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Ancient origin of high taxonomic richness among insects

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Abstract

Insects are a hyper-diverse group, comprising nearly three-quarters of all named animal species on Earth, but the environmental drivers of their richness and the roles of ecological interactions and evolutionary innovations remain unclear. Previous studies have argued that family-level insect richness increased continuously over the evolutionary history of the group, but inclusion of extant family records artificially inflated the relative richness of younger time intervals. Here we apply sampling-standardisation methods to a species-level database of fossil insect occurrences, removing biases present in previous richness curves. We show that insect family richness peaked 125 million years ago and that Recent values are only 1.5-3 times as high as the late Palaeozoic. Rarefied species richness data also tentatively suggest little or no net increase in richness over the past 125 Myr. The Cretaceous peak in family richness was coincident with major radiations within extant groups but occurred prior to extinctions within more basal groups. Those extinctions may in part be linked to mid-Cretaceous floral turnover following the evolution of flowering plants. Negligible net richness change over the past 125 Myr implies that major radiations within extant groups were offset by reduced richness within groups that are now relict or extinct.

1. Introduction

Nearly three-quarters of all named living animal species are insects, yet the factors enabling this immense richness remain unclear [1]. Evolutionary innovations such as the evolution of flight and the origin of complete metamorphosis may be among the key drivers [2–4]. Ecological characteristics of insect clades likely also played an important role in their rapid diversification. The evolution of herbivory [5] and interactions between insects and their host plants, most notably flowering plants [6], have been hypothesised to be important drivers of diversification. Despite the importance of insects across ecosystems, the history of their taxonomic richness remains as uncertain as the causes of rapid diversification.

In the fossil record, insect family richness has traditionally been quantified on the basis of first and last appearances of families ("range-through diversity"), extending the range of extant families beyond the youngest fossil occurrence to the Recent [7–10]. These results have suggested that insects diversified steadily over their evolutionary history to reach unparalled family-level richness in the Recent. The range-through curves further imply that modern family richness may be twice as great as the Early Cretaceous, 125-150 million years (Myr) ago. However, such range-through measures are known to be biased, particularly at their edges, whereas extending fossil ranges of extant families will inflate diversity estimates in younger time intervals (the "Pull of the Recent") because the living insect fauna is substantially better sampled than fossil faunas [11,12]. We compiled a species-level, occurrence-based dataset, which records more than 37,000 individual insect fossil occurrences (representing more than 24,500 valid species) rather than only the oldest and youngest known records. This database enables us to apply less-biased methods of counting diversity, which can account for variable sampling intensity and eliminate the Pull of the Recent bias [12]. Our dataset closely approximates previously-published diversity curves when we use the same range-through counting methods and extant records, but reveals new insights when we apply less biased methods of reconstructing diversity.

2. Methods

We compiled a species-level database of insect occurrences from 6334 primary references, recording more than 39,000 insect fossil occurrences of more than 24,500 valid species, available through the Paleobiology Database (www.paleobiodb.org). Each occurrence is a record of the presence of a taxon in a collection, which is a group of fossils from a single stratigraphic interval at a particular geographic locality. We constructed diversity curves using the "10 million year bin" timescale available in the Paleobiology Database (bins composed of adjacent geological stages totalling approximately 10 million years in length). Although the ages of many insect collections are resolved more precisely, there are too few occurrences in many finer time bins for subsampling calculations. We used the diversity curve tools at Fossilworks (www.fossilworks.org) to perform sampling standardisation on sampled-in-bin richness, downloading occurrences identified to the genus level (without ? or “” qualifiers) and excluding trace fossils and form taxa.

We focus our analyses on the family-level record of insect richness. Despite potentially inconsistent definitions of higher taxa [13], the family-level has traditionally been used to reconstruct changes in fossil insect richness [7–9], although some studies have also analyzed genus-level data[8]. At the family level, we used shareholder quorum subsampling (SQS)[12] to account for large variations in the number of insect occurrences over time. SQS is designed to subsample a constant fraction of the occurrence frequency distribution, selecting taxa until the sum of their occurrence frequencies reaches the chosen quorum. Family-level data were subsampled at a quorum of 0.64 for all records, the highest value that allowed us to evaluate all time bins other than the extremely sparse Early Triassic (28 occurrences) and Maastrichtian (15 occurrences), although the relative richness pattern is unaffected by the choice of sampling quorum (Fig. S1). We also downloaded all insects using the same criteria as previously outlined but excluding records with lithology marked as amber (which occur in the Cretaceous-Recent only). Those occurrences were subsampled with the SQS method at the same quorum (0.64) to reconstruct richness trends within a consistent taphonomic category (compression/impression fossils) through time. For both analyses, Good’s u (a measure of data coverage) was calculated from single-reference taxa, ignoring the most common taxon and the largest collection, following Alroy[12], although these choices have only negligible effects on richness trends (Fig. S2). We did not downweight collections coming from large references because most collections contain occurrences derived from multiple references (therefore the identity of the primary reference is less meaningful). This choice also had no effect on the results (Fig. S2). Although classical rarefaction (CR), which subsamples a uniform number of occurrences, tends to flatten relative richness differences[12], we also analyzed family-level richness at a quota of 170 occurrences. We used both SQS and CR subsampling to assess the robustness of richness trends because the two methods respond differently to changes in the occurrence frequency distribution of the underlying taxon pool by sampling either a uniform frequency (SQS) or absolute quota (CR) of occurrences.

We also downloaded species-level insect occurrences from the Paleobiology Database API (www.paleobiodb.org/data1.2), again removing occurrences that did not fall within a “10 million year” bin. We kept all species-level occurrences regardless of the qualifiers applied to the genus identification. Because paleoentomologists rarely mention additional occurrences of a species after its initial description, Good’s u cannot be estimated reliably for SQS subsampling. Therefore, we used CR subsampling of species-level data at 500, 1000, and 2000 occurrences, despite its problems[12]. All code is available at https://github.com/mclapham/insect_div.

3. Results

(a) Family Richness Trends

The underlying data within Paleobiology Database captures the information contained in range-based compilations (Fig. 1A, S3), but the family-richness curve after shareholder quorum subsampling (SQS) differs considerably from previous range-through curves and does not show a continuous increase in family-level richness to the present (Fig. 1B). Much of the post-Jurassic increase in previous range-through curves arises from Pull of the Recent bias. All fossil ranges are incomplete relative to the true duration of the taxon and the unidirectional range extension enabled by extremely well-known modern data artificially inflates the magnitude of richness increase (Fig. 1A). Range-through curves also suffer from edge effects introduced by artificial range truncations; this effect is most noticeable in the youngest time interval of the fossil-only range-through richness curve (Fig. 1A). These and other biases can be reduced by assessing richness only from taxa recorded within each time interval and by applying subsampling methods [12]. In the subsampled curve, insect family richness increased by about 50% from the mid-Carboniferous to the Middle Jurassic and then more rapidly to a peak in the Early Cretaceous. Subsampled richness in most Cenozoic intervals was lower than the Early Cretaceous peak; only the Cenozoic 3 interval, which contains the exceptionally well-sampled Baltic amber, is equal or higher. However, extreme volatility within the Cretaceous and Cenozoic makes it difficult to determine typical richness levels for the interval, so the presence and magnitude of any decrease are uncertain.

Nevertheless, the SQS record strongly argues against a large increase in family richness since the Early Cretaceous.

When excluding amber fossils to allow direct comparison with pre-Cretaceous intervals (prior to common amber fossilisation), Cenozoic richness of roughly 50 subsampled families per interval is comparable to the Triassic and Jurassic and only 50% higher than the Carboniferous. The youngest time interval (late Miocene-Pleistocene) has unusually low subsampled richness because most localities represent a fundamentally different preservation mode (unlithified sediments) and are overwhelmingly dominated by a few families of ground-dwelling beetles. After excluding unlithified sediments, late Miocene-Pleistocene subsampled richness is comparable to the compression fossil record from other Cenozoic time intervals.

(b) Species Richness Trends

Although there are many extant insect families, the notion of insects as a hyper-diverse group arises primarily from the immense number of insect species. Extant species richness is disproportionately driven by a few clades with extremely high diversity (e.g., ichneumonid wasps, staphylinid beetles)[4]. Those clades are also diverse and abundant in the fossil record; however, the true ancient richness of such hyper-diverse groups is likely underestimated for two reasons. First, in many cases their small body size may reduce the likelihood of collection and identification. Second, fossil specimens, especially those preserved as rock compressions, typically do not preserve all of the subtle anatomical features used for species discrimination of living specimens. Those biases, however, should be consistently present in deposits of similar preservation type throughout the geological record and therefore are unlikely to produce spurious trends in richness estimates when comparing fossil faunas of different ages. Fragile clades (such as the hyper-diverse Lepidoptera) will also be underrepresented relative to more robust taxa, but this also should be true throughout the insect record.

