE, everything else being equal to the TreePar analyses above). We compared models with 0, 1 or 2 rate mass-extinction events in TreePar using the AICc, while BF comparisons were used to assess model fit between models with varying number and time of changes in speciation/extinction rates and mass extinctions in TESS.

Results

Origin and extinction of major dictyopteran lineages

For Dictyoptera *sensu stricto*, we assembled a fossil dataset at the family level comprising 2277 occurrences and a genus-level dataset including 2458 occurrences (more occurrences because several genera are not assigned to a family). The family dataset contains 45 extinct dictyopteran families and 16 extant families, while the genus dataset comprises 513 genera of which 442 are extinct and 71 are extant. With the fossil occurrences of the putative extinct sister lineage Paoliida, the family-level dataset includes 2450 occurrences for 16 extant and 71 extinct families, while the genus-level dataset comprises 2631 occurrences for 71 extant and 497 extinct genera.

The PyRate analyses on the family-level dataset estimate the origin of Dictyoptera in the Late Carboniferous (median = 324.02 Myrs ago, 95% HPD: 321.94 – 329.71 Myrs ago). Overall, the fossil record shows four main periods of clades' origins: in the Late Carboniferous, in the Early-Middle Triassic, in the Early Cretaceous, and in the middle Paleogene (**Fig. 2**). The PyRate analyses also bring insights into the origin of extant families, for instance Blaberidae at 94.77 Myrs ago (95% HPD 90.02 – 104.93 Myrs ago), Blattidae at 183.32 Myrs ago (95% HPD 175.66 – 197.43 Myrs ago), Ectobiidae at 127.98 Myrs ago (95% HPD 125.52 – 131.09 Myrs ago), Mantidae at 59.79 Myrs ago (95% HPD 56.01 – 79.52 Myrs ago), Mantoididae at 56.27 Myrs ago (95% HPD 48.24 – 80.42 Myrs ago), Mastotermitidae at 132.28 Myrs ago (95% HPD 129.54 – 137.16 Myrs ago), and Termitidae at 53.84 Myrs ago (95% HPD 49.26 – 56.80 Myrs ago). Based on the posterior samples of the ages of origin derived from all replicates, we computed the estimated parameter values (offset, scale and shape), which may be directly used for other studies as calibrations to date molecular phylogenetic trees using relaxed molecular clock models. The estimated

parameters and offset values are given following the parameterization used in BEAST or MrBayes (see **Table 1** for families, and Appendix S2 for genera), two popular programs for molecular dating. It is important to note that these ages predate those of the oldest fossil occurrences for each group because they reflect the use of all available occurrence data to model the preservation process while incorporating the uncertainties around the fossil ages. To our knowledge, we are not aware of any study using such parameters and offset values to estimate divergence times, however they can be useful for future dictyopteran phylogenetic studies.

The fossil record shows three main periods for the extinction of clades: in the Carboniferous-Permian boundary, at the Permian-Triassic boundary, and in the mid-Late Cretaceous (**Fig. 3**). Fourth and fifth, albeit lesser, extinction periods are recovered in the middle Permian and at the Jurassic-Cretaceous boundary. The Cenozoic witnessed the extinction of only three families.

Fossil-based diversification dynamics

Regardless of the time intervals (10-Myr-bins or geological epochs) used for the birth-death analyses of PyRate, a dynamic diversification pattern is inferred along the evolutionary history of Dictyoptera (**Fig. 4**; Appendix S3). The analyses based on the 10-Myr-bins bring more insights into the effect of mass extinctions. Dictyoptera had an early burst of speciation in the Late Carboniferous, followed by a sharp four-fold decrease of speciation in the Permian. The Permian period is characterized by high extinction rates, except in the mid-Permian, until the mass extinction 252 Myrs ago. The decrease of speciation associated with the increase of extinction results in a negative net diversification in the Permian, recovered at both taxonomic levels in all analyses (**Fig. 4**; Appendix S3).

The recovery after the mass extinction in the Early and Middle Triassic is characterized by a two-fold increase of speciation, with a decrease of extinction in the Middle Triassic at both the family and genus levels (rates of diversification became positive). The speciation rate significantly dropped to almost zero in the Late Triassic resulting in negative net diversification rate while approaching the Triassic-Jurassic extinction at the family level but not for genera (**Fig. 4**). The Early Jurassic has equal speciation and extinction rates resulting in a null net diversification (high turnover). While the PyRate analyses show a concomitant increase of speciation and decrease of extinction in the Middle Jurassic turning the net diversification to positive, the analyses further show a concomitant decrease of speciation and increase of extinction in the Late Jurassic indicating a negative diversification rate at the end of the Jurassic, a result supported by all analyses (**Fig. 4**; Appendix S3).

The Cretaceous period is divided in two contrasted speciation trends with the Early Cretaceous having speciation rates twice as high as the speciation during the Late Cretaceous; the latter potentially due to a lack of post-Cenomanian localities. Interestingly the extinction rate is low in the earliest and latest Cretaceous epochs but is very high in the mid-Cretaceous (**Fig. 4**; Appendix S3). Nonetheless, we find a difference between the analyses with 10-Myr-bins and geological epochs. The 10-Myrs-bins analyses reveal an important extinction period at the end of the Early Cretaceous (Albian-Aptian, 100 – 120 Myrs ago, **Fig. 4**), explained by a nearly null speciation rate and the highest extinction rate inferred thus resulting in negative net diversification (mean = -0.045, 95% HPD: -0.01 to -0.08). In contrast, with the analyses based on the geological epochs, net diversification rates were positive in the Early Cretaceous and became negative in the Late Cretaceous while approaching the K-Pg boundary (Appendix S3). Such discrepancy might be due to the fact that the Cretaceous (~80 Myrs long) is only divided into two epochs, and we unveil clear temporal variations of diversification rates within each epoch with the analyses using 10-Myrs-bins intervals.

Alternatively, the mid-Cretaceous represents an important turnover period for the entomofauna, but is not perceived in the marine invertebrate fossil record, probably because the data were only analyzed for the two Cretaceous epochs and not through eight time intervals as in our 10-Myrs-bins analyses.

A boom of origination in the Paleocene and Eocene with high net diversification rates characterized the Cenozoic dictyopteran diversification, but the Oligocene was a turnover period with null net diversification. We do not find substantial shifts in origination and extinction rates in the Neogene: net diversification rates are estimated to be close to zero (**Fig. 4**; Appendix S3).

