Paleontology

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Relevant Relicts: The Impact of Fossil Distributions on Biogeographic Reconstruction

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Abstract

Localized extinction can play a significant role in obscuring reconstructions of historical biogeography. Insects, one of the most diverse clades in the tree of life, have complex patterns of local endemism, patterns of relictual distributions, and clades which are rather widespread and cosmopolitan. At the same time, insects have a rich fossil record that can contribute to the inference of ancestral geographical distributions, in light of present ranges. Here, we review current and ancestral insect distributions to explore the impact of fossil ranges on ancestral area reconstruction. Known examples of relictual distributions within Phasmatodea and termites are discussed, while we test the impact of fossil inclusion on biogeographic reconstruction within ants and dragonflies. The inclusion of fossil distributions increases the breadth of ancestral ranges across several nodes in ant and dragonfly phylogenies, which has implications for biogeographically based interpretations of past evolutionary ecology for these groups. More broadly, the incorporation of fossil data into estimates of ancestral distributions will not only improve the accuracy of those estimates but also provide additional temporal context.

Key words: biogeography, dragonfly, fossil, termite, ant

Present-day distributions of organisms are the direct consequence of past instances of dispersal, vicariance, and extinction (Wiens and Donoghue 2004). While it is not possible to directly observe historic events, the distributional patterns of modern and extinct taxa nevertheless provide valuable insight into the spatial history of life over both short and long periods of geological time. Historically, disjunct and relictual distributions have both confounded and inspired biologists. Disjunct distributions—typified by closely related taxa with distant, nonoverlapping, and nonadjacent ranges—aided in the acceptance of plate-tectonics (Fulford 1963, Cracraft 1974) even as prominent biologists viewed continental drift with suspicion (Darlington 1957). How else to explain the reduced range of ancient groups illustrated, for example, by the silverfish *Tricholepidion gertschi* Wygodzinsky 1961, a single living species in present day Northern California closely related to fossils in Europe (Engel 2006). Similarly, subsocial wood roaches, *Cryptocercus* Scudder, have sister lineages occupying distinct putatively 'relictual' ranges in present-day North America and Asia (Lo et al. 2006). Relictual distributions—in which ancestral ranges are contracted due to local extinction—have enriched our understanding of how vital extinction has been in shaping modern biota. Fossils, as direct windows into the past, provide otherwise unknowable insight into past distributional patterns and therefore can be regarded as the often sole indicator of historical range contraction. Even so, the role of fossils in tracing the

biogeographic history of organisms remains unclear given available methodology.

The reconstruction of ancestral patterns of geographic occupation has remained a perpetual goal of evolutionary biologists for centuries (Nelson 1978), and methods have rapidly shifted to better fit what is now known to impact historical hypotheses. A key insight into biogeographic reconstruction was that phylogenetic trees hold information that can directly contribute to an estimation of ancestral ranges (Hennig 1966, Nelson 1969). Not unlike methods of phylogenetic reconstruction themselves, the philosophical underpinnings of biogeographic reconstruction—namely ancestral area estimation, which seeks to assign hypothetical ranges to extinct common ancestors—ultimately split between those employing a cladistic (parsimony) approach and those rooted in statistical optimization. Initial cladistic methodology treated geographic distributional data the same as any phenotypic character system: optimizing the presence or absence of each terminal in a set of ranges, generating ancestral ranges based on reducing the amount of total dispersals or range losses throughout the tree (Bremer 1992, Ronquist 1997). Model-based approaches have improved the sophistication of biogeographic reconstruction, allowing for more complex parameterization which incorporates biotic and abiotic factors into analyses: namely estimated rates of speciation, extinction, and the probability of movement between ranges at any given time (Ree et al. 2005, Ree

and Sanmartín 2009, Ree and Smith 2008). While the accuracy and precision of such analyses have increased, some hypotheses remain irrecoverable absent of the direct inclusion of fossil data. Localized extinctions, which result in relictual distributions, are particularly masked under extant-only sampling regimes. In parsimony- and likelihood-based reconstructions, such as in DIVA (Ronquist 1996) or Lagrange (Ree and Smith 2008), relictual taxonomic distributions are often considered to be endemism, which could fundamentally alter interpretations of speciation and biogeographic history. In other words, modern patterns of range occupation, while inform-ative, may belie the complexity of life history.

