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## Fossil evidence for key innovations in the evolution of insect diversity

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# **Fossil evidence for key innovations in the evolution of insect diversity**

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## 1 **Summary**

2 Explaining the taxonomic richness of the insects, comprising over half of all described  
3 species, is a major challenge in evolutionary biology. Previously, several evolutionary  
4 novelties (key innovations) have been posited to contribute to that richness, including  
5 the insect *bauplan*, wings, wing folding, and complete metamorphosis, but evidence  
6 over their relative importance and modes of action is sparse and equivocal. Here, a new  
7 dataset on the first and last occurrences of fossil hexapod (insects and close relatives)  
8 families is used to show that basal families of winged insects (Palaeoptera e.g.  
9 dragonflies) show higher origination and extinction rates in the fossil record than basal  
10 wingless groups (Apterygota e.g. silverfish). Origination and extinction rates were  
11 maintained at levels similar to Palaeoptera in the more derived Polyneoptera (e.g.  
12 cockroaches) and Paraneoptera (e.g. true bugs), but extinction rates subsequently  
13 reduced in the very rich group of insects with complete metamorphosis (Holometabola  
14 e.g. beetles). Holometabola show evidence of a recent slow-down in their high net  
15 diversification rate, whilst other winged taxa continue to diversify at constant but low  
16 rates. These data suggest that wings and complete metamorphosis have had the most  
17 effect on family level insect macroevolution, and point to specific mechanisms by which  
18 they have influenced insect diversity through time.

19 **Keywords:** adaptive radiation, extinction, flight, Hexapoda, macroevolution, complete  
20 metamorphosis

21

## 22 1. Introduction

23 Why some groups of organism are very speciose, whilst others are species-poor, is a  
24 problem that has fascinated evolutionary biologists ever since Darwin [1–3]. The  
25 insects, with over half of all described species [4,5], have long stood out as a very  
26 speciose group whose richness requires explanation [6]. Of the many hypotheses  
27 proposed to explain this richness, some of the most prominent include the origin of  
28 novel phenotypic characters known as key innovations [7]. Here we use a new dataset  
29 on the fossil record of the hexapods (insects and their six-legged relatives such as  
30 springtails) to assess the relative importance of, and mechanisms underlying, several  
31 putative key innovations.

32 Macroevolutionary approaches to understanding current standing diversity require  
33 data on the past history of life, which comes from two complementary sources of  
34 information [8]. The neontological approach uses phylogenies of extant taxa to infer  
35 changes in past processes [9]. The palaeontological approach uses information from the  
36 fossil record [10]. Phylogenies of extant taxa allow one to study processes at the species  
37 level and in the absence of a fossil record, but inferences about speciation and extinction  
38 rates are problematic (e.g. [11]). Fossils, although often studied at taxonomic levels  
39 above the species, and though prone to sampling biases [12], provide direct evidence  
40 about the timing of changes in rate, as well as extinctions [13].

41 Ultimate causes of macroevolutionary change can include extrinsic factors such as  
42 environmental change [14,15], as well as intrinsic ones such as evolutionary novelties  
43 [16]. Key innovations are novel phenotypic characters such as morphologies,  
44 behaviours, or developmental strategies that enhance species richness [8,17], seen  
45 through an increase in net diversification rate. The underlying macroevolutionary

46 process could be an increase in speciation, decrease in extinction or some combination  
47 of changes in both. Three general ecological mechanisms have been proposed to explain  
48 the macroevolutionary effects of key innovations [8], corresponding to changes in three  
49 macroevolutionary parameters [7]: a) escape from competition into a new adaptive  
50 zone, thus changing the carrying capacity of taxa in the environment; b) decreasing the  
51 probability of extinction; and c) ecological or reproductive specialization, thus  
52 increasing the speciation rate. For neontological studies, explicit data supporting these  
53 macroevolutionary parameters may be lacking because they work with the net outcome  
54 rather than the underlying origination and extinction rates, making it hard to tease the  
55 different underlying parameters apart. In contrast, fossil studies are intrinsically better  
56 able to provide data on these different macroevolutionary parameters, thus aiding  
57 inference of the mechanism.

