

Does extinction wield an axe or pruning shears? How interactions between phylogeny and ecology affect patterns of extinction

Walton A. Green, Gene Hunt, Scott L. Wing, and William A. DiMichele

Abstract.—Extinctions are caused by environmental and ecological change but are recognized and measured in the fossil record by the disappearance of clades or lineages. If the ecological preferences of lineages or taxa are weakly congruent with their phylogenetic relationships, even large ecological perturbations are unlikely to drive major clades extinct because the factors that eliminate some species are unlikely to affect close relatives with different ecological preferences. In contrast, if phylogenetic relatedness and ecological preferences are congruent, then ecological perturbations can more easily cause extinctions of large clades. In order to quantify this effect, we used a computer model to simulate the diversification and extinction of clades based on ecological criteria. By varying the parameters of the model, we explored (1) the relationship between the extinction probability for a clade of a given size (number of terminals) and the overall intensity of extinction (the proportion of the terminals that go extinct), and (2) the congruence between ecological traits of the terminals and their phylogenetic relationships. Data from two extinctions (planktonic foraminifera at the Eocene/Oligocene boundary and vascular land plants at the Middle/Late Pennsylvanian boundary) show phylogenetic clustering of both ecological traits and extinction probability and demonstrate the interaction of these factors. The disappearance of large clades is observed in the fossil record, but our model suggests that it is very improbable without both high overall extinction intensities and high congruence between ecology and phylogeny.

Walton A. Green,* Gene Hunt, Scott L. Wing, and William A. DiMichele. Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Post Office Box 37012, MRC 121, Washington, D.C. 20013-7012. E-mail: wagreen@bricol.net

*Present address: Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts 02138

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*Comes the blind Fury with th'abhorred shears,
And slits the thin spun life.*

—Milton *Lycidas* 75f.

Introduction

Despite extensive study and debate (e.g., Raup 1972, 1991, 1993; Raup and Sepkoski 1982; Knoll 1984; Sepkoski 1993; Seilacher 1998; Purvis et al. 2000; Wing 2004; Jablonski 2001, 2004, 2005; Rabosky 2009) there remain questions about the importance of extinctions in the history of life compared with other factors like competition, integration, and evolutionary innovation. Because historical events are unique it is often difficult to establish a causal relationship between a particular extinction event and its ecological trigger. Of the “big five” mass extinctions identified by Raup and Sepkoski (1982) only one, at the Cretaceous/Paleogene boundary, has a generally accepted cause (Alvarez et al. 1980), and even its evolutionary consequences remain incompletely understood. For in-

stance, Wilf and Johnson (2004) describe an extinction of almost 60% of plant morphotypes in the terrestrial flora of North Dakota at the Cretaceous/Paleogene boundary. It is not clear, however, that this local species extinction is associated with loss of taxa above the level of genus at a continental scale (Green and Hickey 2005). Throughout this paper we use the term “extinction” broadly, to include local extirpations; the significance of any extinction can be appreciated only at a specific spatial, temporal, and taxonomic scale.

In order to avoid the problems of scale dependence and repeatability, in this paper we offer an approach based on computer modeling. Such models have the obvious disadvantage of lacking realism, but the compensating advantages of being scale-independent and easy to generalize and replicate. As is described below in depth, our model assumes a strictly dichotomizing tree of life whose twigs are organisms or

clades that live in an environment represented as a vector space defined by ecological variables (ecospace). We compare the output of this model to data from the fossil record of planktonic foraminifera at the Eocene/Oligocene (E/O) boundary and vascular land plants at the Middle/Late Pennsylvanian boundary, which following DiMichele and Phillips (1996) we will refer to as the Westphalian/Stephanian (W/S) boundary, despite difficulties precisely correlating the W/S boundary with the global timescale (DiMichele et al. 2009). Our model should be generalizable to any taxonomic group and to any scale of analysis, provided a strictly branching tree does a good job of summarizing historical relationships among taxa.

Typically, the intensity of an extinction is measured as the proportion of described species or higher taxa that disappear in a particular time interval (or metrics derived from similar quantities; see Foote 2000). There are no standard criteria for determining when a mass extinction rises above background levels, but the “big five” mass extinctions were originally identified exclusively by their intensities at the family rank (the proportion of marine families that went extinct in a geological stage) and are generally accepted as influential in the marine realm (Raup and Sepkoski 1982). In contrast, global compilations of the stratigraphic ranges of fossil plants do not show sharp declines in diversity like those defining the largest extinctions in the animal fossil record (Niklas et al. 1980, 1985; Niklas and Tiffney 1994). The apparent absence of mass extinctions in plants has been attributed to the resistance of plant individuals and populations to environmental shocks—individuals can regrow from buried storage organs after major tissue loss, and populations can survive bad conditions as spores or seeds in the soil (Knoll 1984). If the absence of global mass extinctions in plants reflects the resistance of individuals and populations to perturbations, then low extinction levels should also be observed in local, high-resolution studies. When the record is examined at the temporal scale of local stratigraphic sections and the geographic scale of a sedimentary basin, however, more

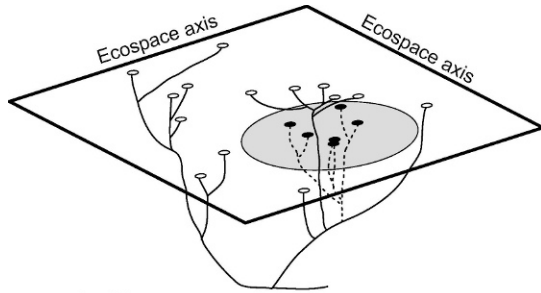
than half the described species or morphotypes sometimes disappear at a boundary (e.g., Looy et al. 2001; Wilf and Johnson 2004; McElwain et al. 2007, 2009).

The apparent conflict between high extinction levels at local to regional geographic scales and low extinction levels globally, or extinctions in some groups but not in others, can be resolved if the probability of a species going extinct is uncorrelated with its membership in higher groups (Wing 2004). Hierarchically higher groups can persist even when most of the species in them go extinct. Extinctions would then be seen only in taxonomically detailed studies of local sections, because on larger temporal, spatial, and taxonomic scales the extinction would be masked by the rapid appearance during the recovery of new species similar to or even indistinguishable from the old ones (Wing 2004).

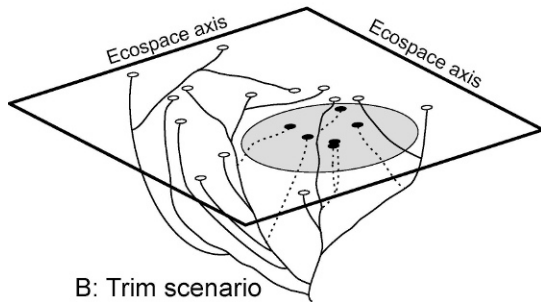
In this paper, we try to determine the effect of an extinction on lineages that vary in the degree to which their phylogeny is congruent with their ecology. Many studies (e.g., McKinney 1995; DiMichele et al. 2001; Prinzing et al. 2001; Crisp et al. 2009) have pointed out that clades often show ecological preferences or “centroids” in ecospace that inhere through time. To the best of our knowledge, however, there have been no attempts to relate ecology-phylogeny congruence to extinction dynamics quantitatively.

Figure 1 illustrates the two extreme scenarios, which we are calling the *chop* and the *trim* situations. In chop extinctions (Fig. 1A) closely related species are clustered in ecospace, and ecologically selective extinctions remove large branches from the phylogenetic tree. In trim extinctions (Fig. 1B) closely related species are ecologically dissimilar and extinctions are therefore dispersed across the phylogenetic tree.

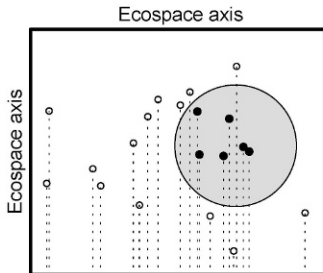
The models described in the following section are intended to quantify the importance of the chop and trim scenarios in determining the phylogenetic effect of an extinction event that drives a particular proportion of species extinct. (Note that the terms “terminal” and “species” are used interchangeably without implying that the



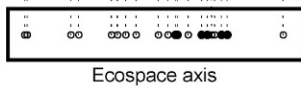
A: Chop scenario
one clade with six terminals goes extinct



B: Trim scenario
one clade with two terminals and
four clades with one terminal go extinct



C: Extinction in two ecodimensions



D: Extinction in one ecodimension

FIGURE 1. Schematic relationships between phylogeny and ecology at an extinction. All scenarios have the same distribution of terminal taxa in ecospace. A, High congruence between ecology and phylogeny; extinctions *chop* off major branches of the phylogeny because related species tend to occupy similar niches. B, Low congruence between ecology and phylogeny; extinctions *trim* only small clades because close relatives occupy niches that are unlikely to be affected by the same environmental changes. C, The extinction viewed in two-dimensional ecospace at the time of the extinction. D, The same extinction event projected onto a single ecological dimension.

terminals of a phylogenetic tree have to represent biological species.) In this paper, we ask if extinctions have different effects when individual clades are broadly distributed ecologically as opposed to being clustered in ecospace. How important are phylogenetic relationships in determining survival of lineages in ecologically targeted extinctions?

