Comparing Extinction Rates: Past, Present, and Future

Vânia Proença and Henrique Miguel Pereira, Faculdade de Ciências da Universidade de Lisboa, Lisboa, Portugal

---

Glossary

Background extinction rate The natural rate of extinction over geological time, measured from the fossil record and independent of anthropogenic influence.

Extinction rate The number or proportion of taxa becoming extinct per unit time.

Mass extinction Rare events in Earth's history when extinction rates escalated and extinction reached devastating magnitudes in a relatively short period of geological time. Mass extinction events affected species from a wide variety of taxa and had a global impact, affecting all regions. There were five mass extinction events in Earth history with magnitudes of 75% or more of species loss.

Species committed to extinction Species whose populations have already experienced, or will probably experience, severe population declines that compromise the viability of their genetic and demographic base and anticipate the eventual extinction.

The IUCN Red List of Threatened Species™ A list built by the International Union for Conservation of Nature (IUCN) that provides information on the global conservation status of assessed species of plants and animals.

Why to Assess and Compare Extinction Rates?

Current estimates of biodiversity range from 5 million to 30 million species (a recent estimate of Mora et al. (2011) suggests a value of 8.7 million terrestrial eukaryotes), but living species may represent only a small fraction, 2–4%, of all species that have ever existed on Earth (Mace et al., 2005). The reasons for this small fraction of remaining species include species evolving, with species giving origin to others (this is called pseudo-extinction), species becoming extinct not only due to competitive exclusion or failing to cope in their environment, but also the occurrence of discrete extinction events associated with abrupt peaks of environmental stress (Raup, 1992; Green et al., 2011).

Species extinction, like species origination, is a natural process in species evolution and diversification. The natural disappearance of species has occurred on a rather constant and low rate through geological time (Raup, 1986). This natural rate of extinction is called the background extinction rate. The background extinction rate was interrupted by five events of mass extinction (in the Ordovician, Devonian, Permian, Triassic, and Cretaceous) when extinction rates escalated and extinction reached devastating proportions of at least 75% loss of all existent species in a relatively limited time interval at the geological scale (Barnosky et al., 2011). Mass extinction events affected species from a wide variety of taxa and had a global impact, affecting all regions. Biodiversity recovery after each mass extinction was a slow and long process as new species evolved during millions of years (Kirchner and Weil, 2000).

Current and recent past extinction rates, measured from records of species loss from the last few centuries, and future extinctions rates, estimated using scenarios and modeling approaches, are much higher than the background extinction rate (Figure 1), or in other words than the expected natural rate of species loss (Mace et al., 2005; Pereira et al., 2010a). This is very worrying because species extinction is a definitive and irreversible form of biodiversity loss. The increase of extinction rates is directly or indirectly driven by human activities and may have negative consequences for humankind. The impoverishment of natural communities and the disruption of ecosystem functioning are caused by several drivers, in particular habitat change, climate change, invasive species, pollution, and unsustainable use of biological resources (MA, 2005; SCBD, 2010). These drivers act together, creating combined pressures over ecosystems and showing complex dynamics at different temporal and spatial scales, which pose huge challenges to their understanding and control (Pereira et al., 2010a).

The comparison between past extinction rates, estimated from the fossil record before human-era disturbances, and anthropogenic extinction rates, derived from documented extinctions and from quantitative models, is a way of discriminating human-induced extinction from natural extinctions. This allows us to put into perspective the extent of the modern biodiversity crisis and to evaluate the severity of human impacts on biodiversity. This information is essential for the prioritization and design of conservation measures that may reduce extinctions and prevent harmful and severe consequences for natural systems and humankind.

Metrics of Extinction

Metrics of Magnitude and Rate

Extinction can be measured using different metrics (Table 1) that can be classified in measures of magnitude or measures of rate. The first includes the number or proportion of extinctions and the latter correspond to the number or percentage of extinctions over a time interval. Using a measure of magnitude or rate depends on the purpose of the assessment. Measures of magnitude provide information on the extent of the extinction. The proportion of extinctions normalizes the number of extinctions over the total number of species in the species pool, thus controlling the effect of sample size (i.e., the species pool). However, this metric, like other measures of magnitude, lacks information on the duration of the time interval along which extinctions occurred, being therefore less suitable for comparing past and modern extinctions due to the disparity in
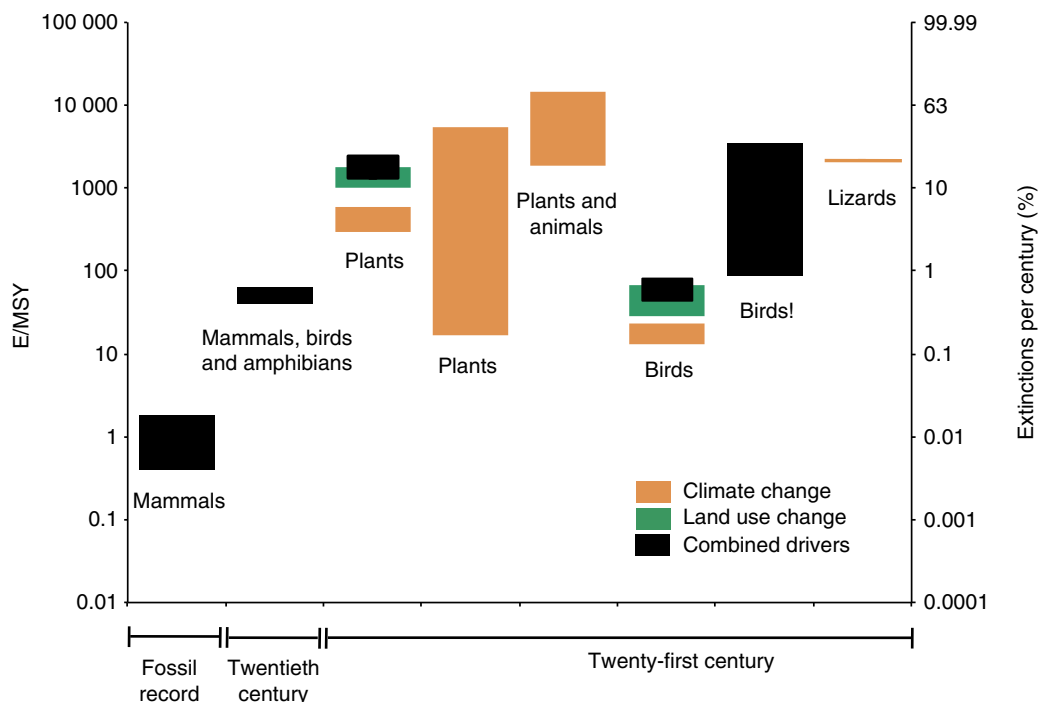

