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TITLE: The complex effects of mass extinctions on morphological disparity

Short title: Mass extinctions and morphological disparity

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Author contributions:

MNP devised the project, wrote the code, carried out experiments, and wrote the manuscript. TG and MAW assisted in devising the experiments and writing the manuscript and subsequence drafts.

Data Sharing and Data Accessibility

Users can freely download the R code as part of the package PETER from GitHub (https://github.com/PuttickMacroevolution/PETER). The whole procedure for running these simulations is available and documented on GitHub.

ABSTRACT

Studies of biodiversity through deep time have been a staple for biologists and palaeontologists for over 60 years. Investigations of species richness (diversity) revealed that at least five mass extinctions punctuated the last half billion years, each seeing the rapid demise of a large proportion

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of contemporary taxa. In contrast to diversity, the response of morphological diversity (disparity) to mass extinctions is unclear. Generally, diversity and disparity are decoupled, such that diversity may decline as morphological disparity increases, and vice versa. Here, we develop simulations to model disparity changes across mass extinctions using continuous traits and birth-death trees. We find no simple null for disparity change following a mass extinction but do observe general patterns. The range of trait values decreases following either random or trait-selective mass extinctions, whereas variance and the density of morphospace occupation only decline following trait-selective events. General trends may differentiate random and trait-selective mass extinctions, but methods struggle to identify trait selectivity. Long-term effects of mass extinction trait selectivity change support for phylogenetic comparative methods away from the simulated Brownian motion towards Ornstein-Uhlenbeck and Early Burst models. We find that morphological change over mass extinction is best studied by quantifying multiple aspects of morphospace occupation.

Keywords: disparity, mass extinctions, phylogenetic comparative methods, traits, macroevolution

INTRODUCTION

Evolutionary biologists and paleobiologists have long quantified diversity in terms of species numbers or species richness, making comparisons both horizontally between clades and higher taxa (Wiens 2017) and vertically throughout evolutionary time (Smith 2007). However, diversity takes no account of the morphological differences between species, a property known as morphological disparity (Wills et al. 1994). Researchers have attempted to formally define disparity in different ways, but most of the indices that derive from these definitions quantify variation in morphology or phenotype (Wills 2001; Hopkins and Gerber 2017; Guillerme et al. 2020a).

There have been numerous empirical analyses of the diversity of the global biota through evolutionary time (Raup and Sepkoski 1982; Alroy 2010) with an overall null expectation of symmetry as clades rise and fall in diversity (Gilinsky and Good 1989; Liow et al. 2010). For disparity, by contrast, there is no such simple null (Pie and Weitz 2005; Hughes et al. 2013; Oyston et al. 2015, 2016) but see (Foote 1996). Quantifying disparity alongside diversity is essential to fully understand the evolution of biodiversity (Roy and Foote 1997) as a series of empirical studies have demonstrated that diversity and disparity are largely decoupled (Wills et al. 1994; Fortey et al. 1996; Bapst et al. 2012). Analyses of disparity have accordingly proven invaluable for studying the tempo and mode of evolution (Simpson 1944), how clades diversify through time and throughout morphological “form space” (Gould 1990), and the patterns of drift and selection that have produced the distribution of living diversity (Raup 1981).

Extinction has had an immediate and potentially catastrophic role in sculpting patterns of biodiversity through time (Sepkoski 1981), particularly mass extinctions (Bond and Grasby 2017). Mass extinctions are defined, by convention, as geologically brief events that remove at least 75% of contemporary diversity (Barnosky et al. 2011). Researchers accept that the effect of a mass extinction upon disparity will depend upon whether species are selectivity or randomly removed by extinction (Foote 1997; Korn et al. 2013). Discrete events in which extinction acts selectively are expected to decrease disparity by eliminating the majority of an enclosed area of morphospace. Non-selective events, by contrast, may not lead to disparity decreases (Foote 1991, 1993; Roy and Foote 1997; Villier and Korn 2004; Korn et al. 2013), particularly when disparity is measured using a variance-based index (Korn et al. 2013).

Empirical studies have demonstrated cases where mass extinctions acted both selectively and non-selectively with regards to particular traits (Foote 1993; Roy 1996; Lockwood 2004; Erwin 2007; Halliday and Goswami 2016). Phylogenetic comparative studies indicate that there is trait selectivity on some groups, such as vascular plants (Green et al. 2011), but there is little evidence to link traits and extinction susceptibility during mass crises in the fossil record (Friedman 2009; Puttick et al. 2017; Allen et al. 2019). Many studies reveal a phylogenetic signal of extinction (Hardy et al. 2012; Harnik et al. 2014; Krug and Patzkowsky 2015; Puttick et al. 2017; Soul and Friedman 2017), without demonstrating links to trait selectivity. We note that in studies of fossil record disparity, it is only possible to analyze traits with fossilization potential, which excludes soft body parts and behavior.

In order to investigate the consequences of extinctions on traits, one approach would be to analyze empirical data, as simulations may lack biological realism. Importantly, however, simulations provide an underpinning framework for such empirical analyses (Foote 1991, 1997; Ciampaglio et al. 2001; Bapst et al. 2012; Korn et al. 2013), as it is possible to test scenarios in which we know the definitive underlying patterns; an impossibility with empirical data. Here we use a novel simulation approach to determine the expected, null patterns of disparity change through mass extinction events and to investigate how quickly diversity and disparity might be expected to recover to pre-extinction levels under many scenarios. We simulate birth-death trees (Ma 2010; Stadler 2010; Mooers et al. 2012) and traits under Brownian motion with a variety of parameter values. During our simulations, a mass extinction removes a proportion of contemporary diversity. We show that disparity generally reduces following a mass extinction event, but that all patterns are variable. Alternative disparity indices imply different patterns of disparity change, such that there is a fundamental link between how we conceptualize and quantify disparity (Wills 1998b; Korn et al. 2013). Finally, we assess how mass extinctions bias comparative phylogenetic models of trait evolution in the extant lineages that survive such events. Phylogenetic regressions do not distinguish selective and non-selective mass extinction events under the simplest simulation models and the selective removal of taxa according to trait value causes comparative models to support non-BM models in preference to the (true) simulated BM process.

METHODS

Overview

We summarize the full simulation procedure in Fig 1. We simulated birth-death trees and Brownian motion traits simultaneously. We ran simulations until 50, 100, or 200 contemporary lineages were present, after which an extinction event removed 50, 75, or 90% of standing diversity. Simulations finished when diversity had recovered to pre-extinction levels (i.e., 50, 100, 200 tips). We chose the severity of mass extinctions (50, 75, 90%) to reflect known extinction values in the fossil record (Stanley 2016; Bond and Grasby 2017). The upper figure (90%) reflects the severity often quoted for the end-Permian event, although this has been questioned (Stanley 2016). The middle figure (75% of species lost) reflects the severest estimates for end-Ordovician and end-Cretaceous events and is accepted as the necessary threshold for a mass extinction (Barnosky et al. 2011). We used 50% for a ‘smaller’ extinction events, such as the Frasnian extinction in the Late Devonian (Stanley 2016; Bond and Grasby 2017).