It is possible, therefore, that increases in the number of species per family led to large increases in insect species richness, despite the lack of trend in family-level richness since the Early Cretaceous.

However, the nature of the published insect fossil record, unusually dominated by species with occurrences reported only from a single reference (91% of species) and from a single database collection (82% of species), poses a challenge for construction of sampling-standardised, particularly SQS, species-level richness curves. Classical rarefaction subsampling can be applied instead, even though only a few intervals have a sufficient number of occurrences for robust subsampling. The resulting species richness curves (Fig. 2) exhibit a mid-Jurassic increase (visible at 1000 occurrences) and suggest no or a small net increase in species richness since the Early Cretaceous (at 1000 and 2000 occurrences, respectively), both broadly similar to the family-level richness curve.

4. Discussion

(a) Biases and Reliability of the Record

Our findings contrast markedly with previous studies that suggested a nearly-continuous, sixfold net increase in insect family richness from the late Paleozoic to Cenozoic [7,8]. We also argue that there was no net increase (perhaps even a decrease) in family-level richness over the past 125 Myr, rather than the near-doubling previously proposed [7]. Furthermore, species-level results suggest little net change over the past 125 Myr despite molecular evidence for major radiations among extant groups. Even though the previous range-through curves contain known artefacts, most notably from the Pull of the Recent bias, it is important to explore the reliability of the subsampled results.

The SQS curve (Fig. 1B) exhibits abrupt peaks and troughs with substantial volatility even between successive time intervals, which seems implausible over such short timescales. The episodic nature of exceptional preservation in amber provides one explanation for the volatility, because amber fossilisation enhances recorded richness in certain time intervals relative to others that lack rich amber deposits. Enhanced richness does not result simply from additional insect occurrences provided by amber fossilisation; instead, amber and compression fossils tend to sample overlapping but distinct subsets of the insect fauna, largely because of different size-selectivity in the two preservation modes [14]. When combined, amber and compression fossils capture a broader taxon pool that is reflected as higher subsampled richness by the SQS method.

Although amber fossilisation produces sharp peaks in sampled family richness (Fig. 1), the compression fossil record also exhibits considerable and likely also artificial volatility, particularly in the Cretaceous. That volatility is best explained by tectonically-driven variations in the nature of depositional environments in which insects were fossilized. We assessed the role of tectonic setting by assigning each collection to "higher-subsidence" (extensional, pull-apart, and volcanic caldera basins) or "lower-subsidence" basins (forearc or foreland basins, passive margins, and cratonic basins). We then tested the role of tectonic setting with linear regression, first with changes in higher-subsidence occurrences as the independent variable and, in a separate analysis, with changes in lower-subsidence occurrences as the independent variable. All time-series data was differenced and we excluded unlithified or poorly lithified occurrences. Richness changes between successive time intervals are significantly associated (R^2=0.225, p = 0.025) with shifts in the number of insect occurrences deriving from higher-subsidence basin types (Fig. 3A). In contrast, there is no relationship (R^2=0.0004, p = 0.93) with changes in the number of occurrences from basin types with lower subsidence rates on average (Fig. 3B). Basins with high subsidence rates generate greater accommodation space for the formation of larger or deeper lakes, where finer grain size, lower energy, and potentially anoxic bottom waters promote high-quality preservation of a broad range of insect families [15–17].

There is a strong association between richness changes and the abundance of occurrences in extensional or other high-subsidence basin types, yet not all extensional basins yield exceptional insect localities [18]. Although each basin has a unique subsidence history, initial fault-controlled subsidence rates typically are higher in rift basins in regions of greater lithospheric thickness [19], consistent with the occurrence of exceptional insect localities in extensional basins associated with collapse of orogenically-thickened continental crust [e.g., 20]. A bimodal paleolatitudinal distribution of insect occurrences (Fig. S4), with peaks near the equator and at temperate mid-latitudes, also suggests that precipitation exceeding evaporation is an important additional control on the formation of exceptional localities. This bimodal pattern is likely not driven by the location of well-sampled regions like North America or Europe because it independently occurs within each region (Fig. S4) and within a single time interval, when sufficient sampling breadth is available (Fig. S5). However, it is difficult to distinguish our preservation hypothesis from true variations in the abundance of insects, which may be less abundant in arid climate zones. Large-scale insect abundance patterns are not well described, and the contributing factors are likely complex[21], but water availability is one important control on richness in insects and other terrestrial groups[22,23].

Only a small fraction of all discovered fossil insect specimens have been formally described. The number of described fossil insects varies considerably among time intervals, in part due to the area of suitable basins, but also likely due to worker effort concentrated on richer time intervals [24,25]. We use sampling standardisation to account for variations in the number of published occurrences, but non-random researcher practices, such as the logical preference for describing well-preserved, rare, or unusual specimens, may also influence the occurrence-frequency distribution in a particular interval. This effect is likely to introduce noise and perhaps amplifies volatility in the record, because extremely rich intervals also yield a greater number of rare and better-preserved specimens, enabling paleoentomologists to focus on describing rare or unique taxa. It is unlikely, however, to vary systematically or predictably with the geological age of the deposit (excluding differences between amber and compression fossils). The insect fossil record is also dominated by only a small number of localities in most time periods, but there is no evidence that geographic extent of sampling, as measured by the length of the minimum spanning tree between all localities [26], biases subsampled richness overall or with compression fossils (Fig. S6).

Short-term fluctuations in the SQS family richness record are therefore best explained as artefacts from changes in the underlying taxon pool driven by tectonic setting and climate, as well as by episodic amber preservation. These biases are particularly likely explanations of the volatility in the Late Cretaceous record and the abrupt decrease in the youngest interval (late Miocene-Pleistocene). Given that, can any conclusions be drawn about the overall trajectory of insect family richness? The classical rarefaction (CR) method of subsampling provides the opposite end-member case for richness estimation by drawing a uniform number of occurrences from each time interval independent of variations in the taxon pool [12]. The overall shape of the CR family-level richness curve closely matches SQS data (Fig. 1), even if potentially less reliable older literature is excluded from the analyses (Fig. S7). Furthermore, net family-level richness change since the beginning of the Cretaceous is negligible even in range-through data after accounting for the Pull of the Recent (Fig. 1A). Because CR and SQS make different assumptions about subsampling from the broader taxon pool, yet result in consistent overall richness trends through time, the broad shape of the sampling-standardised family-richness curve is likely a robust result. Short-term fluctuations are difficult to resolve with confidence, but all methods yield a Late Jurassic-Early Cretaceous increase followed by little net change or perhaps decreasing family-level richness.

The classical-rarefaction species-richness curve appears to record the same major features as the family-richness curves, despite the limited number of intervals meeting a quota of 1000 or 2000 occurrences. However, there are additional caveats to its interpretation. First, richness differences between intervals will be muted by the rarefaction method, especially at smaller quotas [12]. Second, subsampling assumes that the rank-order distribution of published occurrences is an accurate representation of the underlying rank-order distribution of fossil occurrences among collections. The dominance of single-collection or single-reference fossil insect species suggests that the rank-order distribution may be artificially flattened by non-random publication practices in which new species, rather than additional records of existing taxa, are preferentially described. If that effect varies systematically among time periods, which seems unlikely but cannot be ruled out, it may obscure true richness changes. Taken at face value, species-level richness trends (Fig. 2) appear to broadly follow our family-level curve (Fig. 1B): a more pronounced increase from the mid-Jurassic to Early Cretaceous followed by little change over the past 125 million years. In contrast to the family-level curve, which implies decreasing richness from an Early Cretaceous peak, the species-level curve provides more support for little net change or a small net increase in richness since the Early Cretaceous (Fig. 2).

(b) Ecological and Environmental Controls on Insect Richness

Our analyses suggest that the net increase in insect richness from the late Paleozoic to Recent was much less than previously estimated, primarily due to bias from the Pull of the Recent in previous range-through curves. This implies that insects had evolved high richness early in their evolutionary history; family-level richness may have reached one-third (on the basis of range-through data excluding the Pull of the Recent) to three-quarters (on the basis of SQS richness of compression fossils) of modern levels by the Permian. Rapid early diversification is consistent with the hypothesis that the evolution of flight was among the key innovations enabling high richness in insects [1,2]. All methods show a more rapid increase in richness from the mid-Jurassic to the Early Cretaceous. The Late Jurassic also marked a fundamental shift in the preservation quality of insect compression fossils [17], so we cannot rule out taphonomic biases artificially reducing richness in older intervals. However, a pronounced richness increase in the Late Jurassic and Early Cretaceous is supported by phylogenomic evidence for rapid diversification within extant lineages, particularly Holometabola [4,27].