After describing the sensitivity of our model to various parameters, we examine two case studies: the extinction of planktonic foraminifera at the Eocene/Oligocene boundary and the extinction of vascular plants at the Westphalian/Stephanian boundary. In both cases extinction propensity appears to be phylogenetically clustered, as are some measured traits. This finding has wider implications both for our evaluation of the significance of extinction events in the past and potentially for helping to minimize long-term consequences of current anthropogenic extinctions.

Methods

Modeling

In the basic model used in this paper, we construct a random phylogenetic tree of a given size using a pure birth model (function *birthdeath.tree* in the R package *geiger*; Harmon et al. 2008). We then apply one or more ecological variables (drawn from a centered multivariate normal distribution) to the tips of this tree to give a specified congruence between the ecological measure and the relationships shown by the tree. This congruence of ecology with phylogeny is measured by Pagel's λ (Pagel 1997, 1999; Freckleton et al. 2002), a parameter that transforms a phylogenetic tree as follows. The transformation is performed on a tree's phylogenetic variance-covariance matrix, which represents the statistical dependence among tips of a phylogenetic hypothesis (Fig. 2). Entries in the phylogenetic variance-covariance matrix on the main diagonal represent the distance between each terminal and the root of the tree, and off-diagonal elements represent the shared path-length for each pair of tips (i.e., the distance between their most recent common ancestor and the root of the tree). These

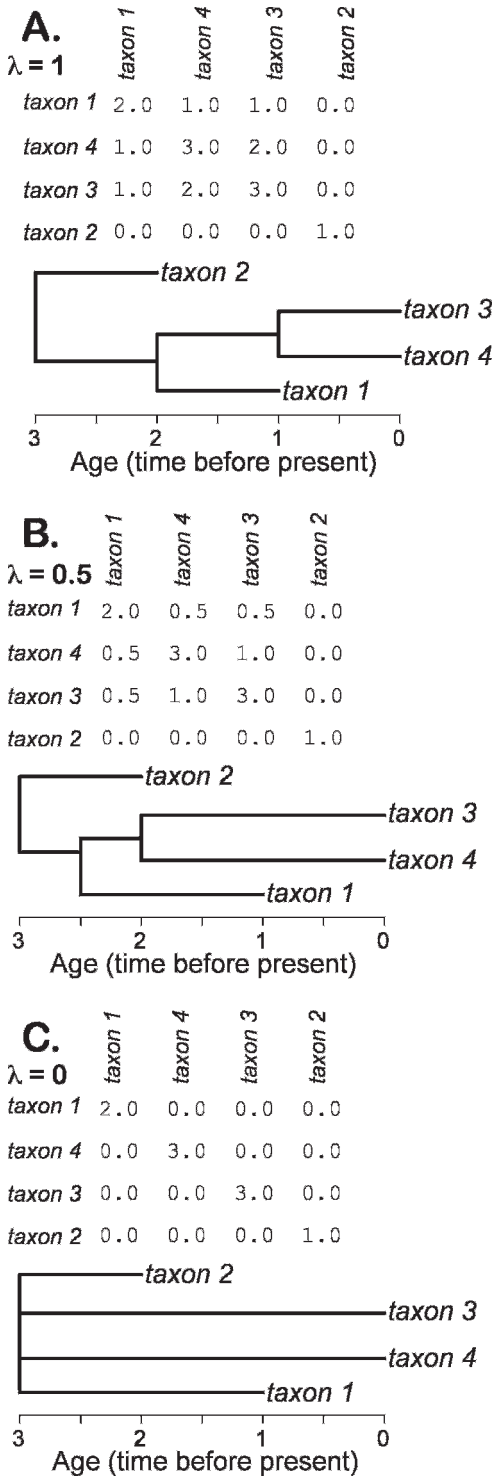


FIGURE 2. Schematic examples of a tree, transformed with different values of λ and the resulting variance-covariance matrices. A, $\lambda = 1.0$. B, $\lambda = 0.5$. C, $\lambda = 0.0$.

entries are in the same units as the branch lengths of the tree, usually time or a proxy thereof. This matrix is called a variance-covariance matrix because traits evolving according to a random walk model are multivariate normal, with variances and covariances among tips given by this matrix multiplied by the rate parameter (Pagel 1999; Freckleton et al. 2002). For a particular topology, the λ transformation multiplies off-diagonal elements of the phylogenetic variance-covariance matrix by λ , where λ ranges from zero to one. Low values of λ shorten internal tree branches, resulting in a tree with proportionately more evolutionary history in the terminal branches and less history shared among taxa. When λ equals zero, internal branches disappear, leaving a star phylogeny, in which case there is no phylogenetic structure to traits and their evolution (Fig. 2). A tree with λ equal to 1 is unaltered by this transformation.

If we evolve traits as random walks (Brownian motion) on these transformed trees, the resulting traits will have high phylogenetic congruence when λ is near 1, and low congruence when λ is close to zero. It is mathematically possible for λ to exceed one, but such values are not readily interpreted, and commonly only values between zero and one are considered (Freckleton et al. 2002).

In addition to its phylogenetic location, each terminal on the tree also has a location in ecospace whose dimensions are biotic or abiotic variables along which an environment can vary (this is a fundamental niche in ecospace, sensu Hutchinson 1978: p.159). Note that the ecological variables represented by the dimensions of our ecospace need not represent single traits, but can be composite axes of variation, like principal components, which come from a rotation and rescaling of an empirical ecospace of higher dimensionality.

Modeled extinctions are deterministic (non-probabilistic), are centered in ecospace on the location of a randomly chosen terminal, and affect all taxa within a given radius of the extinction center. The intensity of extinction is determined by the proportion of tree termi-

nals that go extinct. So for a tree with number of terminals nt and extinction intensity x_{ti} , one terminal is chosen at random to go extinct and then the $nt \times x_{ti}$ other terminals closest in ecospace also go extinct. The measure of ecological proximity is the euclidean distance, which simplifies to the scalar distance (difference) in the one-dimensional case.

The model also allows an ecospace of any number of dimensions. For example, if the single ecological axis is soil wetness, and the extinction is centered at the wet end of the spectrum, this may represent climatic drying in which species requiring wet substrates will go extinct, whereas species preferring drier soils go unaffected. A two-dimensional case might add the effect of soil fertility, so that the extinction is centered in habitats that have high soil moisture and low fertility, preferentially affecting plants of oligotrophic wetlands. As demonstrated in Figure 1C,D, the same schematic extinction may be viewed in two dimensions or projected onto a single axis of variation.

The following are parameters of the model that can be independently varied: the number of tree terminals, nt ; the intensity of extinction (proportion of terminals that go extinct), x_{ti} ; the congruence of the ecological signal with phylogeny, λ ; the ecological dimensionality, $dims$; and the number of replicates or different random tree topologies, n . We measure the response to these simulated extinction events by recording the mean size of extinct clades and the proportion of surviving clades of a given size, s , that go extinct. After extinction, we identify the number and size of clades that are entirely eliminated by this extinction of terminals and are not subclades of larger clades that also go extinct. All programming is done in R (R Development Core Team 2008) and the scripts and results of model runs are available as supplementary data (<http://dx.doi.org/10.1666/09078.s1> and <http://dx.doi.org/10.1666/09078.s2>).

The mean size of extinct clades is calculated from the distribution of extinct clade sizes, which is heavily right-skewed. In most cases, more than half the extinct clades are singletons, so the median extinct clade size is seldom larger than 1. The mean extinct clade

size is also a problematic response variable because it is heavily dependent on the largest clade to go extinct. Hence in addition to showing the variation in mean clade size (Fig. 3), we also illustrate the proportion of clades of a given size that go extinct (Fig. 4). This probability of extinction of a clade with a particular number of terminals seems to be more informative about extinction effects, though when necessary we rely on the mean extinct clade size as a point estimate for extinct clade size.

Case Studies

In addition to exploring the sensitivity of the model to variation in its parameters, we compare its output with two real extinctions for which the phylogenetic, stratigraphic, and ecological data needed to test the model are available. We found relatively few extinctions for which all three types of data had been recorded at the species level. Our conclusions are naturally dependent on the data being reanalyzed, but small errors (for instance of taxonomic lumping or splitting) inherited from the cited sources should affect our results only incrementally without biasing our overall conclusions.

