IDEA AND PERSPECTIVE

Macroevolutionary perspectives to environmental change

Fabien L. Condamine[1]* Jonathan Rolland[1] and Hélène Morlon[1]*

Abstract

Predicting how biodiversity will be affected and will respond to human-induced environmental changes is one of the most critical challenges facing ecologists today. Here, we put current environmental changes and their effects on biodiversity in a macroevolutionary perspective. We build on research in palaeontology and recent developments in phylogenetic approaches to ask how macroevolution can help us understand how environmental changes have affected biodiversity in the past, and how they will affect biodiversity in the future. More and more paleontological and phylogenetic data are accumulated, and we argue that much of the potential these data have for understanding environmental changes remains to be explored.

Keywords

Biodiversity, birth–death models, diversification rates, extinction, fossils, global change, mass extinctions, paleoenvironment, speciation.

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INTRODUCTION

Human activities generate major environmental changes on our planet, in both the land and the sea (Barnosky *et al.* 2012). Habitat loss, global warming, increased UV-radiation, overexploitation and pollution exert high pressure on ecosystems and biodiversity (Barnosky *et al.* 2012). Species in all groups from vertebrates to invertebrates and plants are threatened by extinctions. It has been estimated that one-fifth of animal and plant species are threatened or face extinction, with some groups like cycads, amphibians, and corals particularly affected (Hoffmann *et al.* 2010; Barnosky *et al.* 2011). On the basis of extinctions that have happened million years ago (Ma) and on projected extinctions for the next 50 years, we could be entering one of the largest extinction events ever (Pimm *et al.* 1995; Barnosky *et al.* 2011).

It is not the first time that the Earth has experienced dramatic species loss (Raup & Sepkoski 1982). More than 99% of all species that ever lived are now extinct (Benton 1995). Interspecific competition, environmental changes, and stochastic factors drive species extinct, and clades wax and wane (Benton 2009). Five mass extinctions – characterised by more than 75% species loss in a very short time period (Barnosky *et al.* 2011) – have punctuated the history of life, shaping biodiversity by eliminating whole groups of organisms while fostering the subsequent diversification of others (Raup & Sepkoski 1982; Alroy 2010; Fig. 1). During the most drastic extinction event (the Permian-Triassic extinction), 80–96% of global biodiversity was lost (Chen & Benton 2012).

As environmental changes and extinctions are part of the history of life, studying the past can shed light on the current crisis (Hadly & Barnosky 2009; Barnosky *et al.* 2011). Analysing past extinction events allows evaluating background and exceptional extinction rates (Roy *et al.* 2009; Turvey & Fritz 2011), better understanding causes of extinctions such as long-term environmental changes or geological events (Peters 2005, 2008; Hannisdal & Peters 2011; Lorenzen *et al.* 2011), and assessing if, how and which biodiversity recovers from mass extinction events (Erwin 1998; Chen & Benton 2012).

The most straightforward approach to examining the past to inform the present is to analyse the fossil record (Hadly & Barnosky 2009). The paleontological record can be used to evaluate speciation and extinction rates through time (Roy *et al.* 2009) and to detect major extinction events (Raup & Sepkoski 1982; Alroy 2010). It is also a temporal window into how Earth's biodiversity coped with environmental changes in the past (Peters 2005, 2008; Erwin 2009; Benton 2009; Hannisdal & Peters 2011; Chen & Benton 2012; Fig. 1). However, the picture of the past provided by fossil data is not exhaustive (Benton 1995). Macroevolutionary dynamics during the Phanerozoic have mainly been documented with the marine fossil record because the terrestrial record is incomplete and uneven (Raup & Sepkoski 1982; Peters 2008; Alroy 2010; Song *et al.* 2011), but what happened on the land might be quite different from what happened in the sea (Sahney *et al.* 2010; Chen & Benton 2012).

Gaps in the fossil record have encouraged the development of alternative approaches to analyse long-term diversity dynamics. Methods have been developed to analyse the past using 'reconstructed' phylogenies (Harvey *et al.* 1994; Nee *et al.* 1994). Reconstructed phylogenies – branching trees describing the evolutionary relationships among extant species – can be inferred from molecular DNA sequence data. Phylogenies are becoming increasingly available, and along with recent macroevolutionary models in which diversification is modelled as a birth–death process, they can be used to infer speciation and extinction rates, how they vary through time, across clades, and with species' ecology (Maddison *et al.* 2007; Rabosky & Lovette 2008; Morlon *et al.* 2010, 2011; Stadler 2011a; Etienne *et al.* 2012). These approaches are playing an ever-growing role in the analysis of long-term diversity dynamics (Crisp & Cook 2009; Wiens *et al.* 2011; Condamine *et al.* 2012).

In parallel to a growing role in macroevolutionary studies, phylogenies have played an increasing role in ecology, in particular in community ecology with the recent advent of community phyloge-

[1]*CNRS, UMR 7641 Centre de Mathématiques Appliquées (École Polytechnique), Route de Saclay, 91128 Palaiseau, France*

Correspondence: E-mail: fabien.condamine@gmail.com; helene.morlon@cmap.polytechnique.fr
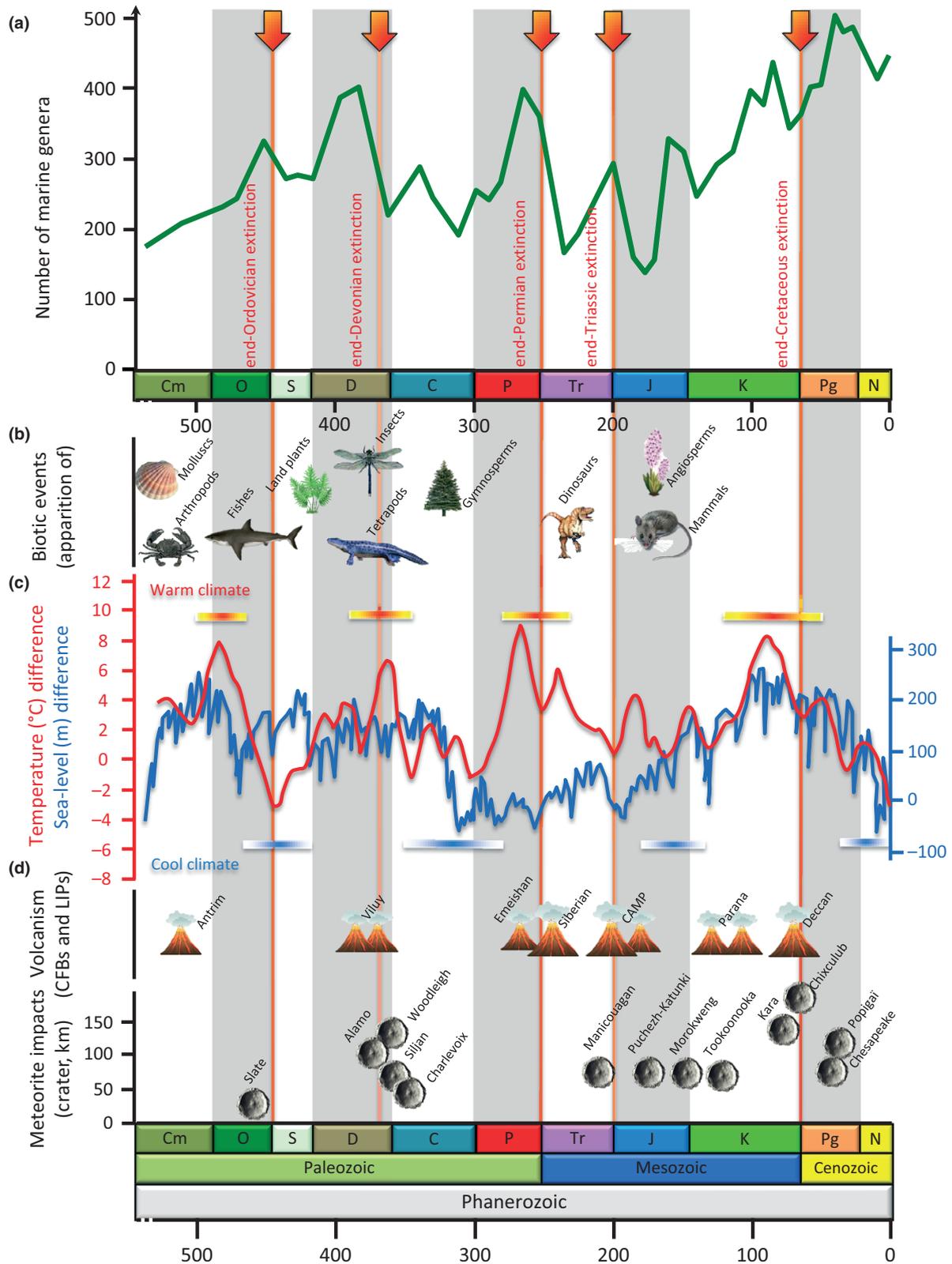
Figure 1 Paleontological setting. (a) The marine biodiversity curve through the Phanerozoic (adapted from Alroy (2010)) is punctuated by five mass extinction events, known as the Big Five (red arrows); (b) rise of major clades; (c) global cooling or warming events (red curve) and other environmental changes such as sea-level fluctuations (blue curve) are major determinants of diversity dynamics; (d) geological events such as volcanism due to tectonic movements (CFBs, continental flood basalts; LIPs, large igneous provinces), or meteorite impacts, modify atmosphere composition and impact diversity.

