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Explaining global insect species richness: lessons from a decade of macroevolutionary entomology

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Explaining global insect species richness: lessons from a decade of macroevolutionary entomology

26 Running title: Insect macroevolution

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52 Key words: biogeography, climate change, comparative method,
53 diversification, extinction, fossil record, herbivory, Hexapoda, key
54 innovation, macroevolution, phylogeny, speciation
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1 Abstract

2 The last ten years have seen more research on insect macroevolution than all the
3 previous years combined. Here I summarize and criticise the claims that have been
4 made by comparative phylogenetic and fossil studies, and identify some future
5 opportunities. We know the fossil record and phylogeny of insects much better than
6 we did ten years ago. We cannot simply ascribe the richness of insects, or their
7 subtaxa, to either age or diversification rate. There is evidence that fossil family
8 richness peaked much earlier than previously suspected. Phylogenetic evidence
9 however suggests that species-level net diversification rates are accelerating, though
10 this is highly variable across taxa, implying ongoing changes in global taxonomic
11 composition. Although there is evidence that wings and metamorphosis have had
12 some macroevolutionary effects, the most definitive broad phylogenetic study does
13 not suggest that they directly elevated net diversification of species. There is little
14 evidence that insect body size influences net diversification rate. Compared to other
15 phyla, arthropod richness, of which insects comprise the major part, is best explained
16 by non-marine habit, presence of parasitic lifestyles, a skeleton, vision and dioecy.
17 Herbivory cannot yet robustly be said to increase diversification over other diets
18 across all insects: there are contrary analyses, and effects differ in different taxa.
19 Many phylogenetic studies now document how it sometimes does: from co-speciation,
20 to diffuse coevolution with host shifting. The last decade has shown that climate
21 change and biogeographic processes are likely important in generating or limiting
22 insect diversification, but there is a need for greater statistical rigour in such studies.
23 There is also a need to understand the validity of some widely used statistical methods
24 better, and to make better use of the data and methods that exist. Macroevolutionary
25 entomology could greatly benefit from online data integration platforms to facilitate
26 analyses of broader scope.

32 Introduction

33 Every entomologist needs an opinion about why there are so many insect species
34 because insect richness is one of the chief justifications for studying them at all. I like
35 to imagine that the proverbial exobiologist from Mars, landing on Earth for the first
36 time, would very quickly be persuaded that macroevolutionary entomology should be
37 a top priority. To help inform these opinions amongst humans, and any Martians out
38 there who might be reading, I previously published a review on the macroevolutionary
39 explanations for insect species richness, focussing on **comparative** evidence from
40 fossils and phylogenies, (Mayhew, 2007). I hoped to widen appreciation of what we
41 had actually discovered about this question, and encourage others to fill the remaining
42 gaps.

43 Ten years after publication, an update of that paper was timely. The data
44 needed to support studies of insect macroevolution have increased substantially over
45 the last decade. The total number of described fossil insect families has increased by
46 over 400 since 1994, whilst over half of the previously known families have different
47 known stratigraphic ranges (Nicholson et al., 2015). Insects also now have a
48 significant presence in the Paleobiology Database which allows a broader suite of
49 analytical tools to be applied to taxonomic occurrence data, controlling for many of
50 the biases in the raw fossil record (Clapham et al., 2016; Condamine et al., 2016). A
51 major use of fossil insect data is also now to time-calibrate molecular phylogenies
52 (Parham et al., 2012; Wolfe et al., 2016), something that had barely been attempted
53 ten years ago. The need to do this accurately has put a premium on accurate fossil
54 identification and new technologies have begun to impact this (Haug & Haug, 2017;
55 Perreau & Tafforeau, 2011).

56 Genomic and transcriptomic data have now begun to resolve some of the most
57 difficult questions in hexapod phylogenetics (Johnson et al., 2013; Kawahara &
58 Breinholt, 2014; Misof et al., 2014; Peters et al., 2017; Timmermans et al., 2014;
59 Wahlberg et al., 2013; Wiegmann et al., 2011), whilst the cheapness and availability
60 of widely applicable molecular markers on the one hand, and new analytical tools on
61 the other, means that we can also build much larger and more inclusive phylogenies
62 (Chesters, 2017; Rainford et al., 2014). Perhaps one of the most important changes
63 has been the development and application of new statistical techniques for testing
64 hypotheses about diversification from phylogenies of extant taxa (Alcala et al., 2017;

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3 65 Alfaro et al., 2009; FitzJohn et al., 2009; Maddison et al., 2007; Meredith et al., 2011;
4 66 Mundry, 2014; Rabosky, 2007; 2014). These techniques mean that it is quite rare for a
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6 67 phylogenetic study not to apply them in some way, and get a “diversification”
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8 68 storyline. In some other ways the current decade has not changed much from the
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10 69 preceding one; insects are still poorly known with respect to current extinction risk
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12 70 (Collen et al., 2012; Stuart et al., 2010); most data come from the usual groups in the
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14 71 usual parts of the world; and we still have little idea of the actual richness of many
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16 72 diverse groups. These are problems for which solutions require longer timespans.

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18 73 As well as a change in the approaches used to study insect diversification, the
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20 74 last decade has seen a change in the questions addressed. There has been one notable
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22 75 new hypothesis: Ferns & Jervis (2016) speculated that sclerotized forewings might
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24 76 have promoted species richness across insect orders. Whilst that hypothesis has
25
26 77 previously been promoted with respect to narrower taxonomic groups (Coleoptera)
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28 78 (Linz et al., 2016) it has been interesting to see this applied more generally. Many
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30 79 recent studies have also highlighted the diversifying effects of paleoenvironmental
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32 80 (e.g. climatic) and biogeographic (e.g. vicariance) events. Whilst it is likely that these
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34 81 events affect a great diversity of taxa, there are reasons to suspect that they may apply
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36 82 particularly to specialized insects such as many herbivorous clades (Kergoat et al.,
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38 83 2016; Nyman et al., 2012). The review reflects this with new sections. The number of
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40 84 proximate studies testing diversity-dependent diversification and ultimate studies
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42 85 devoted to interspecific interactions has been vast in the last decade, whilst the effects
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44 86 of mating system and sexual selection have been relatively ignored, at least in this
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46 87 context. In almost every area, however, **there have been significant new findings.**

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48 88 Despite this progress, **our data and techniques are far from perfect.** The insect
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50 89 fossil record, valuable as it is, is not as complete as we would like. Nor is our
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52 90 knowledge of insect phylogeny, the distribution of species richness across taxa, other
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54 91 trait distributions, and the current extinction risks of extant species. This means that
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56 92 **we cannot apply ideal analytical techniques.** There are two defensible attitudes to a
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58 93 situation like this in science: wait it out until the data and techniques improve, so as to
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60 94 avoid adopting wholly false views of the universe, **or continue to perform studies as**
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62 95 **stepping stones to better ones, and using a critical attitude to identify weaknesses and**
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64 96 **future improvements.** I believe that the latter approach is going to get us to accurate
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66 97 answers quicker, **and for that reason I not only summarize recent findings, but point**
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68 98 **out improvements that can be made.**

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3 99 It was convenient to keep the broad scope and framework of the previous
4 100 review (Figure 1), and treat subjects in the same order, so that the current one can be
5 101 read as a supplement to the former, covering work published 2006-2017. People who
6 102 have read both should have a broad overview of what has been discovered about
7 103 insect macroevolution using fossil and phylogenetic approaches. **In common with the**
8 104 **earlier review, I do not cover mechanistic work on speciation and extinction in insects**
9 105 **that relates to population level phenomena, nor community ecology studies, though**
10 106 **such studies provide a vital source of hypotheses for comparative fossil or**
11 107 **phylogenetic work to test, as well as underlying explanations for patterns revealed.**

12 108 There have been contrary views about whether it is best or most convenient to
13 109 consider clade carrying capacity as a proximate, i.e. macroevolutionary, variable
14 110 (Mayhew, 2007) or more ultimate, ecological, factor affecting clade richness (Wiens,
15 111 2017) (Figure 1). Here I retain my original structure and consider it as a proximate
16 112 variable (Figure 1). Potentially valuable alternative ways to classify proximate and
17 113 ultimate factors are given by Wiens (2017).

18 114 As in the previous review, I have tried to restrict myself to quantitative tests of
19 115 specific hypotheses, but this has become more subjective: many studies include some
20 116 quantitative treatment of their data, but not as much as they might, and there is a
21 117 continuum. Other people might have excluded some of the studies I cover, or included
22 118 more, and I apologize for any unjustified omissions: as you will see, there is a lot to
23 119 cover. As in the previous review, I include comparative studies of extinction risk in
24 120 extant taxa. These studies have much in common with studies in deep time, as they
25 121 are often reliant on phylogenetic data, and the ultimate morphological, ecological and
26 122 behavioural forces overlap with those of deep time studies. **It is still not established to**
27 123 **what extent they can** teach us about macroevolutionary processes in general
28 124 (Bromham et al., 2012; Colles et al., 2009).

29 125 The merit of this review rests on the assumption that the observed richness of
30 126 insects is a major challenge in understanding Earth's taxonomic composition. One
31 127 contrary view is that there are many small-bodied or microscopic clades whose
32 128 described richness is currently low but which might actually be substantially greater
33 129 than that of insects. An interesting recent attempt to estimate the taxonomic
34 130 apportionment of global richness (Larsen et al., 2017) **potentially** reinforces the
35 131 importance of understanding insect richness. It concluded that insect richness is
36 132 considerably smaller than that of fungi, some other animals, and notably bacteria.

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3 133 However, a large majority of these other groups are probably insect parasites or
4 134 symbionts, (specifically mites, nematodes, microsporidia and entomopathogenic
5 135 bacteria) hence probably ultimately depend on insect richness. Thus, the central
6 136 importance of explaining insect richness remains.

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9 137 In the paragraphs that follow I outline the more recent **comparative**
10 138 phylogenetic and fossil evidence explaining insect richness. I begin with proximate
11 139 variables, and then move on to ultimate factors as before (Figure 1). After describing
12 140 the evidence, **and some of its strengths and weaknesses**, I reflect on how far we have
13 141 come and what still remains for the next decade of insect macroevolutionary research.

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17 143 **Proximate variables**

18 144 **Time.**

19 145 Our knowledge of insect clade age has considerably advanced in the last decade with
20 146 new fossil discoveries, taxonomic revisions, and the re-dating of deposits (Nicholson
21 147 et al., 2015) and many new molecular dating analyses (see below). At the broadest
22 148 taxonomic scales, Misof et al. (2014) used phylogenomics to estimate an origin of
23 149 crown hexapods (i.e. the last common ancestor of living species) in the Early
24 150 Ordovician (479 Ma), early Devonian for insect flight (406Ma), and Mississippian
25 151 (345Ma) for the origin of many major extant lineages, and broadly similar findings
26 152 were obtained by Rainford et al. (2014) using a wider sample of families but only
27 153 using the eight most widely sampled markers. **These timings are of course older than**
28 154 **the raw record of higher taxa would suggest** (Nicholson et al., 2015). Phylogenomic
29 155 **and other evidence tentatively suggests Remipedia as the sister group to hexapods**
30 156 **(Legg et al., 2013; von Reumont et al., 2011) , though there are other posited sister**
31 157 **groups (Meusemann et al., 2010; Regier et al., 2010), and the date of the split from**
32 158 **other Pancrustacea (i.e. the stem age) must be held in doubt until the sister group**
33 159 **relationship is more certain (Edgecombe, 2010). Doubt has also been cast on some of**
34 160 **the deep hexapod date inferences since a widely used calibration fossil (*Rhyniognatha***
35 161 ***hirsti*, previously interpreted as a basal pterygote) has recently been tentatively**
36 162 **reinterpreted as a centipede (Haug & Haug, 2017).**

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51 163 There has been much recent interest in statistical correlations between age (as
52 164 opposed to diversification rate) and richness, largely because they have been used to
53 165 argue for or against the existence of **diversity-dependent** clade growth (Rabosky,

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3 166 2009; Wiens, 2011). Such studies can also be used to argue about which proximate
4 167 variables best explain variation in richness (Wiens, 2017). In studies involving
5 168 hexapods, variable results have been found. A positive correlation between age and
6 169 richness has been found across animal classes in a multivariate model (Etienne et al.,
7 170 2012), across numerous taxa including crown insect orders (McPeck & Brown, 2007)
8 171 (Figure 2), across stem insect orders after accounting for other factors (Ferns & Jervis,
9 172 2016), across water beetle lineages after removing the most diverse taxon (Bloom et
10 173 al., 2014), and across beetle families but not subfamilies (Rabosky et al., 2012). **Thus,**
11 174 **perhaps unsurprisingly, it is sometimes true that the richer clades, of a collection**
12 175 **being studied, are older ones.** However, across the tree of life at several higher
13 176 taxonomic levels stem age does not predict richness well (Scholl & Wiens, 2016),
14 177 suggesting that the age of arthropods (and hence hexapods) cannot explain their
15 178 richness in a broader taxonomic setting. Indeed, in several analyses, age is negatively
16 179 correlated with richness, a probably consequence of diversification rates increasing in
17 180 derived taxa (see below). Age also does not predict richness across Diptera higher
18 181 taxa (Wiegmann et al., 2011) nor across Apameini moths (Toussaint et al., 2012), nor
19 182 ant genera (Pie & Tschá, 2009) nor across many individual or aggregate taxa
20 183 (Rabosky et al., 2012). **Wiens (2017) has also argued that using crown ages, as in**
21 184 **(McPeck & Brown, 2007), inflates the rates of species-poor and ancient groups that**
22 185 **have suffered extinction.** We must therefore turn to net diversification rates and the
23 186 two processes underlying it, speciation and extinction, to further understand insect
24 187 richness.

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189 **Net rates of diversification**

190 Across higher taxa of the tree of life at all taxonomic levels examined, net
191 diversification rates better explain species richness than stem group age (Scholl &
192 Wiens, 2016) (Figure 3). In that study, insects were apparently not represented in an
193 analysis across classes, although they featured in the order and family level analyses.
194 Rates increase and show higher variability from higher to lower taxonomic levels: for
195 example, that of Arthropoda as a whole, assuming an extinction fraction of 0.5, is
196 0.0183 My^{-1} , insect orders vary from 0.006 to 0.0378 My^{-1} , and families from zero to
197 0.457 My^{-1} . The richest insect orders and families however show high richness for a
198 given diversification rate (Figure 3). **A study of how the richness of orders and**
199 **families is predicted by stem age and diversification rate has never been conducted**

200 solely for insects, but is necessary to make solid conclusions about the relative
201 contributions of these proximate variables to richness heterogeneity in the group.

