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Phylogenetically patterned speciation rates and extinction risks change the loss of evolutionary history during extinctions

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If we are to plan conservation strategies that minimize the loss of evolutionary history through human-caused extinctions, we must understand how this loss is related to phylogenetic patterns in current extinction risks and past speciation rates. Nee & May (1997, *Science* **278**, 692–694) showed that for a randomly evolving clade (i) a single round of random extinction removed relatively little evolutionary history, and (ii) extinction management (choosing which taxa to sacrifice) offered only marginal improvement. However, both speciation rates and extinction risks vary across lineages within real clades. We simulated evolutionary trees with phylogenetically patterned speciation rates and extinction risks (closely related lineages having similar rates and risks) and then subjected them to several biologically informed models of extinction. Increasing speciation rate variation increases the extinction-management pay-off. When extinction risks vary among lineages but are uncorrelated with speciation rates, extinction removes more history (compared with random trees), but the difference is small. When extinction risks vary and are correlated with speciation rates, history loss can dramatically increase (negative correlation) or decrease (positive correlation) with speciation rate variation. The loss of evolutionary history via human-caused extinctions may therefore be more severe, yet more manageable, than first suggested.

Keywords: biodiversity; biodiversity calculus; evolutionary history; extinction; phylogenetic tree shape; branch lengths

1. INTRODUCTION

Barring major advances in molecular genetics, each time a species goes extinct the independent evolutionary history embodied in that lineage is lost forever. In our present age of extinction we have the potential, through choice of conservation strategies, to decide which species are saved and which are sacrificed. May (1990) coined the phrase 'calculus of biodiversity' for the quantitative methods we employ to give relative worth to species, and Vane-Wright *et al.* (1991) referred to the 'agony of choice' associated with setting conservation priorities. While there are a variety of grounds on which such choices might be based (e.g. May 1990; Altschul & Lipman 1990; Vane-Wright *et al.* 1991; Faith 1992, 1994; Forey *et al.* 1994; Humphries *et al.* 1995; Crozier 1997), evolutionary distinctiveness is an important part of the calculation of value (IUCN 1980; Krajewski 1991; Faith 1992; Wilson 1992; Humphries *et al.* 1995; Crozier 1997; Vazquez & Gittleman 1998). Distinctiveness can be measured in many ways, but it is often correlated with the time a species has been separated from its closest relatives, measured by its taxonomic distinctiveness or the branch lengths of a phylogenetic tree (Williams *et al.* 1994; Crozier 1997; Nee & May 1997). For instance, the coelacanth is more distinct from its living relatives than is any one damselfish from its many cousins, and the difference in distinctiveness might suggest a difference in our conservation priorities. In such cases, if two species must be ranked, the one whose closest living relatives are (phylogenetically) more distant is considered to be more distinct and to embody more evolutionary history and so to be of higher worth (figure 1).

Nee & May (1997) studied the relationship between extinction and the loss of evolutionary history in a theoretical framework. They simulated trees under two models of random evolution, and then subjected them either to random extinction or to an algorithm that preserved the greatest proportion of evolutionary history possible (with history measured as the sum of all branch lengths in a tree). They focused on two important results. First, the relationship between random extinction and loss of evolutionary history is curvilinear, with early extinctions carrying little cost. Losing 50% of the species from a tree leaves 70–80% of the total evolutionary history, depending on the evolutionary model used. Second, the minimizing algorithm allows only a modest increase in history saved: for instance, at 50% extinction on an exponentially growing clade, management (preserving as much distinctiveness as possible) increases history saved only from about 70% to about 80%.

These results have important implications for conservation, as well as for studies of past extinction events, but more realistic models of speciation and extinction must be explored. We consider two biologically relevant patterns. First, phylogenies are markedly non-random in shape in ways that imply variation in speciation rates among lineages and through time (Guyer & Slowinski 1991, 1993; Heard 1992, 1996; Nee *et al.* 1992; Kirkpatrick & Slatkin 1993; Heard & Hauser 1995; Purvis 1996; Owens *et al.* 1999; for a review, see Mooers & Heard 1997). Second, present-day extinction risk is rarely random but shows a strong phylogenetic component (Gaston & Blackburn 1995, 1997; IUCN 1996; Bennett & Owens 1997;

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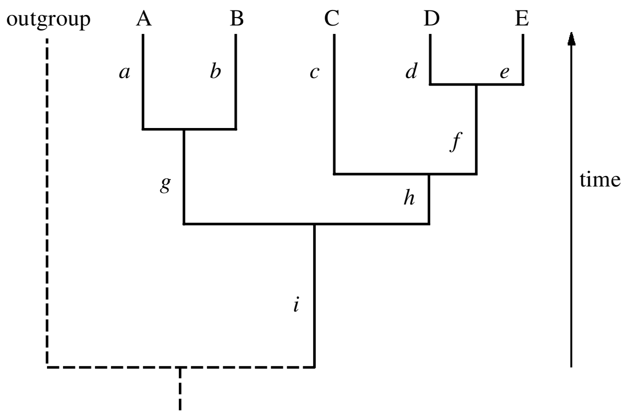

Figure 1. Loss of evolutionary history. Branch lengths represent time and the total evolutionary history of clade (A–E) $= a + b + c + d + e + f + g + h + i$. History i is common to the entire clade, and may represent an important proportion of the sum. If A goes extinct, we lose an amount a of history. If both A and B go extinct, history lost $= a + b + g$, the independent history of the two species plus their common history back to their nearest sister group. Using the biodiversity calculus based on branch length, species C is of more conservation worth then either A or B alone. The minimizing algorithm for 20% extinction (one out of five species lost) would sacrifice one of D or E; for 40% extinction, one of A or B and one of D or E.

