Check for updates Cambridge Philosophical Society

Biol. Rev. (2022), 97, pp. 640-663.

doi: 10.1111/brv.12816

640

The Sixth Mass Extinction: fact, fiction or speculation?

Robert H. Cowie^{1*}, Philippe Bouchet² and Benoît Fontaine³

ABSTRACT

There have been five Mass Extinction events in the history of Earth's biodiversity, all caused by dramatic but natural phenomena. It has been claimed that the Sixth Mass Extinction may be underway, this time caused entirely by humans. Although considerable evidence indicates that there is a biodiversity crisis of increasing extinctions and plummeting abundances, some do not accept that this amounts to a Sixth Mass Extinction. Often, they use the IUCN Red List to support their stance, arguing that the rate of species loss does not differ from the background rate. However, the Red List is heavily biased: almost all birds and mammals but only a minute fraction of invertebrates have been evaluated against conservation criteria. Incorporating estimates of the true number of invertebrate extinctions leads to the conclusion that the rate vastly exceeds the background rate and that we may indeed be witnessing the start of the Sixth Mass Extinction. As an example, we focus on molluscs, the second largest phylum in numbers of known species, and, extrapolating boldly, estimate that, since around AD 1500, possibly as many as 7.5-13% (150,000–260,000) of all ~2 million known species have already gone extinct, orders of magnitude greater than the 882 (0.04%) on the Red List. We review differences in extinction rates according to realms: marine species face significant threats but, although previous mass extinctions were largely defined by marine invertebrates, there is no evidence that the marine biota has reached the same crisis as the non-marine biota. Island species have suffered far greater rates than continental ones. Plants face similar conservation biases as do invertebrates, although there are hints they may have suffered lower extinction rates. There are also those who do not deny an extinction crisis but accept it as a new trajectory of evolution, because humans are part of the natural world; some even embrace it, with a desire to manipulate it for human benefit. We take issue with these stances. Humans are the only species able to manipulate the Earth on a grand scale, and they have allowed the current crisis to happen. Despite multiple conservation initiatives at various levels, most are not species oriented (certain charismatic vertebrates excepted) and specific actions to protect every living species individually are simply unfeasible because of the tyranny of numbers. As systematic biologists, we encourage the nurturing of the innate human appreciation of biodiversity, but we reaffirm the message that the biodiversity that makes our world so fascinating, beautiful and functional is vanishing unnoticed at an unprecedented rate. In the face of a mounting crisis, scientists must adopt the practices of preventive archaeology, and collect and document as many species as possible before they disappear. All this depends on reviving the venerable study of natural history and taxonomy. Denying the crisis, simply accepting it and doing nothing, or even embracing it for the ostensible benefit of humanity, are not appropriate options and pave the way for the Earth to continue on its sad trajectory towards a Sixth Mass Extinction.

Key words: biodiversity crisis, conservation, denial, extinction, invertebrates, IUCN Red List, land snails, molluscs, Sixth Extinction, undescribed species

¹Pacific Biosciences Research Center, University of Hawaii, Honolulu, Hawaii 96822, U.S.A.

²Institut Systématique Evolution Biodiversité (ISYEB), Muséum National d'Histoire Naturelle, CNRS, Sorbonne Université, EPHE, Université des Antilles, 57 rue Cuvier CP 51, 75005 Paris, France

³ UMS 2006 Patrinat (OFB, CNRS, MNHN), Centre d'Écologie et des Sciences de la Conservation (UMR 7204), Muséum National d'Histoire Naturelle, 43 rue Buffon CP 135, 75005 Paris, France

Address for correspondence (Tel: +1 808 956 4909; E-mail: cowie@hawaii.edu).

CONTENTS

I.	Introduction	. 641
II.	Defining the sixth mass extinction	. 642
	The Red List as a tool for measuring extinction	
	(1) Mammals and birds are not representative of overall extinctions	
	(2) Known extinctions since A.D. 1500 not listed	
	(3) Extinctions prior to A.D. 1500	
	(4) Centinelan extinctions	
	(5) The invertebrate problem	
IV.	Other approaches	
	(1) The need to address invertebrates	
	(2) The value of terrestrial molluscs for assessing invertebrate extinction rates	.649
	(3) An assessment of global extinction based on molluscs	
V.	Current versus background extinction rates	. 651
	Islands and other insular habitats	
VII.	Marine species	. 652
	Plants	
IX.	What should we do now?	. 654
X.	Conclusions	. 656
XI.	Acknowledgments	. 657
XII.	Author contributions	. 657
XIII.	References	. 657

I. INTRODUCTION

In her book The Sixth Extinction: an Unnatural History, Elizabeth Kolbert (2014) presented the mounting evidence that the Earth is at the start of, or perhaps in the midst of, the sixth major episode of mass biodiversity extinction since life on Earth arose, the first such event to be caused entirely by humans. She is by no means the first to have drawn this conclusion (e.g. Diamond, 1987, 1989; Leakey & Lewin, 1995; Wake & Vredenburg, 2008) and it continues to be reiterated (e.g. Ceballos et al., 2015; McCallum, 2015; Régnier et al., 2015a; Plotnick, Smith & Lyons, 2016; Ceballos, Ehrlich & Dirzo, 2017; Cowie et al., 2017; Ceballos & Ehrlich, 2018; Dasgupta & Ehrlich, 2019; IPBES, 2019; Ceballos, Ehrlich & Raven, 2020). The evidence for a major biodiversity crisis appears overwhelming. Yet there are some who deny that such evidence really exists and consider that it has been exaggerated by conservation and biodiversity scientists to attract greater public and political attention to biodiversity loss and to enhance opportunities to obtain research grants (e.g. Lomborg, 2001; Briggs, 2014b, 2014c, 2016, 2017). Such denials made the headlines when the IPBES (2019) report was released (e.g. Platt, 2019); they continue to increase, as noted by Lees et al. (2020).

Denial differs from scepticism (Jylhä, 2018; Washington, 2018). The latter is a genuine component of scientific research and discovery, questioning assumptions, results, interpretations and conclusions, until the weight of evidence supports one conclusion or another. Denial, on the other hand is plain disbelief in that weight of evidence. The notion of the Sixth Mass Extinction, or at least a major biodiversity crisis, faces both scepticism and denial, as does

the notion of anthropogenic climate change (Jylhä, 2018; Washington, 2018), the fact of evolution (Ayala, 2008; Nieminen, Ryökäs & Mustonen, 2015; Hansson, 2017), the negative impacts of invasive species (Tassin, 2014; and see Ricciardi & Ryan, 2018a, 2018b), and many other aspects of science in general (Hansson, 2017; Rutjens, van der Linden & van der Lee, 2021). Scepticism and denial may be fuelled by media headlines over-dramatising dire short-term prognoses combined with exaggeration of perceived professional differences of opinion among scientists, regarding, for instance, analysis and interpretation of data (e.g. Leung et al., 2020) and the likelihood of insect 'Armageddon' (Leather, 2017; Desquilbet et al., 2020; Van Klink et al., 2020). Much of this denial of science is not published in reputable peer-reviewed scientific journals, and some may have political undertones, as was the case with the reaction of Republican officials in the USA after the release of the IPBES report in 2019 (Tobias, 2019).

Two primary critiques have been levelled at those who claim we are at what may be a watershed point in the history of our planet. First is the claim that estimated extinction rates have been exaggerated and that the current extinction rate is not significantly greater than the natural background rate (e.g. Lomborg, 2001; Briggs, 2014b, 2014c, 2015, 2016, 2017). Second are the inter-related claims that any extinctions are offset by an equivalent or greater origination of newly evolved species, and that because humans are part of the natural world, human-caused extinctions are a natural phenomenon, a part of the evolutionary trajectory of life on Earth. This view has appeared in various forms in the popular press (e.g. Pyron, 2017), websites (e.g. Brand, 2015; Middleton, 2017) and the writings of some

academic ecologists (e.g. Thomas, 2017). The consequence of this opinion is that we should embrace this new trajectory of evolution (Briggs, 2014*b*, 2014*c*, 2015, 2016, 2017). Thomas (2017) suggested that the rate of evolution, and therefore speciation, is now increasing in the face of change wrought by humans.

Some acknowledge that although they consider there is no mass extinction, at least not yet, many species are becoming rarer or more localised, with an accompanying loss of genetic diversity, and that this is where we should focus our efforts, as rarity could have dire consequences for global ecosystems (e.g. Heywood & Stuart, 1992; Stork, 2010; Briggs, 2014*a*, 2014*b*, 2014*c*, 2015, 2017; Hull, Darroch & Erwin, 2015). Notably, increased rarity may result in functional extinction, which can drive further declines *via* coextinction (Dunn *et al.*, 2009; Sellman, Säterberg & Ebenman, 2016). Increased rarity is undoubtedly true (Dirzo *et al.*, 2014; Ceballos *et al.*, 2017; Hallmann *et al.*, 2017) but that does not mean that mass extinction is not also occurring.

Does the current episode differ from previous mass extinctions? There have been a number of such episodes in the history of the Earth, with most authors accepting five substantial mass extinctions since the Cambrian (e.g. Sepkoski, 1996; Avise, Hubbell & Ayala, 2008; Barnosky et al., 2011; Harper, Hammarlund & Rasmussen, 2014). These have all been caused by a diversity of natural phenomena (Bond & Grasby, 2017) and have been defined, for instance by Barnosky et al. (2011), as events standing out from a steadier background rate of extinction in having extinction rates spiking higher than in any other geological interval of the last 540 million years and involving, somewhat arbitrarily, a loss of over 75% of estimated species. By contrast, the current high rate of extinction is being caused directly by humans. Alroy (2008, p. 11541) emphasised this difference succinctly in stating that "the numerous anthropogenic causes of today's mass extinction are deeply unrelated to the known causes of earlier ones." Indeed, while the current crisis is essentially a non-marine phenomenon, the previous events were mostly defined based on marine, largely invertebrate, fossils, although the end-Cretaceous event involved the demise of non-avian dinosaurs. Furthermore, various authors have arrived at as few as two or as many as 61 mass extinctions, as reviewed by Bambach (2006), who concluded there were 18 but that only three stood out from the continuum of surrounding extinction intensities, although many continue to accept the traditional (e.g. Hull, 2015; Hull et al., 2020). Wiens, Sweet & Worsley (2020), while arguing philosophically that the terms 'background extinction' and 'mass extinction' are inappropriate because these phenomena are indeed the two extremes of a continuum, nonetheless acknowledged that the current crisis is qualitatively different because of its anthropogenic

Implicit in all the arguments denying the current crisis is that there is no need to worry, either because there is no such mass extinction event, or, as suggested hypothetically by Doug Erwin (as quoted by Brannen, 2017), if we really are

in the midst of a mass extinction, then it is too late and there is no point in trying to do anything about it anyway (note that Erwin himself in fact seemed to believe that there is no mass extinction or that the process is only beginning, and that we may have a chance to prevent it if we figure out how). Along with numerous others, we take issue with these conclusions primarily for three reasons: (i) there is mounting evidence that the extinction rate is not normal; (ii) the exponential rise in the human population and in human impacts on the natural world are abnormally rapid; and crucially (iii) we are not just another species evolving in the face of external influences because we have conscious choice regarding our future and that of Earth's biodiversity. Thus not only are we losing species at a greater than normal rate, but also the processes of evolution (speciation) cannot keep up with this loss (Barnosky et al., 2011; Ceballos & Ehrlich, 2018). We consider that the Sixth Mass Extinction has probably started and present arguments to counter those who would deny this. We will probably not convince those who consider this episode part of the natural evolution of life on Earth and therefore that it is acceptable to just let it happen, that is, that they are wrong. Nor will we convince those who think that it is too late to stop it and that we should therefore embrace it, that is, that they also are wrong. However, we hope that we will at least give pause to those who by denying or downplaying it play into the hands of those who advocate doing nothing about it, or those who, accepting it, advocate that we should do our best to manipulate biodiversity primarily if not solely for human, essentially economic, benefit. This latter view has been expressed to a greater or lesser extent by some prominent conservationists (Kareiva & Marvier, 2007, 2012; Kareiva, Lalasz & Marvier, 2011; Thomas, 2017) and has become a key feature of the 'New Conservation' or 'Neoliberal Conservation', although the paradigm has been strongly criticised, for example by Büscher et al. (2012), Soulé (2013) and Rolston (2018).

II. DEFINING THE SIXTH MASS EXTINCTION

If one considers a mass extinction event as a short period when at least 75% of species are lost (Barnosky et al., 2011), the current ongoing extinction crisis, whether labelled the 'Sixth Mass Extinction' or not, has not yet occurred; it is "a potential event that may occur in the future" (MacLeod, 2014, p. 2). But the fact that it has not yet happened – which can only be asserted once it has happened – does not mean that it will not happen or is not in the process of happening. Indeed it could happen within just one or a few centuries if nothing is done to slow or stop the current rate of biodiversity loss (Barnosky et al., 2011). But it has surely begun (Thomas, 2017), and is being caused by human activities.

But when did it begin? Did it begin with the first expansion of modern humans out of Africa, 200–45 thousand years ago (kya) (Henn, Cavalli-Sforza & Feldman, 2012; López, van

Dorp & Hellenthal, 2015; Harcourt, 2016; Bae, Douka & Petraglia, 2017; Hershkovitz *et al.*, 2018), or 12–10 kya during the Neolithic Revolution when human populations began to increase rapidly as a result of the development of agriculture (Bocquet-Appel, 2011; Lenton, 2019), or did it begin much more recently, even as late as during the 19th century industrial revolution? Avise *et al.*, (2008) characterised these as the three phases of the Sixth Mass Extinction, implicitly including all human-caused extinctions, and considering the status of biodiversity now to have reached a crisis point. We concur with Avise *et al.*, (2008) in considering the Sixth Mass Extinction, should that be what the current crisis becomes, to include all anthropogenic extinctions.