202 Differences in net diversification are frequently necessary to explain the
203 differences in richness across insect sister groups (which have identical stem ages).
204 Numerous studies have demonstrated this in recent years (Bloom et al., 2014;
205 Branstetter et al., 2017; Condamine et al., 2016; Condamine et al., 2012; Cunha et al.,
206 2011; Davis et al., 2009; Davis et al., 2010a; b; De-Silva et al., 2016; Edger et al.,
207 2015; Fagua et al., 2017; Gohli et al., 2017; Hamm & Fordyce, 2015; Hunt et al.,
208 2007; Kozak et al., 2015; Letsch et al., 2016; McKenna & Farrell, 2006; Mckenna et
209 al., 2015; McLeish et al., 2007; Morales-Hojas & Vieira, 2012; Moreau & Bell, 2013;
210 Nylín & Wahlberg, 2008; Peña & Espeland, 2015; Pie & Tschá, 2009; Rainford et al.,
211 2014; Sahoo et al., 2017; Song et al., 2015; Toussaint et al., 2012; Wahlberg et al.,
212 2013; Wiegmann et al., 2011). The importance of rate variation in explaining richness
213 in insects therefore seems unquestionable. A given net diversification rate can
214 however be produced by speciation and extinction rates of very different magnitudes.
215 It is sometimes possible to estimate speciation/origination and extinction rates
216 separately to distinguish these possibilities.

218 **Speciation/origination and extinction rates**

219 Nicholson et al. (2014) showed that fossil family origination rates were not higher in
220 more derived and rich taxa (e.g. from Palaeoptera to Holometabola, Figure 4), in
221 contrast to a previous study that used less robust data and methodologies (Mayhew,
222 2007), but that extinction rates were lower instead. The family level record through
223 time shows generally that origination rates are higher than extinction rates
224 (Condamine et al., 2016; Nicholson et al., 2015), though there are some periods
225 (notably the Permian-Triassic extinction) when extinction rates rise above origination
226 rates. Studies of the Coleoptera fossil record confirm low family extinction rates too
227 (Smith & Marcot, 2015). Overall, the family level data on insects represent the best
228 we can currently do to estimate extinction rate variation through time from fossils, but
229 seem intuitively unlikely to represent species level rates or rate variation.

230 Some recent fossil studies have suggested that insects may have been more
231 vulnerable to some extinction events than previously supposed. Fossil studies have
232 not detected extinction at the K-Pg boundary at the family level in insects (Condamine
233 et al., 2016; Nicholson et al., 2015). However, studies of insect trace fossils have

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3 234 shown a depletion of the quantity and types of feeding damage on plants, suggesting
4 235 that extinction did occur at finer taxonomic or functional scales (Donovan et al., 2014;
5 236 Labandeira & Currano, 2013; Wappler et al., 2009; Wilf et al., 2006). It is difficult to
7 237 know how these rates compare to those in other taxa because of the differences in
8 238 types of data used.

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11 239 Some fossil studies continue to imply long insect species lifetimes (i.e. low
12 240 extinction risk) by describing extant species from ancient deposits (Hörschemeyer et
13 241 al., 2010). In addition, very few Palaeartic insect species are known to have gone
14 242 extinct during Pleistocene climate fluctuations (Langford et al., 2014; Larkin et al.,
15 243 2014) and this seems also to be true of New Zealand beetles (Marra & Leschen,
16 244 2011). More geographically widespread studies of this nature are needed to tell if such
17 245 data are representative of Pleistocene extinction rates in insects.

18
19 246 Phylogenetic analyses of diversification shifts through time have attempted to
20 247 separate out speciation and extinction, but have produced heterogeneous results.
21 248 Given that molecular phylogenetic methods are generally known to poorly estimate
22 249 extinction rates (Rabosky, 2010), especially when the trees are incompletely sampled
23 250 (May & Moore, 2016; Meyer & Wiens, 2017; Moore et al., 2016; Rabosky et al.,
24 251 2017), this heterogeneity probably just reflects low signal in the data. Using the
25 252 maximum likelihood application *TreePar* (Meredith et al., 2011) suggest that the ratio
26 253 of extinction to speciation is very close to zero through the evolutionary history of the
27 254 insects (Condamine et al., 2016). Wiegmann et al. (2011) also found that extinction
28 255 rates were generally low in Diptera. However, analyses of clade-specific
29 256 diversification shifts using the maximum likelihood application *MEDUSA* (Alfaro et
30 257 al., 2009) across a tree of most insect families suggested that the speciation and
31 258 extinction rates were almost identical over large parts of the tree (Rainford et al.,
32 259 2014). The same has been inferred from a large dataset on species richness, body size
33 260 and clade age involving both insects and other taxa (Etienne et al., 2012). Analyses of
34 261 the *Heraclides* swallowtail tree suggested no extinction (Lewis et al., 2015), a result
35 262 that has been found in many similar non-insect studies and may be an artefact, whilst
36 263 in *Cinara* aphids extinction rates are about half that of speciation rates (Meseguer et
37 264 al., 2015), as in Orthoptera (Song et al., 2015). Extinction rate to speciation rate ratios
38 265 were highly variable across ants (Moreau & Bell, 2013).

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40 266 Other studies have attributed changes in net diversification in particular clades
41 267 to either changes in speciation or extinction rates. There is no particular a priori

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3 268 reason to expect that speciation or extinction should be the dominant driver of such
4 269 changes, though the fact that the focal taxa often contain diverse but derived clades,
5 270 and that molecular phylogenies do not contain extinct taxa, may predispose studies
6 271 towards detecting rises in speciation rate. Such changes have indeed been suggested,
7 272 and are probably more robust generally than inferences about extinction rate changes.
8
9 273 Letsch et al. (2016) inferred a higher speciation rate in lentic than lotic Odonata
10 274 species being the reason for their higher net diversification rate. Fagua et al. (2017)
11 275 inferred speciation and extinction rates in tortricid moths and found high initial
12 276 diversification resulting from speciation being almost double extinction, with
13 277 significant shifts in speciation rate in one major clade followed by declines in both
14 278 speciation and extinction rates. In *Heliconius* butterflies too, diversification rate
15 279 variation has been mostly due to speciation rate changes (Kozak et al., 2015). In
16 280 nymphalid butterflies, species feeding on Solanaceae have higher net diversification
17 281 rates as a result of higher speciation rates.

18
19 282 Other studies have found changes to be driven by extinction. Kergoat et al.
20 283 (2014) found that a rise in the extinction rate of tenebrionid beetles was mainly
21 284 responsible for the slow-down in its diversification, as did Condamine et al. (2015)
22 285 for birdwing butterflies. (Peña & Espeland, 2015). In scale insects, specialist species
23 286 were inferred to have lower net diversification rates than generalist species as a result
24 287 of rises in both extinction and speciation rates, with extinction rates rising more
25 288 (Hardy et al., 2016). Hamm & Fordyce (2015) found that clades with higher net
26 289 diversification in Nymphalidae also had elevated turnover (i.e. higher ratios of
27 290 extinction to speciation rates). They also estimated speciation and extinction rates for
28 291 specialist and generalist clades (see also Hardy & Otto (2014), although others have
29 292 found these not to be robust (Janz et al., 2016). Despite the misgivings about overall
30 293 extinction rate estimation above, some of the above studies (e.g. (Kergoat et al., 2014)
31 294 display remarkable changes in phylogenetic branching patterns at particular time
32 295 periods that suggest that some extinction signal has been detected by these
33 296 approaches.

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35 297 There has recently been a concerted approach to try to be more inclusive of
36 298 invertebrates in extinction risk assessment of extant species (Baillie et al., 2008;
37 299 Cardoso et al., 2011; Stuart et al., 2010), and this has begun to bear fruit (Clausnitzer
38 300 et al., 2009; Collen et al., 2012) although so far only a single order (Odonata) has
39 301 been assessed globally, showing a relatively low proportion was threatened (14%)

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3 302 compared to other freshwater invertebrate groups. National assessments predominate
4 303 elsewhere, and of the usual taxa and regions (Collen et al., 2012). On land, 45% of
5 304 North American Orthoptera have been assessed as threatened, 22% of globally
6 305 assessed bumblebees are threatened, whilst in other Hymenoptera threat levels vary
7 306 dramatically on a national basis: from 90% in North America, to 5% in Norway. In
8 307 the USA, 17% of butterflies are threatened, 30% in Canada and 8.5% in Europe. Ten
9 308 percent of Norwegian beetles are threatened, and 42% in Germany. For other orders,
10 309 threat levels range from 2% in the UK to 31% in Germany **but the diversity of orders**
11 310 **is very poorly represented in the data. In short, we still have little idea about whether**
12 311 **current extinction rates in insects differ on average from those in other taxa.**
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21 313 **Carrying capacity**

22 314 Tests for a slowing of net diversification over time, such as might be expected under
23 315 **diversity**-dependent diversification, have been frequent over the last decade.
24 316 Nicholson et al. (2015) showed a continual increase in family richness in the raw
25 317 fossil record, but there was variability across taxa in the best-fit model (Nicholson et
26 318 al., 2014), with sigmoidal growth of families in the most rich taxa (e.g. Holometabola)
27 319 and exponential in the least rich (e.g. Palaeoptera). The Coleoptera show a matching
28 320 pattern with a continual increase although net diversification rates have fallen (Smith
29 321 & Marcot, 2015), whilst Lepidoptera families better fit an exponential than linear
30 322 model (Sohn et al., 2015). **Studies of the raw record may however be suspect, because**
31 323 **of sampling and other biases, especially the ‘pull-of-the-recent’, which tends to**
32 324 **overemphasize recent diversity.** Clapham et al. (2016) showed that the pull of the
33 325 recent was indeed very significant, and that when richness was sample-standardized,
34 326 there was no strong evidence of an increase in diversity since the Cretaceous (Figure
35 327 5), with net diversification rates reduced to near-zero (Condamine et al. 2016). This is
36 328 much more indicative of **diversity-dependent** clade growth. A different approach to
37 329 removing fossil record biases was used by Davis et al. (2011), using phylogeny to fill
38 330 in fossil gaps. The Odonatoidea families best fit a linear model of growth if the raw
39 331 record is taken, but if the ages of sister groups are equalized, growth is more
40 332 sigmoidal, again suggesting **diversity-dependence.**
41 333 Tests of **diversity-dependence** have also been conducted on numerous
42 334 phylogenies of extant taxa, **though the absence of extinct lineages cautions against**
43 335 **uncritical acceptance of their findings.** Across the hexapods as a whole, net
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3 336 diversification rates appear to be increasing (Condamine et al., 2016) (Figure 6), a
4 337 finding consistent with the observation that younger orders have higher net rates of
5 338 diversification (Ferns & Jervis, 2016). This would suggest that there is still room on
6 339 Earth to accommodate many more insect species than currently exist, **and is possibly**
7 340 **robust for two reasons: the tip taxa (e.g. families) in the phylogenies are often very**
8 341 **rich, implying much more rapid branching than is found below them. In addition these**
9 342 **tip richness values are likely vast underestimates as they only include described**
10 343 **species. Similar trends have been reported** in *Heliconius* butterflies (Kozak et al.,
11 344 2015), in the Aeshnidae (Odonata) (Letsch et al., 2016) (Figure 7), in Orthoptera
12 345 (Song et al., 2015), and in apameine moths (Toussaint et al., 2012). Several clades
13 346 show no evidence for change over time in their diversification rates: *Drosophila* flies
14 347 (Morales-Hojas & Vieira, 2012), *Cinara* aphids (Meseguer et al., 2015), *Heraclides*
15 348 butterflies (Lewis et al., 2015), ants (Pie & Tschá, 2009), Iberian dung beetles (Cunha
16 349 et al., 2011) and swallowtail butterflies (Condamine et al., 2012), indicating that they
17 350 have not yet approached any carrying capacity. In contrast, several clades show
18 351 declining rates over time: beetles in general (Condamine et al., 2016), birdwing
19 352 butterflies (Condamine et al., 2015), Libellulidae (Odonata) (Letsch et al., 2016)
20 353 (Figure 7), tortricid moths (Fagua et al., 2017), *Nicrophorus* beetles (Toussaint &
21 354 Condamine, 2016), ants (Moreau & Bell, 2013), ithomiine butterflies (De-Silva et al.,
22 355 2016; Elias et al., 2009), *Eois* moths (Strutzenberger & Fiedler, 2011) and
23 356 *Cephaloleia* beetles (McKenna & Farrell, 2006). Overall **this heterogeneity across**
24 357 **taxa seems unlikely to be an artefact of biases in the method, and suggests an**
25 358 **interesting pattern; that continual insect diversification is supported by the continuing**
26 359 **emergence of new radiations that more-than-compensate for the slow-downs**
27 360 **experienced in some clades (Figure 6). It also suggests that the global taxonomic**
28 361 **composition of insect faunas is continuing to change (Figure 7).**

29 362 How are we to reconcile the fossil evidence for **diversity-dependence** across
30 363 all hexapods (Clapham et al., 2016) (Figure 5) with the lack of phylogenetic evidence
31 364 for it (Condamine et al., 2016) (Figure 6)? The critical difference may be the
32 365 taxonomic level under consideration: a slow-down in family diversification may be
33 366 entirely compatible with an increase in diversification at the species level. It is
34 367 interesting therefore that the species level fossil record, such as it is, also provides no
35 368 evidence for an increase in richness since the Cretaceous (Clapham et al., 2016).
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3 370 **Ultimate factors**

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5 371 **Morphological variables**

6 372 There is still no evidence from fossils or phylogenies that the insect body groundplan,
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8 373 in-of-itself led to an increase in diversification rate: there is no evidence of a change
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10 374 in fossil family diversification rate with the origin of insects (Nicholson et al., 2014),
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12 375 and no studies have found a shift in diversification rate on phylogenies coincident
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14 376 with that (Condamine et al., 2016; Davis et al., 2010a; Rainford et al., 2014) (Figure
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16 377 8). Thus, it ironically remains true that we should technically not try to explain the
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18 378 richness of ‘insects’, but some other sets of taxa, both more and less inclusive.

