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## When Darwin's Special Difficulty Promotes Diversification in Insects

Frédéric Legendre, Fabien Condamine

► **To cite this version:**

Frédéric Legendre, Fabien Condamine. When Darwin's Special Difficulty Promotes Diversification in Insects. *Systematic Biology*, 2018, 67 (5), pp.873-887. 10.1093/sysbio/syy014 . mnhn-02170200

**HAL Id: mnhn-02170200**

**<https://mnhn.hal.science/mnhn-02170200>**

Submitted on 1 Jul 2019

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1 ***Running head***

2 EUSOCIALITY AND DIVERSIFICATION

3

4 ***Title***

5 **When Darwin's Special Difficulty Promotes Diversification in Insects**

6

7 ***Authors' names***

8 FRÉDÉRIC LEGENDRE<sup>1¶\*</sup> & FABIEN L. CONDAMINE<sup>2¶\*</sup>

9

10 ***Authors' affiliations***

11 <sup>1</sup>*Muséum national d'Histoire naturelle, UMR 7205 Institut de Systématique, Evolution,*  
12 *Biodiversité ISYEB – UMR 7205 – MNHN CNRS UPMC EPHE, Sorbonne Universités, 57*  
13 *rue Cuvier, 75231 Paris Cedex 05, France*

14 <sup>2</sup>*CNRS, UMR 5554 Institut des Sciences de l'Evolution (Université de Montpellier), Place*  
15 *Eugène Bataillon, 34095 Montpellier, France*

16

17 *\*Correspondence to be sent to: Muséum national d'Histoire naturelle, UMR 7205 Institut de*  
18 *Systématique, Evolution, Biodiversité ISYEB – UMR 7205 – MNHN CNRS UPMC EPHE,*  
19 *Sorbonne Universités, 57 rue Cuvier, 75231 Paris Cedex 05, France; E-mail:*

20 [frederic.legendre@mnhn.fr](mailto:frederic.legendre@mnhn.fr); *CNRS, UMR 5554 Institut des Sciences de l'Evolution*  
21 *(Université de Montpellier), Place Eugène Bataillon, Bât. 22 RDC, CC064, 34095*  
22 *Montpellier, France; E-mail: fabien.condamine@gmail.com.*

23

24 <sup>¶</sup>*Both authors contributed equally to this work.*

25

26 *Abstract.*—Eusociality, Darwin’s special difficulty, has been widely investigated but remains  
27 a topic of great debate in organismal biology. Eusocial species challenge existing theories,  
28 and the impact of highly integrated societies on diversification dynamics is controversial with  
29 opposing assertions and hypotheses in the literature. Here, using phylogenetic approaches in  
30 termites – the first group that has evolved eusociality – we assessed the fundamental  
31 prediction that eusocial lineages have higher diversification rates than non-eusocial clades.  
32 We found multiple lines of evidence that eusociality provided higher diversification as  
33 compared to non-eusociality. This is particularly exacerbated for eusocial species with ‘true’  
34 workers as compared to species with ‘false’ workers. Because most species with ‘true’  
35 workers have an entirely prokaryotic microbiota, the latter feature is also related to higher  
36 diversification rates, but it should be investigated further, notably in relation to angiosperm  
37 diversification. Overall, this study suggests that societies with ‘true’ workers are not only  
38 more successful at ecological timescales but also over millions of years, which further implies  
39 that both organism- and species-level traits act on species selection.

40

41 *Keywords.*—Aggregate trait, emergent trait, eusocial insects, macroevolution, species  
42 selection, termites

43

44 Eusociality is the most integrated organizational level of animal sociality and is  
45 defined by cooperative brood care, overlapping generations within a colony of adults, and  
46 division of labour into reproductive and non-reproductive groups (Wilson and Hölldobler  
47 2005). Although the origin of eusociality is still widely investigated and debated (e.g. Nowak  
48 et al. 2010; Nonacs 2011; Rousset and Lion 2011; Johnstone et al. 2012), this rare but  
49 widespread behavioural characteristic has independently appeared in insects (at least 7-20  
50 times depending on the definition of eusociality), crustaceans (at least thrice), and mammals  
51 (at least twice) (**Fig. 1**; Bourke 2011). Within insects, eusocial species have colonies with  
52 caste differences: queens and reproductive males take the roles of sole reproducers, while  
53 soldiers defending the colony and workers foraging and maintaining resources contribute to  
54 creating a living situation favourable for the colony (Wilson 1971). In his theory of natural  
55 selection, Darwin (1859) famously portrayed the eusocial insects as a “*special difficulty,*  
56 *which at first appeared to [him] insuperable and actually fatal to [his] theory*”. Indeed,  
57 eusociality presents an apparent paradox: if adaptive evolution is mediated by differential  
58 reproduction of individuals on which natural selection acts, how can individuals incapable of  
59 passing on their genes evolve and persist?

60

61 **Figure 1.** Origin and timeline of eusocial lineages for mammals, crustaceans and insects  
62 (bees, wasps, ants, and termites). Bars represent temporal ranges with solid lines based on the  
63 fossil record, whereas broken lines indicate possible eusociality supported by molecular  
64 dating studies (ants: Moreau et al. 2006; bees: Cardinal and Danforth 2011, wasps: Hines et  
65 al. 2007, termites: Ware et al. 2010; Legendre et al. 2015b) but not supported by fossil  
66 evidence.

67

68           The multilevel selection theory could settle this paradox. This theory has a long and  
69 troubled history (Okasha 2006) but is increasingly accepted and supported, especially at the  
70 species level (Jablonski 2008). Species selection results from differences in speciation and  
71 extinction rates among species within a clade, and these differences are not merely related to  
72 the fitness at the level of individuals (Jablonski 2008; Rabosky and McCune 2010). Data and  
73 theory suggest that both organism-level and species-level traits (called aggregate and  
74 emergent traits, respectively) act on species selection. Aggregate traits are characteristics of  
75 individual organisms (e.g. body size), whereas emergent traits are species properties that are  
76 not reducible to organismal traits such as eusociality. Extending this vocabulary, authors often  
77 refer to the emergent fitness of species within clades when discussing species selection  
78 (Jablonski 2008).

79           At the macroevolutionary timescale, the origin and evolution of eusociality are  
80 increasingly well-understood due to recent phylogenetic analyses, along with estimates of  
81 divergence times and diversification rates notably for arthropod groups (ants: Moreau et al.  
82 2006; Pie and Feitosa 2016, bees: Cardinal and Danforth 2011, beetles: Farrell et al. 2001,  
83 wasps: Hines et al. 2007, spiders: Agnarsson et al. 2006, termites: Ware et al. 2010). These  
84 studies have investigated the number of origins of eusociality and the putative factors behind  
85 the extraordinary diversification of eusocial groups (e.g. the Cretaceous radiation of  
86 Angiosperms: Moreau et al. 2006; Cardinal and Danforth 2013). But another challenge  
87 surrounds eusocial organism evolution: the impact of highly integrated societies on the  
88 dynamics of diversification in these organisms (Davis et al. 2009; Ware et al. 2010). This  
89 topic has received less attention probably due to a lack of methods to handle large  
90 phylogenies that include both non-eusocial and eusocial lineages. Although the role of  
91 eusociality has not been formally studied with state-of-the-art diversification methods, the  
92 literature is filled with opposing assertions and hypotheses. In terms of ecological and

93 evolutionary success, modern eusocial insects can either be seen as species-rich groups such  
94 as ants, bees, or termites (Chapman and Bourke 2001; Wilson 1990) or as a group with lower  
95 species diversity than non-eusocial relatives such as ambrosia beetles, or poplar spiral gall  
96 aphids (Wilson 1992). Although the success of eusocial groups could naively lead us to think  
97 that eusociality was a trigger of diversification, Wilson (1992) argued that social insects  
98 (contrary to social vertebrates) show lower diversification (because they are “*less speciose*”)  
99 than non-eusocial insects. Based on studies of population genetics and molecular evolution,  
100 sociality reduces effective population size and possibly reduces levels of genetic variation,  
101 which would in turn increase the risk of extinction of social organisms (Lanfear et al. 2014).  
102 Hence, eusociality could indeed be seen as an impediment to diversification. The fossil record  
103 shows that taxa went extinct within eusocial groups (ants: LaPolla et al. 2013, termites:  
104 Krishna et al. 2010) but, so far, eusocial insect groups have been successful at the  
105 macroevolutionary scale. For the most part, they have persisted since the origins of these  
106 highly integrated behaviours, leading Wilson (1990) to state that “*eusociality conveys*  
107 *evolutionary long life to social insects*”. In reality, several emergent traits influence both  
108 extinction and speciation rates, resulting in unpredictable trade-offs (Jablonski 2008).

109         The ensuing questions ‘does eusociality confer higher diversification rates than non-  
110 eusocial species?’ and ‘what is the dynamic of diversification of social insects and what factor  
111 could explain their success and potential shift in diversification rates?’ are long-standing  
112 research topics (Darwin 1859; Wilson 1992; Wilson and Hölldobler 2005). Biotic and abiotic  
113 factors are important in diversification processes (Benton 2009) and range from  
114 climatic/geologic events (e.g. Condamine et al. 2013), to competition (e.g. Liow et al. 2015;  
115 Silvestro et al. 2015a), and key innovations (e.g. Rainford et al. 2014; Sánchez-García and  
116 Matheny 2016). Eusociality can be classified as a key innovation, but has surprisingly been  
117 understudied when one considers the ecological success that eusocial insect species have

118 experienced (Wilson 1971, 1992; Chapman and Bourke 2001). This ecological dominance is  
119 mainly explained by one property of eusociality: the reproductive division of labour. In other  
120 words, some individuals do not reproduce (i.e. they belong to sterile castes), and this has been  
121 qualified as the most important feature of eusociality (Wilson 1990).