However, within this overarching framework, the beginning of human-caused extinction varies by location (Pimm et al., 2014; Turvey & Crees, 2019). For instance, from a global perspective, modern humans reached Europe at least 43 kya, and Asia and Australia at least 65 kya (Benazzi et al., 2011; Bae et al., 2017; Clarkson et al., 2017), with the earliest forays out of Africa dated to around 200 kya (Hershkovitz et al., 2018), long before they reached the Americas, 20-15 kya (Henn et al., 2012; Harcourt, 2016). And from a narrower, more recent perspective, humans colonised islands of western Oceania (e.g. Vanuatu, New Caledonia) 4-3 kya but only reached the furthest parts of Oceania (e.g. New Zealand, Hawaii) <1 kya (Rieth et al., 2011; Soares et al., 2011; Matisoo-Smith & Daugherty, 2012). Thus the beginning of the so-called 'Anthropocene' is dependent on when humans arrived at a particular location. [We avoid further use of the term 'Anthropocene' (cf. Smith, 2019). Although initially it was coined in an Earth system context largely emphasizing anthropogenic changes in climate and geochemistry (Crutzen & Stoermer, 2000; Crutzen, 2002), it has come to be seen as simply referring to the modern era of human domination of the Earth, embracing wider biological, sociological, political and philosophical issues. But it is poorly defined and has many critics – although also many supporters (reviewed by Malhi, 2017). It has been suggested that it may engender complacency and allow us to reconcile ourselves to a 'new normal' (Laurance, 2019), or at worst reflect an anthropocentric view that the Earth and its resources should be managed primarily, if not solely, for the benefit of humankind (as critiqued by Rolston, 2018) - a view, in one form or another, that is gaining traction at inter-governmental levels (e.g. Masood, 2018). Others have coined alternative names that have not yet gained a wide following (see Malhi, 2017; López-Corona & Magellanes-Guijón, 2020).]

Nonetheless, differences of a few thousand years, for instance among locations in the western Pacific and the central and eastern Pacific, when looking back a few million years from now, will be insignificant. If all human-caused extinctions (i.e. over a period of up to 200 ky so far) are to be included in the current event, while realising that the rate has increased dramatically in more recent times (Ceballos *et al.*, 2015; Régnier *et al.*, 2015*a*, 2015*b*), the time span is of a roughly similar order of magnitude as that over which

extinctions took place in the five traditional previous mass extinction events. For instance, among the three stand-out events identified by Bambach (2006), the end-Permian event lasted 60 ky (Burgess, Bowring & Shen, 2014), the end-Ordovician event ~0.2 Ma (Ling et al., 2019), and the Cretaceous-Palaeogene event, associated primarily with asteroid impact and renowned for the end of the non-avian dinosaurs, lasted <20 ky (Renne et al., 2013) or as little as a few years or decades (Molina, 2015), although there is much discussion about the cause(s) and timing/duration of this event (Henehan et al., 2016; Mateo et al., 2017; Tobin, Bitz & Archer, 2017; Hull et al., 2020). These are the durations of the actual period of extinction (Erwin, 2014) and not the times from the beginning of the event to full recovery of ecosystem function and eventually of species richness (Sheehan, 2001; Sallan & Coates, 2010; Hull, 2015; Hull et al., 2015; Henehan et al., 2016; Alvarez et al., 2019), which are much longer. The Sixth Mass Extinction, if it happens and depending on how its start is defined, could take place in a not dissimilar timeframe.

III. THE *RED LIST* AS A TOOL FOR MEASURING EXTINCTION

The International Union for Conservation of Nature (IUCN) Red List (IUCN, 2020, and its previous iterations) is widely recognised as the most comprehensive compilation of the global conservation status of plants and animals, with the number of assessed species increasing year after year, and is now an irreplaceable tool for conservation planning, management, monitoring and decision making. Its explicit goal is to assess relative extinction risk of species (Rodrigues et al., 2006; Collen et al., 2016; Lacher & Hilton-Taylor, 2018). In the course of assessments, some species are declared extinct, but listing extinct species is a by-product of the *Red List*. However, various studies have used the Red List to ascertain the numbers of recorded modern extinctions, that is, since the year 1500, the date IUCN now uses as a cut-off for listing a species as having gone extinct (see the text under Tables 3 and 4 of the Red List Summary Statistics; IUCN, 2020), and to extrapolate from these numbers to an overall rate of extinction. Often, the focus is on vertebrates, mostly mammals and birds but sometimes including herptiles and fish (e.g. Mace, 1994; McCallum, 2007, 2015; Stork, 2010; Ceballos et al., 2015; Pimm & Raven, 2019; Ceballos et al., 2020). Most such studies acknowledge the limitations of the Red List data. Others, however, have used the Red List data without such acknowledgement and in support of their view that rates of extinction are not dramatically heightened, arguing that these are the dependable and true data from which to calculate rates, notably Lomborg (2001) and Briggs (2014b, 2014c, 2015, 2016, 2017) but also Lamkin & Miller (2016).

IUCN (2020) has evaluated all known bird species and 91% of mammal species. Most estimates of extinction rates for these taxa have been based on the *Red List*, and for mammals the

CREO list (http://creo.amnh.org) (Loehle & Eschenbach, 2012), which also lists only species considered to have gone extinct since 1500. Estimates of extinctions of these taxa since 1500 may be quite accurate (see Section III.1), especially with new approaches combining the timing and reliability of records, the timing and adequacy of surveys, and the timing, extent and intensity of threats (Butchart et al., 2018). However, the *Red List* as a whole, and mammals and birds specifically, is not a good surrogate for assessing the entire extent of the current extinction event, as defined above, for a number of reasons outlined in the following sections, and analyses based on the Red List inevitably under-estimate real levels. This should be no surprise, as it was never designed as a comprehensive compilation of known extinct species.

(1) Mammals and birds are not representative of overall extinctions

IUCN (2020) assessed 120,372 species overall, including 52,649 vertebrates. Although a huge amount of detailed work, this represents only 5.6% of the total of ~2.14 million described animal and plant species accepted by IUCN (2020). [The Catalogue of Life, which is the basis for many of the IUCN (2020) estimates of numbers of species in various groups, estimates that there are 2.2 million living species known to taxonomists (Roskov *et al.*, 2019)]. The number assessed is thus a tiny fraction of described species, heavily biased towards non-marine vertebrates, and especially mammals and birds (Régnier, Fontaine & Bouchet, 2009; Cardoso *et al.*, 2011; Régnier *et al.*, 2015*a*; Cowie *et al.*, 2017; Cowie, Fontaine & Bouchet, in press).

Nonetheless, many of the arguments both for and against the reality of the Sixth Mass Extinction have been based on analyses of vertebrates, primarily mammals and birds (Loehle & Eschenbach, 2012), and to some degree amphibians, which have suffered significant declines and extinctions (McCallum, 2007; Moore, 2014), most recently as a result of chytrid fungal infection, perhaps exacerbated by global warming (Wake & Vredenburg, 2008). Coral reefs are sometimes incorporated into such analyses, as are plants, but invertebrates are rarely considered (e.g. Brooks et al., 2002; Butchart et al., 2010). The implicit, and sometimes explicit, assumption is often made that assessments of extinction rates of mammals and birds are reflective of extinction rates of all biodiversity, an assumption accepted not only among the vertebrate-centric media but also among many vertebrate-centric scientific and conservation organisations and seemingly sometimes even among vertebrate-centric scientists themselves (e.g. Ceballos et al., 2015, 2017, 2020; McCallum, 2015; Tilman et al., 2017).

IUCN (2020) accepts an estimated 6,495 described mammal species and 11,147 described bird species, total 17,642, with 91% of mammals and all bird species evaluated (Fig. 1). Of these 17,046 evaluated species, only 922 (~5%) were placed in the IUCN category Data Deficient, that is, they lacked sufficient information to assess their conservation status according to the IUCN *Red List* Categories and Criteria (IUCN, 2012). Thus, the number of extinctions (249, 1.5% of the total 16,124 evaluated, excluding those evaluated as Data Deficient) listed for mammals and birds since 1500 by IUCN (2020) is probably quite accurate, except perhaps for Polynesian and other island birds (see Section III.3).

Although a small sample of overall biodiversity, if the estimates of extinction in mammals and birds could be considered a random sample of biodiversity, some confidence could perhaps be placed in extrapolations from these estimates to estimates of the overall biodiversity extinction rate. However, it is not a random but a highly biased sample.

Mammals and birds have received considerable conservation support, without which their rate of extinction would

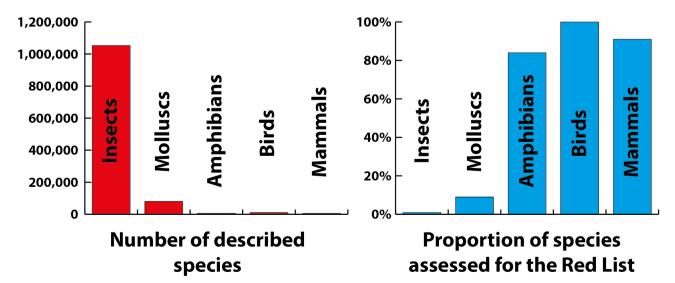


Fig. 1. Taxonomic bias in the *Red List*. Total numbers of described species in selected major vertebrate and invertebrate groups [data from Roskov *et al.* (2019) and MolluscaBase editors (2021)] and the proportions of those species evaluated for the *Red List* (IUCN, 2020).

have been greater, such that extrapolating from them to biodiversity as a whole would under-estimate the overall extinction rate (Butchart, Stattersfield & Collar, 2006; Pimm et al., 2006; Young et al., 2014; Bolam et al., 2020). Another bias lies in the fact that species with large body size (e.g. mammals and birds, and vertebrates in general) tend to have larger ranges than smaller species (insects and invertebrates in general) (Gaston & Blackburn, 1996), and hence will not become extinct because of local habitat destruction. Furthermore, many rare invertebrate species, for instance many species only known from their type localities or even from just a single specimen, inhabit remote tropical regions, which is why they are so little studied and so poorly known. Given their probably small ranges, they may well be very prone to extinction, yet there is insufficient knowledge to evaluate them (e.g. Meiri et al., 2018), which means Red List assessments are biased towards better known species. Even among insects, Red List assessments have been heavily biased towards Odonata, Lepidoptera (Rhopalocera), certain Coleoptera and Orthoptera (e.g. Rocha-Ortega, Rodriguez & Córdoba-Aguilar, 2021). Red List assessments may also be biased towards threatened species, towards groups benefitting from being the target of IUCN Specialist Groups, or in some cases towards regions with higher species richness, as has been shown for plants (Bachman et al., 2019). For all these reasons, although public perception is that charismatic megafauna are the first victims of anthropogenic extinction (they may well have been during the prehistoric beginnings of the process) and thus attract great concern, the untold thousands of invertebrate species that have gone extinct unknown to humanity vastly outweigh the small number of much better known vertebrate extinctions.

(2) Known extinctions since A.D. 1500 not listed

The IUCN guidelines (IUCN Standards and Petitions Subcommittee, 2019, pp. 80–81) state that

The category of Extinct is used when 'there is no reasonable doubt that the last individual has died'. However, extinction—the disappearance of the last individual of a species— is very difficult to detect. Listing of a species as Extinct requires that exhaustive surveys have been undertaken in all known or likely habitat throughout its historic range, at appropriate times (diurnal, seasonal, annual) and over a timeframe appropriate to its life cycle and life form. Listing as Extinct has significant conservation implications, because protective measures and conservation funding are usually not targeted at species believed to be extinct. Therefore, a species should not be listed in the Extinct (EX) or Extinct in the Wild (EW) categories if there is any reasonable possibility that they may still be extant, in order to avoid the 'Romeo Error' (Collar, 1998), where any protective measures and funding are removed from threatened species in the mistaken belief that they are already extinct.

For a very large proportion of described species, there will never be dedicated exhaustive fieldwork, at the appropriate time and over the appropriate timeframe because they are too numerous, and knowledge is too scarce to know the timeframe and even the range to be searched. Moreover, since the *Red List* seeks to avoid the Romeo Error – "uncritical acceptance of pronouncements and assumptions of extinction" (Collar, 1998, p. 240) – it will under-estimate the number of extinct species, even in well-known groups such as birds or amphibians. This is even acknowledged by the IUCN itself (IUCN Standards and Petitions Subcommittee, 2019), which has created a Possibly Extinct tag for "Critically Endangered species that are, on the balance of evidence, likely to be extinct, but for which there is a small chance that they may be extant" (p. 81); they also created an analogous Possibly Extinct in the Wild tag (see also Butchart *et al.*, 2018). IUCN (2020) listed 986 taxa with these tags.

The taxonomic literature is full of examples of species for which the authors suggest they are probably extinct but do not dare to declare them so (e.g. Tan & Hua, 2008; Hedges & Conn, 2012). For example, the Eskimo curlew, Numenius borealis (Forster) (Fig. 2), a Nearctic wader, probably became extinct by the end of the 20th century and has been considered subsequently as such, the last reliable sighting dating from 1963 (e.g. Elphick, Roberts & Reed, 2010; Roberts & Jarić, 2016). However, Butchart et al. (2018) recommended that it remain evaluated as Critically Endangered (Possibly Extinct) based on a probabilistic approach. Another example is Bachman's warbler, Vermivora bachmani (Audubon) (Fig. 2), of which there has been no confirmed sighting since 1988 (BirdLife International, 2021), despite targeted searches (National Park Service, 2018), and which has also been recognised as extinct (Elphick et al., 2010). Both species are still listed as Critically Endangered by IUCN because of the slim chance that one or more birds may still be alive, that is, not committing the Romeo Error. Such species are therefore not counted among extinct species, and vast sums of money are often spent in the vain hope that they will be found again. Incidentally, the US government has very recently proposed that Bachman's warbler be considered extinct (Williams, 2021). More generally, Diamond (1987, 1989) emphasised "the gulf between 'proved extinct' and 'not proved extant'" (Diamond, 1989, p. 471) and that if extinction must be based on definitive proof, then the true extinction rate will be under-estimated and a lot of the limited funding available will be directed at lost causes.

(3) Extinctions prior to A.D. 1500

Humans were instrumental in the global megafauna extinction almost as soon as they started migrating out of Africa (Sandom et al., 2014; Smith et al., 2018), although within Africa some megafauna species (e.g. some proboscidians and sabretooth cats) had gone extinct prior to Homo sapiens expanding beyond the continent, perhaps related to evolution of Homo erectus into the carnivore niche space (Malhi et al., 2016). The Aboriginal colonisation of Australia occurred around 65 kya (Clarkson et al., 2017), earlier than previously thought (i.e. 45 kya; Henn et al., 2012), and may

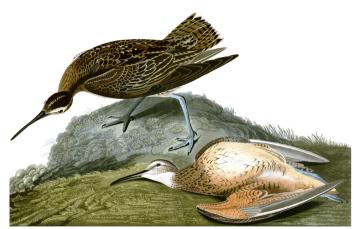




Fig. 2. Extinct but not listed as such, for fear of committing the 'Romeo Error'. Left: Eskimo curlew (*Numenius borealis* (Forster)), from Audubon (1827–1838: plate 208; Wikimedia Commons). Right: Bachman's warbler (*Vermivora bachmani* (Audubon)), from Audubon (1827–1838: plate 185 (detail); Creative Commons, Rawpixel).

have resulted in extinction of the characteristic prehistoric megafauna, although the interaction of human spread with climate change may have been important (Bird et al., 2013; Saltré et al., 2019), as has also been discussed for Eurasia (Stuart, 1991), North America (Meltzer, 2020) and the Caribbean (Orihuela et al., 2020). The consensus seems to be that on a global scale, both humans and climate change were involved in megafaunal extinction but with the former generally of greater significance (Bartlett et al., 2016; Malhi et al., 2016). Avian extinction following initial colonisation of western Pacific islands by native Pacific people has been estimated as extending back to at least 30 kya (Steadman, 1995) and of central Pacific islands to around 3-4 kya (Pimm, Moulton & Justice, 1994). In the islands of the tropical Pacific, Steadman (1995) suggested that prehistoric anthropogenic bird extinctions (primarily rails) may have exceeded 2,000 species (possibly an over-estimate; Livezey, 2003), which, at that time, Steadman considered to be 20% of global bird diversity, although now around 15%. IUCN uses the year 1500 as a cut-off for listing a species as having gone extinct. However, even in the 500 years prior to discovery of the Hawaiian Islands by westerners in 1778, during which time the islands were colonised by native Pacific people (Rieth et al., 2011), roughly 50% of the avifauna of the islands went extinct as a result of both habitat destruction and predation (James & Olson, 1991; Olson & James, 1991; Pimm et al., 1994, 2006). Similar rail extinctions took place on the Macaronesian Islands of the north Atlantic (Alcover et al., 2015). None of these species is included in the Red List.