We simulated extinction in two different ways. Taxa were either eliminated at random in a non-selective event or removed according to their trait values to simulate a selective extinction. In separate analyses, we ran models to simulate one, two, and five traits. We then assessed disparity through time and analyzed the ability of models to recover the signal of trait change across extinctions. We wrote new code in *R* to simulate data; users can freely download this as part of the package *Phylogenetic Evolution of Traits and Extinction in R* (PETER) from *GitHub* (https://github.com/PuttickMacroevolution/PETER).

The first objective of this study is to provide a simple null model for change in disparity across mass extinctions, given a number of varying parameters. In our simulations, we have an extremely high resolution of extinction through time as we record the trait values for all simulated internal nodes and tips. In the fossil record, however, it is often necessary to aggregate data into time bins. Therefore, we also undertook steps to study binned values of disparity through time. For the majority of our analyses, we focused on studies with one continuous trait, as there is often just a single measurement available for a large group of species (e.g., body size in fossil vertebrates). For these simulations, we attempted to control for properties that are likely to vary across the tree of life, such as rates of background extinction and the total number of species. Our multivariate approach was designed to extend the single trait approach, albeit that selectivity was simulated as acting on a single trait. Evolution in this directly selected focal trait was correlated with evolution in the other trait(s), so that these latter traits experienced indirect selectivity (Lande and Arnold 1983). We also ran simulations in which traits evolved independently.

The second objective is to examine the effectiveness of methods commonly used to investigate mass extinctions. For example, we determine whether it is possible to differentiate trait-selective and trait-independent mass extinctions, and how mass extinctions influence models of continuous trait evolution through time.

Simulation of trees and traits

We simulated trees evolving from the root to the tips with time-homogeneous speciation (λ) and extinction rates (μ). We used the same speciation rate ($\lambda = 1$) for all simulations, but different levels of background extinction ($\mu = 0, 0.4, 0.8$).

We simulated traits under a Brownian motion process (Felsenstein 1973, 1985). At the start of each simulation, we sampled the root state from a normal distribution with a mean of zero and a standard deviation of one. In simulations with two and five traits, we set the co-variance either to zero such that the traits were independent or to a co-variance of 0.75 so that the evolution of traits was linked but not identical. The use of a moderate co-variance (0.75) implies that although selectivity (when present) would act on one trait only, the mass extinction would also affect the remaining, non-directly selected traits. We designed this to mimic a scenario in which selectivity acts on one analyzed trait that is known to co-vary with many other traits, such as body size.

Disparity indices

We summarized diversity using lineage-through-time plots, and we used three indices of disparity (Fig 1C): *median pairwise distance*, which is the median pairwise Euclidean distance between all points (Wills et al. 1994); *Sum of Variances* (SOV) from each trait (Foote 1992a); and *Sum of Ranges* (SOR) (Wills 1998a, 2001; Brusatte et al. 2011; Ruta et al. 2013). We use these disparity indices to elucidate different aspects of morphospace occupation: we interpret *median pairwise distance* as an index of the density of morphospace occupation; and we consider *Sum Of Variance*s as an index of dispersion, and *Sum Of Ranges* as an index of the overall magnitude or volume of morphospace occupation (Guillerme et al. 2020b). Unless stated, all analyses were conducted using the R package *dispRity* (Guillerme 2018).

Our simulations produced trait estimates for every node in the tree. We estimated disparity indices using these traits, but for most analyses, we binned trait values into equal-size time bins and subsequently calculated disparity for each bin using a time-slicing approach. We explored the impacts of using different bin sizes (4, 8, 10, 16-time bins), and used the highest resolution, sixteen-time bins to assess if there were significant differences in using each bin size. We used sixteen time-bins throughout the remaining analyses, but we observed the same general trends with all bin sizes (Table 1). After each simulation, we scaled disparity and diversity to unity by dividing each by their maximum values.

Simulation of mass extinctions

For a given quantile of extinction, we set different strengths of selectivity:

(i) *Strict selectivity*. All lineages with traits larger than the cut-off went extinct and all other lineages survived.

(ii) *Strong selectivity*. To investigate events in which the vast majority of extinction related to the size of traits, lineages larger than the cut off had a probability of 0.99 to go extinct whilst lineages smaller than the cut off had a probability of 0.01 to go extinct.

(iii) *Random selectivity*. Trait values had no influence on extinction susceptibility.

(iv) *Weak selectivity.* An intermediate scenario in which lineages larger than the cut off had a probability of 0.75 of extinction whilst lineages smaller than the cut off had an extinction probability of 0.25 (i.e, there was a 25% chance of random extinction).

In each case of selectivity strength, we set the cut-off by using the contemporary distribution of traits at the extinction boundary; lineages with trait values above the 0.5, 0.25, or 0.1 quantiles of the contemporary distribution were more prone to extinction in those simulations with *directional selectivity*. The quantiles were chosen to directly reflect the selectivity of extinction. So, for simulations with *strict selectivity* there was a zero probability of extinction for taxa with trait values below a certain cut-off value. As an example, for simulations with 75% loss of taxa at an extinction boundary and *strict selectivity*, there was a zero probability of extinction for taxa with trait values below the 0.25 quantile of all contemporary trait values.

We binned and summarized simulated data by pooling all parameters: *n* lineages lost, background extinction, and the number of tips for *strict*, *strong*, and *random* extinctions. We used three levels of background extinction in all other simulations (i.e., 0, 0.4, 0.8). In analyses with one trait only, we also ran simulations with a background extinction rate of 1.

Finally, we ran *disruptive selectivity* mass extinction simulations for a single trait in which lineages with trait values closer to the mean were prone to extinction, such that lineages with smaller or larger trait values were more likely to survive. For these simulations, we set the selective extinctions to remove lineages from the 0.5, 0.75, and 0.9 quantiles symmetrical around the mean.

Phylogenetic analysis of mass extinctions

We tested whether survivors and extinct lineages differed significantly in their trait values using Ordinary Least Squares (OLS) and Phylogenetic Generalized Least Squares (pGLS) regressions (Grafen 1989). In these models, we set the response as the continuous trait value and coded the predictor as a binary variable indicating whether or not the lineage survived the mass extinction. We pruned the phylogeny and trait values to include only those lineages that existed at the boundary (Puttick et al. 2017), such that we did not consider values from lineages that were lost before the extinction or arose after it. We estimated the phylogenetic signal in trait values using Pagel's lambda (Pagel 1997, 1999) alongside the regression parameters in the R package *motmot* (Puttick et al. 2020).

We tested the phylogenetic signal in extinction itself, without consideration of trait values, using the *phyloD* statistic (Fritz and Purvis 2010). This method used phylogenetic contrasts to estimate internal node values of binary traits (zero = survivors, one = extinct lineages), and used these node values to estimate the number of binary transitions. The number of changes indicated the phylogenetic signal, with the number of changes and signal strength being inversely correlated (more changes means a weaker phylogenetic signal). A Brownian motion model will produce a *d* value close to 0 under the *phyloD* statistic. Values larger than 0 denote increasingly random signal, and values under 0 are indicative of over-conserved signals.