We find no evidence for a net increase in family-level insect richness, and perhaps also in species richness, since the Early Cretaceous, despite major biotic changes such as the mid-Cretaceous diversification of flowering plants. Negligible effects of the angiosperm radiation are consistent with previous findings [7] and suggest that positive ecological interactions in some groups may have been offset by negative effects in others, for example from disruption of existing habitats and resources during the floral turnover [28]. Limited net richness change over the last 125 million years agrees with the pattern exhibited by beetles, the richest extant insect order, which also have not increased in richness since the Early Cretaceous when the Pull of the Recent bias is excluded [supplementary figures in 29]. Although sampling-related volatility in the data preclude interpretation of shorter-term or more subtle richness changes, a post-Early Cretaceous decrease in subsampled family richness is supported by both SQS and CR methods. This is consistent with beta diversity data (the difference in taxonomic composition among sites), which also argues for Paleogene global insect richness higher than present-day levels [30]. Archibald et al.[31] also found that local species richness within a Paleogene mid-latitude community was comparable to a modern tropical example and greater than a modern mid-latitude community, potentially consistent with a broader-scale reduction in richness since the Paleogene. Our subsampled species-level richness data tentatively imply a small net richness increase since the Early Cretaceous at that taxonomic level, although we lack resolution to assess finer patterns. Regardless, these multiple lines of evidence argue against large increases in richness over the past 50-125 million years.

The Early Cretaceous richness peak may therefore reflect a transitional period in insect evolution where radiating extant families coexisted with basal taxa that are rare today or that became extinct [32–35], consistent with phylogenetic evidence for downshifted diversification rates during the Cretaceous in some basal members of groups [4]. Minimal net richness change since the Early Cretaceous implies that the spectacular evolutionary radiations within extant clades were offset by decreasing diversity in extinct or relict groups. Biotic changes, like the transition to angiosperm-dominated plant communities, and climatic shifts, likely provided evolutionary opportunities for some groups but negatively influenced others. Thus, the evolution of insects, rather than representing a continuous accumulation of taxa to the present-day, has been shaped by ecological and environmental forces and the waxing and waning of clades over their long history.

Data accessibility: All data are deposited and available in the Paleobiology Database (www.paleobiodb.org).

Competing interests: We have no competing interests.

Author contributions: M.E.C. and J.A.K. conceived the study and collected the data. M.E.C. analyzed the data and wrote the first draft of the manuscript. All authors contributed to interpretation of the data and revisions of the manuscript.

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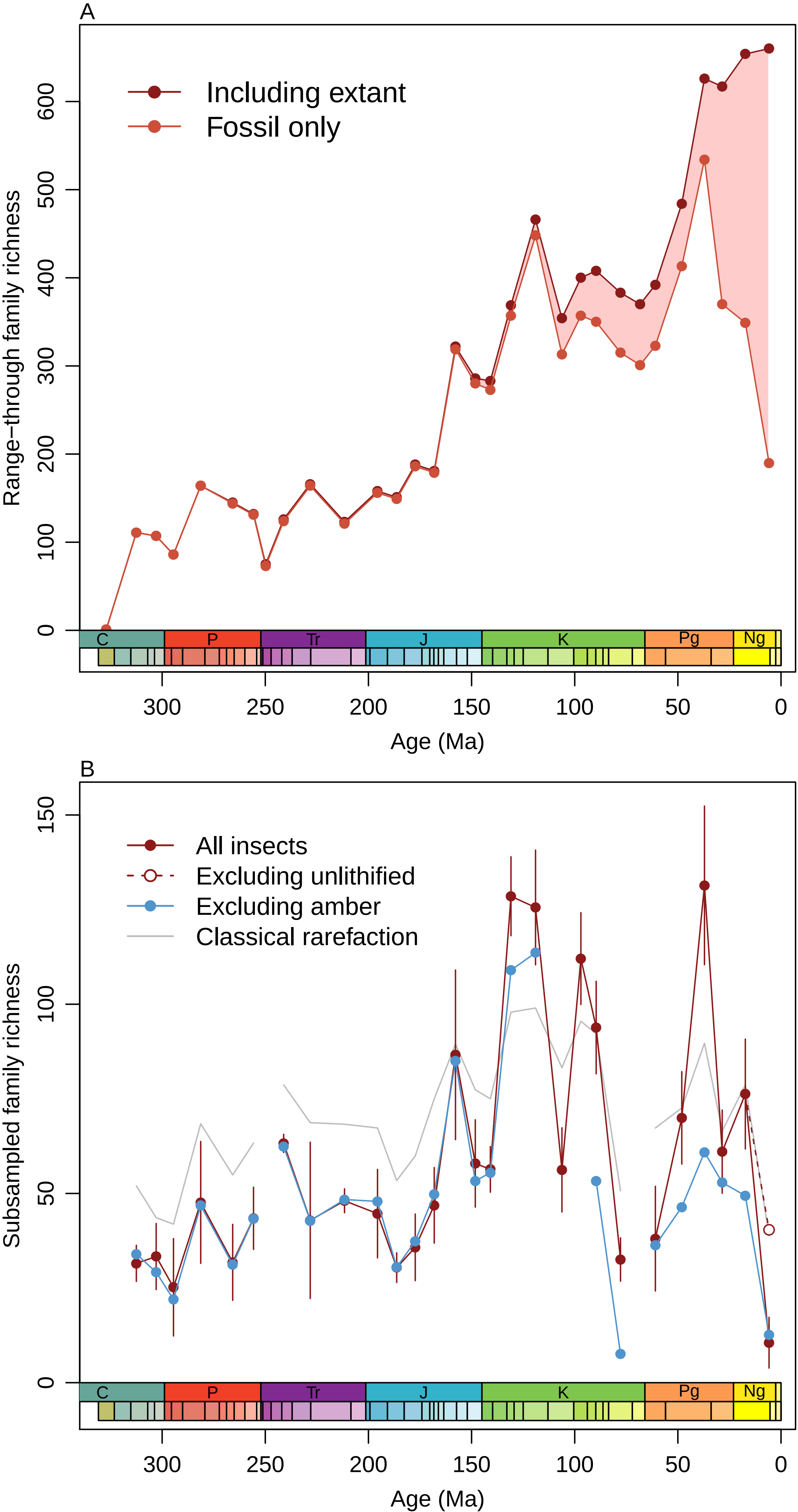
Figure captions

Fig. 1. (*A*) Range-through family richness trends generated by extending ranges of extant families to the Recent (dark red) and only considering fossil data (light red). Including extant data imposes the Pull of the Recent bias (shaded area), while the fossil-only curve suffers from edge effects (notably the decrease in the youngest interval). As a result, these curves are not accurate records of insect richness, particularly when including extant data. (*B*) Sampling-standardised trends in insect family richness. Curves show shareholder quorum subsampling of all insects (red) and excluding amber fossils (blue), as well as classical rarefaction subsampling (gray line). Error bars (shown for all insects only) are one standard deviation. The open circle shows richness after excluding unlithified and poorly lithified occurrences. Differences between the pre-Cretaceous curves for all insects and when excluding amber arise because sampling-standardisation methods take random subsamples of the dataset. The Early Triassic and Maastrichtian intervals are poorly sampled and cannot be analyzed with these methods.

Fig. 2. Species richness estimates from classical rarefaction at quotas of 500, 1000, and 2000 occurrences. The analyses were performed after removing occurrences from unlithified and poorly lithified sediments (only affecting the youngest interval). One standard deviation error bars are smaller than the symbols. Rarefied species richness increases in the mid-Jurassic, similar to the family-level curve, and has a small net increase from the Early Cretaceous to the Neogene.

