

Reconsidering the Loss of Evolutionary History: How Does Non-random Extinction Prune the Tree-of-Life?

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Abstract Analysing extinction within a phylogenetic framework may seem counter-intuitive because extinction is *a priori* a non-heritable trait. However, extinction risk is correlated with other traits, such as body size, that show a strong phylogenetic signal. Further, there has been much effort in identifying key traits important for diversification, and recent evidence has demonstrated that the processes of speciation and extinction may be inextricably linked. A phylogenetic approach also allows us to quantify the impact of extinction, for example, as the loss of branches from the tree-of-life. Early work suggested that extinctions might result in little loss of evolutionary history, but subsequent studies indicated that non-random extinctions might prune more of the evolutionary tree. Loss of phylogenetic diversity might have ecosystem consequences because functional differences between species tend to be correlated with the evolutionary distances between them. Here we explore how extinction prunes the tree-of-life. Our review indicates that the loss of evolutionary history under non-random extinction (the emerging pattern in extinction biology) might be less pronounced than some previous studies have suggested. However, the loss of functional diversity might still be large, depending on the evolutionary model of trait change. Under a punctuated model of evolution, in which trait differences accrue in bursts at speciation, the number of branches lost is more important than their summed lengths. We suggest that evolutionary models need to be incorporated more explicitly into measures of phylogenetic diversity if we are to use phylogeny as a proxy for functional diversity.

Keywords Extinction risk • Phylogenetic comparative methods • Punctuated evolution • Phylogenetic diversity • Feature diversity

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Introduction

There is mounting evidence that we are entering a sixth mass extinction (Millennium Ecosystem Assessment 2005), and the future of biodiversity is at risk due to the high rates at which biological diversity – species, habitats, evolutionary diversity – is being eroded. Species are experiencing unprecedented pressures across their ranges owing to global change, including increased invasion success of aliens (Winter et al. 2009), habitat destruction (Vitousek et al. 1997; Haberl et al. 2007), climate change and climate variability (Willis et al. 2008, 2010). Consequently, approximately 30 % of assessed species are currently categorised as threatened by the IUCN, and a greater proportion may be committed to extinction in the near future (Thomas et al. 2004). Current rates of species loss might be 1,000–10,000 times greater than past extinction rates (Pimm et al. 1995; Millennium Ecosystem Assessment 2005) with particularly elevated rates in tropical biomes (Vamosi and Vamosi 2008), known for their unique life-form diversity. At the ecosystem level, with the loss of species, we also lose their contributions to overall ecosystem functioning and services. The loss of ecosystem services is of particular concern because human survival relies strongly on key services such as food production, plant pollination, medicinal plants, clean water, clean air, nutrient cycling, carbon sequestration, climate stability, recreation, tourism, etc. – which are provided by a well functioning system of biological diversity.

It is well established that human activities can drive extinctions within a short period of time (Baillie et al. 2004; Mace et al. 2005a). Because human population has increased exponentially over the last centuries, and is expected to reach nine billion by 2050 (www.un.org/esa/population/publications/longrange2/2004worldpop2300reportfinalc.pdf), pressure on natural ecosystems is also predicted to increase, yet at the same time there will be an even greater demand for the ecosystem services provided by biologically diverse natural systems. As a result, the rate of species extinction is projected to rise by at least a further order of magnitude over the next few hundred years (Mace et al. 2005b), potentially decreasing the provisioning of ecosystem services at a time when demand is growing. Understanding how the ongoing extinction crisis will impact the provisioning of critical ecosystem services is therefore a matter of urgency.

Quantifying the ecosystem contributions of individual species is a major challenge. Current estimates of global diversity vary by over an order of magnitude (see e.g. May 2010), with the vast majority of species (86 % and 91 % of terrestrial and oceanic diversity, respectively) remaining unknown to science (Mora et al. 2011). An in-depth understanding of species ecologies is therefore impractical for most of life; at best, we might be able to infer their placement on the tree-of-life. Whilst there is now a general consensus on the positive link between biodiversity and ecosystem function (Hooper et al. 2012), there has been growing evidence suggesting that evolutionary history provides a more informative measure of biological diversity than traditional metrics based upon richness and abundance (e.g. Faith 1992; Faith et al. 2010; Davies and Cadotte 2011; see also Srivastava et al. 2012 for a comprehensive review). It is suggested that evolutionary history might better capture

functional diversity including unmeasured or hard-to-measure traits (Crozier 1997; Faith 2002). As such, phylogeny provides a unique framework that captures both known (Forest et al. 2007; Saslis-Lagoudakis et al. 2011) and unknown ecosystem services (Faith et al. 2010). Understanding how the current extinction crisis will prune the tree-of-life is therefore critical for ensuring a continued provisioning of the ecosystem services upon which we rely, but for which we might lack detailed ecological knowledge of underlying process or mechanism (Faith et al. 2010).

There has been growing effort to incorporate species evolutionary histories into conservation decision-making (e.g. Purvis et al. 2000a, 2005; Isaac et al. 2007, 2012; Faith 2008). This effort has been facilitated by the rapid rise in analytical tools, and the availability of large comprehensive phylogenetic trees for well studied taxonomic groups such as mammals (Bininda-Emonds et al. 2007), birds (McCormack et al. 2013), amphibians (Pyron and Wiens 2013), and flowering plants (e.g. Davies et al. 2004). Here, we review recent insights from phylogenetic studies of extinction risk, and re-examine how extinctions impact the tree-of-life.

