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

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Peter J Mayhew

Department of Biology,
University of York,
Heslington,
York
YO10 5DD

Tel: +44 (0)1904 328644
e-mail: peter.mayhew@york.ac.uk

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Abstract

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

Introduction

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

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

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

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

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

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

It was convenient to keep the broad scope and framework of the previous review (Figure 1), and treat subjects in the same order, so that the current one can be read as a supplement to the former, covering work published 2006-2017. People who have read both should have a broad overview of what has been discovered about insect macroevolution using fossil and phylogenetic approaches. In common with the earlier review, I do not cover mechanistic work on speciation and extinction in insects that relates to population level phenomena, nor community ecology studies, though such studies provide a vital source of hypotheses for comparative fossil or phylogenetic work to test, as well as underlying explanations for patterns revealed. There have been contrary views about whether it is best or most convenient to consider clade carrying capacity as a proximate, i.e. macroevolutionary, variable (Mayhew, 2007) or more ultimate, ecological, factor affecting clade richness (Wiens, 2017) (Figure 1). Here I retain my original structure and consider it as a proximate variable (Figure 1). Potentially valuable alternative ways to classify proximate and ultimate factors are given by Wiens (2017).

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

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

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

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

Proximate variables

Time.

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

There has been much recent interest in statistical correlations between age (as opposed to diversification rate) and richness, largely because they have been used to argue for or against the existence of diversity-dependent clade growth (Rabosky, 2009; Wiens, 2011). Such studies can also be used to argue about which proximate variables best explain variation in richness (Wiens, 2017). In studies involving hexapods, variable results have been found. A positive correlation between age and richness has been found across animal classes in a multivariate model (Etienne et al., 2012), across numerous taxa including crown insect orders (McPeek & Brown, 2007) (Figure 2), across stem insect orders after accounting for other factors (Ferns & Jervis, 2016), across water beetle lineages after removing the most diverse taxon (Bloom et al., 2014), and across beetle families but not subfamilies (Rabosky et al., 2012). Thus, perhaps unsurprisingly, it is sometimes true that the richer clades, of a collection being studied, are older ones. However, across the tree of life at several higher taxonomic levels stem age does not predict richness well (Scholl & Wiens, 2016), suggesting that the age of arthropods (and hence hexapods) cannot explain their richness in a broader taxonomic setting. Indeed, in several analyses, age is negatively correlated with richness, a probably consequence of diversification rates increasing in derived taxa (see below). Age also does not predict richness across Diptera higher taxa (Wiegmann et al., 2011) nor across Apameini moths (Toussaint et al., 2012), nor ant genera (Pie & Tschá, 2009) nor across many individual or aggregate taxa (Rabosky et al., 2012). Wiens (2017) has also argued that using crown ages, as in (McPeek & Brown, 2007), inflates the rates of species-poor and ancient groups that have suffered extinction. We must therefore turn to net diversification rates and the two processes underlying it, speciation and extinction, to further understand insect richness.

Net rates of diversification

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

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

Speciation/origination and extinction rates

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

Some recent fossil studies have suggested that insects may have been more vulnerable to some extinction events than previously supposed. Fossil studies have not detected extinction at the K-Pg boundary at the family level in insects (Condamine et al., 2016; Nicholson et al., 2015). However, studies of insect trace fossils have shown a depletion of the quantity and types of feeding damage on plants, suggesting that extinction did occur at finer taxonomic or functional scales (Donovan et al., 2014; Labandeira & Currano, 2013; Wappler et al., 2009; Wilf et al., 2006). It is difficult to know how these rates compare to those in other taxa because of the differences in types of data used.

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

Phylogenetic analyses of diversification shifts through time have attempted to separate out speciation and extinction, but have produced heterogeneous results. Given that molecular phylogenetic methods are generally known to poorly estimate extinction rates (Rabosky, 2010), especially when the trees are incompletely sampled (May & Moore, 2016; Meyer & Wiens, 2017; Moore et al., 2016; Rabosky et al., 2017), this heterogeneity probably just reflects low signal in the data. Using the maximum likelihood application *TreePar* (Meredith et al., 2011) suggest that the ratio of extinction to speciation is very close to zero through the evolutionary history of the insects (Condamine et al., 2016). Wiegmann et al. (2011) also found that extinction rates were generally low in Diptera. However, analyses of clade-specific diversification shifts using the maximum likelihood application *MEDUSA* (Alfaro et al., 2009) across a tree of most insect families suggested that the speciation and extinction rates were almost identical over large parts of the tree (Rainford et al., 2014). The same has been inferred from a large dataset on species richness, body size and clade age involving both insects and other taxa (Etienne et al., 2012). Analyses of the *Heraclides* swallowtail tree suggested no extinction (Lewis et al., 2015), a result that has been found in many similar non-insect studies and may be an artefact, whilst in *Cinara* aphids extinction rates are about half that of speciation rates (Meseguer et al., 2015), as in Orthoptera (Song et al., 2015). Extinction rate to speciation rate ratios were highly variable across ants (Moreau & Bell, 2013).

Other studies have attributed changes in net diversification in particular clades to either changes in speciation or extinction rates. There is no particular a priori reason to expect that speciation or extinction should be the dominant driver of such changes, though the fact that the focal taxa often contain diverse but derived clades, and that molecular phylogenies do not contain extinct taxa, may predispose studies towards detecting rises in speciation rate. Such changes have indeed been suggested, and are probably more robust generally than inferences about extinction rate changes. Letsch et al. (2016) inferred a higher speciation rate in lentic than lotic Odonata species being the reason for their higher net diversification rate. Fagua et al. (2017) inferred speciation and extinction rates in tortricid moths and found high initial diversification resulting from speciation being almost double extinction, with significant shifts in speciation rate in one major clade followed by declines in both speciation and extinction rates. In *Heliconius* butterflies too, diversification rate variation has been mostly due to speciation rate changes (Kozak et al., 2015). In nymphalid butterflies, species feeding on Solanaceae have higher net diversification rates as a result of higher speciation rates.

Other studies have found changes to be driven by extinction. Kergoat et al. (2014) found that a rise in the extinction rate of tenebrionid beetles was mainly responsible for the slow- down in its diversification, as did Condamine et al. (2015) for birdwing butterflies. (Peña & Espeland, 2015). In scale insects, specialist species were inferred to have lower net diversification rates than generalist species as a result of rises in both extinction and speciation rates, with extinction rates rising more (Hardy et al., 2016). Hamm & Fordyce (2015) found that clades with higher net diversification in Nymphalidae also had elevated turnover (i.e. higher ratios of extinction to speciation rates). They also estimated speciation and extinction rates for specialist and generalist clades (see also Hardy & Otto (2014), although others have found these not to be robust (Janz et al., 2016). Despite the misgivings about overall extinction rate estimation above, some of the above studies (e.g. (Kergoat et al., 2014) display remarkable changes in phylogenetic branching patterns at particular time periods that suggest that some extinction signal has been detected by these approaches.

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

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

Carrying capacity

Tests for a slowing of net diversification over time, such as might be expected under diversity-dependent diversification, have been frequent over the last decade. Nicholson et al. (2015) showed a continual increase in family richness in the raw fossil record, but there was variability across taxa in the best-fit model (Nicholson et al., 2014), with sigmoidal growth of families in the most rich taxa (e.g. Holometabola) and exponential in the least rich (e.g. Palaeoptera). The Coleoptera show a matching pattern with a continual increase although net diversification rates have fallen (Smith & Marcot, 2015), whilst Lepidoptera families better fit an exponential than linear model (Sohn et al., 2015). Studies of the raw record may however be suspect, because of sampling and other biases, especially the 'pull-of-the-recent', which tends to overemphasize recent diversity. Clapham et al. (2016) showed that the pull of the recent was indeed very significant, and that when richness was sample-standardized, there was no strong evidence of an increase in diversity since the Cretaceous (Figure 5), with net diversification rates reduced to near-zero (Condamine et al. 2016). This is much more indicative of diversity-dependent clade growth. A different approach to removing fossil record biases was used by Davis et al. (2011), using phylogeny to fill in fossil gaps. The Odonatoidea families best fit a linear model of growth if the raw record is taken, but if the ages of sister groups are equalized, growth is more sigmoidal, again suggesting diversity-dependence.