Fig. 3. Relationship between changes in the tectonic setting of insect occurrences and interval-to-interval changes in subsampled richness. (*A*) Changes in the number of occurrences in typically high-subsidence

basin types (extensional, pull-apart, and volcanic caldera basins) are closely linked with changes in subsampled family diversity (R^2=0.225, p = 0.025). (*B*) Changes in the number of occurrences in other basins have no effect on subsampled diversity (R^2=0.0004, p = 0.93).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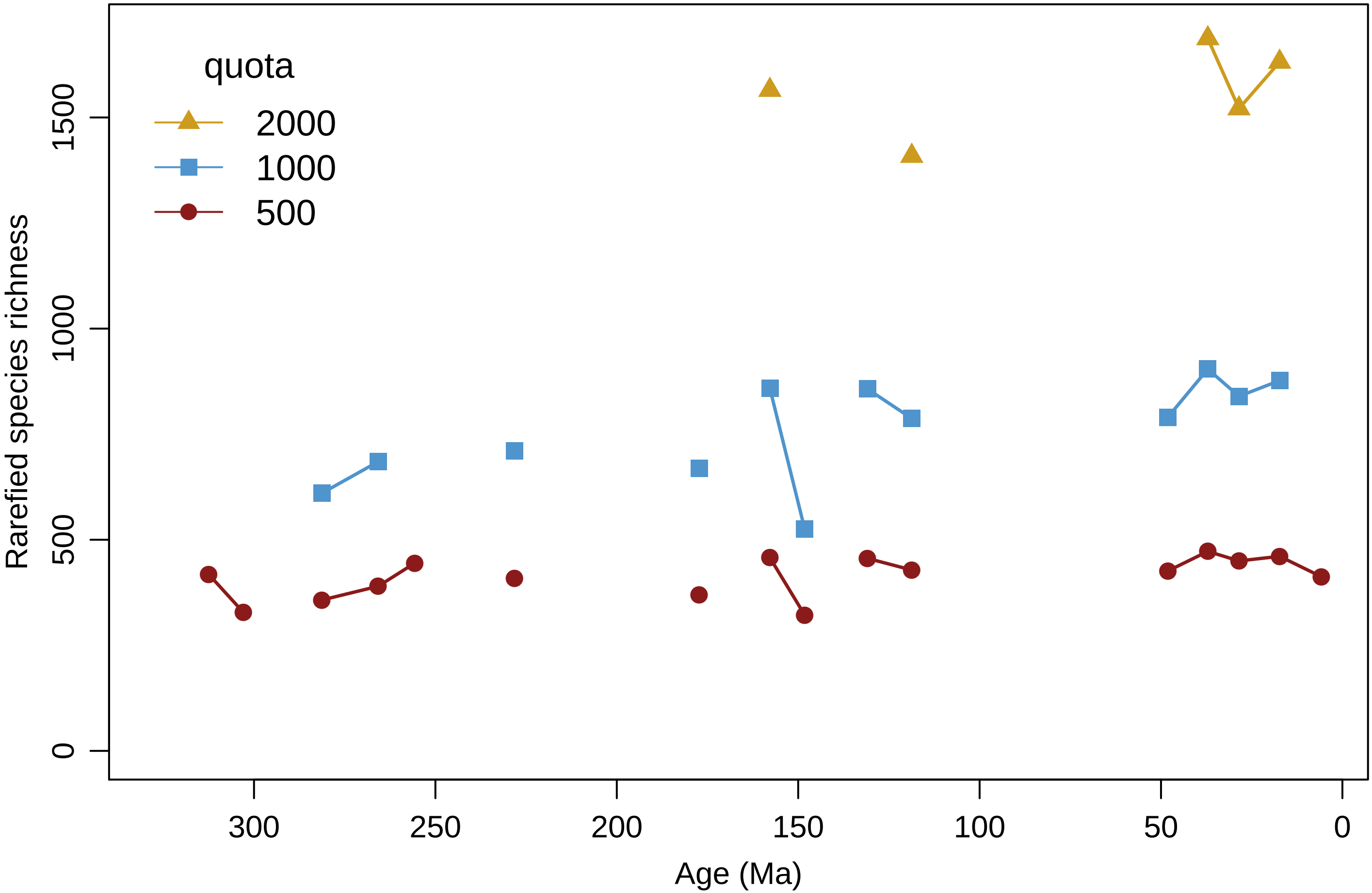
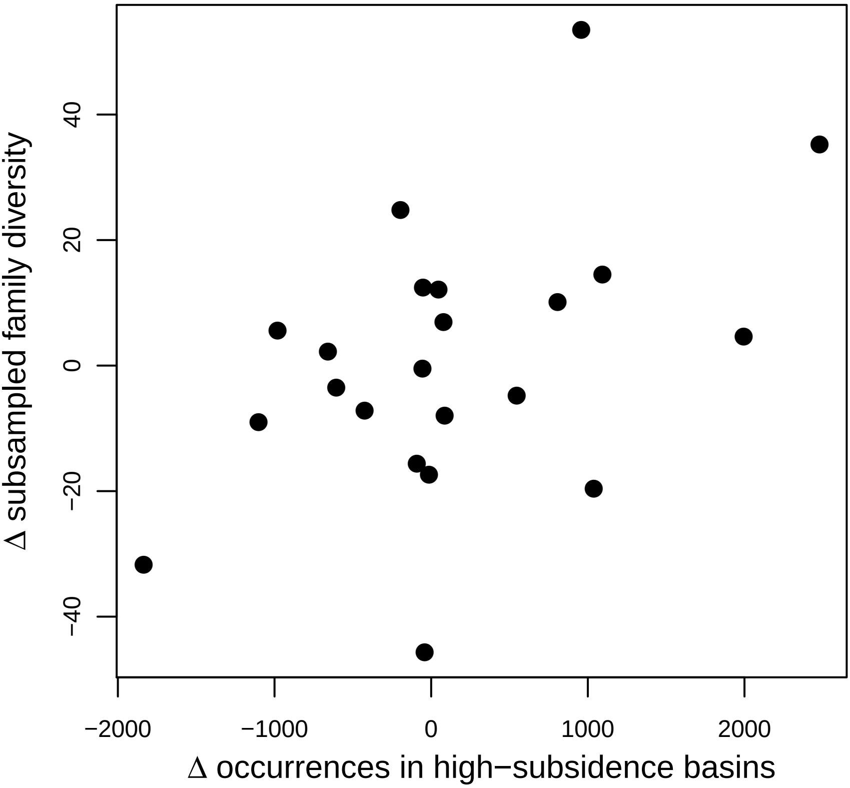
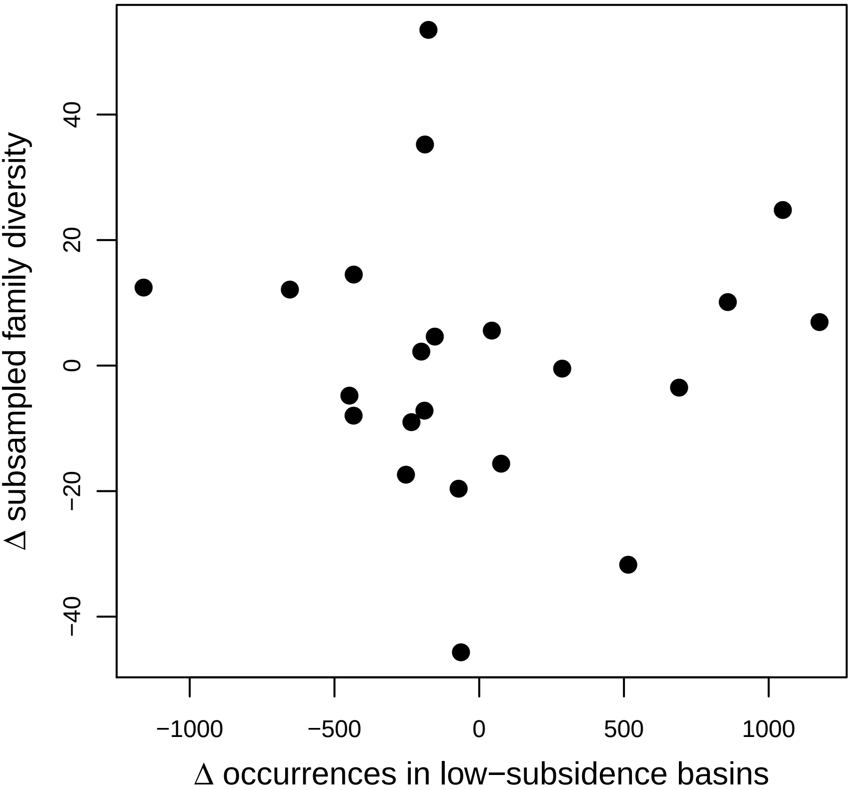
Range−through family richness
0
100
200
300
400
500
600
C
P
Tr
J
K
Pg
Ng
300
250
200
150
100
50
0
Age (Ma)
B
All insects
Excluding unlithified
Excluding amber
Classical rarefaction
Subsampled family richness
0
50
100
150
C
P
Tr
J
K
Pg
Ng
300
250
200
150
100
50
0
Age (Ma)


quota
▲ 2000
■ 1000
● 500
Rarefied species richness
0
500
1000
1500
Age (Ma)
300
250
200
150
100
50
0


Δ subsampled family diversity
40
20
0
−20
−40
−2000
−1000
0
1000
2000
Δ occurrences in high−subsidence basins


Δ subsampled family diversity
40
20
0
−20
−40
−1000
−500
0
500
1000
Δ occurrences in low−subsidence basins

Supplementary figure captions

Fig. S1. Subsampled richness at different quorum levels of shareholder quorum subsampling [1]. Although fewer time intervals are included when the quorum level is larger, the relative trends are not altered.