netics (Cavender-Bares *et al.* 2009), and in conservation biology with the interest in preserving the tree of life (Mace *et al.* 2003; Purvis 2008; Thuiller *et al.* 2011). In comparison, phylogenies have been rarely used to estimate background extinction rates (Barnosky *et al.* 2011), the extinction proneness of species (Purvis 2008), and more generally to analyse speciation-extinction with the aim of informing how biodiversity might respond to current environmental changes. Phylogenies have just begun being used to estimate the capacity for species to adapt to a changing environment (Lavergne *et al.* 2010). Their potential to bring insights into the effects of environmental changes remains largely unexplored (Rolland *et al.* 2012).

In this article, we highlight the role that macroevolutionary thinking can play to understand ecological effects of environmental change. We focus on three specific topics: (1) major extinction events, (2) background speciation and extinction and (3) vulnerability and evolutionary potential. For each of these topics, we review how fossil-based studies have been used and detail how phylogenies, combined with developments from birth–death models, paleoclimate, species traits and global change biology may be used. We illustrate our approach using the cetaceans (whales, dolphins and porpoises), which have both a nearly complete time-calibrated phylogeny (Steeman *et al.* 2009; Appendix S1) and a comprehensive fossil record (Quental & Marshall 2010). We end by outlining current limitations and prospects for future research.

MASS EXTINCTIONS AND RECOVERY IN RELATION TO ENVIRONMENTAL CHANGE

To predict how biodiversity might respond to the current crisis, it can be useful to estimate when mass extinctions occurred (Raup & Sepkoski 1982; Alroy 2010), how many species were lost (extinction intensity, Barnosky *et al.* 2011), which clades were impacted and what traits were associated with high extinction or survival probabilities (extinction selectivity, Peters 2008; Roy *et al.* 2009; Kiessling & Simpson 2011; Finnegan *et al.* 2012), as well as at which level of extinction biodiversity was able to recover (Erwin 1998; Brayard *et al.* 2009; Chen & Benton 2012).

Paleontological perspective

Paleontologists identified five mass extinction events over the last 542 Myrs, often referred to as the 'Big Five' (Raup & Sepkoski 1982; Alroy 2010): the Ordovician–Silurian extinction event (~443 Ma, ~86% species loss), the Late Devonian extinction event (~359 Ma, ~75% species loss), the Permian–Triassic extinction event (~252 Ma, ~96% species loss), the Triassic–Jurassic extinction event (~200 Ma, ~80% species loss) and the Cretaceous–Paleogene extinction event (~65 Ma, ~76% species loss) (Fig. 1).

The causes of mass extinctions have been the subject of much paleontological research, and they are still debated. Arens & West (2008) suggested a 'press/pulse model' in which mass extinctions generally require both long-term pressure on the ecosystem (press) and a sudden catastrophe (pulse) towards the end of the period of pressure, neither of these two causes alone being sufficient to induce a mass extinction. Mass extinctions often occurred following major climatic changes (cooling or warming, Harnik *et al.* 2012), suggesting that climate may act as the 'press'. The Cretaceous-Paleogene mass extinction follows a meteorite impact; the Ordovician–Silurian, Permian–Triassic, Triassic–Jurassic and

Cretaceous–Paleogene events concur with geological changes (e.g. tectonic and volcanic activities), and the Late Devonian extinction coincides with major biotic changes (e.g. the apparition of land plants that drastically diminished atmospheric carbon, Hannisdal & Peters 2011; Fig. 1).

None of the Big Five mass extinctions involved humans. The Pleistocene extinction event (which occurred ~50 000 years ago and killed ~178 large mammal species) is the only major extinction that took place when humans were on the planet and expanded rapidly (Lorenzen *et al.* 2011). This event also occurred at a time when Earth experienced a global warming episode. It appears that extinction during the Pleistocene was driven by either climate change alone (for the Eurasian muskox and the woolly rhinoceros) or a combination of climatic and anthropogenic effects (for the Eurasian steppe bison and the wild horse, Lorenzen *et al.* 2011). Global warming strongly affected habitat distribution, resulting in reduced genetic diversity and population sizes (Lorenzen *et al.* 2011). The Pleistocene extinction is thus particularly relevant to understanding the potential consequences of the on-going environmental changes.

The effect of mass extinctions is not only to lose species, but also to potentially lose morphological disparity, a proxy for niche occupancy, which can further hampers a clade's survival (Jablonski 2005; Brayard *et al.* 2009; Song *et al.* 2011) and reset the rules of ecological dominance (Alroy 2010). For example, only three or four ichthyosaur species (pursuit predators) survived the Triassic–Jurassic mass extinction, and although diversity bounced back in the aftermath of the mass extinction, disparity in body sizes remained at less than one-tenth of its pre-extinction level (Thorne *et al.* 2011). Eventually, the ecological niches previously occupied by ichthyosaurs were taken over by plesiosaurs, marine crocodilians, sharks and bony fishes. The Triassic–Jurassic extinction reset the evolution of apex marine predators by affecting ichthyosaurs' morphological disparity (Thorne *et al.* 2011).

As far as recovery from mass extinctions, some clades were able to rebound after an almost complete eradication (the ammonoids during the Permian-Triassic extinction, Brayard *et al.* 2009), while others such as the trilobites, ichthyosaurs and non-avian dinosaurs never recovered (Benton 1995; Jablonski 2005). When biodiversity recovers, it can either rebound 'quickly' (1–2 Myrs for ammonoids, Brayard *et al.* 2009), within roughly the equivalent of a geological period (5–15 Myrs for foraminifers, Song *et al.* 2011), or take over 20 Myrs (brachiopods and crinoids, Chen & Benton 2012). Among the various reasons why recoveries can be so variable from clade to clade, differences in body size, diet, geographical range size and habitat have been emphasised (Erwin 1998; Payne & Finnegan 2007; Kiessling & Simpson 2011). Recovery appears easier in pelagic vs. benthic habitats, likely because higher dispersal abilities in pelagic habitats allow faster niche colonisation and diversification (Song *et al.* 2011). Similarly, ecosystem recovery appears easier for basal vs. higher trophic level species, since top species can only start recovering once their preys have reappeared (Sahney & Benton 2008; Chen & Benton 2012). Recovery also seems easier for widespread species, as well as small, short generation time species that can diversify faster (Jablonski 2005; Payne & Finnegan 2007).