19 379 Wings, which enhance dispersal ability, are long supposed to have increased
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21 380 net diversification either by increasing speciation rates (e.g. by increasing the number
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23 381 of ecological niches available, or by allowing colonization of new geographic
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25 382 regions), or by decreasing extinction rates (for example by enhancing metapopulation
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27 383 persistence) (Mayhew, 2007). Primitively winged insects (Palaeoptera) show both an
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29 384 increase in fossil family origination, and extinction rates (i.e. greater turnover)
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31 385 (Nicholson et al., 2014) over primitively wingless groups (Apterygota) (Figure 4).
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33 386 However, this finding may be an artefact of differences in preservation potential
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35 387 between the two groups. A phylogenetic study with family level resolution using
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37 388 *MEDUSA* also found an increase in net diversification rate with the origin of wings in
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39 389 some but not all dating scenarios (Rainford et al., 2014). The result has also been
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41 390 found in Phylogenetic Generalized Least Squares (PGLS) modelling (Mundry, 2014)
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43 391 of diversification rates across families (Wiens et al., 2015) and from similar studies
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45 392 across orders (Ferns & Jervis, 2016; Wiens et al., 2015) and from sister taxon
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47 393 comparisons across orders (Davis et al., 2010a).

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49 394 However, diversification rate models using the Bayesian modelling application
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51 395 *BAMM* fail to show any such diversification shift on a family level phylogeny
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53 396 (Condamine et al., 2016) (Figure 8). This latter study must be regarded as more
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55 397 definitive for the present, as *BAMM* contains two advantages over *MEDUSA*: (1) the
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57 398 ability to apply diversity-dependent models; (2) high parameter models do not have to
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59 399 be nested within the best set of lower parameter models (May & Moore, 2016;
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400 Rabosky, 2014). *BAMM* is also, in some respects, an improvement over sister-taxon
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402 comparisons of richness because it is a whole-tree rather than single-node approach
and so can more easily evaluate the location of multiple shifts (Mayhew, 2007).

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3 403 However, *BAMM* itself is limited in performance, especially when clades are poorly
4 404 sampled in the phylogeny and may underestimate the number of rate shifts, biasing
5 405 other estimates (Meyer & Wiens, 2017; Rabosky et al., 2017). The other studies above
6 406 (Ferns & Jervis, 2016; Wiens et al., 2015) did not evaluate a wide range of clade-
7 407 specific rate shift hypotheses. Ultimately the *BAMM* result can only be confirmed
8 408 with a more highly resolved phylogeny (e.g. at genus level or better).

9 409 Comparative studies do show that more dispersive bark beetles diversity
10 410 faster, as expected (Gohli et al., 2017), whilst in contrast flightless Silphinae beetle
11 411 species diversify faster than flighted species (Ikeda et al., 2012). A likely reason for
12 412 this counter-intuitive result is that low dispersal propensity can facilitate geographic
13 413 and reproductive isolation, hence promote speciation, as long as it is not outweighed
14 414 by increased extinction. Studies of extinction risk in extant species across several taxa
15 415 continue to show that extinction risk is lower in more dispersive species (Mattila et
16 416 al., 2011) (Figure 9). Globally, lotic (flowing water) Odonata are more at risk than
17 417 lentic (standing water) species (Collen et al., 2012), a likely result of greater dispersal
18 418 propensity in lentic species. However, Powney et al. (2015) found that lentic UK
19 419 Odonata have declined more in range than lotic species, which they suggested was
20 420 due to greater levels of anthropogenic stressors in those habitats.

21 421 There has been little recent fossil or phylogenetic evidence that wing folding
22 422 has significant effects on diversification. Wing folding is hypothesized to have
23 423 allowed insects to both exploit the advantages of flight but also to utilize niches that
24 424 might otherwise damage outstretched wings (Mayhew, 2007). Only a sister taxon
25 425 study at order level provides partial support for this on some phylogenetic topologies
26 426 (Davis et al., 2010a). More recent studies using whole-tree methods have failed to
27 427 detect a shift in diversification on family level phylogenies (Condamine et al., 2016;
28 428 Rainford et al., 2014) (Figure 8), wing folding is not significant in analyses of
29 429 richness or diversification on order level phylogenies (Ferns & Jervis, 2016), and
30 430 there is no evidence that the Polyneoptera had higher fossil family diversification
31 431 rates than Palaeoptera (Nicholson et al., 2014).

32 432 The role of complete metamorphosis in diversification is not yet settled. It is
33 433 usually hypothesized to have increased diversification rates by allowing adults and
34 434 larvae to use separate food sources, and hence allowing greater specialization of the
35 435 ecological niche through separate adult and larval morphologies (Mayhew, 2007). The
36 436 trait explains diversification rates in PGLS analyses for some phylogenetic topologies

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3 437 but not others (Wiens et al., 2015). However, not all competing key innovations were
4 438 included in models. In *MEDUSA* analyses at family level a diversification shift at the
5 439 origin of metamorphosis is recovered robustly (Rainford et al., 2014), but not in
6 440 sister-taxon comparisons at order level (Davis et al., 2010a), nor in *BAMM* analyses at
7 441 family level, where all the shifts are within the four largest holometabolan orders
8 442 (Condamine et al., 2016) (Figure 8). **For the reasons stated above, the latter study is**
9 443 **currently probably superior to other phylogenetic studies, but may ultimately not be**
10 444 **definitive. Note that this study also leaves open the possibility that metamorphosis is a**
11 445 **contingent key innovation that only exerts its effects in combination with other traits.**
12 446 Fossil family studies show that holometabolan families have lower extinction rates
13 447 than other related groups in the same time interval (Nicholson et al., 2014) (Figure 4),
14 448 **though this does not necessarily mean that species level extinction rates are also**
15 449 **lower.**

16 450 Ferns & Jervis (2016) tested the effects of sclerotized forewings on
17 451 diversification at order level. **Such forewings may provide protection for the**
18 452 **hindwings and body allowing them to use concealed substrates without wing damage,**
19 453 **and also preventing desiccation of the abdomen, better adapting them to dry**
20 454 **environments and potentially both increasing speciation and reducing extinction rates**
21 455 **(Linz et al., 2016).** Such wings are found not just in Coleoptera, but six other orders
22 456 (Dermaptera, Orthoptera, Blattodea, Mantodea, Phasmatodea, Hemiptera). Presence
23 457 of wing sclerotization had a significant positive effect on diversification, equivalent to
24 458 that of wings and parasitism. **Note however that high diversification rates could make**
25 459 **sclerotization more likely to arise (i.e. the causation could be reversed).**

26 460 One comparative study has recently provided evidence for the diversifying
27 461 effects of a skeleton and of sensory sophistication, both features long thought to have
28 462 promoted insect diversity, **potentially through a range of mechanisms such as**
29 463 **expansion of the ecological niche, increasing the potential for sexual selection and**
30 464 **other forces promoting reproductive isolation, and potentially reducing mortality and**
31 465 **extinction rates.** In a comparative study across animal phyla, Jezkova & Wiens (2017)
32 466 showed that both had a significant effect even after controlling for other likely factors
33 467 (Figure 10). The explanatory power of vision and skeletons differed according to
34 468 which other traits were in the models, as well as the assumed species richness values
35 469 and phylogeny and estimated extinction fraction, but in univariate models vision
36 470 explained about 30% of the variation in diversification rate whilst skeletons explained

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3 471 only half that. Arthropods scored positive for all five of the traits that best explained
4 472 diversification rates across phyla, the others being non-marine habitat, parasitism and
5 473 dioecy (Figure 10). Segmentation and presence of legs were never significant. No
6 474 studies seem to have addressed the diversifying effects of mouthpart diversity in the
7 475 last decade, but if insect diversity did in fact peak in the Cretaceous (Clapham et al.,
8 476 2016; Davis et al., 2011) (Figure 5) this would give a better match between the rise of
9 477 insect diversity and the rise of mouthpart diversity than previously inferred (Mayhew,
10 478 2007), making a causal relationship between the traits more likely, **potentially through**
11 479 **allowing adaptation to a broader range of ecological niches.**

12 480 A final morphological variable postulated to contribute to insect species
13 481 richness is small body size. **Small size might promote speciation rates through**
14 482 **allowing greater ecological specialization, increasing clade carrying capacity, or**
15 483 **through reducing extinction rates by increasing population size and vital rates**
16 484 **(Mayhew, 2007).** Size was not significant in the above analysis of animal phyla, and
17 485 size within the insects also does not predict their diversification rate across orders
18 486 (Ferns & Jervis, 2016), nor across a family level phylogeny: Rainford et al. (2016)
19 487 showed that the distribution of body sizes across families and species is
20 488 approximately lognormal, which is what would be expected if it had no consistent
21 489 effect on diversification, as found in sister group contrasts (Figure 11). Size however
22 490 continues to turn up as a significant predictor of the extinction risk of extant insects:
23 491 for example, it is higher for larger bodied Azorean beetles (Terzopoulou et al., 2015),
24 492 saproxylic beetles (Seibold et al., 2015), Swedish longhorn beetles (if they overwinter
25 493 as adults) (Jeppsson & Forslund, 2014), Finnish butterflies (Mattila et al., 2011)
26 494 (Figure 9), Finnish noctuid moths (Mattila et al., 2009), and for monophagous (but not
27 495 polyphagous) Finnish geometrid moths (Mattila et al., 2008). **Size therefore probably**
28 496 **has macroevolutionary effects, but these may not translate to differences in net**
29 497 **diversification rate, as concluded by Etienne et al. (2012).**

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31 499 **Ecology and behaviour**

32 500 *Interspecific interactions*

33 501 The wide variety of interspecific interactions between insects and other organisms has
34 502 so impressed observers that it has long been considered one of the chief reasons for
35 503 their species richness (Mayhew, 2007). A particular focus has been the interactions
36 504 between insects and plants, particularly flowering plants, and particularly herbivory,

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3 505 because feeding on plants allows insects to exploit a variety of specialized ecological
4 506 niches (Futuyma & Agrawal, 2009; Kergoat et al., 2016; Nylin & Wahlberg, 2008;
5 507 Nyman, 2010; Suchan & Alvarez, 2015). Thus, herbivory could increase speciation
6 508 rates, increase clade carrying capacity, and because it involves feeding at a low
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8 509 trophic level, could also reduce extinction rates (Mayhew, 2007).

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11 Studies on the diversifying effects of herbivory across broad taxonomic groups
12 510 in the last decade have produced mixed results (Nakadai, 2017). Hunt et al. (2007)
13 511 detected no significant effect of herbivory on Coleoptera diversification. The same
14 512 was found by Rainford & Mayhew (2015) using sister taxon comparisons across a
15 513 family level phylogeny. However, Wiens et al. (2015) found a significant association
16 514 between herbivory and diversification rate across all orders and at finer relation for
17 515 some groups (Figure 12). The relationship remained non-significant within Coleoptera
18 516 and all other orders except Diptera and Hemiptera. In some cases, non-herbivorous
19 517 groups have radiated very rapidly, whilst in others herbivorous groups have remained
20 518 species poor. One possible reason for the difference in the findings of the latter two
21 519 studies could be their different approaches to coding herbivory: dichotomous, with
22 520 comparisons identified on the basis of ancestral state reconstruction (Rainford &
23 521 Mayhew, 2015), or as the proportion of species that are herbivorous (Wiens et al.,
24 522 2015). Neither of these approaches is free from potential error, and a definitive study
25 523 will also need a better resolved phylogeny to identify the best set of comparisons, and
26 524 potentially more of them.
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37 526 Another series of studies has looked for a temporal coincidence in richness or
38 527 diversification rates and the rise of the angiosperms. The new sample-standardized
39 528 fossil record shows a peak in richness at the time when angiosperms rose to
40 529 dominance, unlike the raw fossil record which shows a flattening in richness
41 530 (Clapham et al., 2016). Labandiera (2014) has shown that many gymnosperm
42 531 associated insect clades declined during this period, whilst a smaller number of clades
43 532 radiated onto angiosperms, so a straightforward increase in insect richness with the
44 533 rise of the angiosperms may be a naïve expectation. Several phylogenetic studies have
45 534 attempted to see if diversification coincided with the rise of angiosperms or of their
46 535 particular associated host plant groups. Rainford et al. (2014) and Condamine et al.
47 536 (2016) both agree that increases in diversification of selected clades occurred then,
48 537 although there was no noticeable effect on overall insect diversification. Specific
49 538 clades which have shown this behaviour include bees (Cardinal & Danforth, 2013),
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3 539 ants (Moreau et al., 2006), tortricid moths (Fagua et al., 2017), Lepidoptera in general
4 540 (Wahlberg et al., 2013), Scaraboidea beetles (Ahrens et al., 2014), some tenebrionid
5 541 beetles (Kergoat et al., 2014) and weevils (McKenna et al., 2009). Satyrinae butterfly
6 542 diversification occurred during the diversification and spread of grasses (Peña &
7 543 Wahlberg, 2008), as did apameine moths (Toussaint et al., 2012), **skipper butterflies**
8 544 **(Sahoo et al., 2017)**, and Australian gall thrips also diversified in concert with their
9 545 hosts (McLeish et al., 2007), as did *Eois* moths (Strutzenberger & Fiedler, 2011), and
10 546 bruchine beetles (Kergoat et al., 2011). **The causal inferences claimed by these studies**
11 547 **need to be treated with caution given that none of them has tested an association**
12 548 **statistically. In contrast to the above studies**, chrysomelid beetles (Gómez-Zurita et al.,
13 549 2007), *Asteromyia* gall midges (Stireman et al., 2010), heterarthrine sawflies
14 550 (Leppänen et al., 2012) and *Phyllonorycter* moths (Lopez-Vaamonde et al., 2006)
15 551 apparently radiated long after their host plants. **Such outcomes are expected since**
16 552 **plant radiations provide the potential for insect radiation at any point after the plant**
17 553 **radiation occurs.**

18 554 **There is evidence that** other types of trophic interactions promote diversity; for
19 555 example, **fungal associations are hypothesized to have increased diversity by**
20 556 **increasing ecological opportunities or through diversifying coevolution. Evidence for**
21 557 bark beetles indeed suggests that they diversify faster if they farm fungi (Gohli et al.,
22 558 2017), **but leaf-cutter ant diversification is not tightly linked to major shifts in their**
23 559 **fungal agriculture (Branstetter et al., 2017)**, and fungal associations have not elevated
24 560 diversification in *Asteromyia* gall midges (Stireman et al., 2010).

