ORIGINAL PAPER

Re-assessing current extinction rates

Nigel E. Stork

Abstract There is a widespread belief that we are experiencing a mass extinction event similar in severity to previous mass extinction events in the last 600 million years where up to 95% of species disappeared. This paper reviews evidence for current extinctions and different methods of assessing extinction rates including species–area relationships and loss of tropical forests, changing threat status of species, co-extinction rates and modelling the impact of climate change. For 30 years some have suggested that extinctions through tropical forest loss are occurring at a rate of up to 100 species a day and yet less than 1,200 extinctions have been recorded in the last 400 years. Reasons for low number of identified global extinctions are suggested here and include success in protecting many endangered species, poor monitoring of most of the rest of species and their level of threat, extinction debt where forests have been lost but species still survive, that regrowth forests may be important in retaining 'old growth' species, fewer co-extinctions of species than expected, and large differences in the vulnerability of different taxa to extinction threats. More recently, others have suggested similar rates of extinction to earlier estimates but with the key cause of extinction being climate change, and in particular rising temperatures, rather than deforestation alone. Here I suggest that climate change, rather than deforestation is likely to bring about such high levels of extinction since the impacts of climate change are local to global and that climate change is acting synergistically with a range of other threats to biodiversity including deforestation.

Keywords Extinction · Extinction crisis · Extinction rates · Red Data lists ·
Threatened species

Introduction

That there is an on-going extinction crisis is widely accepted by scientists, government and non-governmental organisations, the public and the media. Many suggest that the current

N. E. Stork (✉)
Department of Resource Management and Geography, Melbourne School of Land and Environment,
University of Melbourne, 500 Yarra Boulevard, Richmond, VIC 3121, Australia
e-mail: nstork@unimelb.edu.au

extinction phase, frequently referred to as the 'sixth mass extinction event', is as extensive and rapid as the five previous mass extinction events in the last 600 million years when 65–95% of marine animals previously known from fossil records disappeared (Raup 1986). A survey in 1998 suggested that 70% of biologists believe that during the next 30 years as many as one-fifth of all species alive today are committed to extinction, and a third think as many as half the species on Earth will die out in that time (AMNH 1998). There have been a few who have challenged this view (Simon 1995; Lomborg 2001) and their arguments, quite justifiably, have been dismissed as highly selective or unscientific (Pimm et al. 1995; Pimm and Harvey 2001).

The media have a large influence on public opinion, particularly those outlets that are respected for their journalism. For example, the influential magazine, *Time*, ran an article in January 2000 entitled 'Death Row' which noted that surprisingly none of the 25 species of primate that are on the verge of extinction had actually gone extinct in the last century. It stated '*As far as we know, no primate became extinct during the 20th century. That's an impressive record, since the world loses about 100 species a day*'. Almost certainly the latter statement reflects estimates of extinctions which derive from the species–area relationship and loss of tropical forests (e.g. Myers 1988; Wilson 1988) and these are discussed later. In this paper I examine whether figures for extinctions reflect current evidence. I do this by examining the data for recent extinctions and data on the number of all species on Earth, different approaches to estimating extinction rates, and the evidence for differences in the vulnerability of different groups to extinction. In this paper when I use the term *extinction* I am specifically referring to *global extinction* unless otherwise stated. In this respect, I argue that *global extinction* is currently less frequent than many reports indicate and a greater problem is the loss of species at the local and regional level. Finally, I reflect on current evidence that climate change and its interactions with other threats, rather than forest loss alone, may indeed result in the levels of species loss this century that some had previously predicted.

Current data for extinctions and the number of species on Earth

The actual number of species that are officially recognised as extinct since 1600, according to IUCN (IUCN 2009) and other sources, is surprisingly low—around 1,200 species. It is also important to recognise that the most recent 2009 IUCN list of extinct species is in large part a list for 1959 since a species has traditionally only been recognised as 'extinct' when no living individual has been seen for 50 years. This has been changed with a small number of species ($n = 37$) now recognised in a relatively new category of 'extinct in the wild'. There have been remarkable changes in the global environment over the last 50 years with large increases in rates of desertification, the loss of dry and moist tropical forests, and increases in pollution (MEA 2005). Also the threat of extinction for whole faunas and floras has only been measured for a few areas of the world, such as parts of Europe, or globally for only a few groups of organisms such as terrestrial vertebrates, swallowtail butterflies and other well-known animals and plants. Similarly, it is very difficult to determine when the last individual of a species has died (Diamond 1987; Ehrlich and Wilson 1991; Mawdsley and Stork 1995) and figures for recent extinctions are inaccurate. Biologists are still discovering many new species, not all of which are small and cryptic. For example, the large and distinctive Wollemi pine was found 100 km from downtown Sydney (Jones et al. 1995). Even some large vertebrates remain to be described: van Roosmalen et al. (2002) described the 37th and 38th new species of primates

discovered since 1990. We should therefore not be surprised that the last remaining individuals of many threatened species of these vertebrates are often impossible to observe and monitor (Chades et al. 2008). For small vertebrates and invertebrates it is virtually impossible to monitor the fate of such threatened species except where their distribution is small and well-known.