Phylogenetic comparative models of trait distributions that have recovered from a mass extinction

The signal of past mass extinctions may be present in the trait distribution of extant lineages. To explore these patterns, we pruned simulated datasets to yield ultrametric trees comprising only extant taxa (i.e., lineages in existence at the end of the simulation). We applied commonly-used likelihood phylogenetic comparative models of trait evolution to these pruned data: Brownian motion (Felsenstein 1973, 1985) to represent the null model; evolution under a constraint using an Ornstein-Uhlenbeck (OU) model (Hansen 1997; Butler and King 2004; Blomberg et al. 2020) in which variance was constrained to the ancestral value according to the strength of α; and the Early Burst model, in which the rate variance exponentially decreased through time (Blomberg et al. 2003; Harmon et al. 2010).

The whole procedure for running these simulations is available and documented on *GitHub* (https://github.com/PuttickMacroevolution/PETER).

RESULTS

The variance around simulated disparity is higher than the variance around diversity

We ran initial analyses without a mass extinction event. When plotted through time, relative disparity showed an overall pattern of increase (Fig 2). Trends are similar for each index, but there is a more substantial difference between disparity and diversity when the former is measured using the Sum Of Ranges rather than the Sum of Variances or median pairwise distance. We observed similar trends in simulations with two and five traits (Supplementary Fig S1).

Mass extinctions usually cause reductions in disparity, and the precise patterns are related to the index of disparity

As a general rule, selective mass extinctions caused a reduction in disparity (Fig 3, Supplementary Figure S2). However, this pattern was not universal, and changed according to the simulation model (e.g., different strengths of selectivity) and the disparity index used (Fig 4).

All disparity indices showed iterations with both increases and decreases across a mass extinction, such that there is no universal pattern. Pooling the results of all simulations that entailed strict directional selectivity (irrespective of background extinction, number of tips, or extinction severity) we found a median decrease in disparity indexed by median pairwise distance (90%), Sum of Variances (90%), and Sum of Ranges (75%). When selectivity was absent from the simulations, all indices showed a median disparity change of zero across the mass extinction, except for the Sum Of Ranges for which most simulations showed a decrease in disparity across the boundary (75%). For those simulations with one trait, we ran additional simulations that used the special case of $\lambda = \mu = 1$, and these showed patterns similar to those in simulations with other levels of extinction (Supplementary Table S1, Supplementary Figure S2).

For a single trait, we also investigated the effects of varying the simulation parameters individually (viz., strength of selectivity, the proportion of lineages lost, rate of background extinction, number of tips, and disparity index used) (Supplementary Fig S3). Simulations with more tips showed more extreme reductions in disparity across the mass extinction boundary, irrespective of the disparity index used. Only in certain circumstances did all iterations indicate a decrease in disparity across an extinction boundary. For example, there was a consistent decrease in disparity across a mass extinction in simulations with more tips, more severe lineage loss, and higher rates of background extinction (including a background extinction of $\mu = 1$). The Sum Of Ranges index is very sensitive to sample size differences, and a fall in the Sum of Ranges would be expected alongside a reduction in diversity in the wake of a mass extinction. For the *directional selectivity* simulations with one trait, we ran additional simulations that used the special case of $\lambda = \mu = 1$ and these showed similar patterns to simulations with other levels of extinction (Supplementary Table S1).

For simulations with an intermediate level of extinction selectivity (*weak selectivity* with 25% probability of random extinction), the results are generally closer to *random selectivity* models rather than to other models with directional selectivity (Supplementary Table S1).

In simulations with multiple traits, only the extinctions with strict selectivity showed a consistent decrease in disparity across a mass extinction boundary (Fig 4B-C). The median decreases in disparity for multiple traits were smaller than in simulations with one trait, and some multiple trait simulations indicated an increase in disparity across the extinction event. The number of iterations that showed a decrease in disparity across the mass extinction boundary was lower in simulations with no trait co-variance compared to analyses with 0.75 trait co-variance (Table 1A). Again, an exception was the Sum Of Ranges, in which the majority of iterations showed a decrease in disparity with any selectivity strength, and nearly all traits had a decrease in disparity with five traits (Table 1B). We note that increases in range-based indices are only possible because of time binning effects: the *immediate* wake of an extinction event (if not time averaged and therefore excluding new linages) could only show a decrease or no change in range. However, we seek to simulate the temporal sampling that pertains in typical paleontogical data sets. The tendency for a disruptive extinction was for all disparity indices to show an increase or no change across the mass extinction boundary (Fig S4).

Comparative phylogenetic methods do not distinguish selective and non-selective extinctions

pGLS models were more conservative at detecting the true relationship between trait values and extinction selectivity compared to OLS models, but pGLS models have lower type-two error rates in comparison to OLS models (Fig 5). In all simulations with *strict* and *strong* selectivity 99% of OLS models support the correct relationship, compared to only a median of 86% (*strict*) and 68% (*strong*) of pGLS models. With *weak selectivity,* few pGLS (median 6%) models show a significant relationship between extinction and traits, which is much lower than the OLS relationship (80%). When there is no relationship between trait values and extinction selectivity, pGLS models have a lower error rate (median 1%) compared to pGLS models (median 6%).

Models consistently detect the phylogenetic signal of extinction

There was a strong phylogenetic signal, as measured by the *phyloD* statistic, when selectivity was *strict* (median 0.07) and *strong* (median 0.12). Conversely, there was a random signal when selectivity was *weak* (median 0.82) or *random* (median 1.0). Only the strength of selectivity and magnitude of lineage loss were significant factors in explaining the differences in phylogenetic signal. There was no significant difference in the phylogenetic signal for different numbers of tips or different levels of background extinction.

Mass extinctions have long-term impacts on trait distributions

High levels of extinction selectivity increased support for non-Brownian models when analyzed using exclusively extant data that had ancestrally suffered a mass extinction (Fig 6, Supplementary Fig S5). For a single trait with no mass extinction, most simulations supported a

Brownian motion model (median 82%), with relatively few supporting Early Burst (3%) and OU (15%) models.

For simulations of *directional selectivity*, strong or strict selectivity yielded much lower support for Brownian motion (median strict 51%, strong 70%), and higher support for the OU model (strict 49%, strong 28%). When there was no selectivity on the trait value at the mass extinction boundary, the relative support for models was comparable to support for models in simulations with no mass extinctions (BM support, no selectivity 80%). Across all analyses that supported the OU model, the strength of selectivity α had a median half-life of 1.69 (within a range of values from 0.52 to 17.25). Similar patterns were seen in simulations with two traits compared to simulations with one trait.

With higher levels of background selectivity in the simulations with *disruptive selectivity* at mass extinctions, there was lower support for the OU model compared to BM. This was because there was a high turnover of lineages such that the ‘crown’ of these simulated phylogenies emerged after the mass extinction. When only those trees that had at least one ‘crown’ node *predating* the mass extinction were analyzed, the support for OU model was higher (Fig S6). *Disruptive selectivity,* in contrast to directional trait selectivity, resulted in higher support for an early burst model compared with the simulated Brownian motion process.