McKinney 1997; Russell *et al.* 1998; Hughes 1999; Mace & Balmford 2000). We explore the implications of relevant kinds of non-randomness in both speciation rates and extinction risks for the loss of evolutionary history following episodes of extinction. We demonstrate that both the loss of history and the effectiveness of extinction management depend strongly on the degree of variation in speciation rates across lineages, on the kind and degree of interspecific variation in extinction risks, and on the correlation between speciation rate and extinction risk.

2. METHODS

We used a computer program written in QuickBASIC (Microsoft) to simulate the growth of clades by speciation and then the disappearance by sequential extinction of their member species. We explored a number of plausible scenarios for patterns across lineages in both speciation rates and extinction risks. Our focus was on the relationship between intensity of extinction and loss of evolutionary history, and on differences in this relationship among speciation and extinction scenarios.

(a) *Generating evolutionary trees*

We simulated the growth of clades through time as they diversified from a single ancestor species to a target size of 50 species (for clades grown under random evolution and subjected to random or minimum-loss extinction, Nee & May (1997) found only small differences in the loss of history between clades differing tenfold in size). Speciation rates (more precisely, speciation probabilities) of lineages could be constant, or could depend on a quantitative trait of individuals (for instance, body size) that was evolving in a random walk (Felsenstein 1985). Speciation rates in the latter case changed through time and at any instant varied among lineages within a tree (Purvis 1996).

Our algorithm began with a single species (at time t_1) and then stepped through time allowing both trait evolution and speciation events. As the tree grew, we recorded the time (t_i, $i = 1, 2, 3 \ldots 50$) at which each new species i arose. When a tree reached 50 species, we continued to step through time until the next speciation event was predicted. We recorded this time (t_{51}), which we used to terminate branches for all extant species, but we did not actually include the 51st species in the tree. The choice of a termination time is arbitrary, but none of our results are very sensitive to this choice. We chose to stop just before the origin of the 51st species for consistency with Nee & May (1997). Because we focus on the loss of evolutionary history from modern extinctions, for simplicity our models did not include past episodes of extinction (mass or background).

(b) *Trait evolution and speciation*

We modelled the evolution of two quantitative traits, one ($\mathcal{Z}_{\mathrm{s}}$) influencing speciation rate and the other ($\mathcal{Z}_{\mathrm{i}}$) independent of speciation rate. At any point in time, the growing tree consisted of a set of species, each with an associated value for each of the two traits. The speciation trait $\mathcal{Z}_{\mathrm{s}}$ might represent any continuous characteristic of species or individuals that is associated with speciation rate (Eldredge & Gould 1972; Stanley 1975; Vrba & Eldredge 1984; Heard & Hauser 1995; Heard 1996; Purvis 1996): for example, geographical range (Jablonski 1987), dispersal ability, generation time or body size. The independent trait $\mathcal{Z}_{\mathrm{i}}$ could be any other evolving quantitative trait. Importantly, both $\mathcal{Z}_{\mathrm{s}}$ and $\mathcal{Z}_{\mathrm{i}}$ can affect the risk of extinction, but only $\mathcal{Z}_{\mathrm{s}}$ is related to speciation rate. Modelling both $\mathcal{Z}_{\mathrm{s}}$ and $\mathcal{Z}_{\mathrm{i}}$ allows us to compare effects of extinction risks that are non-random with respect to phylogenetic position alone (based on $\mathcal{Z}_{\mathrm{i}}$) with effects of extinction risks correlated with past speciation rates (based on $\mathcal{Z}_{\mathrm{s}}$). We assumed that evolutionary changes in the two traits were independent, punctuated and log Brownian (Heard 1996). By punctuated and log Brownian we mean that evolutionary change occurred only at speciation events, with the logarithm of the trait value changing in a random walk: one daughter lineage 'inherits' the trait value $\mathcal{Z}$ held by its ancestor, modified by a stochastic change: $\log(\mathcal{Z}_{\mathrm{new}}) = \log(\mathcal{Z}_{\mathrm{old}}) + \epsilon$, where ϵ is drawn from a normal distribution with expectation zero and standard deviation $\sigma_{\mathcal{Z}}$. The second daughter species simply inherits the ancestral trait values. We consider random-walk evolution more plausible on a logarithmic scale than an arithmetic one because the logarithmic scale makes equal relative changes (say, ±10%) equally likely for all trait values, rather than equal absolute changes. For our simulations, we varied $\sigma_{\mathcal{Z}}$ from 0 to 0.3, following Heard (1996). This upper bound produces a third of speciation events where species differ by a factor of two in their trait value. For $\mathcal{Z}_{\mathrm{s}}$, this upper bound also produces unbalanced topologies that mimic the shape distribution of trees found in the literature (Heard 1992; Mooers & Heard 1997).