Here, we revisit prominent entomological relicts and present two case studies of fossil distributions impacting ancestral area reconstruc-tion, each representing two extremes of dispersal ability and temporal stratification: dragonflies, as ancient lineages with significant dispersal abilities (some species circumnavigate the globe in current migration events) and ants, recently derived in comparison, with considerably lower dispersal ability. In all presented cases, instances of 'primitive cosmopolitanism' (Platnick and Nelson 1978, Nelson and Platnick 1981) and localized extinction drive misestimation of ancestral range.

Mastotermes, Australia and Beyond

Termites, superfamily Termitoidea in the order Blattodea, comprise ~2,900 species with global geographical ranges. *Mastotermes* Froggatt is a monotypic genus consistently recovered as sister to the remaining extant termites; it has been recovered in a polytomy of stem lineages at the basal nodes of the termite phylogeny (e.g., morphology: Engel et al. 2009; total evidence: Ware et al., 2010; molecules: Bourguignon et al. 2015). *Mastotermes darwinensis* Froggatt is currently restricted to

Queensland, Australia and is considered an invasive in New Zealand. The fossil record of this genus, however, reveals a much broader an-cestral range (Fig. 1) (Pongrácz 1928, Snyder 1949, Emerson 1965, Jarzembowski 1980, Carpenter 1992, Nel and Paicheler 1993, Fontes and Vulcano 2004, Wappler and Engel 2003, Nel and Bourguet 2006, Krishna et al. 2013, Engel et al. 2016). Fossils have been described from the Western Palaearctic: United Kingdom (Eocene), Germany (Eocene), France (Cretaceous, Eocene, and Oligocene), Poland (Miocene), Croatia (Miocene); the Eastern Palaearctic: Russia (Cretaceous) the Afrotropics: Ethiopia (Miocene); and the Neotropics: Dominican Republic and Mexico (Miocene). In the absence of the fos-sil distributions, *Mastotermes* seems like a classic case of endemism in Australia, underscoring the importance of considering fossil bio-geographical data when inferring drivers of current species ranges. Considering the phylogenetic position of *Mastotermes*, these infer-ences are important as they have the potential to inform interpreta-tions of dispersal and extinction in the oldest living termite lineage.

Timema, A Stick Insect With a Relictual Range?