Figure 1   Past, recent, and future extinction rates. Past extinction is represented by the extinction rate of mammals in the Cenozoic fossil record (upper bound from Barnosky *et al.* (2011) and lower bound from Foote and Raupe (1996); recent extinction is represented by the extinction rate of mammals (upper bound), birds, and amphibians (lower bound) in the twentieth century, using documented extinctions (Mace *et al.*, 2005); future extinction is represented by projections of species committed to extinction in the twenty-first century, according to different global scenarios: vascular plants (Malcolm *et al.*, 2006; van Vuuren *et al.*, 2006), plants and animals (Thomas *et al.*, 2004), birds (Jetz *et al.*, 2007; Sekercioglu *et al.*, 2008), and lizards (Sinervo *et al.*, 2010). Extinction rates driven by land-use change or by climate change are discriminated when possible. Modified from Pereira HM, Belnap J, Brummitt N, *et al.* (2010b) Global biodiversity monitoring. *Frontiers in Ecology and the Environment* 8: 459–460, and Pereira HM, Leadley PW, Proença V, *et al.* (2010a) Scenarios for global biodiversity in the 21st century. *Science* 330: 1496–1501.

Table 1   Extinction metrics and their definition

Extinction metric	Definition
Number of extinctions	E
Proportion of extinctions	E/S
Van Valen metric[a]	E/(S − E/2 − O/2)
Total extinction rate	E/t
E/MSY	
Proportional extinction rate (linear model)	(E/S)/t
Proportional extinction rate (exponential model[b])	− ln (1 − (E/S))/t
Van Valen metric per unit of time	(E/(S − E/2 − O/2))/t

[a]The denominator (S − E/2 − O/2) in the Van Valen metric is an estimate of standing diversity. It corresponds to the estimated diversity at the midpoint of a time interval, assuming a linear change in diversity along the interval (see Foote, 1994).
[b]For a given time interval the proportion of species going extinct is $E/S = 1 - e^{-\lambda t}$, where $\lambda = E/MSY$.
E, number of extinctions; S, total diversity in the time interval; O, number of originations; t, time interval, conventionally expressed in million years.

the length of the respective time intervals. Extinction rates constitute a more appropriate metric to compare background extinction with current extinction because extinction is expressed per time unit, thus informing on the pace of species loss. However, extinction rates may be misleading because the

normalization by time assumes that extinctions are distributed evenly along the time interval, which might not be true (Foote, 1994).

Measuring Extinction in E/MSY Units

The E/MSY metric, that is, extinctions per million species-years, has been widely adopted to measure extinction rates (Pimm *et al.*, 1995; Mace *et al.*, 2005). It is a proportional extinction rate measure (Table 1), having the advantage of normalizing the rate of extinction both by time and size of the species pool, allowing the comparison of extinction rates between different periods of time and between species pools of different sizes. For instance, studies suggest an average background extinction rate of terrestrial mammals of 0.4 E/MSY (Foote and Raupe, 1996) to 1.8 E/MSY (Barnosky *et al.*, 2011). A value of 1 E/MSY can be interpreted as one extinction per thousand species per thousand years. Hence, when evaluating current extinction rates, a natural rate of extinction would be, for example, one species extinct in a total of 10,000 species during a time interval of 100 years.

There are several approaches for calculating E/MSY (Table 1): the linear model, the exponential model (also known as per capita extinction rate), and the Van Valen metric

per unit time. The linear model assumes that the proportion of extinctions, E/S, increases linearly with time. This assumption tends to be violated for long time intervals or very high extinction rates (Foote, 1994). Therefore, extinction rate estimates using the linear model are sensitive to the size of the time interval over which they are calculated, tending to decrease as the time interval increases (Foote, 1994; Regan *et al.*, 2001).

A better model of the process of extinction is the exponential model (Foote, 2000). It assumes that the lifetime of each species is given by an exponential distribution. The parameter of the exponential distribution is the per capita rate of extinction and corresponds to the value of E/MSY. Therefore, the inverse of E/MSY is the mean life expectancy of a species, which for a value of 1 E/MSY corresponds to 1 million years. The exponential model is particularly appropriate to compare different estimates of future extinction rates, as several studies report values that are extremely high (Pereira *et al.*, 2010a), which would lead to the saturation of the linear model (i.e., extrapolations of the extinction rates for the future could lead to magnitudes greater than 100% extinction).

Another alternative to the linear model is the Van Valen metric (Foote, 1994). It accounts for both speciation and extinction events (Foote, 1994), and therefore it is commonly used in paleontological studies. The exponential model can also be modified to account for both speciation and extinction (Foote, 2000).

Projected Extinction and Realized Extinction

Although past and recent extinctions refer to the disappearance of a species on the death of its last surviving individual, most projections of future extinction are based on estimates of species committed to extinction. Species committed to extinction are those whose populations have already experienced, or will probably experience, severe population declines that compromise the viability of their genetic and demographic base and anticipate the eventual extinction (Heywood *et al.*, 1994). The time needed for extinction is not certain (Sala *et al.*, 2005; Leadley *et al.*, 2010), because the time lag between impacts, population decline and realized extinction may range from decades to millennia, and in some cases declining trends may even be reverted if measures are taken to halt the causes of endangerment and restore populations.

Currently, 3663 species, from a total of 56,135 species of vertebrates, insects, mollusks, and plants that have already been assessed by the International Union for Conservation of Nature (IUCN) Red List are considered as critically endangered (IUCN, 2011), which means that these species are facing an extremely high risk of extinction in the wild, and will be committed to extinction if the present conditions are maintained or worsened (Heywood *et al.*, 1994). Some of these critically endangered species are species "possibly extinct" (Butchart *et al.*, 2006). "Possibly extinct" species are species that are likely to be extinct because they have not been seen for many years, but for which there is still a small chance that they may be extant (Butchart *et al.*, 2006). These species will only be considered as extinct after adequate efforts to prove their extinction in the wild (Butchart *et al.*, 2006).

Projections of future extinction may include the species that are currently committed to extinction (Barnosky *et al.*, 2011) or the species that might be committed to extinction in the future (Pereira *et al.*, 2010a). The number of species committed to extinction in the future may be assessed by using trends of degradation of species conservation status to extrapolate how many species will be extinct or become critically endangered in the future, or by estimating how many species will become endangered due to projected trends in drivers of change (*see* Future Extinction).