DISCUSSION

Few putative macroevolutionary rules withstand scrutiny (McShea 1998; Hone and Benton 2005; McShea and Brandon 2010; Benson et al. 2018). However, there do appear to be statistical generalities concerning the manner in which major clades evolve through time, with most groups achieving maximum or near maximal morphological disparity relatively early in their existence (Foote 1992a, 1994, 1996; Hughes et al. 2013; Oyston et al. 2015, 2016). The largest environmental crises often appear to disrupt this pattern, with those clades that go extinct coincident with a mass event typically being truncated and having maximum disparity much later in their evolutionary trajectories (Hughes et al. 2013). Despite these empirical observations, there are no null models for the manner in which we expect the disparity of clades to change through time, still less for clades truncated by or (as here) surviving such events with reduced diversity (Korn et al. 2013). Hence, simulations provide a powerful way of analyzing the role of mass extinctions in shaping disparity.

We acknowledge that there is no single, universally agreed index for disparity. Moreover, all empirical assessments of disparity are necessarily relative and constrained within the context of a particular set of descriptors or data set. We also note that disparity is indexed with reference to the constituent entities (species or other operational taxonomic units) within a group (e.g., subclade or time bin), with no reference to species or other entities outside of that group. As such, identical indices of disparity can be reported for clades occupying very different regions of morphospace, or for clades that migrate through that morphospace through time. Strikingly different distributions of points (local densities and clustering structures) can also yield identical disparity indices (Wills et al. 2012). Comparisons of diversity and disparity can nevertheless yield insights into the dynamics of evolutionary change (Foote 1991, 1993, 1994, 1997), while comparisons of a variety of disparity indices can be used to classify patterns of disparity change across mass extinction boundaries (Korn et al. 2013). There are many aspects of evolutionary dynamics (e.g., the directionality or otherwise of selectivity, modes of morphological evolution or speciation) that are more effectively tested and modelled directly rather than via the distributions of taxa in morphospace.

By definition, a mass extinction destroys standing diversity, but our results suggest that it need not always precipitate a fall in disparity (Foote 1991). Across a selective extinction the variance and range of morphological occupation typically decreases (Fig. 3); but the variance is mostly unchanged across a non-selective extinction, even though the range of values still decreases. The patterns of disparity change that we observe depend upon the indices that we use to quantify it, so these indices must therefore be codifying different things. Only the simulations with little deviation from trait-based extinctions show general, predictable patterns of extinction through time. However, when there is more variance around mass extinction selectivity (*weak selectivity*), the observed patterns are much closer to those seen when extinction is random in regard to trait values.

Patterns of disparity are more complicated than patterns of diversity. Here, we principally discuss patterns of directionally selective mass extinctions, but we note that disruptive selectivity can yield disparity increases across extinction boundaries (Fig S4). Many parameters complicate the pattern of disparity change across mass extinction events, including the number of analyzed traits, co-variance between traits, and the index of disparity (Fig 3; Fig S3). For example, when the co-variation between multiple traits is high (0.75), the observed patterns of disparity through time (Fig 4B) are similar to those observed with just one trait (Fig 4A). Thus, there is no single expectation of disparity change across a mass extinction for all clades and all events. Rather, we suggest that in order to understand patterns of disparity change across a mass extinction for a particular group, it is necessary to determine whether this pattern differs from those expected given a similar set of parameters. These expected patterns could be determined using simulations (Foote 1991; Harmon et al. 2003; Slater et al. 2010; Green et al. 2011; Korn et al. 2013). We do note, however, that even with simulation approaches it could be impossible to detect small-scale changes in selectivity at a large scale (Raup et al. 1973), especially in analyses with hundreds or thousands of traits.

Where we find decreases in disparity across mass extinction events, these are often non-linear (Fig 3). Clades evolve through an empirically realized (Stone 1997) or theoretically possible (Novack-Gottshall 2007) multidimensional trait morphospace via a process of branching cladogenesis that is inherently diffusive and with increasing degrees of freedom (McShea 1998). By contrast, random processes of lineage extinction cause a linear decline in diversity, but disparity is a function of the *distribution* of a group of entities, be this morphological range, variance or otherwise (Foote and Gould 1992; Wills et al. 1994; Wills 2001; Ruta et al. 2013; Bazzi et al. 2018). Hence after an extinction event, disparity is expected to decline non-linearly and more slowly than diversity (Foote 1991; Ruta et al. 2013). This expectation is generally echoed in our simulations (Fig 3), but the precise pattern is contingent on the index of disparity used.

Korn et al. (2013) demonstrated that it is possible to differentiate types of mass extinction selectivity by examining changes in morphospace occupation. For example, a random extinction that is non-selective with regards to lineage trait values leads to a minor decrease in the Sum Of Ranges, with no appreciable change in disparity indexed using the Sum Of Variances. For median pairwise distance and Sum Of Variances indices, a substantial decrease in disparity may be indicative of a directionally selective mass extinction. In some instances, these indices may not reflect a decrease in disparity or may reflect a change in the pattern of morphospace occupation (Ciampaglio et al. 2001). The Sum Of Ranges decreases with all types of extinction selectivity and so does not differentiate between selective and random extinctions as well as mean pairwise distance and Sum Of Variances. Because the Sum Of Ranges is sensitive to sample size effects (Foote 1991, 1992b; Butler et al. 2012) it may be an unsuitable index to capture patterns of disparity across a mass extinction event. However, some have argued this is unimportant when sample sizes are large (Simon et al. 2010), and that it can be adjusted using rarefaction approaches (Foote 1992b; Wills 1998a). Median pairwise distances and Sum Of Variances may be able to differentiate selective and non-selective extinction, but no one index of disparity will be sufficient to distinguish all aspects of evolutionary change (Ciampaglio et al. 2001). Moreover, we note that in studies with a higher number of traits than the five simulated here, it will be even more challenging to abstract generalities.

We have primarily investigated the patterns of a directionally selective extinction acting on one trait. Further studies could examine reductions in multi-variate shape space at extinction boundaries (Korn et al. 2013), by employing simulations of non-homogeneous patterns of tree and trait evolution, and patterns of discrete character trait change. Trait evolution in our models is simulated under Brownian motion, such that disparity levels tend to increase linearly through time, and, in the absence of extinction, disparity is higher than relative diversity in the early history of a clade (Figs 2). In the absence of selective extinction (Korn et al. 2013), clades are expected to have top-heavy disparity profiles in which disparity is higher later in time (Gould 1990; Hughes et al. 2013; Deline et al. 2018; Hill et al. 2018). This observations contrasts strikingly with the empirical observation that there is a significant but weak tendency for clades to have low diversity but high disparity relatively *early* in their evolution (Foote 1994; Hughes et al. 2013). In our simulations we employ homogeneous models of speciation and extinction, but alternative patterns are expected to arise from heterogeneous diversification rates through time. Additionally, simulations and evolutionary models can employ different relations between traits and extinction, such as modeling extinction as a logistic function of trait values (Slater et al. 2017).