A critical component in understanding the scale and impact of the 'extinction crisis' is the knowledge of at least a ball park estimate of how many species there are on Earth and how these species are distributed, group by group, and area by area. Only with that knowledge can we start to understand the scale and extent of species extinctions and translate extinction rates into real numbers of species extinctions and vice versa. Estimates of the number of species on Earth escalated in the 1980s from 1–2 million to 30–100 million due to large increases in the number of species of several key taxa—principally insects and their other arthropod relatives, and to a lesser extent, fungi and nematodes (Erwin 1982; May 1988; Stork 1988). Even the number of species of vertebrates and higher plants is uncertain since the use of DNA techniques suggest that the number of recognised species might increase significantly. However, earlier estimates which suggest up to a hundred-fold increase in the total number of species of insects (Erwin 1988), fungi (Hawksworth 1991) or marine invertebrates (Grassle and Maciolek 1992) are disputed (Stork 1988; May 1992) and have been replaced by estimates of 5–15 million species (Hammond 1995; Stork 1997, 1999; May 1998; Novotny et al. 2002; Dirzo and Raven 2003). Recent use of uncertainty modelling with two models (Hamilton et al., submitted) predict medians of 6.3 and 8.6 million arthropod species globally, with 90% confidence intervals of 1.6–16.0 and 2.7–19.7 million. This analysis confirms the very low probability of there being 30 million species of arthropods. The key implications of such estimates with respect to the extinction debate arguably are (i) that arthropods may comprise 80–90% of all species of terrestrial macro-organisms and, (ii) that 85–95% of arthropods, invertebrates and micro-organisms have yet to be named and described, and (iii) that most of these are found in tropical forests. Finally, if the world is losing about 100 species a day, or roughly 36,500 a year, the vast majority of these losses must come from the plants, fungi or invertebrates, since there are arguably only about 45,000 vertebrate species on Earth (Hammond 1992).

Estimates of extinction rates

The approaches to estimating extinction rates (Reid 1992; Stork 1997) can be grouped into five categories: species–area based estimates, estimates from empirical data of known extinctions, estimates from the use of Red Data lists, co-extinctions and lastly models of the impact of climate change. These are discussed in more detail below and in Table 1.

Species area estimates

The earliest estimates of extinction rates variably suggesting the loss of 5–30% of all species on Earth per decade (Lovejoy 1980; Ehrlich and Ehrlich 1981; Raven 1987; Myers 1988, 1993; Wilson 1988) were based on predictions of species loss from the clearing of tropical forests calculated using species–area relationships. Where these estimates differed is in the value of a key constant z (Reid 1992; Simberloff 1992). If some of these higher estimates were true, then we should have already witnessed the extinction of up to 50% of all species on Earth in the last 30 years. Wilson (1988) for example, extrapolating from

Table 1 Estimated rates of extinction (after Reid 1992; Stork 1997, 1999)

Estimate	Taxon (*all taxa* unless otherwise stated)	% global loss per decade	Method of estimation	Reference
(1) Species-area estimates				
One million species between 1975 and 2000		4.00	Extrapolation of past exponentially increasing trend	Myers (1979)
15–20% of species between 1980 and 2000		8–11	Estimated species–area curve; forest loss based on Global 2000 projections	Lovejoy (1980)
50% loss of species by 2000 or soon after; 100% by 2010–2025		20–30	Various assumptions	Ehrlich and Ehrlich (1981)
9% extinction by 2000		7–8	Based on Lovejoy's calculations using updated forest loss estimates	Lugo (1988)
12% of plant species in neotropics, 15% of bird species in Amazon basin	Plants and birds	–	Species–area curve ($z = 0.25$)	Simberloff (1986)
2000 plant species loss per year in tropics and subtropics; 25% loss of species in 1985–2015	Plants	8–9	Loss of half the species in area likely to be deforested by 2015	Raven (1987, 1988)
At least 7% loss of plant species	Plants	7	Half of species lost over next decade in 10 'hot-spots' covering 3.5% of forest area	Myers (1988)
0.2–0.3% species loss per year		2–6	Half of rainforest species assumed lost in tropical rainforests to be local endemics and becoming extinct with forest loss	Wilson (1988, 1989)
2–13% loss between 1990 and 2015		1–5	Species–area curve ($0.15 < z < 0.35$); range includes current rate of forest loss and 50% increase	Reid (1992)
37–50% extinction rate for 5,308 Amazonian plant species by 2020	Amazonian plant species	14.6–19.7	Estimated number of Amazonian species lost by Laurance et al. (2001) predicted forest loss	Hubbell et al. (2008)
5–9% extinction for Amazonian plants by 2050	Amazonian plant species	1.2–2.2	Revision of above estimate reviewing potential habitat loss and species distributions	Feeley and Silman (2009)
Predict: in next 25 years rate of net tropical deforestation to slow on all continents; net increase in forest area in Latin America and Asia at least within 50 years, and in Africa within 100 years			Slowing shifts of people from tropical rural to urban; suggested reduced deforestation, increased secondary forests succession, both reducing extinction pressures	Wright and Muller-Landau (2006a, b)

Table 1 continued

Estimate	Taxon (*all taxa* unless otherwise stated)	% global loss per decade	Method of estimation	Reference
(2) Estimates from empirical data				
Past loss of 50–90% Pacific Island birds	Pacific island birds		Evidence from recent fossil evidence	Pimm et al. (1995), Steadman (1995)
Current extinction rates 100 times background rates and will increase 15 fold by 2100	All bird species		Range of threats to bird species: habitat/forest loss, invasive species and global change	Pimm et al. (2006)
(3) Estimates from Red lists				
50% extinction in 50–100 years (palms and 300–400 years (birds and mammals)	Selected taxa including palms, birds and mammals	1–10	Extrapolating current recorded extinction rates and by dynamics of threatened status	Smith et al. (1993)
6–50% extinction of selected vertebrates in next 100 years	Some vertebrate taxa including reptile, mammal and bird groups	0.6–5	Fitting of exponential extinction functions based on IUCN categories of threat	Mace (1994)
100,000–500,000 insect species extinctions in next 300 years	Insects	0.04–0.21	Extrapolating from British Red Data Books and assuming 8 million species of insects worldwide	Mawdsley and Stork (1995)
(4) Co-extinctions				
3–5% extinction of helminth species parasitising vertebrates in next 50–100 years	Parasitic helminths	0.15–0.5	Loss of parasites due to loss of hosts; developing co-extinction theory (Stork and Lyal 1993; Koh et al. 2004)	Dobson et al. (2008)
213,830–547,500 insect herbivores committed to extinction in 34 biodiversity hot-spots	Herbivorous insects		Assumes that 150,371 endemic plant species have an average of 5.3–10.6 monophagous insect herbivores	Fonseca (2009)
(5) Models of climate change				
15–37% loss of species by 2050	1,103 species including vertebrates & invertebrates	3.2–7.8	Modelled species distributions against IPCC climate change scenarios	Thomas et al. (2004)