Another major determinant of recovery is the underlying diversity dynamics of clades (Fig. 2). If biodiversity is diversity-dependent, limited by the number of niches available, then it will bounce back 'quickly' after a punctuated loss to fill vacant niches (Erwin 1998). For instance, ammonoids took only 1–2 Myrs after the Permian–
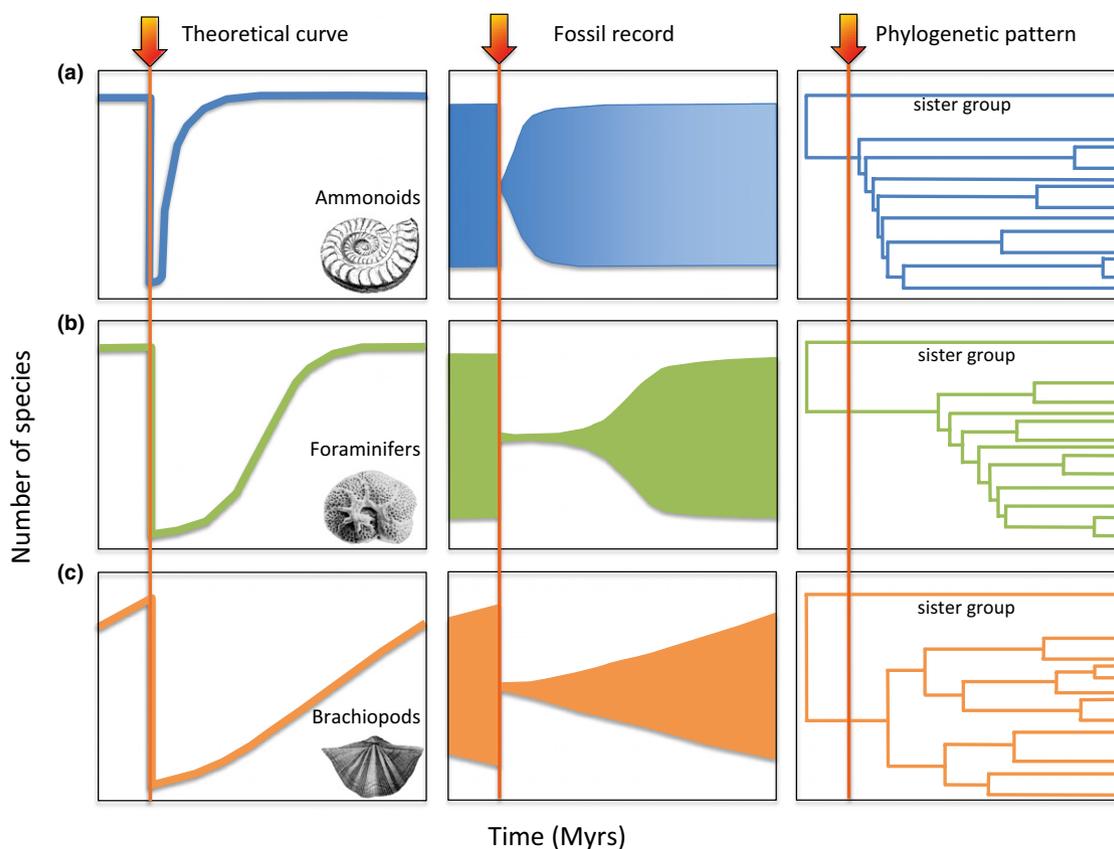
Figure 2 Schematic illustration of how biodiversity might recover from extinction events (red arrows). If species richness follows a logistic curve, as expected under the 'diversity-dependence hypothesis' (a and b), the recovery can be fast (a, ammonoids, Brayard *et al.* 2009) or slower (b, foraminifers, Chen & Benton 2012) depending on the initial net diversification rate. If species richness follows an exponential curve, as expected under the 'time-for-speciation hypothesis', it may take tens of Myrs for biodiversity to reach its pre-extinction level (c, brachiopods, Song *et al.* 2011). Left panels: theoretical curve predicting the recovery; Middle panels: expected pattern in the fossil record; Right panels: expected phylogenetic pattern. These plots are qualitative fabrications drawn by hand for illustrative purposes.

Triassic extinction to reach back the level of diversity they had before the event (Brayard *et al.* 2009). On the contrary, if biodiversity is limited by the time it takes to create new species, also known as the 'time-for-speciation' hypothesis, recovery can take a long time (Chen & Benton 2012). Crinoids and brachiopods were the commonest animals in Permian oceans, but after they experienced a sharp decline in the Permian–Triassic extinction, their diversity did not rebound until the Middle Triassic (Alroy 2010; Chen & Benton 2012).

Phylogenetic perspective

Besides fossils, phylogenies have been used to analyse mass extinctions and their link with environmental change, although to a much smaller extent. In their pioneering study, Harvey *et al.* (1994) analysed the footprint of mass extinctions left in lineage-through-time (LTT) plots, which report how the logarithm of the number of lineages in reconstructed phylogenies accumulates with time (Ricklefs 2007). Mass extinctions result in an anti-sigmoidal LLT plot, characterised by the presence of a plateau that corresponds to long branches without splitting events in the phylogeny (Harvey *et al.* 1994; Crisp & Cook 2009). Some authors have found such anti-sigmoidal curves in empirical phylogenies and tested the presence and intensity of mass extinctions using simulations (Crisp & Cook 2009; Antonelli & Sanmartín 2011). Simulations, however, are not ideal

for parameter estimation. They are not adapted either to distinguish mass extinctions from other scenarios deviating from the constant-rate birth–death model that result in phylogenetic shapes similar to those obtained under mass extinctions, such as diversity-dependent processes (Harvey *et al.* 1994) and periods of stasis followed by radiations (Crisp & Cook 2009).

An approach to analysing major extinction events, formalising Harvey *et al.* (1994)'s work, has been highlighted by Stadler (2011a), who implemented the maximum-likelihood optimisation of a birth–death model with punctuated random sampling (extinction events) in a user-friendly R package (*TreePar*). Under the hypothesis that speciation and extinction rates are identical before and after mass extinctions, the model allows evaluating if and when major extinction events occurred, estimating speciation and extinction rates, and evaluating the probability for species to survive the extinction event (the extinction intensity). By performing these tests on subclades within a phylogeny, it is possible to analyse which clades were impacted by the extinction.

Figure 3 illustrates the approach using the cetacean phylogeny, and compares the results with fossil data. In the case of the cetaceans, the estimated timing of the extinction event (~10 Ma) corresponds well with the beginning of diversity declines evidenced with both other phylogenetic approaches (Morlon *et al.* 2011) and the fossil record (Quental & Marshall 2010). The magnitude of the detected extinction seems high compared to fossil estimates (~86%
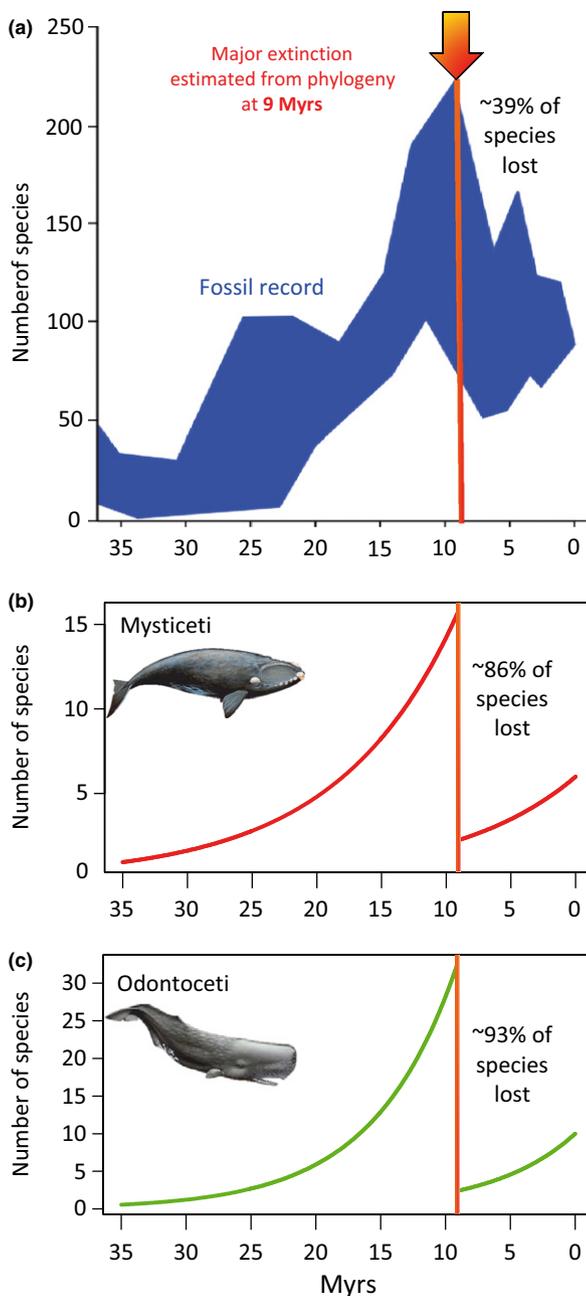
Figure 3 Detecting mass extinctions using phylogenies. (a) The phylogeny of Cetacea suggests a major extinction 9 Ma ($P < 0.05$). This major extinction event coincides with the decline in diversity starting ~10 Ma suggested by the fossil record (in blue, lower and upper estimates of diversity, adapted from Quental & Marshall (2010)). The phylogenies of both the Mysticeti (b) and Odontoceti (c) suggest an extinction event, also occurring 9 Ma ($P < 0.05$ for both groups). Panels b and c describe the corresponding inferred diversity trajectory of the two groups.

in Mysticeti and ~93% in Odontoceti), but the error around fossil estimates is also high (Fig. 3a).