Timema Scudder 1895 is a stick insect in the order Phasmatodea whose extant distribution is restricted to the Western United States and Mexico. The remaining ~3,000 species of Phasmatodea have more widespread distributions. *Timema* is the sole genus in Timematoidea, and the current distribution of the superfamily is Nearctic, restricted to Western United States and northern Mexico. Based on its current distri-bution, this taxon could be considered a Nearctic endemic. The super-family contains a single described stem lineage with a range outside of the Nearctic, however, with *Electrotimema carstengroehni* Zompro present in Eocene Baltic amber (~34–37 Ma; Zompro 2005) from
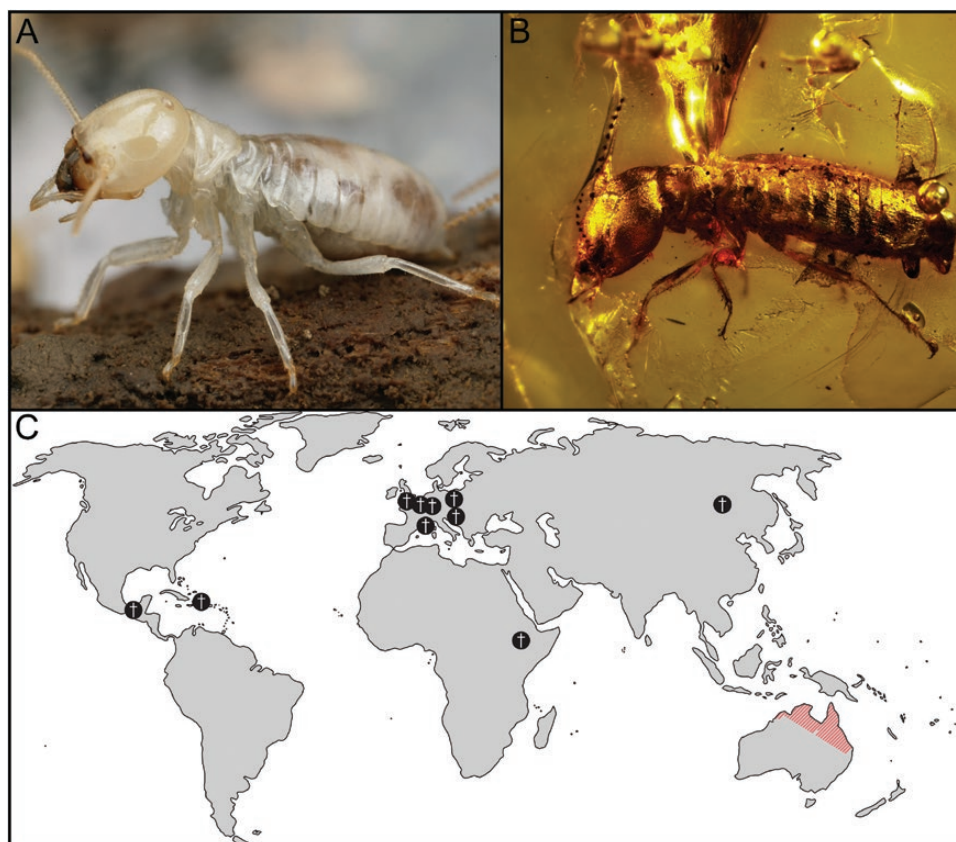
Fig. 1. The relict termite genus *Mastotermes*. (A) Photograph of *Mastotermes darwiniensis* worker in Northern Australia. Licensed under CC-BY-3.0 from CSIRO. (B) Lateral view of *Mastotermes electrodominicus* Krishna & Grimaldi in Miocene aged amber from the Dominican Republic. Specimen AMNH DR-99–136. (C) Approximate extant (in red) and known fossil (deposits denoted by †) range of *Mastotermes* species.

Kaliningrad, in the Russian Federation (54.9°N, 19.9°E). Although this fossil lineage is represented by a single specimen in amber, it suggests that one should use caution when interpreting the ancestral ecological niche of *Timema* based only on its current distribution.

Ancestrally Ambiguous Ants

Ants, as conspicuous members of most terrestrial ecosystems, have a rich fossil record comprising over 700 described species recovered from 67 deposits worldwide (Lapolla et al. 2013, Barden 2017). Perhaps because of this large paleontological sample size, there are numerous fossil-informed examples of significant range loss within the Formicidae. The appropriately named 'Sri Lankan relict ant' *Aneuretus simoni* Emery 1893 is the sole living member of the subfamily Aneuretinae. While the single extant species is restricted to Sri Lanka, there are described fossil aneuretines from Eocene aged deposits in Eastern Russia, the United States, the Isle of Wight, and the Baltic Sea (Wheeler 1915, Carpenter 1930, Dlussky 1988, Dlussky and Rasnitsyn 2003, Antropov et al. 2014, Dlussky et al. 2015), along with putative closely related taxa in Cretaceous Burmese and Canadian amber (Dlussky 1996, Engel and Grimaldi 2005, Boudinot 2015, Barden 2017). A similar subfamilial trend is present in the Myrmeciinae, with all extant species endemic to Australia and New Caledonia and a fossil range extending to several additional continents. Fossil myrmeciines are described from early Eocene to Miocene aged deposits in Argentina, Canada, the United States, Denmark, Germany, Russia, and Baltic amber (Mayr 1868, Cockerell 1923, Viana and Rossi 1957, Archibald et al. 2006, Dlussky 2012, Dlussky et al. 2015). The formicine genus *Oecophylla* Smith comprises two described extant species and is presently distributed throughout sub-Saharan Africa, India, Southeast Asia, and Australia. Often characteristic of relict taxa, there are considerably more extinct *Oecophylla* species described than modern congeners; 12 fossil species span 10 deposits throughout Europe as old as the Eocene and as young as the Messinian approximately 7 million years ago (Dlussky et al. 2008, Antropov et al. 2014, Dlussky and Putyatina 2014). In total with *Oecophylla*, there are 14 extant ant genera with described fossil species that expand geographic ranges beyond those known from living species alone: *Iridomyrmex* Mayr, *Gesomyrmex* Mayr, *Gnamptogenys* Roger, *Odontomachus* Latreille, *Oecophylla*, *Pachycondyla* Smith, *Platythyrea* Roger, *Podomyrma* Wheeler, *Polyrhachis* Smith, *Pristomyrmex* Mayr, *Pseudolasius* Emery, *Rhytidoponera* Mayr, *Tetraponera* Smith, and *Vollenhovia* Mayr. Biogeographically disjunct fossil congeners have also heralded new discovery within the Formicidae. Until recently, all living members of the genus *Leptomyrmex* Mayr were known exclusively from Australasia and a single fossil species present in amber from the Dominican Republic, suggesting a significant biogeographic shift (Lucky and Ward 2010). The complex biogeographic history of this genus was confirmed with the remarkable description of the extant 'lazarus taxon' *Leptomyrmex relictus* in Brazil (Boudinot et al. 2016). While there is some doubt about the taxonomy of congeneric fossils—very few have been evaluated in a phylogenetic context—these putative congeners offer an opportunity to evaluate the potential impact of misestimation given extant-only sampling regimes. The impact of these congeneric disjuncts and relicts on biogeographic reconstruction has never been tested, and so, here we explore the effects of including these lost ranges in ancestral area reconstruction.