Rapid speciation early in a clade's history is expected to result in disparity being higher between (rather than within) clades: this leads to a pattern in which average subclade disparity decreases towards the present (Harmon et al. 2003). However, the patterns we present are not directly comparable to Disparity-Through-Time (DTT) approaches as DTT methods calculate disparity at each point in time using all tip descendants of nodes in a phylogenetic tree (Harmon et al. 2003). Here we estimate disparity based on all of the branches present at a point in time, or we otherwise pool these samples into time bins.

A key question in paleobiology concerns whether mass extinctions selectively remove taxa based on their trait values or whether extinction is random with regards to traits. To this end, previous phylogenetic approaches to detecting extinction selectivity at mass extinctions have utilized pGLS models to test whether surviving and extinct lineages differ significantly in trait values

(Friedman 2009; Puttick et al. 2017; Allen et al. 2019). pGLS models are appropriate in this context to correct for non-independence of residuals in the regression as a result of shared phylogenetic history (Felsenstein 1985), but we show that pGLS models are not able to correctly support the hypothesis that trait values differ in extinct lineages compared to surviving lineage trait values (Fig 5). In contrast, non-phylogenetic Ordinary Least Squares analyses correctly support a significant difference between trait values in survivors and losers at a mass extinction boundary. The cost of Ordinary Least Squares approaches is that they have type-one error rates above 5%, so not using phylogenetic correction cannot be recommended (Felsenstein 1985). Thus, the lack of pGLS support for a selective extinction may not mean that the extinction was random but may reflect a type-two error. This may result from the strictly homogeneous pattern of evolution employed here, which may not reflect biological reality. However, the solution for this problem is unclear, as it is not straightforward to compare non-phylogenetic and phylogenetic modelling results (Freckleton 2009), and impossible to differentiate true signals from model error. One solution, albeit unsatisfactory, is to infer trait-selectivity by analyzing the phylogenetic signal in extinction, without considering traits directly. Previous research has indicated that it is possible to differentiate selectivity types using the phylogenetic signal of extinction (Hardy et al. 2012; Harnik et al. 2014; Krug and Patzkowsky 2015; Puttick et al. 2017; Soul and Friedman 2017). We support these observations because selective and non-selective extinctions have significantly different phylogenetic signals in our simulations (measured using the *phyloD* statistic), and because the amount of phylogenetic diversity lost during an extinction event is dramatically different for random and selective events. We note, however, that even low levels of random noise (25% extinction non-selective, *weak selectivity*) produces results much closer to a fully random extinction simulation rather than one with selectivity.

After recovery from mass extinctions, extant species trait distributions still carry the signature of trait-selective extinction. This selectivity of extinction towards specific morphologies leads to changes in the relative support of phylogenetic comparative methods away from the simulated Brownian motion model to support an Ornstein-Uhlenbeck process (Fig 6A,C). Selective mass extinctions remove the left hand of the trait distributions, so the variance of tip trait values is lower than expected under a Brownian motion model; this trait distribution then resembles the expected distribution under the Ornstein-Uhlenbeck process, so this model is supported (Fig 6E). At face value, this may appear to be a bias that does not support the simulation model (BM) over an erroneous alternative model (OU). If OU is interpreted as a measure of stabilizing selection (Hansen 1997), then support for this model is correct in the context of a selective mass extinction. Taxa in a selective extinction are removed as they possessed trait values that made them prone to extinction. The OU α value from the models here can be interpreted as measuring a discrete event of stabilizing selection (Butler and King 2004) or as an evolutionary optimum (Hansen 1997) that confers survival to a mass extinction event. In an analogous situation, a disruptive extinction event leads to a bi-modal distribution in which a distribution resembles an Early Burst pattern over alternative models (Fig 6b).

Conclusions

Our results indicate that patterns of disparity change across a mass extinction boundary are more complex than patterns of diversity change. As would be expected, disparity generally decreases following a selective extinction, but most indices show both increases and decreases in disparity across boundaries.

Understanding whether mass extinctions are selective or random with regards to traits is a major open question in paleobiology. Our results suggest that differentiating selective and non-selective extinction is difficult with phylogenetic comparative methods, but it is easier to identify phylogenetic signal in extinction itself. Mass extinctions also have long-term impacts on trait distributions and comparative models of trait evolution, even when traits evolve by a simple, time-homogeneous process.

All conclusions here assume that disparity may represent a real biological signal or a phenomenological description of patterns of trait evolution. Whatever trait disparity is measuring, we suggest that multiple indices are necessary in order to capture all aspects of disparity change across an extinction boundary, and a number of parameters need to be considered when inferring extinction disparity patterns.

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FIGURE LEGENDS

Fig 1. Workflow of simulation and analyses. In the simulations, trees and traits are simulated with time-homogeneous birth-death and Brownian motion processes (A). After 50, 100, 200 contemporary tips are present, a mass extinction removes 50, 75, or 90% of lineages (B). We analysed scenarios in which there is a *directional selectivity* so lineages with larger values above a cut-off are prone to extinction, and *disruptive selectivity* in which trait values closer to the mean are liable to extinction. Strict selectivity means only lineages within the cut-off go extinct, strong selectivity applies the same bias but with a non-zero probability of extinction for all lineages, and in a random extinction all lineages are equally susceptible to extinction. (B). For all simulations disparity is measured for traits using a number of indices (C), with summaries of the levels of diversity and disparity (D).