(4) Centinelan extinctions

In his book *The Diversity of Life*, E. O. Wilson (1999) coined the term 'Centinelan extinction' for species going extinct before they are collected and described. We do not know, and in most cases cannot know, how many Centinelan extinctions have occurred, especially for invertebrates (Heywood & Stuart, 1992). An untold number of specimens of undescribed

species lie waiting for us in the world's natural history museum collections, some of which, unbeknownst to us, will have already gone extinct (Fontaine, Perrard & Bouchet, 2012; Bullis & Rundell, 2021). The largest proportion of biodiversity comprises undescribed species (Scheffers et al., 2012), and this problem is especially acute for invertebrates, with the proportion of undescribed insect species perhaps as high as 80% (Stork, 2018). Most undescribed species (notably invertebrates) that went extinct recently cannot be known, unless they left a physical record (e.g. a snail's shell). For vertebrates, the bones of which may be preserved long after a species went extinct, knowledge of such species is more complete (e.g. Hawaiian birds; James & Olson, 1991; Olson & James, 1991), and, with some major assumptions, for instance about constancy of extinction rates, extrapolation back into the past may permit an estimate of the numbers of species that went extinct but that remain unknown (Boehm & Cronk, 2021). According to Tedesco et al. (2014), who based their study on vertebrates only, extinction of undescribed species may account for up to 59% of all extinctions, depending on the taxonomic group and region. In Hawaii, "extinction has ravaged the Lepidoptera ... most without ever being collected" (Rubinoff, 2017, p. 202). Indeed, there are many examples of recent species described after their extinction, in molluscs (see Section IV.2) but also in other groups, even if the authors, probably fearing the Romeo Error, sometimes did not declare them as extinct, for example, plants (Fischer & Rahelivololona, 2002), insects (Tian & Deuve, 2007; Tan & Hua, 2008; Penz, Simonsen & Devries, 2011), mammals (Helgen, Helgen & Wilson, 2009), amphibians (Coloma et al., 2010), reptiles (Hedges & Conn, 2012) and birds (Lees & Pimm, 2015).

(5) The invertebrate problem

Many known invertebrate species are in fact only recorded from one locality and sometimes only one specimen, making them impossible to assess with the *Red List* criteria. For

instance, ~ 20% of Australian Neuroptera are known from a single specimen or a single locality (New, 1997); in a random sample of terrestrial molluscs worldwide, 30% were known only from the original description and 33% from only one locality (Régnier et al., 2015a); in a random sample of Coleoptera, 53% were known only from a single locality and 13% from a single specimen (Stork, 1997); among species of Trichoptera newly described in 2011-2014, 45% were based on singletons (Wells, Johanson & Dostine, 2019); and of 2,198 worldwide mantids, 48% are reported based on single specimens (Battiston, 2014). This extreme paucity of records for invertebrates is the rule, and accounts for the difficulty of assessing them properly against the *Red List* criteria. For aquatic invertebrates, up to 34% of the assessed species (i.e. a sample of species for which there were enough experts and potential knowledge to start the assessment process) were listed as Data Deficient (Collier, Probert & Jeffries, 2016).

IV. OTHER APPROACHES

The primary reasons why the *Red List* is not a good basis on which to assess global extinction rates are thus (*i*) it is far from comprehensive and biased taxonomically, and (*ii*) it is impossible to evaluate the vast numbers of species, notably invertebrates, according to the IUCN categories and criteria, not only because of their sheer numbers but also because we simply do not have adequate data. Even if we did have the data, it would be the fate of many invertebrate species to jump from Data Deficient one year to Extinct a few years later.

In the search for alternative approaches, some have suggested revising and augmenting the *Red List* criteria to permit more realistic evaluations of invertebrates or plants (Cardoso *et al.*, 2011; Bachman *et al.*, 2019; Fox *et al.*, 2019).

More general attempts to assess large-scale extinction have, since long before the prominence of the Red List, been based on species-area relationship (SAR) approaches that are not dependent on known or supposed extinctions of individual species but on projections of, for instance, area of habitat loss extrapolated to proportional loss of species according to various assumptions (Pimm & Raven, 2000). However, there are many problems with using the SAR and many interpretations have been criticised for either over- or under-estimating future extinction rates (e.g. Simberloff, 1992; C. D. Thomas et al., 2004; Lewis, 2006; Stork, 2010; Fattorini & Borges, 2012; He & Hubbell, 2013; Rybicki & Hanski, 2013). Nonetheless, despite the arguments, whether over-estimates or under-estimates, all indicate significant extinction through loss of habitat. Yet all these efforts have even been decried as part of an "exaggeration campaign" (Briggs, 2016, p. 21) that grossly overestimates extinctions, based on theory as opposed to real data (Briggs, 2014b, 2014c), and the approach "remains popular due to [sic] inertia" (Briggs, 2014b, p. 415).

Most recently, efforts have been made to base evaluations on essentially qualitative expert knowledge. Keith et al. (2017)

focused on threats and Thompson *et al.* (2017) on records and surveys; the former adopting a probabilistic approach based on structured reasoning, the latter on a modelling approach, and, as exemplars, using a plant and a bird species, respectively. Butchart *et al.* (2018) extended these approaches to address the probability of extinction for 61 bird species. Using such methods adds quantitative rigour to assessments of extinction but still depends on considerable species-specific knowledge, which for most invertebrates is not available, and is unlikely to become available, in part because the resources to obtain the necessary data are also not available.

Other alternative approaches include: the Red List Index (Butchart *et al.*, 2004, 2007; Brummitt *et al.*, 2015), which was designed to measure extinction risk of sets of species and to track changes in this based on the changes over time of the proportion of species in each category on the *Red List*; extrapolation from well-known taxa (Mawdsley & Stork, 1995; McKinney, 1999); modelling the impact of climate change on extinction risk (e.g. C. D. Thomas *et al.*, 2004; Urban, 2015); or a combination of these approaches (e.g. Van Vuuren, Sala & Pereira, 2006).

(1) The need to address invertebrates

Invertebrates constitute the vast majority, 95–97%, of known animal species (Chapman, 2009; Roskov et al., 2019; IUCN, 2020). It is therefore essential that invertebrates are included in any plausible estimate of overall biodiversity extinction. However, in contrast to the evaluation of all bird and most mammal species (only ~5% listed as Data Deficient), of the ~ 1.5 million described species of invertebrates accepted by IUCN (2020), only 23,808 (1.6%) have been evaluated, of which 6,525 (27%) are Data Deficient (see also Eisenhauer, Bonn & Guerra, 2019). Despite his denial of significantly enhanced rates of extinction (Briggs, 2016), Briggs (2017) acknowledged that "using vertebrate animals to predict global events" (p. 245) was problematic and advocated that we "continue monitoring the well-known groups of insects and use them as surrogates to estimate the overall extinction rate" (p. 257). We agree with this statement, but we extend it to other groups of relatively well-known invertebrates, notably the molluscs.

Most animals are indeed insects; an estimated 1.05 million extant species are known to taxonomists, with 88% of these listed in the Catalogue of Life (Roskov *et al.*, 2019; IUCN, 2020) [IUCN (2020) derived its insect data from Roskov *et al.* (2019)]. IUCN (2020) has evaluated only 9,793 (0.9%) of them (Fig. 1) and lists 2,561 (26%) as Data Deficient and 63 as Extinct (0.9% of those evaluated, excluding those evaluated as Data Deficient). The tiny number listed as extinct reflects the relatively tiny number evaluated and the high proportion of those that are Data Deficient. Few insect groups have been assessed in any way comprehensively – none appears in Fig. 2 of the *Red List* Summary Statistics (IUCN, 2020). Notably, 7,406 (76%) of these insect assessments are of Odonata (4,830 assessed out of an estimated 6,650 known species), Lepidoptera (1,126 of

158,570) and Coleoptera (1,450 of 392,415) (total numbers of known species from Roskov *et al.*, 2019). Among these three groups, 2,000 (27%) are listed as Data Deficient and 43 as Extinct (0.8% of the total, excluding those evaluated as Data Deficient). Many insect species known only from the original descriptions and from the type localities are less likely to be assessed than better known species in the better known groups, and even if they are assessed they are likely to be Data Deficient. Yet these species may well be the most likely to be threatened and therefore to have gone extinct. Thus the numbers assessed as Extinct on the *Red List* are under-estimates, and inappropriate to use to estimate true levels of extinction.

But furthermore, it is inappropriate to argue (Briggs, 2014b, 2014c, 2016, 2017), based on such subsamples of taxonomic groups and the numbers of species assessed by IUCN as Extinct in those subsamples, that those same numbers are the total numbers of Extinct species in each entire group, that is, not just the assessed species but also those not assessed, thus stating that since only 63 insect species are listed as Extinct by IUCN out of the total 1.05 million species, the rate of insect extinction is so low that it is not of concern. Instead, it is necessary, at least, to extrapolate based on the proportion listed as Extinct of only those assessed (excluding Data Deficient) for the group, and not the total known for the group, in order to estimate the proportion extinct for the entire group. Thus, for instance, with 27 Lepidoptera listed as Extinct out of 1,042 assessed (excluding Data Deficient), 4,109 of the 158,570 Lepidoptera species (Roskov et al., 2019) would be estimated as extinct. Similarly, 7,127 Coleoptera (16 listed as Extinct) but no Odonata (none listed as Extinct) would be estimated as extinct. Even within Lepidoptera, for Rhopalocera (butterflies) (19,049 total species; Roskov et al., 2019) four are listed as Extinct out of 973 assessed (excluding Data Deficient species; note that very few moths have been assessed), and extrapolation would estimate 78 extinct species, contrasting with the three acknowledged by Briggs (2014b) but subsequently considered doubtful (Briggs, 2014c, 2015) or discounted by him (Briggs, 2016, 2017). But even the number of extinct species compared to the number of assessed species in a group cannot give an unbiased estimate of extinction rate, as highly threatened or extinct species may be more prone to be listed than species that are not threatened. For instance, for Dytiscidae (4,000 species; Roskov et al., 2019), 24 species have been assessed (none Data Deficient), and six are listed as Extinct (IUCN, 2020). [Incidentally, one of these six species is Carabdytes novaecaledoniae (Balfour-Browne) (included in the Red List since 1996 as Rhantus novacaledoniae), which is not Extinct and has been recorded recently from New Caledonia (Jäch & Balke, 2008)]. Without knowing how the assessed species were selected, it would not be justifiable to infer from these figures that 25% of Dytiscidae species are extinct.

If the proportion of extinct, described insects were the same as the proportion of mammals and birds listed as extinct by IUCN (2020), then there should be roughly 15,000 extinct species of insects. But even if extinction rates for insects are

lower than those for mammals and birds by as much as an order of magnitude (Dunn, 2005; Stork, 2010), which the data above do not seem to support, this still seems unlikely to account for the tiny number listed as extinct on the Red List, which is more likely to be a result of lack of knowledge, or a lack of experts to undertake evaluations for the Red List. To illustrate this last point, among the 139 taxon-specific Specialist Groups of the IUCN Species Survival Commission, only 17 are devoted to invertebrates, yet there are 36 for mammals and 19 for birds. Therefore, extrapolating from the *Red List* numbers for insects (or from a subset of insects) to a global estimate of the number of extinct species will still result in an under-estimate (Dunn, 2005). And because different groups of insects may have suffered different rates of extinction, as suggested by the analysis above, selection of one or a few groups in particular may not be representative of insects as a whole. Incidentally, it is symptomatic that, despite the 373 chordate species listed as extinct (IUCN, 2020), not one of their multicellular (helminths, lice, crustaceans) or unicellular parasites is listed; for example, a species of amphipod that parasitised Steller's sea cow, Hydrodamalis gigas (Boxshall & Hayes, 2019) and six Phthiraptera (lice) that went extinct when their bird hosts disappeared (coextinction), and 2-4 other lice, the extinction of which was due to efforts to save their hosts, including the little spotted kiwi, Apteryx owenii (Fig. 3), and the California condor, Gymnogyps californianus (Rózsa & Vas, 2015).

Briggs (2017, p. 245) stated that

... butterflies, tiger beetles, dragonflies, damselflies ... have been of special interest to amateur and professional entomologists. Each group is well known, it has a worldwide distribution and its species extinction during the past 500 years is documented. Among these four groups, 25 260 species have been evaluated, and only three were found to have become extinct (Briggs, 2016)

It is true that butterflies are more popular and hence probably better known by naturalists globally than other groups of insects, but this does not mean that their extinctions are well documented: there are only four extinct butterflies listed in the *Red List* (IUCN, 2020), despite the fact that more extinctions are reported in the literature (e.g. Penz, Simonsen & Devries, 2011).

The statement that 25,260 species in these groups had been evaluated is not true. In fact only 5,877 of them have been assessed by IUCN (2020): 4,830 odonates out of a total of 5,912, 1,043 of 19,049 butterflies and four of more than 2,300 tiger beetles (Cicindelinae; Cassola & Pearson, 2000; Briggs, 2015). His figure of 25,260 is in fact the total number of then known species of odonates, butterflies and tiger beetles (Briggs, 2014c, 2015, 2017). To conclude, for instance, that none of the >2,300 tiger beetles has gone extinct on the basis of the four that have been evaluated is not appropriate. Thus Briggs' estimates of extinction rates are artificially low. Nonetheless, at least odonates and butterflies do appear to exhibit lower than average extinction rates among insects



Fig. 3. Parasites, such as this louse (Phthiraptera, *Rallicola pilgrimi* Clay, collected June 2014, South Island, New Zealand), which went extinct when its host, the little spotted kiwi (*Apteryx owenii* Gould), was transferred to predator-free islands (Buckley *et al.*, 2012), and which is not on the *Red List*, are almost completely unknown in the assessment of extinctions. Photograph: Creative Commons 4.0. Te Papa (A1.018470).

as a whole, based on *Red List* data, perhaps because higher vagility and concomitant larger range sizes reduce extinction risk in these highly volant groups.