58 Four progressive evolutionary steps have traditionally been recognized in the  
59 evolutionary history of the hexapods, based on the sequence in which they appear in the  
60 fossil record [18,19] and phylogenies (e.g. [20]) (figure 1). These are the evolution of  
61 the insect *bauplan* in wingless insects, wings, wing folding, and complete  
62 metamorphosis (figure 1). Evidence that acquisition of these features increased net  
63 diversification rates, and are therefore key innovations, has largely come from sister-  
64 group species-richness comparisons across orders [21,22], suggesting that shifts in net  
65 diversification rate occurred at or after the origin of wings. However, the results of  
66 these studies are sensitive to phylogenetic uncertainties [22], give no indication of  
67 which macroevolutionary parameters may have changed [21], and may be biased by the  
68 low phylogenetic resolution and simple macroevolutionary models employed (e.g. [11]).  
69 Fossil studies have been rare, but Yang [23] used Lyellian survival analysis on family

70 level data [24] to suggest that extinction rates do not differ between Holometabola and  
71 Paraneoptera, and hence that differences in origination rates probably account for the  
72 larger increase in families in Holometabola. However, Yang only considered this single  
73 key innovation, and the dataset on which his study was based is now considerably  
74 dated. Since 1994 there have been major changes to insect taxonomy (e.g. [25]), the  
75 estimated ages of deposits (e.g. [26]), about 400 additional insect families are known  
76 from the fossil record [27] and 21% of the families in Labandeira [24] have since been  
77 synonymised.

78 Here we use a new compilation of the first and last occurrences of fossil hexapod  
79 families to test for the effects of potential key innovations, by seeking tell-tale significant  
80 differences in the rates of origination, extinction, and accumulation of taxa across major  
81 morphological groupings (figure 1). Specifically, we test for the effect of the insect  
82 *bauplan* by comparing non-insect Entognatha (e.g. springtails) with ectognathan  
83 Apterygota (e.g. silverfish); for the effect of wings by comparing primitively wingless  
84 hexapods (Apterygota) with the primitive winged Palaeoptera (e.g. dragonflies); for the  
85 effect of wing folding by comparing Palaeoptera (which cannot fold their wings) with  
86 Polyneoptera (e.g. cockroaches, which can); and we test for complete metamorphosis by  
87 comparing Holometabola (e.g. beetles, with metamorphosis) with their sister group  
88 Paraneoptera (e.g. true bugs, without metamorphosis) (figure 1). We examine the shape  
89 of the temporal accumulation of taxa across the different groups, and associations  
90 between richness and rates within and across taxa, to test for constraints on richness,  
91 and whether certain key innovations might have elevated diversification rates.

## 92 **2. Methods.**

### 93 **(a) Data collection**

94 Starting with the dataset of Ross & Jarzembowski [28], searches were made of the  
95 published literature to the end of 2009 for the earliest and latest occurrence (stage  
96 resolution) of each fossil family of Hexapoda. Families were classified into higher taxa  
97 following the widely adopted Eur-American scheme [5], with some differences due to  
98 recent revisions (see Supplementary Material). Where there was disagreement over the  
99 taxonomic status of a specimen or family, a consensus approach was taken. The  
100 timescale of Ogg et al. [29] was adopted to date stages.

### 101 **(b) Data analysis**

102 Adjacent geological stages were aggregated to form time bins of approximately equal  
103 length (mean, SD  $9.87 \pm 3.1$  Myr) (see Supplementary Material). Per capita origination  
104 and extinction rates were estimated using Foote's [30] metrics  $\hat{p}$  and  $\hat{q}$  which help  
105 control for variation in interval duration and sampling intensity because they are  
106 instantaneous rates and ignore single interval taxa which are more susceptible to  
107 sampling bias. As the rates time series are highly right skewed (figure S2) and log-  
108 transformation does not normalise their distribution, they were compared across  
109 taxonomic groups using non-parametric Friedman tests. Because the time series began  
110 at different intervals for different groups, tests were implemented pairwise so as not to  
111 discard data unnecessarily, and to reduce Type 1 errors (false positives), tests were  
112 limited to the most essential hypotheses. Because there are so few families of  
113 Apterygota, comparisons between Entognatha and Ectognatha lacked power and were  
114 not pursued beyond these initial basic analyses, which failed to show any significant  
115 differences between them (see Results).

116 Diversification models were investigated using nonlinear least-squares regressions on  
117 the clade richness data through time, with time coded relative to the present (i.e.