The PyRate analyses allow inferring the times of origin and times of extinction (if the taxon is extinct) of each taxon in the fossil dataset. Summing the times of origin and times of extinction through time permits the estimation of the number of genus / family lineages through time (paleodiversity) for the group (**Fig. 5**; Appendix S4). The paleodiversity of the group has substantially fluctuated at both taxonomic levels: it shows the Late Carboniferous, the Middle Triassic, the Early Cretaceous, and the Paleogene as the main periods of taxonomic origination, and shows the Carboniferous-Permian boundary, the Permian-Triassic boundary, the Late Jurassic, and the middle Cretaceous as periods of clade extinction.

Including the fossil occurrences belonging to Paoliida does not alter the global diversification pattern of Dictyoptera. We estimate the same major periods of diversification and extinction and also a similar magnitude in the evolutionary rates (Appendix S5).

Phylogeny-based analyses

The episodic birth-death model of TreePar (with mass extinction disallowed) finds that a model with a single shift time best explains the diversification dynamics of the dictyopteran groups (**Table 2**). Applied to 100 dated trees, the analyses indicate that most of the trees

(81%) had a negative shift of diversification in the Maastrichtian (the last stage of the Late Cretaceous) or even at the K-Pg boundary (median age = 65.3 Myrs ago, **Fig. 6a**). The TreePar analyses do not find support for a diversification shift in deeper times (i.e. models with more shifts are not supported), although models with multiple shifts inferred diversification changes around periods of mass extinction (e.g. 248 Ma with the model including five shifts; **Table 2**).

We further find that this shift of diversification is not due to a mass extinction because the episodic birth-death model of TreePar (with mass extinction allowed) indicates that a model without mass extinction best fits to the diversification dynamics of Dictyoptera: $\Delta\text{AICc} = 6.06$ between a constant-rate model and a model including one mass extinction event, and $\Delta\text{AICc} = 12.17$ against a model with two mass extinction events. Applied to 100 dated trees, the analyses reflect the uncertainty around the estimate of a mass extinction, which could have occurred in three periods: the mid-Permian, the mid-Cretaceous, and the Maastrichtian, but with most trees suggesting an extinction event in the mid-Cretaceous (median age = 117.5 Myrs ago, **Fig. 6b**).

The TESS analyses (Appendix S6) show that diversification increased throughout the Paleozoic, and since the P-T boundary (highest net diversification) the dictyopteran diversification has slowed down drastically until the mid-Cretaceous (lowest net diversification). After the mid-Cretaceous, the diversification increased again, until it dropped abruptly to negative values in the Eocene-Oligocene (~35 Myrs ago). A high turnover is inferred all along the dictyopteran history with a peak in the mid-Cretaceous and the Eocene-Oligocene. Applying the CoMET model, a single possible mass extinction is detected in the mid-Permian but with Bayes factors < 6 (Appendix S7).

Discussion

Diversification and extinction events in Dictyoptera history

Estimated to date back to the Late Carboniferous or even before (Legendre et al., 2015; Evangelista et al., 2019), stem- and crown-Dictyoptera have faced three massive extinction events. How these events have affected their diversification dynamics has however rarely been investigated. It has even been questioned as to whether insects were impacted by mass extinctions (Labandeira and Sepkoski 1993; Mayhew, 2007; Condamine et al., 2016). Here we found that, like for many other organisms, the diversification dynamics of Dictyoptera has alternated between periods of high and low diversification, but these changes are not necessarily correlated with mass extinction events. Far from their misleading stereotypical image of invulnerable insects (Laurentiaux, 1959; Garfield, 1990; Appel, 1995), Dictyoptera have experienced periods of high extinction rates, sometimes resulting in negative net diversification and thus declines in diversity; a result supported by our phylogeny- and fossil-based approaches.

On the basis of the available data, we identified three main periods of diversification for Dictyoptera (i.e. Early Triassic, Early Cretaceous and Paleogene) and three main periods of extinction (i.e. early Permian, late Permian and mid-Cretaceous). The Early Cretaceous diversification seems to have concerned the insects as a whole (Schachat et al., 2019). Phylogeny-based inferences with TESS indicated a possible fourth extinction period in the Eocene-Oligocene, which we will not discuss because it might be due to a methodological artifact given the low sampling of extant species. These diversification and extinction periods conceal different situations that we were able to delineate analyzing phylogeny- and fossil-based results. We discuss below the most remarkable of those patterns and their putative underlying processes.

Dictyoptera diversified greatly during the Early Triassic, which is an epoch with a poor fossil record with only one important Anisian deposit (ca. 247 Myrs ago, Papier et al,

1994, 1996; Papier and Grauvogel-Stamm, 1995; Vršanský, 2010), while the Middle Triassic counts several deposits. This timing also corresponds to the rise of many modern lineages of other insects such as Acercaria and Holometabola (especially beetles, flies and wasps, Papier et al., 2005; Misof et al., 2014; Rainford et al., 2014; Condamine et al., 2016; Montagna et al., 2019). Likewise, during the Cretaceous, the high origination rates of Dictyoptera parallel the rise of most of the modern insect families, currently well-known through recent discoveries in early Cenomanian Burmese amber (Grimaldi and Engel, 2005; Rainford et al., 2014; Ross, 2019), while the high extinction rates match the fall of roachoid fossils, which are not related to crown-Blattodea (Schubnel, 2018). With high origination and extinction rates, the Cretaceous is a period of major turnover in dictyopteran lineages. Interestingly, the Cretaceous underwent drastic environmental changes including the shift in ecological dominance of terrestrial plants with the Angiosperm Revolution (Labandeira and Currano, 2013) and the Cretaceous Terrestrial Revolution (Lloyd et al., 2008). Rather than a mass extinction event, these environmental changes and their aftermath on biotic interactions might explain this period of high turnover in Dictyoptera.

We found a boom-then-bust pattern (boosts of origination followed by boosts of extinction) at the Carboniferous-Permian and P-T boundaries but also in the middle Cretaceous, three periods when diversification rates shifted from positive to negative, hence from expanding to declining diversity (**Fig. 5**). Among these declines, only the P-T boundary corresponds to a known mass extinction, which has been found in the insect fossil record as a whole (Labandeira and Sepkoski, 1993; Condamine et al., 2016) but not recovered in beetles (Smith and Marcot, 2015). The Carboniferous-Permian pattern matches the diversification of the mesophytic flora during the late Carboniferous – early Permian (Cleal and Cascales-Minana, 2014; Servais et al., 2019). It could also reflect the peak of the Late Paleozoic Ice Age that extended throughout the Carboniferous and early Permian (Qie et al., 2019), causing

changes in the entomofaunas. Alternatively, it could be artefactual and merely illustrate the effect of the push of the past, which posits that ancient clades that survived during a long time are more likely to have a slowdown of diversification. Indeed, a high rate of early diversification is a necessary condition for most clades to survive a substantial length of time (Budd and Mann, 2018). Dating back to the Late Carboniferous, a high rate for Dictyoptera is thus expected at this epoch.