122         Within insects, termites (Dictyoptera, order Blattodea, infraorder Isoptera) contain  
123 only eusocial species, and it is thought that they were the first modern eusocial animals to  
124 evolve, sometime in the Late Jurassic (*ca.* 155 Ma) (Legendre et al. 2015b; Engel et al. 2016).  
125 A termite colony is usually differentiated into reproductive, worker and soldier castes (**Fig.**  
126 **2a**). The latter two castes, which are sterile and perform highly specialized tasks, derive from  
127 different stages depending on the species (Noirot and Pasteels 1987). Whereas soldiers likely  
128 have a single origin, the evolution of workers is more controversial (Watson and Sewell 1981;  
129 Noirot and Pasteels 1987; Thompson et al. 2000; Grandcolas and D’Haese 2002; Inward  
130 2007, Legendre et al. 2008, 2013; Roisin and Korb 2011). Importantly, two types of workers  
131 were distinguished early: Some species have a ‘true’ worker caste, while others have a ‘false’  
132 worker caste (also called pseudergates; **Fig. 2a**). ‘True’ workers differ from pseudergates  
133 notably because they diverge early and irreversibly from the imaginal line (Noirot and  
134 Pasteels 1987), while pseudergates do not. Societies with ‘true’ workers have been qualified  
135 as more ‘socially’ highly integrated, which might have consequences for their ecological and  
136 evolutionary success given that >80% of all termites have ‘true’ workers (Korb 2009; Brune  
137 2014).

138

139 **Figure 2.** Eusociality in termites: life cycle (a) and (b) evolutionary origin associated to  
140 putative key innovations. The life cycle differs for species with pseudergates and species with  
141 ‘true workers’ (highlighted by the dashed box). The phylogeny of termites (Isoptera)  
142 illustrates that the origin of eusociality is nested within the radiation of cockroaches (termites

143 and cockroaches together forming the Blattodea). The phylogeny also highlights important  
144 events in the evolution of the digestive symbiosis: the presence of cellulolytic flagellates,  
145 acquired by a common ancestor of termites and Cryptocercidae, is associated to their wood-  
146 feeding lifestyle; the loss of flagellates in Termitidae gave rise to an enormous dietary  
147 diversification (chronogram adapted from Legendre et al. 2015b). Dashed lines for the  
148 common ancestor of cockroaches denote that the group is older than 201 Ma. The asterisk (\*)  
149 specifies that some families or subfamilies are paraphyletic according to the latest studies.

150

151         The study of termite digestive systems might also bring important insights on the  
152 ecological and evolutionary successes of these insects (**Fig. 2b**). Although digestive strategies  
153 and the gut microbiota of termites remain to be fully deciphered, important progress has been  
154 made and two groups can be distinguished by their primary cellulolytic partners and their  
155 hindgut compartmentation (Brune 2014). The first group comprises termite species that  
156 harbour cellulolytic flagellates in their gut; they group all termite species except those  
157 belonging to Termitidae. In the second group (i.e. Termitidae), these flagellates are absent;  
158 instead Termitidae have an entirely prokaryotic microbiota. They also show a higher  
159 compartmentation of the hindgut (except for Macrotermitinae) and a large dietary  
160 diversification (Brune and Dietrich 2015). Because most termite species belong to the family  
161 Termitidae (Beccaloni and Eggleton 2013), their peculiar digestive system might have been a  
162 trigger of diversification. A parallel can be made with cockroach species; even though the gut  
163 microbiota of most cockroach species has not been investigated, flagellates have been found  
164 in some wood-eating species, including, but not restricted to (e.g. Pellens et al. 2002),  
165 *Cryptocercus*, the alleged sister group of termites (Cleveland et al. 1934; Klass et al. 2008).  
166 Because of characteristics shared with ‘lower’ termites (Klass et al. 2008), it is then generally  
167 assumed that *Cryptocercus* belongs to the group with cellulolytic flagellates in their gut

168 (Brune and Dietrich 2015), contrary to other supposedly or asserted wood-eating species (but  
169 see Pellens et al. 2007 and the section *Trait-dependent diversification* for more details and  
170 alternative codings).

171 Our knowledge on the role of eusociality in the dynamic of diversification is limited.  
172 Only one previous study has investigated the diversification of termites (Davis et al. 2009),  
173 suggesting increases in diversification early in termite evolution. However, this study was  
174 based on a family-level supertree, and methods to estimate diversification were still in their  
175 infancy. Besides, this study did not differentiate the potential role of ‘true’ workers or that of  
176 gut microbiota composition in termite diversification. To better understand the triggers of  
177 diversification in Dictyoptera (mantises, cockroaches and termites), we analyze the most  
178 comprehensive time-calibrated phylogeny of the group. We investigate the diversification  
179 dynamic of termites compared to their dictyopteran counterparts using a battery of birth-death  
180 methods to corroborate and strengthen these results. More specifically, we tested the  
181 competing hypotheses in which eusociality is associated with lower (Wilson 1992) or higher  
182 (Davis et al. 2009) net diversification rate compared to non-eusociality. We also tested  
183 whether the presence of ‘true’ workers in termite societies can be considered a key innovation  
184 relative to societies with pseudergates, by assessing the putative role on diversification of  
185 these castes on termite evolution. Similarly, we tested whether an entirely prokaryotic gut  
186 microbiota could also be a key innovation for termite diversification.

187

## 188 MATERIALS AND METHODS

### 189 *Analytical Pipeline*

190 We used a recently published time-calibrated phylogeny of Dictyoptera including 762  
191 species representatives of living dictyopteran diversity (*ca.* 10,000 known species, Legendre  
192 et al. 2015b). This phylogeny resulted from a molecular dataset comprising four

193 mitochondrial and two nuclear markers. Divergence times were estimated using a relaxed-  
194 clock approach coupled with 17 fossils, which were used as minimum age constraints on  
195 different nodes and a maximum age for the tree root (Legendre et al. 2015b).

196 Three putatively key innovations were investigated: eusociality, societies with ‘true’  
197 workers and entirely prokaryotic gut microbiota. To test the role of these innovations, we used  
198 three approaches: (i) the maximum likelihood (ML) approach of time-dependent  
199 diversification (Morlon et al. 2011), implemented in the R-package *RPANDA* v.1.2 (Morlon et  
200 al. 2016), (ii) the Bayesian analysis of macroevolutionary mixture (BAMM v.2.5, Rabosky et  
201 al. 2013), implemented in the R-package *BAMMtools* v.2.1.4 (Rabosky et al. 2014), and (iii)  
202 the ML approach of trait-dependent diversification (Madisson et al. 2007; FitzJohn et al.  
203 2009), implemented in the R-package *diversitree* v.0.9-8 (FitzJohn 2012).

204 Each method is designed to estimate speciation and extinction rates, and the three  
205 methods are used to cross-test hypotheses and corroborate results. Nonetheless, it is worth  
206 mentioning that each method differs at several points in the way speciation and extinction  
207 rates are estimated. For instance, trait-dependent birth-death models (*diversitree*) estimate  
208 constant speciation and extinction rates, while time-dependent birth-death models (*BAMM*  
209 and *RPANDA*) estimate the speciation and extinction rates and their variation through time.  
210 Therefore we expect some differences in the values of the estimated diversification rates that  
211 are inherent to each approach. Our diversification analyses should be seen as complementary  
212 for the inferred diversification trend rather than corroborative on the values and magnitude of  
213 the speciation and extinction rates.

214

#### 215 *Across-Clade and Time-Variation Diversification*

216 The ML approach of Morlon et al. (2011) is a birth-death method that extends  
217 previous birth-death methods such that speciation and/or extinction rates may change

218 continuously through time, and subclades may have different speciation and extinction rates.  
219 This method has the advantage of not assuming constant extinction rate over time (unlike  
220 BAMM, Rabosky et al. 2013), and allows clades to have declining diversity because  
221 extinction can exceed speciation, meaning that diversification rates can be negative (Morlon  
222 et al. 2011).

223 We designed six nested diversification models to test with this approach: *(i)* a Yule  
224 model, where speciation is constant and extinction is null; *(ii)* a constant birth-death model,  
225 where speciation and extinction rates are constant; *(iii)* a variable speciation rate model  
226 without extinction; *(iv)* a variable speciation rate model with constant extinction; *(v)* a rate-  
227 constant speciation and variable extinction rate model; and *(vi)* a model in which both  
228 speciation and extinction rates vary. Models were compared by computing the ML score of  
229 each model and the resulting Akaike information criterion corrected by sample size (AICc).