Note that many of these estimated rates include species 'committed' to extinction. Estimates of % global loss per decade are from Reid (1992) or for later estimates are calculated by the current author based on global estimates for all species on Earth of 10 million and for all insects of 8 million

species area estimates based on logging and forest loss, suggested that 17,500 species are being lost each year based on a total of 5 million species of organisms. Many of these early authors still consider that such extinction rate estimates are valid (e.g. Raven and McNeely 1998; Pimm and Raven 2000; Myers 2003; Dirzo and Raven 2003).

Further concern for the loss of species due to forest loss came from an analysis of the impact of expansion of road networks and other infrastructure in the Amazon that suggested as little as 40% might be unconverted forest by 2020 (Laurance et al. 2001) (but note even the areas termed heavily degraded or deforested are still mostly covered with forests—see also Chazdon et al. 2009 for discussion of regrowth forests). Hubbell et al. (2008) estimated the number, relative abundance and range size of tree species in the Brazilian Amazon using Hubbell's neutral theory (Hubbell 2001) and then examined the optimistic and pessimistic scenarios of Laurance and co-workers to estimate what proportion of species may become extinct. They estimated that this area of the Amazon might contain 11,210 species with 5,308 of these having less than 10,000 individuals each and as such this group of species might suffer a 50% extinction rate under the pessimistic scenario and as high as 37% under the optimistic scenario. These estimates have been criticised (Feeley and Silman 2008) and an improved assessment of the extinction risks of Amazonian plant species suggests that by 2050 land use change may result in 12–24% reduction of forest habitat and that this may result in 5–9% species being committed to extinction (Feeley and Silman 2009).

In contrast, Wright and Muller-Landau (2006a, b), examined United Nations human population data to demonstrate slowing in population growth and population shifts from rural to urban in tropical countries, globally. They suggested that deforestation pressures might reduce and that secondary forests succession might speed up, both reducing the extinction pressures on tropical forests. Their novel approach has reignited what had been a stale argument and sparked new interest in the fate of tropical forest biodiversity (Brook et al. 2006; Sloan 2007; Laurance 2007).

An inspection of Table 1 shows that over time, as data have become more available and as methods of analyses have improved, the species–area based estimates have reduced very considerably. Indeed if the Wright and Muller-Landau calculations are correct then there may even be a recovery of some species rather than extinctions in the long-term. However, the impacts of climate change are likely to more than counteract this trend as is discussed below.

Estimating from empirical data of actual extinctions

The most compelling data for extinctions relate to those provided by Pimm et al. (2006) and others for birds from oceanic islands and in particular the Hawaiian islands. Earlier Pimm et al. (1995) suggested that 50% or more of bird species on many of the Pacific islands including the Hawaiian islands, S.E. Polynesia, the Marianas, and New Caledonia are missing, endangered, extinct or known from bones only. For the Hawaiian islands this figure is closer to 90%. Much of the evidence for such high levels of extinction is from recent fossil evidence which suggests that on these islands the wave of extinction has largely taken place for birds, and in particular flightless birds, after the arrival of man over the last 1,000 years. Steadman (1995) suggested that the Polynesians eliminated 2,000 species of flightless rails alone (see also Curnutt and Pimm 2001). Subsequently, Pimm et al. (2006) suggested that, globally, recent extinction rates for birds are 100 times higher than background rates and that by the end of the twenty-first century they will be 1,500 times higher than background rates. In practice, the extinction phase for birds of the Pacific

Islands has largely taken place, mostly perhaps several hundred years ago (but note there are still species of bird there on the brink of extinction). It is difficult to argue that such extinctions from islands will be replicated on continental landmasses since bird communities there are of different taxa and vary considerably in their extinction vulnerability. In remote island situations, whole biotas which have evolved from a low genetic stock without invasive species for hundreds of thousands if not millions of years are extremely vulnerable to human invasions and the threats that they bring.

Estimating from Red Lists of threatened species

A third approach to estimating extinctions rates by examining the changing threatened status of a number of groups of animals and plants (Smith et al. 1993; Mace 1994; Mawdsley and Stork 1995) provided an alternative to the species–area model that had previously dominated the extinction rate debate (see Table 1). Smith et al. (1993) summed the number of species added to the list of extinctions (as recorded on the World Conservation Monitoring Centre's database) for a 4-year period (1986–1990) for animals, and 2-year period (1990–1992) for plants. With these data and the estimated number of species worldwide for different taxa, they were able to calculate that the time required for 50% of species to go extinct was 1,500 years for birds and 6,500 years for mammals. They also estimated the net changes in the Red Data Book status of species (from rare, vulnerable, endangered to probably extinct) and again estimated 50% extinction values with resulting values of 350, 250 and 70 years for birds, mammals and palms—much lower than those from their first method. A further method of estimating extinction rates by Mace (1994) also used IUCN red list categories but involved species-by-species assessments of extinction probabilities over time (Mace 1994). Her calculations, based on expected extinction times for selected vertebrate taxa, suggested average extinction times of 100–1,000 years or characteristically 300–400 years for 50% extinction of mammals and birds. Although the way such lists are compiled means that their use in such extrapolations may be questionable (Possingham et al. 2002) this work provides further demonstrations that extinction rates vary considerably between different groups.