25 561 In contrast, the evolution of bats may have reduced the diversity of some
26 562 lacewing taxa (Archibald et al., 2014), whilst promoting the diversity of other groups
27 563 with defences against them. **Bats are major predators of lacewings which presumably**
28 564 **has increased extinction risk for some taxa.** The proportion of species that are
29 565 parasitic also predicts richness across orders (Ferns & Jervis, 2016), as well as phyla
30 566 (Jezkova & Wiens, 2017), **again a likely consequence of specialization opening up**
31 567 **ecological opportunities.** However a sister-taxon contrast study across families and
32 568 higher taxa found no consistent association between any broad dietary category and
33 569 species richness (Rainford & Mayhew, 2015). Diets are phylogenetically constrained,
34 570 but to variable extents, and some are more reversible than others, and have originated
35 571 different numbers of times and over different time spans, partially explaining why
36 572 some are more taxonomically widespread than others. **Overall though, many broad**

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3 573 dietary categories have facilitated impressive radiations, whilst none appears to have
4 574 done so entirely consistently.

5 575 Some of the broad-scale mechanisms that might have linked insect and plant
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7 576 diversification have also been investigated. One potential mechanism is co-speciation,
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9 577 which is likely to occur in specialized obligate interactions. Insects in fact provide
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11 578 some of the best evidence there is for co-speciation; it has been observed in figs and
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13 579 fig-wasps (Cruaud et al., 2012), and to a lesser extent between Yuccas and Yucca
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15 580 moths (Althoff et al., 2012), Pocket Gopher lice (Alcala et al., 2017), Sika deer lice
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17 581 (Mizukoshi et al., 2012), parasitoids of *Rhagoletis* flies (Hamerlinck et al., 2016), and
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19 582 sucking lice on rodents (Smith et al., 2008). In the latter cases however, host shifting
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21 583 has also occurred, and this provides, in concert with host specialization, an alternative
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23 584 and probably more widespread mechanism by which interactions can promote
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25 585 diversification.

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27 586 Host shifting accounts for about 20% of speciation events in nematine sawflies
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29 587 (Nyman et al., 2010), and in willow galling sawflies also promotes diversification of
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31 588 their parasitoids (Nyman et al., 2007), whilst parasitoids of *Rhagoletis* flies sometimes
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33 589 speciate by host shifting. Since these shifts are relative recent, it suggests that lineages
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35 590 that originate by host shifts do not persist very long (Hamerlinck et al., 2016).
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37 591 Diversification shifts coincident with use of novel hosts have been identified in pierid
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39 592 butterflies (Edger et al., 2015), delphacid planthoppers (Urban et al., 2010), aphids
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41 593 (Peccoud et al., 2010), heterarthrine sawflies (Leppänen et al., 2012), *Phytomyza* flies
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43 594 (Winkler et al., 2009) and ithomiine butterflies (Peña & Espeland, 2015). Increases in
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45 595 host range across higher taxa also seem to allow diversification in some clades, an
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47 596 possible example of an adaptability trait that promotes diversification (Nylin &
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49 597 Wahlberg, 2008). For example, larval diet range is positively correlated with richness
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51 598 across orders of insects (Ferns & Jervis, 2016). Evidence, sometimes disputed (Hamm
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53 599 & Fordyce, 2015; Janz et al., 2016), has also been presented for a negative
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55 600 relationship between host range and diversification rate in swallowtail butterflies
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57 601 (Hardy & Otto, 2014), longwing butterflies (Hardy & Otto, 2014) and brush-foot
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59 602 butterflies (Janz et al., 2016; Janz et al., 2006), and bark beetles (Gohli et al., 2017).
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61 603 At the species level specialization may however also carry macroevolutionary costs.
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63 604 In scale insects, diversification rates are lower in more specialized groups (Hardy et
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65 605 al., 2016), and across extant taxa extinction risk is often higher in more specialized
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67 606 taxa (Franzén et al., 2012; Jeppsson & Forslund, 2014; Mattila et al., 2011; Mattila et

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3 607 al., 2008; Mattila et al., 2009; Nylin & Bergström, 2009; Powney et al., 2015). For
4 608 this reason, specialization is often regarded as a paradoxical macroevolutionary trait;
5 609 it may promote speciation but also extinction. Rainford & Mayhew (2015) found that
6 610 taxa with diets generally regarded to promote specialization (herbivory,
7 611 ectoparasitism, parasitoidism, fungivory) do not generally have higher richness than
8 612 their sisters with other diets presumed not to promote specialization, though they may
9 613 be diets that are harder to lose. One reason may be that these costs sometimes balance
10 614 out the benefits, though it is also possible that these categories are too coarse to detect
11 615 underlying patterns.
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19 617 *Latitude and other biogeographic factors.*

20 618 At least one study in the last decade has investigated the macroevolutionary effects of
21 619 latitude in insects: Condamine et al. (2012) found that tropical swallowtail butterflies
22 620 diversity faster than temperate ones (Figure 13); a finding already known from
23 621 previous sister-taxon studies (Mayhew, 2007). Some other phylogenetic studies have
24 622 been pertinent to the evolution of latitudinal gradients, showing that the tropics are
25 623 both the site of origination of major groups (a museum), giving them a long time to
26 624 generate species (Branstetter et al., 2017; McKenna & Farrell, 2006; Moreau & Bell,
27 625 2013), and also generate many species over time (a cradle).
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34 626 A number of other studies have addressed how biogeographic processes might
35 627 have contributed to the radiation of various insect groups. The contribution of
36 628 biogeography to diversification is a soft hypothesis, because for any diverse group
37 629 geographic ranges will vary across taxa, and therefore some biogeographic process
38 630 can be inferred to have taken place. The interest is therefore primarily in which
39 631 processes. In Central/South America, the formation of the isthmus of Panama and the
40 632 rise of the Andes are inferred to have promoted diversification in *Cephaloleia* leaf
41 633 beetles (McKenna & Farrell, 2006), ithomiine butterflies (De-Silva et al., 2016; Elias
42 634 et al., 2009) and *Eois* moths (Strutzenberger & Fiedler, 2011), presumably by
43 635 increasing speciation rates through range expansion in the former, and through
44 636 increasing habitat diversity and fragmentation in the latter. Unsurprisingly, dispersal
45 637 events, creating geographically isolated populations, are inferred to be important in
46 638 island radiations such as the *Heracles* swallowtails (Lewis et al., 2015) and
47 639 birdwing butterflies (Condamine et al., 2015). The colonization of different
48 640 continents, with similar and sometimes dramatic results, has been important in a
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3 641 number of groups of wide distribution, including *Nicrophorus* beetles (Toussaint &
4 642 Condamine, 2016), apameine moths (Toussaint et al., 2012), **metalmark moths (Rota**
5 643 **et al., 2016)**, tortricid moths (Fagua et al., 2017), *Drosophila* flies (Morales-Hojas &
6 644 Vieira, 2012), and *Cinara* aphids (Meseguer et al., 2015). **To what extent these**
7 645 **processes are more common, or promote diversification more, in insects than other**
8 646 **taxa is an open question.**

647 648 *Climate change*

649 There are reasons to suspect that climate change might stimulate the diversification of
650 insects more than other taxa, **for example by affecting the distribution of species,**
651 **notably plants, with which they interact** (Nyman et al., 2012). Almost all studies
652 statistically linking climate to insect diversification have covered events in the last
653 150Ma (Cretaceous onwards), and most have been based on phylogenies of extant
654 taxa. A few however have been based on fossils. Currano et al. (2010; 2008) found
655 that insect herbivory was high at a site in North America during the Palaeocene-
656 Eocene thermal maximum, and that herbivory tracked temperature well over a six
657 million year period (Figure 14), suggesting a positive effect of temperature on
658 diversification. **This conclusion is correlative but relies on robust time series statistics,**
659 **and mirrors temporally the positive spatial effect of temperature on biodiversity,**
660 **suggesting that similar mechanisms may underlie both.** Wappler et al. (2009) also
661 **found high diversity of herbivory during this period** at a site in Germany. Archibald et
662 al. (2014) attributed the diversification of green lacewings in the Neogene, **a period of**
663 **climatic fluctuation and cooling**, to their higher climatic tolerance, whilst other less
664 tolerant taxa became more ecologically restricted, **but this conclusion, whilst**
665 **plausible, rests on a comparison of very few higher taxa.** **It suggests however that**
666 **whilst climate changes may restrict the diversification of some taxa, they may open**
667 **opportunities for others.**

668 **Studies using phylogenies of extant taxa have been variable in their statistical**
669 **sophistication.** Peña & Wahlberg (2008) found that grass feeding Satyrini butterflies
670 **diversified during the Miocene cooling, at the same time as spread of grasslands, but**
671 **this study did not formally test null hypotheses of association between diversification**
672 **and climate, nor attempt to detect shifts in diversification rates.** Damm et al. (2010)
673 **similarly attributed the diversification of *Trithemis* dragonflies in Africa to Pliocene**
674 **aridification, though without formal hypothesis testing.**

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3 675 A further suite of studies has also tested for significant shifts in diversification
4 676 rate in the focal insect taxon, and then attributed them post-hoc to climatic events in a
5 677 verbal way. For example, the slow-down in tenebrionid beetle diversification has been
6 678 attributed to climatic events during the mid-Cretaceous terrestrial revolution, during
7 679 which this largely arid-adapted and poorly-dispersive clade experienced an increase in
8 680 both speciation and extinction rates, but the increase in extinction rates was higher
9 681 (Kergoat et al., 2014). This is attributed to the spread of wet forested habitats at that
10 682 period, and is the opposite of that experienced by other taxa that, as already noted
11 683 above, diversified in the Cretaceous. This study also implies that some of the other
12 684 groups in which diversification has slowed towards the present (see above) may be
13 685 due to climate-related phenomena rather than an expression of diversity-dependence.

14 686 Using similar approaches, *Cephaloleia* leaf beetles were shown to diversify
15 687 faster during the Paleocene-Eocene thermal maximum, in agreement with the fossil
16 688 studies mentioned above (McKenna & Farrell, 2006). The spread of Miocene
17 689 grasslands and open habitats has been inferred as the cause of the diversification of
18 690 leaf-cutter ants (Branstetter et al., 2017; Schultz & Brady, 2008), apameine moths
19 691 (Toussaint et al., 2012), and skipper butterflies (Sahoo et al., 2017), all grass
20 692 associated taxa. Similar but later events were inferred to have caused the Pliocene and
21 693 Pleistocene diversification of soil-dwelling cockroaches in Australia (Lo et al., 2016),
22 694 East African grasshoppers (Voje et al., 2009) and Australian gall thrips (McLeish et
23 695 al., 2007). Whilst it is useful that such studies have actually demonstrated
24 696 diversification events to explain, and whilst climatic events are plausible causes, these
25 697 studies do not test the link formally.

26 698 Other studies have tested for differences in diversification rate between *a*
27 699 *priori* defined climatic events, adding some further statistical rigour. These have
28 700 shown that Oligocene and Miocene events have also been linked to the diversification
29 701 of swallowtail butterflies (Condamine et al., 2012). Interestingly, warming events
30 702 seem to have increased diversification of a temperate clade, whilst cooling events
31 703 have increased diversification in a tropical clade (Figure 13). No effect of Oligocene
32 704 climate change was found on *Phytomyza* flies, but they did diversify with the spread
33 705 of grasslands in the Miocene cooling (Winkler et al., 2009).

34 706 Another level of statistical rigour has been added by one study incorporating
35 707 climate change into statistical models of diversification. In birdwing butterflies, high
36 708 temperatures and high sea levels seem to have decreased net diversification through

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3 709 increased extinction rates (Condamine et al., 2015) (Figure 15). This might have been
4 710 due to the reduction of island area and increased isolation of populations. However,
5 711 the conclusion that extinction rates drive the changes may be suspect, because these
6 712 are generally poorly estimated from molecular phylogenies.

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9 713 Researchers are also now beginning to assess extinction risk from climate
10 714 change in extant taxa (Pacifci et al., 2015). Comparative studies of insects in this
11 715 regard may yet shed light on large scale macroevolutionary patterns related to climate,
12 716 though geographic and taxonomic biases are likely to apply just as heavily here as in
13 717 more general assessments of extinction risk in insects. It will be interesting to see if
14 718 these studies can also be reconciled with the persistence of Pleistocene insects in the
15 719 Palaeartic and elsewhere (Langford et al., 2014; Larkin et al., 2014; Marra &
16 720 Leschen, 2011).

721 722 *Other ecological factors*

723 Ellis & Oakley (2016) found that animal clades, including some insects, that use
724 bioluminescence for sexual selection have diversified more than their sisters. This
725 study supports the general notion that intensity of sexual selection, as a driver of rapid
726 evolution of the mating system, can promote reproductive isolation (Mayhew, 2007).
727 A number of studies of extant species have shown that short generation times reduce
728 the risk of extinction; in Swedish Lepidoptera (Franzén et al., 2012), European
729 butterflies (Essens et al., 2017; Nylin & Bergström, 2009), and Swedish longhorn
730 beetles (Jeppsson & Forslund, 2014). This is likely because populations can grow and
731 recover more rapidly.

732 733 **Looking back**

734 At the end of the previous review (Mayhew, 2007), I made several suggestions for
735 future work. How far have these wishes been fulfilled? With respect to proximate
736 variables, I suggested that phylogenetic studies of extant taxa would provide the chief
737 source of estimates of speciation and extinction rates; that we might detect limits on
738 species richness with phylogenies of ancient taxa; that there should be a concerted
739 effort to improve our knowledge of current extinction risk in insects and of
740 Pleistocene fossil insects.