230 First, the Dictyoptera tree was analyzed as a whole using this approach and taking into  
231 account missing species ( $f=0.08$ ). To test the hypotheses that eusociality, societies with ‘true’  
232 workers and gut microbiota composition act on diversification rates, we compared the  
233 likelihoods of models that allow for different patterns of rate variation in different clades.  
234 More specifically, we first allowed for a rate shift along the branch corresponding to the  
235 apparition of eusociality (the termite crown node), and we sequentially tested for a rate shift  
236 between the crown node of termites and the node corresponding to the family Termitidae  
237 (prokaryotic microbiota). Therefore, we partitioned the Dictyoptera phylogeny into seven  
238 evolutionary scenarios: from a backbone without the termites, and the termites as a subtree; to  
239 a backbone without the Termitidae, and the Termitidae as a subtree (with all five possibilities  
240 in between; for a schematic illustration see Fig. S1 in the Supplementary Material that  
241 accompanies this article available on Dryad at <http://dx.doi.org/10.5061/dryad.2tg34>). After  
242 creating these backbones and corresponding subtrees, and accounting for the missing species

243 in each of them, we fitted the same diversification models as detailed above but independently  
244 on each subtree and its corresponding backbone tree (Fig. S1 on Dryad). The global log-  
245 likelihood was calculated as the sum of both subclade and backbone log-likelihoods as  
246 determined by the corresponding best-fitting models. This approach allowed us to compare  
247 the global log-likelihood (under the assumption of a single speciation rate and extinction rate)  
248 to the log-likelihood of one shift at the termite crown (eusociality), and to the log-likelihood  
249 of one shift at the crown of Termitidae (prokaryotic microbiota). We directly compare the  
250 seven scenarios using AICc.

251 We also used BAMM to estimate speciation and extinction rates through time and  
252 among/within clades (Rabosky et al. 2013). BAMM was constructed to study complex  
253 evolutionary processes on phylogenetic trees, potentially shaped by a heterogeneous mixture  
254 of distinct evolutionary dynamics of speciation and extinction across clades. BAMM can  
255 automatically detect rate shifts and sample distinct evolutionary dynamics that explain the  
256 diversification dynamics of a clade without *a priori* hypotheses on how many and where these  
257 shifts might occur. Evolutionary dynamics can involve time-variable diversification rates; in  
258 BAMM, speciation is allowed to vary exponentially through time while extinction is  
259 maintained constant: subclades in a tree may diversify faster (or slower) than others. This  
260 Bayesian approach can be useful in detecting shifts of diversification potentially associated  
261 with key innovations (Rabosky 2014).

262 We ran BAMM by setting four Markov chain Monte Carlo running (MCMC) for 20  
263 million generations and sampled every 2,000 generations. A compound Poisson process is  
264 implemented for the prior probability of a rate shift along any branch. We used a gradient of  
265 prior values ranging from 0.1 to 50 to test the sensitivity to the prior, because it has been  
266 shown that BAMM can be affected by the prior (Moore et al. 2016 but see Rabosky et al.  
267 2017). We accounted for non-random incomplete taxon sampling using the implemented

268 analytical correction; we set a sampling fraction for mantises ( $f=0.118$ ), cockroaches  
269 ( $f=0.042$ ), and termites ( $f=0.094$ ). We performed independent runs (with a 15% burn-in) using  
270 different seeds to assess the convergence of the runs with effective sample size. We processed  
271 the output data using the *BAMMtools* (Rabosky et al. 2014) by estimating (i) the mean global  
272 rates of diversification through time, (ii) the configuration of the diversification rate shifts  
273 evaluating alternative diversification models as compared by posterior probabilities, and (iii)  
274 the clade-specific rates through time when a distinct macroevolutionary regime is identified.

275

### 276 *Trait-Dependent Diversification*

277 We used trait-dependent diversification models to simultaneously model trait  
278 evolution and its impact on diversification (Maddison et al. 2007). In those models, species  
279 are characterized by an evolving trait, and their diversification follows a birth-death process in  
280 which speciation and extinction rates may depend on the trait state. We created three datasets  
281 of traits. First, we categorized all dictyopteran species as being non-eusocial or eusocial. This  
282 two-trait scheme distinguishes the termites (all species are eusocial) from the rest of  
283 dictyopterans (all non-eusocial). Second, we made a three-trait scheme by keeping the non-  
284 eusocial category, and dividing the eusocial trait into two: eusocial with pseudergates (‘false’  
285 workers) and eusocial with ‘true’ workers. Third, we made another three-trait scheme to test  
286 the role of the primary cellulolytic partners in diversification. We followed Brune and  
287 Dietrich (2015) to distinguish Termitidae (entirely prokaryotic microbiota), *Cryptocercus* +  
288 other termites (cellulolytic flagellates), and the remaining Dictyoptera (no specialized  
289 microbiota for lignocellulose digestion). All these coding schemes are imperfect because, like  
290 any broad categorization process, they might oversimplify the reality found in nature  
291 (Legendre et al. 2015a; Goutte et al. 2016). The category ‘remaining Dictyoptera’ in the latter  
292 coding scheme, for instance, is imperfect because it is delineated by default and because of a

293 lack of information for some cockroach species. However, this three-state coding reflects our  
294 current understanding of the primary cellulolytic partners in Dictyoptera as reviewed in Brune  
295 and Dietrich (2015). Anyway, to take into account our lack of knowledge on cockroach  
296 microbiota and the existence of species that, arguably, could not fit well in these three  
297 categories – while limiting the number of categories to save statistical power, we created two  
298 supplementary trait datasets. In the first alternative coding, the wood-feeding non-eusocial  
299 lineages were coded with cellulolytic flagellates (same as ‘lower’ termites) even though the  
300 existence and role of cellulolytic flagellates have not always been investigated and proved.  
301 These lineages represent several genera of the subfamily Panesthiinae, and the genera  
302 *Cyrtotria*, *Lauraesilpha*, *Paramuzoa*, *Parasphaeria*, and *Colapteroblatta* (Grandcolas 1993;  
303 Grandcolas et al. 2002; Pellens et al. 2002). In the second alternative coding, the  
304 Macrotermitinae were not coded with the Termitidae (i.e. initial coding supported by their  
305 entirely prokaryotic gut microbiota) but with the other termites (coding supported by their  
306 relatively simple hindgut structure).

307 We applied the Binary State Speciation and Extinction model (BiSSE, Maddison et al.  
308 2007) with constant diversification rate for the two-trait dataset. We then performed the  
309 Multi-State Speciation and Extinction model (MuSSE, FitzJohn et al. 2009) on the three-trait  
310 datasets. Both BiSSE and MuSSE models account for incomplete taxon sampling, which is  
311 informed as a sampling fraction of species at present having a given trait (FitzJohn et al.  
312 2009). Simulation studies have shown that a large, well-sampled tree is required by these  
313 methods, whereas trees containing fewer than 300 species may lack sufficient phylogenetic  
314 signal to produce enough statistical power (Davis et al. 2013).

315 The BiSSE model has six distinct parameters: two speciation rates without character  
316 change (i.e. *in situ* speciation) associated with non-eusocial species ( $\lambda_N$ ) and eusocial species  
317 ( $\lambda_E$ ), two extinction rates associated with non-eusocial ( $\mu_N$ ) and eusocial species ( $\mu_E$ ), and two

318 transition rates (i.e. anagenetic change) with one from non-eusocial to eusocial ( $q_{N-E}$ ), and  
319 from eusocial to non-eusocial ( $q_{E-N}$ ). Using the same rationale, but applied to three traits, the  
320 MuSSE model has 12 distinct parameters (three for speciation, three for extinction, and six for  
321 transitions).

322 Here we used 100 dictyopteran phylogenies (sampled from the Bayesian analysis in  
323 Legendre et al. 2015b) and combined them with our three datasets of traits. Analyses were  
324 performed using the R-package *diversitree* (FitzJohn 2012) using the functions *make.bisse*  
325 and *make.musse* to construct the likelihood functions for each model based on the data, and  
326 the functions *constrain* and *find.mle* to apply different diversification scenarios.

327 For each model, we computed the AICc based on the log-likelihood and the number of  
328 parameters. We checked support for the selected model against all models using the  
329 difference between AICc ( $\Delta AIC$ ) and the Akaike weight ( $AIC\omega$ ). The scenario supported with  
330 the lowest AICc was considered the best when  $\Delta AIC > 2$  against other models and with  
331  $AIC\omega > 0.5$  (otherwise the model with less parameter was instead considered the best). Finally,  
332 we used the consensus tree and MCMC simulations with the best model to examine the  
333 confidence interval of the parameter estimates. We used an exponential prior and started the  
334 chain with the parameters obtained by maximum likelihood (FitzJohn 2012). We ran 20,000  
335 MCMC steps and applied a 10% burn-in. Net diversification rates were then computed.

336 SSE models have recently been criticized due to type I error (Rabosky and Goldberg  
337 2015). To test whether our diversification results were biased, we estimated the difference of  
338 fit ( $\Delta AIC$ ) between the best model and a null model (i.e. with no state dependence) and  
339 compared this with the difference between the same models as estimated from 100 simulated  
340 trait datasets for each SSE model.