Dragonflies: Relicts Mistaken for Endemics?

Dragonflies, Anisoptera, are highly mobile predators, comprising nine families (Aeshnidae, Petaluridae, Gomphidae, Chlorogomphidae, Cordulegastridae, Synthemistidae, Macromiidae, Corduliidae, and Libellulidae). The Synthemistidae are members of the superfamily Cavilabiata and have a largely Gondwanan distribution currently, including putative Australian endemics, as well as African, South American, European, and Indomalayan genera. The genus *Neophya* Selys (Fig. 2) is monotypic, with *Neophya rutherfordii* Selys found exclusively in Africa; sequences of *N. rutherfordi* have not yet been published, but preliminary data (Ware lab, in prep.) suggest it is recovered in Synthemistidae with only two other African genera (*Idomacromia* Karsch and *Syncordulia* Selys). The family also comprises the Indomalayan genus *Macromidia* Martin, which is found in India and Japan, the South American genus *Gomphomacromia* Brauer and European genus *Oxygastra* Selys. More than a dozen other genera are all considered to be 'endemic' to Australia: *Apocordulia* Watson, *Archaeophya* Fraser, *Archaeosynthemis* Carle, *Austrosynthemis* Carle, *Choristhemis* Tillyard, *Cordulephya* Selys, *Eusynthemis* Förster, *Hesperocordulia* Tillyard, *Idionyx* Hagen, *Lathrocordulia* Tillyard, *Micromidia* Fraser, *Parasynthemis* Carle, *Pseudocordulia* Tillyard, *Synthemis* Selys, *Sythemiopsis* Tillyard, and *Toniosynthemis* Theischinger. The fossil record of Synthemistidae is patchy, with several fossils that are putative members of the family but many of uncertain status. Cavilabiata fossils are known from China, Brazil, England, Mongolia, and Argentina (Pritykina 1986; Nel and Paicheler 1994; Jarzembowski and Nel 1996; Zhang et al. 2006; Petrulevičius and Nel 2009; Nel and Fleck 2014). Among these, the fossil genus *Palaeophya* Petrulevicius & Nel (Argentina) is suggested to belong to the Synthemistidae subfamily Neophyinae, which comprises *Neophya* and *Palaeophya*. While the modern examples of *Neophya* are restricted to the Afrotropical region (it has often been called a near endemic to Africa; e.g., Dijkstra 2007), the fossil lineage *Neophya legrandi* Nel & Fleck has been recently described from the Isle of Wight (Western Palaearctic; NHMUK In. 24606, Nel and Fleck 2014). *Eocordulia* Pritykina is suggested to belong to the Gomphomacromiinae, a subfamily that is poorly understood but comprises at least the genus *Gomphomacromia*, which is South American, and likely also Australian Synthemistidae.