Finally, Dictyoptera underwent an extinction event at the end of the Early Cretaceous at the boundary of the Aptian and Albian (~115 Myrs ago), which does not correspond to a mass extinction event. Strikingly, both phylogeny- and fossil-based analyses recovered the signal of this extinction event. A high extinction rate during the Aptian and Albian stages has already been observed in insects (Labandeira, 2005). Different underlying reasons have been postulated, the most convincing being a change and increase in angiosperm food resources as a trigger of clade extinction through competition (Labandeira, 2005). During the Aptian-Albian, the angiosperms (aquatic and strictly terrestrial) began to be quite frequent in sedimentary deposits with numerous fossils with exceptional preservation, and a high diversity in many clades (i.e. konservat lagerstätten) like the Crato Formation in Brazil (Martill et al., 2007). In beetles, families of Polyphaga thrived during this period, while non-Polyphaga families experienced high extinction rates and diversity declines (Smith and Marcot, 2015). Beyond the causes that our study cannot decipher, our results confirm that this period has been critical for several insect groups, be they detritivorous like most Blattodea or carnivorous like Mantodea that underwent an important diversification at that time (Delclòs et al., 2016). The Aptian-Albian is also the period of the first known diversification of the eusocial ‘lower’ termites (mastotermitid- and hodotermitid-like taxa, and Kalotermitidae, Engel et al., 2009; Zhao et al., 2019).

Although these results must be considered in light of the heterogeneity of the fossil record (see below), they suggest that Dictyoptera, and likely other insects, have not been impacted as heavily as other organisms by mass extinction events (Labandeira and Sepkoski, 1993; Condamine et al., 2016). This agrees with, for instance, both a steady diversification of insect mouthparts (diets) for which no massive extinction events have been revealed (Nel et al., 2018), and with the origin of major innovations (e.g. diets, wings, metamorphosis) that did not parallel main era or period transitions (Rainford and Mayhew, 2015). A noticeable exception for Dictyoptera is the K-Pg transition. This crisis matches the main shift of diversification in Dictyoptera (**Fig. 6a**), with the rise of the first eusocial Dictyoptera, the termites, that were already quite diverse during the Cretaceous (Engel et al., 2009; Legendre and Condamine, 2018). However, there could be a bias around the K-Pg crisis because the insect fossil record for the Maastrichtian remains poorly studied, hence potentially leading to some uncertainty in the timing of these changes. But, apart from this exception, mass extinctions in insects seem to have played a lesser role than biotic interactions, which deserves further studies (Labandeira and Currano, 2013).

Fossil record, phylogeny and the study of extinction

Estimating extinction rates is a major hurdle to the study of the clades' diversification dynamics, especially from molecular phylogenies of extant species (Rabosky, 2010; Quental and Marshall, 2010; Morlon et al., 2011; Beaulieu and O'Meara, 2015; Rabosky, 2016; Hagen et al., 2018). To overcome this difficulty, fossils have a key role (Quental and Marshall, 2010; Fritz et al., 2013). Indeed, fossils are direct evidence of the diversification processes and they contribute to improve our estimates and understanding of the role of extinction during life history (Wagner and Lyons, 2010). However, two general issues may influence any diversification analysis: (i) the fossil record is biased and incomplete (Kidwell

and Holland, 2012), and (ii) the taxonomic ranks used to perform diversification studies may impact the outcomes of the analyses.

Notorious gaps in insect fossil records exist (Nel et al., 2018). The main Lagerstätten for insects are not spread homogeneously over geological time (e.g. Smith and Marcot, 2015; Clapham et al., 2016). A major “Hexapod gap” is known from the Early Carboniferous, which hinders our understanding of the first winged insects (Nel et al., 2013), whose origin remains unclear (e.g. decrease of atmospheric oxygen level, rarity, or preservation artifacts – Retallack, 2011; Schachat et al., 2018). The lack of a rich fossil record in the late Permian, Early Triassic, Early Jurassic, and latest Cretaceous (Nel et al., 2018) might blur the diversification dynamics of Dictyoptera. Conversely, the rich fossil record in the Paleogene, mostly due to Eocene Baltic ambers, might lead us to overestimate origination rates at this time. Rich Paleocene outcrops like Menat (60 Myrs ago, France) remain to be studied. However, in the case of PyRate, simulations confirm the absence of consistent biases due to the incompleteness of the data in the fossil record (Silvestro et al., 2014). Incomplete taxon sampling appears to have fewer problematic effects on the estimation of speciation and extinction rates because, in contrast to molecular phylogenies (e.g. Cusimano and Renner, 2010; Brock et al., 2011), removing a random set of taxa does not affect the observed occurrences of other lineages (Silvestro et al., 2014; 2019). We estimated a substantial extinction effect of the P-T event in the fossil-based analyses, a result not found with phylogeny-based analyses. Although filling gaps in the fossil record is a primary objective to better understand insect evolution, we identified changes in the diversification dynamics of Dictyoptera with this incomplete fossil record, changes we were unable to measure with the phylogeny-based analyses of this study. In parallel, molecular phylogenies of Dictyoptera are now in their genomic era (Evangelista et al., 2019), with termites (Bourguignon et al., 2017) and cockroaches (Bourguignon et al., 2018) being more and more sampled and sequenced,

resulting in unprecedented topological resolutions. Applying phylogeny-based diversification models to future dated dictyopteran phylogenies would allow revising our results.

We also found that family-, genus- or species-level diversification analyses of the fossil record differ in their advantages and drawbacks. A species-level analysis of the fossil record would seem the most appropriate, but because of biases in the insect fossil record and the few specimens per species (most fossil species are known from singletons), we risk deriving wrong conclusions. Genus- and family-level analyses are less prone to these issues. They have commonly been used to estimate insect diversification (Labandeira and Sepkoski, 1993; Clapham et al., 2016; Condamine et al., 2016), but have other limitations. For Dictyoptera, family-level analyses are questionable because several families were not defined according to accurate synapomorphies and are most likely para- or polyphyletic (e.g. Mesoblattinidae, Blattulidae). All of the Paleozoic dictyopteran families have never been revised under a phylogenetic perspective and are mainly based on unpolarized wing venation characters subject to important intraspecific variations (see Schneider, 1983, 1984). Counting non-monophyletic entities is dubious for deriving any evolutionary conclusion. This problem is, however, less significant at the genus level. Here, the importance of this effect was downplayed by running analyses at both the family and genus levels.