The main limitation of current models is that mass extinction events, when modelled as instantaneous sampling events (Harvey *et al.* 1994), are indistinguishable from rate shifts (i.e. instantaneous change in diversification rate, Stadler 2011b). Consequently, to recover mass extinction events, one needs to assume that speciation and extinction rates are identical before and after these events. This
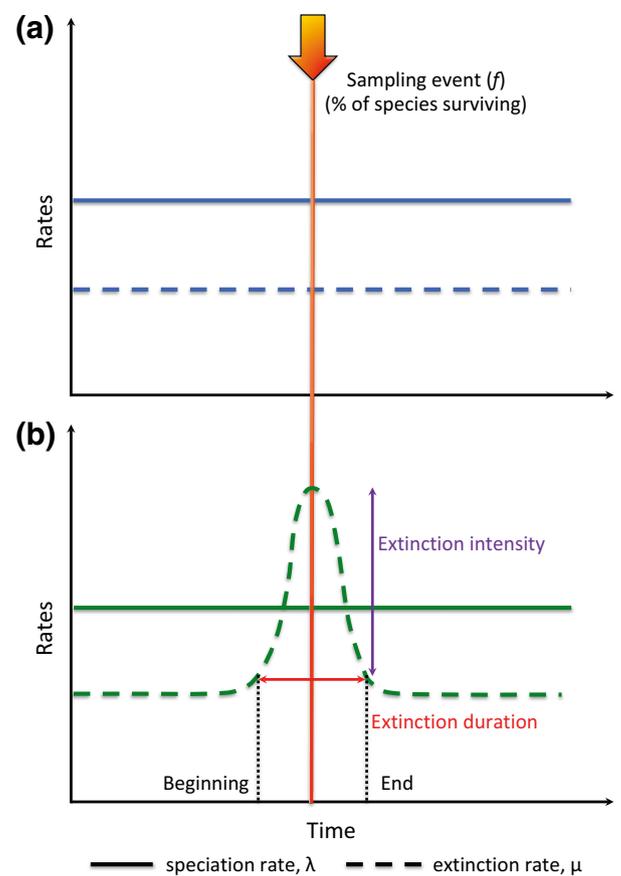

Figure 4 Models of diversification with mass extinction. (a) Current models treat mass extinctions as an instantaneous sampling process (Harvey *et al.* 1994; Stadler 2011a). At the time of the mass extinction (red arrow), a fraction f of all species, chosen at random, go extinct. f measures the intensity of the extinction (b) Future models, based on existing time-dependent models (Nee *et al.* 1994; Rabosky & Lovette 2008; Morlon *et al.* 2011), could use functional forms of the time-dependence of extinction that would account for the non-zero duration of mass extinctions.

assumption cannot be relaxed, as the signature of mass extinctions and rate shifts in the likelihood expression is exactly the same. This is problematic, because there is fossil evidence for long-term shift in diversification rates following mass extinctions (Krug *et al.* 2009).

Taking the duration of mass extinctions into account could help distinguish them from rate shifts. This would also provide a more realistic modelling approach, given that mass extinctions do not necessarily have a short time-span (the Devonian mass extinction lasted 2–29 Myrs). One way to do so would be to consider continuous descriptions of elevated extinction rates throughout the period of the mass extinction (Fig. 4), implemented within continuously varying time models (Nee *et al.* 1994; Rabosky & Lovette 2008; Morlon *et al.* 2011). Alternatively, background and mass extinction events could be modelled within the same continuous-time framework, in which mass extinctions are simply the extremes of a background continuum of extinction intensities and durations. This would remove at once the artificial distinction made between these two types of extinctions and hence the difficulty to distinguish between them. Such analyses, and more generally further empirical phylogenetic analyses of mass extinctions, could well reveal that the signal of mass extinction in phylogenies is more common than previously thought.

Current phylogenetic approaches to analysing mass extinctions do not take diversity-dependence into account. However, recovery from mass extinctions is expected to be quite different if diversity-dependent processes regulate diversity (Fig. 2a and b) or if they do not (Fig. 2c). Mass extinctions have yet to be incorporated in diversity-dependent models (Etienne et al. 2012), or time-dependent models mimicking diversity-dependence (Nee et al. 1994; Rabosky & Lovette 2008; Morlon et al. 2011). In the current state, one way that mass extinctions could be analysed while allowing a form of diversity-dependence is by building on coalescent approaches to diversification (Morlon et al. 2010; Fig. 1 Model 1, each extinction event – happening at rate τ – is immediately followed by a speciation event). Using these approaches and assuming a constant turnover rate, one could derive the likelihood of a phylogeny under the following scenario: diversity is at 'carrying capacity' before the extinction event, an instantaneous mass extinction event reduces diversity during a period of time, and finally diversity rebounds either to the pre-extinction carrying capacity, or to another carrying capacity corresponding to ecological constraints reset by the extinction event (Erwin 1998; Thorne et al. 2011).

Coalescent approaches may also be relevant to predicting how diversity might rebound from the current crisis, by testing whether current diversity has reached equilibrium or is expanding (Morlon et al. 2010). A test of these alternative hypotheses on 289 phylogenies indicate that diversity has not reached its equilibrium level (Morlon et al. 2010), meaning that current biodiversity is limited by the time it takes to create new species, and suggesting that recovery from the current crisis might be a long rather than short process.

BACKGROUND SPECIATION AND EXTINCTION IN RELATION TO ENVIRONMENTAL CHANGE

Earth's history has been punctuated by major environmental changes. Environments have changed as a result of biotic and abiotic factors such as the colonisation of land by plants, geological events (e.g. volcanism and tectonics) and global warming and cooling events (Hannisdal & Peters 2011; Barnosky et al. 2012). Many studies have suggested a prominent role of these environmental changes on diversification (Peters 2005, 2008; Benton 2009; Erwin 2009; Condamine et al. 2012). Temperature, for example, is believed to influence rates of molecular evolution and speciation, potentially as a result of energetic constraints (Allen et al. 2006). Understanding the role that changing abiotic factors had in shaping biodiversity dynamics can help predict the potential effect that current changes will have on biodiversity.

Paleontological perspective

Drastic environmental changes have occurred at virtually all temporal and spatial scales during the Phanerozoic (Hannisdal & Peters 2011). The most widely documented environmental changes concern the climate (red in Fig. 1c) and the rise and fall of sea levels (blue in Fig. 1c). The Phanerozoic is mostly characterised by four successive phases of warming and cooling events (Fig. 1c). These changes are often linked to periods of intense tectonic activity that remodelled Earth's configuration, changed major oceanic currents, and caused volcanic eruptions that released carbon dioxide in the atmosphere. Environmental changes during the Cenozoic (from

65.5 Ma to present) are well documented (Miller et al. 2005; Zachos et al. 2008; Figs 1 and 5a).

Paleontological studies have revealed that environmental changes are major macroevolutionary drivers of diversity dynamics (Jaramillo et al. 2006, 2010; Ezard et al. 2011; Hannisdal & Peters 2011). Climate change, tectonic activity, sea-level variations and the resulting marine transgressions and regressions profoundly affected diversity dynamics during the Phanerozoic by modifying the extent of near-shore environments compared to other marine environments (Peters 2005, 2008; Hannisdal & Peters 2011). Cenozoic climatic change had a strong influence on Neotropical plant diversity (Jaramillo et al. 2006) and macroperforate planktonic foraminifera (Ezard et al. 2011). Diversity in both groups increased with temperature during the early Eocene, and dropped sharply at the Eocene-Oligocene Glacial Maximum.

Environmental changes are extinction-selective, in the sense that they affect different organisms in different ways. During the climatic fluctuations of the Carboniferous 305 Ma, cooling events exceeding species' ability to adapt resulted in the fragmentation of large rainforest ecosystems into small refuges, decimating amphibian clades and spurring the evolution of 'reptiles' (Sahney et al. 2010). Marine clades adapted to shallow seas were much more impacted than those adapted to deep seas during the Late Ordovician glaciation (Finnegan et al. 2012), and ocean acidification and rapid warming impacted reef clades during the Phanerozoic (Kiessling & Simpson 2011). In addition to speciation and extinction, environmental changes affected ecological interactions (Wilf & Labandeira 1999), the frequency and intensity of ecological disturbances, the distribution and abundance of organisms and the structure and composition of ecological communities (Erwin 2009).

Phylogenetic perspective

Phylogenies have been used to understand diversification in light of underlying environmental changes. For instance, phylogenies in combination with the Cenozoic climate (Zachos et al. 2008) or sea-level (Miller et al. 2005) curves have revealed the impact of warming or cooling events on diversity dynamics (Steeman et al. 2009; Antonelli & Sanmartín 2011). These studies, however, have mostly relied on purely visual and descriptive inspections of phylogenies in parallel to paleoenvironmental curves.