Fig. S2. Comparison of the effects of different choices for calculation of Good's u and other SQS procedures. (A) We calculated Good's u based on single-reference taxa, excluding the most common taxon and the largest collection ("Refs, common, largest"). However, the shape of the richness curve is unchanged if we calculate Good's u based on single-reference taxa, excluding the most common taxon but not the largest collection ("Refs, common"). It is likewise unchanged if we calculate Good's u only from single-reference taxa without any adjustments ("Refs"). Use of occurrences rather than references, regardless of other choices, also has little effect. (B) We did not downweight references that yielded many collections because most PBDB insect collections contain occurrences from multiple references. The subsampled richness curve is unchanged if we do downweight large references.

Fig. S3. Comparison of Paleobiology Database data with existing range-through diversity curves[2,3]. The Paleobiology Database (PBDB) yields comparable diversity curves to previously published studies when it is treated with range-through counting methods including extant records (the Pull of the Recent). The Nicholson et al. curve[3] reaches slightly greater heights because it includes some families known only from trace fossils and because the PBDB curve is only based on records identified to genus level or lower.

Fig. S4. Paleolatitudinal distribution of fossil insect occurrences from compression fossil localities (excluding amber). North America, Europe, and countries of the former Soviet Union all have a peak around 45 degrees paleolatitude, with fewer occurrences around 10-30 degrees. North American and Europe independently have a bimodal distribution with a smaller peak of occurrences centered around the paleo-equator.

Fig. S5. Paleolatitudinal distribution of compression fossil occurrences in PBDB "10 million year" time intervals. Distributions are shown as beanplots [4], which contour the occurrences with a Gaussian smoothing curve. The width of the bean is scaled to the number of occurrences at a given paleolatitude. Sampling is concentrated in the northern hemisphere, due to extensive research in North America, Europe, countries of the former Soviet Union, and China. Like in figure S4, insect occurrences preferentially derive from paleo-equatorial regions or mid-latitudes (around 45 degrees). Some time intervals (e.g., Permian 2 and Cretaceous 3) have bimodal distributions with a low at 10-30 degrees paleolatitude.

Fig. S6. Effect of the geographic extent of sampling on subsampled family richness. Geographic extent was calculated as the distance along the minimum spanning tree connecting unique paleolatitude/paleolongitude coordinates for insect collections. If multiple collections occurred at a single location, only one paleolat/paleolongitude value was used. Unlithified and poorly lithified occurrences were excluded from both analyses. (A) SQS family richness against minimum spanning tree distance for all insect localities. (B) SQS family richness for compression fossils against minimum spanning tree distance for compression fossil localities.

There is no clear relationship between minimum spanning tree distance and subsampled richness in either analysis.

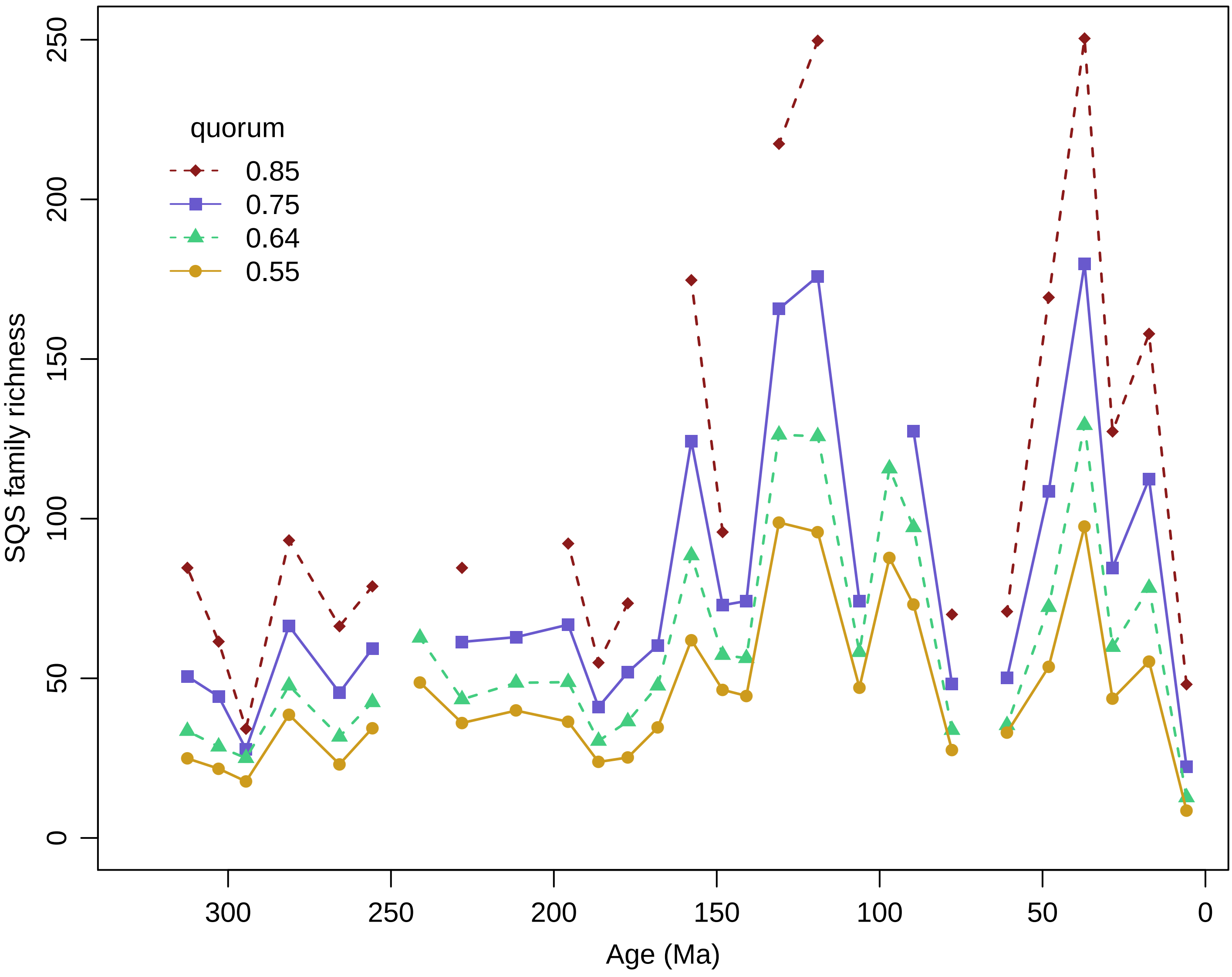
Fig. S7. Comparison of rarefied diversity curves constructed from different subsets of the published literature. (A) Bars indicate the proportion of occurrences published after 1900 (red) and 1950 (blue) in each time interval. (B) Rarefied diversity curves from all publications (gray curve with one standard deviation error bars), only papers published after 1900 (red curve), and only papers published after 1950. Diversity trends are not significantly changed when older literature, which may contain less reliable identifications, is excluded.