Eocene/Oligocene Planktonic Foraminifera.—The E/O boundary marks a significant turnover in planktonic foraminifer assemblages, including the extinction of an entire family, the Hantkeninidae (Pearson et al. 2008). Extinctions in these and other taxa are linked to changes in ocean circulation and climatic cooling (Wade and Pearson 2008). In our analyses, we consider the extinction of all species of planktonic foraminifera extant during the last biozone of the Eocene (E16, duration ~ 600 Kyr). We scored species as victims if they did not survive into the Oligocene according to range charts in Pearson et al. (2006), updated to reflect the recently reported range extension of *Subbotina hagni* into the Oligocene (Wade and Pearson 2008). Because the survivorship of *Acarinina echinata* through this interval is questionable, this species was omitted from the analysis.

A species-level phylogenetic tree was assembled for species extant in the last interval of the Eocene using the phylogenetic hypoth-

eses of Pearson et al. (2006), supplemented where necessary by inferred relationships among Paleocene taxa (Olsson et al. 1999). Branch lengths were set according to the divergence dates reported in these references. In a few cases, there was reported uncertainty in some of the inferred relationships. For purposes of analysis, the following relationships were assumed: *Dentoglobigerina* was considered to descend from the acarininids; the clade composed of *Chilguembelina* + *Streptochilus* was considered to descend from the Cretaceous/Paleogene survivor *Guembeltia* via the intermediate *Woodringina*; and *Cassigerinella* + *Tenuitella* was interpreted as having descended from an independent evolution of the planktonic habit from a benthic ancestor. The divergence date of this last group is not known, but was set to be mid-Jurassic, which is the interval in which planktonic foraminifera first appear in the fossil record.

Body sizes were taken from Pearson et al. (2006), who list maximum dimensions, usually for type specimens. When sizes were reported as ranges, the range midpoint was used. Any bias introduced by using the mid-range as a point estimate of a distribution of body sizes should be small relative to the six-fold range of body sizes recorded (0.11–0.69 mm), uncorrelated with phylogeny, and have the effect of reducing somewhat the concordance between body size similarity and phylogenetic relatedness. Because body size evolution is generally best considered on a proportional rather than absolute scale (Foote 1991), size measures were log-transformed before analysis.

Westphalian/Stephanian Vascular Plants.—The W/S boundary (Middle/Late Pennsylvanian transition) marks a change in the composition and diversity of lowland wetland vegetation in North America and Europe, particularly in peat-forming environments (Phillips et al. 1974; Peppers 1996; DiMichele and Phillips 1996). Middle Pennsylvanian peat swamps were dominated by large lycopsids (*Lepidophloios*, *Diaphorodendron*, *Synchysidendron*, *Paralycopodites*, *Sigillaria*) with subdominant tree ferns and pteridosperms. These assemblages were even-

tually replaced by communities dominated by tree ferns and pteridosperms, with a much reduced array of locally abundant lycopsid trees (mainly *Sigillaria*) and smaller lycopsids (*Chaloneria*). Similar patterns are found in clastic adpression floras (Pfefferkorn and Thomson 1982; Blake et al. 1999; Dimitrova et al. 2005; Dimitrova and Cleal 2007). In both settings, tree ferns began to rise in importance before the W/S boundary.

The data used in this paper come from coal balls, masses of permineralized peat found in coal beds that preserve the original vegetation of the peat swamp (DeMaris 2000). Coal balls were collected from coals of both late Middle Pennsylvanian and early Late Pennsylvanian age, an interval of several million years; methods of collection and quantification are described by Phillips et al. (1977).

Of the 85 taxa identified in Westphalian and Stephanian coals, 54 were observed in the latest zone of the Westphalian (Westphalian D), of which 35 went extinct at the W/S boundary. There are no published phylogenies of Pennsylvanian plants resolved to the level of detail needed for this study. Therefore, a phylogeny was constructed by combining published phylogenies or schemes of evolutionary descent with various degrees of resolution into a basic phylogenetic framework for the major plant groups. The intent was to create a phylogeny not for all known Carboniferous wetland plants, but only for those taxa present in the study interval. For many of these groups, whole plants are not known. In those instances, one organ was used as proxy for the parent plant (e.g., seeds for pteridosperms). The most reliable sources are reconstructed whole-plant phylogenies (e.g., representative tree lycopsids [Bateman et al. 1992]; marattialean tree ferns [Lesniakowska 1989]; cordaitaleans [Trivett 1992; Costanza 1985]). In groups where only a few whole plants have been reconstructed, whole-plant attributes were inferred from organ phylogenies (e.g., medullosan pteridosperms based on seeds [Taylor 1965]). In other instances, a phylogeny was compiled from one or more partial phylogenies based on single organs used as proxies for the whole plant (e.g., inclusion of *Albertlongia incostata*,

Taylor 1967, in the larger phylogeny of *Pachytesta*, Taylor 1965). Relationships were based on published interpretations of species or genera within various clades and among related clades (e.g., filicalean ferns [Phillips 1974; Rothwell 1991; Galtier and Phillips 1996; Phillips and Galtier 2005]). Finally, relationships were sometimes inferred from a combination of stratigraphic and morphological data, in the absence of a relationship scheme (e.g., *Heterangium* [Pigg et al. 1987]). Our phylogeny includes a few taxa for which placement was highly uncertain (e.g., *Stellastellara*: DiMichele and Phillips, 1979), but in no case was without some rationale. Because of the large number of papers and variety of data that had to be synthesized in this process, full documentation is not possible, but no taxon was included without consultation of a published phylogeny, a published discussion of its possible evolutionary relationships, or a published description of its morphology adequate to support reasonable speculation about its relationships.

After arranging the 54 taxa present in the latest Westphalian in a phylogenetic tree, we constrained the branch lengths of the phylogeny by known stratigraphic ranges where possible, and recorded two morphological variables of ecological importance for each terminal: disseminule size (megaspore or seed volume in cubic millimeters, log-transformed for analysis) and growth form (scored semiquantitatively as herb, shrub, small tree, large tree). Both stature and disseminule size are considered to be related to plant ecological strategies. Plant stature relates to overall adult body size, which is correlated with environmental features like site stability and resource availability, as well as the ability to compete with other plants for light (Grime 2002). The ecological significance of disseminule size is strongly correlated with dispersal mode and the light environment of seedling establishment, among other factors (Moles et al. 2005). Seed size and adult height are two of the three dimensions proposed by Westoby (1998) for a comprehensive description of plant ecological strategy space. Homosporous plants lacking macroscopic disseminules were assigned a small arbitrary disseminule

size (equal to 90% of the size of the smallest macrospore size), and stem or foliage taxa whose associated disseminules are not known were scored as missing data.

Analysis.—For each case study, we measured the phylogenetic signal in each ecological variable using Pagel's λ (estimated with the function *fitContinuous* in the R package *geiger* [Harmon et al. 2008]). For comparison, we also assessed phylogenetic signal using Blomberg's *K* statistic (Blomberg and Garland 2002; Blomberg et al. 2003), using the functions *phylosignal* and *Kcalc* in the R package *picante* (Kembel et al. 2008). λ and *K* as well as other descriptive statistics are given for both groups in Table 1. The metrics λ and *K* are designed to measure phylogenetic signal in continuously varying characters like disseminule or body size. As such, they cannot be used directly to measure the phylogenetic signal in discrete traits like extinction. Although lineage extinction is clearly a binary outcome, it can reasonably be related to an underlying probability or susceptibility to extinction, which can be seen as varying continuously, like the threshold model for quantitative phenotypic traits (Felsenstein 2005).

Thus, if we treat "extinction susceptibility" as a continuous variable that is characteristic of a clade, we can estimate its λ using simulations similar to those described earlier but run with constraints, using the known phylogenies of the groups and observed extinction intensities as data (0.37 = 17 extinctions among 46 foraminifer species; 0.65 = 35 extinctions among 54 vascular plant species). For a wide range of λ transformations of the tree, we simulated the evolution of extinction susceptibility according to a random walk model. Assuming that the species with the highest susceptibilities were the ones that went extinct, we recorded the simulated distribution of extinct clade sizes in each simulated run and computed the proportion of runs in which the simulated distribution exactly matched the observed distribution of extinct clade sizes (see Table 1). For instance, in the E/O case study, we run our model with a 46-terminal tree and extinction intensity equal to 0.37 (the values

TABLE 1. Range estimates for values are given in parentheses: for x_{ti} , ± 1 binomial standard deviation, and for λ , ± 1 log likelihood unit. Estimated mean extinct clade size is produced by runs of our model with parameters set to their observed values.