Speciation was a stochastic process in which any extant lineage at any time possessed a relative speciation rate s directly proportional to its speciation trait value $\mathcal{Z}_{\mathrm{s}}$. In particular, s was simply $\mathcal{Z}_{\mathrm{s}}$ divided by a sufficiently large number (constant within the set of trees for any scenario–parameter value combination) to ensure that the probability of more than one lineage speciating at a single iteration was negligible. This means that our time-scale is entirely arbitrary, but because we are interested only in relative changes in the time-based measure of evolutionary history, the choice of a divisor to convert $\mathcal{Z}_{\mathrm{s}}$ to s is unimportant. Variation in s was entirely dependent on variation

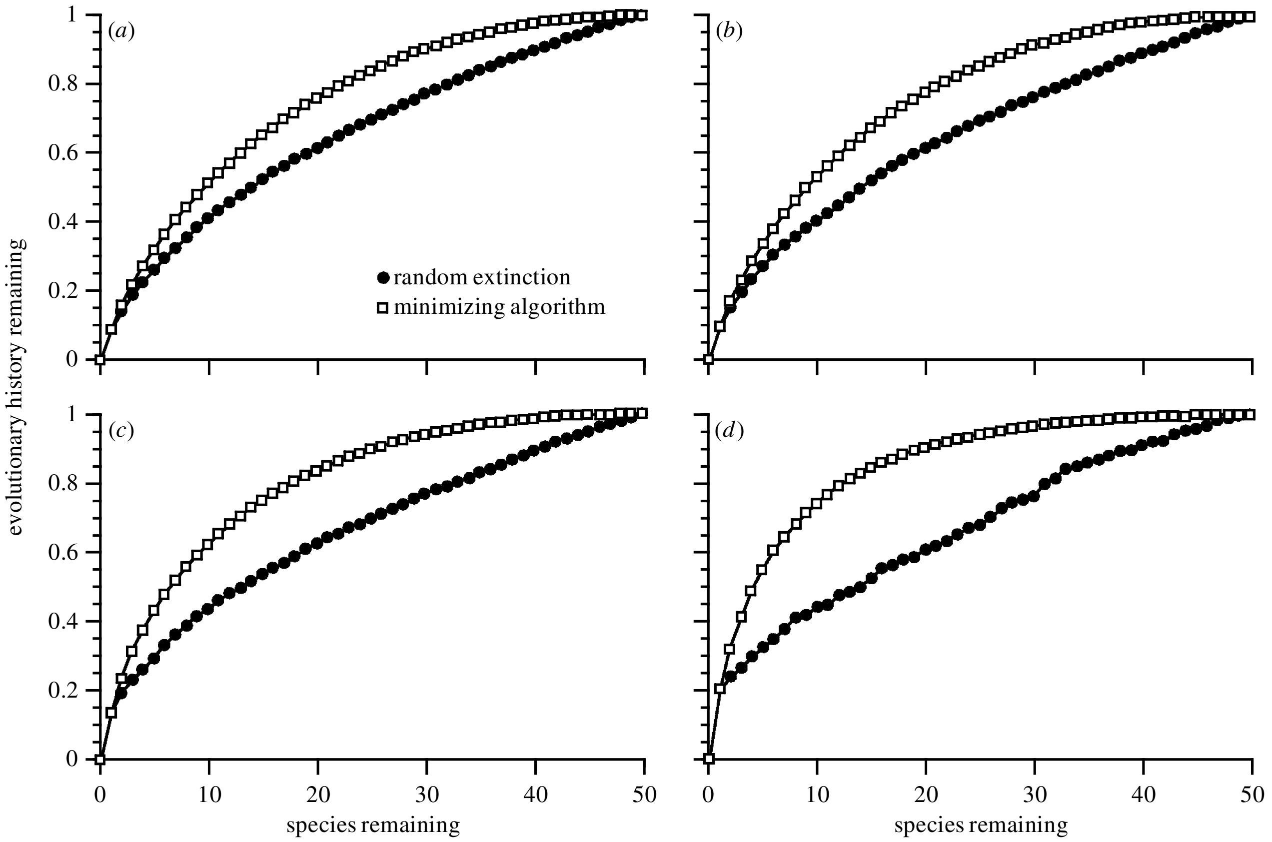

Figure 2. EHR as a function of tree shape ($N = 50$ tips). (*a–d*) EHR under random extinction (filled circles) and the minimizing algorithm (open squares) as variation among tips in speciation rate increases (*a*) equal-rate Markov trees, $\sigma_{\mathcal{Z}_\mathrm{s}} = 0.0$, $I_\mathrm{c} = 0.12$; (*b*) $\sigma_{\mathcal{Z}_\mathrm{s}} = 0.1$, $I_\mathrm{c} = 0.14$; (*c*) $\sigma_{\mathcal{Z}_\mathrm{s}} = 0.2$, $I_\mathrm{c} = 0.19$; (*d*) $\sigma_{\mathcal{Z}_\mathrm{s}} = 0.3$, $I_\mathrm{c} = 0.33$.