Methodology

To explore the impact of fossil distributions on ancestral area reconstruction in both libelluloid dragonflies and ants, previously

Fig. 2. *Neophya,* an African taxon with restricted distribution (Photo credit: K. D. Djikstra, with permission).

generated genus-level phylogenetic hypotheses were utilized along with modern and putative fossil ranges. Because the paleontological records of ants and dragonflies differ significantly, we employed a different fossil-inclusion approach for each group. In the case of ants, we relied on assumed taxonomy of fossil and extant congeners, limiting our analyses to terminals of extant genera (and limiting fossil inclusion to described fossils with modern congeneric relatives). While assuming that species named as congeneric are indeed closely related is a potential source of error, the focus here lies more on the potential for biogeographic impact, rather than a definitive new biogeographic hypothesis itself. When treating dragonflies, we placed extinct genera as terminals (with one congener exception) based on their putative phylogenetic positions. This difference in approach was driven by the number of fossil taxa known for ants and libelluloid dragonflies, as well as the respective feasibility of placing extinct genera. There are fewer than 30 extinct libelluloid genera; however, only a single biogeographically disjunct fossil species is currently placed within a modern genus. This contrasts with ants, with 123 extinct ant genera and 14 cases of fossil species that are biogeographically disjunct from living congeners. While the phylogenetic placement of a great majority of extinct ant genera is unknown, it is possible to infer the placement of multiple fossil libelluloid genera based on taxonomic affinities related to wing venation.

In the case of ants, the tree of Moreau and Bell (2013) was reduced to a genus-level phylogeny with 174 terminals by removing all but one member of monophyletic genera. In cases where genera were resolved as polyphyletic, all lineages were included and each terminal was coded for all known biogeographic generic ranges. This coding scheme likely reduces the accuracy of reconstruction, however limits the subjective nature of determining the ranges for polyphyletic taxa, including cases of polyphyletic genera corresponding to those with fossil range expansions (as in *Gnamptogenys* and *Pachycondyla* which are present as two terminals). Each genus was scored for seven ranges (Nearctic, Neotropical, Western Palearctic, Eastern Palearctic, Afrotropical, Indomalayan, and Australasia). Distributional ranges were obtained from AntWeb (2017), AntCat (2017), and previous genus- and species-level biogeographic analyses (Ward et al. 2010, 2015, Schmidt 2013, Blaimer et al. 2015). Generic fossil ranges were appended for 13 out of 14 range-expanding fossil distributions outlined above, with the exception of *Gesomyrmex*, which was not present in the phylogeny utilized.

For the Odonata data set, Letsch et al. (2016) was reduced to a data set comprising the Cordulegastridae and a subset of Cavilabiata, the superfamily to which Synthemistidae, Corduliidae, Macromiidae, and Libellulidae are members (as in Letsch et al. 2016); the phylogenetic placement of *Neophya* was inferred based on molecular and morphological data (Ware et al., in prep; Ware 2008). In contrast to the ant tree, fossil genera were included as tips, with 35 extant and four extinct genera. The phylogenetic placement of the fossil lineages was inferred from the original fossil descriptions, which place them in either Neophyinae or Gomphomacromiinae; Gomphomacromiinae as originally defined is likely not a valid subfamily, based on Ware et al. (2007), Letsch et al. (2007), and Letsch et al. (2016), so we placed the putative fossil gomphomacromiines at the base of a clade which contains *Gomphomacromia*. As in the ant data set, each genus was scored for seven biogeographical ranges based on documented geographic ranges (Steinmann 1997; World Odonata List). In addition to the extinct genera, the genus *Neophya*, which contains a single fossil species, was coded for both extant-only and fossil-inclusive ranges. We reconstructed ancestral biogeographical states for the nodes of each phylogeny using parsimony in Mesquite 2.75 (Maddison and Maddison 2017), optimizing both extant-only and fossil-inclusive distribution matrices. Briefly, we compared geographical state reconstructions using the current distributions and again with current and fossil distributions included in the same matrix. While other statistical methods exist for ancestral state reconstruction, parsimony analysis was chosen for the binary nature of results, allowing for straightforward comparison of extant-only and fossil-inclusive results.