Speciation and Extinction as Two Natural Processes

Extant species represent just a small fraction of all the species that have ever lived (Jablonski 1995; May et al. 1995; Niklas 1997). This standing biodiversity is the net difference between cumulative speciation and extinction over the evolutionary history of life on Earth. Both the processes of speciation and extinction are therefore intrinsic parts of Earth's natural history. Much effort has gone into exploring geographic and taxonomic patterns of diversity, looking to answer why some regions and some taxa are more species-rich than others. Recent debate has contrasted explanations based upon ecological limits and times for speciation (e.g. see Rabosky and Lovette 2008). Comparisons between sister taxa, which are by definition of equal age, allow us to control for time for speciation, and thus differences in richness must reflect either variation in speciation or extinction rates (Barraclough et al. 1998). Such comparisons have shown that diversification rates have been higher in more tropical lineages (Davies et al. 2004; Rolland et al. 2014), but that higher tropical species richness is most likely a product of both faster rates and longer times for speciation (Jansson and Davies 2008). However, high diversification might be explained by high speciation rates, low extinction rates or a combination of both, and until recently, it has not been possible to reliably disentangle the two.

Unraveling the processes of extinction and speciation remains a major challenge (Benton and Emerson 2007). The fossil record is often thought to provide the most reliable documentation of speciation and extinction, yet the cumulative fossil record suggests that speciation rate increases inexorably through time (Raup 1991; Nee 2006; Benton and Emerson 2007), whereas there is growing evidence suggesting that species accumulate in bursts, and speciation rates decline over time (Simpson 1953; Schluter 2000; Gavrillets and Vose 2005; Scantlebury 2013). Phylogeny provides an alternative tool for reconstructing evolutionary process (Harvey et al.

1994). Nee et al. (1994) illustrated how extinction rates could be estimated from phylogenetic trees (but see Rabosky 2010), but assumed constant rates model. New methods, for example, BiSSE (Maddison et al. 2007) and GeoSSE (Goldberg et al. 2011), relax this assumption, and allow us to estimate extinction and speciation rates simultaneously, for example, with the gain or loss of particular character states (BiSSE) or shifts in geographic distributions (GeoSSE). Phylogeny-based analysis of diversification provides some limited evidence for increasing speciation through time (e.g. Barraclough and Vogler 2002; Linder et al. 2003; Turgeon et al. 2005), but again, a scenario of rapid radiation followed by a decline in speciation rate over time appears to be more common (Harmon et al. 2003; Shaw et al. 2003; Kadereit et al. 2004; Machordom and Macpherson 2004; Morrison et al. 2004; Williams and Reid 2004; Xiang et al. 2005; Kozak et al. 2006; Weir 2006; Phillimore and Price 2008; Scantlebury 2013). This pattern could be linked to a density-dependent model of ecological opportunity and/or reflect punctual mass extinctions (e.g. Yessoufou et al. 2014) that open up new niche space for subsequent radiations (Crisp and Crook 2009). Recently, using phylogenetic information on the Cape Floristic Region, Davies et al. (2011) suggested that the processes of speciation and extinction may be inextricably linked.

Speciation and extinction are part of life's natural history, and to achieve equilibrium in standing diversity, speciation must equal extinction (Raup 1986). Even the classic MacArthur and Wilson (1963, 1967) model of island biogeography suggests that species richness is a dynamic equilibrium between immigration, speciation and extinction. However, today this balance is increasingly biased towards extinction (Millennium Ecosystem Assessment 2005), and we risk moving towards a new low-diversity state as it is not possible to manipulate speciation rates to match current losses (Barraclough and Davies 2005). Whilst there is increasing evidence that evolutionary processes can occur over ecological time scales (Kettlewell 1972; Endler 1986; Kinnison and Hendry 2001; Ashley et al. 2003), speciation can take a longer time to complete, whereas extinctions are occurring over much shorter time spans (Barraclough and Davies 2005). Even for the most famous examples of rapid speciation, such as Lake Victoria cichlids, diversification rates are estimated over 100's to 1000's of years, and evidence of 'reverse-speciation' indicates that speciation might not have been complete (Seehausen 2006). By contrast, rates of extinction are now estimated at many times background rates (Vitousek et al. 1997; Butchart et al. 2004), and are occurring over 10's to 100's of years.

Shifting the Balance Towards a Low-Diversity Earth

Extinction Trends

Whilst the scale of current species loss parallels that of mass extinction events in the paleontological past (May et al. 1995; Millennium Ecosystem Assessment 2005), unlike past extinctions which were caused by abiotic factors such as asteroid strikes,

volcanic eruptions, and natural climate shifts, the current crisis is driven largely by human activities, and is perhaps the first mass extinction event that can be attributed to a biotic cause. Current estimates indicate that 10–30 % of mammals, amphibians and birds are threatened with extinction (Millennium Ecosystem Assessment 2005). Taxonomic groups are not, however, equally at risk of extinction. Among terrestrial vertebrates, amphibians have the highest proportion at at-risk species, with at least a third of ~6600 known amphibians threatened with extinction (Wake and Vredenburg 2008). It is estimated that 12 % and 20 % of continental birds and mammals, respectively, have already been lost (Wilson 1992), but with a higher rate of loss observed on islands (Lohle and Eschenbach 2011). In fish, of the ~2,000 species that have been assessed 21 % are considered at risk of extinction (IUCN 2010). Our knowledge of extinction risks in invertebrates is much poorer; however, of the 1.3 million known invertebrates, less than 10,000 species have been assessed, of which 30 % are threatened (IUCN 2010).

In plants, extinction trends appear to be even more alarming, but estimates need to be interpreted carefully. For example, over 70 % of Red-listed species of flowering plants are classified as at risk of extinction (category VU or higher) (IUCN 2010). This proportion is much higher than that reported for vertebrate groups (22 %), but as yet only a very small fraction of total plant diversity has been assessed (~13,000 of >300,000 species), and a trend towards focusing on some of the most obviously vulnerable species might bias our estimates of threat upwards. For clades with more complete sampling, such as cycads, the proportion of threatened species remains high (>80 %), but perhaps this ancient group that peaked in diversity in the Jurassic–Cretaceous (Jones 2002; Taylor et al. 2009) when dinosaurs roamed the Earth, is not representative of current seed plant diversity. One recent attempt to estimate the true proportion of threatened species within angiosperms using a statistical model to correct for sampling bias – the sampled Red List – has suggested that the percent of at-risk plant species might actually be more comparable to that for mammals (<http://threatenedplants.myspecies.info/>).