No single large insect group has been comprehensively assessed for the *Red List*. For this reason, using the proportion of species listed as extinct by the *Red List* in a given group of insects compared to the number of described species in that group to assess extinction rates is misleading.

(2) The value of terrestrial molluscs for assessing invertebrate extinction rates

In attempts to surmount this apparently intractable invertebrate problem, Régnier *et al.* (2009, 2015*a*, 2015*b*) and Cowie *et al.* (2017) focused on molluscs. Molluscs are a reasonably well-known group of invertebrates, which makes them valuable from the perspective of extrapolating extinction rates to biodiversity more broadly. They constitute the second largest animal phylum after arthropods in terms of numbers of known valid extant species (83,584 catalogued in MolluscaBase as of 13 October 2021; MolluscaBase editors, 2021), with estimates of up to 200,000 molluscan species in total (Chapman, 2009) and even of 200,000 marine species alone (Bouchet *et al.*, 2016).

Of the known mollusc species, 8,772 (~10.5%) have been evaluated (Fig. 1), and of these 2,213 are Data Deficient.

IUCN (2020) lists 299 as extinct, which is 4.6% of the total evaluated, excluding those that are Data Deficient. Thus, molluscs have suffered a considerably higher rate of extinction than birds and mammals (1.5%; see Section III.1), based on analysis of the IUCN *Red List* data, with the caveat that there is probably some bias towards listing extinct species. Despite the relative lack of data on invertebrates compared with vertebrates, almost the same number of molluscs (299) are listed as extinct by IUCN (2020) as all mammals, birds, reptiles and amphibians combined (314); most of those molluscs (273) are gastropods, with the great majority being land snails from oceanic islands and more than half of these (135) being Pacific island snails.

Preservation potential of organism remains is important in assessing extinctions, but there are inherent preservation biases that can influence such assessments (Plotnick et al., 2016). For instance the preservation potential of mammals is much greater than that of amphibians (McCallum, 2007) and that of large vertebrates is much greater than that of small vertebrates (McCallum, 2015). Among terrestrial invertebrates, molluscs are a good candidate for assessing species losses, as they leave long-lasting remains (shells) in the fossil and archaeological records when they die (Fig. 4). On islands, especially where limestone substrates with a high calcium content allow longterm persistence of empty shells (Říhová et al., 2018), many surveys have revealed a recently vanished fauna (Fig. 5), and species new to science, although already extinct, have been described (e.g. Christensen, 1982; Abdou & Bouchet, 2000; Bouchet & Abdou, 2001; Zimmermann, Gargominy & Fontaine, 2009; Richling & Bouchet, 2013; Sartori, Gargominy & Fontaine, 2013, 2014; Gerlach, 2016; Christensen, Kahn & Kirch, 2018) (Fig. 4). Insects or other arthropods, many of which do not leave identifiable remains, generally cannot provide such an insight into recent extinctions as molluscs can, unless time-demanding sample analysis methods are used (e.g. swamp coring), in which case recent insect extinctions and their possible causes may be revealed (e.g. Whitehouse, 2004, 2006; Craig & Porch, 2013; Porch & Smith, 2017). Nonetheless, many insects are preserved in amber (Poinar, 1993) and others are well known from, for instance, lacustrine deposits, fen and bog peat deposits, and oil seeps (Durden, 1966; Elias, 1991; Smith & Moe-Hoffman, 2007; Smith & Marcot, 2015; Holden et al., 2017).

(3) An assessment of global extinction based on molluscs

Despite major efforts by IUCN, the *Red List* data for mollusc extinctions remain far from comprehensive. We have undertaken assessments that have shown that many more mollusc species are known by the scientific community to be extinct than are included in the *Red List* (Régnier *et al.*, 2009, 2015*a*, 2015*b*; Cowie *et al.*, 2017). Our approaches were a combination of expert and survey/records approaches (*cf.* Keith *et al.*, 2017; Thompson *et al.*, 2017). However, they were not probabilistic, structured reasoning approaches (Keith *et al.*, 2017), although they did incorporate probability modelling aspects.



Fig. 4. Recently extinct Endodontidae from Rurutu (Austral Islands, French Polynesia). Photographs: O. Gargominy, A. Sartori (Muséum national d'Histoire naturelle, Paris).



Fig. 5. Rurutu (Austral Islands, French Polynesia) was once home to 19 species of endemic Endodontidae (Mollusca). Despite extensive searches in the remaining patches of native vegetation, such as at the foot of this cliff, only empty shells were found. All 19 species are now considered extinct. Photograph: B. Fontaine.

Our most recent numbers (Cowie et al., 2017) are 638 species extinct, 380 possibly extinct, and 14 extinct in the wild, a total of 1,032 species in these combined categories, and more than twice as many as listed by IUCN (2020) in these categories (462). Furthermore, based on expert assessment of a rigorously random global sample of 200 land snail species (Régnier et al., 2015a), extrapolation estimated that of the

 $\sim\!30,\!000$ land snail species – the number recognised at that time by Rosenberg (2014) – 3,000–5,100 (10–17%) may have gone extinct [based on re-assessment of the data of Régnier et al. (2015a) by Cowie et al. (2017)]. When extinctions of the $\sim\!44,\!000$ marine molluscs (Rosenberg, 2014) were taken as effectively zero (three Extinct, three Possibly Extinct; Cowie et al., 2017), then 4–7% of the 73,000–75,000

(Rosenberg, 2014) described mollusc species had gone extinct (Cowie *et al.*, 2017). According to MolluscaBase (MolluscaBase editors, 2021), the total number of known valid extant mollusc species is somewhat higher than the estimates of Rosenberg (2014) that Régnier *et al.* (2015*a*) and Cowie *et al.* (2017) used in their calculations; however, the overall picture of extinction has not changed.

If we assume that (*i*) the 200 land snail species sampled by Régnier *et al.* (2015*a*) are representative of known nonmarine invertebrate diversity and their extinction rate (admittedly a bold assumption), (*ii*) three-quarters of species are non-marine (Mora *et al.*, 2011), and (*iii*) marine extinctions are negligible compared with non-marine extinctions, then approximately 7.5–13% (150,000–260,000) of all ~2 million species have gone extinct since around 1500. This is orders of magnitude greater than the 882 (0.04%) listed as extinct by IUCN (2020). But is it a biodiversity crisis, or even the Sixth Mass Extinction?

V. CURRENT VERSUS BACKGROUND EXTINCTION RATES

Arguments surrounding the question of whether current extinction rates are artificially high depend on an assessment of the background rate of extinction. Since Pimm et al. (1995) introduced the E/MSY metric (number of extinctions per million species-years), this statistic has been used frequently to describe the background rate, with most authors reaching estimates of 0.1–1 E/MSY (Ceballos et al., 2015), with some suggesting that typical rates may be closer to 0.1 E/MSY (De Vos et al., 2015; Lamkin & Miller, 2016; Pimm & Raven, 2019). However, based on mammals, Ceballos et al. (2015) estimated a background rate of ~2 E/MSY. Nonetheless, Briggs (2016, 2017) preferred to use a Pleistocene background extinction rate of about 0.5 species per year for comparison with modern extinctions. However, the great value of E/MSY is that the rate of extinction (proportion of the biota going extinct) is independent of the total number of species, while a specific number of species going extinct says nothing about the rate. Nonetheless, for ease of comparison, and under the assumption of a total of ~2 million described species, a background rate of 2 E/MSY (Ceballos et al., 2015) equates to 4 species extinctions per year, but 0.5 species per year (Briggs, 2017) equates to only 0.25 E/MSY. Using the 2 E/MSY value of Ceballos et al. (2015) for comparison with modern rates is therefore eight times more conservative than using the 0.5 species per year of Briggs (2016, 2017) because the difference between 4 per year and the modern rate will be smaller than that between 0.5 per year and the modern rate, and will thus de-emphasise the inference of a biodiversity crisis. Further, in the present timeframe of hundreds of years (i.e. IUCN listing extinctions since 1500), for ease of understanding, E/MSY is equivalent to the number of extinctions per 10,000 species per 100 years.

Hence, our estimate of 150,000-260,000 extinctions of all species during the roughly 500 years since 1500 (300-520 extinctions per year) among ~2 million species equates to 150-260 E/MSY, far greater than even the high and conservative background rate of Ceballos et al. (2015). If, more conservatively, we base our calculations on the 638 mollusc species we (Cowie et al., 2017) considered extinct, out of ~80,000 extant (not fossil-only) mollusc species (MolluscaBase editors, 2021), including marine species that have suffered negligible extinction, we obtain a rate of 16 E/MSY, or 26 E/MSY if we also include species we considered possibly extinct (380) and extinct in the wild (14); however, these estimates are artificially low because we compared known (by us) extinctions with total known species, as opposed to only those known species the status of which we had screened (additional known species might be extinct, unbeknown to us). If we use the IUCN (2020) numbers of 299 mollusc species extinct out of 6,559 non-Data Deficient mollusc species evaluated, we obtain a rate of 91 E/MSY, although this is artificially high because of bias in listing known extinct species. The average of these various estimates of mollusc extinctions falls a little over 100 E/MSY but with a huge variance dependent on the data used.

For amphibians, McCallum (2007) estimated modern extinction rates (based on IUCN *Red List* data) of 10–61 E/MSY. Pimm *et al.* (2014) estimated rates for species of birds, amphibians and mammals, respectively, described before 1900 as 49, 66 and 72 E/MSY, and described after 1900 as 132, 107 and 243 E/MSY. For plants, Humphreys *et al.* (2019) estimated modern extinction rates at 171 E/MSY for plants described before 1900, and 60 E/MSY for species described after 1900. All these estimates of E/MSY fall within the range 10–243, with an average of just over 100 E/MSY but again a wide variance.

Taken together, therefore, these estimates fall within a similar range to those of previous studies (e.g. Table 2 of Lamkin & Miller, 2016) and suggest a contemporary rate 100–1,000 times greater than the background rate, that is, based on a background rate of 1 or 0.1 E/MSY, respectively. Lamkin & Miller (2016) estimated E/MSY as ~1.05 based on the IUCN number of extinct species, but as a proportion of all known species, an approach that, as discussed above, seriously under-estimates true extinctions. Nonetheless, they also estimated E/MSY based on numbers of extinct plus additional ~1,000 suspected extinct species for a value of ~10 E/MSY, and then included all ~20,000 Threatened species for a value of ~58 E/MSY, which is of the same order of magnitude as found by other studies. Regardless of the relative numbers, whether one accepts a background rate of 1.0 or 0.1 E/MSY, extinction rates assessed in many studies have increased within the last 500 years and, despite the problem that rates estimated over longer time intervals are lower than those estimated over shorter intervals, they are many times higher than the background extinction rate derived from the fossil record (Barnosky et al., 2011).

VI. ISLANDS AND OTHER INSULAR HABITATS

Most estimates of extinction rates, including ours (Régnier et al., 2009, 2015a, 2015b; Chiba & Cowie, 2016; Cowie et al., 2017), indicate that island species have suffered far greater rates than have continental species, a fact that is widely acknowledged (Manne, Brooks & Pimm, 1999; Stork, 2010; Triantis et al., 2010). However, Briggs (2017) discounted this as not representative of a Sixth Mass Extinction, focusing on continental faunas with much lower extinction rates. But ignoring island species downplays the seriousness of these losses, with figures such as 2,000 bird species extinctions on Pacific islands after human colonisation beginning just a few thousand years ago (Steadman, 1995), that is, the loss of almost one sixth of the current worldwide bird fauna. While it has generally been thought that the vast jungles of the Amazon Basin and Central Africa may not be populated by extremely narrow endemic species, at least not on the scale of island endemics inhabiting only a few square kilometres, there are nonetheless many habitat islands within continental regions that do indeed support relatively narrow endemics that are just as threatened as those of oceanic islands (Manne et al., 1999).

The land snails of karst outcrops in South-East Asia and elsewhere are highly diverse and narrowly endemic, often to single outcrops, and are under severe threat (Clements et al., 2008; Vermeulen & Marzuki, 2014). Freshwater springsnails are particularly vulnerable because of their typically narrow ranges, often just a single spring or spring complex (Ponder & Clark, 1990; Hershler, Liu & Howard, 2014), as are amphipods (Murphy, Adams & Austin, 2009) and other taxa including plants (Rossini et al., 2018) of artesian springs in Australian deserts. Cave faunas in many parts of the world harbour highly endemic invertebrate faunas, with

some species restricted to single caves, for example in Romania (Moldovan et al., 2020) and South Africa (Ferreira et al., 2020). Fish species in isolated Chinese plateau lakes exhibit high levels of single-lake endemism (Ding et al., 2017), as do freshwater snails endemic to one or a few of these lakes (Zhang et al., 2015). Ancient lakes in the Balkans support radiations of endemic snails (Stelbrink et al., 2016) and crustaceans (Korovchinsky Petkovski, 2014). Equally, the biota of single isolated mountain tops (sky islands) often include endemic species of many groups (Leite, Kok & Weksler, 2015; Merckx et al., 2015; Breure, 2019; Rull et al., 2019). All these ecosystems are isolated by the surrounding habitat and in this regard are equivalent to oceanic islands. But the biodiversity of many of these isolated habitats has been only poorly surveyed and no doubt large numbers of endemic species await discovery. While it certainly seems that island biota are more subject to extinction than continental species (Fig. 6), such a broad conclusion may hide the vulnerability of the great diversity of narrowly endemic continental species occurring on such island equivalents. Even in the Amazon basin it is increasingly recognised that many cryptic taxa may not only be restricted to areas of endemism bounded by major rivers but also only occur in mini-interfluvia within these areas (Fernandes, 2013).