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3 741 Whilst many studies have indeed applied birth-death models to dated
4 742 phylogenies and estimated both speciation and extinction rates (Figures 7, 15), **there is**
5 743 **a general consensus that the extinction rate estimates are likely not robust, or at least**
6 744 **less robust than speciation and net diversification** (May & Moore, 2016; Meyer &
7 745 Wiens, 2017; Moore et al., 2016; Rabosky, 2010; Rabosky et al., 2017). A plethora of
8 746 phylogenetic studies have now also detected reductions in diversification rate through
9 747 time in insects, and in most, the taxa are relatively young (Figure 7). Though efforts
10 748 are ongoing to better assess current extinction risks in insects (Baillie et al., 2008;
11 749 Clausnitzer et al., 2009; Collen et al., 2012), this situation will take time to produce
12 750 useful comparative results for macroevolutionary biology. A similar situation exists
13 751 for the study of Pleistocene insects (Marra & Leschen, 2011).

14 752 Regarding ultimate variables, I suggested testing for key innovations in the
15 753 fossil record, and comparative studies of species richness against evolutionary
16 754 flexibility, mouthpart diversity, appendages and segmentation, sensory systems, and
17 755 ecological generalization. **With the exception of studies of mouthpart diversity, such**
18 756 **studies have all been carried out** (Hardy et al., 2016; Janz et al., 2016; Jezkova &
19 757 Wiens, 2017; Nicholson et al., 2014) (Figures 4, 10).

20 758 With respect to data, I expressed a need for a better understanding of order
21 759 level phylogeny; for phylogenies at family level of the most diverse orders; a
22 760 comprehensive phylogeny of higher insect taxa; an update of the family level fossil
23 761 record; for a single catalogue of extant richness; for studies attempting to extrapolate
24 762 asymptotic richness; and for more comprehensive assessments of current insect
25 763 extinction risk. The first four wishes have been fulfilled (Clapham et al., 2016;
26 764 Mckenna et al., 2015; Misof et al., 2014; Nicholson et al., 2015; Peters et al., 2017;
27 765 Rainford et al., 2014; Timmermans et al., 2014; Wiegmann et al., 2011) (Figures 5, 7,
28 766 8, 12). Whilst platforms do exist that might eventually provide comprehensive and up-
29 767 to-date data on described richness, these are currently highly incomplete for insects,
30 768 so in practice researchers currently have to dig through various separate specialist
31 769 sources (Jezkova & Wiens, 2017; Rainford et al., 2014; Scholl & Wiens, 2016; Wiens
32 770 et al., 2015). Some of these studies include analyses on extrapolated richness (Jezkova
33 771 & Wiens, 2017) for higher taxa that include hexapods, but nobody, to my knowledge,
34 772 has done this yet for a broad suite of subtaxa of insects. As indicated above, we now
35 773 have a global assessment of extinction risk for a single Order, Odonata, though even
36 774 for that there are still many data-deficient species (Clausnitzer et al., 2009).

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3 775 Many of the problems with data analysis and interpretation highlighted in the
4 776 last review have also now been addressed. The estimated relative effect size of
5 777 diversification shifts can now relatively easily be quantified by the techniques that
6 778 automatically assign rates to branches (Alfaro et al., 2009; Rabosky, 2014). For
7 779 example, Rainford et al. (2014) used the modelled rates to show that an inferred shifts
8 780 at the origin of Pterygota and Holometabola, if correct, had by far the greatest effect
9 781 on extant richness of all those considered, each accounting for nearly a million species
10 782 once the effects of other shifts were discounted.

11 783 Studies have continued to address multiple explanatory variables and allow
12 784 their explanatory power to be compared: for example, Ferns & Jervis (2016) found
13 785 that larval diet range, the proportion of flying species, and presence of wing
14 786 sclerotization were more important than the proportion of species that were parasitic
15 787 and order age at explaining species richness across orders. Wiens et al. (2015) found
16 788 that the relative importance of herbivory, wings and metamorphosis in explaining
17 789 diversification rates across orders varied according to the study, although collectively
18 790 they explained about 60% of the variation. Across the Misof et al. (2014) phylogeny,
19 791 wings and herbivory each explained about 30% of the variation on their own, and
20 792 metamorphosis less (Figure 12). As before, studies of current extinction risk in insects
21 793 continue to explore many explanatory variables simultaneously.

22 794 Several studies have also explicitly linked ultimate and proximate factors. For
23 795 example, using a phylogeny of tenebrionid beetles, Kergoat et al. (2014) linked the
24 796 climatic changes in the Cretaceous to both an increase in speciation and an increase in
25 797 extinction. Because the former was smaller than the latter, the net outcome has been a
26 798 reduction in the net rate of diversification. Using fossils, Nicholson et al. (2014)
27 799 linked the increase in family level diversification in Holometabola to an decrease in
28 800 extinction rates, rather than an increase in origination rates (Figure 4). There are many
29 801 other examples (see above).

30 802 How have broad conclusions changed in the last decade? The acceleration of
31 803 net diversification rates overall at the species (but not family) level (Figures 5, 6),
32 804 with heterogeneity across subtaxa (Figure 7), is **an interesting new** finding. This has
33 805 been realized through phylogenetic studies which have filled in our knowledge gap
34 806 about insect evolution the Cenozoic (Figure 13), which for fossils is dominated by
35 807 noise rather than signal (Figure 5). Wings and metamorphosis still feature as likely
36 808 key innovations in recent studies (Figure 12), **but the best broad phylogenetic study**

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3 809 **does not implicate either** (Figure 8). The importance of skeletons, vision, non-marine
4 810 habit, parasitism, and dieocy across animal phyla (Figure 10) also brings a useful
5
6 811 broader context to understanding insect richness. Whilst it is still contentious overall
7
8 812 whether herbivory has tended to have diversifying effects, there is enough evidence to
9
10 813 say that it does at least in some taxa, and we can say that host-shifting, and sometimes
11
12 814 cospeciation, are important processes. We are now much more aware of the
13
14 815 importance of climatic changes and biogeographic processes (Figures 13-15) than we
15
16 816 were a decade ago, **but studies of the former need greater statistical rigour.**

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18 818 **Looking forward**

19 819 **It will be apparent from the above** that there are still many unsolved controversies,
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21 820 and for most of the questions above, the last word has probably not been said. **There is**
22
23 821 **a major need to refine our knowledge of the appropriateness and validity of new**
24
25 822 **statistical methods, and doubtless further methods will be developed and shape studies**
26
27 823 **in the next decade. There is also a need to take more studies further with these as**
28
29 824 **appropriate, so that more is made of the potential raw data beyond discursive stories.**
30
31 825 **When one looks at the potential set of interesting questions that can be posed by insect**
32
33 826 **macroevolution studies, it becomes clear how few of them are ever addressed in a**
34
35 827 **given research project. We need to do more with what is in front of us. There is much**
36
37 828 **potential still to address ultimate factors, such as diet and ecology, with fossil studies.**
38
39 829 **A study of the effect of clade age and diversification rate on species richness in all**
40
41 830 **insects across different higher taxa would be valuable, as current studies do not focus**
42
43 831 **on them and this makes interpretation of more generic findings more difficult. Tests**
44
45 832 **of diversity-dependence need to be more direct and relate rate changes to each other**
46
47 833 **or actual densities rather than just testing for slow-downs in rate, as well as ruling out**
48
49 834 **climate change as an alternative explanatory variable. Much more can be done with**
50
51 835 **life history and morphology to address diversity-disparity relationships through time.**

52 836 **Fossil and phylogenetic information will continue to flow in, and now that the**
53
54 837 **novelty of detecting shifts in diversification, and hypothesizing about why, has worn**
55
56 838 **off, studies need to focus more on testing those hypotheses in convincing ways,**
57
58 839 **emphasizing a shift from quantity to quality of studies.** One likely area where insect
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60 840 studies will benefit is from the growth of open access informatics. Publically available
841 databases have begun to make an impact in some studies, and I would hope to see that
842 continue, but they are often restricted to particular data types, or taxonomic groups.

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3 843 As well as more such datasets, proper multi-variate hubs are needed where different
4 844 datasets can mix and integrate. Big data are the natural product of entomology.

5 845 Given that most of the broad-scale studies discussed above work with less-
6
7 846 than-ideal data, and hence methods, it is difficult to predict if the preliminary findings
8
9 847 of the last decade will still stand a decade from now. We can however hope that gaps
10
11 848 will be filled in questions addressed, and that the quality of studies increases either
12
13 849 through improvements (e.g. veracity, completeness) in underlying datasets, as well as
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15 850 analytical techniques (e.g. more valid techniques, or used in more appropriate ways).
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17 851 That leads to the further hope that a decade or more from now, another review will be
18
19 852 able to claim a more confident understanding of the reasons for insect species richness
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21 853 than we currently have.

22 854

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3 1325 **Figure legends**
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6 1327 Figure 1. The types of explanation for hexapod richness and their interrelationships,
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8 1328 as presented in this review.

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10
11 1330 Figure 2. Extant richness and crown group age in orders of insects (*red diamonds*),
12
13 1331 teleost fishes (*blue circles*), amphibians (*blue squares*), reptiles (*green diamonds*),
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15 1332 birds (*pink circles*), and mammals (*red squares*). The point for the Sphenodontida
16
17 1333 (green diamond at 228 MY on the crown group age axis) was excluded as an outlier.

18 1334 **Reproduced from Figure 4 of McPeck & Brown (2007) with permission from**
19
20 1335 **University of Chicago Press, © 2007 by The University of Chicago.**

21 1336

22 1337 Figure 3. Diversification rate predicts richness for phyla and orders across the tree of
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24 1338 life. Arthropods and three of the richest insect orders are labelled. **Reproduced with**
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26 1339 **modifications from Figure 3 of Scholl & Wiens (2016) by permission of the Royal**
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28 1340 **Society.**

29 1341

30 1342 Figure 4. Family level origination and extinction rates for major insect higher taxa.
31
32 1343 Both rates are elevated in Palaeoptera and extinction rates reduced in Holometabola.
33
34 1344 **This also appears as Figure 2 in Nicholson et al. (2014), published by Wiley and the**
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36 1345 **Royal Society, © the authors.**

37 1346

38 1347 Figure 5. Fossil family richness through time using (a) the raw family record as
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40 1348 represented in the Paleobiology database by “range-through” measures, and with the
41
42 1349 pull-of-the-recent removed by considering only last occurrences from the fossil
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44 1350 record, and (b) using standardized subsamples. **This also appears as Figure 1 in**
45
46 1351 **Clapham et al. (2016), published by Wiley and the Royal Society, © the authors.**

47 1352

48 1353 Figure 6. Net rates of diversification estimated from a family level phylogeny of
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50 1354 insects and their described species richness (a) for the whole clade and (b) for
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52 1355 particular subclades. **Reproduced from Figure 3 of Condamine et al. (2016) under**
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1
2
3 1358 Figure 7. Speciation rates (scale bar) inferred from a phylogeny of Anisoptera
4 1359 (Odonata) (Letsch et al., 2016). Shifts inferred from Bayesian modelling of
5 1360 diversification are shown by red circles. Speciation rates have sped up in Aeshnidae,
6 1361 but slowed in Libellulidae. **Reproduced from Figure 2 of Letsch et al. (2016) with
7 1362 permission from Wiley, © 2016 John Wiley & Sons Ltd.**

8 1363
9 1364 Figure 8. Shifts in diversification rate inferred from Bayesian analysis of described
10 1365 species richness plotted onto a family level phylogeny of insects. Colours indicate
11 1366 different net rates (right hand scale bar), and empty circles represent shift points
12 1367 (abrupt colour changes), including major upshifts in the four richest orders
13 1368 (illustrated). The origins of Holometabola (H) and Pterygota (P) are not accompanied
14 1369 by shifts. **Reproduced from Figure 4 of Condamine et al. (2016) under Creative
15 1370 Commons Attribution Licence (CC-BY) 4.0.**

16 1371
17 1372 Figure 9. Partial regressions showing the effect of body size and dispersal ability on
18 1373 range change in Finnish butterflies. 1=Hesperiidae, 2=Pieridae, 3=Lycaenidae,
19 1374 4=Nymphalidae, 5=Satyridae, 6=Papilionidae. **Reproduced from Figure 2 of Mattila
20 1375 et al. (2011) with permission from Wiley, © 2011 The Royal Entomological Society.**

21 1376
22 1377 Figure 10. Species richness, diversification, and ultimate factors explaining them
23 1378 across animal phyla. Proportion of species displaying each trait is shown across taxa
24 1379 for the five most important explanatory variables, and Arthropoda are the only
25 1380 Phylum showing species with all five traits. The proportion of species displaying
26 1381 parasitism is an underestimate as parasitism is very strictly defined. **Reproduced from
27 1382 Figure 1 of Jezkova & Wiens (2017) with permission from University of Chicago
28 1383 Press, © 2017 by The University of Chicago. All rights reserved.**

29 1384
30 1385 Figure 11. The lack of association between body size and species richness in
31 1386 Hexapoda and Holometabola. **Reproduced from Figure 3 of Rainford et al. (2016)
32 1387 under Creative Commons Attribution Licence (CC-BY) 4.0.**

33 1388
34 1389 Figure 12. Traits affecting diversification across the hexapod orders. The distribution
35 1390 of two morphological variables (wings and metamorphosis) (a) is plotted against the
36 1391 species richness of taxa and the number of species that are herbivorous (b).

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3 1392 Reproduced from Figure 1 of Wiens et al. (2015) under Creative Commons

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7 1395 Figure 13. Diversification of a tropical (top) and temperate (bottom) clade of
8 1396 swallowtail butterflies depicted as lineage-through-time plots. Also shown is the
9 1397 Cenozoic global climate cooling as depicted by Benthic $\delta^{18}\text{O}$. Vertical bars show
10 1398 periods of cooling (blue) and warming (orange). The tropical clade has diversified
11 1399 faster than the temperate clade, but does so more after cooling events, whilst the
12 1400 temperate clade diversifies faster after warming events. Reproduced from Figure 4 of
13 1401 Condamine et al. (2012) with permission from Wiley, © 2012 Blackwell Publishing
14 1402 Ltd/CNRS.

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17 1404 Figure 14. Change in leaf damage types (DT) (A, B) and amount of damage (C, D)
18 1405 with mean annual temperature (MAT) over six millions years of the Paleocene-
19 1406 Eocene thermal maximum at a site in the USA. Reproduced from Figure 7 of Currano
20 1407 et al. (2010) with permission from Wiley, © 2010 by the Ecological Society of
21 1408 America.