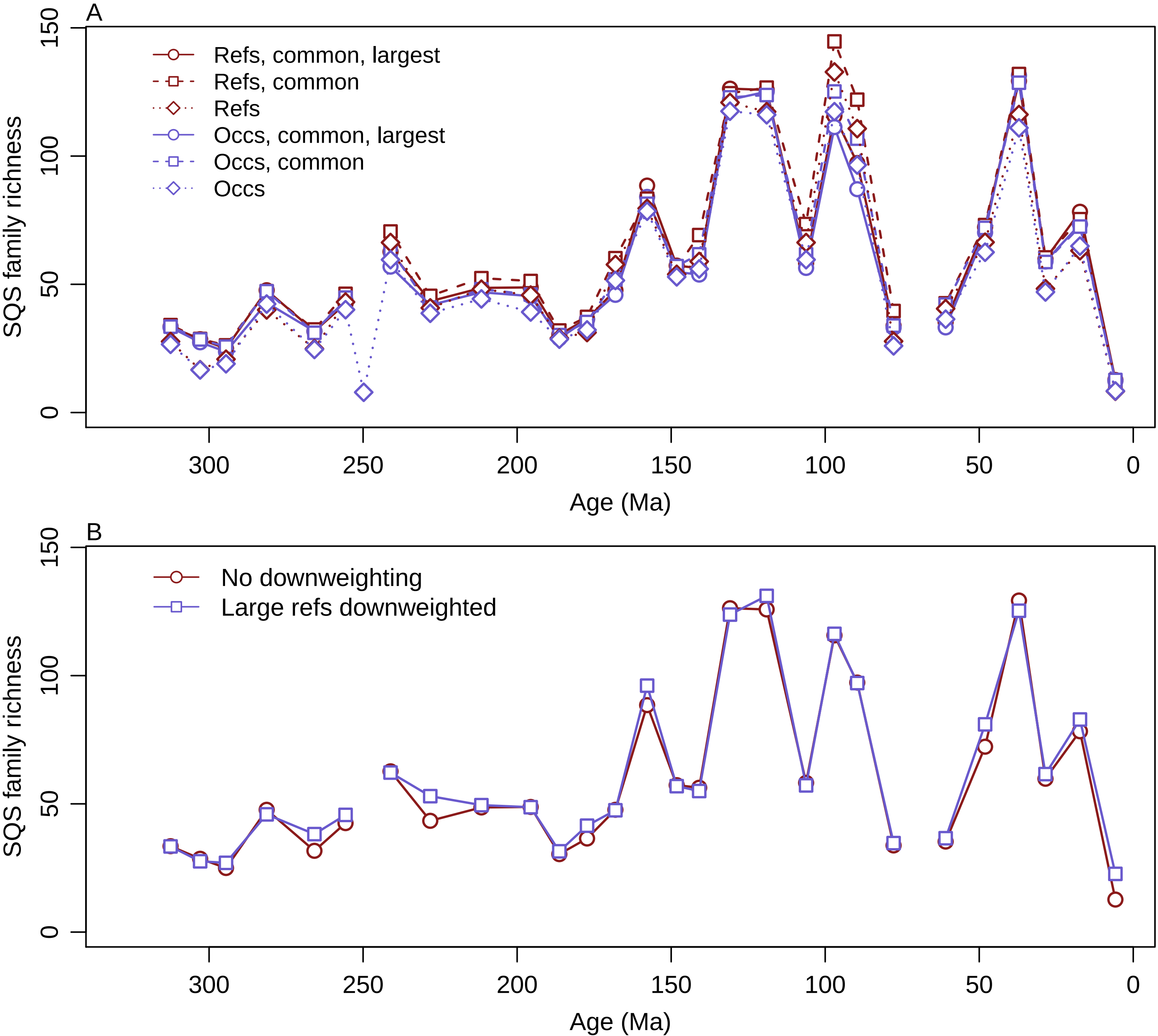
1. Alroy, J. 2010 Fair sampling of taxonomic richness and unbiased estimation of origination and extinction rates. In *Quantitative Methods in Paleobiology. The Paleontological Society Papers, Vol 16* (eds J. Alroy & G. Hunt), pp. 55–80.

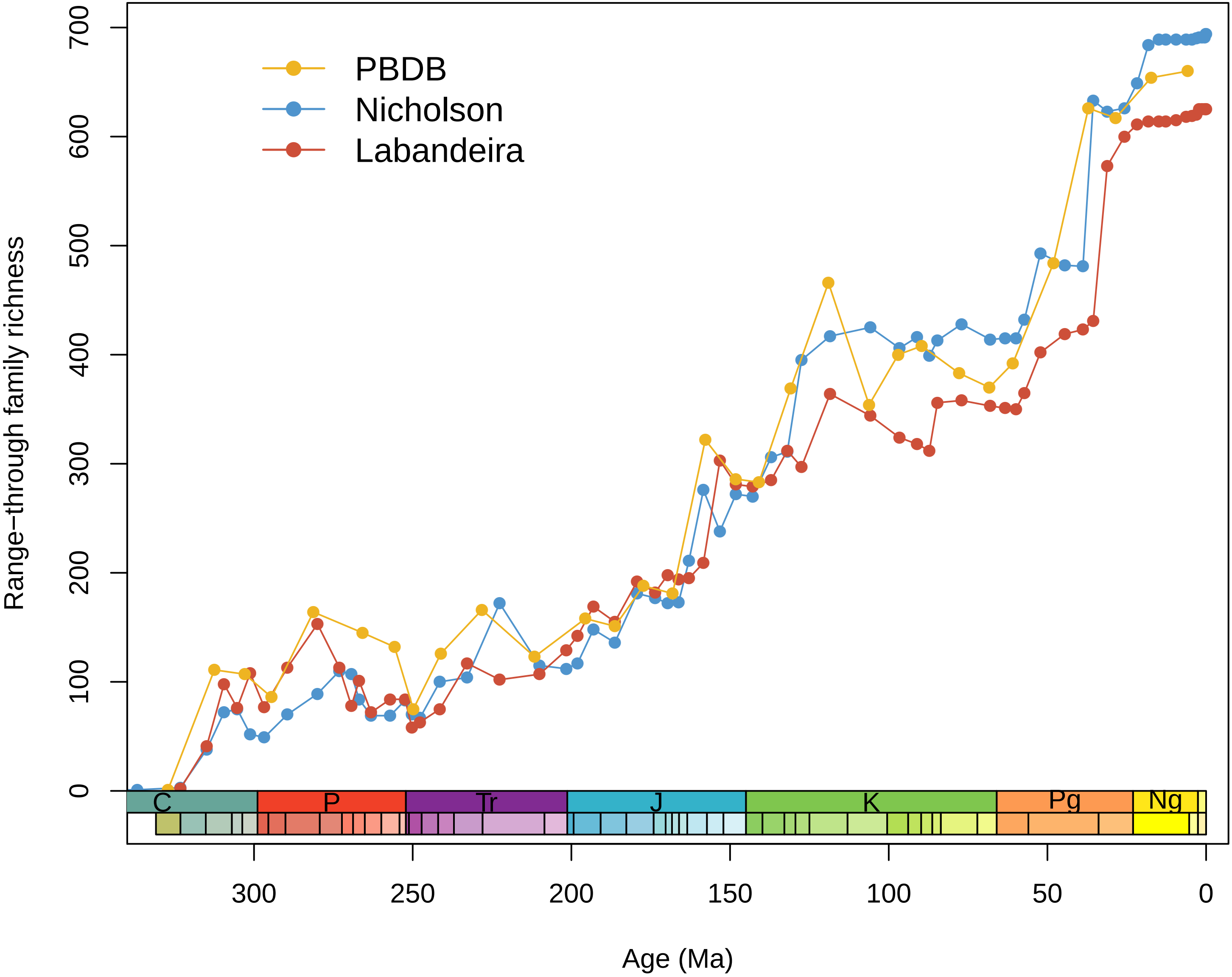
2. Labandeira, C. C. & Sepkoski, J. J. 1993 Insect diversity in the fossil record. *Science.* **261**, 310–315.