VII. MARINE SPECIES

Environmental health of the oceans is the subject of considerable media attention, that to a large extent tends to treat pollution (e.g. the "seventh continent" of plastic; Ter Halle & Perez, 2020), the collapse of fisheries, and extinction as





Fig. 6. Right: Tropical islands such as Anjouan in the Comoros, have suffered extensive deforestation for agriculture. Native vegetation is generally completely lacking at lower altitudes, and the highest ridges and mountaintops are now the last refuges of the remaining extant endemic species. Left: Other islands such as Rapa in the Austral Islands, French Polynesia, which has an area of only 40 km² and used to have more than 100 endemic land snail species, 59 endemic plant species and 67 endemic weevil species, are now mostly barren. Fires and overgrazing by introduced herbivores have destroyed much of the upper elevation habitat, and the vegetation at lower altitudes is dominated by invasive species. Photographs: B. Fontaine.

different manifestations of the same problem. Ironically, although the first five mass extinctions are documented based on the marine fossil record, there is remarkably little evidence that a Sixth Mass Extinction may have begun in the oceans. Two much cited studies (Myers & Worm, 2003; Worm et al., 2006) have documented the overfishing, past, present and projected, of commercial fish stocks and their collapse by the middle of the 21st century, leading to media statements such as "seafood off the menu by 2048" (Biello, 2006) and "no more fish by 2048" (Burrows, 2018). However, commentators have confused commercial extinction (the economic and ecological collapse of fish stocks) and biological extinction (the disappearance of all individuals of a species). It cannot be denied that commercial fish stocks have been, and continue to be depleted and the reduction of size in target fishes throughout the 20th century provides compelling evidence of "shifting baselines" (Pauly, 1995; Jackson et al., 2001; Pauly, Watson & Alder, 2005; Zeller & Pauly, 2018). It is, therefore, remarkable that, in contrast to this massive body of evidence, there is a just one documented extinction of a truly marine fish: Sympterichthys unipennis (Cuvier), known from a single specimen collected in Tasmania in 1802 (Last, Edgar & Stuart-Smith, 2020). Additionally, the houting, Coregonus oxyrinchus (L.), from the estuaries of the North Sea basin, and the amphidromous New Zealand grayling, Prototroctes oxyrhynchus Günther, are also extinct (Freyhof & Kottelat, 2008; West, David & Ling, 2014). All other 72 fish species listed as Extinct (62) or Extinct in the Wild (10) on the Red List (IUCN, 2020) are strictly from fresh water. In addition to fishes, marine species listed as extinct include the iconic Steller's Sea Cow, Hydrodamalis gigas (Zimmermann) (Fig. 7), the Caribbean monk seal, Neomonachus tropicalis (Gray), the great auk, Pinguinus impennis (L.), and several other seabird species (although the monk seal and the seabirds faced threats when on land rather than in the sea), as well as just one alga species (the rhodophyte Vanvoorstia bennettiana (Harvey) Papenfuss), from Sydney Harbour, not recorded since 1886, and four species of marine molluscs. Of these molluscs, Littoraria flammea (Philippi) from

the mangroves and saltmarshes of China, has been rediscovered (Dong, Huang & Reid, 2015), although its survival remains uncertain; and the assimineid *Omphalotropis plicosa* (Pfeiffer) from Mauritius qualifies more as a halophile terrestrial species than as a marine snail. In fact, the New England eel-grass limpet, *Lottia alveus* (Conrad), remains the only marine invertebrate the taxonomic status of which is undisputed and which has a well-documented extinction history (Carlton *et al.*, 1991). The decline of the fourth mollusc species, *Lottia edmitchelli* (Lipps), first described as a Pleistocene fossil, is not linked to obvious modern environmental changes and may have been natural.

Roberts & Hawkins (1999, p. 245) argued that "there are several reasons to suspect that many marine extinctions have gone unnoticed", an assertion with which we agree. But we do not share their judgement that "compared with terrestrial ecosystems, the sea has been far less studied and the historical baseline of information tends to be brief. It is harder to sample marine ecosystems" (p. 245); whereas their statement that "our taxonomic knowledge of many groups remains fragmentary" (p. 245) applies just as well to most non-marine invertebrate groups.

Beyond the *Red List*, there are indeed additional cases of marine species declared extinct (e.g. Carlton, 1993; Peters *et al.*, 2013; White, Kyne & Harris, 2019; Tenorio *et al.*, 2020), and Gravili *et al.* (2015) even speculated that of 53 species of Mediterranean Hydrozoa not recorded in the literature in the preceding 41 years, 60% (i.e. 32 species) could be declared Extinct. Just as on land, species declared extinct may also be rediscovered (de Weerdt & Glynn, 1991; Glynn & Feingold, 1992; Díaz, Gast & Torres, 2009).

Admittedly, the vastness of the marine realm and the remoteness of some places make it difficult to conduct exhaustive surveys to document the conservation status of many of its species components. However, this vastness and this remoteness are precisely what makes marine species less prone to global extinction.

We agree with Roberts & Hawkins (1999, p. 245) that "what is now beyond doubt is that many marine species have



Fig. 7. Steller's sea cow (*Hydrodamalis gigas* (Zimmerman)), one of the few documented marine extinctions, skeleton in the Musée des Confluences, Lyon. Photograph: Vassil, via Wikimedia Commons.

begun walking the path to global extinction", that the various threats continue to mount (e.g. Sullivan, Constant & Lubchenco, 2019) and that extreme rarity may be the harbinger of extinction (Hull *et al.*, 2015), but we conclude, in line with the review of Monte-Luna *et al.* (2007) and with the views defended by Briggs (2017), that there is no evidence that a Sixth Mass Extinction has already hit marine biota.

VIII. PLANTS

This commentary has focussed on animals, and especially non-marine animals. But plants, although probably more fully described than the myriads of invertebrates, are poorly covered by the Red List (Humphreys et al., 2019). The 2016 Kew Royal Botanical Garden report (RBG Kew, 2016) acknowledged that proving extinction in plants is difficult because species may be difficult to detect, especially those that do not flower every year, and because of lack of surveying effort. Moreover, only 10% of known plant species have been assessed by IUCN (2020), a small sample skewed towards species that are supposed to be more prone to extinction by Red List assessors (RBG Kew, 2016). While stating that 21% of plant species are threatened with extinction according to the IUCN criteria, the Kew report did not give any figure for known extinctions in plants. IUCN (2020) has evaluated 43,556 plant species and lists 120 species as Extinct and 39 Extinct in the Wild (0.32% combined of those evaluated), with 17,507 in the threatened categories of Critically Endangered, Endangered and Vulnerable (41% of those evaluated and 4.1% of the total diversity).

There have been several attempts to produce regional counts of plant extinctions, generally producing low figures: 0.53% of the native flora in California (Reimánek, 2018), 0.38% of the Spanish flora (Aedo et al., 2015), and 0.55% of the overall flora of Mediterranean Europe but 2% of the native flora of Europe and Israel (Essl et al., 2013). Based on literature reviews, Humphreys et al. (2019) compiled the first ever global list of known extinct plants, a total of 571 species. This included 491 species that were not on the *Red List*, which currently (IUCN, 2020) lists 120, and excluded others that were previously listed as Extinct but had been rediscovered or synonymised. De Vos et al. (2015) also showed that the current extinction rate for plants is up to 500 times their background extinction rate. However, this figure is far less than an earlier estimate of ~30,000 plants likely to go extinct by 2015, which was extrapolated from a species-area approach applied to the loss of tropical forests (Heywood & Stuart, 1992). Cronk (2016) explained the discrepancy between these estimates and the IUCN figure as a result of two factors: (i) the general fact, also applicable to animals, that extinction lists are highly conservative because of the difficulty of proving that a species is extinct and the fear of the Romeo Error; but mostly (ii) the long extinction lag time, that is, the time between the occurrence of the event leading to extinction (habitat degradation, or extinction of a species

needed to accomplish the life cycle such as a seed disperser or pollinator) and the demise of the last individual of the species - the phenomenon known as extinction debt (Tilman et al., 1994; Triantis et al., 2010; Figueiredo et al., 2019). For plants, this lag time may last several centuries. This phenomenon is illustrated by the fact that in highly degraded ecosystems, such as agricultural areas where the native forest has been cleared, for instance in Costa Rica (Janzen, 2001), individual indigenous trees may survive for decades although there is no recruitment; these trees were called "the living dead" by Janzen (2001). This lag time is usually much longer in plants than in animals because (i) many plants have longer lifespans than animals, (ii) the presence of a soil seed bank that may produce individuals until it is exhausted, and (iii) many plants can reproduce asexually, which allows the last individual to produce successors.

However, several studies comparing local extinction rates among various taxonomic groups have shown that plants usually have lower extinction rates than invertebrates (J. A. Thomas *et al.*, 2004; Essl *et al.*, 2013). It remains to be demonstrated that this is true at a global level, but it may be that plants indeed have a lower rate of extinction than animals.

The phenomenon of long extinction lag times may also occur in long-lived animals such as freshwater pearl mussels (Unionidae), which may have living populations of old animals but no recruitment when the fish hosts of the larvae have been extirpated.

IX. WHAT SHOULD WE DO NOW?

As we have shown, many publications based on independent methods demonstrate the reality of the crisis. The Sixth Mass Extinction may have not occurred yet, but heightened rates of extinction and huge range and population declines have already occurred, and whatever it is called, biodiversity is changing at a greater rate than it would in the absence of anthropogenic influences. This is a fact. Denying it is simply flying in the face of the mountain of data that is rapidly accumulating, and there is no longer room for scepticism, wondering whether it really is happening.

We understand the costs of over-estimating extinction rates (Akçakaya et al., 2017), notably that by doing so, species incorrectly assessed as extinct would be excluded from conservation support, with a loss of credibility should the species subsequently discovered to be (e.g. Battarbee, 2014). Recording an invertebrate as Probably Extinct garners no headlines, but its rediscovery does, especially in this era of science denial. But under-estimating rates provides fuel to those who consider there to be no biodiversity crisis, as stressed by Diamond (1987), which may lead to even greater exclusion from support. With all the uncertainty that is inherent in declaring a species – especially an invertebrate - extinct, our review indicates that the most probable scenario is that the true levels of anthropogenic extinctions rank among what environmental sceptics call

"over-estimation". It is an over-estimation only to those who reject facts that do not conform to their personal or political agendas. That the Sixth Mass Extinction has begun on land and in freshwater seems increasingly likely.

Humankind has the power to manipulate the Earth on a grand scale. We are the only species with such power and choices (Deer, 2019). We are not, therefore, as some would argue (e.g. Thomas, 2017), just another species going about its business in the greater evolutionary scheme of things, an argument that gives carte blanche to those who would destroy the Earth for their own short-term gain. Neither should we, as others argue, focus solely (or at least primarily) on manipulating the Earth for human well-being, whatever that means. Such attitudes, reviewed and criticised by Meine (2018) and Rolston (2018), are an abdication of responsibility - indeed an abdication of morality (e.g. Cafaro & Primack, 2014; Rolston, 2018). In our power, we are qualitatively different from all other organisms. Neither is our impact on the Earth just another major impact like an asteroid collision; we have choice, asteroids do not. We have a moral and ethical obligation to use that power judiciously not capriciously (Dasgupta & Ehrlich, 2019; Sullivan et al., 2019).

But we cannot help but feel that humanity is allowing a probable Sixth Mass Extinction to unfold, and it is pie in the sky to think that this situation will change in any major way, despite attempts by some to influence politicians and business people. Specific conservation programs try to save a species here and another there, mostly birds and mammals; and some will indeed be successful (e.g. Bolam et al., 2020) – even if ex situ – giving the false impression, which will be touted by the deniers, that we are successful in combatting the crisis. Agencies, including IUCN, document threats but have little impact in terms of ameliorating those threats on a large scale. Editors exhort us to conclude our publications with an effort to be positive but it is surely better to be realistic. So what can we do?

The good news is that conservation efforts may sometimes be effective. When specific threats are removed, target species may recover from being on the brink of extinction. For example: recoveries of marine mammal species following hunting bans (Lowry et al., 2014; Bejder et al., 2016); recovery of native faunas, including invertebrate species, after invasive species eradication on islands (Jones et al., 2016); peregrine falcon, Falco peregrinus Tunstall, 1771, recovery from near-extinction in North America after banning of DDT (Cade & Burnham, 2003). However, these rare successes should not hide the fact that since most species population decreases are caused either multifactorially or by large-scale habitat degradation or loss, removing the cause of the decrease is usually beyond the reach of single conservation actions. Moreover, most such bright spots target vertebrates; for the vast majority of threatened invertebrate species, targeted actions to remove threats will never be undertaken. There are multiple initiatives, at various levels, to try to slow or prevent the Sixth Mass Extinction: initiatives by individuals, non-governmental organisations, and green parties at the political/social level (e.g. Extinction Rebellion; or the ban of neonicotinoids by the European Union in 2018 after decades of lobbying by environmentalists and already suffering exceptions), efforts by conservation agencies to protect individual species or set up protected areas, etc. None of these initiatives is enough, many will have little or no impact, but all are needed to try to slow the process, even though they may barely reduce the rate of extinction (Engel et al., 2021). Most such initiatives are not species oriented (except for some charismatic vertebrates) and work at a large scale (protected areas, environmental legislation, environmental education). We know that there cannot be specific actions to protect all living species individually.

In the context of limited time, funding and people to fight the biodiversity crisis, conservationists have suggested several approaches to help establish taxonomic or geographic priorities for action, including, among many others: selecting areas with both the highest diversity and highest threat level, that is, biodiversity hotspots (Myers et al., 2000; Myers, 2003); selecting species based on threat level and phylogenetic value (Redding & Mooers, 2006; Isaac et al., 2007; Volkmann et al., 2014); taking into account taxonomic, phylogenetic and functional diversity (Cadotte & Tucker, 2018); incorporating comprehensiveness, representativeness, surrogacy, but also persistence of investments and cost-efficiency in spatial prioritisation (Wilson, Cabeza & Klein, 2009); integrating ecosystem services in conservation planning (Chan et al., 2006); taking into account human population pressure, habitat and protection status (Shi et al., 2005); capacity building in megadiverse countries (Fan et al., 2020; Tong, 2020); and increased efforts to combat extinction denial (Lees et al., 2020) and improve public education and outreach to address science denial in general (Rutjens et al., 2021). The list is almost endless, and although these tools may help conservation planning and are certainly useful, we should admit that they are not sufficient to solve the crisis.

But this is where we, as taxonomists and systematists, should play our part, since we are better informed than most other scientists about the fate of individual species. We must nurture the innate human appreciation of biodiversity – why is David Attenborough so popular and famous? We must spread the message that the biodiversity that makes our world so fascinating and beautiful is going extinct unnoticed at an unprecedented rate, far faster than some would have us believe, and that preserving ecosystem function (e.g. by restoring habitats) is not enough to prevent extinctions. And because it is not feasible to conserve all species we must do our best to collect (and if possible describe) species before they go extinct - "salvage sampling" (Mesibov, 2004) - an effort emphasised by Boehm & Cronk (2021) and Engel et al. (2021). All this will depend on reviving the venerable but no longer trendy study of natural history and taxonomy - "bionomy" as espoused by Dijkstra (2016), especially in academic institutions in the Global North where it has declined drastically. Much of this has been said many times by many people, but rarely more eloquently than by Dijkstra (2016, p. 174): "In an era of extinction, there are no greater priorities than to accelerate the synthesis of life, salvage knowledge and increase awareness. To do so, we need

our strongest familiarity with all species." Furthermore, to develop a sound view of all life on Earth it is crucial that in addition to the large, beautiful and charismatic animals we also focus our attention on the "endless forms most stupid, icky, and small" — the non-charismatic invertebrates (Czekanski-Moir & Rundell, 2020, p. 12638).