341

342 RESULTS

343 *Diversification Across-Clade and Time*

344         The BAMM analyses supported a model with six evolutionary regimes (i.e. five rate  
345 shifts; Fig. S2 and Table S1 available on Dryad). The post burn-in posterior distribution  
346 indicated that five shifts occur with a posterior probability (PP) of 0.54, and PP=0.33 and 0.10  
347 for four and six shifts, respectively (less or more shifts occur with PP<0.05; Table S1  
348 available on Dryad). The 95% credible set of shift configurations and marginal shift  
349 probabilities strongly favoured a model that includes shifts along branches within termites  
350 (Figs S3-S4 available on Dryad). The shift configurations within this credible set contained  
351 also shifts at internal nodes in mantises and at a more derived position within cockroaches  
352 (Blaberidae: Panesthiinae). The different shift configurations in the credible set allowed  
353 quantifying uncertainty in placement of a termite shift (Fig. S4 available on Dryad). The shift  
354 configurations sampled at the highest frequency always contained a shift within termites  
355 (cumulative posterior probability of 0.62). The best configuration shift retained five core  
356 shifts, one located within the termites (crown Termitidae), two within Mantodea and two  
357 others within cockroaches (Fig. S5 available on Dryad). We repeated the analyses by  
358 changing the Poisson process for the prior probability of a rate shift along any branch: these  
359 analyses supported a similar diversification pattern, although we found an additional clade-  
360 specific macroevolutionary regime when a higher prior probability of rate shift was used (Fig.  
361 S6 and Table S1 available on Dryad).

362         We found evidence for low and constant-rate diversification through time for  
363 Dictyoptera punctuated by few shifts. When diversification changed, speciation rates  
364 increased for the termites in particular at the base of Termitidae (**Fig. 3**). Although other  
365 increases of speciation were found, the most elevated speciation rate (and also net  
366 diversification rate) occurred within termites. Interestingly, when termite macroevolutionary  
367 regime was studied in isolation, the net diversification rate of the clade increased towards the

368 present (**Fig. 3**). On the contrary, the other macroevolutionary regimes showed a more  
369 common pattern of diversification slowdown over time.

370

371 **Figure 3.** Diversification and eusociality in Dictyoptera. (a) Time-calibrated phylogeny of  
372 Dictyoptera (adapted from Legendre et al. 2015b) showing the origin of eusociality (all  
373 termites), the origin of an entirely prokaryotic microbiota (Termitidae), and the shifts in  
374 diversification rate identified with BAMM. (b) Results of BiSSE show that lineages with  
375 eusocial species have higher net diversification rates than non-eusocial species. (c) Results of  
376 MuSSE show that lineages with ‘true’ workers have higher net diversification rates than other  
377 dictyopteran lineages, including termite lineages with pseudergates. (d) Results of MuSSE  
378 show that lineages with an entirely prokaryotic microbiota (and a complex hindgut  
379 compartmentation) have a higher diversification rate than other dictyopteran lineages. For  
380 BiSSE and MuSSE plots, Bayesian posterior distributions represent the 95% credibility  
381 interval of each estimated parameter. (e) BAMM analyses suggest a strong increase in net  
382 diversification rate of termites towards the present, especially in termites with ‘true’ workers  
383 (mostly Termitidae and Rhinotermitidae). The shaded areas represent the 95% credibility  
384 interval of each estimated parameter.

385

### 386 *Termite Key Innovations and Diversification*

387 The *RPANDA* analyses refined the location of the rate shift within termites, and  
388 allowed testing the effect of three termite key innovations: eusociality, societies with ‘true’  
389 workers, and entirely prokaryotic gut microbiota, which have evolved sequentially from the  
390 origin of termites to the origin of Termitidae. Applying a series of time-dependent birth-death  
391 models (including a rate shift at the crown node of a termite subclade), we compared the fit of  
392 alternative scenarios to locate the best change of diversification rates. We first found that any

393 scenario including a rate shift within termites is better than a scenario having no shift at all  
394 (**Table 1**). Comparing all diversification scenarios including a shift in the termite tree, we  
395 found that the best-fitting scenario includes a shift along a branch supporting termites that  
396 only contain species with ‘true’ workers in their societies (*scenario 6*, **Table 1**). There is  
397 strong support for this scenario (lowest  $\Delta\text{AIC}=12.7$ ) as compared to competing hypotheses of  
398 other locations in the termite tree such as the evolution of eusociality (*scenario 1*), or the  
399 change in gut microbiota composition (*scenario 7*).

400 BMM identified an important rate shift within the mantises (166.8 Ma, **Fig. 3**),  
401 which corresponds to an increase of diversification. Using *RPANDA*, we tested whether a  
402 model including this shift performs better than the model with the best-fitting shift in termites.  
403 We reproduced the approach explained above but we isolated the mantis clade as a subtree,  
404 from the rest of the Dictyoptera (this time including termites). We analyzed all the same  
405 models and found that the shift within the Mantodea does not improve the likelihood as  
406 compared with the model including the shift within termites (AICc for the shift in  
407 mantises=7640.83; resulting in a  $\Delta\text{AIC}=327$  between the best scenario including a shift within  
408 termites and this scenario, **Table 1**).

409 *RPANDA* analyses endorsed BMM results: The best-fit scenario indicated a  
410 speciation rate increasing through time for both the termite tree and the backbone.  
411 Nonetheless, we estimated an elevated speciation rate of 0.193 lineage/Myr for termites,  
412 strikingly contrasting with the speciation rate of the remaining dictyopteran lineages (0.058  
413 lineage/Myr). Moreover, we found the termite clade diversified with low or zero extinction  
414 rates, again contrasting with the extinction rate for the rest of the tree (0.023 lineage/Myr).  
415 Consequently, the net diversification rate of the termite tree is 5.5 times higher than the  
416 remaining part of the dictyopteran tree (*scenario 7*, **Table 1**).

417 We corroborated the BAMM and *RPANDA* analyses with BiSSE and MuSSE applied  
418 to a two-trait dataset and two three-trait datasets, respectively. We found that the best-fitting  
419 BiSSE model was the one with different speciation and extinction, but with equal transition  
420 rates. Simpler or more complex models were not supported ( $\Delta\text{AIC}=4.13$  with the second best-  
421 fit BiSSE model, which has one extra parameter, **Table 2a**, Table S2 available on Dryad). In  
422 the best-fit model, both speciation and extinction rates were higher for eusocial species  
423 (**Table 2a**), and the net diversification rate was two-fold higher for eusocial lineages (**Fig. 3**).  
424 Bayesian MCMC analysis showed that speciation, extinction, and net diversification rates  
425 were significantly different between the two traits (Fig. S7 available on Dryad).

426 We further investigated whether difference of diversification rates occurred within the  
427 termites by splitting the eusociality trait into two (societies with pseudergates or societies with  
428 ‘true’ workers). We found that the best-fitting MuSSE model supported the most complex  
429 model, in which all parameters are free. Simpler models were not supported ( $\Delta\text{AICc}=15.8$   
430 with the second best-fit MuSSE model, which has one less parameter, **Table 2b**, Table S2  
431 available on Dryad). In the best-fit model, speciation and extinction rates were higher for  
432 eusocial lineages with ‘true’ workers. Speciation and extinction rates were both low for the  
433 two other traits (non-eusocial, and eusocial with pseudergates). The net diversification rate  
434 was higher for eusocial lineages with ‘true’ workers (**Fig. 3**). The trait-dependent rates of  
435 speciation, extinction, and net diversification for the eusocial species with ‘true’ workers were  
436 significantly different from the rates of the two other traits, and the two other traits were not  
437 significantly different from each other (Fig. S8 available on Dryad).

438 As for the primary cellulolytic partners, we found that the net diversification rate was  
439 higher for the Termitidae, the lineage with an entirely prokaryotic gut microbiota (**Fig. 3**;  
440 **Table 2c**; Fig. S9 and Table S2 available on Dryad). The two other traits were not  
441 significantly different in terms of diversification even though the lineages with cellulolytic

442 flagellates showed higher speciation and extinction rates than mantises and cockroaches  
443 (except *Cryptocercus* that harbours flagellates).

444 Randomization analyses of the three datasets of traits showed that all the SSE-based  
445 results were robust to type-I error (Fig. S10 available on Dryad) indicating that our inferences  
446 are not biased. We performed additional MuSSE analyses by re-coding either the wood-  
447 feeding non-eusocial lineages or Macrotermitinae with *Cryptocercus* spp. and all the termites  
448 but the other Termitidae, and we found that the results were not sensitive to this effect:  
449 eusocial lineages with a prokaryotic microbiota or with a complex hindgut compartmentation  
450 diversified significantly faster than their counterparts (Figs. S11-S12 available on Dryad).

451

## 452 DISCUSSION

453 The origin of eusociality has been widely investigated at the organismal level. For  
454 instance, Hall and Goodisman (2012) explored the differences in rate of substitution for  
455 queen- and worker-selected loci, whereas Rehan and Toth (2015) reviewed several  
456 hypotheses about molecular evolution of eusociality and tried to integrate them in a synthetic  
457 framework. Above the species level, the origin and evolution of eusociality has been also  
458 addressed with molecular dated phylogenies of eusocial groups (Farrell et al. 2001;  
459 Agnarsson et al. 2006; Moreau et al. 2006; Hines et al. 2007; Cardinal and Danforth 2011,  
460 2013; Pie and Feitosa 2016). These studies have shown that eusociality is a labile trait that has  
461 appeared independently in many clades. However, the consequences of eusociality as a driver  
462 of species diversification have received less attention (Davis et al. 2009; Ware et al. 2010).  
463 What role does eusociality play at this macroevolutionary scale? In social insects, only two  
464 studies mentioned this aspect and suggested contradictory hypotheses. Edward O. Wilson  
465 (1992) proposed that social insects would have a lower diversification rate than non-eusocial  
466 insects, while Davis et al. (2009) suggested that termites would have a higher diversification

467 rate than their close relatives; the study of Ware et al. (2010) did not compare termite  
468 diversification with the non-eusocial clades. These opposite predictions are in fact not so  
469 surprising because, for numerous aggregate and emergent traits, both low speciation and  
470 extinction rates are predicted (Jablonski 2008). These traits would then lead either to increase  
471 or decrease in diversification depending on the intensity of speciation and extinction.