Overall, extinction rates in the future will probably be lower than what is suggested by projected extinction rates because not all species committed to extinction will become extinct. However, current extinction rates, based on recent extinction data, correspond to conservative estimates because some "possibly extinct" species will eventually be classified as extinct.

Present Extinction

Human-Induced Extinction Rates

Human-induced extinctions followed the growth and expansion of human populations across the globe. The extinction of megafauna species in the late Pleistocene (ca. 50,000 BP–12,000 BP) was at least partly a consequence of overexploitation and habitat change, although climate change may have also contributed to extinctions, especially in the northern hemisphere (Barnosky *et al.*, 2004). Human migration through land and sea lead humans to regions where biota had evolved without human disturbance. The coincidence between records of first human arrival and records of widespread extinction suggest that humans were responsible for or prompted species disappearance (Steadman, 1995). Islands provide a paradigmatic example: after the first human arrivals, 1500–2000 years ago, between 70 and 90 endemic birds were extinct in the Hawaiian archipelago, in an estimated pool of about 150 species, and 40% of large mammals were extinct in Madagascar (Pimm *et al.*, 2006). Overall, at the global level around one-third of autochthonous mammals were extinct from oceanic islands and oceanic-like islands, such as the Mediterranean islands (Alcover *et al.*, 1998).

The IUCN Red List (www.iucnredlist.org) includes more than 800 records of extinctions since the 1500s, including nearly 200 extinctions of birds and mammals (Baillie *et al.*, 2004; Mace *et al.*, 2005). Most records refer to realized extinctions and less than 10% refer to extinctions in the wild (i.e., species that disappeared from their natural habitat but still survive in captivity). Considering mammals, birds and amphibians all together, there were about 100 documented extinctions since the start of the twentieth century (Mace *et al.*, 2005), in a total pool of nearly 21,000 described species, which corresponds to an extinction rate of 48 E/MSY, which is 30–120 times greater than the background extinction rate of 0.4–1.8 E/MSY for mammals. If possibly extinct species are included, then the number of extinctions rises to 215, resulting in an extinction rate of 102 E/MSY (Mace *et al.*, 2005).

There are several sources of uncertainty that affect the assessment of current extinction magnitudes and rates. A basic

problem is that we do not know with an adequate certainty how many species exist in the world today and we only know a very small fraction of species. In addition, systematic species description only started during the eighteenth century and only about 1.7 million species have been described up to the present day (IUCN, 2011). That means that many taxa may have become extinct, or will become extinct, before being described. Another problem is that existing data are biased toward terrestrial vertebrates, which are better known and monitored than all other taxa but represent only around 2% of described species (Mace *et al.*, 2005). Moreover, several species are rare or have secretive habits, which constrains the assessment of their current status, including extinction. Finally, the time lag between impacts and extinction also limits an accurate estimation of extinction rates.

Therefore, estimates of the magnitude of contemporary extinctions, derived from documented extinctions, are very conservative, because only a small fraction of species has been described and monitored. In addition, estimates of current extinction rates are probably very conservative as well, since only realized extinctions are considered (Baillie *et al.*, 2004; Pimm *et al.*, 2006). Still, estimates of current extinction rates are already very high when compared with background extinction rates (**Figure 1**). This value will probably rise in the near future due to the continuous degradation of species conservation status, as revealed by the Red List Index (RLI) (**Figure 2**), which measures trends of species extinction risk across time (Hilton-Taylor *et al.*, 2009; Butchart *et al.*, 2010; Hoffmann *et al.*, 2010).

Species extinction rates can also be estimated indirectly using data on drivers of species extinction, such as habitat loss. For example, species extinction along time after habitat fragmentation can be modeled by assessing species loss in habitat fragments of different size and age since fragmentation (for more details see Pimm and Brooks (1999)). These modeling studies tend to deliver higher rates of extinction than the conservative approach, on the range of three to four orders of magnitude higher than a background extinction rate of 1 E/ MSY (Pimm and Brooks, 1999). True values of current extinction are probably found between the estimates delivered by both approaches, but nevertheless they will always be much higher than the background extinction rate.

Patterns of Modern Extinction

Patterns of contemporary extinction are not homogenous across the globe and across species groups. Islands have been the stage of most documented extinctions so far (**Figure 3**), encompassing 62% of mammal extinctions, 88% of bird extinctions, 54% of amphibian extinctions, and 68% of mollusc extinctions (Baillie *et al.*, 2004). The main causes of extinction were habitat loss, the introduction of invasive species, which includes the introduction of predators, competitors, and pathogens, and overexploitation (Baillie *et al.*, 2004). In the case of large birds and mammals, overexploitation and direct persecution were important causes of extinction. Species extinction in continents has become more frequent during the past century (**Figure 3**). Habitat change has been the main driver of species extinction in continental areas, but climate change is also becoming increasingly important (Leadley *et al.*, 2010).

The extinction record of terrestrial species is still very incomplete; even so this is the group for which present conservation status and recent extinctions are better studied. In contrast, the conservation status of freshwater and marine
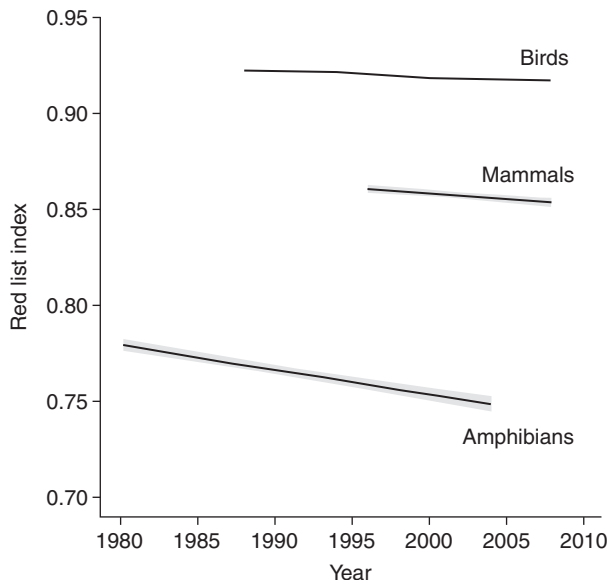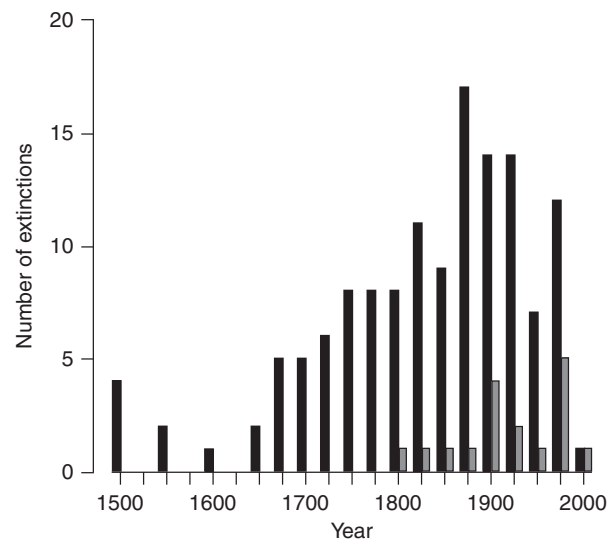