Despite unavoidable limitations inherent to infer diversification dynamics with phylogenies or fossils, we are confident that the recent methodological developments (e.g. the birth-death chronospecies (BDC) model in Silvestro et al., 2018) will continue improving the estimation of speciation and extinction rates thanks to joint analyses of fossils and phylogenetic data.

Conclusion

In this study, using both the fossil record and molecular phylogeny coupled with state-of-the-art diversification models, we show that Dictyoptera have experienced alternative periods of high and low diversification, but instead of massive extinction events (except at the end of the Permian), other factors might have played key roles. We thus deemphasize the importance of mass extinction events in the diversification dynamics of dictyopteran insects. We rather underline that the causes and consequences of extinction must be studied beyond mass extinction events alone to gain a broader understanding of how clades wax and wane. With the current biodiversity crisis where thousands of species face extinction (Régnier et al., 2015; Ceballos et al., 2017; Sánchez-Bayo and Wyckhuys, 2019; Simmons et al., 2019; Seibold et al., 2019), such general knowledge is urgent and critical.

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Figure legends

Figure 1. Images of extant and extinct species of praying mantises, cockroaches and termites.

(a) An unidentified fossil mantis from Cretaceous amber of Myanmar (© Wikimedia commons). (b) *Paratithrone royi* Lombardo, 1996 (© S. Hugel). (c) †*Etolblattina klebsi* Meunier, 1921 (© G. Doitteau – type specimen MNHN.F.R51484). (d) *Notolampra punctata* (Saussure, 1873) (© S. Hugel). (e) Fossil termite †*Meiatermes bertrani* Lacasa Ruiz and Martínez-Delclòs 1986 from Cretaceous of Spain (© Wikimedia commons). (f) A physogastrous queen with a worker of an unidentified termite species (© F. Legendre).

Figure 2. Estimated times of origin (crown ages) for dictyopteran families. Bold names are extant families. The four main periods of origination are in shaded grey in the background. The distributions were obtained from modeling the preservation process in PyRate and after combining 10 replicated analyses to incorporate the uncertainties around the ages of the fossil occurrences. The time of origin of Dictyoptera (not shown here) was 324.02 Myrs ago (95% HPD: 321.94 – 329.71 Myrs ago). These distributions (Table 1) can be directly implemented as calibration priors for dating the phylogenies of these clades using Bayesian relaxed molecular clocks. The parameterization provided here follows that implemented in popular molecular dating approaches. Asterisks indicate the illustrated families with pictures of *Parastylotermes krishnai*, *Lithoblatta lithophila*, and *Parvifuzia peregrina* from © Wikimedia commons. Abbreviations: Ng = Neogene.

Figure 3. Estimated times of extinction for dictyopteran families. Bold names are extant families. The three main periods of extinction are in shaded grey in the background. The distributions were obtained from modeling the preservation process in PyRate and after combining 10 replicated analyses to incorporate the uncertainties around the ages of the fossil

occurrences. Asterisks indicate the illustrated families with pictures of *Parastylotermes krishnai*, *Lithoblatta lithophila*, and *Parvifuzia peregrina* from © Wikimedia commons. Abbreviations: Ng = Neogene.

Figure 4. Fossil-based diversification analysis of dictyopteran families (a) and genera (b).

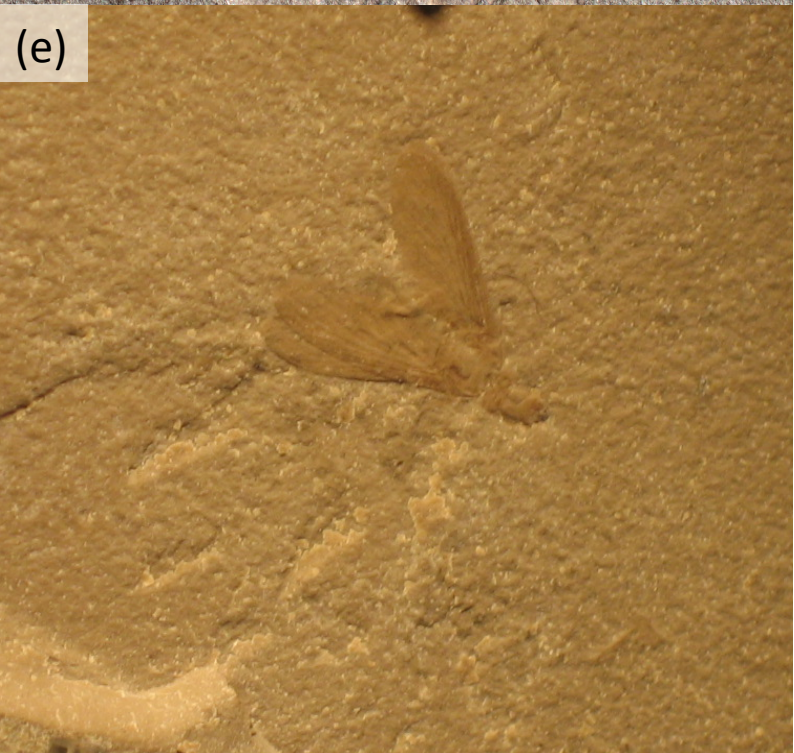
Origination (blue), extinction (red), and net diversification (grey) rates were estimated using the Bayesian approach implemented in PyRate with time shifts defined every 10 million years (results with time shifts defined by epochs of the geologic timescale are shown in Appendix S3). Solid lines indicate mean posterior rates, whereas the shaded areas show 95% credibility intervals. The vertical dashed lines indicate the major mass extinction events: at the Permian–Triassic (P-Tr), Triassic–Jurassic (Tr-J), and Cretaceous–Paleogene (K-Pg) boundaries. C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Pg, Paleogene; Ng, Neogene.