118 negative numbers becoming less negative through time). Linear, exponential, logistic  
119 and Gompertz models were fitted using the `nls()` function from the `nlrwr` package,  
120 and the preferred model for each clade identified by comparison of AICc values [31,32]  
121 using the `akaike.weight()` function in the `qpcR` package in R [33; supplementary  
122 information]. For Palaeoptera and Polyneoptera, logistic and Gompertz model runs  
123 failed to converge on a solution. Examination of terminated model runs showed  
124 selection for an ever-increasing (and unrealistically large) value of the richness  
125 asymptote. The fitted values resembled exponential or linear growth, with little sign of a  
126 richness asymptote in the data, whilst the AICc scores were relatively high, indicating  
127 that the assumption of a richness asymptote was inappropriate. For these cases, model  
128 runs were terminated after 500 iterations and output for illustrative purposes, noted  
129 where appropriate in Table 1.

130 Associations between richness, origination and extinction in the time series for different  
131 groups were investigated using bivariate correlation of the first differences. First  
132 differencing is a simple detrender that removes short-term autocorrelation, long term  
133 patterns and the spurious correlations that may derive from them, as well as removing  
134 random walk effects. Significance was assessed using bootstrapping of the test statistic  
135 to reduce the necessary underlying assumptions about the data.

### 136 **3. Results**

#### 137 **(a) Origination and extinction rates**

138 Instantaneous per capita family origination and extinction rates [30] are mostly low but  
139 with occasional high values, mostly restricted to the early half of the record (figure 2).

140 Unsurprisingly, origination rates are generally higher than extinction rates in all  
141 morphological groups (figure 2, table S1). Through time, however, there is

142 heterogeneity in the difference between these rates. There are intervals when extinction  
143 rates temporarily outweigh origination rates, most noticeably during the Permian (299–  
144 251Ma) in Palaeoptera and Polyneoptera, but not in Holometabola (figure 2), and Upper  
145 Triassic (229–200Ma) in Polyneoptera. Episodes when origination rates are much  
146 higher than extinction rates include the Pennsylvanian (318–299Ma), Lower Triassic  
147 (251–246Ma), Barremian (130–125Ma), and Eocene (56–34Ma) (figure 2 and  
148 Supplementary Data). Both rates are higher for Palaeoptera than Apterygota (Friedman  
149 tests,  $p < 0.0001$ ). However, origination rates do not differ significantly between  
150 Palaeoptera and Polyneoptera, or Paraneoptera and Holometabola (figure 2, table S2,  
151 figure S1). Extinction rates do not differ significantly between Palaeoptera and  
152 Polyneoptera (figure 2, table S2, figure S1), but are significantly lower in Holometabola  
153 than Paraneoptera (Friedman test,  $p = 0.041$ ). The median net diversification rate is  
154 highest in Holometabola and lowest in Apterygota, and differs significantly between  
155 them (Friedman test,  $p = 0.02$ ), but not between other groups (figure 2, table S2).

156 **(b) Rates of family accumulation and correlations amongst time series.**

157 The best-fit diversification model varies by clade: logistic for Apterygota, exponential  
158 for Palaeoptera and Polyneoptera, and Gompertz for Paraneoptera and Holometabola  
159 (figure 3), although for Paraneoptera the exponential and logistic models are only  
160 marginally worse, as is the linear model for Polyneoptera (see table 1). This indicates a  
161 decrease in the rate of accumulation of taxa in the more-derived and richer  
162 Paraneoptera and Holometabola (most strongly in the latter) towards the present, with  
163 the more-basal Palaeoptera and Polyneoptera showing no slow-down in diversification  
164 despite an overall slow rate of taxon accumulation (figure 3). There is also a strong

165 preference for a logistic growth model for Apterygota, indicating a low current rate of  
166 diversification.

167 The first differences in log richness were most highly correlated between Paraneoptera  
168 and Holometabola ( $r = 0.848, n = 29, p < 0.001$ ), and between Palaeoptera and  
169 Polyneoptera ( $r = 0.623, n=29, p < 0.01$ ), reflecting similar short-term richness  
170 trajectories in those pairs of taxa (figure 3). First differences in richness were negatively  
171 correlated with future (1 interval step) origination in Palaeoptera ( $r = -0.627, n = 28, p <$   
172  $0.001$ ), Polyneoptera ( $r = -0.540, n = 28, p < 0.05$ ), Paraneoptera ( $r = -0.657, n = 28, p <$   
173  $0.001$ ) and Holometabola ( $r = -0.548, n = 28, p < 0.001$ ). However, there was no  
174 significant relationship between the first differences in extinction rate and future  
175 origination rate except in Palaeoptera, where it was negative ( $r = -0.505, n = 28, p <$   
176  $0.01$ ). There were significant positive relationships between (first differences in)  
177 Holometabola richness and Polyneoptera extinction ( $r = 0.651, n = 29, p < 0.001$ ) and  
178 Palaeoptera extinction ( $r = 0.556, n = 29, p < 0.05$ ), whilst first differences in  
179 Holometabola richness are also negatively correlated with future richness in  
180 Polyneoptera ( $r = -0.549, n = 28, p < 0.05$ ) and Palaeoptera ( $r = -0.569, n = 28, p < 0.01$ ).