Tests of diversity-dependence have also been conducted on numerous phylogenies of extant taxa, though the absence of extinct lineages cautions against uncritical acceptance of their findings. Across the hexapods as a whole, net diversification rates appear to be increasing (Condamine et al., 2016) (Figure 6), a finding consistent with the observation that younger orders have higher net rates of diversification (Ferns & Jervis, 2016). This would suggest that there is still room on Earth to accommodate many more insect species than currently exist, and is possibly robust for two reasons: the tip taxa (e.g. families) in the phylogenies are often very rich, implying much more rapid branching than is found below them. In addition these tip richness values are likely vast underestimates as they only include described species. Similar trends have been reported in *Heliconius* butterflies (Kozak et al., 2015), in the Aeshnidae (Odonata) (Letsch et al., 2016) (Figure 7), in Orthoptera (Song et al., 2015), and in apameine moths (Toussaint et al., 2012). Several clades show no evidence for change over time in their diversification rates: *Drosophila* flies (Morales-Hojas & Vieira, 2012), *Cinara* aphids (Meseguer et al., 2015), *Heraclides* butterflies (Lewis et al., 2015), ants (Pie & Tschá, 2009), Iberian dung beetles (Cunha et al., 2011) and swallowtail butterflies (Condamine et al., 2012), indicating that they have not yet approached any carrying capacity. In contrast, several clades show declining rates over time: beetles in general (Condamine et al., 2016), birdwing butterflies (Condamine et al., 2015), Libelluidae (Odonata) (Letsch et al., 2016) (Figure 7), tortricid moths (Fagua et al., 2017), *Nicrophrorus* beetles (Toussaint & Condamine, 2016), ants (Moreau & Bell, 2013), ithomiine butterflies (De-Silva et al., 2016; Elias et al., 2009), *Eois* moths (Strutzenberger & Fiedler, 2011) and *Cephaloleia* beetles (McKenna & Farrell, 2006). Overall this heterogeneity across taxa seems unlikely to be an artefact of biases in the method, and suggests an interesting pattern; that continual insect diversification is supported by the continuing emergence of new radiations that more-than-compensate for the slow-downs experienced in some clades (Figure 6). It also suggests that the global taxonomic composition of insect faunas is continuing to change (Figure 7).

How are we to reconcile the fossil evidence for diversity-dependence across all hexapods (Clapham et al., 2016) (Figure 5) with the lack of phylogenetic evidence for it (Condamine et al., 2016) (Figure 6)? The critical difference may be the taxonomic level under consideration: a slow-down in family diversification may be entirely compatible with an increase in diversification at the species level. It is interesting therefore that the species level fossil record, such as it is, also provides no evidence for an increase in richness since the Cretaceous (Clapham et al., 2016).

Ultimate factors

Morphological variables

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

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

However, diversification rate models using the Bayesian modelling application *BAMM* fail to show any such diversification shift on a family level phylogeny (Condamine et al., 2016) (Figure 8). This latter study must be regarded as more definitive for the present, as *BAMM* contains two advantages over *MEDUSA*: (1) the ability to apply diversity-dependent models; (2) high parameter models do not have to be nested within the best set of lower parameter models (May & Moore, 2016; Rabosky, 2014). *BAMM* is also, in some respects, an improvement over sister-taxon 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).

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

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

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

The role of complete metamorphosis in diversification is not yet settled. It is usually hypothesized to have increased diversification rates by allowing adults and larvae to use separate food sources, and hence allowing greater specialization of the ecological niche through separate adult and larval morphologies (Mayhew, 2007). The trait explains diversification rates in PGLS analyses for some phylogenetic topologies but not others (Wiens et al., 2015). However, not all competing key innovations were included in models. In *MEDUSA* analyses at family level a diversification shift at the origin of metamorphosis is recovered robustly (Rainford et al., 2014), but not in sister-taxon comparisons at order level (Davis et al., 2010a), nor in *BAMM* analyses at family level, where all the shifts are within the four largest holometabolan orders (Condamine et al., 2016) (Figure 8). For the reasons stated above, the latter study is currently probably superior to other phylogenetic studies, but may ultimately not be definitive. Note that this study also leaves open the possibility that metamorphosis is a contingent key innovation that only exerts its effects in combination with other traits. Fossil family studies show that holometabolan families have lower extinction rates than other related groups in the same time interval (Nicholson et al., 2014) (Figure 4), though this does not necessarily mean that species level extinction rates are also lower.

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

One comparative study has recently provided evidence for the diversifying effects of a skeleton and of sensory sophistication, both features long thought to have promoted insect diversity, potentially through a range of mechanisms such as expansion of the ecological niche, increasing the potential for sexual selection and other forces promoting reproductive isolation, and potentially reducing mortality and extinction rates. In a comparative study across animal phyla, Jezkova & Wiens (2017) showed that both had a significant effect even after controlling for other likely factors (Figure 10). The explanatory power of vision and skeletons differed according to which other traits were in the models, as well as the assumed species richness values and phylogeny and estimated extinction fraction, but in univariate models vision explained about 30% of the variation in diversification rate whilst skeletons explained only half that. Arthropods scored positive for all five of the traits that best explained diversification rates across phyla, the others being non-marine habitat, parasitism and dioecy (Figure 10). Segmentation and presence of legs were never significant. No studies seem to have addressed the diversifying effects of mouthpart diversity in the last decade, but if insect diversity did in fact peak in the Cretaceous (Clapham et al., 2016; Davis et al., 2011) (Figure 5) this would give a better match between the rise of insect diversity and the rise of mouthpart diversity than previously inferred (Mayhew, 2007), making a causal relationship between the traits more likely, potentially through allowing adaptation to a broader range of ecological niches.

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

Ecology and behaviour

Interspecific interactions

The wide variety of interspecific interactions between insects and other organisms has so impressed observers that it has long been considered one of the chief reasons for their species richness (Mayhew, 2007). A particular focus has been the interactions between insects and plants, particularly flowering plants, and particularly herbivory, because feeding on plants allows insects to exploit a variety of specialized ecological niches (Futuyma & Agrawal, 2009; Kergoat et al., 2016; Nylin & Wahlberg, 2008; Nyman, 2010; Suchan & Alvarez, 2015). Thus, herbivory could increase speciation rates, increase clade carrying capacity, and because it involves feeding at a low trophic level, could also reduce extinction rates (Mayhew, 2007).

Studies on the diversifying effects of herbivory across broad taxonomic groups in the last decade have produced mixed results (Nakadai, 2017). Hunt et al. (2007) detected no significant effect of herbivory on Coleoptera diversification. The same was found by Rainford & Mayhew (2015) using sister taxon comparisons across a family level phylogeny. However, Wiens et al. (2015) found a significant association between herbivory and diversification rate across all orders and at finer relation for some groups (Figure 12). The relationship remained non-significant within Coleoptera and all other orders except Diptera and Hemiptera. In some cases, non-herbivorous groups have radiated very rapidly, whilst in others herbivorous groups have remained species poor. One possible reason for the difference in the findings of the latter two studies could be their different approaches to coding herbivory: dichotomous, with comparisons identified on the basis of ancestral state reconstruction (Rainford & Mayhew, 2015), or as the proportion of species that are herbivorous (Wiens et al., 2015). Neither of these approaches is free from potential error, and a definitive study will also need a better resolved phylogeny to identify the best set of comparisons, and potentially more of them.