in $\mathcal{Z}_\mathrm{s}$; when $\mathcal{Z}_\mathrm{s}$ did not evolve ($\sigma_{\mathcal{Z}_\mathrm{s}} = 0$) our model simplifies to the well-known equal-rates Markov model (Yule 1924; Heard 1992; Purvis 1996; Mooers & Heard 1997).

(c) *Extinction*

We examined five extinction scenarios, including two variants of the deterministic cull on $\mathcal{Z}_\mathrm{s}$ (see § 2(c)(iv)). In every case, the 50 species making up an evolutionary tree were declared extinct, one at a time, until none remained. The scenarios differed in the rules determining the order in which species became extinct, as follows.

(i) *Random cull*

Under our simplest scenario, species are picked at random for extinction, regardless of their phylogenetic position or trait value. This scenario has also been called the 'field of bullets' (Nee & May 1997).

(ii) *Minimum-loss cull*

We followed Nee & May (1997) in implementing a loss-minimizing algorithm under which the next extinction event always hits the extant species whose loss removes the least possible evolutionary history from the tree. Each time an extinction is to occur, the algorithm identifies the most recent speciation event of which both descendants are still extant (for instance, that giving rise to D + E in figure 1); removing one of these two descendants will always remove the shortest possible branch length (least evolutionary history). One of the two is chosen at random for extinction (see figure 1).

(iii) *Deterministic cull on* Z_i

Under the deterministic cull on the independent trait $\mathcal{Z}_\mathrm{i}$, extinction is non-random with respect to phylogenetic position but is not directly correlated with speciation rate. The order of extinction is entirely determined by the values of $\mathcal{Z}_\mathrm{i}$: species are sorted by $\mathcal{Z}_\mathrm{i}$, and extinction proceeds from largest $\mathcal{Z}_\mathrm{i}$ to smallest (reversing the order to cull from smallest to largest made no difference to the results, as expected (S. B. Heard and A. Ø. Mooers, unpublished data)). Because closely related species tend to have similar values of $\mathcal{Z}_\mathrm{i}$, under this scenario extinction tends to remove related species in groups; effectively, extinction risk is higher for some lineages within the clade than for others.

(iv) *Deterministic cull on* Z_s *(two variants)*

The deterministic cull on $\mathcal{Z}_\mathrm{s}$ combines the phylogenetic non-independence of extinction under the deterministic cull on $\mathcal{Z}_\mathrm{i}$ with a second non-random component: extinction rates are correlated (either positively or negatively; see § 4) with speciation rates. If rates are positively correlated (extinction ordered from largest $\mathcal{Z}_\mathrm{s}$ to smallest), lineages with high speciation rates are more prone to extinction; if negatively correlated (extinction ordered from smallest $\mathcal{Z}_\mathrm{s}$ to largest), then lineages with historically low speciation rates are at higher risk.

We also considered extinction scenarios where $\mathcal{Z}_\mathrm{i}$ or $\mathcal{Z}_\mathrm{s}$ affected extinction in a probabilistic rather than in a deterministic matter (i.e. $\mathcal{Z}_\mathrm{s}$ affected the probability of extinction for each species, but did not fully determine the order of extinction). Results closely resembled those of the simpler deterministic scenarios, and so are not presented here.

(d) *Measuring evolutionary history*

We measured the evolutionary history embodied in a phylogenetic tree as the total length of all its branches (figure 1). Following Nee & May (1997), we expressed evolutionary history remaining (EHR) on a relative scale, from 0 (all 50 species extinct) to 1 (all 50 species extant). We made one important addition, however. Our measure of evolutionary history is not from the first speciation event within the clade being considered, as was modelled by Nee & May (1997), but from when that clade first split from its sister clade (e.g. for the clade including species A–E in figure 1, we begin not at the split giving rise to branches *g* and *h*, but instead at the base of branch *i*). This 'root branch' (branch *i*) is definitely part of a clade's total evolutionary history and depending on the initial speciation rate and on changes in this parameter through time, it may represent a sizeable proportion of the total history of the clade. This adds force to Nee & May's (1997) claim that few species may retain much of a clade's total evolutionary history.