#### 181 **4. Discussion**

182 Net rates of diversification vary across taxa [21] but are also highly heritable in the  
183 hexapods [34]. These facts, long casually observed, have suggested that key  
184 evolutionary changes have been responsible for generating much of the richness in this  
185 very diverse group, and four such evolutionary innovations have held centre stage  
186 [18,19]: the insect *bauplan* [35], wings [36], wing folding [21] and complete  
187 metamorphosis [23]. Here we have reported evidence that both fossil family origination  
188 and extinction rates increased in groups that have wings but not the other key

189 innovations, whilst insects with complete metamorphosis have lower extinction rates  
190 than their sister group without this innovation. There is evidence from the most derived  
191 groups that the rate at which described richness accumulates has slowed through their  
192 history, with taxonomic replacement evident between Palaeozoic and post-Palaeozoic  
193 faunas. These results suggest specific modes by which taxonomic richness has been  
194 generated by key innovations in the hexapods.

195 The contrast between the rates of origination and extinction in Palaeoptera and  
196 Apterygota, taken at face value, suggests that the origin of wings, in-of-itself, led to large  
197 macroevolutionary changes, a fact that has long been suspected [36], although the  
198 phylogenetic evidence for this is equivocal since the richness of Palaeopteran orders is  
199 not very much greater than that of some apterygote orders [21]. Previous authors have  
200 suggested that dispersal via wings could not only lower rates of extinction (e.g. [37]), for  
201 example via increased immigration rates within metapopulations, but also raise  
202 speciation rates via dispersal to isolated habitat patches [7]. Our data indicate that  
203 winged insects had both increased speciation and extinction rates. Many Paleozoic  
204 Palaeoptera families did not survive into the Mesozoic (figure 2), suggesting that the  
205 Permo-Triassic extinction is one reason for the high extinction rates in this group,  
206 although extinction rates also remained high after the P-T boundary (figure 2). *Prima*  
207 *facie*, this suggests that susceptibility to extinction has tempered the evolutionary  
208 potential of basal winged insects. It is debateable, on the strength of this evidence,  
209 whether wings should be regarded as a key innovation in of themselves, as the  
210 difference between the speciation and extinction rates is not significantly greater than  
211 Apterygota, and family richness, like species richness, is not particularly enhanced  
212 (figure 3).

213 The other potential key innovation highlighted by our results is complete  
214 metamorphosis. A decline in extinction in Holometabola was previously proposed by  
215 Ross et al. [38] who considered Holometabola less susceptible to mass extinction than  
216 other groups. However, another fossil analysis [23] suggested that origination rates  
217 have increased in Holometabola, and suggested that extinction rates are unchanged. Our  
218 results suggest that the difference between the origination and extinction rate has  
219 widened in more derived groups, despite origination rates generally declining. There  
220 are a number of differences between our analyses and Yang's [23] including the  
221 underlying data, the rate metrics used, and the analytical approaches. In all these  
222 characteristics we consider our analysis to be an improvement: the data take account of  
223 more recent discoveries (including 400 more families); we use more robust rate metrics  
224 (estimated per capita rates ignoring single-interval taxa); we use statistical approaches  
225 that take account of repeated measures; we assess origination and extinction directly  
226 and in ways that account for the whole of the time series available (as opposed to  
227 Lyellian survival analysis which mainly reflects the latter part of the time series). How  
228 extinction rates might be lowered by metamorphosis has been little discussed:  
229 metamorphosis might allow greater buffering from environmental variability in the  
230 protected pupal stage [38], faster development, higher population sizes, and reduced  
231 intraspecific competition between adult and offspring. All plausible and testable  
232 contributors [5].