The spatial congruence in taxonomic richness across taxonomic groups has been well described globally (Grenyer et al. 2006), with the richest areas of the world found in highly productive environments at low latitudes and in mountainous regions (Orme et al. 2005). Similarly, there is a geographical pattern in the distribution of rare and threatened taxa, which has been shown at the global scale for vertebrates (e.g. Grenyer et al. 2006), and at various scales for plants (e.g. Zhang and Ma 2008; Davies et al. 2011; Daru et al. 2013). However, hotspots of richness and rarity or threat do not necessarily coincide (Grenyer et al. 2006). For example, vertebrate richness peaks on the Neotropical mainland, but bird rarity concentrates on oceanic island archipelagos, the diversity of rare mammal species peaks on continental shelf islands and rare amphibian species are more centered on continental landmasses (Grenyer et al. 2006). The variation in geographical patterns of rarity may be partially linked to differences in relative dispersal ability across taxa. Spatial variation in extinction risk additionally reflects differences in the distribution of threats facing each group. For example, invasive species and overexploitation are key threats for birds whereas overexploitation is the major driver of species loss in mammals

(Baillie et al. 2004), and climate change, pollution and transmissible diseases are important in amphibians (Stuart et al. 2004).

Extinction Drivers: Animals Versus Plants

Extrinsic Versus Intrinsic Factors

Explaining why some species appear predisposed to higher extinction risk than others is an important goal for conservation research (McKinney 1997). The five main extinction drivers include habitat loss, climate change, increased pollution, resources over-exploitation and invasive species (Millennium Ecosystem Assessment 2005), and all are linked directly or indirectly to anthropogenic pressures. These drivers parallel Jarred Diamond's 'evil quartet' (Diamond 1984, 1989), but with the more recent addition of climate change, and Diamond additionally included the possibility of extinction cascades in which secondary extinctions follow the loss of key species, for example, due to the disruption of ecosystem processes. We can further simplify this list into extrinsic (e.g. climate change) and intrinsic factors (e.g. ecological traits such as population density and species life-history traits such as body size and gestation length) (Cardillo et al. 2005). Extrinsic factors might help explain geographic variation in extinction risk, whereas intrinsic factors might better explain taxonomic patterns; however, highest risk is where driver intensity associated with extrinsic factors overlaps with species intrinsic vulnerability. In addition, species are increasingly likely to be exposed to multiple drivers, and this will likely further exacerbate risk of extinction (Brook et al. 2008).

Extinction Drivers in Animals

Correlates of extinction risk in animal kingdom have been explored extensively using data from the IUCN Red List (Bennett and Owens 1997; Russell et al. 1998; Purvis et al. 2000a, b; Cardillo 2003; Cooper et al. 2008) with particular attention to mammals (Russell et al. 1998; Cardillo et al. 2005, 2008; Isaac et al. 2007; Huang et al. 2012), perhaps the best-studied higher taxonomic group. Across studies, high extinction risk is generally associated with large body size, long generation times and small geographic range sizes (Bennett and Owens 1997; Russell et al. 1998; Purvis et al. 2000a; Cardillo 2003; Fisher and Owens 2004; Cooper et al. 2008). Conversely, species at low risk of extinction are small, reproduce rapidly, and have a wide niche breadth.

We know, for example, that mammals that are at risk of extinction are, on average, an order of magnitude heavier than non-threatened species (IUCN 2003). The size-selectivity of extinction risk is not unique to the current extinction crisis; past mass extinction events, such as that of the late Pleistocene, were also biased towards larger species (Martin 1967; Johnson 2002). During the late-Pleistocene – early-

Holocene extinction event, there was a mass extinction of much of the mammalian megafauna, resulting in a loss of several complete ecological guilds and their predators (Cione et al. 2003). Size selectivity in extinction risk has been long-recognised (e.g. Pimm 1991; Lawton 1995; Pimm et al. 1988; Cardillo and Bromham 2001; Johnson 2002), and there are many potential explanations. Large-sized mammals might be more extinction-prone because of generally lower average population densities (Damuth 1981), putting them at greater risk from stochastic population dynamics. High risk in large bodied mammals might also reflect the negative correlation between intrinsic rates of population increase and body mass (Fenshel 1974), and thus longer recovery times following population declines. There might also be an increased propensity for humans to exploit larger species (Bodmer et al. 1997; Jerzolimski and Peres 2003). The relationship between species traits and extinction risk, however, is not straightforward, because of the complex interaction between intrinsic and extrinsic drivers, and different clades might have very different predictors (e.g. see Cardillo et al. 2008).

Cardillo and colleagues (2005) demonstrated that risk in small-sized mammals (<3 kg) was largely determined by extrinsic factors including the size and location of geographical ranges. However, the predisposing factors in the larger size class include both intrinsic species properties (e.g. population density, neonatal mass and litters per year) and extrinsic factors. Such fine-scaled analyses can help address whether extinctions are linked to 'bad genes' or 'bad luck' (Raup 1993; Bennett and Owens 1997). For mammals, it appears that extinction in small bodied species is more likely a case of bad luck, driven by extrinsic factors. For larger bodied species, bad genes, that is, genes controlling intrinsic traits such as body size and life history are additional aggravating factors promoting extinctions.