Figure 2 Changes in the Red List Index (RLI) for the period of 1980–2010, for birds, mammals, and amphibians. The RLI varies between 0 and 1: 1 corresponds to all species having a conservation status of Least Concern, and 0 corresponds to all species being extinct. A decrease in the RLI indicates that species' conservation status are worsening. Shaded areas correspond to 95% confidence intervals. Reproduced from Figure 3A. Trends in the Red List Index (RLI) for the world's birds, mammals and amphibians in Hoffmann M, Hilton-Taylor C, Angulo A, *et al.* (2010) The impact of conservation on the status of the World's vertebrates. *Science* 330: 1503–1509.

Figure 3 Bird extinctions on islands (black) and continents (gray) since 1500 AD. Reproduced from Baillie JEM, Hilton-Taylor C, and Stuart SN (2004) *2004 IUCN Red List of Threatened Species. A Global Species Assessment*. Gland: IUCN.

species is still a major unknown. There are still few records of global extinction in the marine realm, which may be due to the lack of data and adequate detection methods (Dulvy *et al.*, 2003; Baillie *et al.*, 2004). Marine species appear to be as vulnerable to human action as terrestrial species, and given the long history of human use of oceans, especially in coastal areas, one might expect a higher number of extinctions than the extinctions documented (Dulvy *et al.*, 2003). Overexploitation has been identified as the main cause of extinction of local populations, and it may cause the collapse of several world fisheries in the next decades (Worm *et al.*, 2009). Habitat destruction, pollution, and climate change are also important drivers, with severe impacts in coastal regions and in coral reefs (Dulvy *et al.*, 2003; Leadley *et al.*, 2010).

Species extinctions in freshwater systems were best documented in the USA (Baillie *et al.*, 2004). Data reveal a high magnitude of extinction, with 105 documented extinctions due to habitat destruction, pollution, and invasive alien species (Baillie *et al.*, 2004). In addition, data of freshwater fishes conservation status on the IUCN Red List indicate that more than 50% of species in the Mediterranean and Madagascar and nearly 50% of species in Europe may be threatened (Darwall *et al.*, 2009). These values are alarming, because they suggest that freshwater species could be even more threatened than terrestrial species.

A characteristic shared by many extinct species and seriously threatened species is their low total abundance, that is, a relatively small number of individuals at the global level (Pimm and Jenkins, 2010). This includes species that have limited distribution ranges and species that have large distribution ranges but are rare. In the first case, examples include the endemic species on islands, which could be rare or have high local population densities, but always have a low global abundance due to their limited distribution, and also endemic species in continental areas whose distribution is also limited. The second case includes species with large distribution ranges but with low densities and therefore with a low total abundance, this is the case with top predators, such as large carnivores.

When analyzing regional patterns of extinction, the regions that concentrate a high number of endemics are also the ones where species loss is more probable. This is the case of the biodiversity hotspots that concentrate a high diversity of endemics, and which were exposed to extensive habitat change and continue to face a severe threat of further habitat loss (Myers *et al.*, 2000; Brooks *et al.*, 2002). Extinctions may be less pronounced in regions with few endemics even when the level of impacts is considerable, such as in eastern North America, where intense deforestation since the 1600s caused the extinction of four species only from a total of 162 forest species (Pimm and Jenkins, 2010).

Future Extinction

Projecting Extinction Rates

Future extinction rates will depend on several factors, including demographic and socio-economical variables, trends in drivers of environmental change (e.g., climate change) and

ecosystems and species responses to drivers of change. Research approaches to estimate future extinction rates generally include three main components: socio-economic scenarios, models to project the future state of environmental change drivers, and models to project ecosystems and species response to those drivers (Pereira *et al.*, 2010a).

Socio-economic scenarios are used to characterize changes in demographic and socio-economic variables, such as population growth, fossil fuel use, or implementation of environmental policies. Demographic and socio-economic variables act like indirect drivers of biodiversity change affecting the trajectory of environmental change drivers (e.g., climate change and land use change), which will have a direct effect on species and ecosystems. Finally, projections on the future levels of direct drivers are used to assess ecosystems and species responses to environmental changes. The response of species to drivers of change is usually estimated using phenomenological models or process-based models.

Phenomenological models are built on empirical relationships between environmental variables, such as area of natural habitat or precipitation, and biodiversity metrics, such as species richness or presence/absence of particular species. Examples of phenomenological models to assess species extinction include species–area relationships, niche-based models, and dose-response models (Leadley *et al.*, 2010). Species–area relationships are based on the known correlation between habitat area and species richness (Sala *et al.*, 2005; van Vuuren *et al.*, 2006). These models derive species extinction from the extent of predicted habitat loss. Niche-base models (or species distribution models) are based on the effect of environmental variables, namely climatic variables, on species distribution. These models use species' current distributions to define their environmental niche, or their "climate envelope" in the case of climatic variables (Thuiller *et al.*, 2008). Changes in environmental conditions will have effects on species distribution ranges, thus the future distribution of a species is estimated by combining current environmental niches with future environmental conditions. Species extinction may occur if species fail to change their distribution range in order to adapt to environmental changes, for example, due to limitations to migration, such as physical barriers or species inability to migrate. Dose-response models establish the relations between the intensity of a global change driver, which is the "dose", and the species responses (Alkemade *et al.*, 2009). An example is the decrease in plant species richness with increasing levels of nitrogen deposition.

Process-based models simulate biological processes such as population growth or mechanisms such as ecophysiological responses (e.g., changes in climatic variables affecting rates of photosynthesis, respiration and evapotranspiration in plants, or affecting demography of animal populations) to mimic species or population responses to environmental changes (Thuiller *et al.*, 2008).