233 The richness time series of the different taxa appear *prima facie* consistent with the  
234 macroevolutionary changes described above. Over the majority of the time series,  
235 richness is highest in the derived Holometabola, and lowest in the basal Apterygota  
236 (figure 2, figure S4). Palaeozoic richness was dominated by Palaeoptera and

237 Polyneoptera, which gave way to the more derived groups Paraneoptera and  
238 Holometabola (see also [39]), with lower extinction rates. This reflects a more general  
239 tendency in the fossil record for high turnover groups to dominate the earlier record  
240 [40]. The first differences in the time series confirm that these pairs of taxa (Palaeoptera  
241 and Polyneoptera; Paraneoptera and Holometabola) show very similar short-term  
242 trajectories. Only Holometabola and Apterygota show clear evidence of a slow-down in  
243 the rate of addition of taxa (figure 3, table 1), although with Apterygota it is difficult to  
244 say if this is simply due to the paucity of data from the fossil record. Palaeoptera and  
245 Polyneoptera best fit exponential or linear models of diversification, implying that limits  
246 to family richness, if there are any, have not yet been met by these groups. By contrast,  
247 the Holometabola only show signs of possible limits to richness after attaining  
248 considerably higher richness than the less derived Palaeoptera and Polyneoptera, limits  
249 that are apparently not yet fully attained. The Paraneoptera show signs of a slow-down  
250 with a preferred Gompertz growth model, but the evidence for this is not much better  
251 than that for an exponential model (table 1). These patterns of richness through time  
252 provide equivocal support for the idea of new adaptive zones [17]: Holometabola have  
253 attained richnesses far above those ever achieved by the other taxa, but there is not  
254 strong evidence that the richness has been constrained by carrying capacity limits in  
255 Paraneoptera, Palaeoptera, or Polyneoptera. The latter clades therefore conform to  
256 other terrestrial studies showing exponential clade growth [e.g. 41–44], whilst the  
257 others conform to a pattern that may be more common in marine taxa [but see 45].  
258 Whilst increases in richness tend to be associated with decreases in future origination,  
259 which in the marine record has been interpreted as density-dependent cladogenesis  
260 [13], in insects it likely simply reflects the episodic nature of origination in the record  
261 [5], an interpretation supported by the lack of a predicted positive relationship between

262 current extinction and future origination [13]. The associations between increases in  
263 Holometabola richness and current extinction and future reductions in richness in  
264 Polyneoptera and Palaeoptera may suggest that the latter faunas have been negatively  
265 affected by the rise of more derived faunas.

266 Our data provide no support for the idea that the basic or primitive insect *bauplan* is a  
267 key innovation, in common with previous phylogenetic tests [21,22]. Zeh et al. [35]  
268 made the case for modification to the egg and egg-laying apparatus in apterygote insects  
269 as a key innovation, though as with wings, the low diversity of basal groups with this  
270 innovation suggests that it is insufficient for generating high diversity, though perhaps  
271 necessary. There is also little support for wing folding, and in fact Polyneoptera show a  
272 marginally non-significant decline in origination rates relative to Palaeoptera (Table  
273 S2), as well as a quite similar richness. It is however likely that the diversity of  
274 Holometabola is in some way contingent [16] on this innovation given the richness of  
275 species, such as beetles, that depend on it.

276 Recently, analyses of fossil richness and rates have paid much attention to the effect of  
277 sampling bias through time as an explanation for patterns (e.g. [12,44–46]). Since our  
278 analyses focus on variability across groups rather than through time, and because it is  
279 doubtful that even standardized subsampling of occurrence data could eliminate the  
280 taphonomic biases that likely accrue across time intervals in hexapods, this issue is less  
281 important than an alternative one; that sampling may be biased due to uneven  
282 preservation potential of different taxa. However, Labandeira & Sepkoski [39] tested  
283 variation in preservation potential across orders by observing the correlation between  
284 the number of extant families per order and the number fossilized in the latest Tertiary.  
285 They found a very high correlation in which the only outlying order was Lepidoptera,

286 suggesting little support for such bias at the scale of this analysis. Standardized  
287 estimates of richness through time would likely depress the apparent growth of clades  
288 near the present [46], but are unlikely to affect the rank order of richness across the  
289 major taxa considered here.

290 Our analyses suggest a new model of insect macroevolution; that of a major up-shift in  
291 both family-level origination rates and extinction rates (but not net diversification rate)  
292 with the origin of wings, giving rise to a group of families vulnerable to extinction. This  
293 was followed by a decline in extinction rates in Holometabola, allowing richness to rise  
294 towards an apparent limit that has never been attained by the other groups. In this  
295 latter respect, Holometabola conform to the classical notion of an adaptive radiation  
296 [17]. The mechanism of change, through a reduction in sub-clade extinction rate [17],  
297 has also been suggested as an explanation for the radiation of the angiosperms [47]. In  
298 contrast, there is little evidence from the fossil record that wing folding or the insect  
299 *bauplan* were sufficient to alter insect family macroevolution, although they may have  
300 been necessary. The different extinction propensities of taxa shown here may also imply  
301 differing resistance to anthropogenic extinction, and hence contribute to debate on the  
302 vulnerability of extant insects to environmental change [7]. In the future, better-  
303 resolved phylogenetic studies may allow additional tests of the importance of  
304 metamorphosis and there is a need to elucidate the ecological or life history  
305 determinants of the proximate macroevolutionary forces suggested above.