However, at the current pace of exploration and discovery (IISE, 2012), it will take over 300 years to describe the remaining undocumented 6 million species of the planet (Bouchet *et al.*, 2016). Yet the bottlenecks to finding, collecting, describing and naming the remaining species of the world are not technical or technological, but sociological and regulatory. For example, with all good intentions, the 1992 Convention on Biological Diversity (CBD) and in particular its 2010 appendix, the Nagoya Protocol, introduced regulatory changes that, rather than facilitating it, have made biodiversity collecting and research extremely difficult to undertake, especially in some of the most biodiverse countries and for the multitudes of little-known invertebrates for which local capacity to describe species is lacking (Bouchet *et al.*, 2016; Prathapan *et al.*, 2018).

In the preparation for the 15th meeting of the Conference of the Parties (COP 15) to the CBD, numerous world leaders, in September 2020, made declarations that biodiversity extinction must be stopped by 2030. And the first resolution of the Kunming Declaration (COP 15, 2021), released on 13 October 2021 during the first part of the COP 15, "commits ... to reverse the current loss of biodiversity and ensure that biodiversity is put on a path to recovery by 2030 at the latest ...". We naturally hope that the COP 15 will go beyond declarations of goodwill, and will constrain the parties to set up capacity building in megadiverse countries, combat extinction denial and scepticism and promote better public outreach, among many other effective steps humanity can take to fight the crisis. Sound ideas for action are many, and encompass a vast array of subjects, from proper design of protected areas to taxation, family planning and green agriculture, as listed in reviews such as IPBES (2019) and Ripple et al. (2017), but it seems that political will is lacking. Furthermore, we feel that overly strict restriction of international collaboration, aimed at protecting individual countries' biological resources from external commercial exploitation, should be revisited as it is currently putting roadblocks in the way of a deeper basic understanding of biodiversity and the crisis it faces, especially in the tropics. Local capacity building may go some way to ameliorating this problem. The precedent of the European Union, that had earlier failed to reach its ambitious target of halting the loss of biodiversity by 2010, and the failure of the world's countries (IPBES, 2019) to reach the Aichi target number 12 set in 2010 by the CBD in Nagoya ("By 2020 the extinction of known threatened species has been prevented and their conservation status, particularly of those most in decline, has been improved and sustained"), admittedly does not lead to optimism, on top of which there are concerns that indicators used to measure biodiversity erosion do not measure extinction risk (Fontaine et al., 2007).

But we are not throwing up our hands and embracing a likely Sixth Mass Extinction. Rather, we are realistically accepting that there will be many more losses and suggesting that it is important to preserve and document representatives of those future losses. But perhaps, with efforts to publicise the crisis, biodiversity scientists may achieve some successes, such that a significant component of currently extant global biodiversity can be preserved in the wild, and many of those species that will be lost from the wild can at least be preserved in museums for future generations to study and marvel at.

Denying the Sixth Mass Extinction, simply accepting it and doing nothing about it or even embracing it for the benefit (defined by whom?) of humanity, paves the way for it to happen.

X. CONCLUSIONS

- (1) The Sixth Mass Extinction of Earth's biodiversity, distinct from previous such events because it is caused by human activities, has been acknowledged by many for at least 30 years. We define this crisis for biodiversity as including all anthropogenic extinctions since modern humans expanded out of Africa between 200,000 and 45,000 years ago, although extinction rates are now much greater than they were at the start. Yet some deny that there is a crisis, based on two primary critiques: (*i*) the claim that estimated extinction rates have been exaggerated and that the current extinction rate is not significantly greater than the natural background rate, and (*ii*) that because humans are part of the natural world, human-caused extinctions are a natural phenomenon, a part of the evolutionary trajectory of life on Earth.
- (2) We counter these arguments by showing that current extinction rates, notably in terrestrial invertebrates, are far higher than background extinction rates. We also show that use of IUCN *Red List* extinction data to determine current extinction rates inevitably leads to dramatic under-estimation of rates, except for birds, mammals and perhaps amphibians. *Red List* data have been used inappropriately by some to deny that there is a crisis. And as humanity has the power of choice, we further argue that a *laissez-faire* attitude to the current extinction crisis is morally wrong.
- (3) We review alternative approaches for assessing extinctions, focusing on the need to address invertebrates, and argue that molluscs have significant advantages among invertebrates because of their shells, which remain after death as a permanent record, while most other invertebrates vanish without trace and would therefore never be known had they not been collected prior to going extinct. (We note, however, the notinsignificant body of work on fossil insects.) We review our own studies of extinction in molluscs and by logical extrapolation conclude that 7.5–13% (150,000-260,000) of all ~2 million known species may already have gone extinct since around 1500. This is orders of magnitude

- greater than the 882~(0.04%) listed as extinct by IUCN (2020).
- (4) We briefly discuss the marine realm and conclude that many marine species face significant threats, which continue to increase, but we also conclude that there have been relatively few extinctions and that there is no evidence that the Sixth Mass Extinction has already involved the marine biota. Plants, however, face many of the threats faced by terrestrial animals and suffer from similar conservation biases as do invertebrates, although there are hints that they may have suffered lower rates of extinction.
- (5) The prognosis for the survival of a large proportion of extant species is not good. Our review lays out arguments clearly demonstrating that there is a biodiversity crisis, quite probably the start of the Sixth Mass Extinction. Dedicated conservation biologists and conservation agencies are doing what they can, focused mainly on threatened birds and mammals, among which some species may be saved from the extinction that would otherwise ensue. But we are pessimistic about the fate of most of the Earth's biodiversity, much of which is going to vanish without us ever knowing of its existence. Denying the crisis, accepting it and doing nothing about it, or embracing it and manipulating it for the fickle benefit of people, defined no doubt by politicians and business interests, is an abrogation of moral responsibility.

XI. ACKNOWLEDGMENTS

R.H.C. is grateful for the opportunity to work on this publication while at the Muséum national d'Histoire naturelle, Paris, during the summers of 2018, 2019 and 2021. We thank Olivier Gargominy and André Sartori for photographs of extinct Pacific island snails (Endodontidae). This is publication number 11425 of the University of Hawaii School of Ocean and Earth Science and Technology.

XII. AUTHOR CONTRIBUTIONS

All authors contributed to the conception, development and writing of this publication.

XIII. REFERENCES

- ABDOU, A. & BOUCHET, P. (2000). Nouveaux gastéropodes Endodontidae et Punctidae (Mollusca, Pulmonata) récemment éteints de l'archipel des Gambier (Polynésie). Zoasystema 22(4), 689–707.
- AEDO, C., MEDINA, L., BARBERÁ, P. & FERNÁNDEZ-ALBERT, M. (2015). Extinctions of vascular plants in Spain. Nordic Journal of Botany 33, 83–100.
- AKÇAKAYA, H. R., KEITH, D. A., BURGMAN, M., BUTCHART, S. H. M., HOFFMANN, M., REGAN, H. M., HARRISON, I. & BOAKES, E. (2017). Inferring extinctions III: a cost-benefit framework for listing extinct species. *Biological Conservation* 214, 336–342.

- ALCOVER, J. A., PIEPER, H., PEREIRA, F. & RANDO, J. C. (2015). Five new extinct species of rails (Aves: Gruiformes: Rallidae) from the Macaronesian Islands (North Atlantic Ocean). Zootaxa 4057(2), 151–190.
- ALROY, J. (2008). Dynamics of origination and extinction in the marine fossil record. Proceedings of the National Academy of Sciences of the United States of America 105(suppl. 1), 11536–11542.
- ALVAREZ, S. A., GIBBS, S. J., BOWN, P. R., KIM, H., SHEWARD, R. M. & RIDGWELL, A. (2019). Diversity decoupled from ecosystem function and resilience during mass extinction recovery. *Nature* 574, 242–245.
- AUDUBON, J. J. (1827–1838). The Birds of America; from Original Drawings by John James Audubon. The Author, London.
- AVISE, J. C., HUBBELL, S. P. & AYALA, F. J. (2008). In the light of evolution II: biodiversity and extinction. Proceedings of the National Academy of Sciences of the United States of America 105(Suppl. 1), 11453–11457.
- AYALA, F. J. (2008). Science, evolution, and creationism. Proceedings of the National Academy of Sciences of the United States of America 105(1), 3–4.
- Bachman, S. P., Field, R., Reader, T., Raimondo, D., Donaldson, J., Schatz, G. E. & Lughadha, E. N. (2019). Progress, challenges and opportunities for red listing. *Biological Conservation* **234**, 45–55.
- BAE, C. J., DOUKA, K. & PETRAGLIA, M. D. (2017). On the origin of modern humans: Asian perspectives. *Science* **358**(6368), eaai9067.
- BAMBACH, R. K. (2006). Phanerozoic biodiversity mass extinctions. Annual Review of Earth and Planetary Science 34, 127–155.
- Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O. U., Swartz, B., Quental, T. B., Marshall, C., McGuire, J. L., Lindsey, E. L., Maguire, K. C., Mersey, B. & Ferrer, E. A. (2011). Has the Earth's sixth mass extinction already arrived? *Nature* 471(7336), 51–57.
- BARTLETT, L. J., WILLIAMS, D. R., PRESCOTT, G. W., BALMFORD, A., GREEN, R. E., ERIKSSON, A., VALDES, P. J., SINGARAYER, J. S. & MANICA, A. (2016). Robustness despite uncertainty: regional climate data reveal the dominant role of humans in explaining global extinctions of late quaternary megafauna. *Ecography* 39, 152–161.
- BATTARBEE, R. W. (2014). The rediscovery of the Aldabra banded snail, *Rhachistia aldabrae*. Biology Letters 10, 20140771.
- BATTISTON, R. (2014) Species diversity and conservation of mantids: threatened species or merely Data Deficient? *Antenna* Special Edition, 10th European Congress of Entomology, York, UK 3–8 August 2014, 36–37.
- BEJDER, M., JOHNSTON, D. W., SMITH, J. N., FRIEDLAENDER, A. & BEJDER, L. (2016). Embracing conservation success of recovering humpback whale populations: evaluating the case for downlisting their conservation status in Australia. Marine Policy 66, 137–141.
- Benazzi, S., Douka, K., Fornai, C., Bauer, C. C., Kullmer, O., Svoboda, J., Pap, I., Mallegni, F., Bayle, P., Coquerelle, M., Condemi, S., Ronchitelli, A., Harvati, K. & Weber, G. W. (2011). Early dispersal of modern humans in Europe and implications for Neanderthal behaviour. *Nature* 479(7374), 525–529.
- BIELLO, D. (2006). Overfishing could take seafood off the menu by 2048. Scientific American. Electronic file available at https://www.scientificamerican.com/article/ overfishing-could-take-se/. Accessed 29.07.2020.
- BIRD, M. I., HUTLEY, L. B., LAWES, M. J., LLOYD, J., LULY, J. G., RIDD, P. V., ROBERTS, R. G., ULM, S. & WURSTER, C. M. (2013). Humans, megafauna and environmental change in tropical Australia. *Journal of Quaternary Science* 28(5), 439–452.
- BIRDLIFE INTERNATIONAL (2021) Species factsheet: Vermivora bachmanii. Electronic file available at http://www.birdlife.org. Accessed 21.04.2021.
- BOCQUET-APPEL, J.-P. (2011). When the world's population took off: the springboard of the Neolithic demographic transition. *Science* 333(6042), 560–561.
- BOEHM, M. M. A. & CRONK, Q. C. B. (2021). Dark extinction: the problem of unknown historical extinctions. *Biology Letters* 17, 20210007.
- BOLAM, F. C., MAIR, L., ANGELICO, M., BROOKS, T. M., BURGMAN, M., HERMES, C., HOFFMANN, M., MARTIN, R. W., McGOWAN, P. J. K., RODRIGUES, A. S. L., RONDININI, C., WESTRIP, J. R. S., WHEATLEY, H., BEDOLLA-GUZMÁN, Y., CALZADA, J., CHILD, M. F., et al. (2020). How many bird and mammal extinctions has recent conservation action prevented? *Conservation Letters* 14(1), e12762.
- Bond, D. P. G. & Grasby, S. E. (2017). On the causes of mass extinctions. Palaeogeography, Palaeoclimatology, Palaeoecology 478, 3–29.
- BOUCHET, P. & ABDOU, A. (2001). Recent extinct land snails (Euconulidae) from the Gambier Islands with remarkable apertural barriers. *Pacific Science* 55, 121–127.
- BOUCHET, P., BARY, S., HÉROS, V. & MARANI, G. (2016). How many species of molluscs are there in the world's oceans, and who is going to describe them? Mémoires du Muséum national d'Histoire naturelle 208, 9–24.
- BOXSHALL, G. & HAYES, P. (2019). Biodiversity and taxonomy of the parasitic Crustacea. *Zoological Monographs* 3, 72–134.
- Brand, S. (2015). Rethinking Extinction. The idea that we are edging up to a mass extinction is not just wrong it's a recipe for panic and paralysis. Electronic file available at https://aeon.co/essays/we-are-not-edging-up-to-a-mass-extinction. Accessed 28.11.2019.

Brannen. P. (2017). Earth is not in the midst of a sixth mass extinction. The Atlantic, 13 June. Electronic file available at https://www.theatlantic.com/science/archive/ 2017/06/the-ends-of-the-world/529545/

- Breure, A. S. H. (2019). Land snails. In *Biodiversity of Pantepui: The Pristine "Lost World"* of the Neotropical Guiana Highlands (cds V. Rull, T. Vegas-Vilarrubia, O. Huber and C. Señaris), pp. 247–261. Academic Press, London.
- Briggs, J. C. (2014a). Fauna in decline: beyond extinction. Science 346, 820.
- BRIGGS, J. C. (2014b). Global biodiversity: extinctions and originations. Research & Reviews in BioSciences 8(11), 414–421.
- BRIGGS, J. C. (2014c). Global biodiversity gain is concurrent with declining population sizes. Biodiversity Journal 5(4), 447–452.
- BRIGGS, J. C. (2015). Species extinction: frequency and biogeography. Environmental Skeptics and Critics 4(4), 96–105.
- Briggs, J. C. (2016). Global biodiversity loss: exaggerated versus realistic estimates.