(e) *Analysis*

For each set of tree-generating parameter values ($\mathcal{Z}_\mathrm{s}$ and $\mathcal{Z}_\mathrm{i}$), we generated 200 trees. For each tree, our computer program computed Colless' index of imbalance I_c (Heard 1992), which ranges from 0 for a completely balanced tree (each node splitting a clade exactly in half) to 1 for a completely unbalanced tree (each node splitting just one species from the remainder of a clade). Each tree was then subjected to each of the five extinction scenarios. We calculated mean EHR (and its standard error for each set of 200 trees), for each new tree size (50, 49, 48 . . . 1) as extinction progressed. We do not present formal statistical analyses, because results are obvious: in all plots (figures 2–5) approximate 95% confidence intervals (mean ± 2 s.e.) are hidden by the symbols used to plot the means.

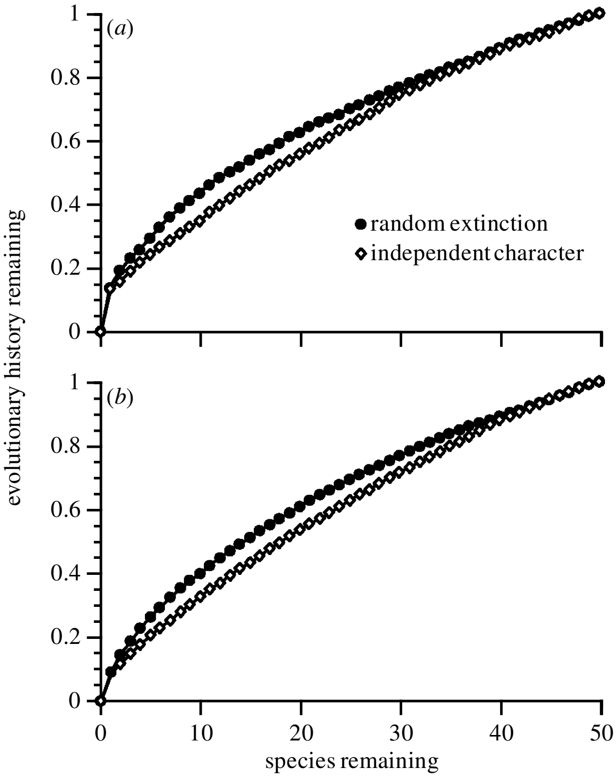

Figure 3. EHR as a function of extinction due to a phylogenetically correlated trait ($N = 50$ tips). (*a*) Random tree ($\sigma_{\mathcal{Z}_\mathrm{s}} = 0.0$, $I_\mathrm{c} = 0.12$). Closed circles: random extinction; open diamonds: independent evolving trait with $\sigma_{\mathcal{Z}_\mathrm{i}} = 0.2$. (*b*) Unbalanced tree ($\sigma_{\mathcal{Z}_\mathrm{s}} = 0.2$, $I_\mathrm{c} = 0.19$). Closed circles, random extinction; open diamonds, independent evolving trait with $\sigma_{\mathcal{Z}_\mathrm{i}} = 0.2$.

3. RESULTS

(a) *Random versus minimum-loss cull: effects of non-random speciation*

Increasing $\sigma_{\mathcal{Z}_\mathrm{s}}$ (the rate of evolution of the trait controlling speciation rate) increases among-lineage variation in speciation rate and changes tree shape (producing more unbalanced trees). As $\sigma_{\mathcal{Z}_\mathrm{s}}$ increases (and simulated trees approach published trees in average balance), the difference between random cull and the minimum-loss cull (which might be termed the extinction-management pay-off) increases (figure 2). For instance, with $\sigma_{\mathcal{Z}_\mathrm{s}} = 0.0$, random extinction of 50% of the species leaves 0.69 of the evolutionary history, while the minimum-loss cull leaves 0.84 (22% pay-off). When $\sigma_{\mathcal{Z}_\mathrm{s}} = 0.2$, random 50% extinction still leaves 0.69 of the history but the minimum-loss cull now leaves 0.89 (a 29% pay-off). The effect of speciation rate variation can be marked: at $\sigma_{\mathcal{Z}_\mathrm{s}} = 0.3$, the maximum extinction-management pay-off (at 14 species remaining) is almost three times the maximum pay-off (at 20 species remaining) under the equal speciation rate model (70 versus 24%).

(b) *Phylogenetically patterned extinction risks*

Non-randomness in extinction risks has important effects on the loss of evolutionary history. These effects depend critically on whether or not the pattern in extinction rates is correlated with past speciation rates. In our model, this is represented by the dependence of extinction on $\mathcal{Z}_\mathrm{i}$ or $\mathcal{Z}_\mathrm{s}$.

When extinction depends on $\mathcal{Z}_\mathrm{i}$, extinctions are phylogenetically clustered, but there is no expected correlation with speciation rate. Such phylogenetically clustered extinction is more costly than random extinction for the range of $\sigma_{\mathcal{Z}_\mathrm{i}}$-values we used (0.01–0.3; see figure 3). This holds for both randomly evolved trees (figure 3*a*) or quite unbalanced trees (figure 3*b*). In our punctuated model, any degree of variation in $\mathcal{Z}_\mathrm{i}$ suffices to allow phylogenetically clustered extinctions; we show curves for $\sigma_{\mathcal{Z}_\mathrm{i}} = 0.2$ but other values would give closely similar results. The amount of added history lost, however, is not dramatic; for instance, at 50% extinction on random trees ($\sigma_{\mathcal{Z}_\mathrm{s}} = 0.0$, figure 3*a*), non-random extinction (e.g. $\sigma_{\mathcal{Z}_\mathrm{i}} = 0.2$) removed only 9% more history (0.63 retained under cull on $\mathcal{Z}_\mathrm{i}$ versus 0.69 under random cull).