Another series of studies has looked for a temporal coincidence in richness or diversification rates and the rise of the angiosperms. The new sample-standardized fossil record shows a peak in richness at the time when angiosperms rose to dominance, unlike the raw fossil record which shows a flattening in richness (Clapham et al., 2016). Labandiera (2014) has shown that many gymnosperm associated insect clades declined during this period, whilst a smaller number of clades radiated onto angiosperms, so a straightforward increase in insect richness with the rise of the angiosperms may be a naïve expectation. Several phylogenetic studies have attempted to see if diversification coincided with the rise of angiosperms or of their particular associated host plant groups. Rainford et al. (2014) and Condamine et al. (2016) both agree that increases in diversification of selected clades occurred then, although there was no noticeable effect on overall insect diversification. Specific clades which have shown this behaviour include bees (Cardinal & Danforth, 2013), ants (Moreau et al., 2006), tortricid moths (Fagua et al., 2017), Lepidoptera in general (Wahlberg et al., 2013), Scaraboidea beetles (Ahrens et al., 2014), some tenebrionid beetles (Kergoat et al., 2014) and weevils (McKenna et al., 2009). Satyrinae butterfly diversification occurred during the diversification and spread of grasses (Peña & Wahlberg, 2008), as did apameine moths (Toussaint et al., 2012), skipper butterflies (Sahoo et al., 2017), and Australian gall thrips also diversified in concert with their hosts (McLeish et al., 2007), as did *Eois* moths (Strutzenberger & Fiedler, 2011), and bruchine beetles (Kergoat et al., 2011). The causal inferences claimed by these studies need to be treated with caution given that none of them has tested an association statistically. In contrast to the above studies, chrysomelid beetles (Gómez-Zurita et al., 2007), *Asteromyia* gall midges (Stireman et al., 2010), heterarthrine sawflies (Leppänen et al., 2012) and *Phyllonorycter* moths (Lopez-Vaamonde et al., 2006) apparently radiated long after their host plants. Such outcomes are expected since plant radiations provide the potential for insect radiation at any point after the plant radiation occurs.

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

In contrast, the evolution of bats may have reduced the diversity of some lacewing taxa (Archibald et al., 2014), whilst promoting the diversity of other groups with defences against them. Bats are major predators of lacewings which presumably has increased extinction risk for some taxa. The proportion of species that are parasitic also predicts richness across orders (Ferns & Jervis, 2016), as well as phyla (Jezkova & Wiens, 2017), again a likely consequence of specialization opening up ecological opportunities. However a sister-taxon contrast study across families and higher taxa found no consistent association between any broad dietary category and species richness (Rainford & Mayhew, 2015). Diets are phylogenetically constrained, but to variable extents, and some are more reversible than others, and have originated different numbers of times and over different time spans, partially explaining why some are more taxonomically widespread than others. Overall though, many broad dietary categories have facilitated impressive radiations, whilst none appears to have done so entirely consistently.

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

Host shifting accounts for about 20% of speciation events in nematine sawflies (Nyman et al., 2010), and in willow galling sawflies also promotes diversification of their parasitoids (Nyman et al., 2007), whilst parasitoids of *Rhagoletis* flies sometimes speciate by host shifting. Since these shifts are relative recent, it suggests that lineages that originate by host shifts do not persist very long (Hamerlinck et al., 2016). Diversification shifts coincident with use of novel hosts have been identified in pierid butterflies (Edger et al., 2015), delphacid planthoppers (Urban et al., 2010), aphids (Peccoud et al., 2010), heterarthrine sawflies (Leppänen et al., 2012), *Phytomyza* flies (Winkler et al., 2009) and ithomiine butterflies (Peña & Espeland, 2015). Increases in host range across higher taxa also seem to allow diversification in some clades, an possible example of an adaptability trait that promotes diversification (Nylin & Wahlberg, 2008). For example, larval diet range is positively correlated with richness across orders of insects (Ferns & Jervis, 2016). Evidence, sometimes disputed (Hamm & Fordyce, 2015; Janz et al., 2016), has also been presented for a negative relationship between host range and diversification rate in swallowtail butterflies (Hardy & Otto, 2014), longwing butterflies (Hardy & Otto, 2014) and brush-foot butterflies (Janz et al., 2016; Janz et al., 2006), and bark beetles (Gohli et al., 2017). At the species level specialization may however also carry macroevolutionary costs. In scale insects, diversification rates are lower in more specialized groups (Hardy et al., 2016), and across extant taxa extinction risk is often higher in more specialized taxa (Franzén et al., 2012; Jeppsson & Forslund, 2014; Mattila et al., 2011; Mattila et al., 2008; Mattila et al., 2009; Nylin & Bergström, 2009; Powney et al., 2015). For this reason, specialization is often regarded as a paradoxical macroevolutionary trait; it may promote speciation but also extinction. Rainford & Mayhew (2015) found that taxa with diets generally regarded to promote specialization (herbivory, ectoparasitism, parasitoidism, fungivory) do not generally have higher richness than their sisters with other diets presumed not to promote specialization, though they may be diets that are harder to lose. One reason may be that these costs sometimes balance out the benefits, though it is also possible that these categories are too coarse to detect underlying patterns.

Latitude and other biogeographic factors.

At least one study in the last decade has investigated the macroevolutionary effects of latitude in insects: Condamine et al. (2012) found that tropical swallowtail butterflies diversity faster than temperate ones (Figure 13); a finding already known from previous sister-taxon studies (Mayhew, 2007). Some other phylogenetic studies have been pertinent to the evolution of latitudinal gradients, showing that the tropics are both the site of origination of major groups (a museum), giving them a long time to generate species (Branstetter et al., 2017; McKenna & Farrell, 2006; Moreau & Bell, 2013), and also generate many species over time (a cradle).

A number of other studies have addressed how biogeographic processes might have contributed to the radiation of various insect groups. The contribution of biogeography to diversification is a soft hypothesis, because for any diverse group geographic ranges will vary across taxa, and therefore some biogeographic process can be inferred to have taken place. The interest is therefore primarily in which processes. In Central/South America, the formation of the isthmus of Panama and the rise of the Andes are inferred to have promoted diversification in *Cephaloleia* leaf beetles (McKenna & Farrell, 2006), ithomiine butterflies (De-Silva et al., 2016; Elias et al., 2009) and *Eois* moths (Strutzenberger & Fiedler, 2011), presumably by increasing speciation rates through range expansion in the former, and through increasing habitat diversity and fragmentation in the latter. Unsurprisingly, dispersal events, creating geographically isolated populations, are inferred to be important in island radiations such as the *Heraclides* swallowtails (Lewis et al., 2015) and birdwing butterflies (Condamine et al., 2015). The colonization of different continents, with similar and sometimes dramatic results, has been important in a number of groups of wide distribution, including *Nicrophorus* beetles (Toussaint & Condamine, 2016), apameine moths (Toussaint et al., 2012), metalmark moths (Rota et al., 2016), tortricid moths (Fagua et al., 2017), *Drosophila* flies (Morales-Hojas & Vieira, 2012), and *Cinara* aphids (Meseguer et al., 2015). To what extent these processes are more common, or promote diversification more, in insects than other taxa is an open question.

Climate change

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

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

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

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

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

Another level of statistical rigour has been added by one study incorporating climate change into statistical models of diversification. In birdwing butterflies, high temperatures and high sea levels seem to have decreased net diversification through increased extinction rates (Condamine et al., 2015) (Figure 15). This might have been due to the reduction of island area and increased isolation of populations. However, the conclusion that extinction rates drive the changes may be suspect, because these are generally poorly estimated from molecular phylogenies.

Researchers are also now beginning to assess extinction risk from climate change in extant taxa (Pacifici et al., 2015). Comparative studies of insects in this regard may yet shed light on large scale macroevolutionary patterns related to climate, though geographic and taxonomic biases are likely to apply just as heavily here as in more general assessments of extinction risk in insects. It will be interesting to see if these studies can also be reconciled with the persistence of Pleistocene insects in the Palaearctic and elsewhere (Langford et al., 2014; Larkin et al., 2014; Marra & Leschen, 2011).