Compared to vertebrates, the distribution and drivers of extinction risk in invertebrate communities has been poorly explored. However, a recent study estimated that one-fifth of invertebrate species may be threatened with extinction, with freshwater species at particular high risk (Collen et al. 2012). Collen and colleagues suggested that the greater threat to freshwater species was predominantly driven by agricultural pollution and dam construction, invasive species and waterborne diseases. More generally, and perhaps unsurprisingly, species that are less mobile and with limited geographic ranges, such as freshwater mollusks, tend to be at higher risk (Collen et al. 2012). In marine ecosystems, however, the market values of some invertebrates correlate strongly with their risk of extinction, e.g. invertebrate species considered luxury seafood (Purcell et al. 2014), providing an exception to the general trend for greater threat to be observed in larger-sized species.

The phylogenetic distribution of extinction risk in mammals has also been of much interest. In mammals, it has been suggested that species subtending from longer phylogenetic branches, and thus representing greater unique evolutionary history, are at higher risk of extinction (Russell et al. 1998; Purvis et al. 2000a). This pattern matches to Wilson's (1961) 'taxon cycle', which predicts that older species would have higher extinction probabilities as species expand and contract in their geographical distributions over their evolutionary lifetimes. Although, as originally described, the taxon cycle referred to the distribution of species on islands (ants on

islands in Melanesia), the concept has been extended to include species on continents (e.g. see Ricklefs and Bermingham 2002). Alternatively, it might simply echo the pattern of historical extinctions, in which older species represent survivors of once more diverse clades (Purvis et al. 2000a). However, the precise relationship between extinction risk and evolutionary age remains debated (Verde et al. 2013). Further, patterns of extinction risk in plants appears to show an opposite trend, with higher risk associated with young species in species rich (Schwartz and Simberloff 2001; Meijaard et al. 2007) and more rapidly diversifying clades (Davies et al. 2011), suggesting that predictors of extinction in plants might be very different to those for mammals.

Extinction Drivers in Plants

Species extinction in the plant kingdom is predominantly the result of habitat loss, for example through deforestation. Tropical forests, which cover less than 7 % of the world land area, contain over 50 % of global biodiversity (Dirzo and Raven 2003), but these unique habitats are being destroyed at unprecedented rates (Laurance 1991; Achard et al. 2002) as a result of rapid human population growth and economic development. In tropical Asia and Africa, over 40 % of the primary forests is already lost (Wright 2005). This drastic reduction in forest cover has had a devastating impact on plant diversity (Sodhi and Brook 2006). Although there is some evidence that, globally, recent rates of deforestation are slowing, we likely owe a large extinction debt due to the time lag between habitat loss and species losses predicted from the reduction in area. Thus, even should we be successful in preserving the remaining forest cover, many species might still be predicted to be lost over the following decades as habitats return to a new, lower diversity, equilibrium state. This extinction event will likely be exacerbated by the effects of ongoing climate change as local climate conditions shift and species are forced to either adapt to new conditions or track climate space (Willis et al. 2008).

Plant responses to environmental change are difficult to predict. With warming, plants might adapt by shifting their phenologies – the timing of life history strategies – for example flowering earlier and losing leaves later (Parmesan 2007). Recent work indicates significant phylogenetic conservatism in flowering phenology (Davies et al. 2013), suggesting that there might be some evolutionary constraints to species adaptive responses. If the velocity of climate change is high, species may not have the necessary time to adjust their phenological responses. Alternatively, species might track suitable climates, for example by shifting their distribution northwards or towards higher elevations (Sandel et al. 2011). Species already restricted to high elevation biomes might then be particularly vulnerable as increased warming may result in the reduction of suitable habitat and, at the extremes, complete habitat loss. In the biodiversity hotspots of the Eastern Arc Mountains of East

Africa, species at higher elevations already tend to be more threatened, perhaps reflecting recent climate shifts (Yessoufou et al. 2012). Species that are unable to adapt their phenology or track climate through space will be most vulnerable to extinction. In data from Thoreau's woods in Concord, MA, spanning 100 years, it is already possible to detect declines in populations among species that have failed to shift their phenologies to match recent climate change (Willis et al. 2008, 2010). These data also revealed phylogenetic structure in species responses, suggesting evolutionary conservatism not only in flowering times, but also plasticity in flowering times (see also Davies et al. 2013).

As for animals, there has been much work aimed at identifying intrinsic life-history traits that predispose some plant species towards extinction (Sodhi et al. 2008). However, investigating the correlates of extinction risk within the plant kingdom has proven somewhat more challenging, as key traits frequently differ between studies (Walker and Preston 2006; Sodhi et al. 2008). In addition, traits explain only a small proportion of the variation in extinction risk and, with the exception of geographic range size, we have yet to reveal any single strong correlate equivalent to, for example, body size in mammals. Life-history traits that have been found to correlate with plant extinction include pollination syndrome (e.g. wind or animal mediated), sexual system, habit, height, and dispersal mode (Sodhi et al. 2008). For tropical angiosperms, these traits can explain ~10 % of extinction risk (Sodhi et al. 2008), whereas equivalent models of intrinsic drivers for mammals can explain up to 30 % of the variation in extinction risk (Cardillo et al. 2008). However, even for mammals, explanatory power tends to be lower when exploring predictors across disparate clades (Cardillo et al. 2008), reflecting clade specific sensitivities to different drivers. Perhaps, therefore, it is unsurprising that in flowering plants, a group containing up to 500,000 species, predictive models are often poor.

An alternative avenue of exploration has considered the importance of evolutionary history in models of extinction risk (Sodhi et al. 2008; Davies et al. 2011). In plants, there is increasing evidence that a species evolutionary history might be more important than its life history in explaining extinction risk. As mentioned above, threatened terrestrial plants generally fall within species-rich clades (Schwartz and Simberloff 2001; Pilgrim et al. 2004) that represent recent radiations (Davies et al. 2011). However, when we look at the distribution of extinction risks across plant families, species-poor and especially monotypic families also appear to contain species at higher risk of extinction (Vamosi and Wilson 2008). It is therefore possible that mechanistic explanations for variation in extinction risk differ between old and young clades. Old and species-poor families may represent remnants of once more diverse clades, with species vulnerabilities associated with intrinsic life history traits and long generation times, as in mammals. In contrast, extinction risk in younger, still diversifying clades, may be more closely linked to the speciation process, with high extinction risk more closely associated with traits driving speciation, such as small geographic range size and short generation times.