Results and Discussion

With respect to ants, the inclusion of fossil ranges for 13 genera (present as 15 terminals due to polyphyletic taxa) ultimately impacted 33 node reconstructions (Fig. 3). The most common and impactful regional addition was the Western Palearctic, driven largely by Baltic amber which accounts for over 130 described fossil ant species. The trend of West Palearctic extinction has been identified in the past, most recently in a worldwide comparison of generic similarity for fossil and extant ants (Guénard et al. 2015). Three additional ranges within the Myrmicinae had the greatest effect, remarkably altering 18 ancestral area estimations. In contrast, a number of expanded fossil ranges produced subtler effects, impacting only a single upstream node or, as with *Oecophylla*, no parsimony-informed ancestral area changes. *Oecophylla* highlights the context-dependent impact of fossils ranges on ancestral area reconstruction. While extant species are limited to an old-world equatorial distribution, fossils indicate that the genus may have originated in present-day Europe. However, because *Oecophylla* most probably represents the sole example of localized Western Palearctic extinction among closely related taxa; the addition of a Western Palearctic distribution has no impact on ancestral reconstruction.

Including fossil Cavilabiata ranges in our reconstruction of dragonfly biogeographical history impacted the ancestral range predictions for the Synthemistidae (*sensu* Carle et al. 2015; Fig. 4). The ranges for four nodes within Synthemistidae are broader when fossils are included as tips in the analysis. Although, including fossils as tips also requires that additional nodes be present, and so, three out of four impacted nodes were not present in the extant-only tree. For our evaluation of odonate ancestral biogeographical ranges here, the addition of Palaearctic *Neophya* fossil data affects the range of the entire clade and makes it possible to infer that *Neophya* is relictual rather than endemic. The inclusion of fossil Neophyinae and Gomphomacromiinae impacted the immediate ancestral node and the entire clade, respectively.