 Environmental Skeptics and Critics 5(2), 20–27.
- BRIGGS, J. C. (2017). Emergence of a sixth mass extinction? Biological Journal of the Linnean Society 122, 243–248.
- BROOKS, T. M., MITTERMEIER, R. A., MITTERMEIER, C. G., DA FONSECA, G. A. B., RYLANDS, A. B., KONSTANT, W. R., FLICK, P., PILGRIM, J., OLDFIELD, S., MAGIN, G. & HILTON-TAYLOR, C. (2002). Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology* 16, 909–923.
- Brummitt, N. A., Bachman, S. P., Griffiths-Lee, J., Lutz, M., Moat, J. F., Farjon, A., Donaldson, J. S., Hilton-Taylor, C., Meagher, T. R., Albuquerque, S., Aletrari, E., Andrews, A. K., Atchison, G., Baloch, E., Barlozzini, B., et al (2015). Green plants in the red: a baseline global assessment for the IUCN Sampled Red List index for plants. PLoS One 10(8), e0135159
- BUCKLEY, T. R., PALMA, R. L., JOHNS, P. M., GLEESON, D. M., HEATH, A. C. G., HITCHMOUGH, R. A. & STRINGER, I. A. N. (2012). The conservation status of small or less well known groups of New Zealand terrestrial invertebrates. New Zealand Entomologist 35(2), 137–143.
- BULLIS, D. A. & RUNDELL, R. J. (2021). Molecular phylogenetics and premating isolation in the punctoid land snails of Belau (Republic of Palau, Oceania). Zoologica Scripta 50(5), 555–570.
- BURGESS, S. D., BOWRING, S. & SHEN, S.-Z. (2014). High-precision timeline for Earth's most severe extinction. *Proceedings of the National Academy of Sciences of the United States of America* 111, 3316–3321.
- BURROWS, S. (2018). Ocean fish could be extinct by 2048, ecologists warn. Return to Now. Electronic file available at https://returntonow.net/2018/04/05/ocean-fishcould-be-extinct-by-2048-ecologists-warn/. Accessed 29.07.2020.
- BÜSCHER, B., SULLIVAN, S., NEVES, K., IGOE, J. & BROCKINGTON, D. (2012). Towards a synthesized critique of neoliberal biodiversity conservation. *Capitalism Nature Socialism* 23(2), 4–30.
- Butchart, S. H., Akçakaya, H. R., Chanson, J., Baillie, J. E., Collen, B., Quader, S., Turner, W. R., Amin, R., Stuart, S. N. & Hilton-Taylor, C. (2007). Improvements to the Red List Index. *PLoS One* 2(1), e140.
- BUTCHART, S. H., LOWE, S., MARTIN, R. W., SYMES, A., WESTRIP, J. R. & WHEATLEY, H. (2018). Which bird species have gone extinct? A novel quantitative classification approach. *Biological Conservation* **227**, 9–18.
- BUTCHART, S. H., STATTERSFIELD, A. J., BENNUN, L. A., SHUTES, S. M., AKÇAKAYA, H. R., BAILLIE, J. E., STUART, S. N., HILTON-TAYLOR, C. & MACE, G. M. (2004). Measuring global trends in the status of biodiversity: Red List Indices for birds. *PLoS Biology* 2(12), e383.
- BUTCHART, S. H., STATTERSFIELD, A. J. & COLLAR, N. J. (2006). How many bird extinctions have we prevented? *Orpx* **40**(3), 266–278.
- BUTCHART, S. H., WALPOLE, M., COLLEN, B., VAN STRIEN, A., SCHARLEMANN, J. P., ALMOND, R. E., BAILLIE, J. E. M., BOMHARD, B., BROWN, C., BRUNO, J., CARPENTER, K. E., CARR, G. M., CHANSON, J., CHENERY, A. M., CSIRKE, J., et al. (2010). Global biodiversity: indicators of recent declines. Science 328(5982), 1164–1168.
- CADE, T. J. & BURNHAM, W. (eds) (2003). Return of the Peregrine: A North American Saga of Tenacity and Teamwork. The Peregrine Fund, Boise.
- CADOTTE, M. W. & TUCKER, C. M. (2018). Difficult decisions: strategies for conservation prioritization when taxonomic, phylogenetic and functional diversity are not spatially congruent. *Biological Conservation* 225, 128–133.
- CAFARO, P. & PRIMACK, R. (2014). Species extinction is a great moral wrong. Biological Conservation 170, 1–2.
- CARDOSO, P., BORGES, P. A., TRIANTIS, K. A., FERRÁNDEZ, M. A. & MARTÍN, J. L. (2011). Adapting the IUCN Red List criteria for invertebrates. *Biological Conservation* 144(10), 2432–2440.
- CARLTON, J. T. (1993). Neoextinctions of marine invertebrates. American Zoologist 33, 499–509.
- CARLTON, J. T., VERMEIJ, G. J., LINDBERG, D. R., CARLTON, D. A. & DUBLEY, E. C. (1991). The first historical extinction of a marine invertebrate in an ocean basin: the demise of the eelgrass limpet *Lottia alveus. Biological Bulletin* 180(1), 72–80.

- CASSOLA, F. & PEARSON, D. L. (2000). Global patterns of tiger beetle species richness (Coleoptera: Cicindelidae): their use in conservation planning. *Biological Conservation* 95, 197–208.
- CEBALLOS, G. & EHRLICH, P. R. (2018). The misunderstood sixth mass extinction. Science 360(6393), 1080–1081.
- CEBALLOS, G., EHRLICH, P. R., BARNOSKY, A. D., GARCÍA, A., PRINGLE, R. M. & PALMER, T. M. (2015). Accelerated modern human-induced species losses: entering the sixth mass extinction. *Science Advances* 1(5), e1400253.
- CEBALLOS, G., EHRLICH, P. R. & DIRZO, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proceedings of the National Academy of Sciences of the United States of America 114(30), E6089–E6096.
- CEBALLOS, G., EHRLICH, P. R. & RAVEN, P. H. (2020). Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction. *Proceedings* of the National Academy of Sciences of the United States of America 117(24), 13596– 13602.
- CHAN, K. M., SHAW, M. R., CAMERON, D. R., UNDERWOOD, E. C. & DAILY, G. C. (2006). Conservation planning for ecosystem services. *PLoS Biology* 4(11), e379.
- CHAPMAN, A. D. (2009). Number of Living Species in Australia and the World, Second Edition. Department of the Environment, Water, Heritage and the Arts, Australian Government, Canberra.
- CHIBA, S. & COWIE, R. H. (2016). Evolution and extinction of land snails on oceanic islands. Annual Review of Ecology, Evolution, and Systematics 47, 123–141.
- CHRISTENSEN, C. C. (1982). A new species of Endodonta (Pulmonata, Endodontidae) from Oahu, Hawaii. Malacological Review 15, 135–136.
- Christensen, C. C., Kahn, J. G. & Kirch, P. V. (2018). Nonmarine mollusks from archaeological sites on Moʻorea, Society Islands, French Polynesia, with descriptions of four new species of recently extinct land snails (Gastropoda: Pulmonata: Endodontidae). *Pacific Science* 72(1), 95–123.
- CLARKSON, C., JACOBS, Z., MARWICK, B., FULLAGAR, R., WALLIS, L., SMITH, M., ROBERTS, R. G., HAYES, E., LOWE, K., CARAH, X., FLORIN, S. A., MCNEIL, J., COX, D., ARNOLD, L. J., HUA, Q., et al. (2017). Human occupation of northern Australia by 65,000 years ago. Nature 547(7663), 306–310.
- CLEMENTS, R., NG, P. K. L., Lu, X. X., AMBU, S., SCHILTHUIZEN, M. & BRADSHAW, C. J. A. (2008). Using biogeographical patterns of endemic land snails to improve conservation planning for limestone karsts. *Biological Conservation* 141, 2751–2764.
- Collar, N. J. (1998). Extinction by assumption; or, the Romeo error on Cebu. *Oryx* 32, 239–243.
- Collen, B., Dulvy, N. K., Gaston, K. J., Gärdenfors, U., Keith, D. A., Punt, A. E., Regan, H. M., Böhm, M., Hedges, S., Seddon, M., Butchart, S. H. M., Hilton-Taylor, C., Hoffmann, M., Bachman, S. P. & Akçakaya, H. R. (2016). Clarifying misconceptions of extinction risk assessment with the IUCN Red List. *Biology Letters* 12, 20150843.
- COLLIER, K. J., PROBERT, P. K. & JEFFRIES, M. (2016). Conservation of aquatic invertebrates: concerns, challenges and conundrums. Aquatic Conservation: Marine and Freshwater Ecosystems 26(5), 817–837.
- COLOMA, L. A., DUELLMAN, W. E., ALMENDÀRIZ, A. & RON, S. R. (2010). Five new (extinct?) species of Atelopus (Anura: Bufonidae) from Andean Colombia, Ecuador, and Peru. Zootaxa 2574, 1–54.
- COP 15 (2021). Kunning Declaration. Electronic file available at https://www.cbd.int/doc/c/df35/4b94/5e86e1ee09bc8c7d4b35aaf0/kunmingdeclaration-en.pdf. Accessed 17.10.2021.
- COWIE, R. H., FONTAINE, B. & BOUCHET, P. (in press). Non-marine molluscs. In *The Living Planet: The State of the World's Wildlife* (ed. N. Maclean). Cambridge University Press, Cambridge.
- COWIE, R. H., RÉGNIER, C., FONTAINE, B. & BOUCHET, P. (2017). Measuring the Sixth Extinction: what do mollusks tell us? The Nautilus 131, 3–41.
- CRAIG, D. A. & PORCH, N. (2013). Subfossils of extinct and extant species of Simuliidae (Diptera) from Austral and Cook Islands (Polynesia): anthropogenic extirpation of an aquatic insect? *Zootaxa* 3641(4), 448–462.
- CRONK, Q. (2016). Plant extinctions take time. Science 353(6298), 446–447.
- CRUTZEN, P. J. (2002). Geology of mankind. Nature 415, 23.
- CRUTZEN, P. J. & STOERMER, E. F. (2000). The "Anthropocene". Global Change Newsletter 41, 17–18.
- CZEKANSKI-MOIR, J. & RUNDELL, R. J. (2020). Endless forms most stupid, icky, and small: the preponderance of noncharismatic invertebrates as integral to a biologically sound view of life. *Ecology and Evolution* 10, 12638–12649.
- Dasgupta, P. S. & Ehrlich, P. R. (2019). Why we're in the Sixth Great Extinction and what it means to humanity. In *Biological Extinction: New Perspectives* (eds P. Dasgupta, P. H. Raven and A. L. McIvor), pp. 262–284. Cambridge University Press, Cambridge.
- Deer, J. (2019). Quenched: five fires for thinking extinction. Oxford Literary Review 41, 1–17.
- DESQUILBET, M., GAUME, L., GRIPPA, M., CÉRÉGHINO, R., HUMBERT, J. F., BONMATIN, J. M., CORNILLON, P. A., MAES, D., VAN DYCK, H. & GOULSON, D.

(2020). Comment on "Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances". Science 370(6523), eabd8947.

- De Vos, J. M., Joppa, L. N., Gittleman, J. L., Stephens, P. R. & Pimm, S. L. (2015). Estimating the normal background rate of species extinction. *Conservation Biology* 29(2), 452–462.
- DE WEERDT, W. H. & GLYNN, P. W. (1991). A new and presumably now extinct species of *Millepora* (Hydrozoa) in the eastern Pacific. *Zoologische Mededelingen* **65**(20), 267–276.
- DIAMOND, J. M. (1987). Extant unless proven extinct? Or, extinct unless proven extant? Conservation Biology 1, 77–79.
- DIAMOND, J. M. (1989). The present, past and future of human-caused extinctions. Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences 325(1228), 469–477.
- DÍAZ, J. M., GAST, F. & TORRES, D. C. (2009). Rediscovery of a Caribbean living fossil: Pholadomya candida G. B. Sowerby I, 1823 (Bivalvia: Anomalodesmata: Pholadomyoidea). The Nautilus 123(1), 19–20.
- DIJKSTRA, K.-D. B. (2016). Restore our sense of species. Nature 533, 172–174.
- DING, C., JIANG, X., XIW, Z. & BROSSE, S. (2017). Seventy-five years of biodiversity decline of fish assemblages in Chinese isolated plateau lakes: widespread introductions and extirpations of narrow endemics lead to regional loss of dissimilarity. *Diversity and Distributions* 23, 171–184.
- DIRZO, R., YOUNG, H. S., GALETTI, M., CEBALLOS, G., ISAAC, N. J. B. & COLLEN, B. (2014). Defaunation in the Anthropocene. *Science* 345, 401–406.
- DONG, Y.-W., HUANG, X.-W. & REID, D. C. (2015). Rediscovery of one of the very few 'unequivocally extinct' species of marine molluses: *Littoraria flammea* (Philippi, 1847) lost, found — and lost again? *Journal of Molluscan Studies* 81(3), 313–321.
- Dunn, R. R. (2005). Modern insect extinctions, the neglected majority. *Conservation Biology* 19, 1030–1036.
- DUNN, R. R., HARRIS, N. C., COLWELL, R. K., KOH, L. P. & SODHI, N. S. (2009). The sixth mass coextinction: are most endangered species parasites and mutualists? *Proceedings of the Royal Society B* 276, 3037–3045.
- Durden, C. J. (1966). Lake deposits in central Colorado and a new fossil insect locality. $Journal\ of\ Paleontology\ 40(1),\ 215-219.$
- EISENHAUER, N., BONN, A. & GUERRA, C. A. (2019). Recognizing the quiet extinction of invertebrates. Nature Communications 10, 1–3.
- ELIAS, S. A. (1991). Insects and climate change. Fossil evidence from the Rocky Mountains. BioScience 41(8), 552–559.
- ELPHICK, C. S., ROBERTS, D. L. & REED, J. M. (2010). Estimated dates of recent extinctions for North American and Hawaiian birds. *Biological Conservation* 143(3), 617–624.
- ENGEL, M. S., CERÍACO, L. M. P., DANIEL, G. M., DELLAPÉ, P. M., LÖBL, I., MARINOV, M., REIS, R. E., YOUNG, M. T., DUBOIS, A., AGARWAL, A., LEHMANN, A.,. P., ALVARADO, M., ALVAREZ, N., ANDREONE, F., ARAUJO-VIEIRA, K., et al. (2021). The taxonomic impediment: a shortage of taxonomists, not the lack of technical approaches. Zoological Journal of the Linnean Society 193, 381–387.
- ERWIN, D. H. (2014). Temporal acuity and the rate and dynamics of mass extinctions. Proceedings of the National Academy of Sciences of the United States of America 111, 3203–3204.
- ESSL, F., MOSER, D., DIRNBÖCK, T., DULLINGER, S., MILASOWSZKY, N., WINTER, M. & RABITCH, W. (2013). Native, alien, endemic, threatened, and extinct species diversity in European countries. *Biological Conservation* 164, 90–97.
- FAN, P.-F., YANG, L., LIU, Y. & LEE, T. M. (2020). Build up conservation research capacity in China for biodiversity governance. *Nature Ecology & Evolution* 4, 162–167.
- FATTORINI, S. & BORGES, P. A. V. (2012). Species-area relationships underestimate extinction rates. Acta Oecologica 40, 27–30.
- FERNANDES, A. M. (2013). Fine-scale endemism of Amazonian birds in a threatened landscape. Biodiversity and Conservation 22(11), 2683–2694.
- Ferreira, R. L., Giribet, G., Du Preez, G., Ventouras, O., Janion, C. & Silva, M. S. (2020). The Wynberg cave system, the most important site for cave fauna in South Africa at risk. *Subterranean Biology* **36**, 73–81.
- FIGUEIREDO, L., KRAUSS, J., STEFFAN-DEWENTER, I. & CABRAL, J. S. (2019). Understanding extinction debts: spatio-temporal scales, mechanisms and a roadmap for future research. *Ecography* 42, 1973–1990.
- FISCHER, E. & RAHELIVOLOLONA, M. E. (2002). New taxa of *Impatiens* (Balsaminaceae) from Madagascar. I. Adansonia 24(2), 271–294.
- Fontaine, B., Bouchet, P., Van Achterberg, K., Alonso-Zarazaga, M. A., Araujo, R., Asche, M., Aspöck, U., Audisio, P., Aukema, B., Bailly, N., Balsamo, M., Bank, R. A., Barnard, P., Belfiore, C., Bogdanowicz, W., et al. (2007). The European Union's 2010 target: putting rare species in focus. Biological Conservation 139, 167–185.
- FONTAINE, B., PERRARD, A. & BOUCHET, P. (2012). 21 years of shelf life between discovery and description of new species. Current Biology 22(22), R943–R944.
- FOX, R., HARROWER, C. A., BELL, J. R., SHORTALL, C. R., MIDDLEBROOK, I. & WILSON, R. J. (2019). Insect population trends and the IUCN Red List process. *Journal of Insect Conservation* 23(2), 269–278.