472         Speciation rate supposedly increases with molecular rate (Webster et al. 2003; Lanfear  
473 et al. 2010; but see Rabosky and Matute 2013), which in turn depends on several features  
474 including population size, population abundance, and genetic population. Harvey et al. (2017)  
475 showed, for instance, a link between population differentiation within species and speciation  
476 rates inferred from phylogenies in New World birds. All the aforementioned features are  
477 emergent traits connected to eusociality. In termites, the archetype society mode involves  
478 large and abundant populations headed by pairs of reproductives, resulting in colonies with  
479 strong genetic structures and genetically isolated by distance (Goodisman and Crozier 2002;  
480 Thompson et al. 2007; Dupont et al. 2009; Eggleton 2011; Vargo and Hussedener 2011).  
481 According to classical predictions, high abundance would imply low extinction and low  
482 speciation rates, while highly structured populations would imply both high extinction and  
483 speciation rates. As for large population size, predictions suggest low extinction rates and are  
484 contradictory about speciation rates (Jablonski 2008). For Dictyoptera, we found here higher  
485 extinction and speciation rates for eusocial lineages when compared to non-eusocial lineages  
486 (using three different approaches). Because speciation is much higher than extinction, the net  
487 diversification rate is higher for eusocial species than for non-eusocial species, resulting in a  
488 strong positive link between eusociality and net diversification.

489         These results suggest that a high level of genetic structure could be the main factor  
490 acting on Dictyoptera diversification. However, the classical vision of termites is outdated.  
491 Population structure in termites probably shows a large spectrum of variation that should be

492 investigated further (Vargo and Husseneder 2011) and compared to cockroach population  
493 structures that should also vary between solitary, gregarious and subsocial species (Bell et al.  
494 2007), or flying and wingless species. Population size – and size-dependent properties – is  
495 also poorly known (Korb 2009) but range from a few hundreds to millions of individuals.  
496 Even within the family Termitidae comprising only species with ‘true’ workers, there is a  
497 large variance with nest population of a few thousands to a few millions of individuals  
498 (Lepage and Darlington 2000). But, even though the underlying factors remain to be  
499 investigated further, eusociality seems to act as a key innovation favouring diversification in  
500 Dictyoptera.

501         Key innovations are alluded to whenever an evolutionary novelty is thought to have  
502 favoured the diversification of a clade. Three main categories of key innovations can be  
503 distinguished (Heard and Hauser 1995): *(i)* innovations opening new adaptive zones *sensu*  
504 Simpson (1944); *(ii)* innovations increasing fitness and allowing to outcompete other species;  
505 and *(iii)* innovations increasing the propensity for reproductive or ecological specialization.  
506 These three categories are not necessarily exclusive. For termites, eusociality unlikely opened  
507 new adaptive zones (definition 1). Termites act mainly as decomposers, a niche already  
508 existing and occupied before the emergence of this clade (Raymond et al. 2000). However, a  
509 highly integrated society, especially with ‘true’ workers, might have allowed termites to  
510 outcompete other species and increased their propensity for reproductive and ecological  
511 specialization (definitions 2 and 3). This scenario is classically put forward at the ecological  
512 timescales, wherein the higher dominance and the large ecological success of termites are  
513 known, and could be here translated at the macroevolutionary timescale. Interestingly, all the  
514 diversification analyses (three different types of models) show that both speciation and  
515 extinction rates were higher for eusocial lineages with ‘true’ workers resulting in a higher net  
516 diversification rate for these lineages. Accordingly, our results suggest that societies with

517 'true' workers are not only more successful at ecological timescales but also over millions of  
518 years, which further implies that both organism- and species-level traits (aggregate and  
519 emergent traits, respectively) act on species selection.

520 Other factors are also probably at play in Dictyoptera diversification and they should  
521 be examined in future research (Jablonski 2008; Benton 2009). The diversification of  
522 angiosperms in the Cretaceous is often proposed to have played an important role in insect  
523 diversification, especially social insects (Moreau et al. 2006; Cardinal and Danforth 2013).  
524 Interestingly, molecular dating phylogenies of termites concur to show that termites appeared  
525 in the very Late Jurassic – Early Cretaceous (Ware et al. 2010; Bourguignon et al. 2015;  
526 Legendre et al. 2015b). Although there is a debate on the origin of angiosperms, from the  
527 Early Cretaceous to Triassic (e.g. Beaulieu et al. 2015; Magallón et al. 2015; Silvestro et al.  
528 2015b; Foster et al. 2017), the main period of diversification always occurred in the  
529 Cretaceous and coincides well with the rise of many extant insect clades. It is nonetheless  
530 questioned whether the angiosperm radiation has boosted insect diversification (Rainford and  
531 Mayhew 2015; Condamine et al. 2016). The increase in termite diversification in the  
532 Cretaceous can be associated with the rise to dominance of angiosperms; a similar scenario is  
533 proposed for another important eusocial insect clade, the ants (Moreau et al. 2006). Other  
534 dramatic landscape modifications that happened in the last 300 million years might have  
535 promoted shifts in diversification in termites. For instance, global climate changes or the  
536 break-up of ancient continents (Bourguignon et al. 2015) could have induced different  
537 dynamics of diversification between non-eusocial and eusocial lineages. Future studies could  
538 investigate the impact of such important environmental changes using both phylogenies and  
539 fossil data. Also, to better understand these intricate mechanisms, approaches integrating  
540 various factors such as caste and colony size but also foraging types, dispersal abilities, diets  
541 and digestive capacity (Abe 1987; Jeanson and Deneubourg 2009; Brune and Dietrich 2015),

542 should be used to sort out the effect of these factors. Regarding diet specialization, which is  
543 strongly related to gut anatomy and microbiota composition (Bignell and Eggleton 1995;  
544 Köhler et al. 2012; Mikaelyan et al. 2015), the concomitance of termite and angiosperm  
545 diversifications brings credit to its importance in termite diversification because changes in  
546 intestinal anatomy and microbiota complexity would have opened new niches to diversify in.

547 Rabosky (2009) underlined the possible change in species “carrying capacity” for  
548 some clades in a given area. Instead of playing on diversification rates *per se*, may eusociality  
549 impact ecological limits in a given environment, which would in turn increase termite  
550 diversification? This remains a possibility that could be linked to our side-result that net  
551 diversification rates within termites increase towards the present, which is unusual, but the  
552 underlying mechanisms are still to be deciphered. The apparent increased diversification rate  
553 in termites at the present can be caused by a phenomenon, called the pull of the recent, which  
554 is due to a more complete sampling of recent and still extant species than in the past  
555 (Jablonsky 2008). This is slightly different from the pull of the present that is due to constant  
556 birth-death models showing an upward turn in species number towards the present (Nee  
557 2006). Most of the phylogenies are better explained by a slowdown of speciation rates  
558 towards the present (e.g. Phillimore and Price 2008; Morlon et al. 2010). An increase in  
559 speciation through time is rarely inferred, thus the increase in termite speciation goes against  
560 the classical pattern. We do not think the increase in speciation can be attributed to the pull of  
561 the present/recent because the increase started tens of million years ago, while the effect of  
562 the pull of the present/recent is usually considered to be important in the last million years  
563 (Nee 2006). The species sampling is relatively homogeneous across the phylogenetic tree,  
564 except for the Panesthiinae which are more sampled than the rest, but more importantly the  
565 termite subtree is not better sampled than the other groups (Legendre et al. 2015b). Therefore,  
566 we think the impact of the pull of the present/recent is limited here.

567           Finally, even though there were probably multiple origins of the ‘true’ worker caste in  
568 termites (Legendre et al. 2008, 2013), Dictyoptera offers a single replicate to investigate the  
569 role of eusociality in clade diversification. We expect advances in our understanding of the  
570 role of eusociality at the species selection level, when similar studies would be conducted  
571 with other eusocial organisms, especially in the insect order Hymenoptera (Peters et al. 2017)  
572 where ants, bees and wasps constitute conspicuous elements of ecosystems and have evolved  
573 eusociality independently.

574

#### 575 SUPPLEMENTARY MATERIAL

576 Supplementary material can be found in the Dryad Digital Repository at <http://datadryad.org>,  
577 <http://dx.doi.org/10.5061/dryad.2tg34>.

578

#### 579 ACKNOWLEDGMENTS

580 We thank the associate editor Brian Wiegmann and two anonymous referees for the excellent  
581 comments that improved the study. We also thank Giovanni Fagua, Gaël Kergoat, H el ene  
582 Morlon, Andr e Nel and Felix Sperling for proofreading and commenting on this manuscript.

583

#### 584 FUNDING

585 Financial support was provided by a Marie Curie International Outgoing Fellowship (project  
586 627684 BIOMME) to FLC.

587

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TABLE 1. Support for an increase of diversification rates for termites, especially for lineages including ‘true’ workers.