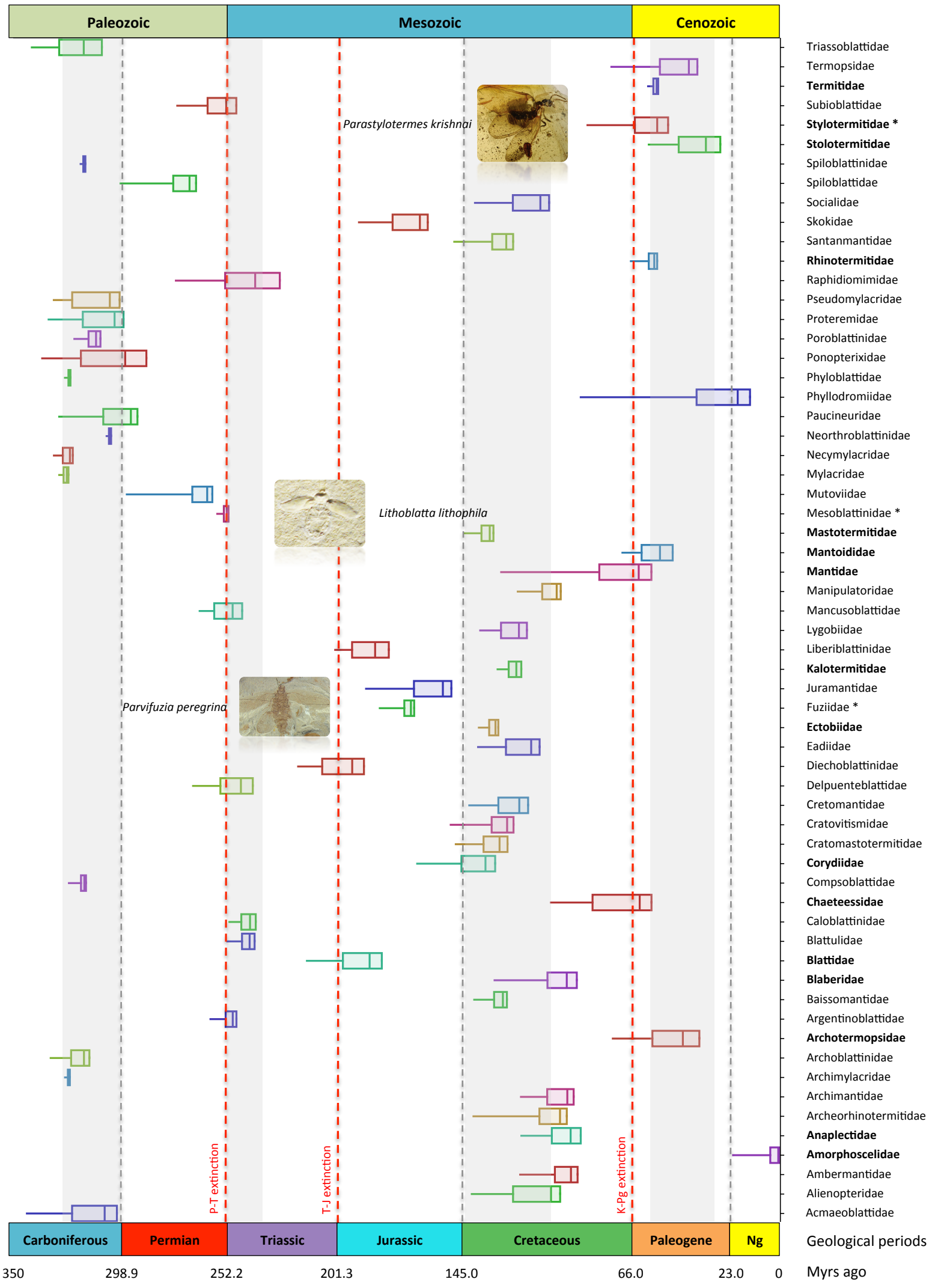
Figure 5. The paleodiversity trajectories of dictyopteran families (a) and genera (b).

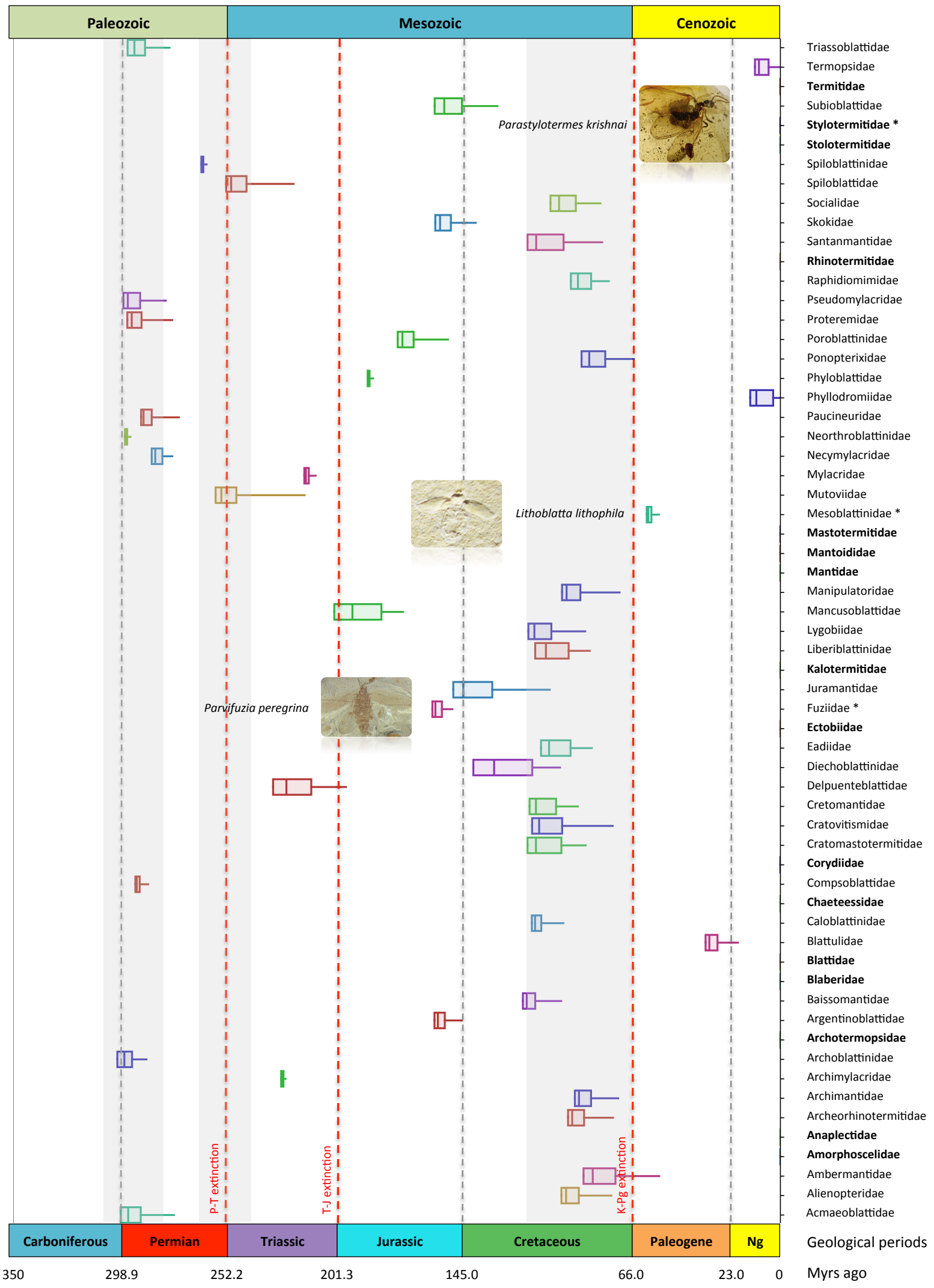
Reconstructions of diversity trajectories are based on times of origin and times of extinction of each taxon, and are replicated 10 times to incorporate uncertainties around the age of the fossil occurrences (results with time shifts defined by epochs of the geologic timescale are shown in Appendix S4). The vertical dashed lines indicate the major mass extinction events: at the Permian–Triassic (P-T), Triassic–Jurassic (T-J), and Cretaceous–Paleogene (K-Pg) boundaries.