Other ecological factors

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

Looking back

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

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

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

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

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

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

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

How have broad conclusions changed in the last decade? The acceleration of net diversification rates overall at the species (but not family) level (Figures 5, 6), with heterogeneity across subtaxa (Figure 7), is an interesting new finding. This has been realized through phylogenetic studies which have filled in our knowledge gap about insect evolution the Cenozoic (Figure 13), which for fossils is dominated by noise rather than signal (Figure 5). Wings and metamorphosis still feature as likely key innovations in recent studies (Figure 12), but the best broad phylogenetic study does not implicate either (Figure 8). The importance of skeletons, vision, non-marine habit, parasitism, and dieocy across animal phyla (Figure 10) also brings a useful broader context to understanding insect richness. Whilst it is still contentious overall whether herbivory has tended to have diversifying effects, there is enough evidence to say that it does at least in some taxa, and we can say that host-shifting, and sometimes cospeciation, are important processes. We are now much more aware of the importance of climatic changes and biogeographic processes (Figures 13-15) than we were a decade ago, but studies of the former need greater statistical rigour.

Looking forward

It will be apparent from the above that there are still many unsolved controversies, and for most of the questions above, the last word has probably not been said. There is a major need to refine our knowledge of the appropriateness and validity of new statistical methods, and doubtless further methods will be developed and shape studies in the next decade. There is also a need to take more studies further with these as appropriate, so that more is made of the potential raw data beyond discursive stories. When one looks at the potential set of interesting questions that can be posed by insect macroevolution studies, it becomes clear how few of them are ever addressed in a given research project. We need to do more with what is in front of us. There is much potential still to address ultimate factors, such as diet and ecology, with fossil studies. A study of the effect of clade age and diversification rate on species richness in all insects across different higher taxa would be valuable, as current studies do not focus on them and this makes interpretation of more generic findings more difficult. Tests of diversity-dependence need to be more direct and relate rate changes to each other or actual densities rather than just testing for slow-downs in rate, as well as ruling out climate change as an alternative explanatory variable. Much more can be done with life history and morphology to address diversity-disparity relationships through time.

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

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

Given that most of the broad-scale studies discussed above work with less-than-ideal data, and hence methods, it is difficult to predict if the preliminary findings of the last decade will still stand a decade from now. We can however hope that gaps will be filled in questions addressed, and that the quality of studies increases either through improvements (e.g. veracity, completeness) in underlying datasets, as well as analytical techniques (e.g. more valid techniques, or used in more appropriate ways). That leads to the further hope that a decade or more from now, another review will be able to claim a more confident understanding of the reasons for insect species richness than we currently have.

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Figure legends

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

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 McPeek & Brown (2007) with permission from University of Chicago Press, © 2007 by The University of Chicago.

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.

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.

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.

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.

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.

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.

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.

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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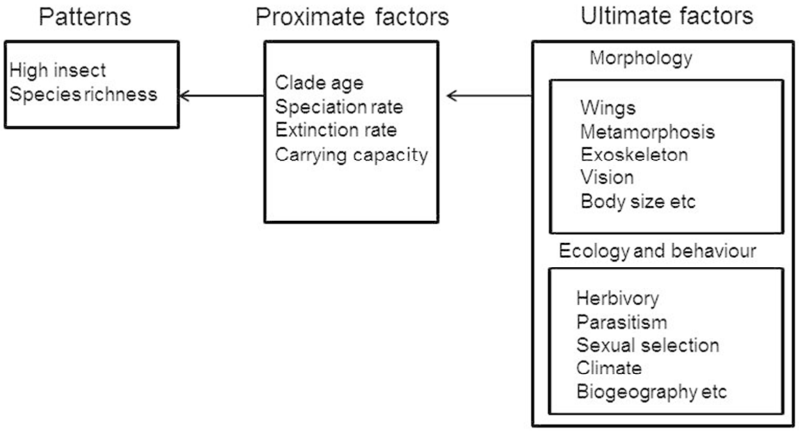

Figure 1. The types of explanation for hexapod richness and their interrelationships, as presented in this review.

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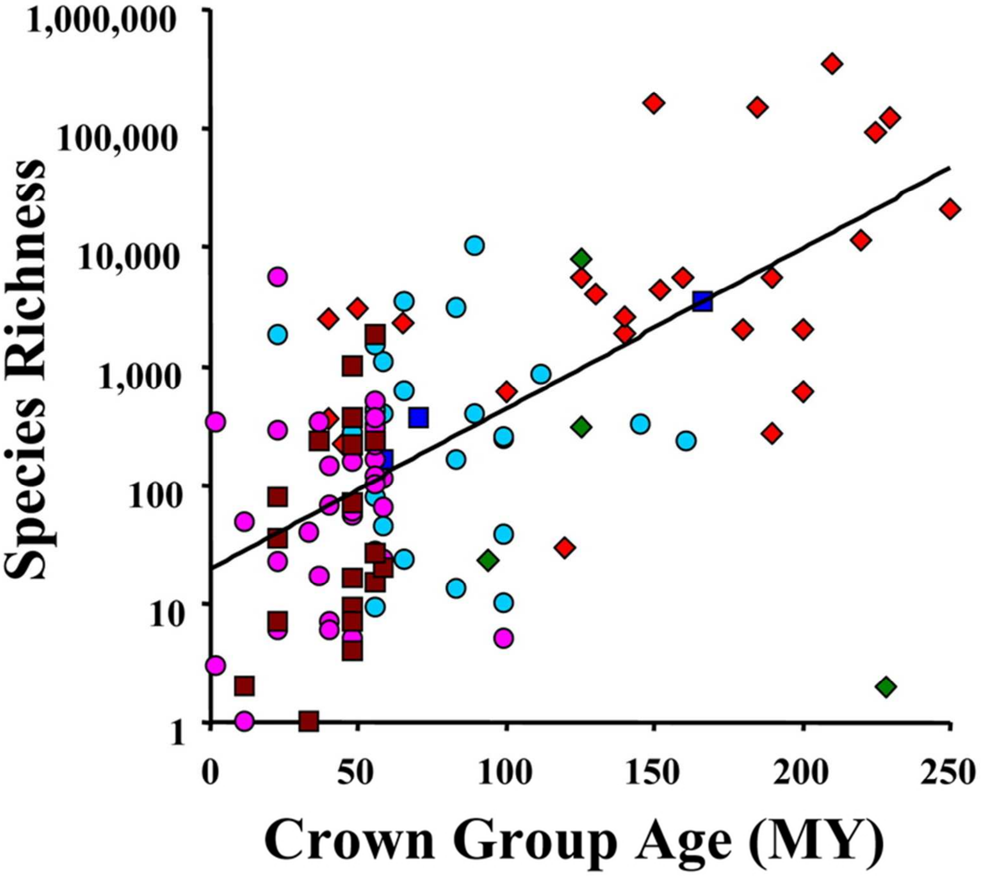

Figure 2. Extant richness and crown group age in orders of insects (red diamonds), teleost fishes (blue circles), amphibians (blue squares), reptiles (green diamonds), birds (pink circles), and mammals (red squares). The point for the Sphenodontida (green diamond at 228 MY on the crown group age axis)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

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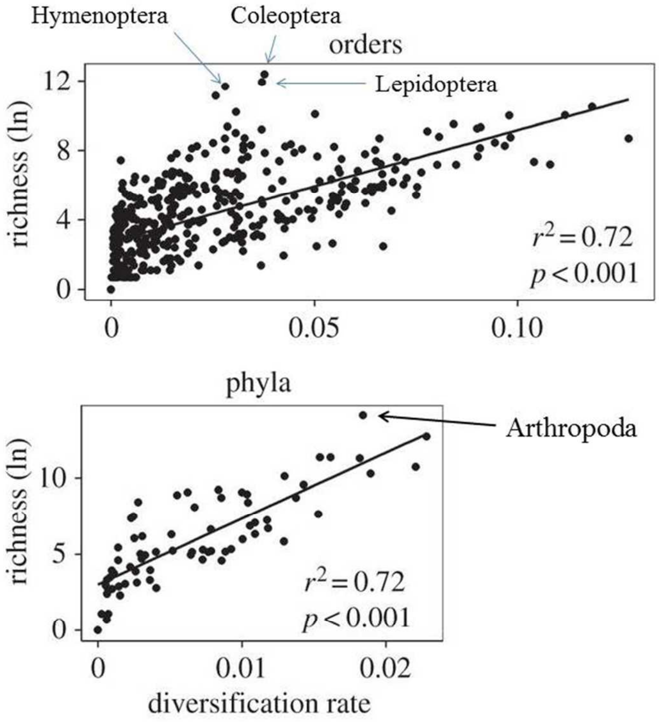