The Importance of Phylogeny in Conservation

Why We Need to Evaluate Extinction Risk within a Phylogenetic Framework

Phylogenetic approaches are now well accepted in many ecological disciplines. Phylogenetic methods are also increasingly commonplace in extinction biology (see Purvis 2008). The necessity of employing a phylogenetic framework for exploring a non-evolving trait such as risk of extinction has been questioned (Grandcolas et al. 2011). Reasons for doing so are multifold. First, as we have discussed above, many drivers of extinction risks can be linked to phylogenetically conserved traits, such as body mass (Cardillo et al. 2005, 2008) and phenology (Willis et al. 2008, 2010). Therefore, phylogenetic comparative methods, such as independent contrasts (Felsenstein 1985) or phylogenetic regression are important because species cannot be considered as statistically independent (see Purvis 2008 for further discussion). Second, species evolutionary history might itself be an important predictor of extinction risk, for example, with higher risks associated with either more evolutionarily distinct lineages (Purvis et al. 2000a; Mace et al. 2003) or centres of diversification (Davies et al. 2011), depending on the clade and taxonomic scale. Third, by considering extinction within a phylogenetic framework, we can quantify directly its impacts on the tree-of-life as the loss of phylogenetic diversity (PD) (Purvis et al. 2000a; Mace et al. 2003). This measure of evolutionary heritage provides a useful conservation metric, typically measured in millions of years, it is easily comprehensible, and simple to calculate for particular regions or taxa (Moore et al. 2005). Although, there remain practical obstacles in the implementation of phylogenetic approaches for conservation planning, there is now increasing appreciation of the importance of including an evolutionary perspective within conservation goals, as illustrated by the Zoological Society of London's EDGE of existence programme (<http://www.edgeofexistence.org/>) that emphasises the conservation of evolutionary distinct and threatened species (Isaac et al. 2007).

Practical Contribution of Phylogeny to Conservation

The practical contribution of phylogeny to conservation actions has recently been discussed (Cardillo and Meijaard 2012; Winter et al. 2013). In part, the conservation value of the phylogenetic approach is in its ability to guide pre-emptive actions towards identifying and prioritizing the most at-risk species. For example, by identifying species with traits or in regions that predispose them to high risk of extinction, we can identify species that are not yet at risk of extinction but which might become threatened in the near future if current extinction drivers increase in intensity or geographic extent. Cardillo et al. (2006) referred to such species as having high 'latent risk' of extinction. Given limited conservation funding, focusing efforts on species with high latent risk might make economic sense as it is likely to be more

cost effective to prevent species declines before they begin versus reestablishing viable populations for species that have already suffered declines and may have lost much of their natural range. Preserving intact habitats will almost always be easier and cheaper than returning transformed habitats to their natural states.

A justification for placing emphasis on the preservation of phylogenetic diversity per se is that phylogenetic diversity captures feature diversity (Faith 1992; Crozier 1997; see also section “[Feature diversity and evolutionary models of character change](#)”), and thus preserving the set of species that maximizes phylogenetic diversity also maximizes the possibility of having the right set of features in an uncertain future. Forest et al. (2007) provided an example of the utility of phylogenetic diversity in the Cape Floristic Region of South Africa by demonstrating that preserving the phylogenetic diversity of the flora would maximize future options for the benefit of society through a continued provisioning of key ecosystem services. To date, empirical examples of conservation actions implemented explicitly to protect phylogenetic diversity are rare; however, one recent effort spearheaded by the Zoological Society of London’s EDGE programme specifically aims at focusing conservation attention on evolutionary distinct species at risk of extinction. These EDGE species are distinct not only in the history of their evolutionary past, but perhaps also in the functional roles they might fill within ecosystems. The extinction of EDGE species might therefore result in the loss of important ecosystem functions and services for which we have no species substitute. Some EDGE species (e.g. elephants and pandas) are well known, but many others (e.g. Chinese giant salamanders and the peculiar long-beaked echidnas) have been overlooked by traditional conservation strategies (see Isaac et al. 2007, 2012).

Critically, the utility of phylogenetic metrics and methods in conservation biology relies upon the accuracy of the underlying phylogenetic topology and, if we are interested in capturing feature diversity, the evolutionary model of character change along the branches of the tree, a point we explore further in the following sections.

Extinction and the Loss of Evolutionary History

Phylogenetic Structure in Extinction Risks

We have discussed above how the process of extinction is non-random with respect to species traits and geography. For example, extinction will tend to remove large-bodied species with slow life histories and narrow niches, and species in regions with high intensity of extinction drivers. Because many of the traits linked to extinction risk (e.g. body size, generation time, dispersal ability etc.) demonstrate phylogenetic conservatism (Fritz and Purvis 2010), such that they tend to be clustered on the phylogeny, extinctions will also tend to cluster on the phylogeny. Whereas evidence for trait-based explanations for plant extinctions is mixed (Freville et al. 2007; Bradshaw et al. 2008; Sodhi et al. 2008; Davies et al. 2011; Daru et al. 2013),

phylogenetic selectivity in extinction risk might also result from a geographical pattern in the drivers of extinction, for example, range elevation might determine a species vulnerability to climate change (Sandel et al. 2011). If closely related species also tend to have close geographical proximities, perhaps reflecting shared habitat preferences or the geographical process of speciation, they will then also be exposed to similar intensity of extinction drivers. There is an increasing weight of evidence suggesting that extinction risk is generally more clustered on a phylogeny than expected by chance (Bennett and Owens 1997; Purvis et al. 2000a; Schwartz and Simberloff 2001), a pattern also observed within the fossil record. Extinction will thus prune the tree-of-life non-randomly. However, how this non-random pruning might impact the loss of evolutionary history has been a subject of recent debate.