Fossil range inclusion in biogeographical analyses may extend the ancestral range of taxa, and when the fossil placement is unambiguous, fossil ranges should be considered for inclusion along with present ranges when attempting to reconstruct past distributions. This is especially true when biogeographical analyses are implemented in larger ecological studies evaluating endemism and ecological niche patterns. Many fossils have not yet been treated with a phylogenetic evaluation, and their position within a phylogeny of modern lineages is uncertain. Researchers should include fossils in their biogeographical analysis with caution if the fossil position is ambiguous, as this will add error to the ancestral range estimation. As in our assessment of ancestral ranges, relying on assumed taxonomy suggests interpreting results with skepticism. Nevertheless, the potential impact of including extinct ranges is clear, and the results presented here are themselves considerable underestimates of the impact of fossil ant distributions on biogeographic reconstruction: there are 123 extinct genera that were not included in this assessment of relict impact. The vast majority of these extinct lineages have no definitive phylogenetic placement and may reshape our estimates of
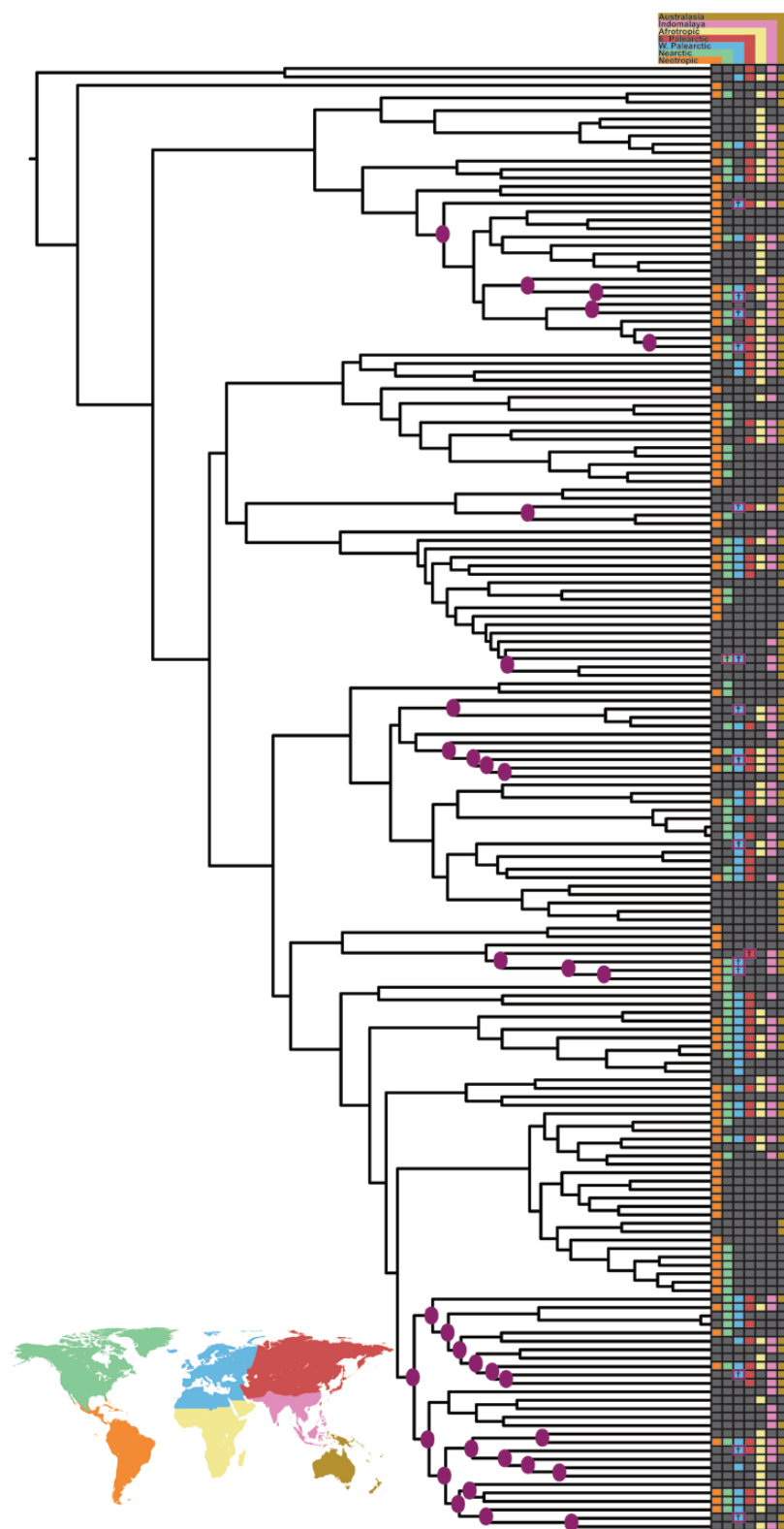
Fig. 3. Demonstration of the impact of congeneric fossil distributions on ancestral area reconstruction in Formicidae. Terminal colors represent genus-level distributions, with extinct ranges highlighted in purple and denoted with dagger symbol (†). Purple node icons indicate an ancestral area reconstruction impacted by the inclusion of an extinct range. Tree topology from Moreau and Bell (2013). Terminal names available in Suppl. Fig. 1.

biogeographic history within the Formicidae. With respect to the relict subfamilies Myrmeciinae and Aneuretinae, no fossil species have been described as members of living genera and so they were not included here; however, it is clear that extant taxa do not carry