Models	Whole phylogeny	Scenario with a rate shift located at:						
		the MRCA of Isoptera	the MRCA of Euisoptera	the MRCA of Kalotermitidae and Neoisoptera	the MRCA of Neoisoptera	the MRCA of Neoisoptera minus Rhinotermitinae	the MRCA of Termitidae, Coptotermitinae and Heterotermitinae	the MRCA of Termitidae
NP	3	4	4	5	4	5	<b>5</b>	4
logL	-3889.247	-3709.158	-3706.857	-3693.107	-3658.84	-3659.554	<b>-3651.496</b>	-3691.284
AICc	7784.526	7426.385	7421.781	7396.308	7325.754	7329.206	<b>7313.092</b>	7390.653
$\Delta AIC$	471.434	113.293	108.689	83.216	12.662	16.114	<b>0</b>	77.561
AIC $\omega$	0	0	0	0	$\approx 0.002$	<0.0001	<b>0.998</b>	0
Subclade speciation rate	0.191	0.177	0.178	0.185	0.186	0.191	<b>0.193</b>	0.197
Subclade extinction rate	0.175	0	0	0	0	0	<b>0</b>	0
Subclade net div. rate	0.016	0.177	0.178	0.185	0.186	0.191	<b>0.193</b>	0.197
Backbone speciation rate	-	0.044	0.044	0.057	0.044	0.058	<b>0.058</b>	0.084
Backbone extinction rate	-	0	0	0.024	0	0.024	<b>0.023</b>	0.06
Backbone net. div. rate	-	0.044	0.044	0.033	0.044	0.034	<b>0.035</b>	0.024

Notes: The table reports the log-likelihood (*logL*) and the corrected Akaike Information Criterion (*AICc*) calculated for the whole phylogeny of Dictyoptera (assuming no shift of diversification) and seven evolutionary scenarios including a shift of diversification (as specified in the table). For each model, the parameter values of the best-fitting model are reported (rates are in events/Myr). The 'backbone' rates represent the estimated diversification parameters for the tree containing all Dictyoptera species except the termite subclades. The termite subclades are analyzed aside. The *logL*, the number of parameters (*NP*), and *AICc* are thus the sum of the *logL*/parameters/*AICc* of the backbone tree plus the *logL*/parameters/*AICc* of the termite subclade. The best-fitting scenario is determined by  $\Delta AIC$  and *AIC*  $\omega$  and includes a shift within the termites that only include species with 'true' workers in their societies (*scenario 7*, highlighted in bold).

TABLE 2. Supports for eusociality as a driver of diversification

Models	NP	logL	AICc	$\Delta AICc$	AIC $\omega$	$\lambda_0$	$\lambda_1$	$\mu_0$	$\mu_1$	q01	q10
<i>Null model</i>	3	-3831.072	7668.175	218.2023	0	0.1980		0.1786		2.01E-05	
$\lambda_0 \neq \lambda_1, \mu_0 = \mu_1, q_01 = q_10$	4	-3752.206	7512.465	62.492	0	0.1335	0.1867	0.1129		1.64E-05	
$\lambda_0 = \lambda_1, \mu_0 \neq \mu_1, q_01 = q_10$	4	-3773.267	7554.586	104.6133	0	0.1626		0.1441	0.0921	1.24E-05	
$\lambda_0 = \lambda_1, \mu_0 = \mu_1, q_01 \neq q_10$	4	-3830.967	7669.988	220.0149	0	0.1979		0.1784		2.43E-05	4.97E-06
<b><math>\lambda_0 \neq \lambda_1, \mu_0 \neq \mu_1, q_01 = q_10</math></b>	<b>5</b>	<b>-3719.947</b>	<b>7449.973</b>	<b>0</b>	<b>0.887</b>	<b>0.1004</b>	<b>0.4145</b>	<b>0.0766</b>	<b>0.3721</b>	<b>0.3721</b>	
$\lambda_0 \neq \lambda_1, \mu_0 = \mu_1, q_01 \neq q_10$	5	-3752.346	7514.772	64.7993	0	0.1280	0.1815	0.1071		1.81E-05	1.20E-05
$\lambda_0 = \lambda_1, \mu_0 \neq \mu_1, q_01 \neq q_10$	5	-3774.607	7559.294	109.3214	0	0.1541		0.1349	0.0810	1.27E-05	7.40E-06
$\lambda_0 \neq \lambda_1, \mu_0 \neq \mu_1, q_01 \neq q_10$	6	-3720.997	7454.106	4.1336	0.113	0.0910	0.4099	0.0667	0.3674	4.35E-05	5.91E-06

Notes: The table reports the models applied, their number of parameters (*NP*), the means for the log-likelihood (*logL*) and the corrected Akaike Information Criterion (*AICc*), the difference of *AICc* between the best model (lowest *AIC*) and a given model ( $\Delta AICc$ ), the Akaike weight (*AIC $\omega$* ) and the values for each parameter of the corresponding model based on 100 dated trees. The best model is highlighted in bold. Standard errors for each parameter estimate are reported in Table S2.  $\theta$  = non-eusocial and  $I$  = eusocial;  $\lambda$  = speciation rate (one for each character state,  $\lambda I$  is the speciation rate for eusocial species);  $\mu$  = extinction rate (one for each character state,  $\mu I$  is the extinction rate for eusocial species); and  $q$  = transition rate between character states.

TABLE 3. Supports for eusociality with true workers as drivers of diversification

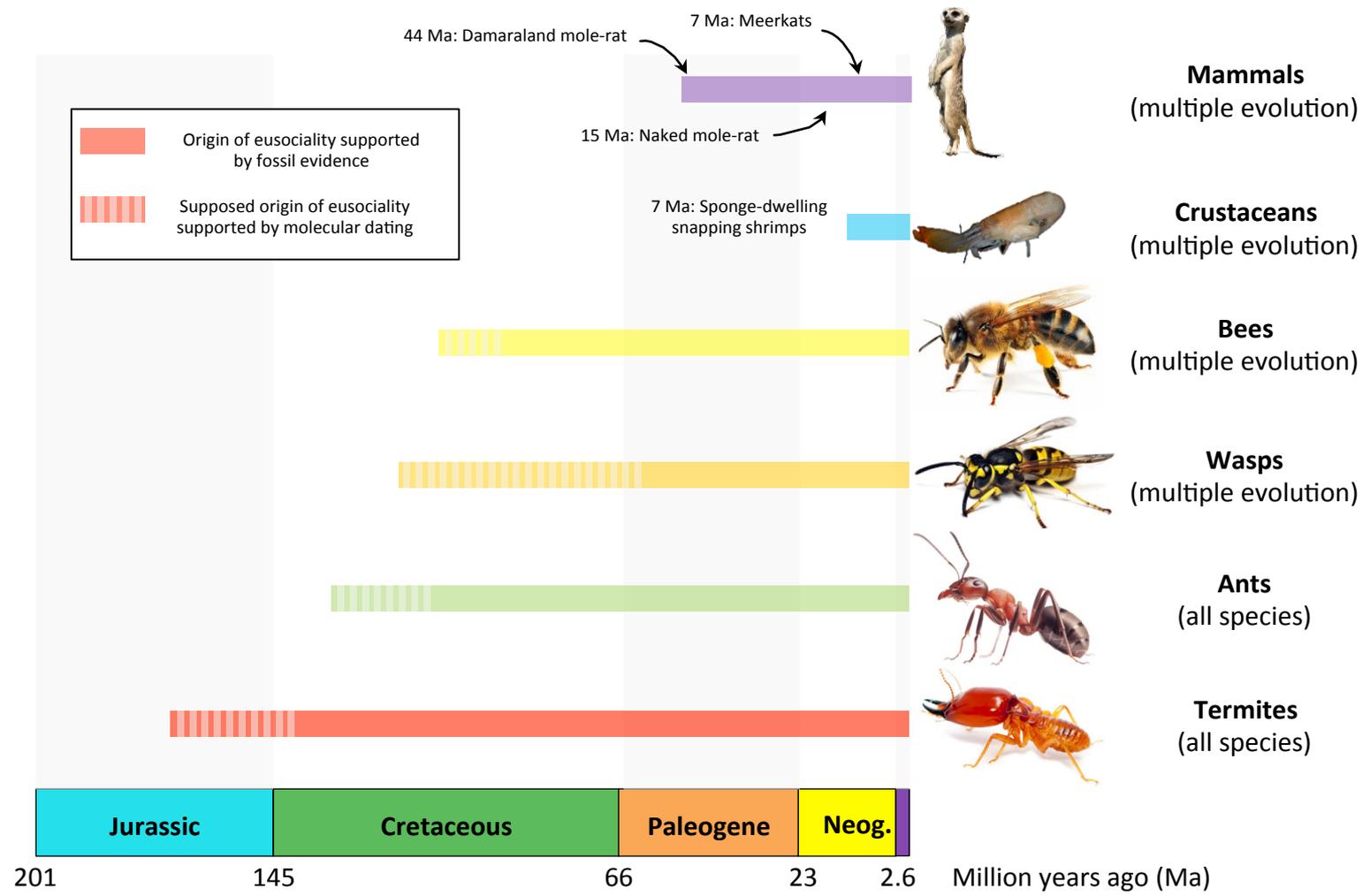
Models	NP	logL	AICc	$\Delta AIC$	AIC $\omega$	$\lambda_1$	$\lambda_2$	$\lambda_3$	$\mu_1$	$\mu_2$	$\mu_3$	q12	q13	q21	q23	q31	q32
<i>Null model</i>	3	-3889.534	7785.100	373.94	0		0.1719			0.1525				4.21E-05			
all $\lambda$ are varying	5	-3717.017	7444.114	32.95	0	0.0683	0.0727	0.1699		0.0438				2.43E-05			
all $\mu$ are varying	5	-3751.789	7513.657	102.49	0		0.1214		0.1020	0.0974	0.0000			1.43E-05			
all $q$ are varying	8	-3879.999	7776.191	365.03	0		0.1713			0.1519		1.29E-05	6.67E-07	1.67E-06	0.00161	4.64E-06	0.00023
all $\lambda$ and $\mu$ are varying	7	-3706.089	7426.327	15.16	$\approx 0.005$	0.0637	0.0580	0.3198	0.0384	0.0266	0.2267			3.85E-05			
all $\lambda$ and $q$ are varying	10	-3703.355	7427.005	15.84	$\approx 0.005$	0.0645	0.0693	0.1736		0.0394		1.55E-05	1.33E-07	7.90E-07	0.00155	9.81E-06	2.73E-06
all $\mu$ and $q$ are varying	10	-3738.133	7496.560	85.40	0		0.1258		0.1067	0.1030	0.0000	1.87E-05	7.14E-08	2.63E-07	0.00043	2.73E-06	0.00044
<b>All rates are free</b>	<b>12</b>	<b>-3693.372</b>	<b>7411.163</b>	<b>0</b>	<b>0.99</b>	<b>0.0649</b>	<b>0.0378</b>	<b>0.3196</b>	<b>0.0398</b>	<b>0.0000</b>	<b>0.2244</b>	<b>1.09E-05</b>	<b>2.43E-07</b>	<b>6.45E-07</b>	<b>0.00224</b>	<b>1.32E-06</b>	<b>0.00027</b>