Quantifying the Loss of Evolutionary History

Extinction prunes species from the tips of the tree-of-life, resulting in the loss of terminal branches. In a frequently cited paper, Nee and May (1997) used simulations to explore the expected loss of evolutionary history (quantified as the summed branch lengths from the tree-of-life) under various extinction intensities. Perhaps surprisingly, they found that up to 80 % of the tree would remain under even extreme extinction scenarios in which 95 % of species were lost. However, their simulations were unrealistic in two regards. First, they assumed extinction events were random – the field-of-bullets model, in which extinction is independent of species' traits and thus also phylogeny. If extinctions are clustered on a phylogeny, we might also lose the internal branches of the tree that connect them, and thus experience a greater overall loss of phylogenetic diversity (Russell et al. 1998; Purvis et al. 2000a). Second, their expectation was derived assuming a phylogeny based on a coalescent model, which generates a highly unrealistic distribution of branching times, with most branches clustered towards the present (see Fig. 1a), and does not fit to most empirical estimates of phylogenies. Importantly, coalescent trees tend to be 'tip-heavy' such that most branching events are short and clustered towards the present (tips of the tree). Therefore, under this model, most extinctions remove only short terminal branches from the tree, and most major lineages survive even extreme pruning of tips. Empirical phylogenies tend to have a very different distribution of branching times (e.g. Rabosky and Lovette 2008; see also Fig. 1b, c for pure birth and birth-death tree). Mooers et al. (2012) explore further how tree shape impacts the expected loss of phylogenetic diversity. The phylogenetic non-random distribution of extinction risk and the shape of empirical phylogenies might therefore suggest that we risk losing a disproportionate amount of evolutionary history from the tree-of-life.

A suite of empirical studies were to follow on from the early work of Nee and May, and emphasized both the phylogenetically non-random nature of species' extinctions and a greater than random loss of phylogenetic diversity (e.g. Purvis et al. 2000a; Purvis 2008; Vamosi and Wilson 2008). A link between non-random

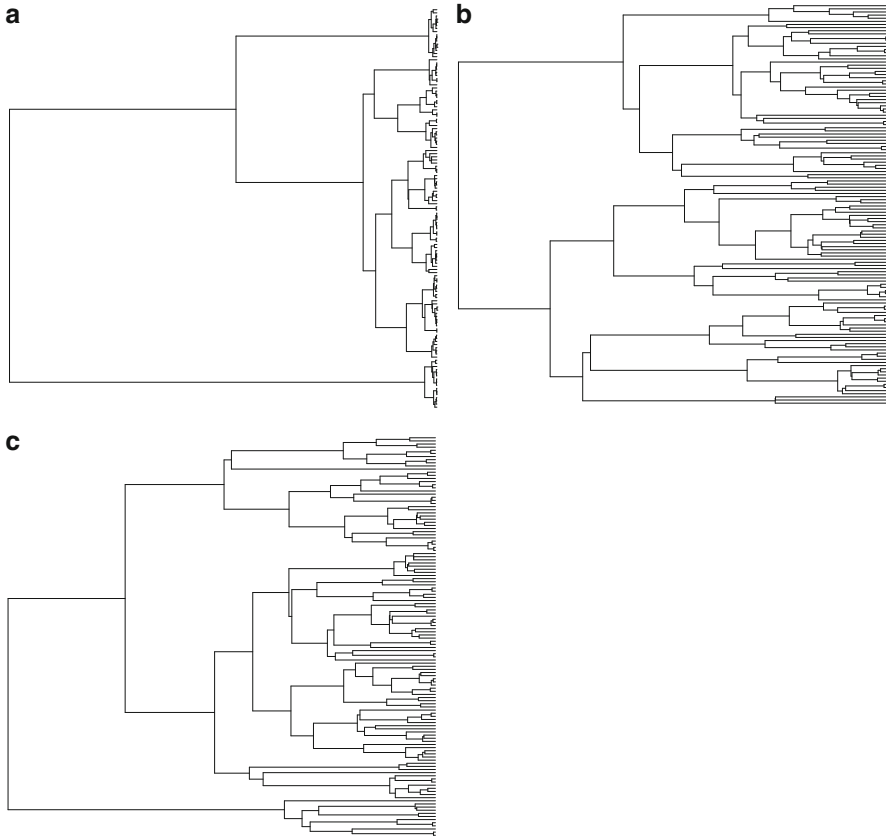


Fig. 1 Comparison of branching times for different tree reconstruction models of size 128 tips. **a** Coalescent model in which branching clusters towards present; **b** pure birth model in which all lineages have an equal probability of splitting ($b=1.0$) and no lineages go extinct ($d=0$); **c** birth-death model in which lineages have equal rates of splitting and extinction ($\text{birth}=1.0$, $\text{death}=0.2$)

extinction and greater than random loss of phylogenetic diversity seemed intuitive; if two sister species are lost to extinction, not only do we lose the unique phylogenetic diversity captured in the branches from which they subtend, but we also lose the ancestral branch that is shared between them (see Fig. 2). However, in a more recent study, again using simulations, but this time assuming both a more realistic model of diversification and a range of phylogenetic signal in extinction probabilities, Parhar and Mooers (2011) suggested that the loss of phylogenetic diversity under phylogenetically non-random extinctions was more or less indistinguishable from random (see also Heard and Mooers 2000). Seemingly, the observation of phylogenetic signal in extinction risks and the non-random loss of phylogenetic diversity are not necessarily connected directly.