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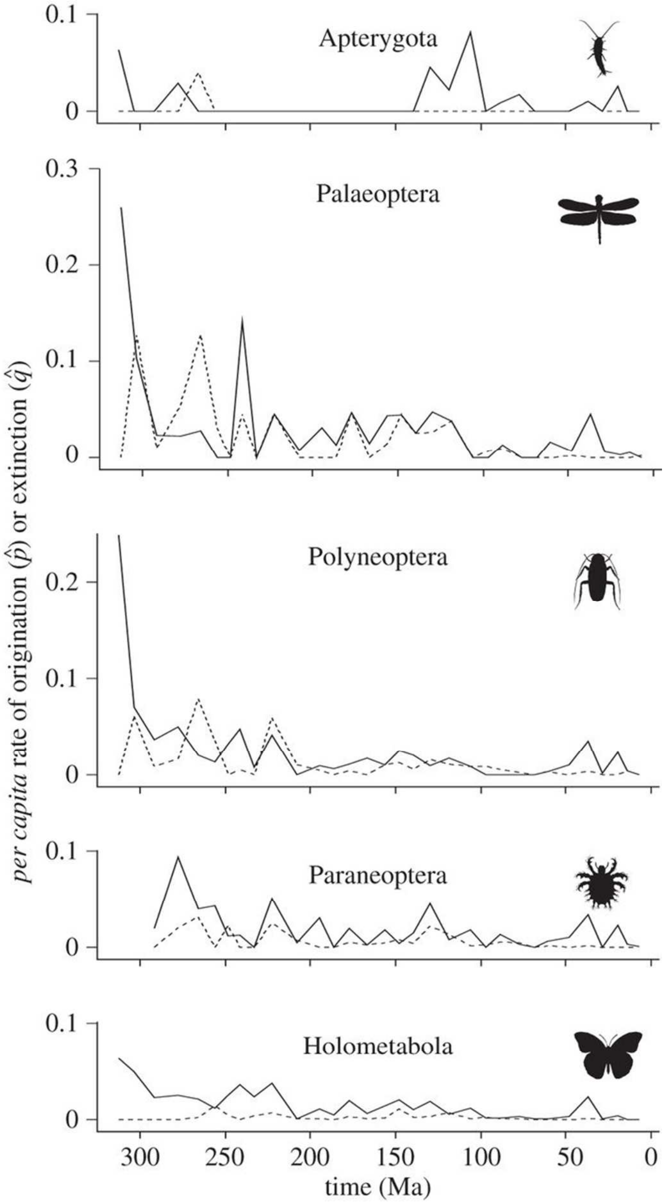

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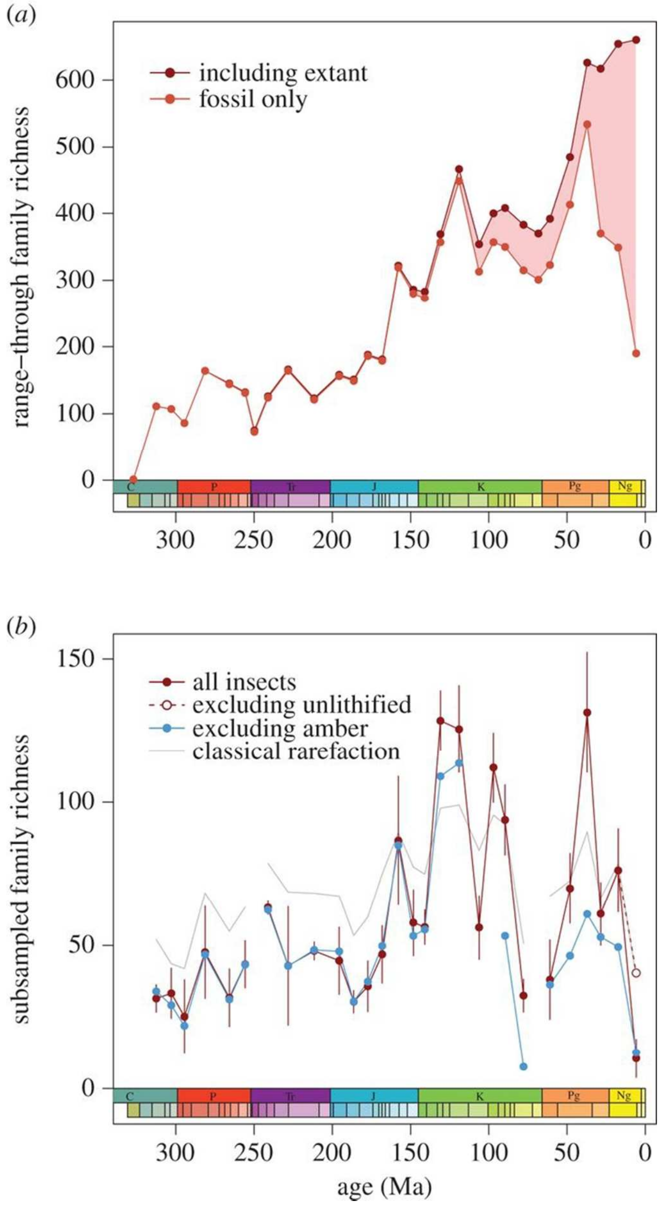

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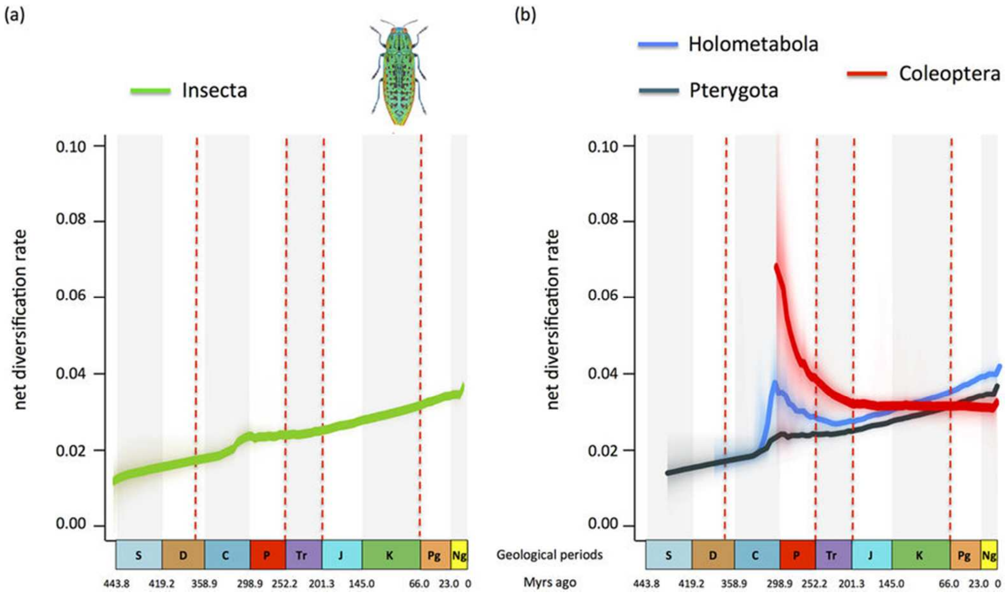