306

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313 **Data accessibility.** Data presented in this paper are available as an Electronic Data  
314 Supplement.

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- 426

427 Fig. 1 Four putative hexapod key innovations, together with the taxa defined by them  
428 [7].

429

430 Fig 2. Family level origination ( $\hat{p}$  - solid lines) and extinction rates ( $\hat{q}$  - dashed lines)  
431 through time in the five major groups of hexapods.

432

433 Fig 3. Accumulation of hexapod families through time in the major groups. The thick  
434 lines show the fitted values of different models. **Apt** (circles) = Apterygota (logistic  
435 model), **Pal** (Xs) = Palaeoptera (exponential model), **Poly** (squares) = Polyneoptera  
436 (exponential model), **Para** (triangles) = Paraneoptera (Gompertz model), **Holo** (+s) =  
437 Holometabola (Gompertz model). Relative support for these models can be seen in table  
438 1.

439

440 **Table 1. Competing nonlinear least squares models for clade diversification, with**  
 441 **AICc scores.** Parameters: Linear a, b; Logistic/Gompertz a, b and c; Exponential  $y_0$ , b;  
 442 NULL intercept only. Parameter significance levels: \* < 0.05; \*\* < 0.01; \*\*\* < 0.001. Note  
 443 that significance may be inflated due to autocorrelation in the time series.

Model	Par 1	Par 2	Par 3	AICc	$\Delta$ AICc	AICc weight	R <sup>2</sup>
<b>Apterygota</b>							
logistic	17.087***	5.757***	0.053***	143.64	0.00	0.74	0.9139
Gompertz	17.363***	0.009	0.040***	145.70	2.06	0.26	0.9083
exponential	22.111***	104.115***	–	157.41	13.77	0.00	0.8593
linear	16.013***	0.057***	–	179.92	36.28	0.00	0.7217
NULL	7.000***	–	–	219.86	76.22	0.00	–
<b>Palaeoptera</b>							
exponential	40.277***	307.667***	–	255.23	0.00	0.69	0.3097
linear <sup>§</sup>	35.998***	0.067**	–	257.78	2.55	0.19	0.2544
Gompertz <sup>§</sup>	22040	6.497	2.82×10 <sup>-4</sup>	260.26	5.02	0.06	0.2533
logistic	1405	-3.737	0.002	260.40	5.17	0.05	0.2500
NULL	25.364***	–	–	265.195	9.96	0.00	–
<b>Polyneoptera</b>							
exponential	52.049***	496.706**	–	260.73	0.00	0.47	0.2817
linear	50.136***	0.073**	–	261.38	0.64	0.34	0.2675
logistic <sup>§</sup>	169.5	-0.880	0.002	263.66	2.93	0.11	0.2707
Gompertz <sup>§</sup>	6414	4.903	2.882×10 <sup>-4</sup>	264.20	3.46	0.08	0.2588
NULL	38.52***	–	–	269.38	8.65	0.00	–
<b>Paraneoptera</b>							
Gompertz	1210.72	2.147	0.997***	221.82	0.00	0.60	0.9647
exponential	149.643***	133.714***	–	223.93	2.10	0.21	0.9591
logistic	331.46	29.69	103.58***	224.06	2.24	0.19	0.9620
linear	124.714***	0.434***	–	236.49	14.67	0.00	0.9386
NULL	60.097***	–	–	320.72	98.90	0.00	–
<b>Holometabola</b>							
Gompertz	745.8***	0.522**	0.993***	301.46	0.00	0.95	0.9739
logistic	519.148***	-95.47***	59.354***	307.41	5.95	0.05	0.9686
linear	411.201***	1.525***	–	324.40	22.93	0.00	0.9423
exponential	508.75***	116.8***	–	324.73	23.27	0.00	0.9417
NULL	176.44***	–	–	413.68	112.22	0.00	–

444 <sup>§</sup>Model run terminated and output after 500 iterations due to non-convergence (see

445 Methods for explanation).

446