	E/O Forams	E/O Forams	W/S Plants	W/S Plants	W/S Plants
Number of terminals (nt)	46		54		
Extinction intensity (x_{ti})	0.37 (0.30,0.44)		0.65 (0.58,0.71)		
Extinct clade sizes	7,3,1,1,1,1,1,1		10,8,3,2,2,1,1,1,1,1,1,1,1,1		
Observed mean extinct clade size	1.89		2.34		
Mean extinct clade size, $\lambda = 0$	1.21 (1.1,1.3)		1.47 (1.3,1.6)		
Ecological character	size*	extinction susceptibility	stature	seed size†	extinction susceptibility
Blomberg's K	0.38		0.89	0.54	
Pagel's λ	0.97	0.97 (0.78,1)	1	0.99	0.7 (0.3,1)
Estimated mean extinct clade size	1.94		3.01	2.91	

* Maximum dimension in mm.

† Volume in mm³.

obtained from the observed foraminifer data). By simulating many trees at different values of λ and recording how frequently the observed pattern of extinctions occurs (one clade with seven species, one clade with three species, and seven clades composed of a single species each), we can generate a likelihood curve for λ —a plot of the probability of observing particular data values, given a model. Values of λ are favored to the extent that they commonly produce the observed data in the form of the distribution of extinct clade sizes. The maximum of this plotted curve is then the maximum likelihood estimate for λ .

Our approach to estimating λ for extinction susceptibility uses simulation to approximate the likelihood function because no direct analytical solution is available. Logistic regression is often used to estimate the relationship between continuous factors and the binary state of survival/extinction (e.g., Payne and Finnegan 2007; Finnegan et al. 2008; Wang and Bush 2008), but this approach assumes that taxon values are independent, and therefore it cannot be used to assess the amount of phylogenetic signal, which is a measure of the statistical dependence among values assigned to the terminals of a tree. General estimating equations have been applied to account for these dependencies in the analysis of discrete traits (Paradis and Claude 2002),

but this approach does not rely on a likelihood foundation, and so λ cannot be estimated using a maximum likelihood approach. In the future, suitable modification of the general estimating equation approach may allow a more direct analytical estimation of λ .

Results

Modeling

The basic model response is shown in Figure 3A,D as a landscape in which elevation (shading) represents the mean size of extinct clades. It can be seen that extinct clade size increases both with species-level extinction rate and with higher phylogenetic congruence of the ecological traits. Note that large clades seldom go extinct except when both species-level extinction and phylogenetic congruence of the ecological traits are high. With a 1000-terminal tree, $\lambda = 0.9$ (phylogenetically clustered ecological preferences), and $x_{ti} = 0.9$ (900 of the 1000 species go extinct), the mean extinct clade size is still smaller than seven terminals per extinct clade.

Because the mean extinct clade size is very sensitive to the high outliers in a right-skewed distribution of extinct clade sizes, we also show probabilities of taxa of given sizes going extinct (Fig. 4). The top panel of Figure 4 shows the probability of going extinct for clades of size 1. Because the extinction of a single species does not depend on the fates of

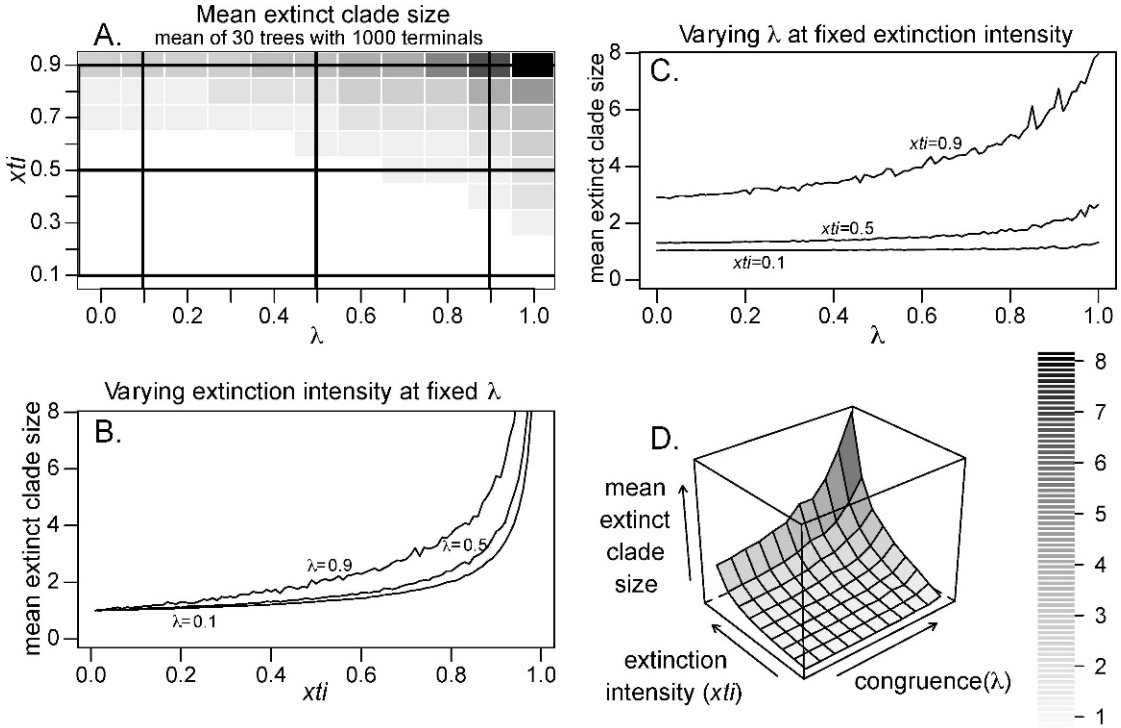


FIGURE 3. λ -extinction intensity landscape. A and D show the same data (a 9×11 pixel landscape in which the elevation or gray scale shows the mean extinct clade size for a given λ and extinction intensity). B and C are higher resolution transects showing three profiles of the same landscape from each margin.

other lineages, it is completely insensitive to λ . As the size of clades increases, moving down through Figure 4, we see an increased dependence on λ . This substantiates the well-known observation (Raup and Sepkoski 1982; Sepkoski 1993; Janevski and Baumiller 2009) that extinctions look less severe at higher taxonomic levels. An extinction that eliminates a given proportion of families will eliminate a higher proportion of genera and even higher proportion of species.

The probability of a clade of a given size going extinct must of course also depend on the total number of species available. If there were only 1000 species in existence, then the probability of 1001 going extinct would be zero, independent of extinction intensity. Empirically, however, this effect only seems to affect the mean extinct clade size at high λ (Fig. 5). With realistic extinction intensities and values of λ below 0.9, the probability of a large clade going extinct is virtually constant above an absolute tree size of about 1000 taxa.

Even with $\lambda = 1$, the effect of overall tree size on extinct clade size is weak (Fig. 5).

Another factor that might influence the mean size of extinct clades is ecological dimensionality. Ecospace (or ecological strategy spaces or morphospaces) are often defined in many dimensions, with an axis for each measurable ecological attribute, which can include measures of biogeographic distribution or climatic tolerance. These are often then reduced to a smaller number of axes that are thought to capture the major features of ecological diversity (Bambach 1983; Westoby 1998; Grime 2002). As can be seen from Figure 6, extinct clade size is independent of the number of ecological dimensions used in our simulations over a wide range of λ and x_{ti} .

Because the ecospace offers only a simplified model of a biological community, it is difficult to interpret this as support for the idea that extinction risk is independent of niche differentiation. In our model, however,