The situation is quite different when past speciation and present extinction rates are correlated (figure 4). With a negative correlation (high extinction risk for slowly speciating lineages, like living fossils), more speciation rate variation (larger $\sigma_{\mathcal{Z}_\mathrm{s}}$) means more—potentially much more—evolutionary history is lost for any level of extinction (bottom traces, figure 4*a–d*). For instance, with $\sigma_{\mathcal{Z}_\mathrm{s}} = 0.2$ and 50% extinction, a negative correlation between speciation rate and extinction risk means a loss of 40% more evolutionary history compared with a random cull. With a positive correlation (high extinction risk for actively speciating lineages), on the other hand, results are more complicated. With low $\sigma_{\mathcal{Z}_\mathrm{s}}$ (little variation in speciation rates), loss of evolutionary history is slightly greater

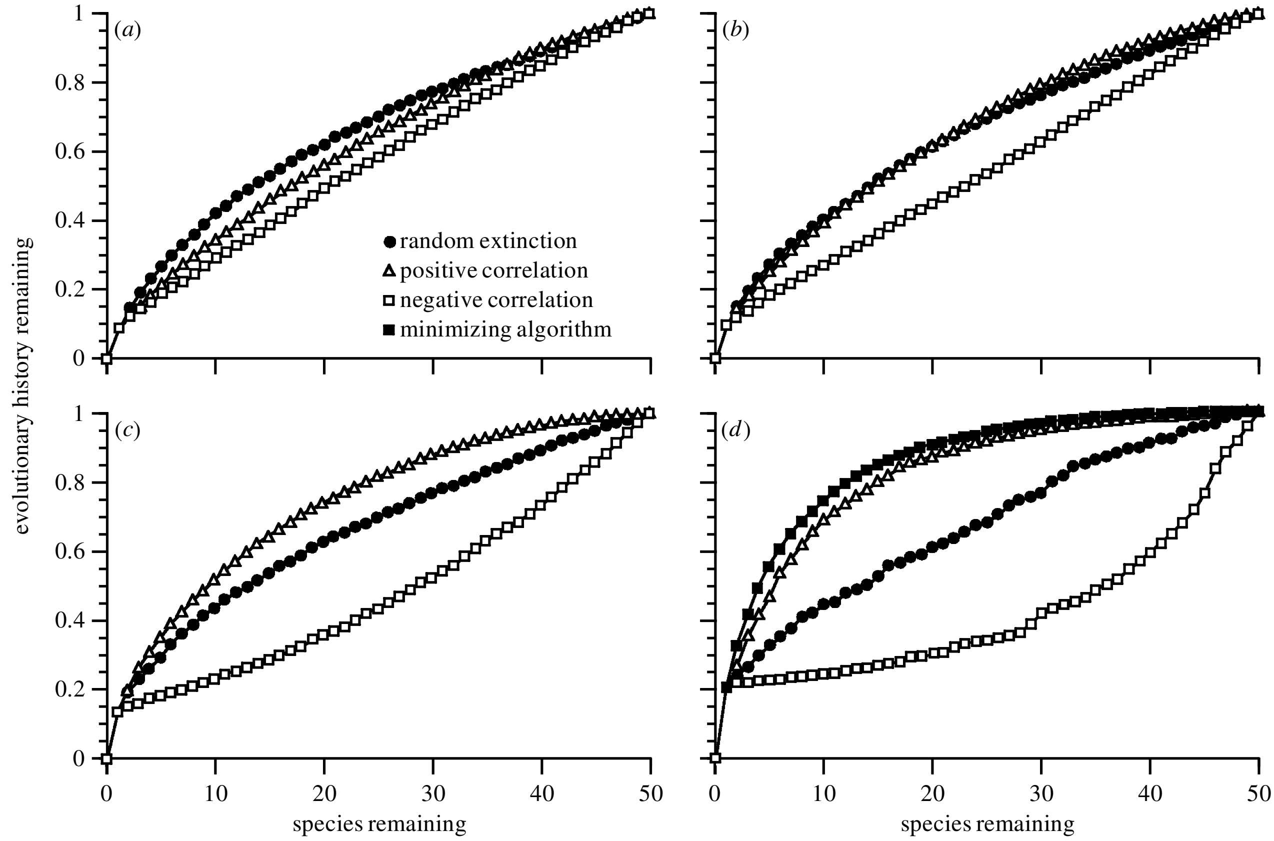

Figure 4. EHR as a function of extinction due to a trait correlated with speciation rate ($N = 50$ tips). (*a–d*) EHR under random extinction (closed circles) and the positive (open triangles) and negative correlation (open squares) with speciation rate as variation among species in speciation rate increases. (*a*) $\sigma_{\zeta_s} = 0.05$, $I_c = 0.13$; (*b*) $\sigma_{\zeta_s} = 0.1$, $I_c = 0.14$; (*c*) $\sigma_{\zeta_s} = 0.2$, $I_c = 0.19$; (*d*) $\sigma_{\zeta_s} = 0.3$, $I_c = 0.33$. Filled squares, results from minimizing algorithm.