In few cases, birth–death likelihood methods have been used to test the hypothesis that a shift in speciation rate occurred at specific Cenozoic climatic events (Winkler et al. 2009; Condamine et al. 2012). In these studies, climatic events were modelled as punctuated events (happening 24 Ma in the case of the Oligocene warming event), and the authors tested support for a two-rates model with shift at the climatic event vs. a one-rate model corresponding to the null hypothesis of no rate shift. While these analyses were performed with a likelihood expression that assumed no extinction, the expression including extinction is now available (Stadler 2011a). In addition, the approach is not restricted to a single rate shift and could thus be used to test support for multiple shifts in speciation or extinction rates over the time-series and their concordance with temperature shifts.

The 'shift' approach might not always be well adapted to analysing the effect of environmental change, in particular when warming or cooling events are not short. The Oligocene warming event lasted 3 Myrs, and other events, such as the one that occurred during the

Permian, lasted even longer (Fig. 1). In addition, the approach is mostly correlative and thus does not allow quantifying how an environmental variable (e.g. temperature) influences diversification rates.

To quantify the effect past environments had on diversification rates, we develop an approach that allows us to relate speciation and extinction rates to the paleoenvironment. This approach builds on time-dependent diversification models (Nee *et al.* 1994; Rabosky & Lovette 2008; Morlon *et al.* 2011); it allows speciation and extinction rates to depend not only on time but also on an external variable, itself depending on time (see Box 1 for details). An illustrative application of the approach to the cetaceans and paleotemperatures identifies a positive relationship between speciation rates and temperature (Fig. 5b), in agreement with the general idea that higher temperatures foster diversification (Allen *et al.* 2006; Jaramillo *et al.* 2006, 2010).

In this illustrative analysis, we considered only temperature as a potential determinant of speciation rates, such that the inferred time-variation in speciation rate matches the time-variation in temperature. More elaborate applications of the approach considering various paleoenvironmental data in combination, and potentially including time directly as an explanatory variable (to indirectly model diversity-dependent processes), as described in Box 1, will yield less straightforward time-variation in speciation rate. Besides temperature, $\Delta^{13}C$ used as a proxy for atmospheric carbon (Zachos *et al.* 2008) and sea level which influences space availability (Miller *et al.* 2005), could be good candidates for such analyses. This would allow assessing the influence of increased carbon concentration (leading to both ocean acidification and warming climate) and sea levels on diversification rates, which would be relevant to the current crisis.

Box 1. Testing the effect of the paleoenvironment on diversification

We assume that a clade has evolved according to a birth–death process. The speciation (λ) and extinction (μ) rates can vary trough time, and they can be influenced by one or several environmental variables $E_1(t)$, $E_2(t)$,…, $E_k(t)$ (e.g. temperature), themselves varying through time. $\tilde{\lambda}(t) = \lambda(t, E_1(t), E_2(t),…, E_k(t))$ and $\tilde{\mu}(t) = \mu(t, E_1(t), E_2(t),…, E_k(t))$ denote the speciation and extinction rate respectively.

We consider the phylogeny of n species sampled at present from this clade, and allow for the possibility that some extant species are not included in the sample by assuming that each extant species was sampled with probability $f \leq 1$. Time is measured from the present to the past; $t_1 > t_2 > … > t_n$ denote branching times in the phylogeny (t_1 is the stem age and t_2 the crown age of the clade). The probability density of observing such a phylogeny, conditioned on the presence of at least one descendant in the sample, is directly adapted from Morlon *et al.* (2011):

$$L(t_1,…,t_n) = \frac{f^n \Psi(t_2, t_1) \prod_{i=2}^n \tilde{\lambda}(t_i) \Psi(s_{i,1}, t_i) \Psi(s_{i,2}, t_i)}{1 - \Phi(t_1)},$$

where $\Phi(t)$, the probability that a lineage alive at time t has no descendant in the sample, is given by

$$\Phi(t) = 1 - \frac{e^{\int_0^t \tilde{\lambda}(u) - \tilde{\mu}(u)du}}{\frac{1}{f} + \int_0^t e^{\int_0^s \tilde{\lambda}(u) - \tilde{\mu}(u)du} \tilde{\lambda}(s)ds},$$

and $\Psi(s,t)$, the probability that a lineage alive at time t leaves exactly one descendant lineage at time $s < t$ in the reconstructed phylogeny, is given by

$$\Psi(s,t) = e^{\int_s^t \tilde{\lambda}(u) - \tilde{\mu}(u)du} \left[1 + \frac{\int_s^t e^{\int_0^\tau \tilde{\lambda}(\sigma)d\sigma} \tilde{\lambda}(\tau)d\tau}{\frac{1}{f} + \int_0^s e^{\int_0^\tau \tilde{\lambda}(\sigma)d\sigma} \tilde{\lambda}(\tau)d\tau} \right]^{-2}.$$

These general expressions can be used to derive likelihoods for any functional form of λ and μ, parameterised by a set X of parameters. For example, λ may be an exponential function of temperature, such that $\tilde{\lambda}(t) = \lambda_0 e^{\alpha T(t)}$, where λ_0 and α are the two parameters to estimate. The time-variations of the environmental variables (i.e. $E_1(t)$, $E_2(t)$,…, $E_k(t)$) are known from paleoenvironmental data. Here, we used paleotemperatures, $T(t)$ across the Cenozoic, obtained from Zachos *et al.* (2008), but one can easily use other variables such as carbon concentration or sea level. Given an empirical phylogeny, the likelihoods can be used to estimate the parameters X as well as their confidence intervals, and quantify the effect that various environmental variables, taken in isolation or in combination, had on diversification. For example, in the case of exponential dependency on temperature, a positive estimated α would indicate that higher temperatures enhance speciation, whereas a negative α would indicate that higher temperatures hamper speciation. Codes for these analyses are available upon request.
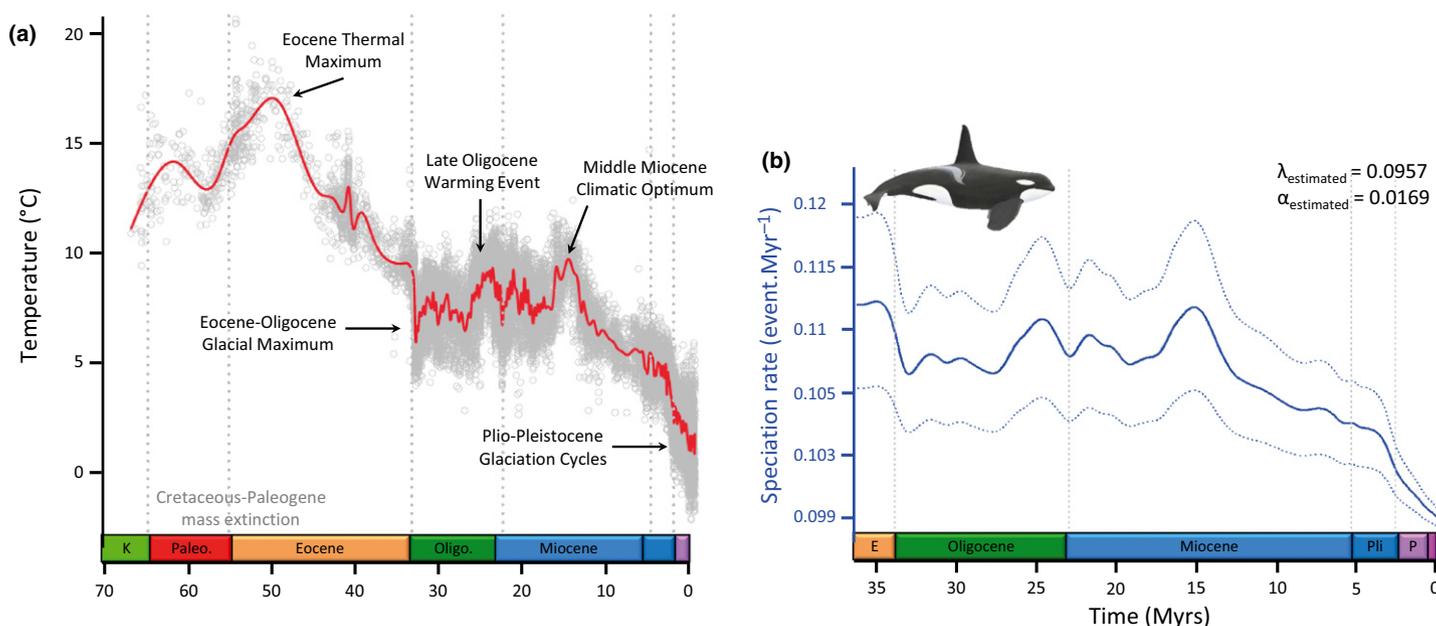
Figure 5 Evaluating how environmental changes affected diversification processes in the past. (a) Major trends in global climate change during the Cenozoic (65 Ma to present), estimated from relative proportions of different oxygen isotopes ($\Delta^{18}O$) in samples of benthic foraminifer shells (Zachos *et al.* 2008). $\Delta^{18}O$ data were converted to absolute temperatures using $T = 16.5 - 4.3 \times \Delta^{18}O + 0.14 \times (\Delta^{18}O)^2$ (Epstein *et al.* 1953). Black arrows indicate major climatic events. (b) Speciation rate through time for the cetaceans obtained from the relationship between speciation rate and paleotemperatures estimated using the approach described in Box 1. The relationship between speciation rate and temperature estimated with the approach is $\lambda(T) = 0.0957e^{0.0169T}$, suggesting a positive dependence of speciation rates on temperature.