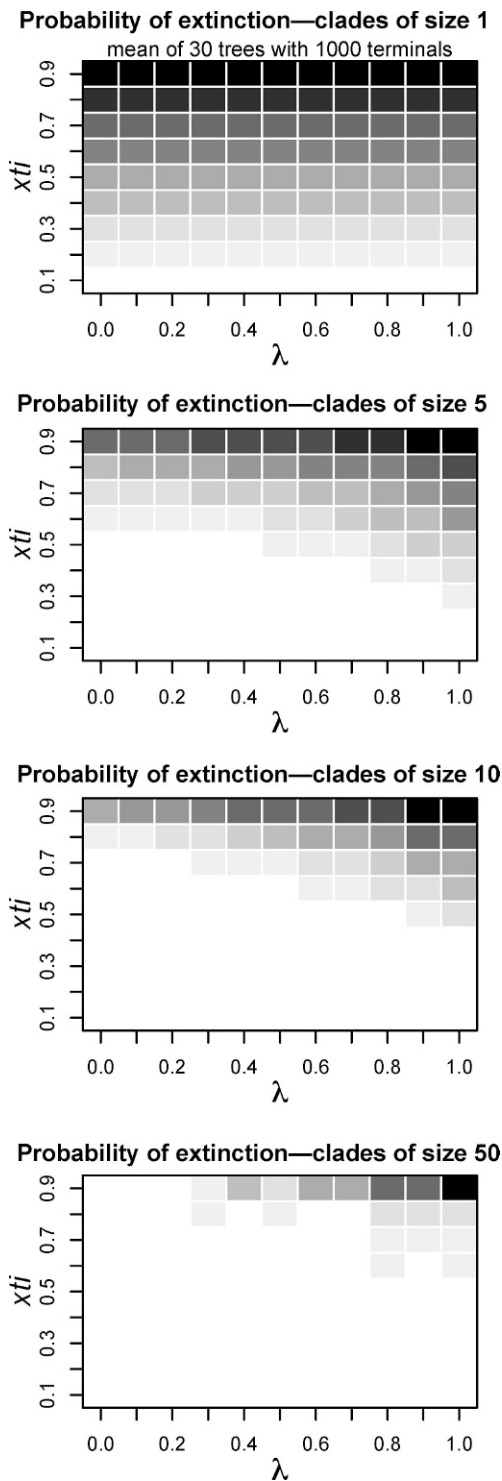


FIGURE 4. Each panel represents a landscape of extinction probabilities like the landscape of mean extinct clade sizes in Figure 3A. The clade size considered increases down through the four panels, showing how the sensitivity to λ increases as the clade size considered

it is clear that the dimensionality of the modeled ecospace does not affect the way that ecological congruence interacts with extinction intensity to determine the sizes of extinct clades.

Case Studies

Figure 7 gives curves showing the proportions of model runs in which the observed pattern of extinctions was observed for each case study. Because these curves are analogous to log-likelihood functions, the modes of the curves can be interpreted as maximum likelihood estimates of the parameter λ for the hypothetical continuous variable measuring extinction susceptibility of a clade.

The statistics describing each case study are given in Table 1. Blomberg's K and Pagel's λ both indicate high levels of phylogenetic signal in foraminifer body size, plant stature, and plant disseminule size.

The inferred phylogenetic relationships among end-Eocene foraminifera lineages are shown in Figure 8. Although it is not entirely determined by phylogeny, body size is mostly consistent among close relatives. There are relatively small-bodied clades such as *Tenuitella* + *Cassigerinella*, and *Pseudohastigerina*, and large-bodied clades such as the hantkeninids. The maximum likelihood estimate of λ for body size is quite high ($\lambda = 0.97$), very close to the random walk prediction ($\lambda = 1$). This pattern is consistent with previous studies that document generally high phylogenetic signal for body size (Freckleton et al. 2002; Blomberg et al. 2003).

Figures 8 and 9 show the phylogeny and survivorship at each extinction. The E/O extinctions are not randomly distributed with respect to phylogeny (Fig. 8). For example, the hantkeninids, a clade of seven species, goes entirely extinct. With independent binomial extinction intensities of 0.37, a clade of seven species is expected to go extinct only about one time in ten thousand ($p = 0.00095$), and thus the extinction of a clade this large

← increases. All results are for simulations with one ecological dimension. Shading as in Figure 3A.

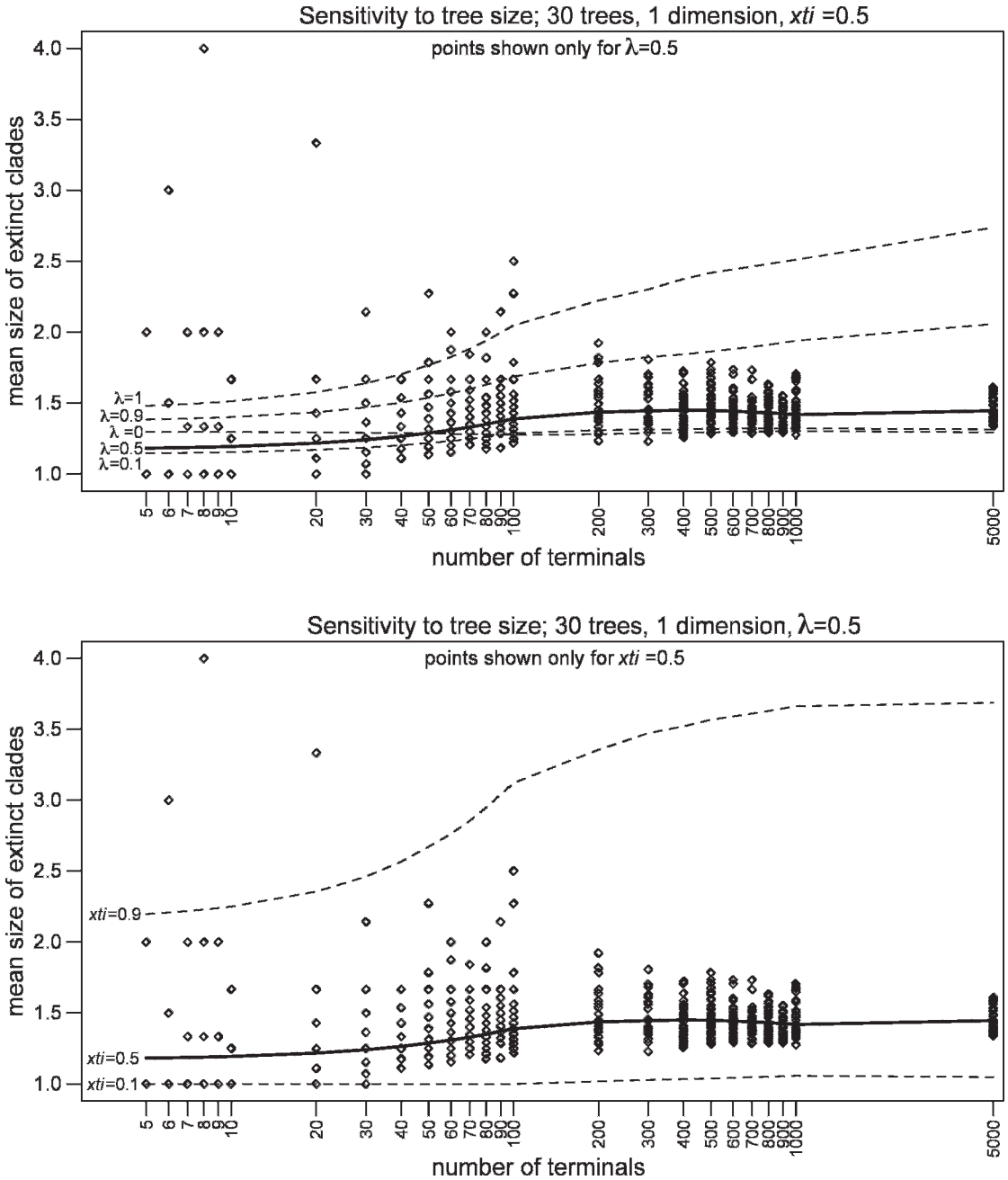


FIGURE 5. Sensitivity of mean extinct clade size to number of terminals. Each plotted point represents a synthesized phylogeny. At small tree sizes there is a great deal of scatter, so points are only shown for the solid line ($\lambda = 0.5$). The points from other values of λ are summarized by dotted locally weighted regression (lowess) curves (Cleveland 1979). Top: change in mean extinct clade size for 30 trees as total tree size increases for different levels of λ . Bottom: same representation, but varying extinction intensity (x_{ti}) instead of λ . The logistic shape of the curves shows how the model stabilizes at relatively small tree sizes except when λ is very high.

would not be likely unless extinction were phylogenetically clumped. This reasoning is confirmed by the simulation-based estimate of λ , which indicates very high phylogenetic

signal in extinction susceptibility ($\lambda = 0.97$). The 95% confidence limits of this estimate (taken as two units of log-likelihood) are quite broad, encompassing λ values as low as 0.62.