the historic signatures of their ancestral ranges. Effort should therefore be devoted to placing taxonomically ambiguous fossil species, as they may significantly alter biogeographic estimation. Analyses that incorporate both molecular and morphological
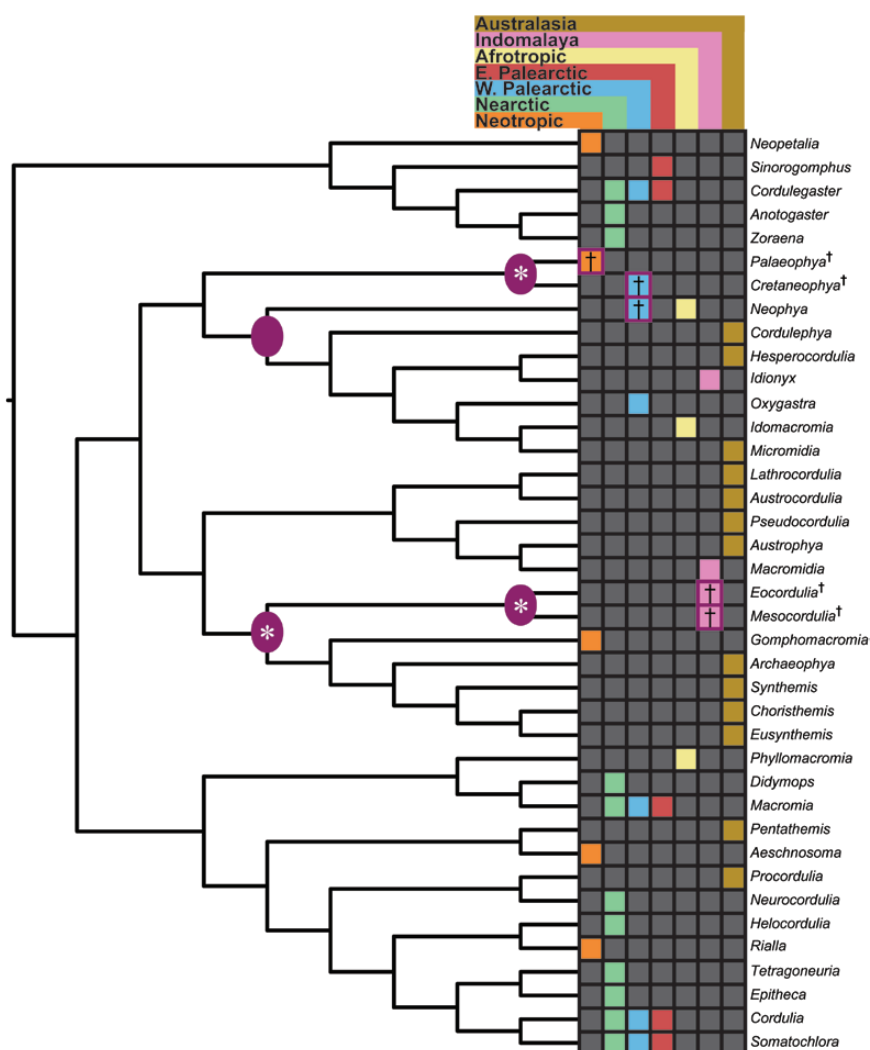
Fig. 4. Demonstration of the impact of extinct congener and fossil genus distributions on ancestral area reconstruction in Anisoptera. Purple node icons indicate an ancestral area reconstruction impacted by the inclusion of an extinct range. Purple icons marked with * indicate nodes that are affected by the inclusion of fossil taxa but would not be present were fossils not included. Tree topology from [modified from Letsch et al. (2016)] with putative fossil relationships appended.

data with the aim of objectively placing fossil taxa have been successful in identifying ancestral biogeographic patterns in spiders, for example, Wood et al. (2013). It is also possible in principle to effectively constrain nodes for reconstruction in a likelihood framework; however, this method also relies on assumed taxonomy, not unlike node calibrations for divergence time estimation (Ree and Smith 2008, Wen et al. 2013). While time was not included in this study, the incorporation of temporal data may improve biogeographical estimation. Future work should consider other methods of node age estimation that implement fossil taxa to reconstruct trees for use in biogeographical analyses. The fossilized birth death model (Heath et al. 2014), for example, can be implemented in a Bayesian framework to estimate node ages with living and fossil taxa; by removing some of the bias from ad hoc calibration points, ages may be more reliable which may in turn improve biogeographical estimates using time-calibrated trees. Future work should continue to examine whether different types of fossils impact biogeographical interpretations in the same way; whether younger and older fossil ranges have the same impact is unclear, and the inclusion of fossil tips at deeper versus shallow nodes of the tree may have different levels of influence on internal node range reconstructions.

Acknowledgments

Supplementary Data

Supplementary data is available at *Insect Systematics and Diversity* online.

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