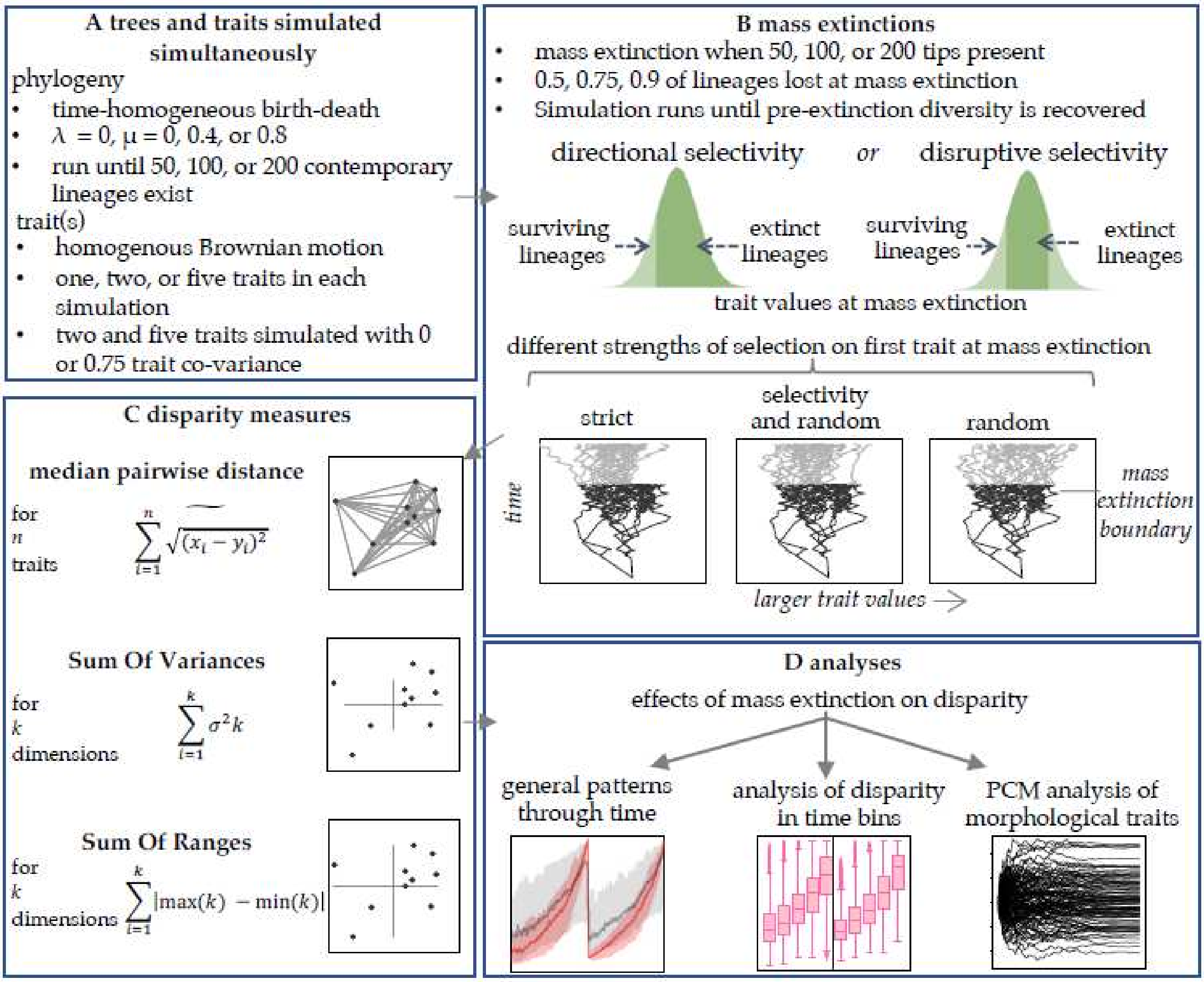


Fig 2. Summarises of relative and disparity through time in simulations with no mass extinctions for iterations run until 50, 100, and 200 contemporary tips are present. For each simulation time, disparity, and diversity measures are scaled to unity, and each line represents a single simulation. The relative disparity patterns through time from Sum Of Ranges are consistent across iterations, but the patterns from other metrics are more variable.

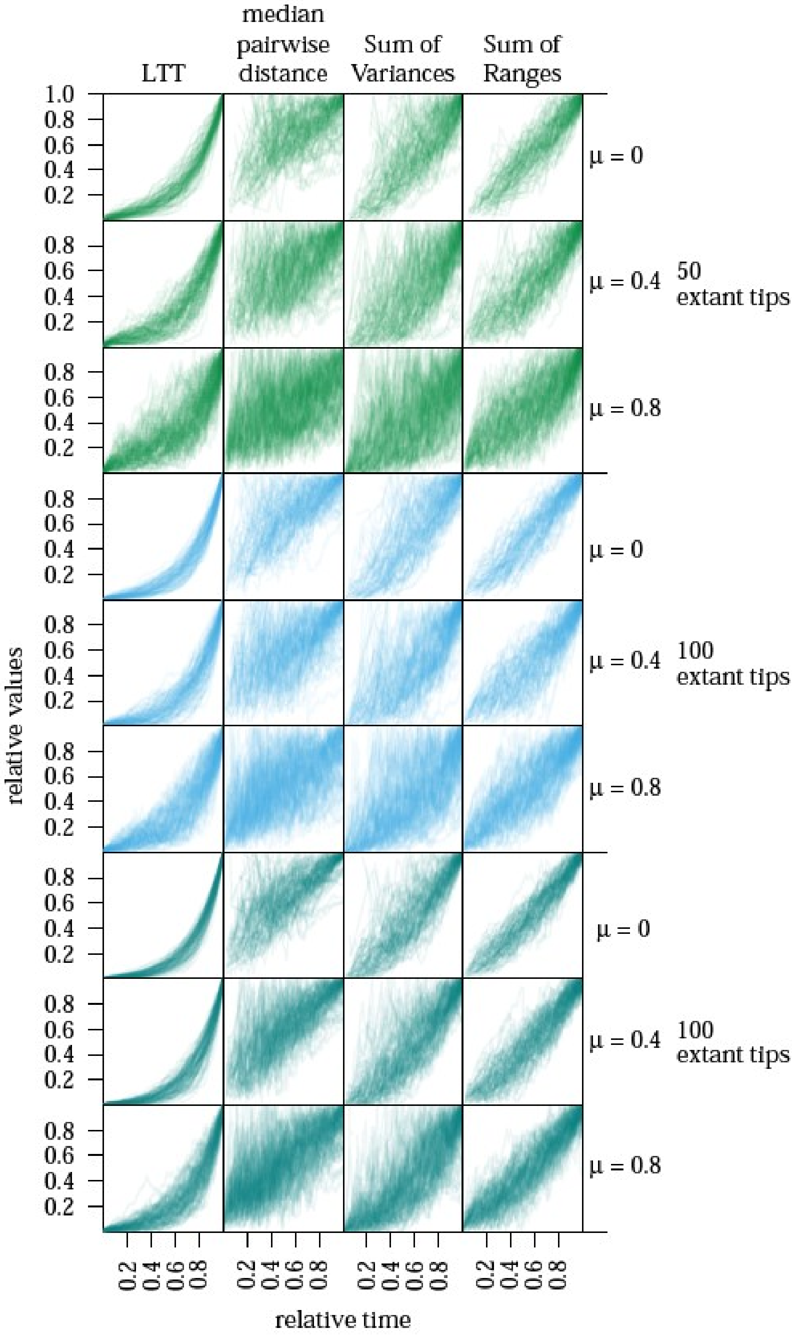


Fig 3. The relative difference between diversity (red lines) and disparity (grey lines) measured in simulations of one trait with 200 extant tips (background extinction 0.8). Results are scaled to show the extinction at the midpoint of each iteration that destroyed 0.5 or 0.9 of contemporary lineages; the median (dark line) and full range (shaded areas) of all iterations are summarised. Full all iterations the variance of disparity indices across all iterations is larger than the trends in diversity patterns. When extinctions are strict or strong diversity and disparity exhibit similar trends with large decreases following extinction, except when disparity is measured using median root distance. Non-selective extinctions do not generally lead to disparity decreases.