Notes: 1 = non-eusocial or societies without worker, 2 = societies with pseudergates, and 3 = societies with true workers;  $\lambda$  = speciation rate (one for each character state,  $\lambda 1$  is the speciation rate for species without worker);  $\mu$  = extinction rate (one for each character state,  $\mu 1$  is the extinction rate for species without worker); and  $q$  = transition rate between character states.

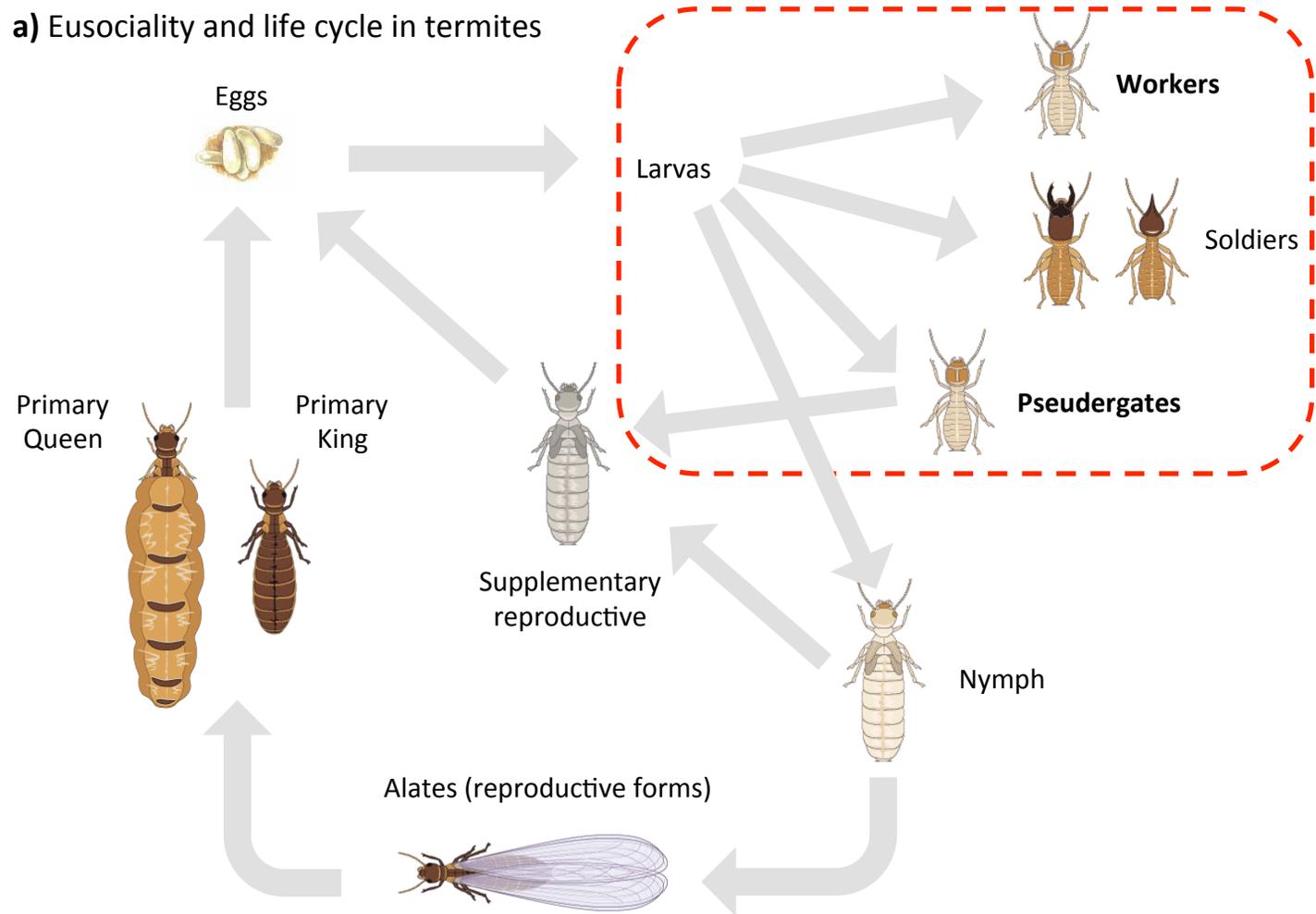
TABLE 4. Supports for gut microbiota as drivers of diversification

Models	NP	logL	AICc	$\Delta$ AIC	AIC $\omega$	$\lambda 1$	$\lambda 2$	$\lambda 3$	$\mu 1$	$\mu 2$	$\mu 3$	q12	q13	q21	q23	q31	q32
<i>Null model</i>	3	-3840.575	7687.181	274.01	0		0.1959			0.1764				3.03E-05			
all $\lambda$ are varying	5	-3710.247	7430.573	17.41	0	0.1166	0.1270	0.2157		0.0941				1.72E-05			
all $\mu$ are varying	5	-3731.518	7473.115	59.95	0		0.1642		0.1456	0.1373	0.0447			1.21E-05			
all q are varying	8	-3835.418	7687.028	273.86	0		0.1957			0.1763		2.40E-05	6.75E-07	4.36E-06	0.00046	1.88E-06	3.10E-06
<b>all <math>\lambda</math> and <math>\mu</math> are varying</b>	<b>7</b>	<b>-3699.510</b>	<b>7413.168</b>	<b>0</b>	<b>0.703</b>	<b>0.1070</b>	<b>0.1894</b>	<b>0.3022</b>	<b>0.0832</b>	<b>0.1652</b>	<b>0.1979</b>			<b>2.39E-05</b>			
ll $\lambda$ and q are varying	10	-3703.777	7427.847	14.68	0	0.1147	0.1254	0.2157		0.0921		1.98E-05	2.74E-07	3.45E-06	0.00025	3.21E-06	2.81E-06
ll $\mu$ and q are varying	10	-3735.700	7491.694	78.53	0		0.1683		0.1500	0.1304	0.0555	2.01E-05	7.33E-07	3.67E-06	0.01504	2.54E-06	0.00221
All rates are free	12	-3695.237	7414.892	1.72	0.297	0.1037	0.1730	0.3033	0.0795	0.1472	0.1975	3.11E-05	4.02E-07	4.87E-06	0.00029	4.52E-06	2.54E-06