Future Extinction Rates

Future global extinction rates have been projected for different taxa. Existing studies are mainly directed at terrestrial species (**Figure 1**, **Table 2**) and very few address the marine and

Table 2   Summary of global scale studies projecting terrestrial species extinction for the twenty-first century

	Plants	Plants[a]	Plants and animals	Birds	Birds	Lizards
E/MSY[b]						
UB (CD/LU/CC)	2489/1775/589	–/–/17	–/–/1886	51/28/23	89/–/–	–/–/2125
LB (CD/LU/CC)	1326/1003/290	–/–/5534	–/–/14,679	79/67/13	3500/–/–	
Global drivers	LU & CC	CC	CC	LU & CC	LU & CC	CC
Socio-economic scenarios	MA socio-economic scenarios[c]	GHG emission scenarios[f]	GHG emission scenarios	MA socio-economic scenarios[c]	MA socio-economic scenarios[c]	IPCC SRES emission scenarios
Drivers models	CC based on IMAGE model.[d] Habitat loss from IMAGE model based on LU and global vegetation response to climate.	Several CC scenarios.[f] Habitat loss based on two global vegetation models	Hadley centre climate model	CC based on IMAGE model.[d] Habitat loss based on LU and IMAGE model for global vegetation response to climate.	CC based on IPCC SRES scenarios.[g] Habitat loss based on LU and IMAGE model[d] for global vegetation response to climate.	Several CC scenarios. Habitat loss not considered
Species distribution model and/or species extinction model	Species–area curves	Species–area curves	Synthesis of regional projections of species ranges changes using niche-based models. Species extinction from species–area curves and IUCN status	Overlap between habitat loss and species distribution (extinction defined by 100% habitat loss/overlap)	Extinction risk based on species tolerance to CC and habitat availability.	Physiological model based on species thermal behavior
Time interval	1995–2100[e] 1995–2050	100 years	2000–2050	1985–2100[e] 1985–2050	2000–2100	1975–2080
Study	Van Vuuren et al. (2006)	Malcolm et al. (2006)	Thomas et al. (2004)	Jetz et al. (2007)	Sekercioglu et al. (2008)	Sinervo et al. (2010)

[a]Malcolm et al. also present projections for vertebrate species but only projections for plants are presented in Figure 1.

[b]Values of E/MSY were derived from data available in each study (see Pereira et al. 2010a). The upper (UB) and lower (LB) bounds correspond to the worst and best case scenarios analyzed in each study, except for Sinervo et al. that present a unique value for global extinction rate. Values are presented for combined drivers (CD), land use change (LU), and climate change (CC) according to available data.

[c]MA, 2005 scenarios (Carpenter et al., 2005).

[d]IMAGE 2.2. model (Alcamo et al., 1998, IMAGE-team, 2001).

[e]Extinctions rates presented in **Figure 1** were based on projections for the longest time interval.

[f]See Neilson et al. (1998).

[g]See IPCC (2007).

LU, Land use change; CC, Climate change; GHG, Greenhouse gas. Projections of species extinction are graphed in Figure 1. Studies are presented in the same order as in Figure 1.

Source: Reproduced from Leadley P, Pereira HM, Alkemade R, et al. (2010) Biodiversity Scenarios: Projections of 21st Century Change in Biodiversity and Associated Ecosystem Services. Montreal: Secretariat of the Convention on Biological Diversity, and Pereira HM, Leadley PW, Proença V, et al. (2010a) Scenarios for global biodiversity in the 21st century. Science 330: 1496–1501.

freshwater realms (Pereira et al., 2010a). Studies on terrestrial species are focused on two main drivers: land-use change and climate change. Each study uses a set of interconnected scenarios, including socio-economic, climatic and land-use change scenarios, to model extinction rates and bound estimates between potential best- and worst-case scenarios (Figure 1, Table 2). All projected extinction rates are much higher than the background extinction rate (fossil record), with several studies projecting species becoming committed to extinction at rates as high as thousands of extinctions per million species-years (Table 2, Figure 1). Even best-case scenarios, that is, the lower bounds of the intervals of variation of projected extinction rates, are projected to be above recent extinction rates in most studies (Figure 1).

All studies in Table 2 except Sinervo et al. (2010) use phenomenological models to project the number of species committed to extinction. These studies estimate extinctions based on habitat loss due to land-use changes and/or climatic changes (e.g., van Vuuren et al., 2006), or due to shifts in species ranges driven by climatic changes (e.g., Thomas et al., 2004). One study, Sinervo et al., 2010, uses a physiological model (process-based model) to project the number of species committed to extinction given climatic changes. The authors project lizard extinction by modeling species thermal tolerance and adapting behavior in the face of increasing environmental temperatures.

Two studies, by van Vuuren et al. (2006) and Jetz et al. (2007), analyze the separate and combined effects of land-use change and climate change on the rate of species extinction of plants and birds, respectively. Both studies predict that land-use change will cause more extinctions than climate change during the twenty-first century. However, the effects of those two drivers will not be uniform across the globe: climate change will mostly affect natural communities in high latitudes and elevated regions, whereas land-use change will be the prevailing driver of species loss in temperate and tropical latitudes, where a higher diversity of endemic and specialist species is also found.

Global studies on future extinction risk of marine species are less common. Cheung et al. (2009) investigated the effect of climate change on distribution ranges of marine species, fish and invertebrates, and predicted patterns of local extinction and invasion. Results point to numerous events of local extinction particularly in the subpolar regions, tropics and semi-enclosed seas, and invasions in the Artic and the Southern ocean. Species turnover will occur at a global scale with potential deleterious effects for ecosystem functioning. The authors found a global average local extinction rate of 3% by 2040–2060 of the initial species richness in 2001–2005. Despite being local extinction values, they are below most projected global extinction rates for terrestrial species. This may be partially explained by a higher dispersal ability of marine species in relation to terrestrial species.

The future extinction risk of freshwater species has been addressed in a study on the consequences of changes in river discharge, due to a decline in run-off caused by climate change and water withdrawal from human activities, in selected river basins across the globe (Xenopoulos et al., 2005). Species extinction was determined at the basin scale and results suggest that 15% of the world's rivers may have more than 20% of

their fish species committed to extinction during the next century.

Uncertainty in Projected Extinction Rates

The large variation in projected extinction rates, within studies and among studies, raises questions about their accuracy and suitability for comparison with past and recent rates. Pereira et al. (2010a) identify three main sources of uncertainty in projected extinction rates: (1) variation in the intensity of the drivers of change, (2) lack of knowledge on species ecology and species response to drivers, and (3) differences in modeling approaches and in model sensitivity.

The first factor (1) underlies much of the variation within studies. Studies test different scenarios, characterized by different degrees of land-use or climate change, to encompass a variety of possible futures and assess the effects of each scenario on biodiversity.