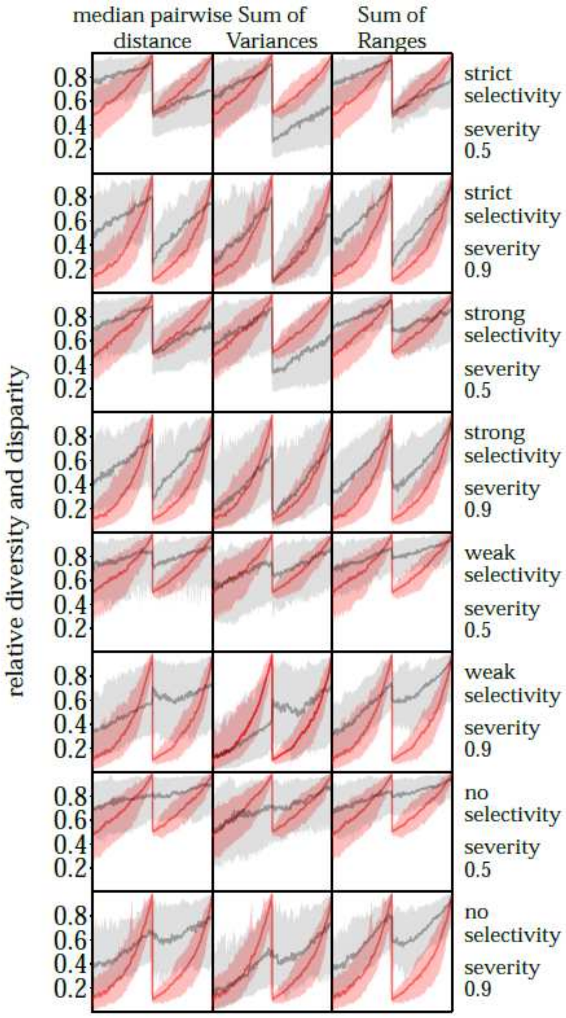


Fig 4. Relative change in disparity across a mass extinction boundary for simulations with one (A), two (B), and five (C) traits. The dark horizontal line at zero indicates a null model of no disparity change across an extinction, values below this line indicate a decrease in disparity, and values above indicate a disparity increase. The figures summarise data for all considered disparity indices, including the amount of lineage loss. For two (B) and five (C) traits the first, darker box shows the traits that evolved independently and the lighter, second box shows traits that were simulated with co-variance. Vertical shading denotes selectivity of trait values.

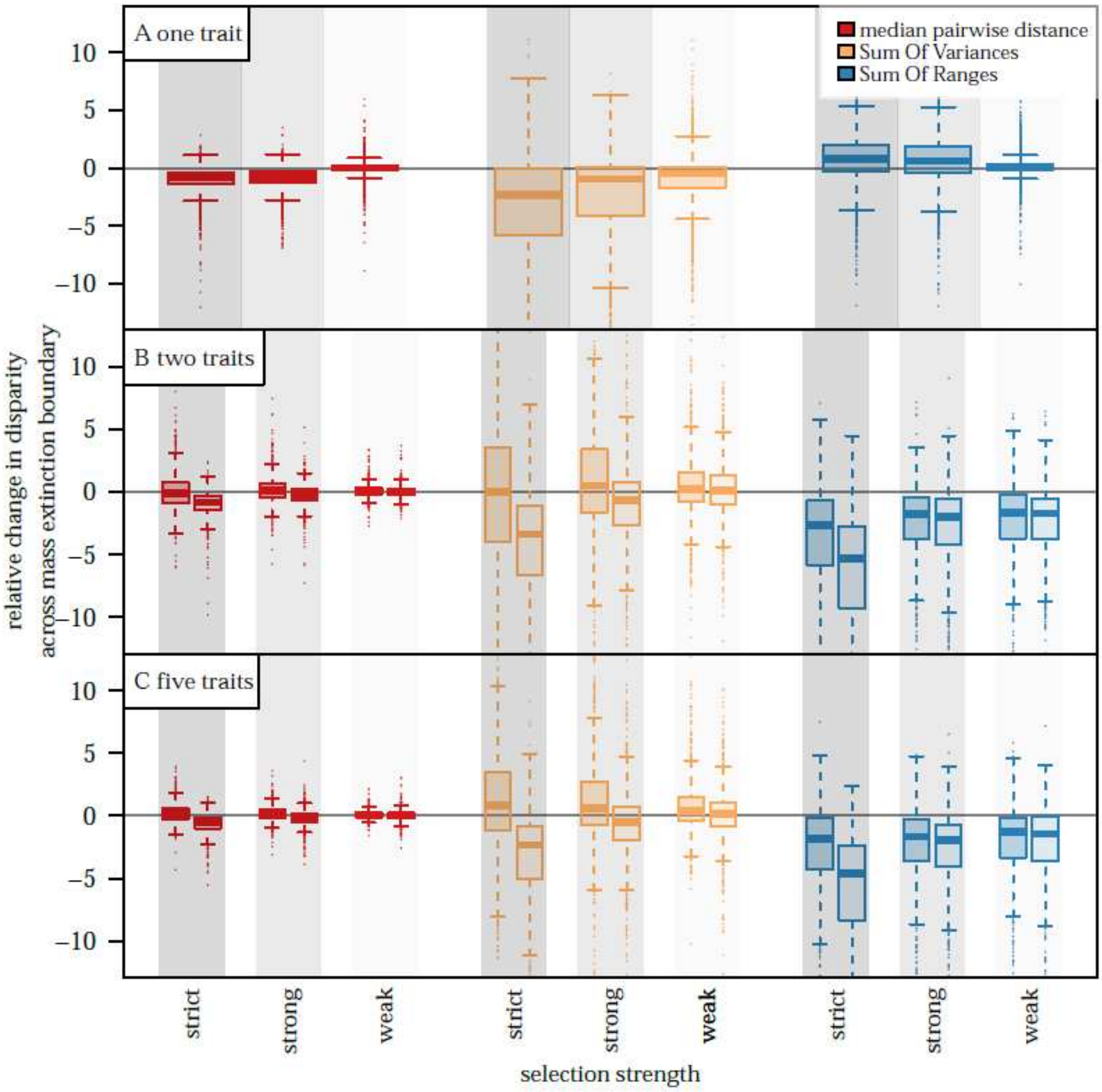


Fig 5. Summary of the number of pGLS (green) and OLS (pink) models that supported a significant relationship between the trait value and extinction for different selectivity levels and severity of extinction. For most simulations there was a true relationship between extinction and trait values (A-C) so it is expected the majority of models would support a significant relationship (gray shading). For the selectivity models (A-C) OLS models more consistently support a significant relationship compared to pGLS, and models perform more poorly as the number of lost lineages at a mass extinction increases. When extinction is random with regards to traits (D) most models should reject a relationship between trait values and extinction (i.e., below 5%, gray shading); OLS models generally have a high type-two error rate but pGLS models consistently and correctly reject a relationship.