Observations for greater than random losses of phylogenetic diversity that have been inferred for many clades under realistic extinction scenarios likely reflect the

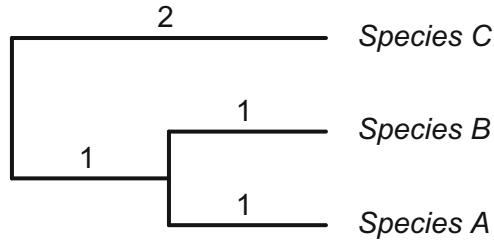


Fig. 2 Ultrametric phylogenetic tree with three tips (A, B and C) and four branches with lengths in millions of years (Myrs). If tip taxa A and C become extinct, we lose two branches and 3 Myrs of evolutionary history from the tree. If sister taxa A and B become extinct, for example, because they share a phylogenetically conserved trait that predisposes them to high risk, we also lose 3 Myrs of evolutionary history, but this time three branches are lost from the phylogeny

particularities of phylogenetic tree topology in combination with a tendency for more extinction prone species to fall within species poor clades (Heard and Mooers 2000; von Euler 2001; Parhar and Mooers 2011). There does seem to be a general trend within some clades for threatened species to be overrepresented in species-poor clades (e.g. in mammals, Purvis et al. 2000b and birds, Bennett and Owens 1997). In plants, patterns appear mixed. As discussed above, there is some evidence suggesting an opposite trend to vertebrates, with a greater proportion of threatened plant species falling within species-rich clades (Schwartz and Simberloff 2001; Lozano and Schwartz 2005), and less evolutionary distinct lineages (Davies et al. 2011). Globally, however, species poor, and especially monotypic plant families, again appear to be more threatened, and their extinction would also result in a disproportionate loss of evolutionary history (Vamosi and Wilson 2008).

Feature Diversity and Evolutionary Models of Character Change

Underpinning the theoretical arguments for maximizing the preservation of phylogenetic diversity is the assumption that it captures feature diversity (i.e. variance in measured ecological and morphological traits), and thus selecting the set of taxa to maximize phylogenetic diversity will also maximize feature diversity (Faith 1992; Crozier 1997). Many biological traits demonstrate significant phylogenetic signal (Blomberg et al. 2003) and therefore this assumption might be broadly valid. However, the relationship between phylogenetic diversity, which is measured in millions of years, and feature diversity is not straightforward, but assumes a linear divergence between species over time, for example, as might be modeled under a Brownian motion process, in which trait variance increases in proportion with time, but for which evidence is mixed. Frequently, traits demonstrate much weaker phylogenetic signal than assumed by a strict Brownian motion model (e.g. Kamilar and Cooper 2013). Although there are a large number of alternative models of

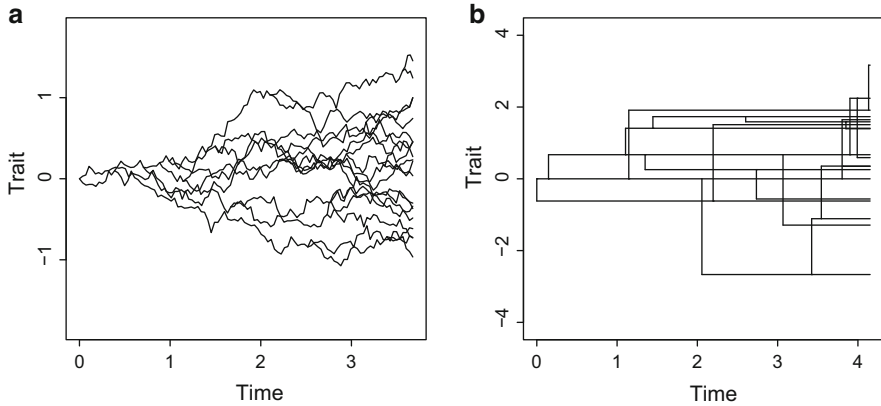


Fig. 3 Simulations showing accumulation of trait variance over time assuming a Brownian motion model of trait evolution **a** in which variance increases in proportion to time, versus a punctuated model of trait evolution **b** in which trait change occurs in bursts at speciation, and a pure-birth process of phylogenetic branching (see also Ingram 2011; Davies 2015)

evolutionary change, including the Ornstein-Uhlenbeck model which approximates stochastic evolution with stabilizing selection (Hansen 1997) and the early burst model that might characterize adaptive radiations (Harmon et al. 2010), we here (see Davies and Yessoufou 2013; Davies 2015) compare the potential loss of phylogenetic diversity under two models with very different assumptions: (1) a model of phylogenetic gradualism as represented by Brownian Motion (Fig. 3a), and (2) a punctuated model of evolution in which trait differences accumulate in bursts at speciation (Fig. 3b).

To date, the model of evolution has rarely been considered explicitly within the conservation phylogenetics literature (e.g. Owens and Bennett 2000). However, if traits evolve following a speciational model – as may be the case for body mass in mammals (Mattila and Bokma 2008) – where trait evolution occurs in bursts at speciation, each individual branch would capture similar feature diversity, and as such, the number of branches might be of equal, or greater conservation value than their summed lengths. Furthermore, because nonrandom extinction may target deeper branches in the tree-of-life (Mckinney 1997; Purvis et al. 2000a; Purvis 2008), we would predict a disproportionate loss of branches without necessarily a concomitant loss of total summed branch lengths (Fig. 2). Non-random extinction might therefore have a greater impact on number of branches lost than on the sum of their branch lengths – which has been the focus of most studies to date.