The second factor (2) is also a significant cause of variation in projected extinction rates within studies. Species may be able to adapt or show different levels of tolerance to changes. When the level of adaptation is weakly understood, the option is to test several alternatives that represent species responses. For example, Thomas et al. (2004) include species ability to migrate in their model and found a large difference in projected extinction depending on that characteristic (38% species loss with unlimited migration vs. 58% species loss with no migration).

The last factor (3) should explain most of the variation between studies, and it is related with differences in the modeling approaches used by the studies and on the criteria used to define species extinction. For example, while Jetz et al. (2007) estimate extinctions based on the number of species projected to lose 100% of their initial habitat from biome changes caused by climate change and land-use change, Thomas et al. (2004) use niche-based models to project decreases in species ranges caused by climate change and estimated extinctions based on species–area relationships.

Reducing uncertainty in projected extinction rates is critical for a more accurate comparison of extinction rates and to better inform decision makers. The evaluation of model projections, by validating models against data and using indicators to compare models outputs, and the harmonization of modeling methods are essential steps toward this objective (Pereira et al., 2010a). Also important is the development of models, particularly process-based models, that integrate the effects of a broader range of drivers, and which capture the feedback of the biodiversity changes to the human system and the drivers of environmental change.

Comparing Past, Present, and Future Extinction Rates

Are We Driving the Sixth Mass Extinction?

Recent extinction rates are up to two orders of magnitude higher than the background extinction rate and future extinction rates are projected to be at least as high as current rates and likely one or two orders of magnitude higher. A

relevant question is whether mankind is driving a new mass extinction. Although past extinction rates provide a useful benchmark to evaluate the extent and severity of modern extinction rates, events of mass extinction are usually defined as the loss of at least 75% of species in a relatively short period in geological time, which provides a measure of magnitude but it is elusive regarding duration. Mass extinction events may have occurred in less than a year, along thousands of years or along millions of years (Raup, 1992; Barnosky et al., 2011).

A way of dealing with this limitation is to compare simultaneously measures of rate and magnitude (Barnosky et al., 2011). With this approach it is possible to assess if current rates of extinction may lead to a magnitude of extinction identical to the magnitude of past mass extinctions. Barnosky et al. (2011) calculated the range of variation of possible extinction rates for each event of mass extinction, using data on their magnitude and the interval of their possible duration, and then compared those values with modern rates of extinction of vertebrates considering not only species extinct in the past 500 years, but also all critically endangered and all threatened species (critically endangered, endangered and vulnerable species) that could became potentially extinct in the near future (Figure 4). Current rates of observed extinctions are already above the rates associated with all mass extinction events but the Cretaceous mass extinction. However, with the

exception of the Cretaceous event that may have spanned from a period of less than a year to 2.5 Myr, all past events spanned for periods much larger than 500 years. If a hypothetical and fixed period of 500 years is set for comparison purposes, then modern rates of extinction will be slower than past rates, but will became dangerously similar to the rates of past mass extinctions if the (hypothetical) extinction of currently threatened species is also considered in that time span.

It is worth noting that future extinction rates derived from scenarios (Figure 1) are in many cases higher than hypothetical extinction rates calculated considering threatened species as inevitably extinct in a period of 500 years (Figure 4).

Following a different approach, one can also ask if modern extinction rates may lead, and in how much time, to a magnitude of 75% species loss. This question may be answered by testing different rates of extinction based on hypothetical assumptions, namely by assuming the loss of all threatened species or of just critically endangered species, in a period of 100 years or of 500 years, and then using those extinction rates to determine the interval of time needed to reach a magnitude of 75% loss. According to Barnosky et al. (2011) reaching 75% of (mammals, birds, and amphibians) species loss may take from a few centuries in a worst-case scenario, if all threatened species are lost in the next century, to about ten millennia, if only critically endangered species become extinct in the next five centuries.
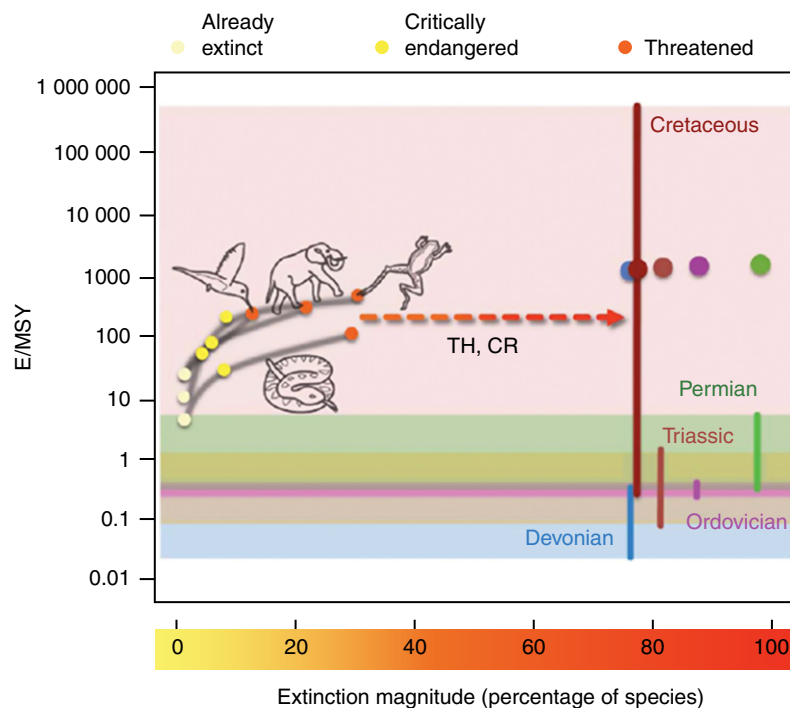

Figure 4 Extinction rate vs. extinction magnitude of past mass extinction events and of modern extinction (past 500 years). Vertical lines on the right illustrate the range of extinction rates for each event of mass extinction that would result in the magnitude associated with each event. The range of extinction rates varies accordingly with the interval of possible duration of each event. Each colored dot on the right represents the extinction rates associated with past events of mass extinction if they have occurred (hypothetically) over only 500 years. Dots and lines on the left represent modern extinction rates computed for a period of 500 years for vertebrates, using data from already extinct species (light yellow) and of species committed to extinction: critically endangered species (dark yellow) and all 'threatened' species (orange). If all threatened (TH) species became extinct in 100 years and that rate was maintained in the future, a magnitude of 75% species loss would be reached within 240–540 years. A similar scenario using the rate of critically endangered (CR) species yields an estimate of 890–2270 years. Reproduced from Figure 3. Extinction rate versus extinction magnitude in Barnosky AD, Matzke N, Tomiya S, et al. (2011) Has the Earth's sixth mass extinction already arrived? *Nature* 471: 51–57, with permission from Nature.