Smith and colleagues were unable to produce extinction estimates for less well-known groups such as insects and other invertebrates because of the lack of adequate information on their threatened status. However, Mawdsley and Stork (1995) suggested that one such source of information was the Red Data Book status of British invertebrates (e.g. Shirt 1987; Batten and 1990; Bratton 1991). The British biota has been so well studied for so many years that the threatened status of most groups is very well known. Mawdsley and Stork noted that the percentages of threatened insects, molluscs and spiders were remarkably similar and that these groups were 7.1 times less threatened than birds in Britain. They argued that if this reflected a true difference in the vulnerability of birds to invertebrates, we might be able to use this 'relative extinction rate' to determine how many invertebrate species have gone globally extinct. Since 1% of birds and mammals have become extinct since 1600, $1/7.1 = 0.14\%$ of insects also may have become extinct in the same period of time—equivalent to 7,000–14,000 species of insect, assuming a figures of 5–10 million insect species on Earth. Using the estimated 12–55 fold increase in extinction rates of birds over the next 300 years (Smith et al. 1993) a further 100,000–500,000 species of insect would also become extinct. Mawdsley and Stork (1995) also showed that since 0.7% of British insects have become extinct since 1600, a relative extinction rate with birds of 7.1 would suggest that 5% or 11 British breeding birds should also have been lost. This concurs with Sharrock (1974) who states that 11 species of bird have become extinct in

Britain and Ireland with two later recolonizing. Attempts to re-examine the viability of the 'relative extinction rate' for other parts of the world have been thwarted by a lack of consistency in the assessment of the threatened status of insects and other invertebrates in different countries.

Estimating co-extinctions

The biologies of some species of organisms are so intimately connected with other host species that the extinction of their hosts may lead to their own extinction. Such 'co-extinctions' (Stork and Lyal 1993) are most likely to occur when species are highly host-specific. Although no one has yet estimated precisely how many species are dependent on other species, I would guess this to be possibly 30–40% of all species on Earth (but see discussion by Fonseca, 2009). A number of authors have attempted to estimate the likelihood of extinction based on estimates of host-specificity variously focussing on insects specific to plants and parasites of vertebrates (Koh et al. 2004; Dobson et al. 2008). Dobson et al. (2008) estimate that there are 75,000–300,000 helminth species parasitising vertebrates and that 3–5% is threatened with extinction in the next 50–100 years because of their intimate relationships with threatened vertebrate species. These estimates suggest that co-extinctions are likely to be in the tens of thousands in the next 100 years. Most recently Fonseca (2009) has estimated that the 150,371 endemic plant species in the world's 34 biodiversity hotspots may have an average of 5.3–10.6 monophagous insect herbivore species feeding on them or a total of 795,971–1,603,423 insect species. He estimates that 213,830–547,500 of these insect species are committed to extinction as their hosts become extinct due to habitat loss. To some extent the co-extinction problem reflects the connectedness of species and is a side issue from the main debate about the importance of the key drivers of extinction—habitat loss and climate change.

Models of the impact of climate change

Another recent set of models have been developed to predict the impact of rising temperatures on organisms (Williams et al. 2003; Thomas et al. 2004). Thomas et al. (2004) looked at six biologically diverse regions around the world covering about 20% of the Earth's land area and modelled the future distributions of 1,103 species including plants, mammals, birds, reptiles, frogs, butterflies and other invertebrates. Using three different IPCC climate change scenarios they found that the 15–37% of these species could become extinct by 2050. Their model is also based on the species–area relationship and the use of this relationship is further critiqued by Lewis (2006) who suggests that these estimates should be considered 'first pass' estimates requiring much greater refinement. The Thomas et al. model and other models have been analysed by Botkin et al. (2008) who suggest how to make such predictions more accurate and reliable. They and others (Willis et al. 2004; Stork et al. 2009) also suggest that we should be making much greater use of the Quaternary record where very few species appeared to go extinct as a consequence of large changes in temperature. In summary, climate envelope models provide an upper limit on the number of extinctions that might be possible rather than the number that might be expected.

There has been considerable attention on the impact of rising temperatures on tropical forest species particularly as poleward range shifts of equatorial species due to global warming are unlikely given the prevailing narrow tropical temperature gradient today (Wright et al. 2009). Upslope elevational range shifts in the tropics are perhaps more likely

(Colwell et al. 2008) but some higher elevation species are likely to disappear as suitable climatic conditions disappear (Williams et al. 2003). Poleward and elevational shifts of tropical species may be hampered in anthropogenically modified and fragmented land-scapes and by the lack of some key seed-dispersing animals previously lost through overhunting.

Why predicted extinction rates do not match empirical data

Conservation efforts to protect species

There is no doubt that the massive conservation efforts in the last 50 years by governments and non-governmental organisations to create protected areas and efforts to protect individual species that are threatened has had a great impact on reducing what might have been almost certain extinctions in many instances. The IUCN Red lists and Global Biodiversity Hotspots, for example, are testament to these efforts.