Figure 6. Phylogenetic diversification dynamics of Dictyoptera inferred with time-dependent models. (a) Episodic birth-death models in TreePar identified a significant negative shift of diversification at the K-Pg boundary. The TreePar model estimated a

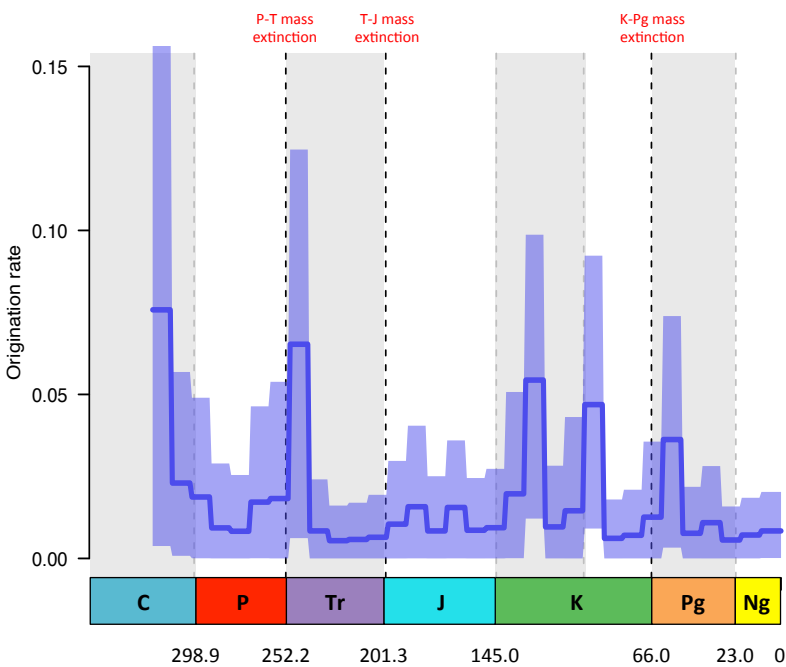
940 decrease in diversification after the K-Pg (Table 2). (b) Mass extinction models in TreePar
941 recovered a possible (not significant) mass extinction event in the mid-Cretaceous (similar
942 results obtained with CoMET, Appendix S7). The histograms show the uncertainty around