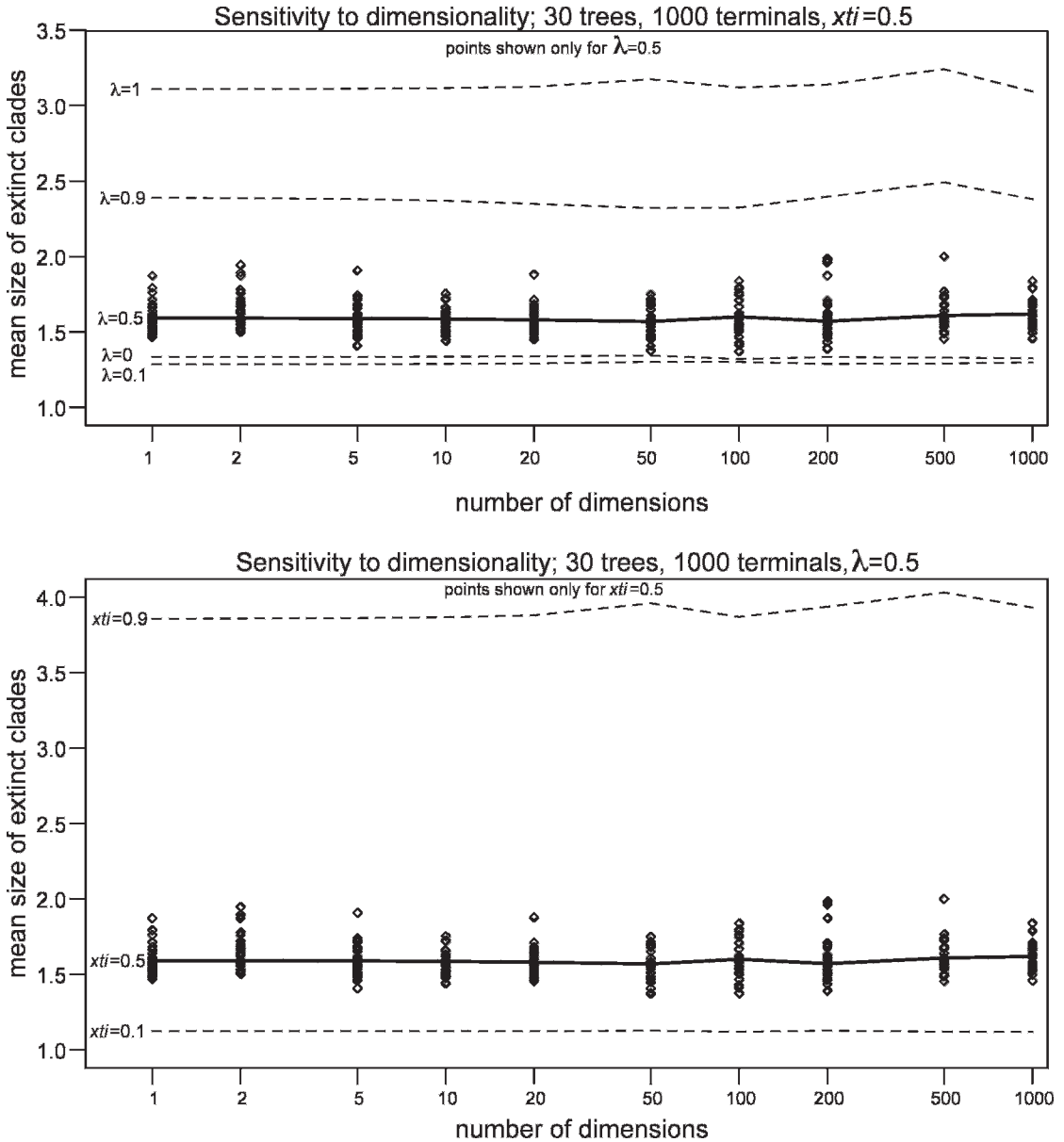


FIGURE 6. Sensitivity to dimensionality, shown as in Figure 5. The change in mean extinct clade size among 30 trees as ecospace dimensionality increases for different levels of λ and x_{ti} . Each plotted point represents a synthesized phylogeny and points are shown only for the solid $\lambda = 0.5$ (top) and $x_{ti} = 0.5$ (bottom) lowest curves. The flat lines indicate no response in the model to changes in dimensionality.

Nevertheless, even this lower limit represents substantial phylogenetic signal. Results from the W/S extinction of vascular land plants (Fig. 9) are similar: an estimated λ of 0.7 suggests lower λ for extinction susceptibility than in the foraminifer case, but because of the large error in the estimate (not statistically

different from 1; with lower 68% confidence limit of 0.3) the two cases are not statistically distinguishable.

The phylogenetic signal in the plant stature and disseminule size measurements is visually apparent when plotted on the phylogeny (Fig. 9). Because there are two measurable

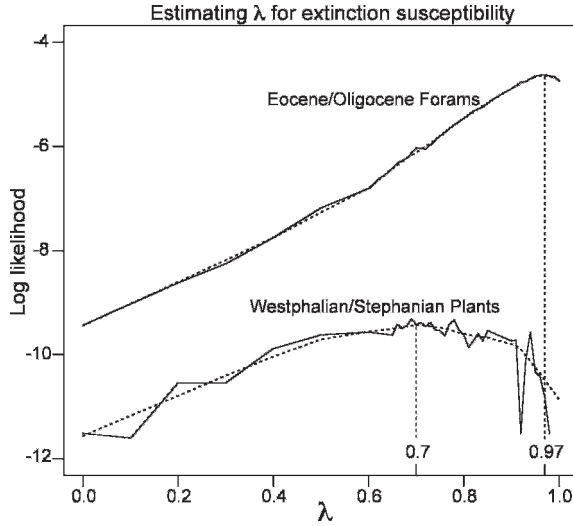


FIGURE 7. Maximum likelihood estimation of λ for extinction susceptibility; solid lines are model output and dotted lines are lowest smoothed curves of data from simulations. Interpreting each curve as a log-likelihood function, the labeled modes are interpreted as maximum likelihood estimates for λ .

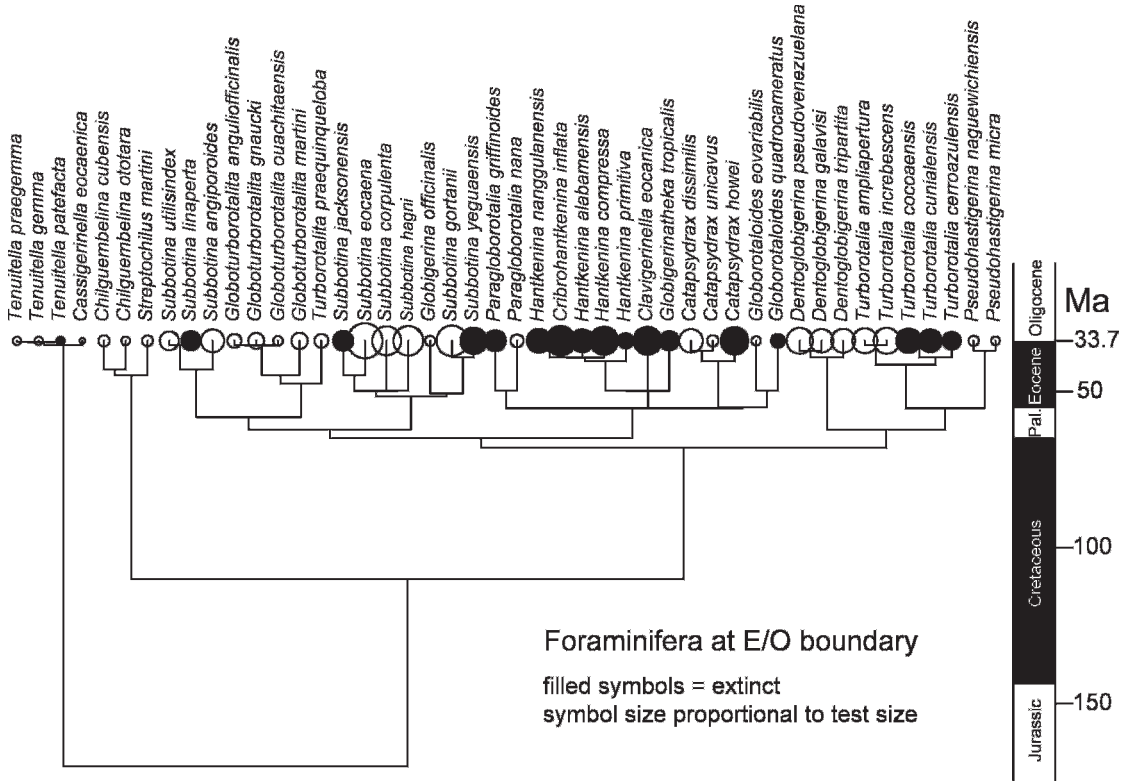


FIGURE 8. Phylogeny of Eocene planktonic foraminifera. Symbol size is proportional to body size and a filled black circle indicates a victim of the Eocene/Oligocene extinction.