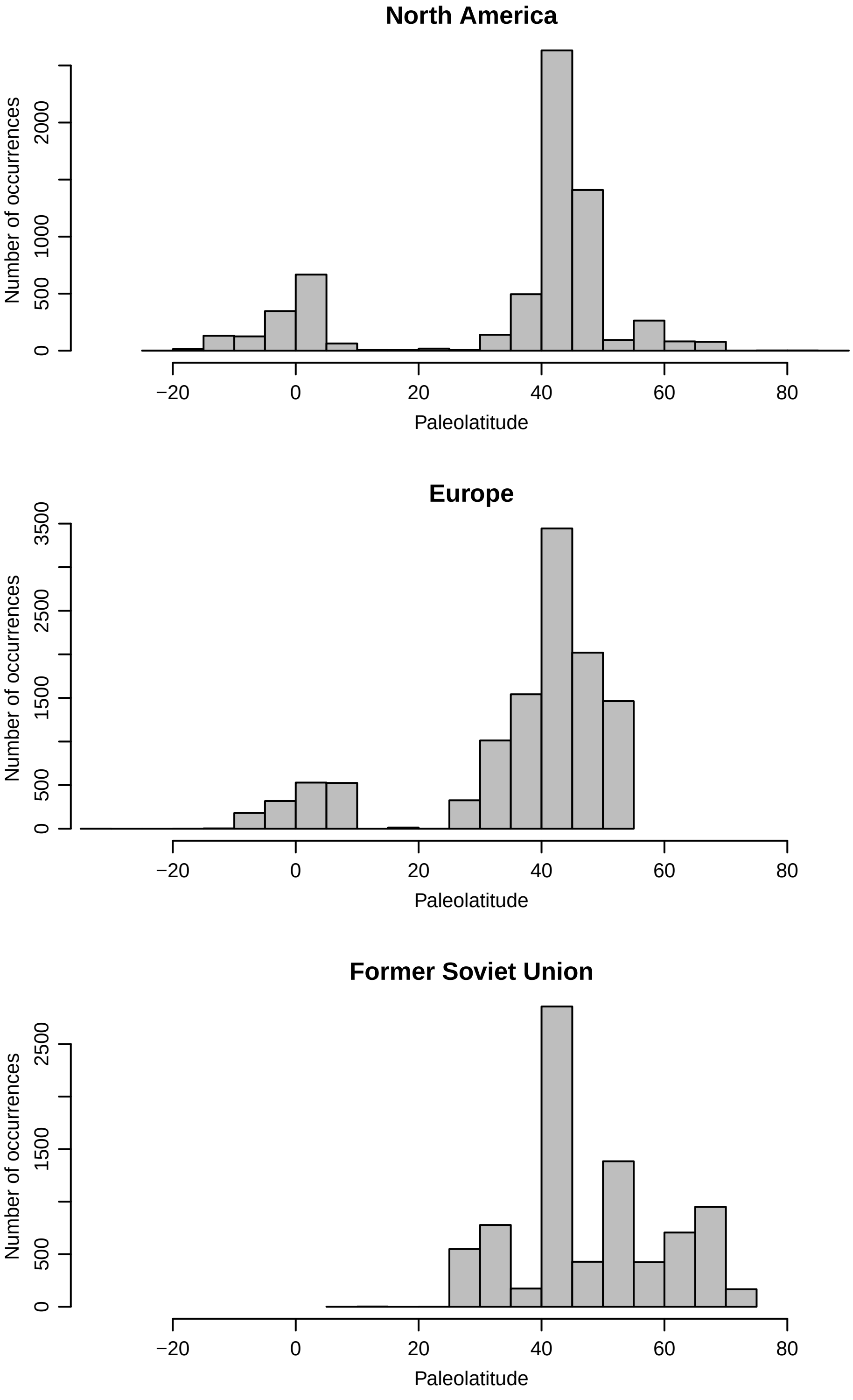
3. Nicholson, D. B., Mayhew, P. J. & Ross, A. J. 2015 Changes to the fossil record of insects through fifteen years of discovery. *PLoS One* **10**, e0128554.

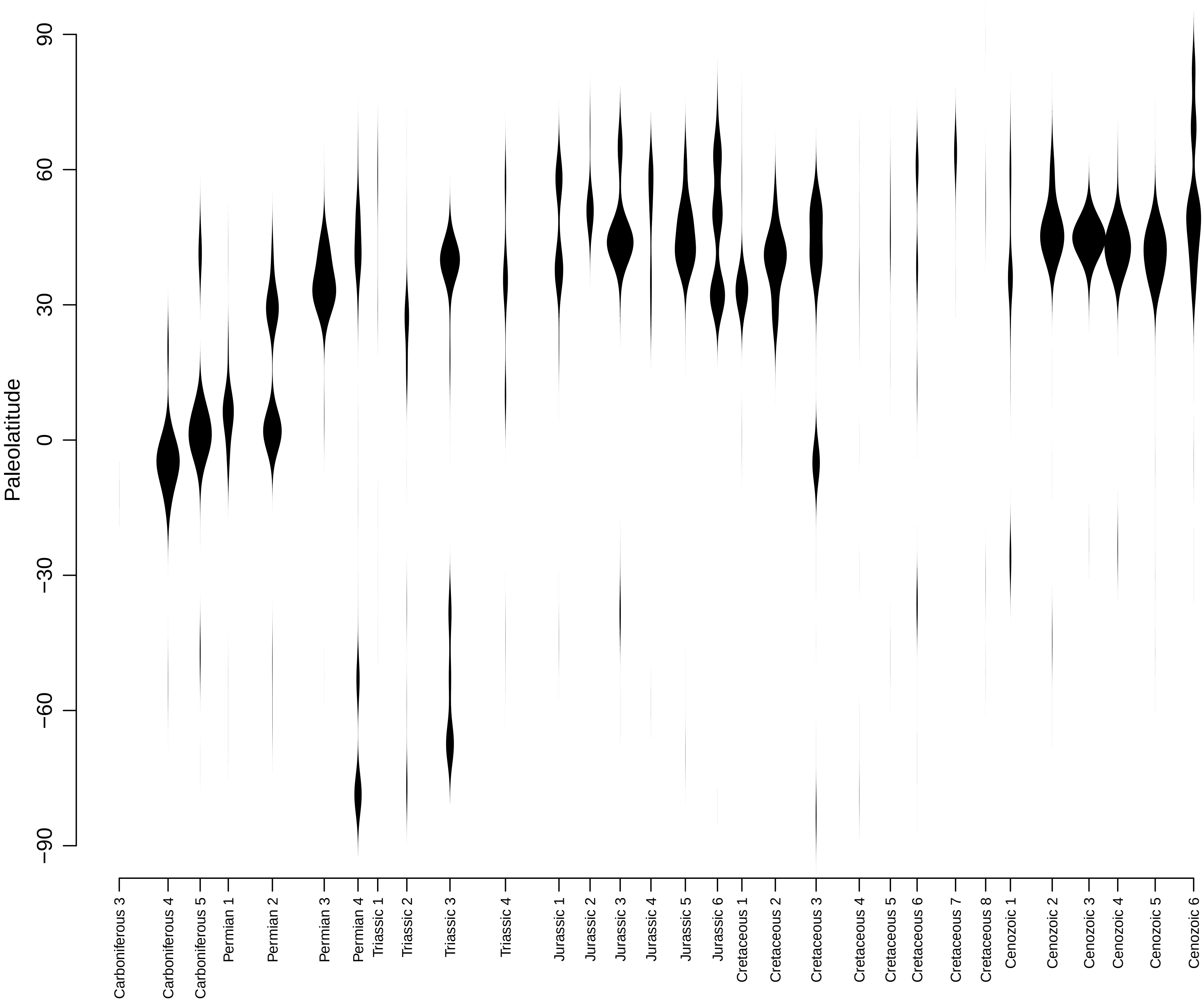
4. Kampstra, P. 2008 Beanplot: a boxplot alternative for visual comparison of distributions. *J. Stat. Software, Code Snippets* **28**, 1–9.