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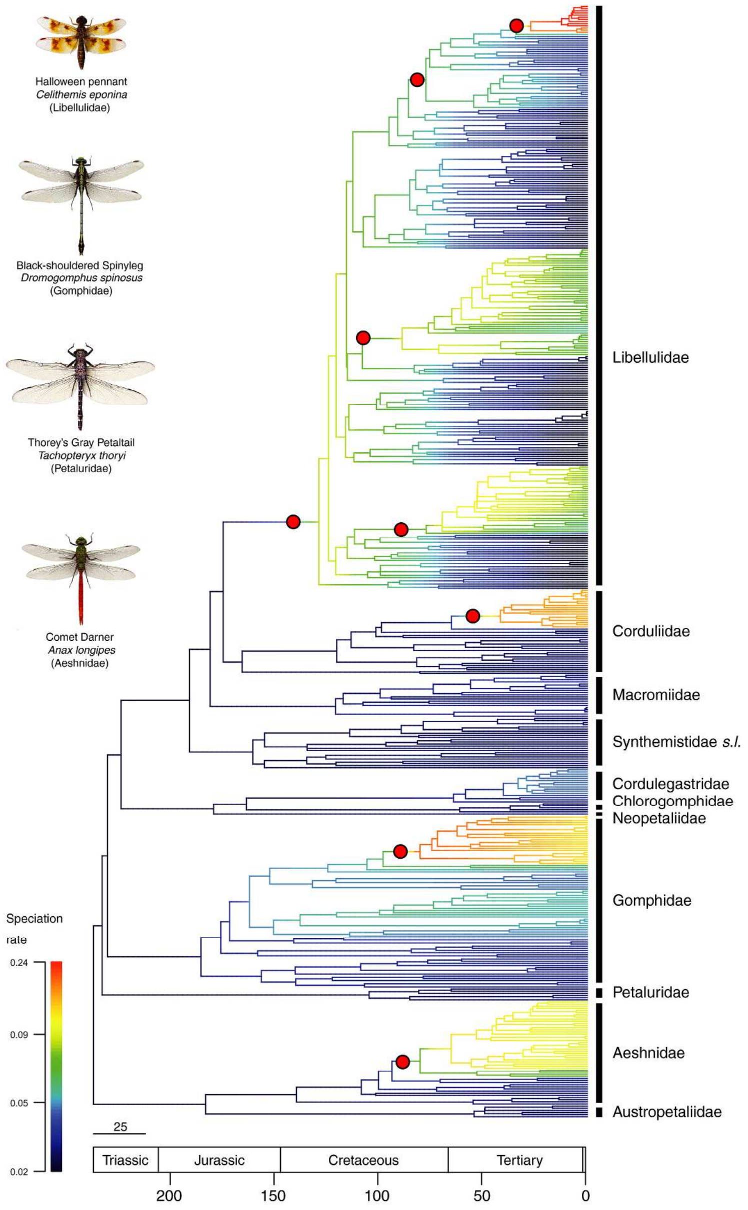

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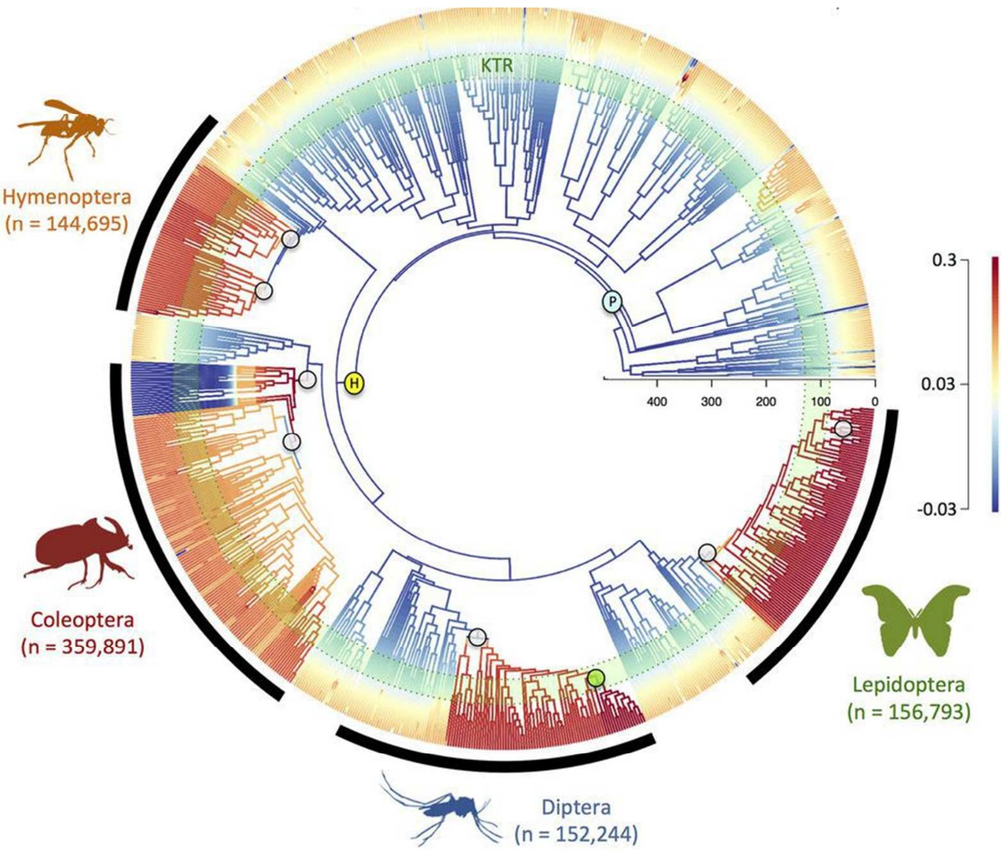

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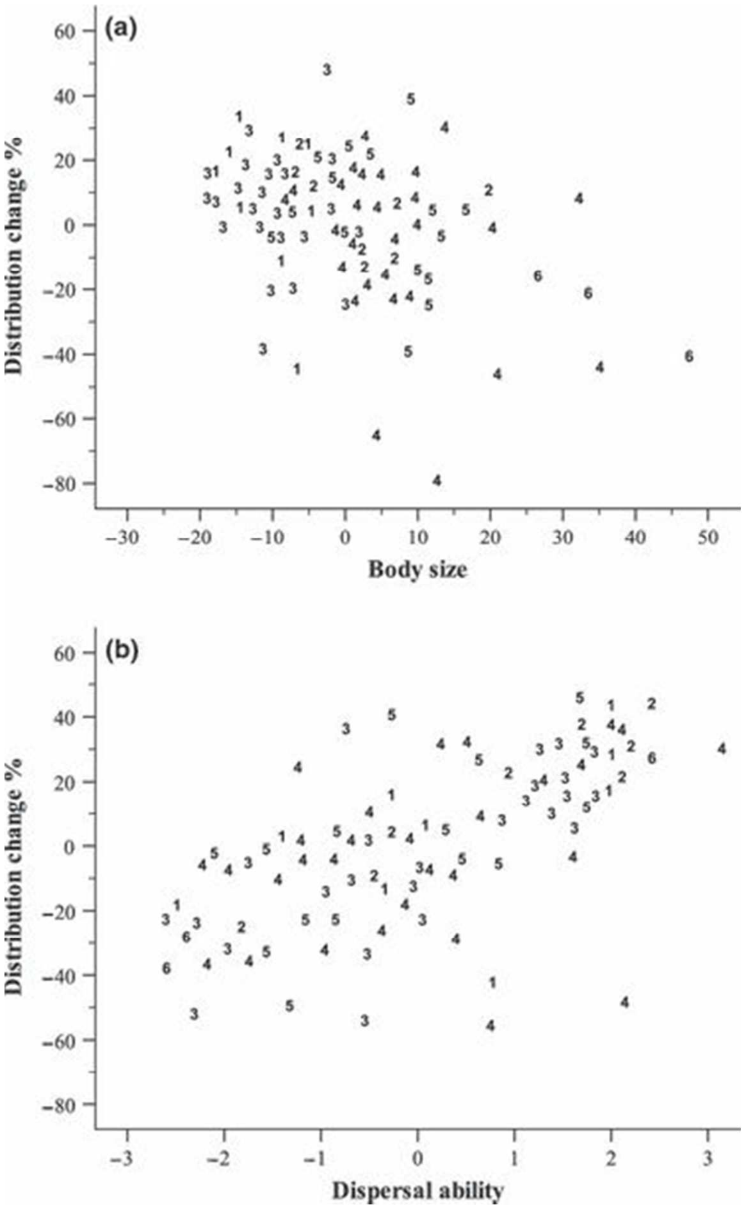