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23 1409

24 1410 Figure 15. Effect of global temperature and sea level change on extinction of birdwing
25 1411 butterflies. Reproduced from Figure 3 of Condamine et al. (2015) under Creative
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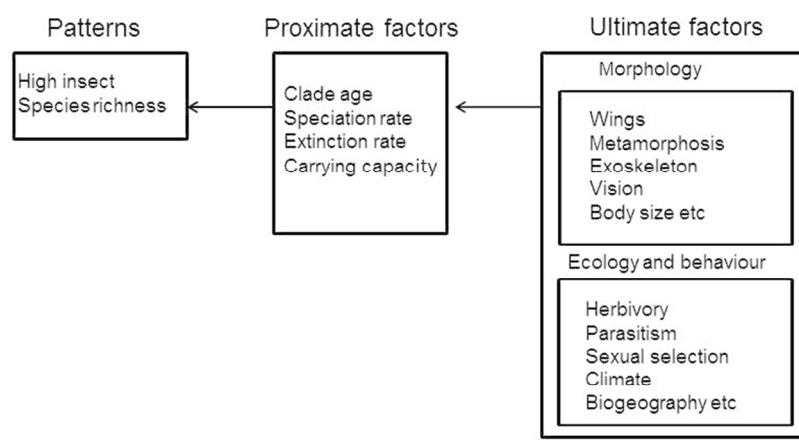


Figure 1. The types of explanation for hexapod richness and their interrelationships, as presented in this review.

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view

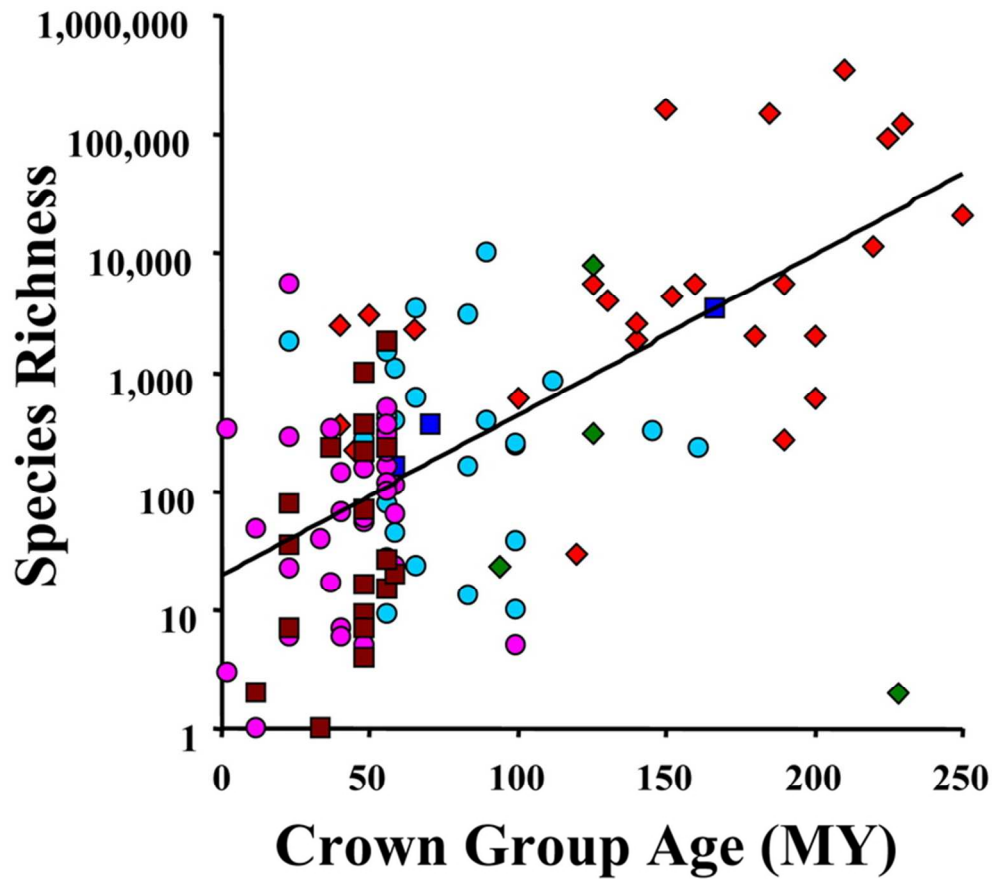


Figure 2. Extant richness and crown group age in orders of insects (red diamonds), teleost fishes (blue circles), amphibians (blue squares), reptiles (green diamonds), birds (pink circles), and mammals (red squares). The point for the Sphenodontida (green diamond at 228 MY on the crown group age axis) was excluded as an outlier. Reproduced from Figure 4 of McPeck & Brown (2007) with permission from University of Chicago Press, © 2007 by The University of Chicago.

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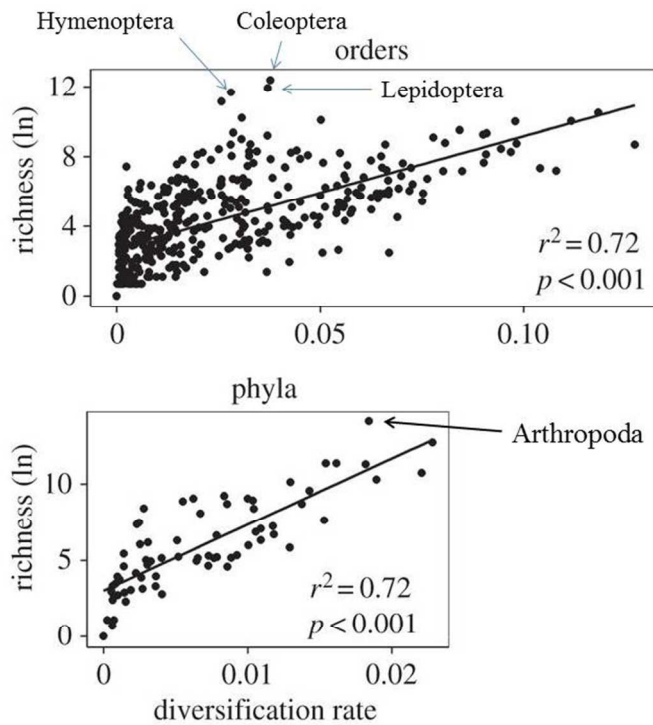


Figure 3. Diversification rate predicts richness for phyla and orders across the tree of life. Arthropods and three of the richest insect orders are labelled. Reproduced with modifications from Figure 3 of Scholl & Wiens (2016) by permission of the Royal Society.

254x190mm (96 x 96 DPI)

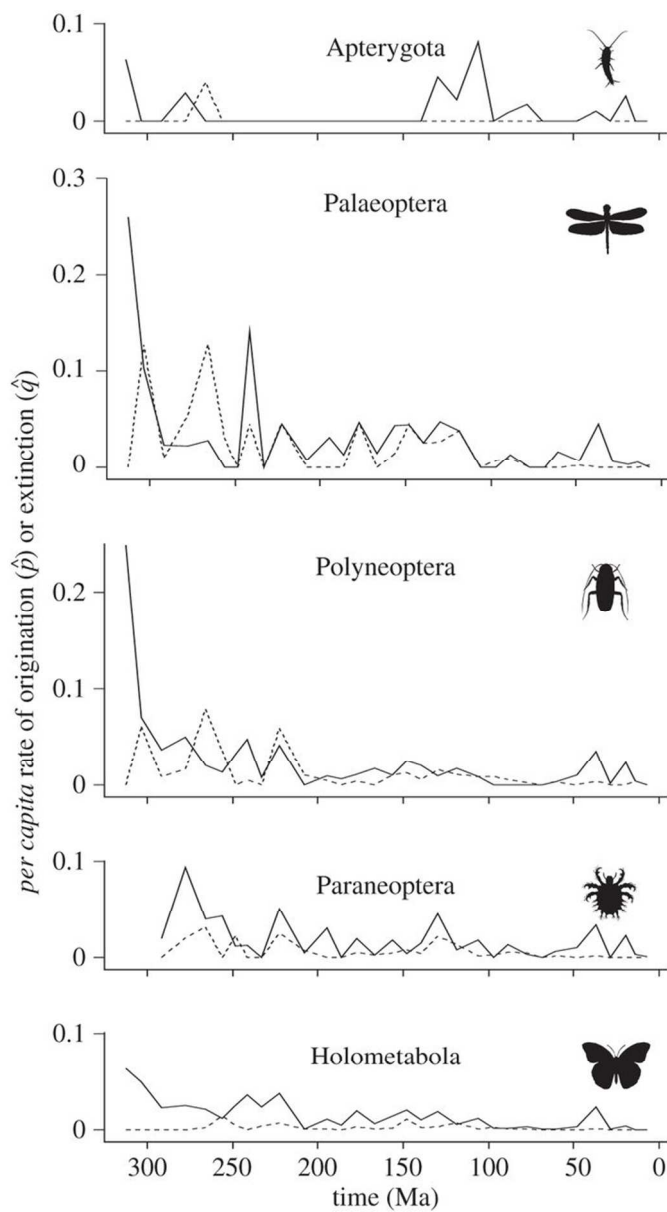


Figure 4. Family level origination and extinction rates for major insect higher taxa. Both rates are elevated in Palaeoptera and extinction rates reduced in Holometabola. This also appears as Figure 2 in Nicholson et al. (2014), published by Wiley and the Royal Society, © the authors.

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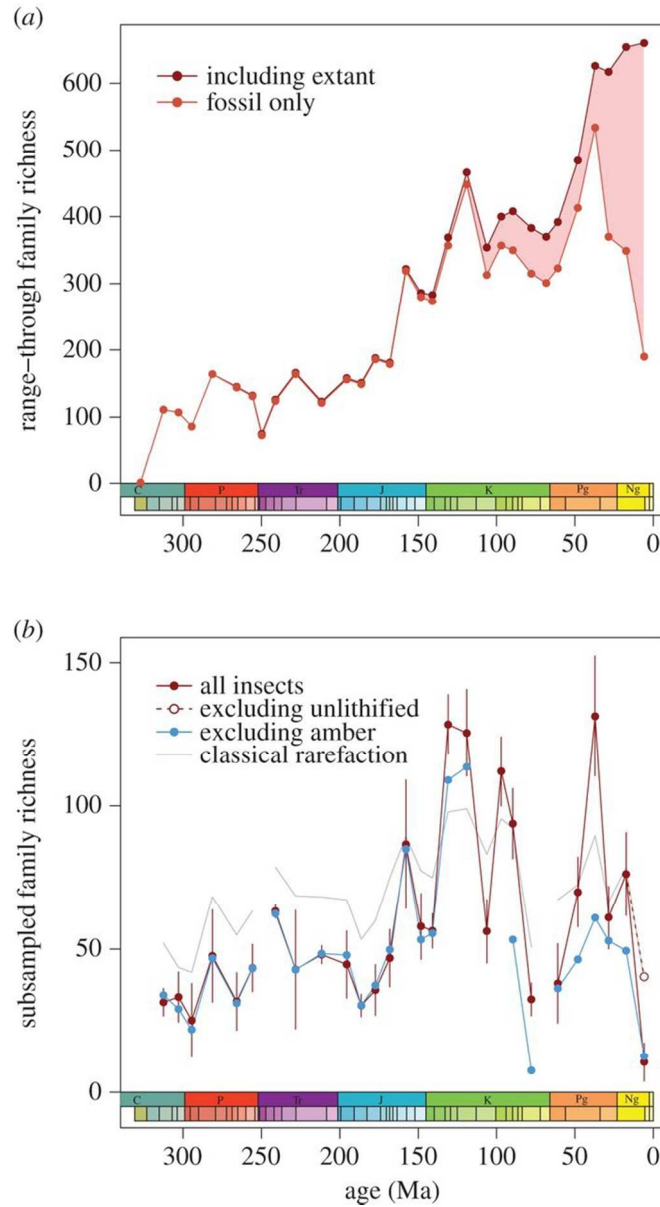


Figure 5. Fossil family richness through time using (a) the raw family record as represented in the Paleobiology database by “range-through” measures, and with the pull-of-the-recent removed by considering only last occurrences from the fossil record, and (b) using standardized subsamples. This also appears as Figure 1 in Clapham et al. (2016), published by Wiley and the Royal Society, © the authors.

58x108mm (300 x 300 DPI)

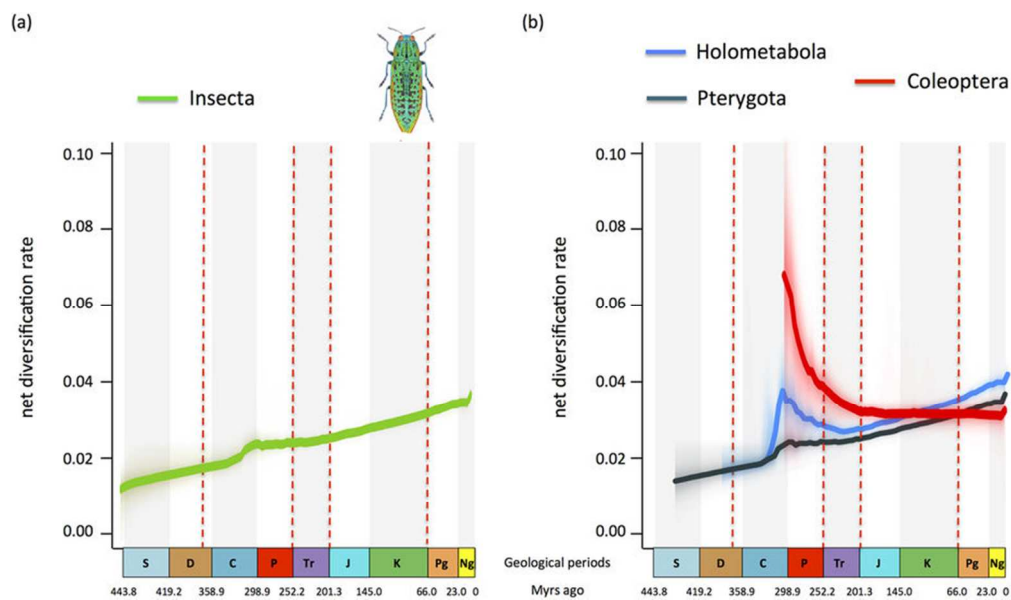


Figure 6. Net rates of diversification estimated from a family level phylogeny of insects and their described species richness (a) for the whole clade and (b) for particular subclades. Reproduced from Figure 3 of Condamine et al. (2016) under Creative Commons Attribution Licence (CC-BY) 4.0.