943 the timing of the shift time (a) and mass extinction event (b) based on the estimates over 100
944 trees with TreePar (the red lines show the median age of shift and mass extinction). C,
945 Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; Pg, Paleogene; Ng,
946 Neogene.
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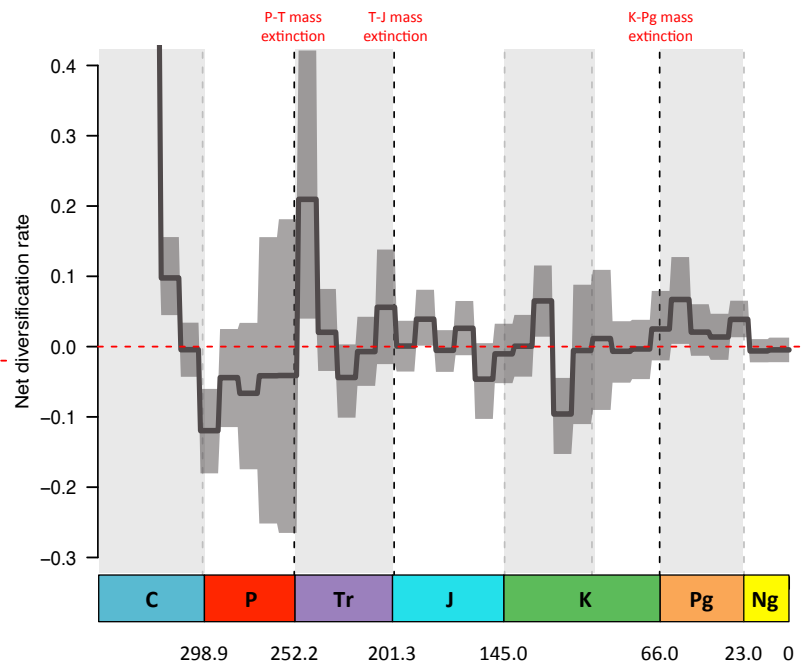
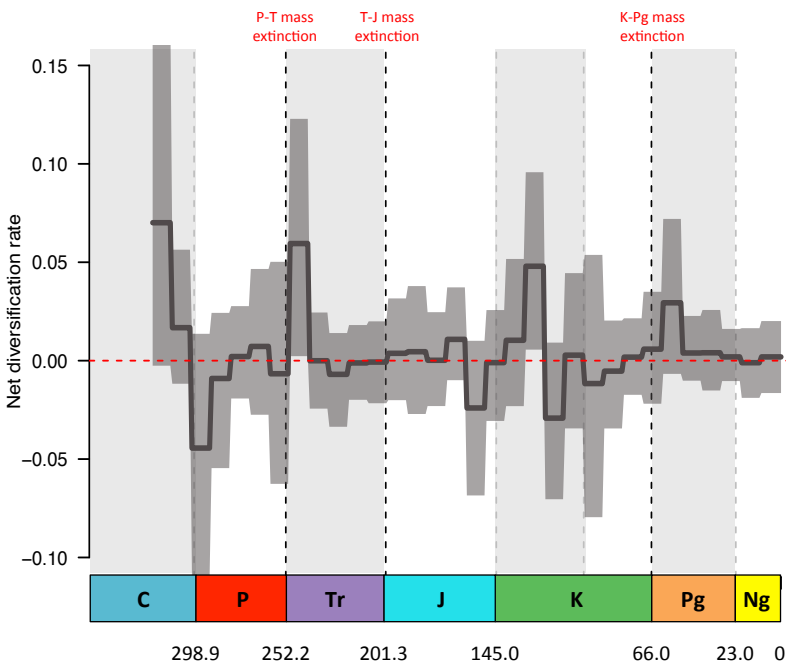
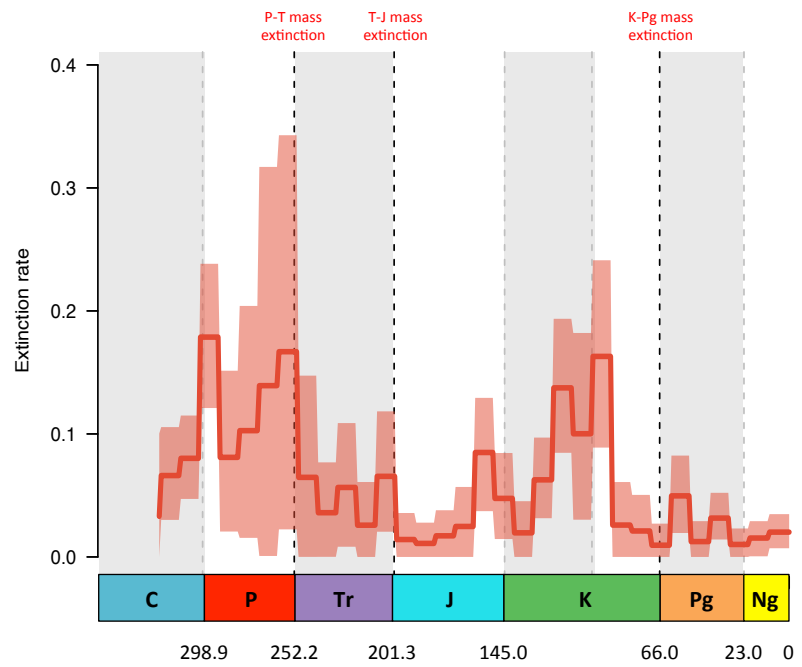
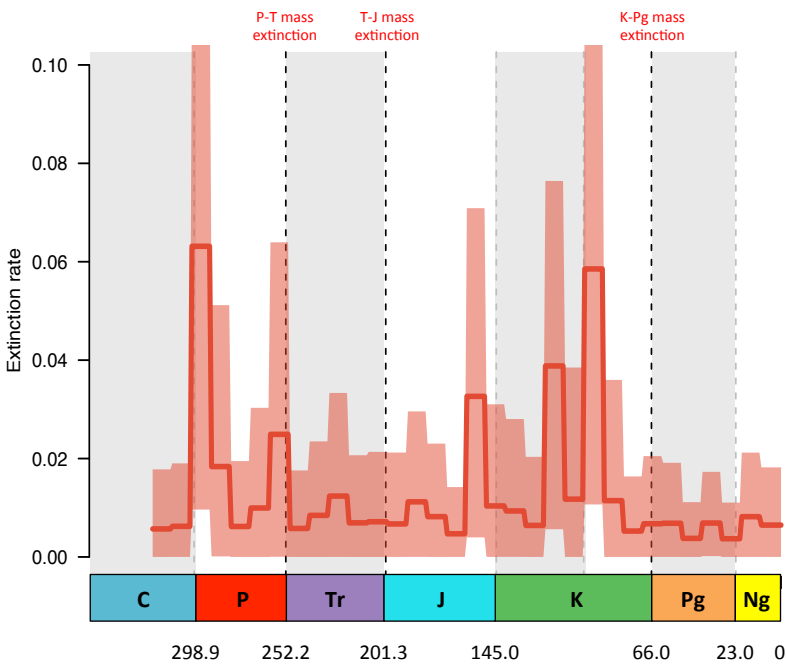
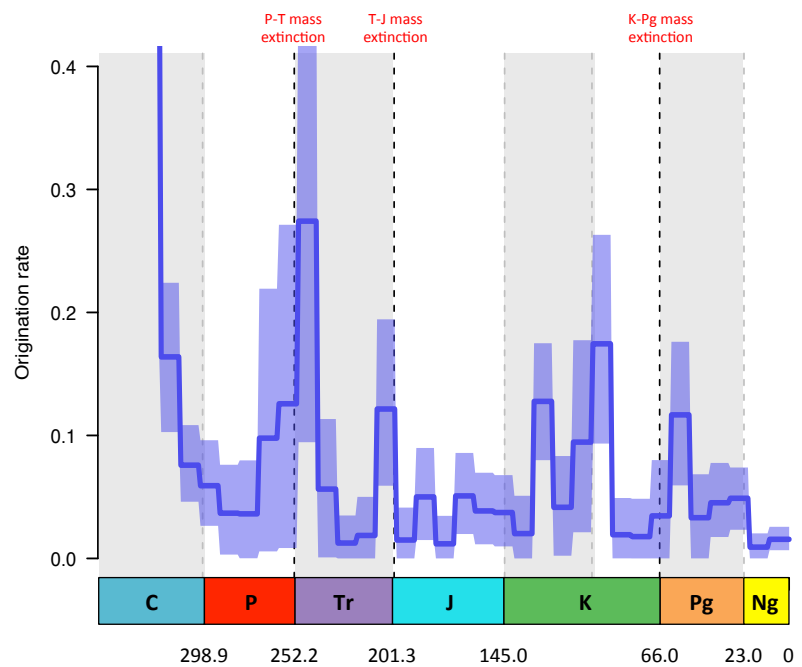