Caveats to Comparison

Differences in criteria and in the quality of the data used to assess past, present, and future extinction rates are major sources of uncertainty limiting their comparison.

Estimates of past extinction are based on the fossil record, which is a very restricted sample of past diversity. Only a very limited (but still impressive) fraction of species left a trace of their existence in the fossil record. Overall around a quarter of a million species have been identified from a total of tens of millions of well-preserved fossils (Raup, 1992). Near-shore aquatic species are among the most common, because sediments in riverbeds, lakebeds, and in the seabed tend to provide a good medium for fossil preservation (Raup, 1992; Barnosky et al., 2011). In addition, organisms with hard body parts, such as bivalves, fossilize better than soft-body organisms, such as insects. The action of decomposers and erosion erased most signs of past terrestrial organisms, and existent fossils usually correspond to individuals that were trapped and died in good preservation settings, such as volcanic ashes or tar pits (Raup, 1992). The best records of fossil vertebrates are for temperate terrestrial mammals (Regan et al., 2001; Barnosky et al., 2011).

The assessment of present and future extinction rates mostly relies on terrestrial vertebrate data for which there is more data available. With the exception of terrestrial mammals, the differences in the composition of past and recent extinction records limit the comparison between past and current extinction rates. Therefore, it is important to improve our knowledge on the conservation status of groups that are well represented in the fossil record but currently less known, such as near-shore marine invertebrates with shells (Barnosky et al., 2011). A caveat would be that selected groups might not be good indicators of other taxa, ascribing a limited utility to comparisons.

A second problem relates with the taxonomic levels used to assess extinction rates and with the concept used to define species (Barnosky et al., 2011). Fossil diversity and extinction rate are usually assessed at the genus level, and species diversity and extinction rate are then extrapolated using species-to-genus ratios, based on proportions of well-known groups. However, modern extinction rates are directly based on species data. Moreover, species in the fossil record are defined using the morphological species concept, whereas modern species are often defined using other criteria, especially the phylogenetic species concept, based on genetic similarity. The type of concept used may affect the number of species in a taxon and influence extinction rate metrics, adding uncertainty to extinction rate comparisons.

A third source of uncertainty when comparing extinction rates is that past extinction rates represent a measure of realized extinction, current extinction rates represent a conservative measure of recent extinction, due to the omission of "possibly extinct" species, and projected extinction rates may represent an overestimated measure of extinction rate, due to the inclusion of species committed to extinction.

Key Messages

Human activities and intervention over ecosystems have been causing the loss of species at rates much higher than the natural rate of extinction. Earth is experiencing a biodiversity crisis and while a sixth mass extinction is still avoidable, modern rates of extinction are already too high and alarming. Although developed regions, namely Europe, have already lost an important share of their biodiversity during millennia of human occupation and resources exploitation, other regions, namely species-rich tropical regions are now experiencing intense human pressure, which may lead to very high rates of biodiversity loss. The risks of biodiversity loss, from species loss to ecosystem degradation, are real and may jeopardize human well-being by affecting the delivery of critical ecosystem services, including food, clean water, and regulation of natural disasters.

Despite these risks our knowledge of biodiversity and of the complex interactions between drivers of change and between them and natural systems is still very incomplete, and limits our capacity of action to target and develop measures to halt biodiversity loss. There is a need for a better understanding of the impacts of drivers on biodiversity, especially of drivers that are still weakly integrated in projections of future biodiversity change (i.e., land-use change, overexploitation, pollution, and invasive species), but there is also a need for data from regions where biodiversity is now under more severe pressure. The implementation of a global network for biodiversity monitoring (Pereira et al., 2010a, 2010b) that delivers data to fill knowledge gaps and to validate and calibrate current models of biodiversity change may contribute to reduce uncertainty in projections and hence to better assess impacts of drivers on biodiversity and relevant conservation measures.

See also: Extinction, Causes of. Extinction in the Fossil Record. Human Impacts on Ecosystems: An Overview. Mass Extinctions, Concept of. Modeling Biodiversity Dynamics in Countryside and Native Habitats. Modern Examples of Extinctions

---

References

Alcamo J, Leemans R, and Kreileman E (eds.) (1998) *Global Change Scenarios of the 21st Century. Results from the IMAGE 2.1 Model*. Oxford, UK: Pergamon and Elsevier Science.

Alcover JA, Sans A, and Palmer M (1998) The extent of extinctions of mammals on islands. *Journal of Biogeography* 25: 913–918.

Alkemade R, van Oorschot M, Miles L, Nellemann C, Bakkenes M, and ten Brink B (2009) GLOBIO3: A Framework to investigate options for reducing global terrestrial biodiversity loss. *Ecosystems* 12: 374–390.

Baillie JEM, Hilton-Taylor C, and Stuart SN (2004) *2004 IUCN Red List of Threatened Species. A Global Species Assessment*. Gland: IUCN.

Barnosky AD, Koch PL, Feranec RS, Wing SL, and Shabel AB (2004) Assessing the causes of late pleistocene extinctions on the continents. *Science* 306: 70–75.

Barnosky AD, Matzke N, Tomiya S, et al. (2011) Has the Earth's sixth mass extinction already arrived? *Nature* 471: 51–57.

Brooks TM, Mittermeier RA, Mittermeier CG, et al. (2002) Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology* 16: 909–923.

Butchart SHM, Stattersfield AJ, and Brooks TM (2006) Going or gone: Defining "Possibly Extinct" species to give a truer picture of recent extinctions. *Bulletin-British Ornithologists Club* 126: 7.

Butchart SHM, Walpole M, Collen B, et al. (2010) Global biodiversity: Indicators of recent declines. *Science* 328: 1164–1168.

Carpenter SR, Pingali PR, Bennett EM, and Zurek MB (eds.) (2005) *Ecosystems and Human Well-Being: Scenarios*. Washington, DC: Island Press.

Cheung WWL, Lam VWY, Sarmiento JL, Kearney K, Watson R, and Pauly D (2009) Projecting global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries* 10: 235–251.

Darwall W, Smith K, Allen D, *et al.* (2009) Freshwater biodiversity: A hidden resource under threat. In: Vié J-C, Hilton-Taylor C, and Stuart SN (eds.) *Wildlife in a Changing World: An Analysis of the 2008 IUCN Red List of Threatened Species.* Gland, Switzerland: IUCN.