78x45mm (300 x 300 DPI)

Review

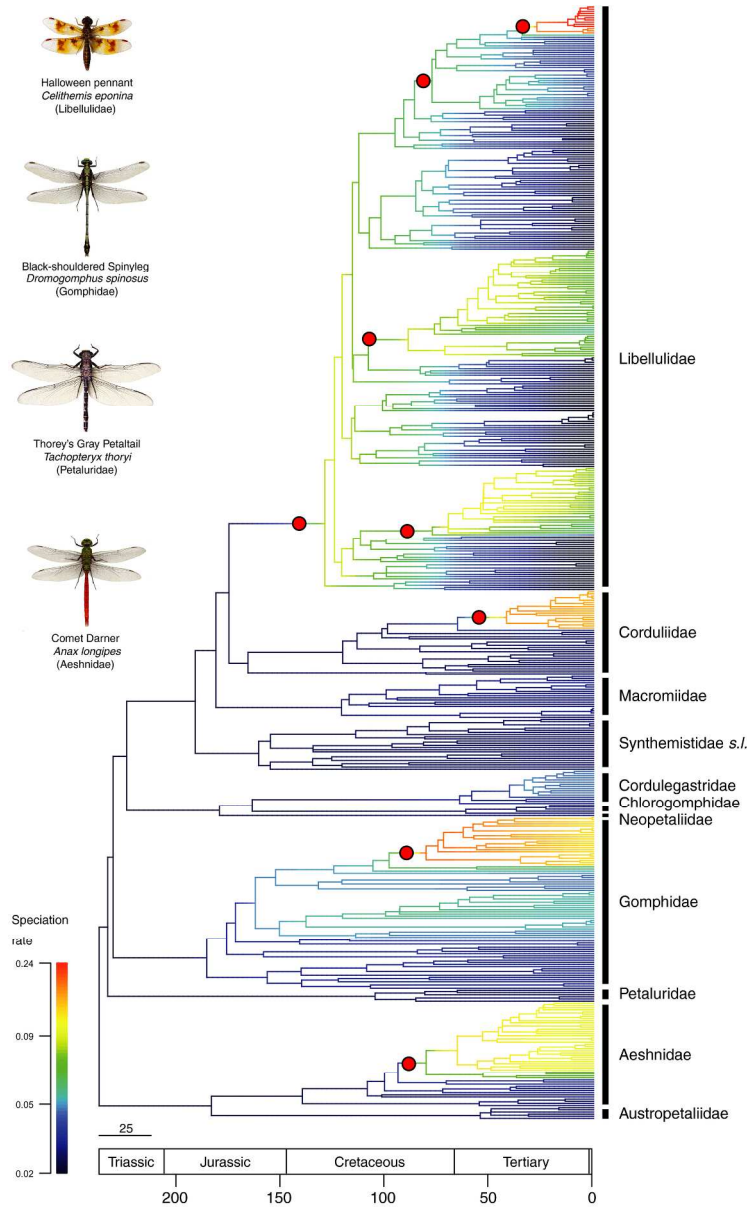


Figure 7. Speciation rates (scale bar) inferred from a phylogeny of Anisoptera (Odonata) (Letsch et al., 2016). Shifts inferred from Bayesian modelling of diversification are shown by red circles. Speciation rates have sped up in Aeshnidae, but slowed in Libellulidae. Reproduced from Figure 2 of Letsch et al. (2016) with permission from Wiley, © 2016 John Wiley & Sons Ltd.

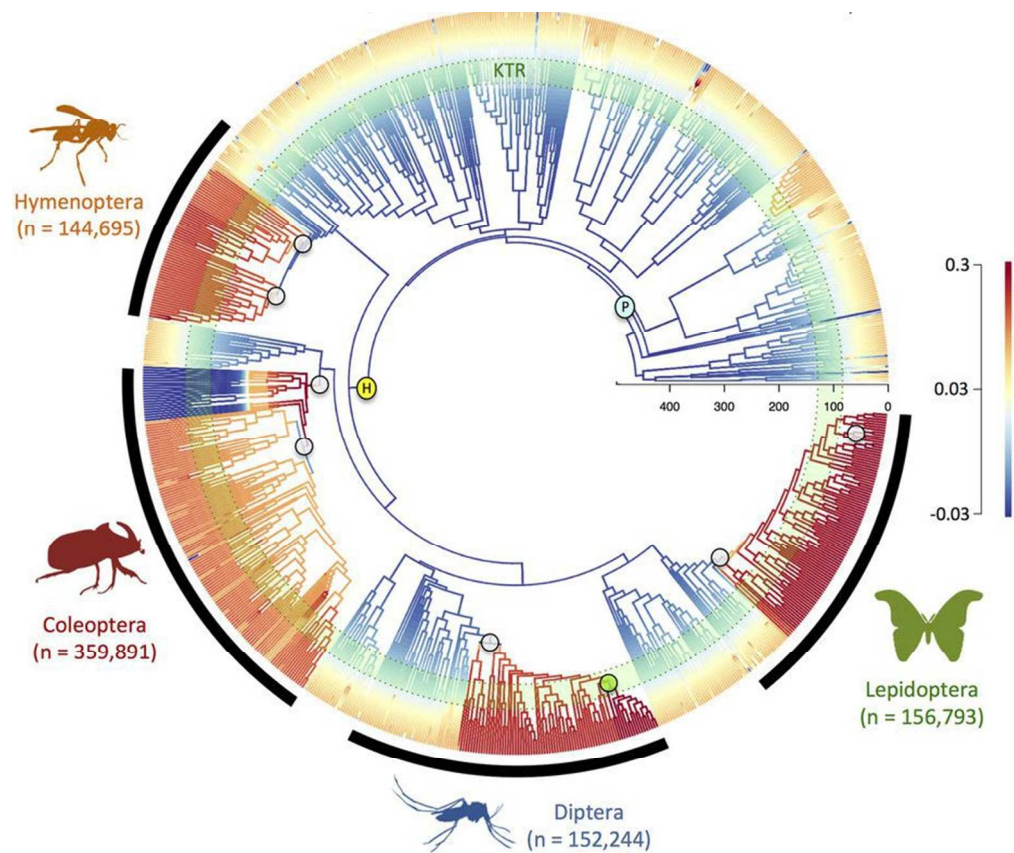


Figure 8. Shifts in diversification rate inferred from Bayesian analysis of described species richness plotted onto a family level phylogeny of insects. Colours indicate different net rates (right hand scale bar), and empty circles represent shift points (abrupt colour changes), including major upshifts in the four richest orders (illustrated). The origins of Holometabola (H) and Pterygota (P) are not accompanied by shifts. Reproduced from Figure 4 of Condamine et al. (2016) under Creative Commons Attribution Licence (CC-BY) 4.0.

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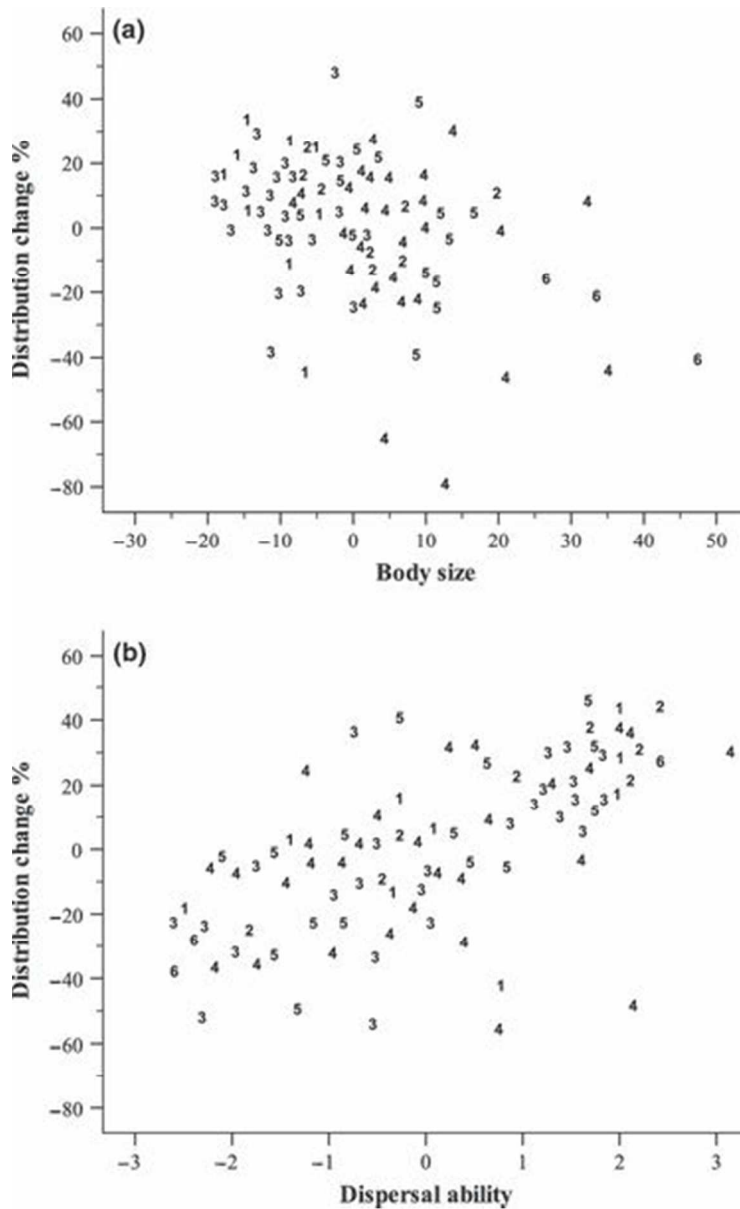


Figure 9. Partial regressions showing the effect of body size and dispersal ability on range change in Finnish butterflies. 1=Hesperiidae, 2=Pieridae, 3=Lycaenidae, 4=Nymphalidae, 5=Satyridae, 6=Papilionidae. Reproduced from Figure 2 of Mattila et al. (2011) with permission from Wiley, © 2011 The Royal Entomological Society.

131x214mm (72 x 72 DPI)

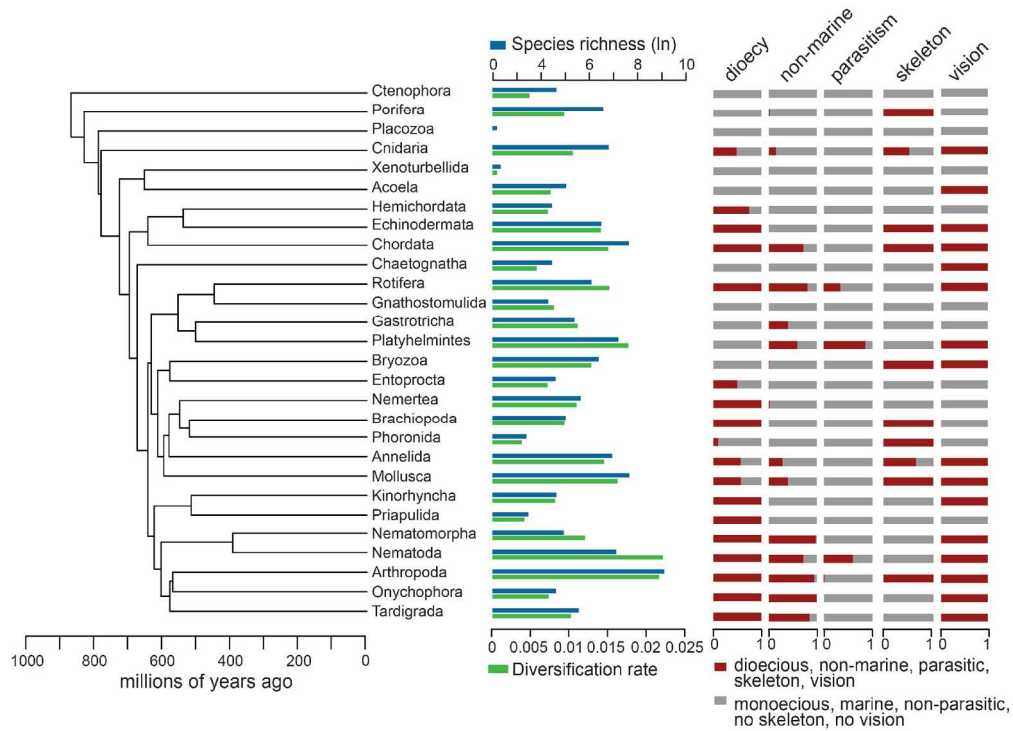


Figure 10. Species richness, diversification, and ultimate factors explaining them across animal phyla. Proportion of species displaying each trait is shown across taxa for the five most important explanatory variables, and Arthropoda are the only Phylum showing species with all five traits. The proportion of species displaying parasitism is an underestimate as parasitism is very strictly defined. Reproduced from Figure 1 of Jezkova & Wiens (2017) with permission from University of Chicago Press, © 2017 by The University of Chicago. All rights reserved.