than under random extinction (figure 4*a*); the difference is attributable to phylogenetically clustered extinctions, as seen when extinction is based on evolving traits not linked to speciation rate (ζ_i). As σ_{ζ_s} increases (more variation in speciation rates), extinctions begin to affect primarily young species embodying little independent evolutionary history. As a result, the loss of evolutionary history for any level of extinction quickly declines until history remaining exceeds the random expectation (figure 4*b–d*). When speciation rates are very variable ($\sigma_{\zeta_s} = 0.3$), much more history remains than under the random cull, nearly as much as that possible under the minimum-loss cull (figure 4*d*).

4. DISCUSSION

We have demonstrated that the loss of evolutionary history associated with any given level of extinction will depend in important ways on two factors. First, history loss will depend on the kind of diversification processes that gave rise to the clade under consideration (in particular, on the topology of the phylogenetic tree, which depends in turn on underlying variation in diversification rates across lineages within the clade). Second, it will depend on patterns in risk of extinction across species (most notably on correlations between extinction risk and speciation rates). The size of the extinction-management pay-off (the difference in history lost between employing the loss-minimizing algorithm and simply doing nothing) depends on the same two factors. Our results should highlight the importance of two questions for the calculus of biodiversity: What is the pattern in speciation rate variation among lineages in real clades, and what is the correlation between this pattern and risk of extinction?

Nee & May (1997) pointed out that random extinction removes more history on unbalanced phylogenies than it does on balanced ones and Vazquez & Gittleman (1998) highlight this observation as potentially important, given that trees come in all variety of shapes. Recent work has suggested that phylogenetic trees taken from the literature are often more unbalanced than those produced by equal-rate Markov and equilibrial models (reviewed in Purvis 1996; Mooers & Heard 1997) and that this is most likely due to differences in speciation rates (or past extinction rates) among extant lineages within a clade (Guyer & Slowinski 1991, 1993; Heard 1992, 1996; Nee *et al.* 1992; Kirkpatrick & Slatkin 1993; Heard & Hauser 1995; Purvis 1996; Owens *et al.* 1999). If such variation is general, this implies that the random speciation models considered by Nee & May (1997) do not bracket the plausible shapes of trees with which conservationists might be concerned. The minimum-loss algorithm does much better (higher extinction-management pay-off) on unbalanced trees created under an evolving speciation rate model than on equal-rate Markov trees. The extinction-management pay-off is different under different extinction regimes but can be substantial (figure 5). Under Nee & May's model (our analyses), the greatest

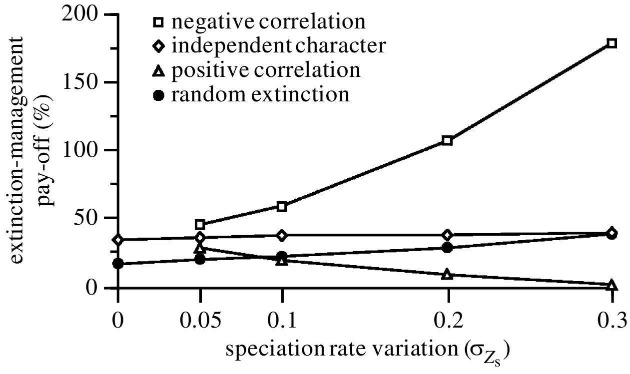

Figure 5. Extinction-management pay-off at 50% extinction for various evolutionary scenarios. The *y*-axis is the percentage improvement of the minimizing algorithm over extinction under one of the following scenarios, for different amounts of variation in speciation rate (*x*-axis). Filled circles, random extinction; open diamonds, extinction based on an evolving trait independent of speciation ($\sigma_{Z_i} = 0.2$); open triangles, present extinction and present speciation rates positively correlated; open squares, present extinction and speciation rates negatively correlated.

possible improvement offered by extinction management (versus doing nothing) is a modest 24%, but with even moderate speciation rate variation (say, $\sigma_{Z_s} = 0.2$), pay-offs can be well over threefold higher. Indeed, pay-offs above 170% are possible when speciation rates and extinction risks are highly variable and when extinction is severe (e.g. with $\sigma_{Z_s} = 0.3$ and a negative speciation–extinction correlation, history retained after 50% extinction can be improved from 0.35 to 0.95; figure 5). In general, the largest pay-offs are expected where extinction risks are phylogenetically clustered but independent of speciation rate (figure 5, open diamonds), or where extinction risks are negatively correlated with speciation rates (figure 5, open squares). Although each tree must be evaluated separately, conservationists employing minimum-loss algorithms in making management decisions (Vane-Wright *et al.* 1991; Crozier 1997) may get a much greater return than previously suggested.