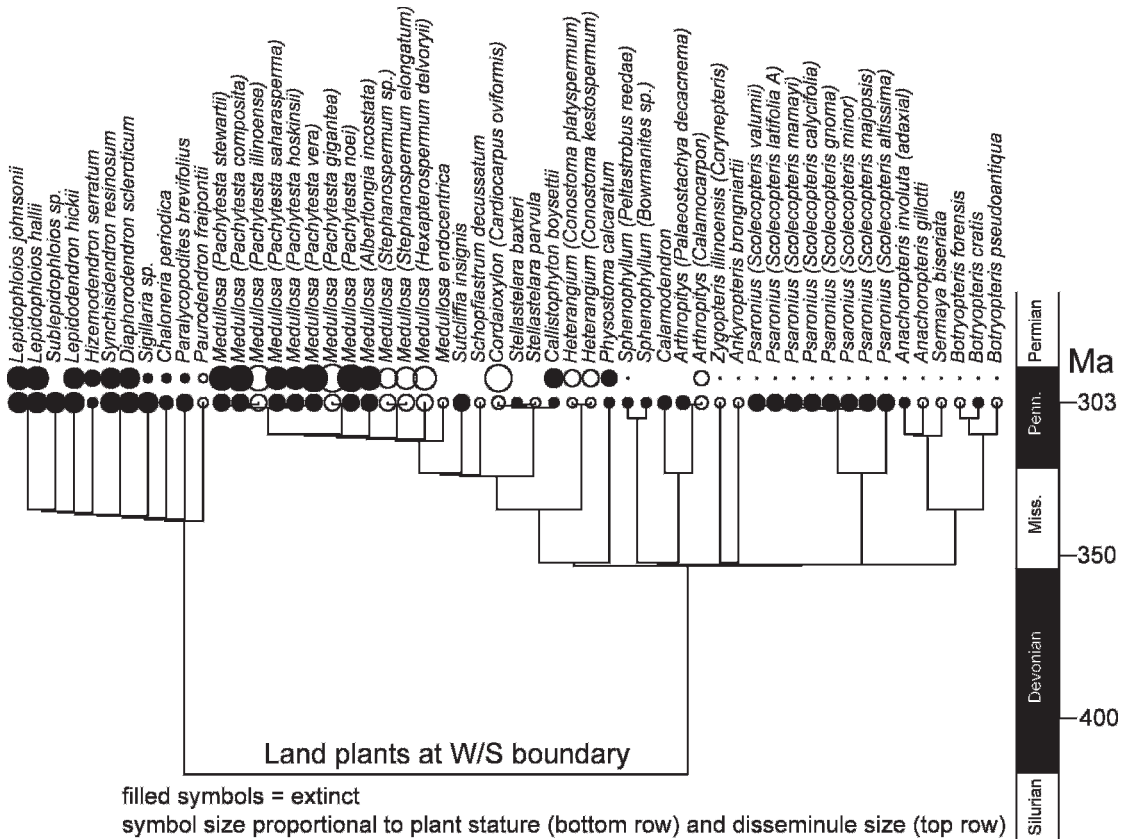


FIGURE 9. Phylogeny of vascular land plants from the Westphalian D. Symbol sizes are proportional to disseminule size and stature, and filled black circles indicate victims of the W/S extinction.

ecological variables, the extinctions can also be plotted in a two-dimensional ecospace (Fig. 10). The W/S extinction is clearly not spherical and determinate in ecospace like the hypothetical extinction shown in Figure 1. The propensity for plants of larger stature to go extinct is also obscured by the granularity of the stature data: because the variable takes only four values (herb, shrub, small tree, large tree), it is not immediately obvious that survival at the W/S boundary is selective with respect to stature (though it is; see Fig. 11). When considering all 54 taxa, there is no significant correlation between stature and disseminule size, but note that there is a weakly significant correlation between the two variables in the sub-population of Stephanian survivors (Pearson's two-sided correlation test; $n = 16$, $p = 0.13$, $r^2 = 0.16$). This appears to be because all of the large (>shrub

size) free-sporing plants went extinct at the W/S boundary, which could suggest a transition to more shaded habitats in the Stephanian (leading to direct selection against taxa with small disseminules) or could be an indirect result of the progressive increase in tree-fern dominance through the Middle Pennsylvanian.

This was a time of glacial-interglacial oscillations during which the Tropics responded by drying out between periods of peat formation. The wet-dry oscillations became progressively, if irregularly, more severe during the later Middle Pennsylvanian. During the drier periods, the wet flora presumably withdrew to refugia including channel bottoms and wet floodplains. As drought severity increased, culminating in a particularly severe wetland constriction at the W/S boundary, tree ferns appear to have

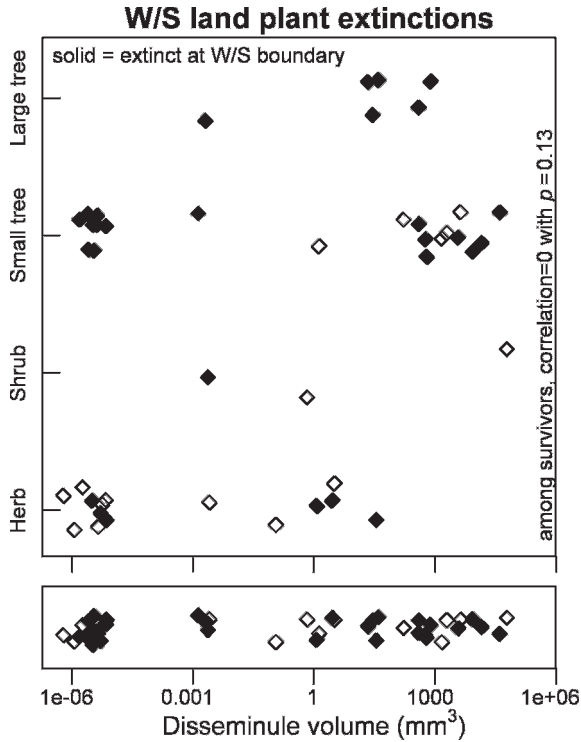


FIGURE 10. The W/S extinction in ecospace; analogous to the schematic diagrams in Figure 1C,D. Each point represents a terminal taxon; solid diamonds are taxa that went extinct at the boundary, unfilled survived. Top: two-dimensional plot with dimensions of plant stature (four-state), and disseminule volume. Bottom: points projected onto the single dimension of disseminule volume. All points are moved by a small random amount to reduce over-plotting of symbols.

been favored increasingly with the return of widespread wet conditions. The selectivity of the extinction with respect to size is probably an indirect effect due to localized environmental change and taxonomic displacement (DiMichele and Phillips 1996; DiMichele et al. 2009).

A non-phylogenetic analysis shows significant differences between survivors and victims in the cases of foraminifer size and plant stature (Fig. 11). Surviving plants did not, however, have significantly different disseminule sizes from those that went extinct. So of the two ecological variables measured for W/S plants, both have very high congruence with phylogeny, but only one has significantly different values among survivors and victims. If this pattern were found more generally, it would suggest that ecological extinctions primarily work on lineages through the congruence of ecological characters with phylogeny.

Discussion

There is a long history in paleontology of investigating the selectivity of extinctions with respect to traits like body size. Many of the traits shown to be selective for some extinctions have also been demonstrated to have phylogenetic signal or congruence: for example, geographic range size (Jablonski 1987; Jablonski and Hunt 2006), ecology or life history (Owens and Bennett 2000), and body size or other morphological features (Freckleton et al. 2002; Blomberg et al. 2003). This suggests that extinction susceptibility itself is likely to be phylogenetically inherited, a phenomenon that would manifest on trees as phylogenetically clumped extinctions, and in traditional taxonomies as systematic variation in extinction rates among higher taxa.

Prior examination of the phylogenetic structure of extinctions has often relied on taxonomy to test for clumping of extinction