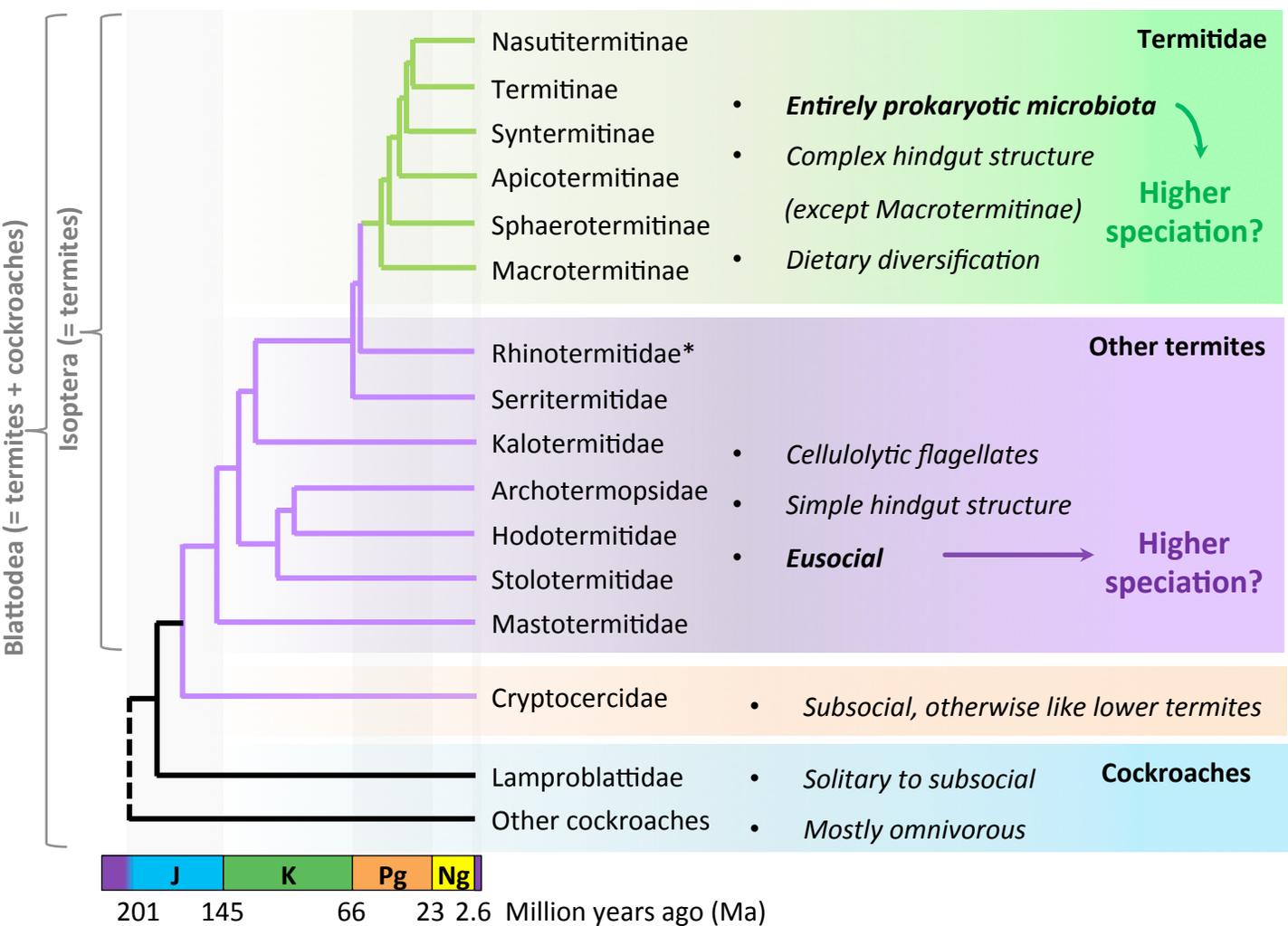
Notes: 1 = gut with no specialized microbiota for lignocellulose digestion, 2\* = gut with cellulolytic flagellates, and 3\* = gut with entirely prokaryotic microbiota;  $\lambda$  = speciation rate (one for each character state,  $\lambda 1$  is the speciation rate for species without microbiota);  $\mu$  = extinction rate (one for each character state,  $\mu 1$  is the extinction rate for species without microbiota); and  $q$  = transition rate between character states. \* Results of alternative coding strategies (see main text) are provided in Figs. S11-S12.



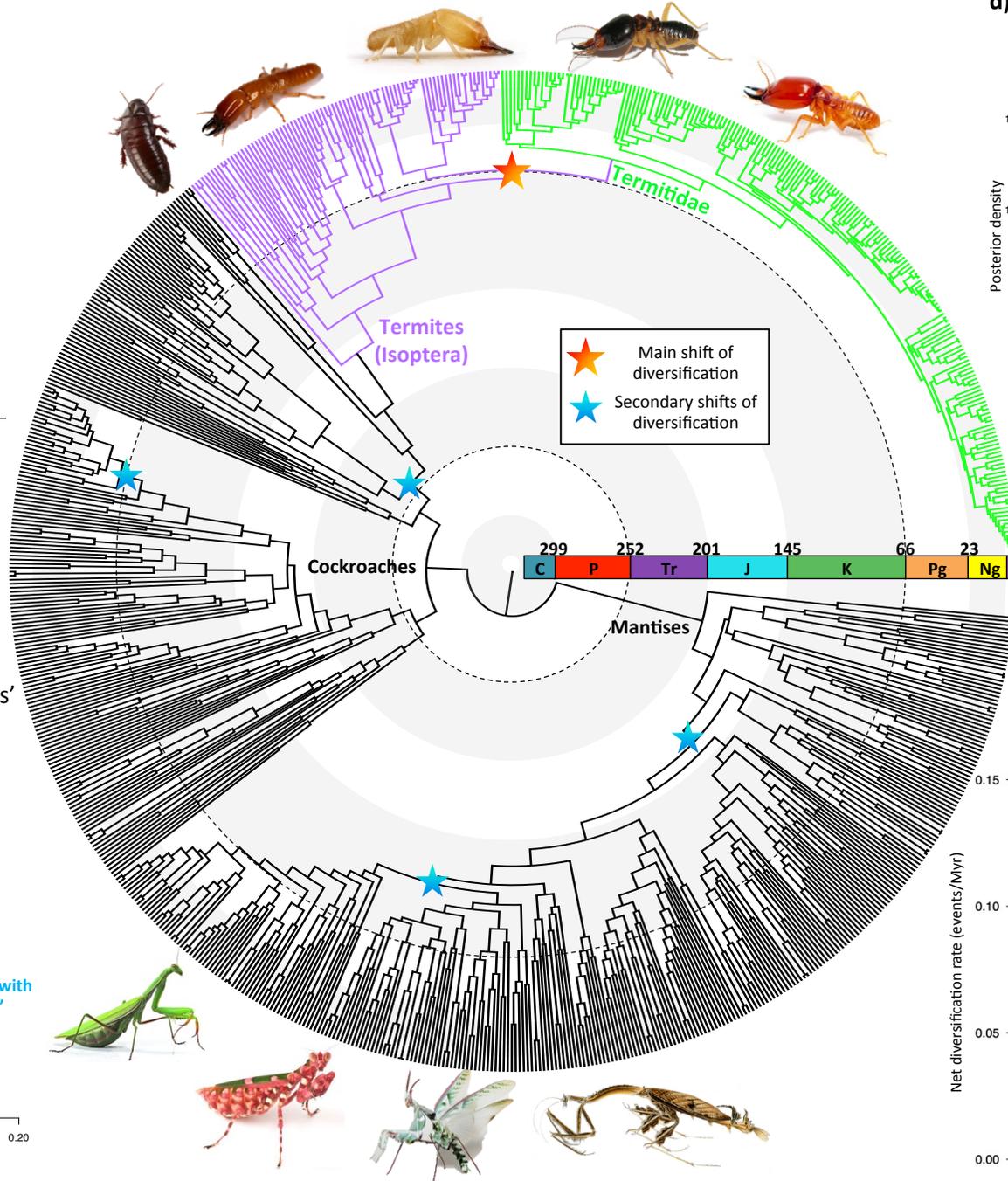
## a) Eusociality and life cycle in termites



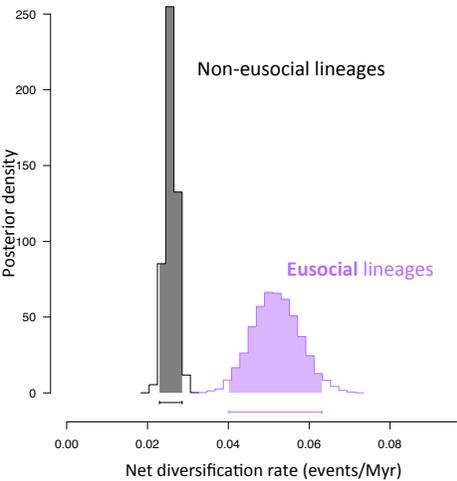
## b) Termite key innovations



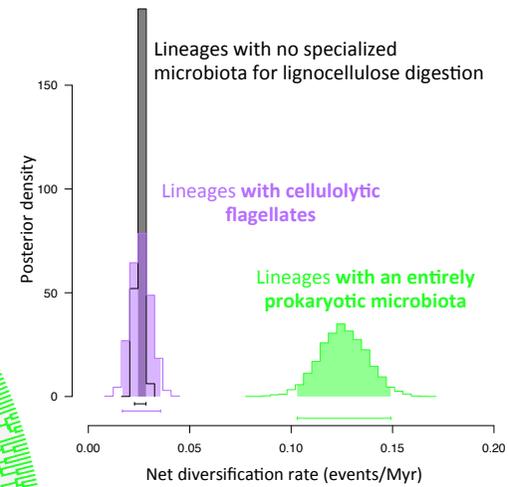
### a) Evolutionary history of Dictyoptera



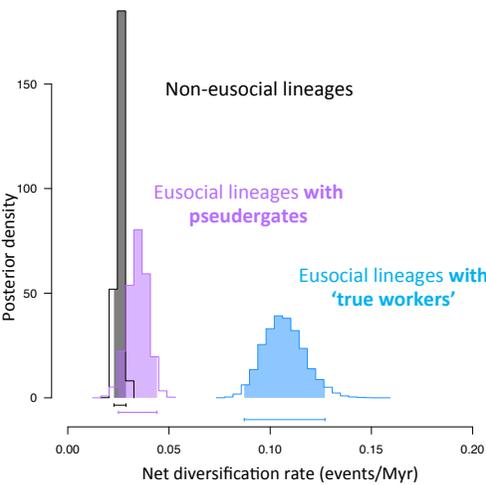
### b) Eusocial lineages diversified faster



### d) Termitidae diversified fast, perhaps due to their hindgut microbiota



### c) Eusocial lineages with 'true workers' diversified even faster



### e) Diversification dynamics through time for termite lineages