VULNERABILITY AND EVOLUTIONARY POTENTIAL

Conservation focusses on preserving threatened species and species-rich geographical areas such as biodiversity hotspots (Myers *et al.* 2000). The necessity to also preserve the evolutionary processes generating biodiversity ('evolutionary potential') has been increasingly recognised in the last years (Forest *et al.* 2007), which has enhanced the use of phylogenies in conservation research (Mace *et al.* 2003; Purvis 2008). Conservation biologists have discussed how to maximise the preservation of phylogenetic diversity, that is, measures of diversity taking into account the evolutionary history of species (Forest *et al.* 2007). Although phylogenies can be used to study speciation and extinction to provide clues about vulnerability and evolutionary potential, they have rarely been used in this context (Davies *et al.* 2011; Rolland *et al.* 2012). This is probably largely due to the fact that the role of speciation and evolutionary potential in current conservation decisions, which have a time horizon of 10s or 100s years, remains unclear. However, if provided to policy-makers, additional information about diversification could progressively be incorporated in conservation decisions.

Evaluating the vulnerability and evolutionary potential of lineages

Rates of speciation and extinction are heterogeneous across the tree of life (Alfaro *et al.* 2009; Wiens *et al.* 2011). Some clades diversify faster than others (Euteleostei fishes compared with coelacanths and lungfishes, Alfaro *et al.* 2009). Similarly, some clades have a higher propensity to go extinct than others: extinction selectivity and phylogenetic signal of extinction risk are evidenced in both the fossil record (Peters 2008; Roy *et al.* 2009; Kiessling & Simpson 2011; Finnegan *et al.* 2012) and extant taxa (Hoffmann *et al.* 2010). Although general tendencies for rapid diversification or extinction proneness can vary over time, and particularly with current anthropogenic disturbance, some of the trends will likely be conserved, such that lineages that diversified faster or were more vulnerable in the past could be more prone to speciation or extinction today. In this case, identifying such lineages can be of valuable interest for conservation priorities.

Macroevolutionary models can help identifying lineages that diversify faster or are more extinction-prone. Phylogenetic approaches allow detecting clades with high or low speciation and extinction rates using either species-level phylogenies (Morlon *et al.* 2011), or higher level phylogenies combined with species richness data (Alfaro *et al.* 2009). Time-dependent diversification models can identify clades that are expanding or on a trajectory of diversity decline, potentially indicating which lineages have the greatest chance of diversifying in the future, or conversely, which ones are the most at risk (Rolland *et al.* 2012).

These predictions about diversification or extinction make the implicit assumption that species have particular characteristics (dispersal limitation, body size, generation time) rendering them more or less prone to diversification or extinction. The approach outlined above identifies lineages with lower or greater evolutionary potential, but does not specify the characteristics of species controlling this potential. Understanding what makes lineages diversify faster or more prone to extinction can however be useful (Purvis 2008; Hadly & Barnosky 2009). Species traits linked with body size, population trends and geographical range sizes are commonly correlated with threat status (Mace *et al.* 2003). Although the particular attributes that influence vulnerability can differ among clades and geographical regions, identifying these key traits can help predicting future declines and implementing preventive conservation measures (Fritz *et al.* 2009).

Traits associated with extinction selectivity have been analysed with the fossil record. For example, Payne & Finnegan (2007) suggested that range size is one of the most significant predictors of extinction risk in the marine fossil record. There is also evidence that extinction risk is related to geographical attributes of species, such as the maximum paleo-latitude at which they occur (Finnegan *et al.* 2012) or the habitat in which they live (shallow vs. deep seas, Kiessling & Simpson 2011).

Given phylogenetic data and the traits of extant species, phylogenetic methods can infer how particular traits affect speciation and extinction (Maddison *et al.* 2007; FitzJohn *et al.* 2009; FitzJohn 2010). Trait evolution is modelled as a Brownian or Ornstein–Uhlenbeck process, and trait value influences diversification rates. These models have already identified a series of traits impacting speciation and extinction rates, such as body size (FitzJohn 2010), reproduction modes within plants (Goldberg *et al.* 2010), colour polymorphism (Hugall & Stuart-Fox 2012), diet (Price *et al.* 2012) or traits associated with the climatic niche of species (estimated with ecological niche models, Pyron & Burbrink 2012). Application to traits related to climatic niche, such as temperature tolerance, could be relevant to assess evolutionary potential in the context of current warming. Similarly, continuity in the geographical range, that is, whether species occupy the integrity of their geographical distribution, or whether individuals are distributed in isolated patches within their range, can be relevant to assess evolutionary potential in the context of current habitat fragmentation.

Another attribute of clades influencing their vulnerability and evolutionary potential is the extent to which their traits are labile. Although clades with high trait lability may be able to rapidly adapt to new environmental conditions and rebound after an extinction event, clades whose traits tend to be conserved may face greater difficulties (Brayard *et al.* 2009; Chen & Benton 2012; Harnik *et al.* 2012). Approaches to estimating trait conservatism (Lavergne *et al.* 2010) may thus be useful for apprehending clades' evolutionary potential.

Evaluating the vulnerability and evolutionary potential of geographical areas

Rates of speciation and extinction are heterogenous across space (Goldberg *et al.* 2005). Some areas functioned as drivers of diversification (sources) while others experienced more extinction than speciation events (sinks) (Goldberg *et al.* 2005; Becerra & Venable 2008). Tropical regions are often regarded as engine of global biodiversity (Jablonski *et al.* 2006; Wiens *et al.* 2011), while polar or desert regions are thought to be sinks (Goldberg *et al.* 2005). We could be interested in protecting areas with high speciation rates (to preserve the 'source', or generation of species), and those with high extinction rates (in order to limit current losses). This could provide conservation criteria different than the ones used today: conservation has focussed on biodiversity hotspots (Myers *et al.* 2000), but areas with high species richness are not necessarily areas of rapid diversification (Forest *et al.* 2007; Becerra & Venable 2008).