682x492mm (72 x 72 DPI)

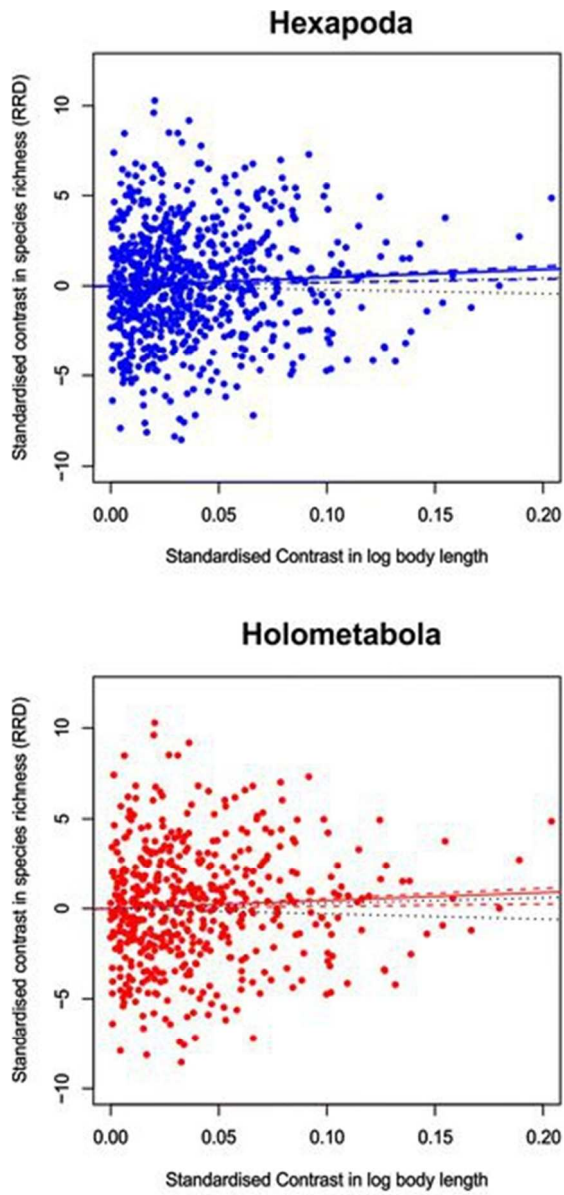


Figure 11. The lack of association between body size and species richness in Hexapoda and Holometabola. Reproduced from Figure 3 of Rainford et al. (2016) under Creative Commons Attribution Licence (CC-BY) 4.0.

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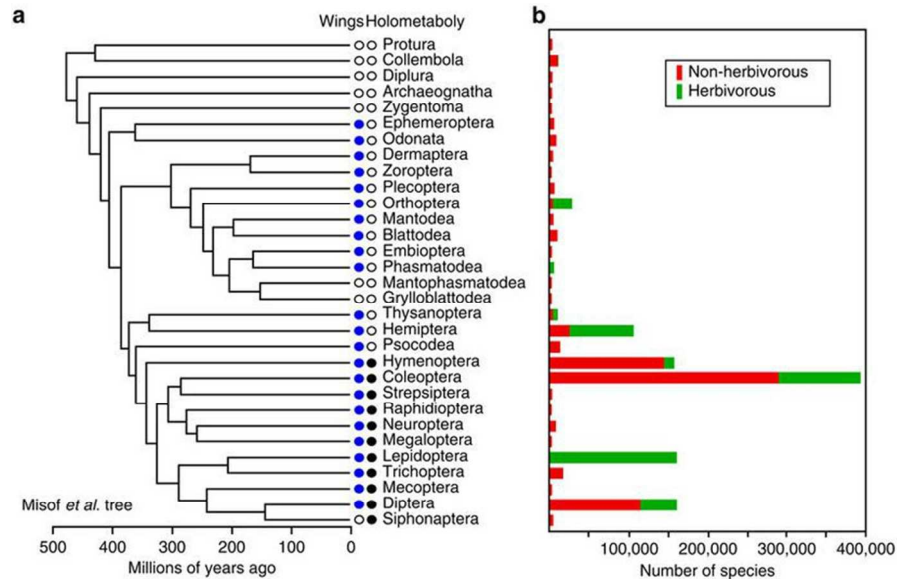


Figure 12. Traits affecting diversification across the hexapod orders. The distribution of two morphological variables (wings and metamorphosis) (a) is plotted against the species richness of taxa and the number of species that are herbivorous (b). Reproduced from Figure 1 of Wiens *et al.* (2015) under Creative Commons Attribution Licence (CC-BY) 4.0.

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review

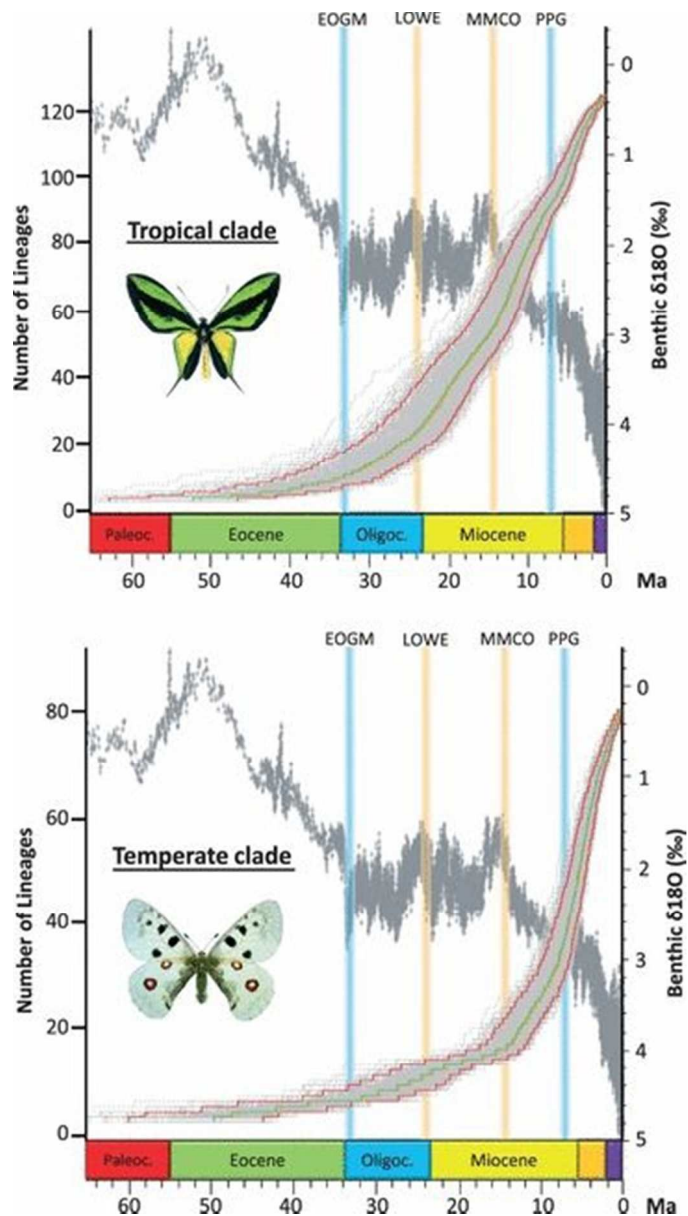


Figure 13. Diversification of a tropical (top) and temperate (bottom) clade of swallowtail butterflies depicted as lineage-through-time plots. Also shown is the Cenozoic global climate cooling as depicted by Benthic $\delta^{18}O$. Vertical bars show periods of cooling (blue) and warming (orange). The tropical clade has diversified faster than the temperate clade, but does so more after cooling events, whilst the temperate clade diversifies faster after warming events. Reproduced from Figure 4 of Condamine et al. (2012) with permission from Wiley, © 2012 Blackwell Publishing Ltd/CNRS.

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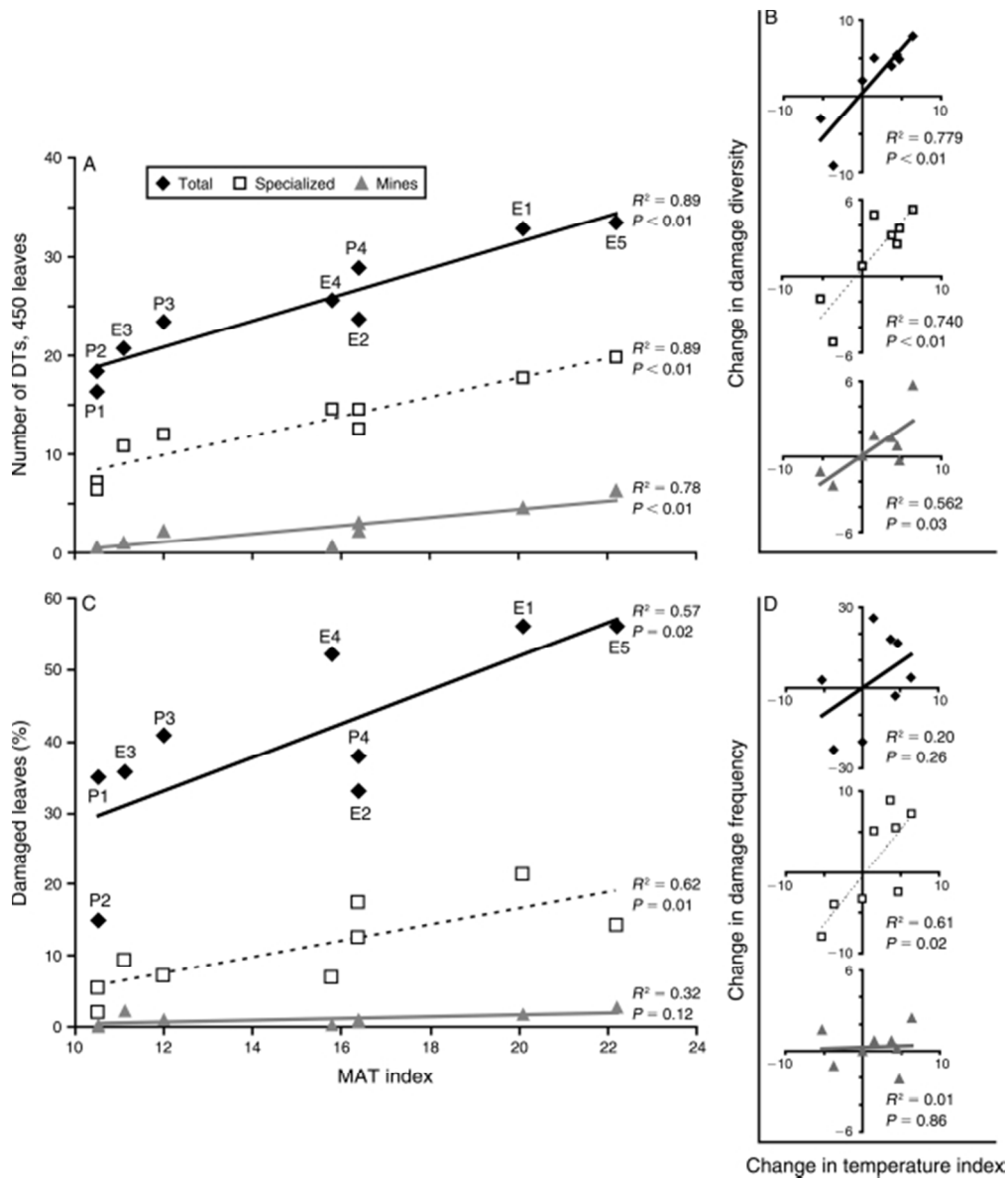


Figure 14. Change in leaf damage types (DT) (A, B) and amount of damage (C, D) with mean annual temperature (MAT) over six million years of the Paleocene-Eocene thermal maximum at a site in the USA. Reproduced from Figure 7 of Currano et al. (2010) with permission from Wiley, © 2010 by the Ecological Society of America.

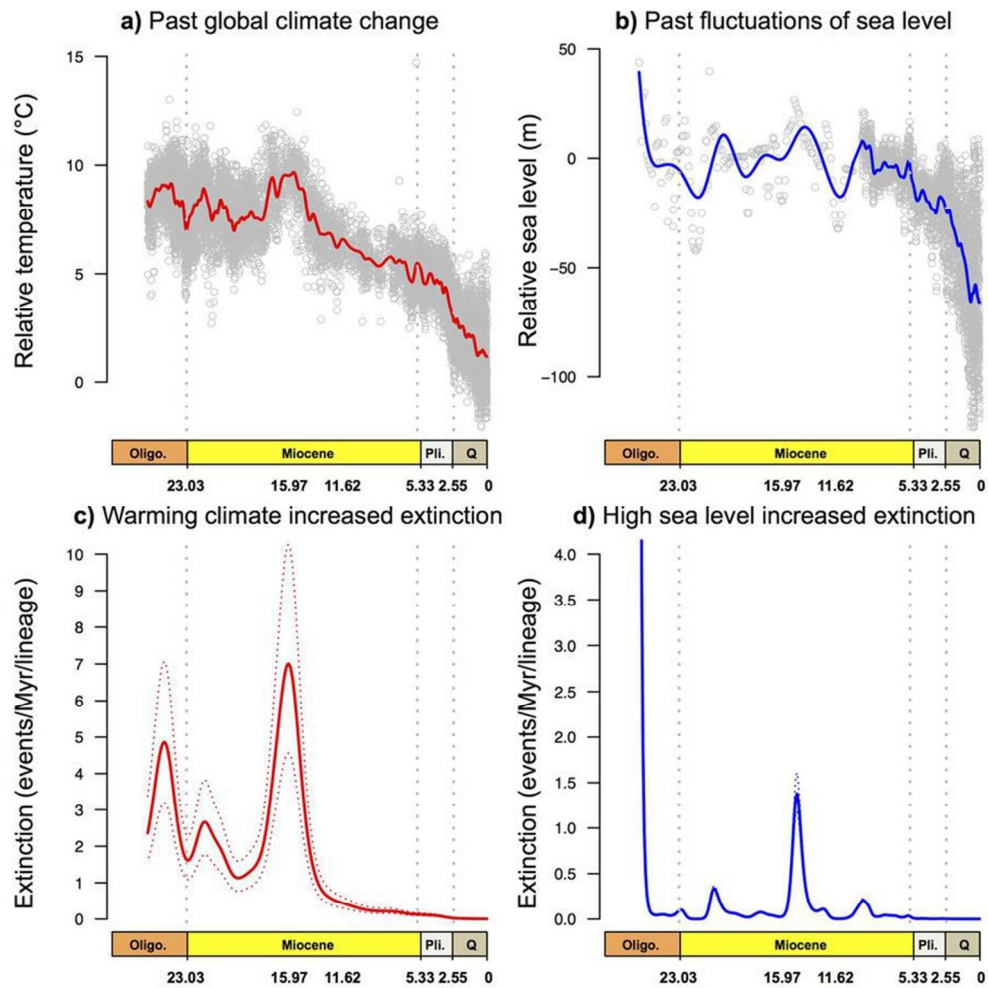


Figure 15. Effect of global temperature and sea level change on extinction of birdwing butterflies. Reproduced from Figure 3 of Condamine et al. (2015) under Creative Commons Attribution Licence (CC-BY) 4.0.

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