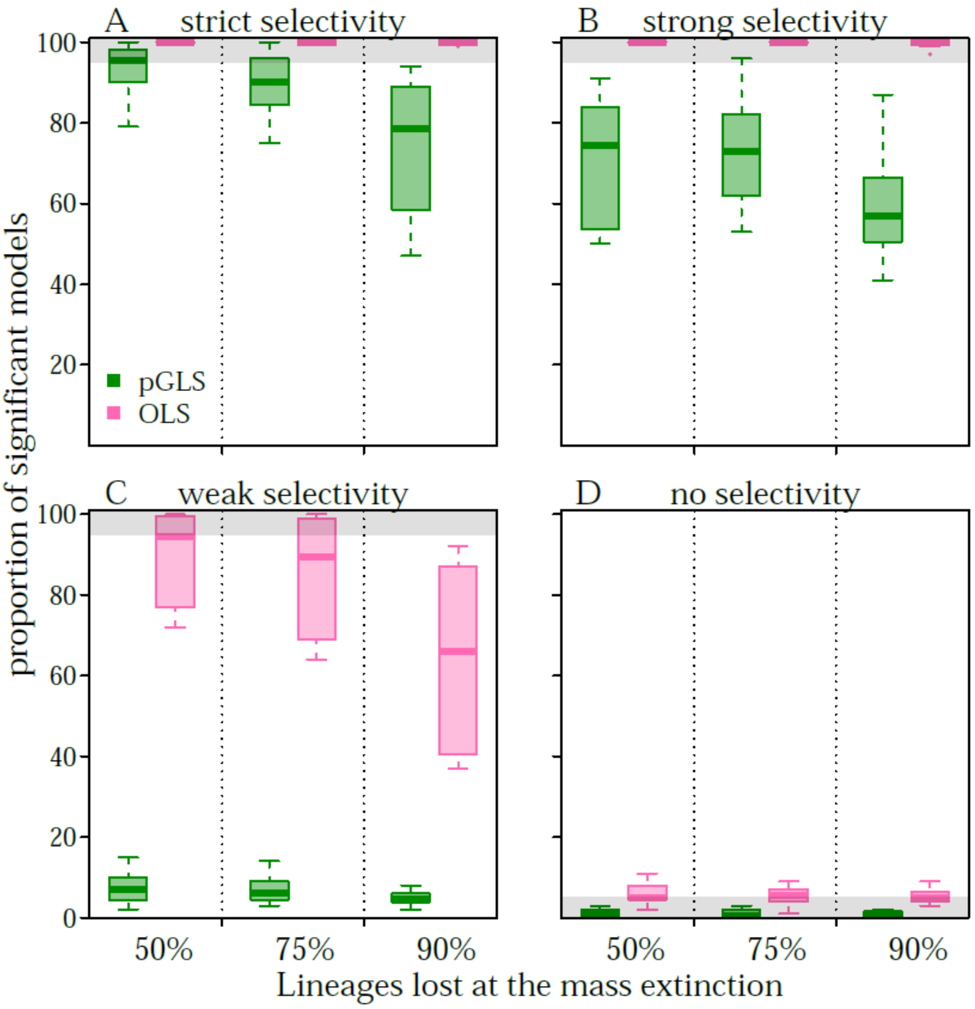
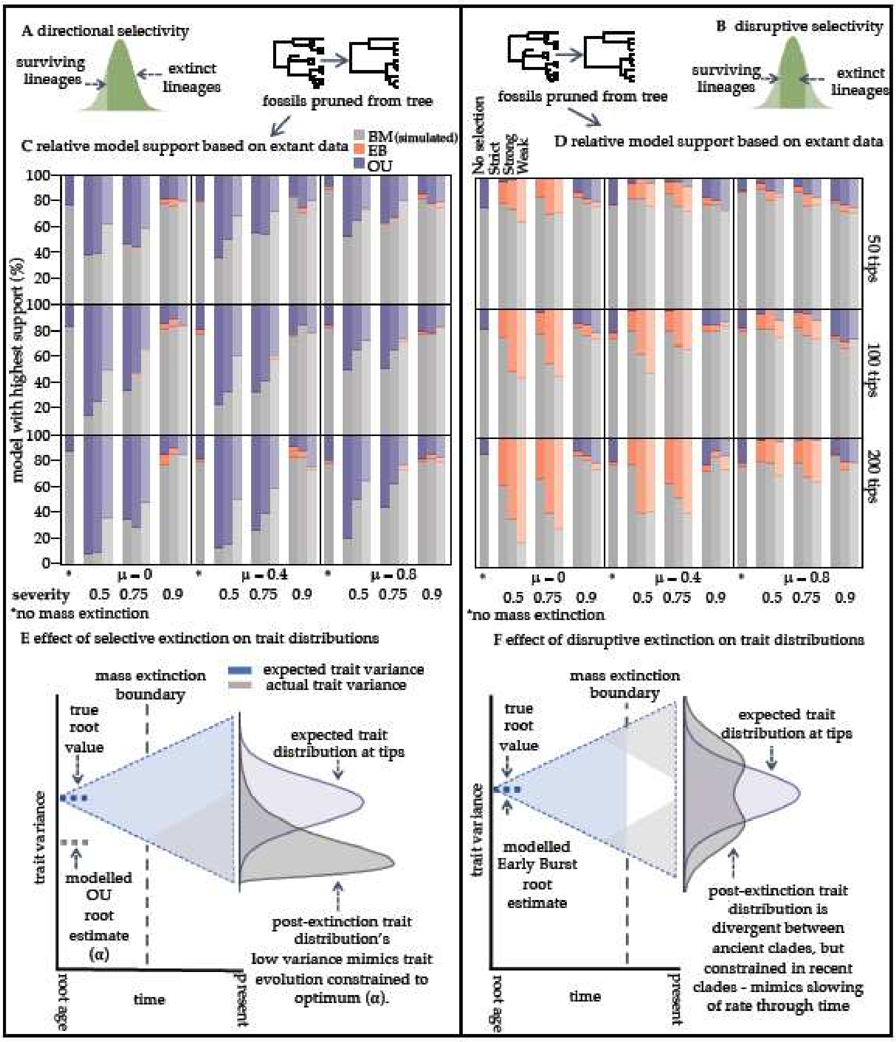


Fig 6. The effects of trait distribution and phylogenetic comparative models applied to extant lineages on a tree that when through a deep-time mass extinction. The results are summarised for a directional selectivity (A) in which selectivity is directed towards lineages with larger trait values and disruptive selectivity (B) in which extinction selectivity is directed towards lineages with trait values at the tails of the distribution. All data were simulated under homogeneous Brownian motion, but models applied to extant data only show higher support for the OU model when selectivity is directional (C) and support for the EB model when selectivity is disruptive (D). A directional selectivity leads to a trait distribution that resembles a distribution expected under an OU process (E), and a disruptive extinction resembles an EB-type distribution (F).



		selectivity strength		
(A) two traits	co-variance	strict	strong	none
median pairwise distance	0	50%	46%	42.3%
	0.75	88%	66%	47%
Sum of Variances	0	51%	44%	43%
	0.75	90%	63%	44%
Sum of Ranges	0	85%	80%	78.79%
	0.75	86%	65.5%	50%
(B) five traits		strict	strong	none
median pairwise distance	0	39.1%	40%	38%
	0.75	88%	62%	44%
Sum of Variances	0	37.11%	38.54 %	36%
	0.75	90%	58%	45.45%
Sum of Ranges	0	79%	78%	78%
	0.75	97%	84%	80%

Table 1. The number of iterations in which there is a decrease in disparity when data are binned into sixteen-time bins for simulations with two (a) and five (b) traits. The disparity for each index is summarised alongside the strength of selectivity for extinction and the trait co-variance.