Extinction debt–relaxation times

Many have observed that loss of forest on continental landmasses does not lead to automatic widespread global extinction of species as predicted by the species–area relationship (Heywood and Stuart 1992, but see Raven and McNeely 1998). For example, there is little evidence so far for large scale extinctions following the massive forest loss in the Atlantic forests in north-east Brazil (Brown and Brown 1992). This lack of extinction in the Atlantic forests and elsewhere where there has been extensive forest conversion may be due both to the often fragmented nature of this conversion, that it can take many years for extinction inducing factors to take effect (Diamond 1972; Tilman et al. 1994; Brooks and Balmford 1996; Brooks et al. 1999), that biodiversity hotspots too have their own hotspots (Hugall et al. 2002; Carnaval et al. 2005) and that hotspots of endemism do not necessarily coincide with hotspots of threat (Orme et al. 2005). This phenomenon of higher species diversity for an area than one would predict following a reduction in that area has been termed 'relaxation time' (Diamond 1972) or 'extinction debt' (Tilman et al. 1994), as the species diversity returns to an equilibrium level that reflects the balance between immigration rates and extinction rates. How long extinction debt may exist after logging and fragmentation is still uncertain but empirical data from Borneo show that regenerating previously selectively logged forests can remain habitat for a range of vertebrate species that might have been considered highly threatened by logging (Johns 1997; Meijaard et al. 2005).

The issue of how important secondary regrowth forests are in maintaining biodiversity and species survival has become increasingly more important as half of all tropical forests now fit that category (Chazdon et al. 2009). With the exception of a few comparative studies (e.g. Lawton et al. 1998; Dunn 2004; Meijaard et al. 2005; Barlow et al. 2007), we still have a poor understanding of what happens to biodiversity (insects, fungi and other microorganisms, as well as birds and mammals) when areas are logged or how biodiversity changes as forests regenerate after logging. A key question is just what proportion of 'old growth' species is found in regrowth forests (Chazdon et al. 2009). Interpretation of the results of existing studies have also been complicated because too often the different or

compounding effects of aspects of forest fragmentation (e.g. edge effects, size of fragments, degree of isolation, length of time of isolation) or forest disturbance (e.g. amount of loss of vegetation cover, degree of soil compaction, degree of soil erosion, hydrological effects, etc.) have not been measured, frequently because it has been difficult to do so.

Species are not equally prone to extinction

Some assume global extinction rates for birds and large mammals can be directly translated to other organisms (e.g. Pimm and Brooks 2000; Pimm and Raven 2000) and yet there is now a vast body of literature and other evidence from the IUCN lists of threatened species which demonstrate that species and different groups of organisms are not all equally prone to extinction. This also includes analysis of variously combined paleontological, phylogenetic, historical and ecological data (McKinney 1997; Purvis et al. 2008; Stork et al. 2009). Why some species are more vulnerable than others has been the subject of many studies for different taxa (e.g. mammals and birds—Laurance 1991; Newmark 1991, insects—Mawdsley and Stork 1995, and plants—Bradshaw et al. 2008; Sodhi et al. 2008). In addition, the biotas of different parts of the Earth also vary in their vulnerability—a key thesis of the biodiversity hotspots theory (Myers 1988; Myers et al. 2000; but see Manne et al. 1999). As discussed previously, the majority of all recorded extinctions are from islands where their biotas have often evolved from a small gene pool and have suffered from human-related impacts such as hunting or over-extraction, land-use change or invasive organisms. Such impacts on these narrowly distributed species have resulted in the loss of all populations simultaneously with the consequent loss of such species. Species on continental islands, such as mountain tops, are similarly prone to such threats because of their small size (Manne et al. 1999).

Concluding remarks

So what can we conclude about extinction rates? First, less than 1% of all organisms are recorded to have become extinct in the last few centuries and there are almost no empirical data to support estimates of current extinctions of 100 or even one species a day. Second, the most frequently used predictions for global extinction rates are still largely based on the species–area relationship and the fact that large areas of forests (in particular) are being converted. As Lewis (2006) suggested these and the first models of the impacts of climate change on biodiversity, are first passes with subsequent more sophisticated analyses frequently reducing first estimates of extinction rates (see Table 1). With the increasing evidence that some species appear to survive in regrowth forests (Chazdon et al. 2009) the key question is how long are the time lags to extinction for those remaining species which are unable to survive in regrowth or fragmented forests? Third, the evidence is so overwhelming that extinction threats vary for different groups of organisms and different faunas and floras that it is surprising that there are still some who seek to draw conclusions on global extinction rates for all organisms based on the knowledge of just a few very highly threatened groups.

Are estimates of extinction rates useful? Yes I believe so but we should consider some of the highest and 'first pass' estimates as upper boundaries rather than real estimates since the assumptions that are made are often unrealistic and require much further modification. However, in spite of the 'first pass' nature of the climate change models and their frequent dependence on the assumptions of the species–area relationship, the pervading global

nature of such temperature increases seems more threatening than any previous threat. There is also growing evidence that many threats are acting synergistically (Brook et al. 2008; Stork et al. 2009, Supplementary data). Most notably synergistic interactions have been recognised between climate change and all other identified threats (Stork et al. 2009). How such synergies may accelerate species loss is as yet largely unknown although there is some experimental evidence indicating rapid acceleration. Habitat fragmentation and overharvesting combined with experimental warming in rotifer zooplankton resulted in population declines up to 50 times greater combined than when acting on their own (Mora et al. 2007). As Brook (2008) has noted, the potential synergies between species invasion and climate change is one of the prime examples of the type of non-linear, mutually reinforcing ecological responses driving ecosystem change and there are few case studies upon which to base projections for the future.