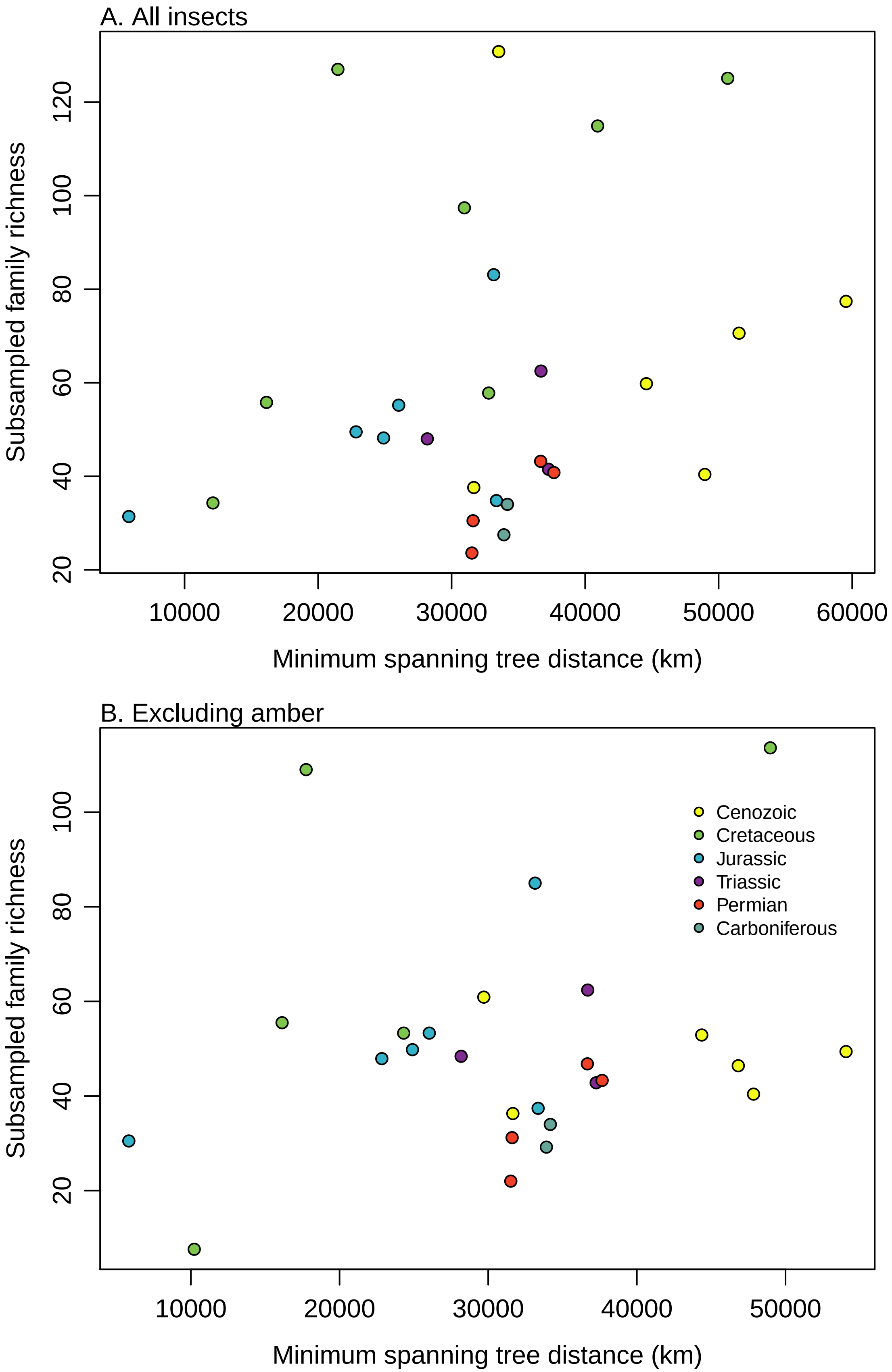

quorum
0.85
0.75
0.64
0.55
SQS family richness
0
50
100
150
200
250
Age (Ma)
300
250
200
150
100
50
0

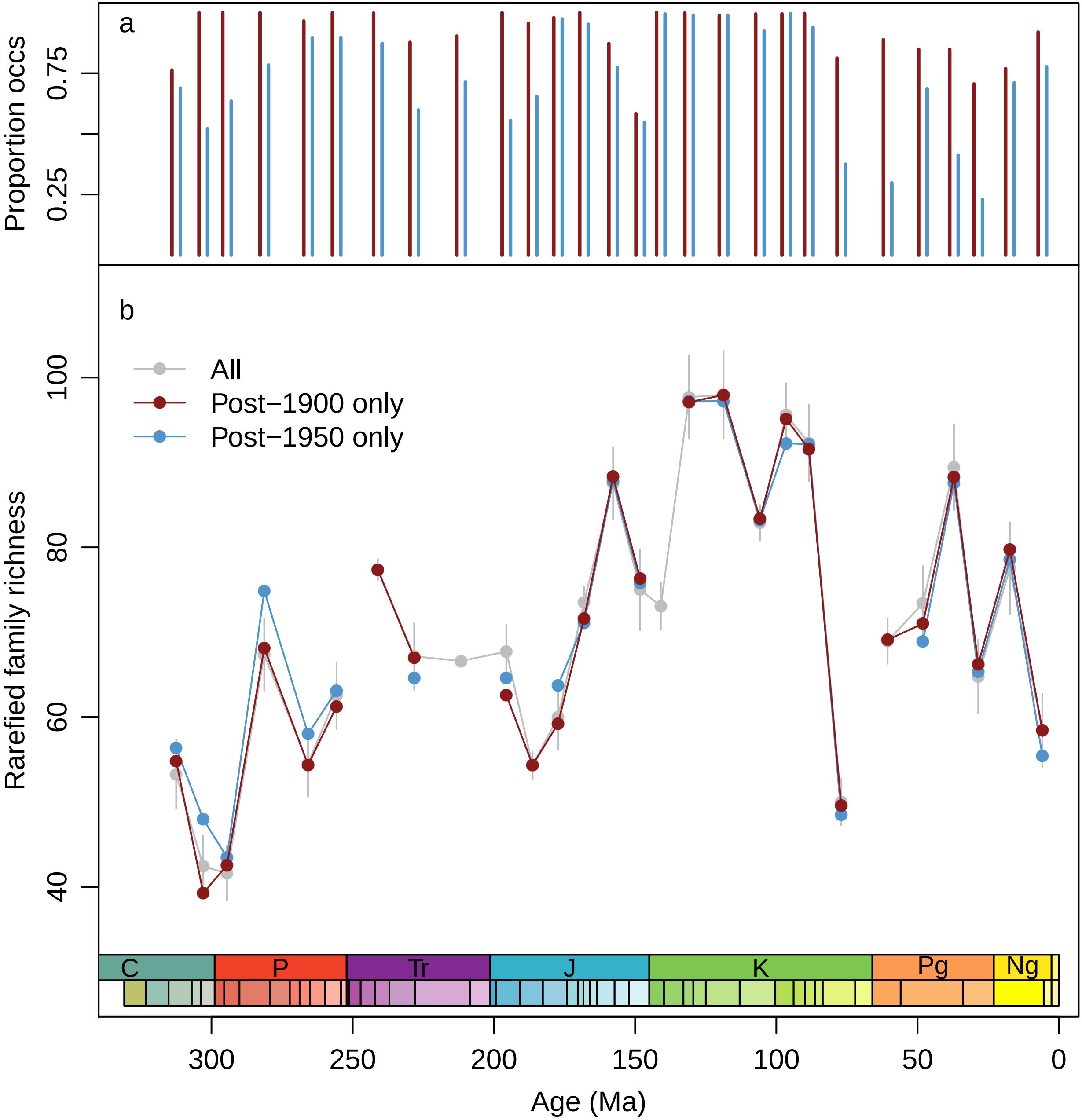

A
Refs, common, largest
Refs, common
Refs
Occs, common, largest
Occs, common
Occs
SQS family richness
0
50
100
150
300
250
200
150
100
50
0
Age (Ma)
B
No downweighting
Large refs downweighted
SQS family richness
0
50
100
150
300
250
200
150
100
50
0
Age (Ma)


PBDB
Nicholson
Labandeira
Range−through family richness
0
100
200
300
400
500
600
700
C
P
Tr
J
K
Pg
Ng
300
250
200
150
100
50
0
Age (Ma)


North America
Number of occurrences
0
500
1000
2000
−20
0
20
40
60
80
Paleolatitude
Europe
Number of occurrences
0
500
1500
2500
3500
−20
0
20
40
60
80
Paleolatitude
Former Soviet Union
Number of occurrences
0
500
1500
2500
−20
0
20
40
60
80
Paleolatitude


Paleolatitude
90
60
30
0
−30
−60
−90
Carboniferous 3
Carboniferous 4
Carboniferous 5
Permian 1
Permian 2
Permian 3
Permian 4
Triassic 1
Triassic 2
Triassic 3
Triassic 4
Jurassic 1
Jurassic 2
Jurassic 3
Jurassic 4
Jurassic 5
Jurassic 6
Cretaceous 1
Cretaceous 2
Cretaceous 3
Cretaceous 4
Cretaceous 5
Cretaceous 6
Cretaceous 7
Cretaceous 8
Cenozoic 1
Cenozoic 2
Cenozoic 3
Cenozoic 4
Cenozoic 5
Cenozoic 6


A. All insects
Subsampled family richness
20
40
60
80
100
120
10000
20000
30000
40000
50000
60000
Minimum spanning tree distance (km)
B. Excluding amber
Subsampled family richness
20
40
60
80
100
10000
20000
30000
40000
50000
Minimum spanning tree distance (km)
Cenozoic
Cretaceous
Jurassic
Triassic
Permian
Carboniferous


a
Proportion occs
0.25
0.75
b
Rarefied family richness
40
60
80
100
All
Post−1900 only
Post−1950 only
C
P
Tr
J
K
Pg
Ng
300
250
200
150
100
50
0
Age (Ma)