Using a dated phylogenetic tree for Primates, Carnivora and Artiodactyla, we (Davies and Yessoufou 2013) combined simulations and empirical extinction risk data from the IUCN Red List of threatened species (<http://www.iucnredlist.org/>) to explore the loss of phylogenetic diversity under two alternative evolutionary models. First, following standard practice, we calculated the expected loss of PD assuming a gradual model of evolution. Second, we also calculated the equivalent loss of diversity under a speciational model of evolution (in which all branches are assigned

equal weights) following the approach of Witting and Loeschcke (1995). Extinction categories were first converted into extinction probabilities, $p(\text{ext})$, following Mooers et al. (2008) and assuming IUCN designations projected to 50 years. We then compared observed losses to expectations from the same distribution of $p(\text{ext})$, but randomly assigned to species at the tips of the phylogeny (100 replicates). Last, we explored the relationship between phylogenetic signal, estimated using Pagel's (1999) Lambda, and the loss of evolutionary history by evolving traits along the branches of simulated phylogenetic trees. Here, we assume a birth–death tree ($b=0.2$, $d=0$, size $n=240$), in contrast to the unrealistic coalescent trees used by Nee and May (1997). Based on the simulated trait values, a constant fraction of species (the top 25 %, as this broadly matches the proportion of threatened mammal species in the IUCN Red List) were then assigned high risk of extinction ($p(\text{ext})=0.75$).

Our results reveal that under a speciation model of evolution, non-random extinction prunes more branches from the tree-of-life (see also Fig. 2), but that the loss of summed branch lengths (Faith's PD) does not depart significantly from random expectation (Davies and Yessoufou 2013). Although there is a weak trend for greater loss of phylogenetic diversity (PD) and number of branches lost with increasing phylogenetic signal in extinction risk, there is large variance in PD loss under random pruning such that observed losses typically overlap to a greater extent with the null distribution. In contrast, there is much less variance in the number of pruned branches such that random extinctions of equivalent intensity would prune similar number of branches. Therefore, observed number of branches loss more often falls outside the null distribution from randomizations (Fig. 4).

Conclusion

There is an increasing call for prioritizing efforts towards the conservation of phylogenetic diversity (Mace et al. 2003; Forest et al. 2007; Davies et al. 2008). Implicit within this conservation agenda is an assumption that species diverge in their ecological and morphological traits more or less linearly through time, and thus that the evolutionary distance between species captures their functional differences. We (Davies and Yessoufou 2013) explored scenarios where this assumption is violated, and feature diversity occurs in bursts at speciation, matching to a punctuated model of trait evolution. Our results illustrate that projected extinctions might prune more branches from the tree-of-life than predicted from the same number of extinctions randomly distributed across the phylogeny; however, the loss of summed branch length might be no greater than expected by chance.

We do not suggest that punctuated evolution is necessarily a better model of trait change, but rather we emphasise the need for a more explicit consideration of evolutionary models if our aim is to maximize feature diversity. Recent advances in comparative methods have allowed comparisons between alternative evolutionary models, and frequently find strict Brownian motion to be a poor fit to observed trait

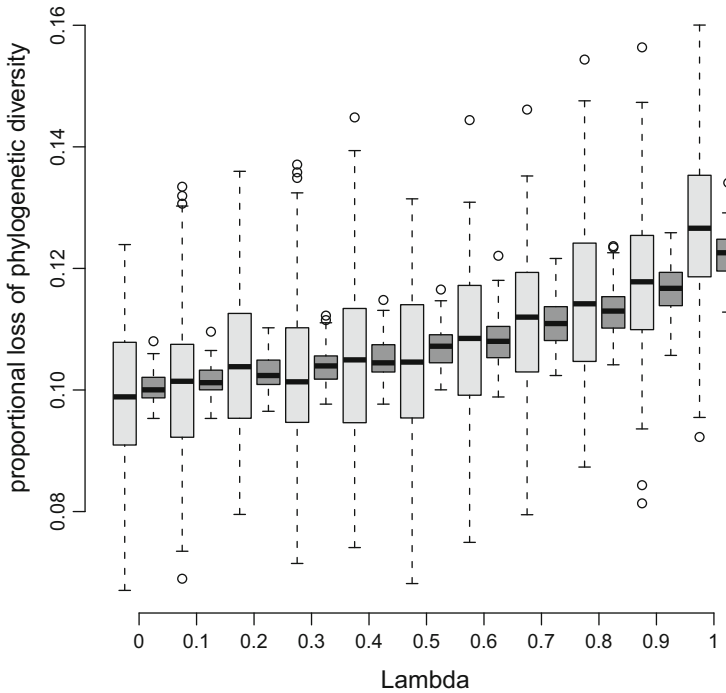


Fig. 4 Results from simulated extinctions with varying levels of phylogenetic clustering (Lambda) across 100 random birth–death trees (see Fig. 1c) assuming $p(\text{ext})=0.75$ for the top 25 % of species. *Light grey boxes* = expected loss of PD for empirical branch lengths (assuming phylogenetic gradualism or a Brownian motion model of trait change); *dark grey boxes* = expected loss of PD assuming equal branch lengths (matching to a punctuated model of trait change). Simulations with Lambda=0 are equivalent to random extinctions. This figure is similar to that in Davies and Yessoufou (2013), but presents a new set of stochastic simulations

data (e.g. Blomberg et al. 2003; O’Meara et al. 2006; Harmon et al. 2010). It remains possible that Brownian motion might still best capture aggregate species differences even when individual traits diverge from a Brownian motion model, assuming traits are evolving independently or when selective regimes fluctuate over time (Felsenstein 1988). However, this expectation has rarely been evaluated using empirical data.

Finally, we note that our understanding of the distribution of phylogenetic diversity across space and among communities might also be informed by further consideration of evolutionary models. For example, traditional metrics of phylogenetic diversity tend to correlate very closely with species richness (Rodrigues et al. 2005), although it is possible to identify regions of greater or lower phylogenetic diversity than predicted from species richness alone, for example, by looking at residual variation (e.g. Forest et al. 2007; Davies et al. 2008). The covariation between evolutionary history and species richness might exhibit very different properties under alternative evolutionary models, but as far as we are aware, there have not yet been any equivalent studies exploring such models in geographical space.

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