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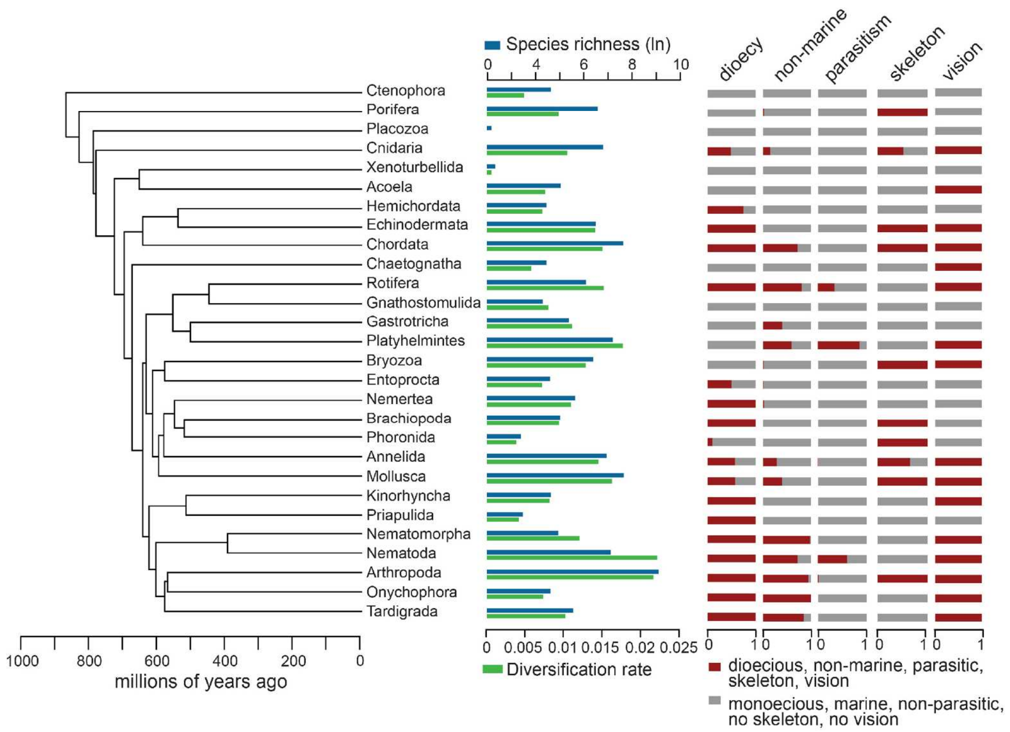

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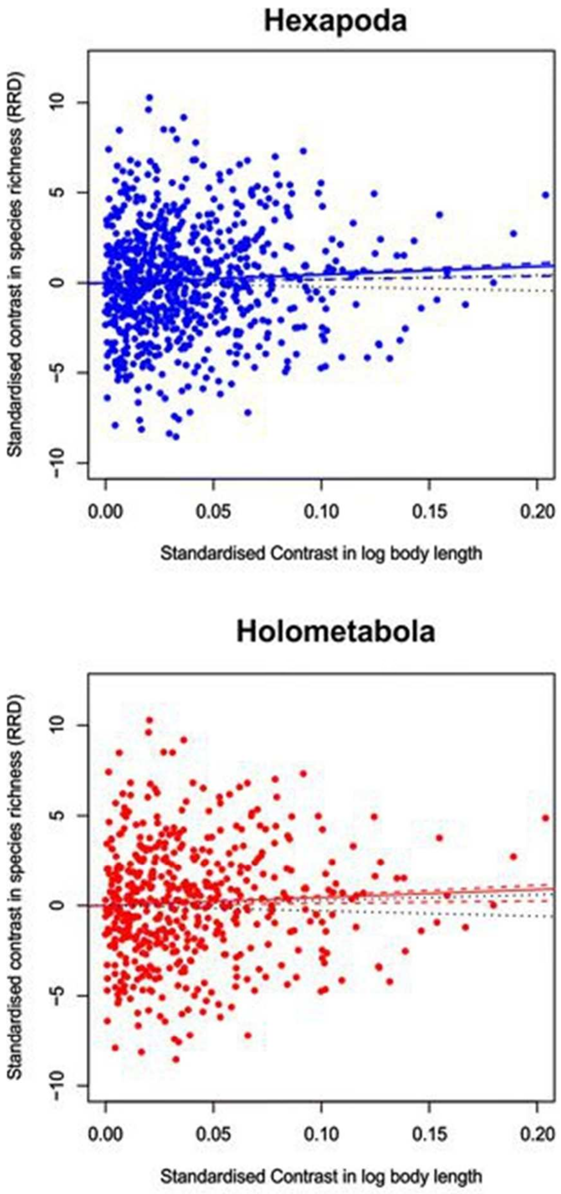

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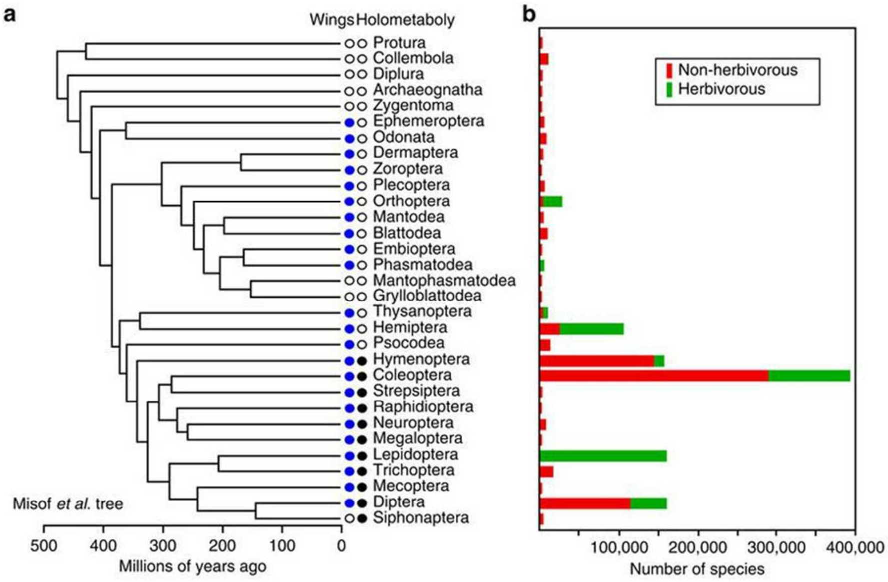

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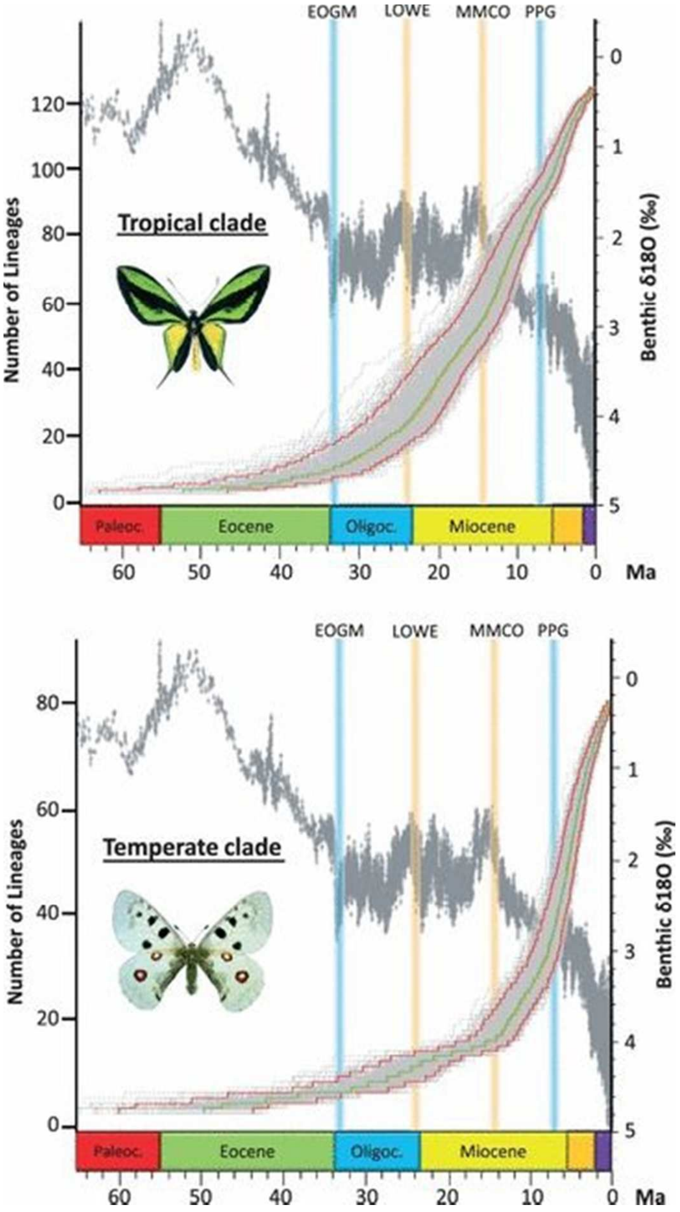