Other models of diversification must also be considered in more detail. Because the pay-off from the minimum-loss algorithm is dependent on the relative waiting times between speciation events, different models of diversification may result in better or worse extinction-management pay-offs. For instance, among exponentially growing clades, those with gradual (as opposed to punctuated) evolution of traits influencing speciation (like our Z_s) tend to be less unbalanced (Heard 1996) and might therefore lose less evolutionary history during extinction. Furthermore, exponential growth is not a good model for all clades; instead, a logistic growth model with long periods of stasis seems to describe phylogenetic patterns among higher taxa and over long periods of evolutionary time (Sepkoski 1979; Wagner 1995; Alroy 1996; Courtillot & Gaudemer 1996; but see dissent from Benton 1995; Hewzulla *et al.* 1999). Nee & May (1997) showed that extreme extinction on such trees removes relatively little evolutionary history, supporting palaeontological evidence concerning the robustness of higher taxonomic groups to mass extinctions (Raup 1979). Finally, past episodes of extinction (particularly mass extinctions) might alter the vulnerability of clades to modern extinction; this is particularly likely where past extinction rates depended on traits of individuals and therefore could have caused changes in phylogenetic tree topology. More work is required to investigate the effects of plausible levels of background and mass extinctions on the results presented here.

The importance of the speciation rate–extinction risk correlation draws attention to the grave lack of empirical knowledge about this relationship. Stanley (1979) documented large-scale positive correlations between speciation and extinction rates over geological time. However, Jablonski (1986) argued that mass extinctions are different, and whether modern extinctions follow the same rules as past background or mass extinctions remains unknown. While it is clear that extinction is often phylogenetically non-random (for evidence from recent extinctions, see for example Newmark 1995; Russell *et al.* 1998; Foufopoulos & Ives 1999; Hughes 1999), the exact pattern of non-randomness will doubtless vary among clades (Lawton 1995). McKinney (1997) suggested that concentrations of extinctions in certain families and genera can accelerate net losses of biodiversity. Our simulations suggest that while this is true, phylogenetically clumped extinction uncorrelated with past diversification decreases EHR by only a relatively small amount; this is good news. If lineages with high speciation rates are more likely to go extinct in our present age, then, depending on the amount of variation, McKinney may be wrong, and the situation may not be as bad as random extinction. Importantly, if lineages with low speciation rates are more liable to extinction, then McKinney's (1997) warning is true and forceful indeed: clumped extinction can result in a great loss of evolutionary history.

Are modern extinction risk and speciation rate positively, negatively, or uncorrelated for real clades? All three patterns seem plausible, and different patterns may hold for different taxonomic groups or guilds. Past speciation and present extinction risk may be uncorrelated. For instance, Gaston & Blackburn (1995) and Bennett & Owens (1997) both argued that large-bodied birds are at a higher risk of extinction than small-bodied ones, but Owens *et al.* (1999) claim that bird body sizes may be unrelated to past speciation rates (for a similar result in primates and carnivores, see Gittleman & Purvis (1998); for a palaeontological perspective, see Jablonski (1996)). Other things being equal, these observations imply that overall loss of evolutionary history within the bird clade may be closer to that suggested by the independent trait model (figure 3) than the speciation trait model (figure 4). (Nevertheless, given the extremely unbalanced nature of the bird tree (Harvey *et al.* 1991; Mooers *et al.* 1994), the minimum-loss algorithm might be expected to yield a large pay-off in this clade.) Positive correlations between speciation rate and extinction risk seems possible when closely related species tend to live in similar habitats (e.g. in threatened tropical habitats), though this must be investigated further. Finally, the worst-case scenario may hold, and extinction risk may be negatively correlated with speciation rate. Stiassny & de Pinna (1994) highlight that basal, depauperate (low diversification rate) taxa of freshwater fish tend to have restricted geographical ranges, rendering them liable to extinction. Russell *et al.* (1998) document the clumping of threatened species in depauperate taxa of birds and mammals (e.g. all three New Zealand kiwi species) and Hughes (1999) presents evidence that historical, human-induced extinctions have been concentrated in monotypic genera of birds.

In general, understanding prospects for managing the loss of evolutionary history due to extinctions will require considerable understanding of the processes by which lineages diversify and by which species go extinct. In particular, we have emphasized the importance of variation in past speciation rates and the correlation between speciation rates and present risk. The studies by Bennett & Owens (1997) and Owens *et al.* (1999) are among the first to empirically connect past diversification rates and present risk. Further surveys that directly consider branch length data from comprehensive phylogenetic trees (see, for example, Bininda-Emonds *et al.* 1999) will shed considerable light on how much evolutionary history we are in the process of losing, and how we can best reduce that amount.

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