Dulvy NK, Sadovy Y, and Reynolds JD (2003) Extinction vulnerability in marine populations. *Fish and Fisheries* 4: 25–64.

Foote M (1994) Temporal variation in extinction risk and temporal scaling of extinction metrics. *Paleobiology* 20: 424–444.

Foote M and Raupe DM (1996) Fossil preservation and the stratigraphic ranges of taxa. *Paleobiology* 22: 121–140.

Foote M (2000) Origination and extinction components of taxonomic diversity: General problems. *Paleobiology* 26: 74–102.

Green WA, Hunt G, Wing SL, and DiMichele WA (2011) Does extinction wield an axe or pruning shears? How interactions between phylogeny and ecology affect patterns of extinction. *Paleobiology* 37: 72–91.

Heywood VH, Mace GM, May RM, and Stuart S (1994) Uncertainties in extinction rates. *Nature* 368: 105.

Hilton-Taylor C, Pollock CM, Chanson JS, Butchart SHM, Oldfield TEE, and Katariya V (2009) State of the world's species. In: Vié J-C, Hilton-Taylor C, and Stuart SN (eds.) *Wildlife in a Changing World: An Analysis of the 2008 IUCN Red List of Threatened Species.* Gland, Switzerland: IUCN.

Hoffmann M, Hilton-Taylor C, Angulo A, *et al.* (2010) The impact of conservation on the status of the World's vertebrates. *Science* 330: 1503–1509.

IMAGE-team (2001) *The IMAGE 2.2 implementation of the SRES scenarios: a comprehensive analysis of emissions, climate change and impacts in the 21st century.* RIVM CD-ROM Publication 481508018. Bilthoven: National Institute of Public Health and the Environment.

IPCC (2007) *Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Geneva, Switzerland: IPCC.

IUCN (2011) *IUCN Red List of Threatened Species. 2011.1.* Summary Statistics.

Jetz W, Wilcove DS, and Dobson AP (2007) Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology* 5.

Kirchner JW and Weil A (2000) Delayed biological recovery from extinctions throughout the fossil record. *Nature* 404: 177–180.

Leadley P, Pereira HM, Alkemade R, *et al.* (2010) *Biodiversity Scenarios: Projections of 21st Century Change in Biodiversity and Associated Ecosystem Services.* Montreal: Secretariat of the Convention on Biological Diversity.

MA – Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-Being: Synthesis.* Washington, DC: Island Press.

Mace GM, Masundire H, and Baillie JEM (2005) Biodiversity. In: Scholes R and Hassan R (eds.) *Ecosystems and Human Well-Being: Current State and Trends*, pp. 77–122. Washington, DC: Island Press.

Malcolm JR, Liu C, Neilson RP, Hansen L, and Hannah L (2006) Global warming and extinctions of endemic species from biodiversity hotspots. *Conservation Biology* 20: 538–548.

Mora C, Tittensor DP, Adl S, Simpson AGB, and Worm B (2011) How many species are there on Earth and in the ocean? *PLoS Biology* 9: e1001127.

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, and Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.

Neilson RP, Prentice IC, Smith B, Kittel TGF, and Viner D (1998) Simulated changes in vegetation distribution under global warming. In: Watson RT, Zinyowera MC, Moss RH, and Dokken DJ, (eds.) *The Regional Impacts of Climate Change: An Assessment of Vulnerability*, pp. 439–456. Cambridge: Cambridge University Press.

Pereira HM, Belnap J, Brummitt N, *et al.* (2010b) Global biodiversity monitoring. *Frontiers in Ecology and the Environment* 8: 459–460.

Pereira HM, Leadley PW, Proença V, *et al.* (2010a) Scenarios for global biodiversity in the 21st century. *Science* 330: 1496–1501.

Pimm S, Raven P, Peterson A, Sekercioglu CH, and Ehrlich PR (2006) Human impacts on the rates of recent, present, and future bird extinctions. *Proceedings of the National Academy of Sciences* 103: 10941–10946.

Pimm SL and Brooks TM (1999) The sixth extinction: How large, how soon, and where? In: Raven P (ed.) *Nature and Human Society: The Quest for a Sustainable World.* Washington, DC: National Academy Press.

Pimm SL and Jenkins CN (2010) Extinctions and the practice of preventing them. In: Sodhi NS and Ehrlich PR (eds.) *Conservation Biology for All.* New York: Oxford University Press.

Pimm SL, Russell GJ, Gittleman JL, and Brooks TM (1995) The future of biodiversity. *Science* 269: 347–350.

Raup D (1986) Biological extinction in earth history. *Science* 231: 1528–1533.

Raup DM (1992) *Extinction: Bad genes or bad luck?.* New York: WW Norton & Company.

Regan HM, Lupia R, Drinnan AN, and Burgman MA (2001) The currency and tempo of extinction. *The American Naturalist* 157: 1–10.

SCBD – Secretariat of the Convention on Biological Diversity (2010) *Global Biodiversity Outlook 3.* Montreal: Secretariat of the Convention on Biological Diversity.

Sala OE, Van Vuuren DP, Pereira HM, *et al.* (2005) Biodiversity across scenarios. In: Carpenter SR, Pingali PL, Bennett EM, *et al.* (eds.) *Ecosystems and Human Well-Being: Scenarios.* Washington, DC: Island Press.

Sekercioglu CH, Schneider SH, Fay JP, and Loarie SR (2008) Climate change, elevational range shifts, and bird extinctions. *Conservation Biology* 22: 140–150.

Sinervo B, Méndez-de-la-Cruz F, Miles DB, *et al.* (2010) Erosion of lizard diversity by climate change and altered thermal niches. *Science* 328: 894–899.

Steadman DW (1995) Prehistoric extinctions of Pacific island birds: Biodiversity meets zooarchaeology. *Science* 267: 1123–1131.

Thomas CD, Cameron A, Green RE, *et al.* (2004) Extinction risk from climate change. *Nature* 427: 145–148.

Thuiller W, Albert C, Araújo MB, *et al.* (2008) Predicting global change impacts on plant species' distributions: Future challenges. *Perspectives in Plant Ecology, Evolution and Systematics* 9: 137–152.

van Vuuren D, Sala O, and Pereira HM (2006) The future of vascular plant diversity under four global scenarios. *Ecology and Society* 11: 25.

Worm B, Hilborn R, Baum JK, *et al.* (2009) Rebuilding global fisheries. *Science* 325: 578–585.

Xenopoulos MA, Lodge DM, Alcamo J, Marker M, Schulze K, and Van Vuuren DP (2005) Scenarios of freshwater fish extinctions from climate change and water withdrawal. *Global Change Biology* 11: 1557–1564.