If we want to preserve regions of high speciation and/or extinction rates, we need tools to identify these regions. Treating the geographical location of species as characters, the character-dependent diversification models outlined above (Maddison *et al.* 2007; FitzJohn 2010) can be used to detect areas with high speciation
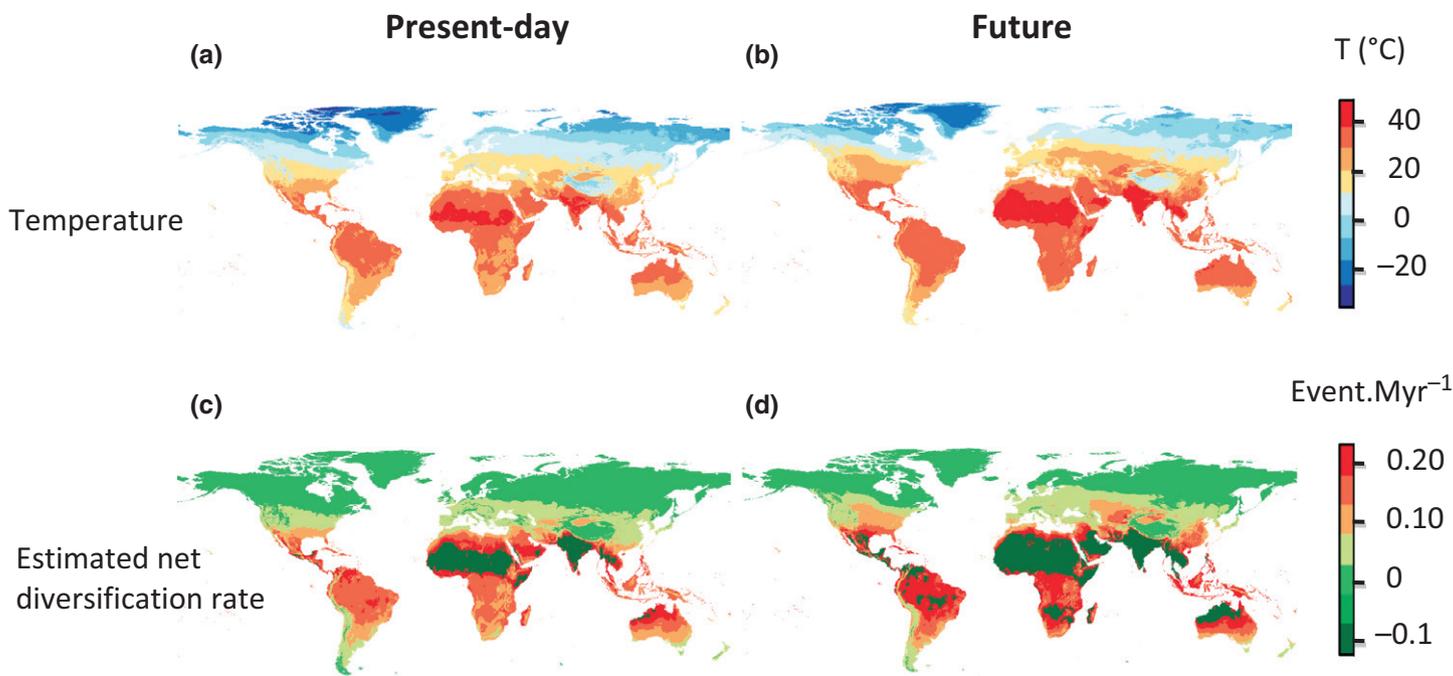

Figure 6 Estimating current and future areas of diversification. For illustrative purposes, we assume that functional dependencies between diversification rates and an environmental variable have been derived. We do not use real data, but the expected relationship between speciation and temperature (T, in °C) provided by the metabolic theory of biodiversity ($\lambda(T) = \lambda_0 e^{-\frac{E}{KT}}$), where E is the activation energy and K is Boltzmann constant (Allen *et al.* 2006); we keep the speciation rate constant above 35 °C ($\lambda_0 = e^{23}$). The dependency of extinction with temperature is given by the step function $\mu(T) = 0.003$ when $T \leq 35$ °C, and $\mu(T) = 0.35$ when $T \geq 35$ °C. Using present-day (a) and projected (year 2080, b) environmental data, we can predict maps of current (c) and future (d) diversification rates.

and/or extinction rates (Goldberg *et al.* 2011). An alternative approach is based on the idea that abiotic factors – such as temperature and precipitation – that affected diversification in the past will affect current diversification (Bellard *et al.* 2012). In this case, for a given clade, we can estimate the functional dependence of speciation and extinction rates on environmental variables, as discussed above. Using the functional dependency of diversification rates on environmental variables, it is then possible to map speciation and extinction rates for this clade (Fig. 6a and c, see the legend for details). To identify areas of high or low diversification for entire groups (mammals or birds), the similar procedure can be applied to a series of subclades, and estimates of diversification rates at a given point on Earth can be obtained by averaging these estimates over the species occurring at this geographical point. This procedure yields a map of current speciation and extinction rates.

Projecting into the future

There is an increasing interest in proposing biodiversity scenarios for the near future (e.g. year 2040 or 2080) based on projected environmental changes (Bellard *et al.* 2012). These scenarios have focussed on projecting species distributions or phylogenetic diversity (Thuiller *et al.* 2011) under various climatic scenarios proposed by the International Panel on Climate Change. Following the approach outlined above, but using projected environmental variables (e.g. for year 2040 or 2080) rather than current ones, it is possible to produce alternative predicted maps of speciation and extinction rates for individual clades (Fig. 6b and d). This can then be used to construct scenarios for entire groups, by identifying the species that will occur at each geographical location (using species distribution models, Bellard *et al.* 2012), and producing an average over these species of the diversification rates of the clade they belong to. If we become interested in integrating diversification in conservation planning, efforts could focus on areas of high projected speciation and/or extinction rates, and on designing corridors between current and future areas of diversification.

PERSPECTIVES AND LIMITATIONS

Past versus current environmental changes

Comparing past and current effects of environmental changes on biodiversity is complicated by differences between human-driven environmental changes and long-term natural processes. Harnik *et al.* (2012) compiled information on the drivers of marine extinctions in the past; they found drivers, such as acidification and anoxia, which are shared with past and predicted environmental conditions, while additional pressures such as overexploitation and pollution are new threats. The two most important pressures on current biodiversity are habitat loss and climate change. Paleontological analogies to habitat loss include glaciation events, sea level increases, major ecological transitions (from tropical forests to savannahs, meaning a loss of habitat for tropical species), and meteorite impacts (such as the impact that caused the Cretaceous–Paleogene mass extinction), which might bear similarities to human-driven habitat degradation and loss today (Harnik *et al.* 2012). Similarly, past climatic changes, linked to volcanic release of carbon dioxide or shifts in the configuration of continental landmasses that

affected oceanic and atmospheric circulation patterns, may be comparable to current human-induced climatic changes.

There is a common belief that we are altering present-day ecosystems at a much faster pace than the pace of natural environmental changes (Pimm *et al.* 1995; Barnosky *et al.* 2012). Habitat transitions typically take millions of years. Global temperatures have increased by ~0.0074 °C per year, which is much faster than the ~0.0003 °C per year increase within 20 000 years during one of the most rapid global warming event, the Paleocene–Eocene Thermal Maximum (Zachos *et al.* 2008). This event is typically used for comparison with current changes, but the variation in temperature was 25-fold slower than the current variation. However, the slow pace of past environmental changes compared with current changes may reflect an observational bias, such as limited temporal resolution for some environmental proxies in the geological record resulting in an artificially slow rate of change. Bolide impacts are instantaneous events with devastating global consequences, and their effects can occur on a timescale as short as a human lifetime. Glaciation cycles are in the order of thousand years. Volcanic activity can be sudden and short with big impacts (Barnosky *et al.* 2012). Hence, although analogies between past and present environmental changes are sometimes far-fetched, they can be relevant.

Estimating extinction rates using phylogenies

Although it is in principle possible to estimate extinction rates using reconstructed phylogenies, as originally described by Nee *et al.* (1994), it has proved difficult in practice (Quental & Marshall 2010; Rabosky 2010). Estimates of extinction rates obtained from empirical phylogenies are often not significantly different from zero, and in general too low to be realistic given what we know from the fossil record (Purvis 2008; Quental & Marshall 2010). This has led some authors to suggest that extinction rates cannot be estimated from phylogenies (Rabosky 2010), and that adding fossil information is necessary to obtain proper estimates of both extinction and speciation rates (Quental & Marshall 2010).

There are several lines of evidence that failure to properly estimate extinction rates comes from fitting models which underlying hypotheses are violated in nature, meaning that better estimates could be obtained with more realistic models. When extinction rate estimates are obtained from phylogenies simulated under the diversification process assumed for the fit (i.e. when hypotheses are not violated), these estimates are unbiased (Morlon *et al.* 2010, 2011). In contrast, if phylogenies are simulated under a diversification process different from the one assumed for the fit, for example, if a model with homogeneous rates across lineages is fitted to phylogenies obtained under a diversification process with heterogeneous rates, then extinction rate estimates are highly sensitive to these violations (Rabosky 2010). As a result, if diversification rates shifted in subclades within a phylogeny but this is not taken into account in the fit, unrealistic extinction rate estimates are obtained (Morlon *et al.* 2011). On the other hand, if the shifts are taken into account, the detected extinctions can be consistent with the fossil record; it is even possible to detect periods of positive and negative diversification rates mimicking periods of 'waxing and waning' observed in the fossil record (Morlon *et al.* 2011).

Although not impossible, estimating extinction from phylogenies remains challenging. Extinction estimates are unbiased when the hypotheses underlying diversification models are met, but finding the good underlying model can be arduous. In addition, extinction

estimates are typically characterised by large confidence intervals (Morlon *et al.* 2010, 2011; Stadler 2011a). Hence, although phylogenies can provide useful information about extinction in the absence of fossil data, further developments, in particular incorporating fossil information, will be critical in refining extinction estimates.