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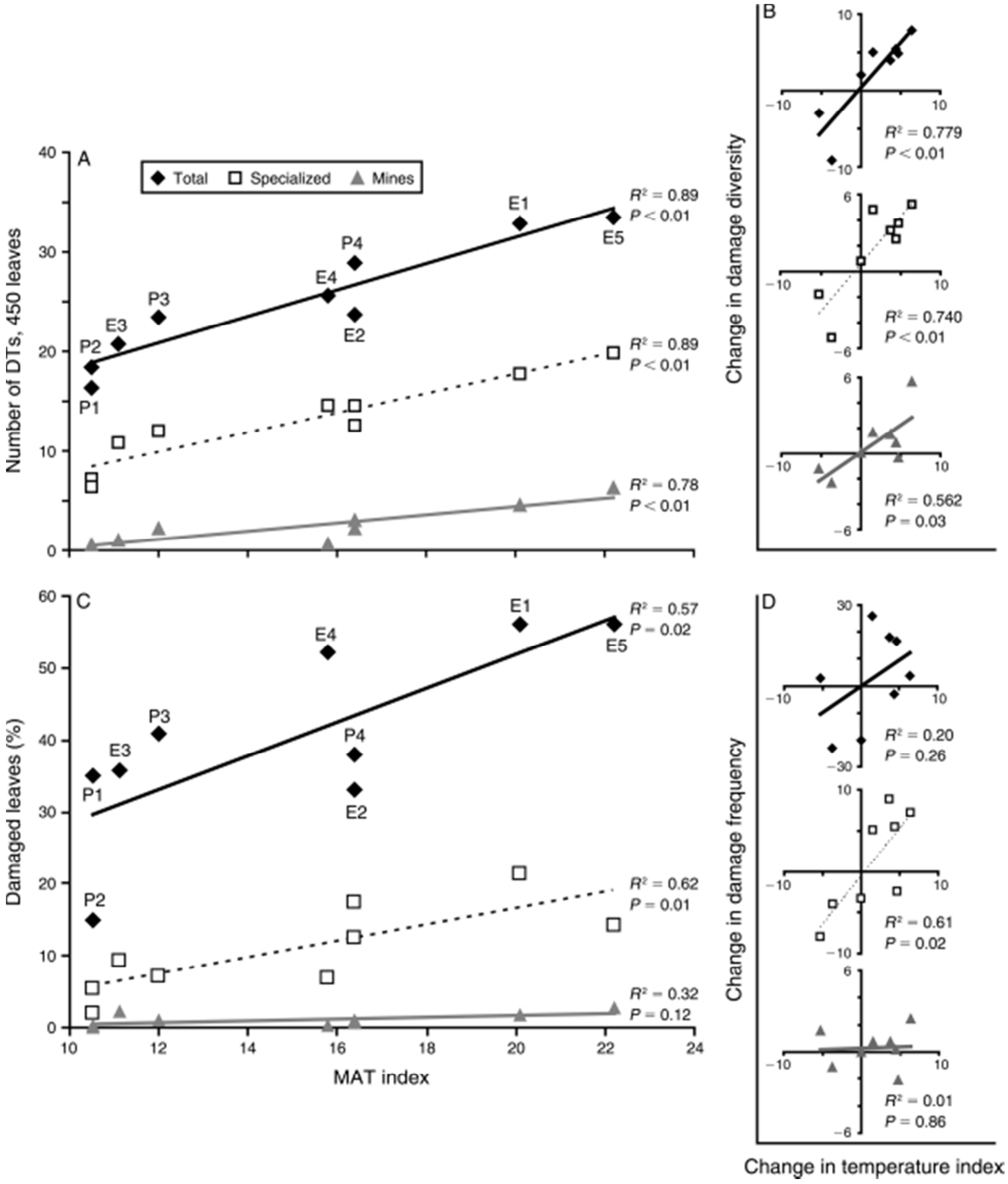

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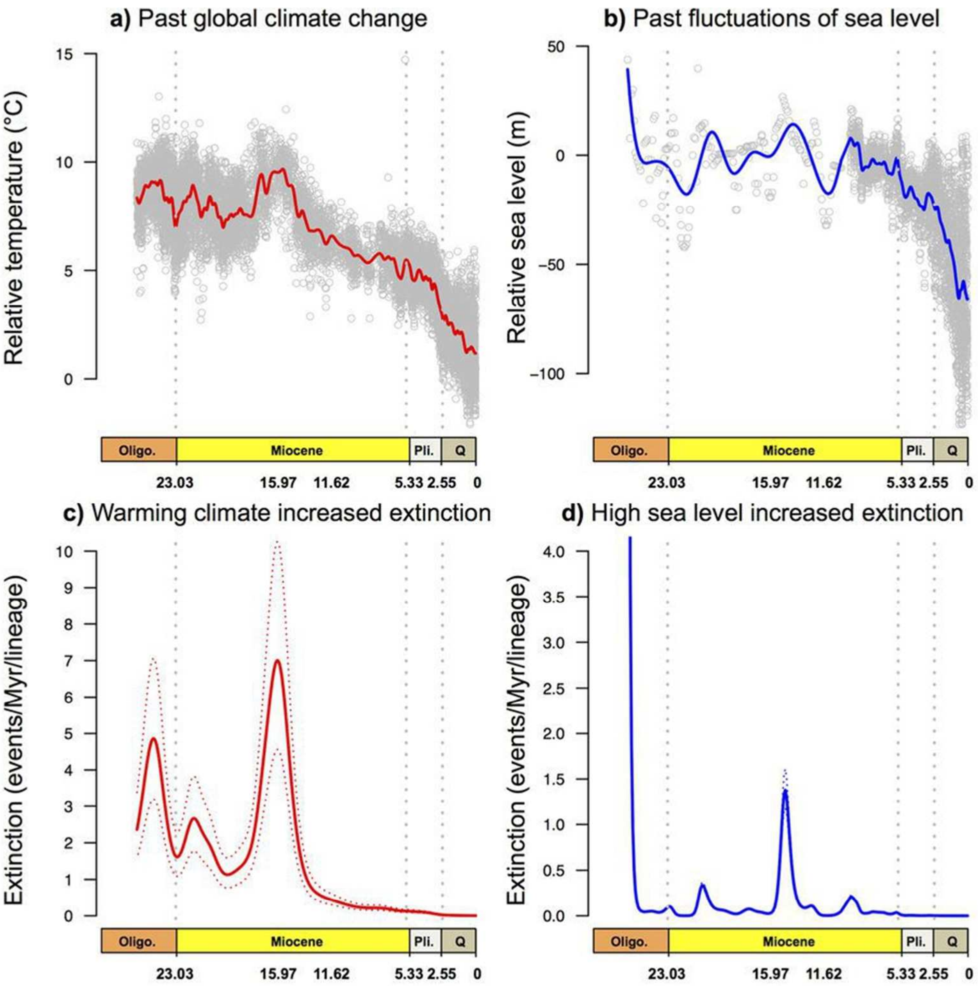

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