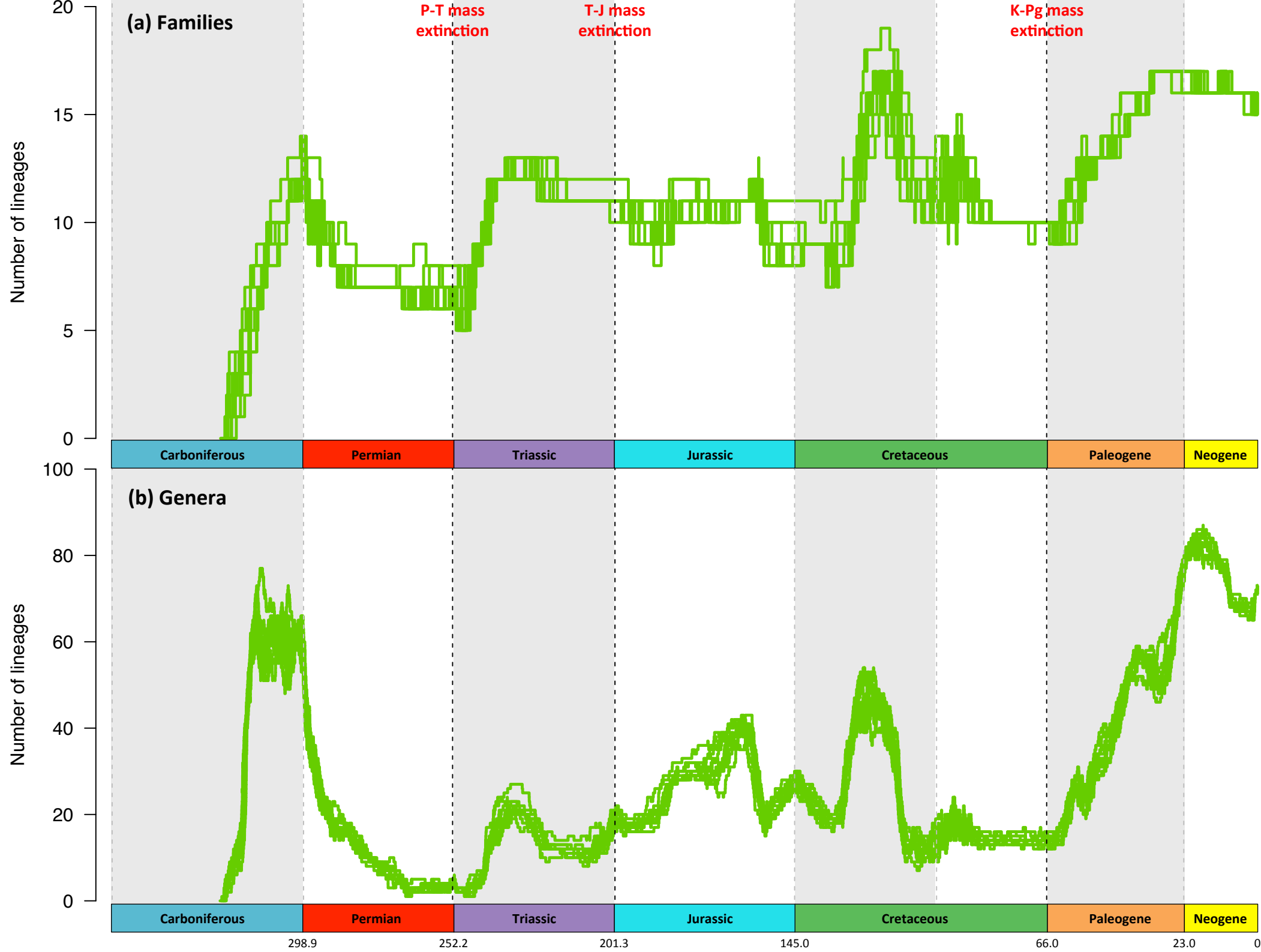


(a) Diversification dynamics of dictyopteran families

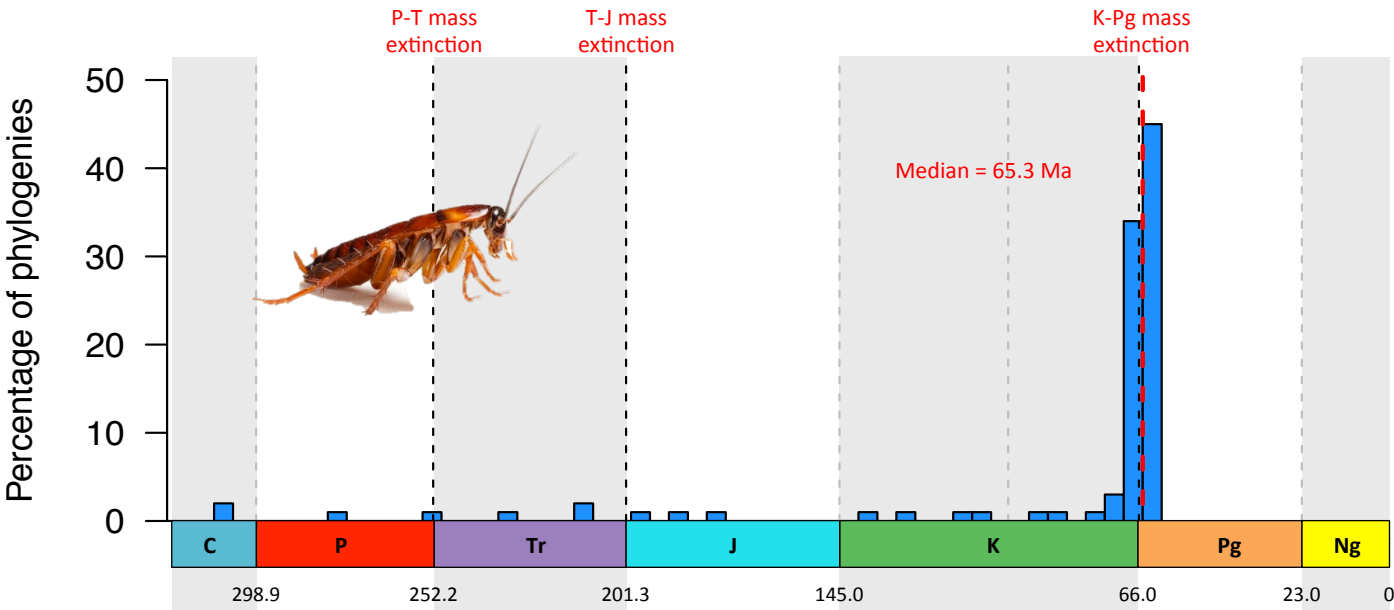


(b) Diversification dynamics of dictyopteran genera





(a) TreePar analyses estimating whether **shifts in diversification occurred**



(b) TreePar analyses estimating whether a **mass extinction occurred**