In contrast to the lack of evidence for mass global extinctions, there is considerable evidence for widespread loss of species at the local and regional level and I suggest that and the consequences of such losses on ecosystem function should be key foci for future research. The loss of this biodiversity, and in particular the loss of the tropical forest megafauna, affects the future regeneration of some key tropical forest plant species. As a consequence, we are now witnessing a massive change in floral composition and the dynamics of many tropical forests around the world (Wright et al. 2007; Wang et al. 2007; Muller-Landau 2007). Corlett (2007), for example, has found that massive range contractions of many of the typical megafauna species in South-East Asian forests including, for example, the Asian elephant, the tiger and the orangutans, mean that less than 2% of this region has an intact or near complete megafauna. Virtually all of these species are still globally extant but their regional contribution to ecosystems has been vastly reduced because of local extinctions.

What can be done to improve our monitoring of extinction beyond the work of IUCN and the Red Data lists? Museums, botanical gardens and other repositories of natural history can play a vital role since their collections provide a historical record of what was found at a particular location. Theoretically we should be able to resurvey some of these locations to determine what has not disappeared and therefore to measure local extinction. One example is the assessments of the species that have gone extinct in Singapore (Brook et al. 2003; Lane et al. 2006). A rapid survey of the largest museums and botanical gardens to identify those species that are most likely to be threatened or are already extinct would be relatively easy to achieve and yet would advance our knowledge of the threatened status of life on Earth enormously.

References

AMNH (1998) National survey reveals biodiversity crisis—scientific experts believe we are in midst of fastest mass extinction in Earth's history. http://www.amnh.org/museum/press/feature/biofact.html

Barlow J, Gardner TA, Araujo IS et al (2007) Quantifying the biodiversity value of tropical primary, secondary and plantation forests. PNAS 47:18555–18560

Batten LA et al (1990) Red Data birds in Britain: action for rare, threatened and important species. NCC and RSPB, T. and A.D. Poyser, London

Botkin DB, Saxe H, Araujo MB et al (2008) Forecasting the effects of global warming on biodiversity. Bioscience 57:227–236

Bradshaw CJA, Giam X, Tan HTW et al (2008) Threat or invasive status in legumes is related to opposite extremes of the same ecological and life-history attributes. J Ecol 96:869–883

Bratton JH (1991) British Red Data Books. 3. Invertebrates other than insects. Joint Nature Conservation Committee, London

Brook BW (2008) Synergies between climate change, extinction and invasive vertebrates. Wildl Res 35:249–252

Brook BW, Sodhi NS, Ng PKL (2003) Catastrophic extinctions follow deforestation in Singapore. Nature 424:420–423

Brook BW, Bradshaw CJA, Koh LP et al (2006) Momentum drives the crash: mass extinction in the tropics. Biotropica 38:302–305

Brook BW, Sodhi NS, Bradshaw CJA (2008) Synergies among extinction drivers under global change. TREE 23:453–460

Brooks TM, Balmford A (1996) Atlantic forest extinctions. Nature 380:115

Brooks TM, Pimm SL, Oyugi JO (1999) Time lag between deforestation and bird extinction in tropical forest fragments. Conserv Biol 15:1140–1150

Brown KS Jr, Brown GG (1992) Habitat alteration and species loss in Brazilian forests. In: Whitmore TC, Sayer JA (eds) Tropical deforestation and species extinction. Chapman & Hall, London, pp 119–142

Carnaval AC, Hickerson MJ, Haddad CFB et al (2005) Stability predicts genetic diversity in the Brazilian Atlantic forest hotspot. Science 323:785–789

Chades I, McDonald-Madden E, McCarthy MA et al (2008) When to stop managing or surveying cryptic threatened species. PNAS 105:13936–13940

Chazdon RL, Peres CA, Dent D et al (2009) Where are the wild things? Assessing the potential for species conservation in tropical secondary forests. Conserv Biol 23:1406–1407

Colwell RK, Brehm G, Cardelús C et al (2008) Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. Science 322:258–261

Corlett RT (2007) The impact of hunting on the mammalian fauna of tropical Asian forests. Biotropica 39:292–303

Curnutt J, Pimm SL (2001) How many bird species in Hawai'i and the Central Pacific before first contact? In: Scott JM, Conant S, van Riper III S (eds) Evolution, ecology, conservation, and management of Hawaiian birds: a vanishing avifauna. Stud Avian Biol 22:15–30

Diamond JM (1972) Biogeographic kinetics: estimation of relaxation times for avifaunas of southwest Pacific Islands. PNAS 69:3199–3204

Diamond JM (1987) Extant unless proven extinct? Or extinct unless proven extant? Conserv Biol 1:77–79

Dirzo R, Raven PH (2003) Global state of biodiversity and loss. Annu Rev Environ Resour 28:137–167

Dobson A, Lafferty KD, Kuris AM et al (2008) Homage to Linnaeus: how many parasites? How many hosts? PNAS 105:11482–11489

Dunn RR (2004) Recovery of faunal communities during tropical forest regeneration. Conserv Biol 18:302–309

Ehrlich PR, Ehrlich AH (1981) Extinction: the causes of the disappearance of species. Random House, New York

Ehrlich PR, Wilson EO (1991) Biodiversity studies: science and policy. Science 253:758–762

Erwin TL (1982) Tropical forests: their richness in Coleoptera and other arthropod species. Coleopt Bull 36:74–75

Erwin TL (1988) The tropical forest canopy: the heart of biotic diversity. In: Wilson EO, Peters FM (eds) Biodiversity. National Academy Press, Washington, DC, pp 123–129

Feeley KJ, Silman MR (2008) Unrealistic assumptions invalidate extinction estimates. PNAS 105:E121

Feeley KJ, Silman MR (2009) Extinction risks of Amazonian plant species. PNAS 106:12382–12387

Fonseca CR (2009) The silent mass extinction of insect herbivores in biodiversity hotspots. Conserv Biol. doi:10.1111/j.1523-1739.2009.01327.x