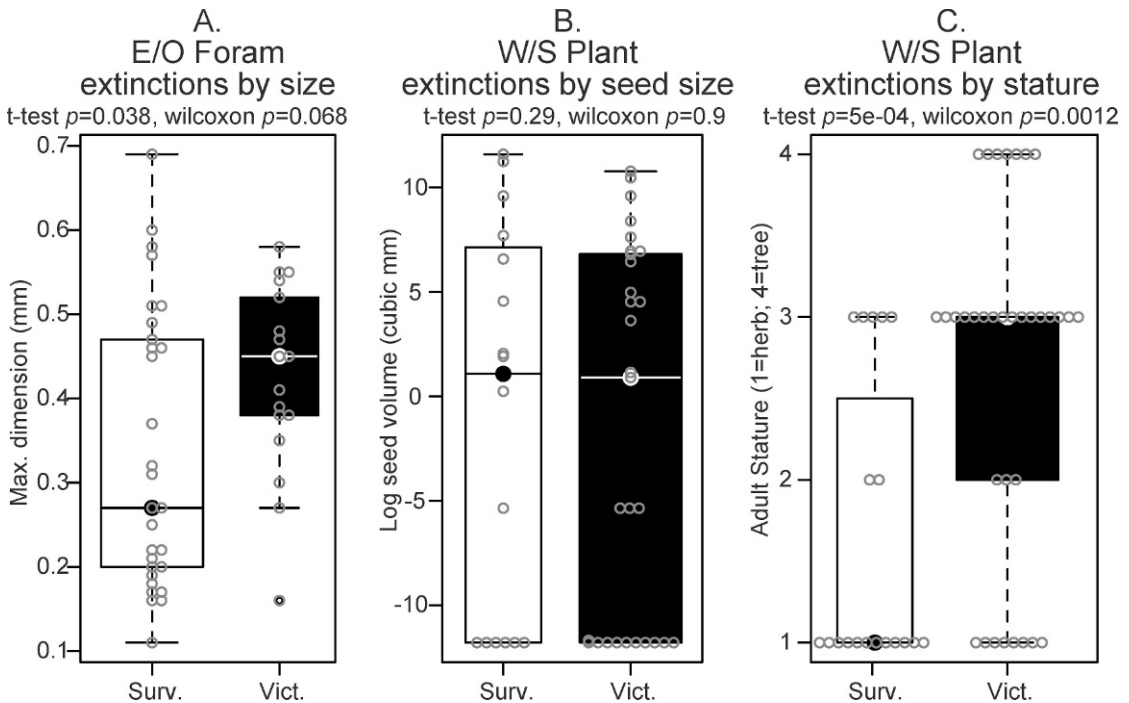


FIGURE 11. Boxplots of survivors versus victims for each ecological measurement–extinction pair. Medians marked by solid points superimposed on boxplots; gray points are actual measurements. A, Eocene/Oligocene foraminifera by test size. B, Westphalian/Stephanian plants by disseminule size; C, Westphalian/Stephanian plants by stature.

risk, asking, for instance, if endangered or extinct species are clumped within genera (e.g., Russell et al. 1998; Lockwood et al. 2002; Bielby et al. 2006; Janevski and Baumiller 2009). In this paper our approach is independent of rank-based Linnean taxonomy, and estimates congruence of ecology and phylogeny directly from phylogenies. Research on living vertebrates has found good evidence that extinction risk can be clustered taxonomically and phylogenetically (Schwartz and Simberloff 2001; Purvis 2008), and the same has been suspected for paleontological extinctions (e.g., Raup 1991; McKinney 1995). Recently, Roy et al. (2009) demonstrated taxonomic and phylogenetic clustering in geological extinctions of bivalve genera. The case studies described here, E/O planktonic foraminifera and W/S land plants, are consistent with this previous work. Extinctions in both systems are phylogenetically clumped, and in each case, at least one readily measured morphological variable also shows significant phylogenetic signal. Given these

results, and the frequency with which biologically important morphological, ecological, and life-history traits show phylogenetic structure (Freckelton et al. 2002; Blomberg et al. 2003), this pattern of phylogenetically clustered extinctions may be a very general property of life.

Roy et al. (2009) report very high phylogenetic selectivity of extinction during the mass extinction at the end of the Cretaceous, even though this interval has consistently shown less selectivity with respect to features (e.g., geographic range, larval mode) than earlier background intervals (Jablonski 1986). In general, selectivity can go undetected because of low statistical power, or it may be masked by differences among clades (Smith and Roy 2006; Purvis 2008). Alternatively, phylogenetic selectivity without trait selectivity can also result from extinctions that are selective with respect to unmeasured (latent) variables that are themselves phylogenetically congruent. Selectivity in extinctions may therefore be even more common than would be surmised

from studies that assess the relatively few traits that paleontologists can measure across many taxa.

The degree of phylogenetic selectivity can have important effects on the macroevolutionary impact of extinctions. Truly random extinctions, as in Raup's (1991) "field of bullets," remove a surprisingly small fraction of total evolutionary history, even when extinction is quite severe (Nee and May 1997), and are not expected to drive large clades (or higher taxa) extinct. Our simulation results support the intuition that clustered ecological traits exacerbate the effects of extinctions. When λ is low, even a numerically intense extinction tends only to trim dispersed tips from trees; when high, whole limbs can sometimes be chopped off. Though we approached the problem from a methodologically different perspective from Janevski and Baumiller (2009), whose examination of fossil occurrence data is taxonomically based and reliant on data analysis instead of computer modeling, we have come to a similar conclusion. Neither intense extinction nor strong congruence alone is sufficient for removing large, diverse clades; both are necessary.

Although our model does not explicitly examine the aftermath of an extinction, it is reasonable to infer that trim-type extinctions will leave smaller gaps in ecospace, and that recovery (diversification into emptied niches) will be more rapid and complete than when large gaps are left in ecospace by chop-type removal of large clades. The distribution of gaps and survivors also may have important effects on the nature of morphological changes that accompany the recovery of pre-extinction diversity (Erwin et al. 1987).

Most observed extinctions have intensities such that the effect of the events will depend on λ , so if plant groups have (on average) lower λ than animal groups, this would provide a plausible explanation for the fact that mass extinctions are less frequently observed in plant groups. Although sufficient data are not yet available to test this directly, as noted by Wing (2004), it may be possible in the future to compare this theory with the alternative idea that properties of individual

plants account for the lack of major extinctions.

Like all models, ours has necessitated some simplifications of reality: for instance, we use a birth-only model, so extinctions come in a single event rather than continuously through time. (This is an extreme pulsed model *sensu* Foote 2005.) Extinction in our model is deterministic rather than probabilistic and has only one ecological focus, whereas real extinctions may have multiple locations in ecospace (or a single non-spherical shape) and are likely to be probabilistic. Our reliance on simulation cannot give the same kind of mathematical insight that might be provided by an analytical model but is a pragmatic choice in a situation where no analytical solution is available.

We also rely heavily on Pagel's λ as a measure of phylogenetic signal. Calculating λ requires measuring an ecological or morphological variable for all terminals, so λ cannot be calculated for groups so divergent that they lack comparable features. The choice of characters may also be biased by practical constraints and the presence of homologies. Therefore, because comparable, ecologically significant features cannot be measured for all organisms, the true distribution in nature of congruence between phylogeny and ecology may be underestimated by λ values calculated for particular groups of organisms. The above difficulties aside, correspondence between modeled and measured phylogenetic signal in susceptibility to extinction suggests that our model is capturing some essentials of the dynamics that are observed in the fossil record. The results of our modeling substantiate our intuition that mass extinctions require both high species-level extinctions and high congruence between phylogenetic position and location in ecospace.

As the scale of current anthropogenic extinctions becomes apparent (Butchart et al. 2005; Willis et al. 2008), it may be useful to apply this result to the anthropogenic extinctions we are now observing. Using the extinction landscape shown in Figure 3, we could predict surviving clade size in any extant clade with known λ and extinction rate. Although the scope of this paper does

not permit an application of our model to extant groups or full consideration of modern conservation questions, it is easy to imagine how such a consideration might help guide conservation efforts toward groups whose susceptibility to extinction is particularly phylogenetically dependent (high λ). Like taxa with restricted geographic ranges or low population densities, clades with greater congruence between phylogeny and ecology may be particularly sensitive to extinction.

Conclusions

1. It is very difficult to drive large clades extinct. The two most important variables controlling extinct clade size are the extinction intensity (the probability of a given terminal going extinct), and the phylogenetic dependence of extinction susceptibility or ecological-phylogenetic congruence (measured with Pagel's λ). The main result of our analyses is a documentation of the mutual reinforcement of these two factors and a quantification of their interaction and importance. Large clades (e.g., >20 species) are likely to be lost at an extinction only when the overall extinction rate is greater than 0.8 and the congruence of ecology with phylogeny yields a λ of greater than 0.6. This puts observed species extinction rates in the fossil record into perspective. A 50% species extinction may sound dramatic, but if ecology-phylogeny congruence is low, then it may be necessary to count even extinctions of this magnitude as merely background—the cost of evolving in a cruel world. Note that this is consistent with the generally accepted consensus that the vast majority of species that ever evolved have gone extinct (Raup 1986). When the sum of extinction intensity and λ is less than 1 (e.g., extinction intensity 0.6, $\lambda = 0.4$), only single terminals are likely to go extinct.
2. Ecospace dimensionality appears to have no effect on extinct clade size in our simulations. Above a tree size of about 1000 terminals, the effect of tree size on extinct clade size is weak and detectable only when λ is greater than about 0.9.

3. The E/O extinction of planktonic foraminifera was selective with respect to body size; the North American W/S vascular plant extinction was selective with respect to plant stature, but not to disseminule size. All traits also showed substantial congruence with phylogenetic relationships. In both case studies, the estimated congruence between phylogeny and extinction susceptibility was significantly greater than would be expected if the terminals were located in ecospace at random with respect to their evolutionary relationships.

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