Comparing current extinction risks to past extinction rates

We have argued that macroevolutionary approaches can be used to detect lineages, traits or geographical areas that may be threatened today. However, given differences between past and present changes and the difficulty to estimate extinction with fossils or phylogenies, it is not clear whether macroevolutionary estimates of extinction rates are relevant to present-day conservation (Rolland *et al.* 2012). A possible test of the relevance of macroevolutionary-based estimates of extinction to actual vulnerability consists in comparing estimates from fossils or phylogenies to classical estimates of current vulnerability such as those recorded by the International Union for Conservation of Nature (IUCN, Hoffmann *et al.* 2010).

To compare fossil estimates of extinction rates with IUCN statuses, one would need to consider taxonomic groups for which both a good fossil record and IUCN statuses are available. Such datasets have just begun to be compiled (Barnosky *et al.* 2011; Harnik *et al.* 2012). Extinction from the fossil record is generally estimated globally rather than clade by clade, and over long rather than short time-periods (but see Harnik *et al.* 2012). In addition, IUCN statuses have been more documented for terrestrial than marine organisms, but the terrestrial fossil record is the most incomplete. Roy *et al.* (2009) carried a clade-by-clade analysis of extinction in the bivalve fossil record, but only 1% of the IUCN statuses are available for this group. On the other hand, IUCN statuses are well documented for groups such as, amphibians, birds, mammals and scleractinian corals, but their fossil record has rarely been examined on a clade-by-clade basis.

Further collection and compilation of combined IUCN and fossil data will improve our ability to assess the relevance of past extinction rates to current threats. Harnik *et al.* (2012) reviewed the extinction rates estimated from the fossil record of several marine clades and compared them with the extinction risks assessed by the IUCN. They found that some abiotic drivers (warming and cooling climate events) and some biotic drivers (body size and geographical range) influenced both ancient extinctions and modern extinctions. This further suggests that some biological attributes that confer resilience and risk are phylogenetically conserved (Purvis 2008; Roy *et al.* 2009) and that information about the past vulnerability of related species might provide meaningful predictions of current and future risk (Harnik *et al.* 2012).

Comparing phylogenetic estimates of extinction with IUCN statuses is straightforward, since phylogenies are available for many of the groups with IUCN statuses. If phylogenetic estimates correlate reasonably well with IUCN statuses, they could provide an idea of extinction risks for the many species which IUCN statuses remain unknown. This approach could be useful for invertebrates and plants, for which few IUCN extinction risks estimates exist (Hoffmann *et al.* 2010).

Our analysis of the correlates of IUCN-based vs. phylogeny-based extinction risks for cetaceans (Table 1) suggests that macroevolutionary rates may at least in part explain current risks. Phylogenetic models of diversification identify four recently radiating

Table 1 Comparison between phylogenetic inference of macroevolutionary dynamics and IUCN statuses for the cetaceans

Clades	Net diversification rates at present		% of threatened	
Balaenopteridae	0.02		25	
Delphinidae	0.224	0.119	13.9	20.4
Phocoenidae	0.141	(± 0.085)	42.9	(± 0.18)
Ziphiidae	0.093		0.0	
Other mysticetes	**−0.528**	**−0.703**	**33.3**	**50**
Other odontocetes	**−0.877**	**(± 0.247)**	**66.7**	**(± 0.23)**

Clades with negative diversification rates at present (i.e. under a trajectory of diversity decline, in bold) have higher IUCN extinction risks. Net diversification rates at present were taken from Morlon *et al.* (2011). Right columns are means and standard deviations over the groups.

clades with low extinction, and two clades that have been in decline since ~10 Ma (Morlon *et al.* 2011). Remarkably, present-day species from the four clades with low extinction (Balaenopteridae, Delphinidae, Phocoenidae and Ziphiidae) tend to be less threatened than present-day species from the two declining clades. More generally, IUCN extinction risks tend to correlate with estimates of net diversification rate at present, although there are exceptions, such as a high percentage of threatened species combined with a positive net diversification rate in Phocoenidae. We hope that these promising preliminary results will encourage similar studies at broader scales.

Integrating phylogenies and the fossil record

A better integration of phylogenetic and fossil data would help obtaining better estimates of both extinction and speciation (Paradis 2004; Quental & Marshall 2010; Didier *et al.* 2012). Ultimately, this would lead to a better understanding of diversity dynamics in relation to environmental changes. Likelihood expressions for reconstructed tree incorporating fossil data have started being developed (Didier *et al.* 2012), but much remains to be done in terms of both method development and application to data.

One of the most natural ways to use combined phylogenetic and fossil information is to incorporate fossils directly into the reconstructed phylogeny using morphological characters. Didier *et al.* (2012) derived the likelihood of a reconstructed tree with fossils under a stochastic process modelling speciation, extinction and fossil finds, which account for the incompleteness of the fossil record. This important advance should foster empirical applications, although the feasibility of accurately placing enough fossils onto the phylogeny remains to be proven. Further developments of the approach are also required to relax current assumptions, such as the homogeneity across time and lineages of speciation, extinction and fossil discovery rates.

Another approach to integrate fossil information into phylogenetic analyses of diversification would be to leverage fossil estimates of diversity. There are some geological periods when environment conditions were favourable to fossil preservation (Benton 1995), such that descent estimates of diversity may be available for these periods. Coalescent approaches to diversification would be especially well adapted to incorporate such information, as the likelihood expression directly involves the number of species at time *t* in the past (Eqn 1 in Morlon *et al.* 2010). Given that fossil data typically

provide a bracket of diversity values rather than direct estimates of diversity (Alroy 2010), it would be useful to develop the methods in such a way that they can incorporate uncertainties in fossil diversity estimates. Morlon *et al.* (2011) provided the likelihood corresponding to a phylogenetic tree tracing back to a given number of ancestral lineages at time *T* in the past and to fossil-based knowledge that at least a certain number of lineages alive at *T* left no observed descendants. Yet, both the full development and the empirical application of this approach remain to be explored.

Once fully developed, methods incorporating phylogenetic and fossil data could allow a better detection and estimation of mass extinctions, their intensity and the time for recovery. They could also be useful for evaluating the influence of environmental change on background speciation and extinction. Finally, they could help assessing vulnerability and evolutionary potential, as well as the traits that influence them, especially if methods that incorporate data on the biological features of extant and extinct species are developed.

Integrating the effect of ecological interactions

We focussed on the direct effect of environmental (abiotic) changes on biodiversity, but indirect effects mediated by biotic interactions may actually have a stronger effect on diversity dynamics. Species are all interdependent in complex ecological networks (food-webs or plant-pollinator networks), and environmental perturbations initially affecting few species may result in a cascade of secondary extinctions. Cahill *et al.* (2013) suggested that changing species interactions are a major cause of current extinctions related to climate change, for example stronger than the direct effect of climate change.

The role of past environmental changes on ecological interactions is crucial as well to determine diversity dynamics on long, geological time scales (Benton 2009; Ezard *et al.* 2011). Higher trophic groups have shown a delay to recover from intense warming events lowering their food availability (Chen & Benton 2012). Hence, current changes affecting ecological interactions (Barnosky *et al.* 2012) will likely have long-term consequences on speciation and extinction processes.

A major limitation of current diversification models is that despite the importance of ecological interactions, they most often ignore them by assuming that all lineages are independent. One exception concerns diversity-dependent models, in which speciation and extinction rates depend on the number of species at any given time, thus taking into account the fact that species are interacting, for example competing for a limited set of resources (Rabosky & Lovette 2008; Etienne *et al.* 2012). These models could be extended to incorporate the effect of environmental change by making the 'carrying capacity' depend on an external environmental variable varying over time (e.g. the amount of space available to species), similarly to the approach we developed here for time-variable models.

Still, diversification models that fully take into account species interactions remain to be developed. This would require developing models for the evolution and diversification of species interaction networks in which some features of interactions (e.g. the degree of specialism or generalism) influence speciation and extinction. Such models have never been developed enough to allow hypothesis testing or parameter inference. Such developments would allow analy-

sing how interaction networks have evolved in relation to environmental change and potentially predicting how they will change in the future.

CONCLUSIONS

One of the biggest challenges facing ecologists today is to predict how biodiversity will be influenced by human-induced environmental changes. We have detailed several ways that a macroevolutionary perspective can help meet this challenge. We suggest that phylogenetic approaches developed with the initial goal to understand long-term diversity dynamics and the historical determinants of present-day richness patterns may also be useful in the context of current environmental changes. Combined with paleobiology, trait-based ecology and species distribution modelling, estimates of extinction and speciation rates derived from phylogenetic data could provide significant and novel insights into how biodiversity may respond to current human pressure. We hope that these possibilities will encourage more integration of macroevolutionary approaches into global change research.

AUTHORSHIP

FLC, JR and HM designed research, FLC and JR analysed the data with the advice of HM, FLC and HM wrote the article.

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