Grassle JF, Maciolek NJ (1992) Deep-sea species richness: regional and local diversity estimates from quantitative bottom samples. Am Nat 139:313–341

Hamilton A, Basset Y, Benke KK et al (submitted) Quantifying uncertainty in estimating global arthropod species richness. Am Nat

Hammond PM (1992) Species inventory. In: Groombridge B (ed) Global biodiversity, status of the Earth's living resources. Chapman and Hall, London, pp 17–39

Hammond PM (1995) Described and estimated species numbers: an objective assessment of current knowledge. In: Allsopp D, Colwell RR, Hawksworth DL (eds) Microbial diversity and ecosystem function. CAB International, Wallingford, pp 29–71

Hawksworth DL (1991) The fungal dimension of biodiversity: magnitude, significance and conservation. Mycol Res 95:641–655

Heywood VH, Stuart SN (1992) Species extinctions in tropical forests. In: Whitmore TC, Sayer JA (eds) Tropical deforestation and species extinction. Chapman and Hall, London, pp 91–117

Hubbell SP (2001) The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton

Hubbell SP, He F, Condit R et al (2008) How many tree species are there in the Amazon and how many of them will go extinct? PNAS 105:11498–11504

Hugall A, Moritz C, Mousali A, Stanisic J (2002) Reconciling paleodistribution models and comparative phylogeography in the Wet Tropics rainforest land snail *Gnarosophia bellendenkerensis* (Brazier 1875). PNAS 99:6112–6117

IUCN (2009) http://www.iucnredlist.org/. Accessed 4 Sep 2009

Johns AG (1997) Timber production and biodiversity conservation in tropical rainforests. Cambridge University Press, Cambridge

Jones WG, Hill KD, Allen JM (1995) *Wollemia nobilis*, a new living Australian genus and species in the Araucariaceae. Telopea 6:173–176

Koh LP, Dunn RR, Sodhi NS et al (2004) Species co-extinctions and the biodiversity crisis. Science 305:1632–1634

Lane DJW, Kingston T, Lee BPY-H (2006) Dramatic decline in bat diversity in Singapore with implications for Southeast Asia. Biol Conserv 131:584–593

Laurance WF (1991) Ecological correlates of extinction proneness in Australian tropical rain forest mammals. Conserv Biol 5:79–89

Laurance WF (2007) Have we overstated the biodiversity crisis? TREE 22:65–70

Laurance WF, Cochrane MA, Bergen S et al (2001) The future of the Brazilian Amazon. Science 291:438–439

Lawton JH, Bignell DE, Bolton B et al (1998) Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. Nature 391:72–76

Lewis OT (2006) Climate change, species–area curves and the extinction crisis. Philos Trans R Soc B 361:163–171

Lomborg B (2001) The sceptical environmentalist: measuring the real state of the world. Cambridge University Press, Cambridge

Lovejoy TE (1980) A projection of species extinctions. In: Council on Environmental Quality (CEQ), The Global 2000 Report to the President, vol CEQ. Washington, DC, pp 328–331

Lugo AE (1988) Estimating reductions in the diversity of tropical forest species. In: Wilson EO, Peter FM (eds) Biodiversity. National Academy of Sciences, Washington, DC, pp 58–70

Mace GM (1994) Classifying threatened species: means and ends. Philos Trans R Soc Lond B 344:91–97

Manne LL, Brooks TM, Pimm SL (1999) Relative risk of extinction of passerine birds on continents and islands. Nature 399:258–261

Mawdsley NA, Stork NE (1995) Species extinctions in insects: ecological and biogeographical considerations. In: Harrington R, Stork NE (eds) Insects in a changing environment. Academic Press, London, pp 322–369

May RM (1988) How many species are there on Earth? Science 241:1441–1449

May RM (1992) Bottoms up for the oceans. Nature 357:278–279

May RM (1998) The dimensions of life on Earth. In: Raven PH (ed) Nature and human society: the quest for a sustainable world. National Academy Press, Washington, DC, pp 30–45

McKinney ML (1997) Extinction vulnerability and selectivity: combining ecological and paleontological views. Ann Rev Ecol Syst 28:495–516

Meijaard E, Sheil D, Nasi R et al (2005) Life after logging: reconciling wildlife conservation and production forestry in Indonesian Borneo. CIFOR, Jakarta Indonesia

Millenium Ecosystem Assessment (2005) Current state and trends, vol 1. Island Press, Washington, DC

Mora C, Metzger R, Rollo A et al (2007) Experimental simulations about the effects of overexploitation and habitat fragmentation on populations facing experimental warming. Proc Biol Sci 274:1023–1028

Muller-Landau HC (2007) Predicting the long-term effects of hunting on plant species composition and diversity in tropical forests. Biotropica 39:372–384

Myers N (1979) The sinking ark: a new look at the problem of disappearing species. Pergamon Press, Oxford

Myers N (1988) Threatened biotas: 'hotspots' in tropical forests. Environmentalist 8:1–20

Myers N (1993) Questions of mass extinction. Biodivers Conserv 2:2–17

Myers N (2003) Conservation of biodiversity: how are we doing? Environmentalist 23:9–15

Myers N, Mittermeier RA, Mittermeier CG et al (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Newmark WD (1991) Tropical forest fragmentation and the local extinction of understory birds in the eastern Usambara mountains, Tanzania. Conserv Biol 5:67–68

Novotny V, Basset Y, Miller SE et al (2002) Low host specificity of herbivorous insects in a tropical forest. Nature 416:841–844

Orme CDL, Davies RG, Burgess M et al (2005) Global hotspots of species richness are not congruent with endemism or threat. Nature 436:1016–1019

Pimm SL, Brooks TM (2000) The sixth extinction: how large, where and when? In: Raven PH (ed) Nature and human society: the quest for a sustainable world. National Academy Press, Washington, DC, p 46

Pimm SL, Harvey J (2001) No need to worry about the future. Nature 414:149–150

Pimm SL, Raven PH (2000) Extinction by numbers. Nature 403:843–845

Pimm SK, Russell GJ, Gittleman JL, Brooks TM (1995) The future of biodiversity. Science 269:347–349

Pimm SL, Raven R, Peterson A et al (2006) Human impacts on the rates of recent, present, and future bird extinctions. PNAS 103:10941–10946

Possingham HP, Andelman SJ, Burgman MA et al (2002) Limits to the use of threatened species lists. TREE 17:503–507

Purvis A, Agapow P-M, Gittleman JL et al (2008) Nonrandom extinction and the loss of evolutionary history. Science 288:328–330

Raup DM (1986) Biological extinction in Earth history. Science 231:1528–1533

Raven PH (1987) The scope of the plant conservation problem world-wide. In: Bramwell D et al (eds) Botanic gardens and the world conservation strategy. Academic Press, London, pp 19–29

Raven PH (1988) Our diminishing tropical forests. In: Wilson EO, Peter FM (eds) Biodiversity. National Academy of Sciences, Washington, DC, pp 119–122

Raven PH, McNeely JA (1998) Biological extinctions: its scope and meaning for us. In: Guruswamy LD, McNeely JA (eds) Protection of global biodiversity: converging strategies. Duke University Press, Durham, pp 13–32

Reid WV (1992) How many species will there be? In: Whitmore TC, Sayer JA (eds) Tropical deforestation and species extinction. Chapman and Hall, London, pp 55–73

Sharrock JTR (1974) The changing status of breeding birds in Britain and Ireland. In: Hawksworth DL (ed) The changing flora and fauna of Britain. Academic Press for the Systematics Association, London, pp 203–220

Shirt DB (ed) (1987) British Red Data Books. 2. Insects. Nature Conservation Council, Peterborough

Simberloff D (1986) Are we on the verge of a mass extinction in tropical rainforests? In: Elliott DK (ed) Dynamics of extinction. Wiley, New York, pp 165–180

Simberloff D (1992) Do species–area curves predict extinction in fragmented forest. In: Whitmore TC, Sayer JA (eds) Tropical deforestation and species extinction. Chapman and Hall, London, pp 75–89

Simon JL (1995) Why do we hear prophecies of doom from every side? The Futurist 29:19–24

Sloan S (2007) Fewer people may not mean more forest for Latin American forest frontiers. Biotropica 39:443–446

Smith FDM, May RM, Pellew R et al (1993) Estimating extinction rates. Nature 364:494–496

Sodhi NS, Koh PL, Peh KS-H, Tan HTW et al (2008) Correlates of extinction proneness in tropical angiosperms. Divers Distrib 14:1–10

Steadman DW (1995) Prehistoric extinctions of Pacific Island Birds: biodiversity meets Zooarchaeology. Science 267:1123–1131

Stork NE (1988) Insect diversity: facts, fiction and speculation. Biol J Linn Soc 35:321–337

Stork NE (1997) Measuring global biodiversity and its decline. In: Reaka-Kudla ML, Wilson DE, Wilson EO (eds) Biodiversity II: understanding and protecting our biological resources. Joseph Henry Press, Washington, DC, pp 41–48

Stork NE (1999) The magnitude of biodiversity and its decline. In: Cracraft J, Grifo JT (eds) The living planet in crisis: biodiversity, science and policy. Columbia University Press, New York, pp 3–32

Stork NE, Lyal CHC (1993) Extinction or 'co-extinction' rates? Nature 366:307

Stork NE, Coddington JA, Colwell RK et al (2009) Vulnerability and resilience of tropical forest species to land use change. Conserv Biol 23:1438–1447

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

Tilman DR, May RM, Lehman CL et al (1994) Habitat destructions and the extinction debt. Nature 371:65–66

van Roosmalen MGM, van Roosmalen T, Mittermeier RA (2002) A taxonomic review of the titi monkeys, Genus Callicebus Thomas, 1903, with the description of two new species, *Callicebus bernhardi* and *Callicebus stephennashi*, from Brazilian Amazonia. Neotrop Primates 10(Suppl):1–53

Wang BC, Sork VL, Leong MT et al (2007) Hunting of mammals reduces seed removal and dispersal of the Afrotropical tree *Antrocaryon klaineanum* (Anacardiaceae). Biotropica 39:340–347

Williams SE, Bolitho EE, Fox S (2003) Climate change in Australian tropical rainforests: an impending environmental catastrophe. Proc R Soc Lond B 270:1887–1892

Willis KJ, Bennett KD, Walker D (2004) The evolutionary legacy of the ice ages. Philos Trans R Soc B 359:15–158

Wilson EO (1988) The current state of biological diversity. In: Wilson EO, Peters FM (eds) Biodiversity. National Academy Press, Washington, DC, pp 3–18

Wilson EO (1989) Threats to biodiversity. Scientific American, September, pp 108–116

Wright SJ, Muller-Landau HC (2006a) The future of tropical forest species. Biotropica 38:287–301

Wright SJ, Muller-Landau HC (2006b) The uncertain future of tropical forest species. Biotropica 38:443–445

Wright SJ, Stoner KE, Beckman N et al (2007) The plight of large animals in tropical forests and the consequences for plant regeneration. Biotropica 39:289–291

Wright SJ, Muller-Landau HC, Schipper J (2009) The future of tropical species on a warmer planet. Conserv Biol 23:1418–1426