FREYHOF, J. & KOTTELAT, M. (2008). Coregonus oxyrinchus. The IUCN Red List of Threatened Species 2008: e.T5380A11126034. Electronic file available at https://doi.org/10.2305/IUCN.UK.2008.RLTS.T5380A11126034.en. Accessed 22.07.2020.

- GASTON, K. J. & BLACKBURN, T. M. (1996). Range size–body size relationships: evidence of scale dependence. Oikos 75, 479–485.
- GERLACH, J. (2016). Icons of Evolution: Pacific Island Tree-Snails of the Family Partulidae. Phelsuma Press, Cambridge.
- GLYNN, P. W. & FEINGOLD, J. S. (1992). Hydrocoral species not extinct. Science 257(5078), 1845.
- GRAVILI, C., BEVILACQUA, S., TERLIZZI, A. & BOERO, F. (2015). Missing species among Mediterranean non-Siphonophoran Hydrozoa. *Biodiversity and Conservation* 24, 1329–1357.
- Hallmann, C. A., Sorg, M., Jongejans, E., Siepel, H., Hofland, N., Schwan, H., Stenmans, W., Müller, A., Sumser, H., Hörren, T., Goulson, D. & de Kroon, H. (2017). More than 75 percent decline over 27 years in total flying insect biomass in protected areas. *PLoS One* 12(10), e0185809.
- HANSSON, S. O. (2017). Science denial as a form of pseudoscience. Studies in History and Philosophy of Science 63, 39–47.
- HARCOURT, A. H. (2016). Human phylogeography and diversity. Proceedings of the National Academy of Sciences of the United States of America 113(29), 8072–8078.
- HARPER, D. A. T., HAMMARLUND, E. U. & RASMUSSEN, C. M. Ø. (2014). End Ordovician extinctions: a coincidence of causes. Gondwana Research 25, 1294–1307.
- He, F. & Hubbell, S. (2013). Estimating extinction from species-area relationships: why the numbers do not add up. *Ecology* 94, 1905–1912.
- HEDGES, S. B. & CONN, C. E. (2012). A new skink fauna from Caribbean islands (Squamata, Mabuyidae, Mabuyinae). Zootaxa 3288, 1–244.
- Helgen, K. M., Helgen, L. E. & Wilson, D. E. (2009). Pacific flying foxes (Mammalia: Chiroptera): two new species of *Pteropus* from Samoa, probably extinct. *American Museum Novitates* 3646, 1–37.
- Henehan, M. J., Hull, P. M., Penman, D. E., Rae, J. & Schmidt, D. N. (2016). Biogeochemical significance of pelagic ecosystem function: an end-Cretaceous case study. *Philosophical Transactions of the Royal Society B* **371**, 20150510.
- HENN, B. M., CAVALLI-SFORZA, L. L. & FELDMAN, M. W. (2012). The great human expansion. Proceedings of the National Academy of Sciences of the United States of America 109(44), 17758–17764.
- Hershkovitz, I., Weber, G. W., Quam, R., Duval, M., Grün, R., Kinsley, L., Ayalon, A., Bar-Matthews, M., Valladas, H., Mercier, N., Arsuaga, J. L., Martinón-Torres, M., Bermúdez de Castro, J. M., Fornai, C., Martín-Francés, L., et al. (2018). The earliest modern humans outside Africa. Science 359, 456–459.
- HERSHLER, R., LIU, H.-P. & HOWARD, J. (2014). Springsnails: a new conservation focus in western North America. BioScience 64, 693–700.
- Heywood, V. H. & Stuart, S. N. (1992). Species extinctions in tropical forests. In *Tropical Deforestation and Species Extinction* (eds T. C. Whitmore and J. A. Sayer), pp. 91–117. Chapman & Hall, London.
- HOLDEN, A. R., SOUTHON, J. R., WILL, K., KIRBY, M. E., AALBU, R. L. & MARKEY, M. J. (2017). A 50,000 year insect record from Rancho La Brea, Southern California: insights into past climate and fossil deposition. *Quaternary Science Reviews* 168, 123–136.
- HULL, P. M. (2015). Life in the aftermath of mass extinctions. Current Biology 25, R941–R952.
- HULL, P. M., DARROCH, S. A. F. & ERWIN, D. H. (2015). Rarity in mass extinctions and the future of ecosystems. *Nature* 528, 345–351.
- HULL, P. M., BORNEMANN, A., PENMAN, D. E., HENEHAN, M. J., NORRIS, R. D., WILSON, P. A., BLUM, P., ALEGRET, L., BATENBURG, S. J., BOWN, P. R., BRALOWER, T. J., COURNEDE, C., DEUTSCH, A., DONNER, B., FRIEDRICH, O., et al. (2020). On impact and volcanism across the Cretaceous-Paleogene boundary. Science 367, 266–272.
- Humphreys, A. M., Govaerts, R., Ficinski, S. Z., Lughadha, E. N. & Vorontsova, M. S. (2019). Global dataset shows geography and life form predict modern plant extinction and rediscovery. *Nature Ecology & Evolution* 3, 1043–1047.
- IISE (2012). Retro SOS 2000–2009, a Decade of Species Discovery in Review. International Institute for Species Exploration, Tempe.
- IPBES (2019). Summary for Policymakers of the Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. IPBES secretariat, Bonn.
- ISAAC, N. B. J., TURVEY, S. T., COLLEN, B., WATERMAN, C. & BAILLIE, J. E. M. (2007). Mammals on the EDGE: conservation priorities based on threat and phylogeny. PLoS One 2, e296.
- IUCN [INTERNATIONAL UNION FOR CONSERVATION OF NATURE] (2012). IUCN Red List Categories and Criteria. Version 3.1, 2nd Edition. IUCN, Gland and Cambridge.
- IUCN [INTERNATIONAL UNION FOR CONSERVATION OF NATURE] STANDARDS AND PETITIONS SUBCOMMITTEE (2019). Guidelines for Using the IUCN Red List Categories and Criteria. Version 14. IUCN, Gland.

IUCN [INTERNATIONAL UNION FOR CONSERVATION OF NATURE] (2020). The IUCN Red List of Threatened Species. Version 2020-2. IUCN, Gland.

- Jäch, M. A. & Balke, M. (2008). Global diversity of water beetles (Colcoptera) in freshwater. Hydrobiologia 595, 419–442.
- JACKSON, J. B. C., KIRBY, M. X., BERGER, W. H., BJORNDAL, K. A., BOTSFORD, L. W., BOURQUE, B. J., BRADBURY, R. H., COOKE, R., ERLANDSON, J., ESTES, J. A., HUGHES, T. P., KIDWELL, S., LANGE, C. B., LENIHAN, H. S., PANDOLFI, J. M., et al. (2001). Historical overfishing and the recent collapse of coastal ecosystems. Science 293(5530), 629–637.
- JAMES, H. F. & OLSON, S. L. (1991). Descriptions of thirty-two new species of Hawaiian birds: part II. Passeriformes. Ornithological Monographs 46, 1–88.
- JANZEN, D. H. (2001). Latent extinction the living dead. Encyclopedia of Biodiversity 4, 590–598
- JONES, H. P., HOLMES, N. D., BUTCHART, S. H. M., TERSHY, B. R., KAPPES, P. J., CORKERY, I., AGUIRRE-MUÑOZ, A., ARMSTRONG, D. P., BONNAUD, E., BURBIDGE, A. A., CAMPBELL, K., COURCHAMP, F., COWAN, P. E., CUTHBERT, R. J., EBBERT, S., et al. (2016). Invasive mammal eradication on islands results in substantial conservation gains. Proceedings of the National Academy of Sciences of the United States of America 113(15), 4033–4038.
- JYLHÄ, K. M. (2018). Denial versus reality of climate change. In Encyclopedia of the Anthropocene Volume 2 (eds D. A. Dellasala and M. I. Goldstein), pp. 487–492. Elsevier, Oxford.
- KAREIVA, P. & MARVIER, M. (2007). Conservation for the people. Scientific American 297(4), 50–57.
- KAREIVA, P. & MARVIER, M. (2012). What is conservation science? BioScience 62(11), 962–969.
- KAREIVA, P., LALASZ, R. & MARVIER, M. (2011). Conservation in the Anthropocene. Beyond solitude and fragility. Breakthrough Journal 2, 29–37.
- KEITH, D. A., BUTCHART, S. H. M., REGAN, H. M., HARRISON, I., AKCAKAYA, H. R., SOLOW, A. R. & BURGMAN, M. A. (2017). Inferring extinctions I: a structured method using information on threats. *Biological Conservation* 214, 320–327.
- KOLBERT, E. (2014). The Sixth Extinction. An Unnatural History. Henry Holt and Company, New York.
- KOROVCHINSKY, N. M. & PETKOVSKI, T. K. (2014). The ancient Balkan lakes harbor a new endemic species of *Diaphanosoma* Fischer, 1850 (Crustacea: Branchiopoda: Cladocera). *Zootaxa* 3784(5), 539–549.
- Lacher, T. E. & Hilton-Taylor, C. (2018). The IUCN Red List: assessing extinction risk in the Anthropocene. In *Encyclopedia of the Anthropocene. Volume 2* (eds D. A. Dellasala and M. I. Goldstein), pp. 333–339. Elsevier, Oxford.
- LAMKIN, M. & MILLER, A. I. (2016). On the challenge of comparing contemporary and deep-time biological-extinction rates. BioScience 66(9), 785–789.
- LAST, P. R., EDGAR, G. & STUART-SMITH, R. (2020). Sympterichthys unipennis. The IUCN Red List of Threatened Species 2020: e.T123423283A123424374. Electronic file available at https://doi.org/10.2305/IUCN.UK.2020-1.RLTS. T123423283A123424374.en. Accessed 21.07.2020.
- LAURANCE, W. F. (2019). The Anthropocene. Current Biology 29, R953-R954.
- Leakey, R. & Lewin, R. (1995). The Sixth Extinction: Patterns of Life and the Future of Humankind. Doubleday, New York.
- LEATHER, S. R. (2017). "Ecological Armageddon" more evidence for the drastic decline in insect numbers. Annals of Applied Biology 172(1), 1–3.
- Lees, A. C., Attwood, S., Barlow, J. & Phalan, B. (2020). Biodiversity scientists must fight the creeping rise of extinction denial. *Nature Ecology & Evolution* 4, 1440–1443.
- Lees, A. C. & Pimm, S. L. (2015). Species extinct before we know them? *Current Biology* **25**(5), R177–R180.
- LEITE, Y. L. R., KOK, P. J. R. & WEKSLER, M. (2015). Evolutionary affinities of the 'Lost World' mouse suggest a late Pliocene connection between the Guiana and Brazilian shields. *Journal of Biogeography* **42**, 706–715.
- Lenton, T. M. (2019). Biodiversity and global change. From Creator to victim. In *Biological Extinction: New Perspectives*, (eds P. Dasgupta, P. H. Raven & A. L. McIvor), pp. 34–79. Cambridge University Press, Cambridge.
- Leung, B., Hargreaves, A. L., Greenberg, D. A., McGill, B., Dornelas, M. & Freeman, R. (2020). Clustered versus catastrophic global vertebrate declines. *Nature* **588**(7837), 267–271.
- LEWIS, O. T. (2006). Climate change, species-area curves and the extinction crisis. Philosophical Transactions of the Royal Society B 361, 163–171.
- Ling, M.-X., Zhan, R.-B., Wang, G.-X., Wang, Y., Amelin, Y., Tang, P., Liu, J.-B., Jin, J., Huang, B., Wu, R.-C., Xue, S., Fu, B., Bennett, V. C., Wei, X., Luan, X.-C., et al. (2019). An extremely brief end Ordovician mass extinction linked to abrupt onset of glaciation. Solid Earth Sciences 4, 190–198.
- LIVEZEY, B. C. (2003). Evolution of flightlessness in rails (Gruiformes: Rallidae): phylogenetic, ecomorphological, and ontogenetic perspectives. *Ornithological Monographs* **53**, 1–654.
- LOEHLE, C. & ESCHENBACH, W. (2012). Historic bird and mammal extinction: rates and causes. *Diversity and Distributions* 18, 84–91.

LOMBORG, B. (2001). The Skeptical Environmentalist: Measuring the Real State of the World. Cambridge University Press, Cambridge.

- LÓPEZ, S., VAN DORP, L. & HELLENTHAL, G. (2015). Human dispersal out of Africa: a lasting debate. Evolutionary Bioinformatics 11(Suppl. 2), 57–68.
- LÓPEZ-CORONA, O. & MAGELLANES-GUIJÓN, G. (2020). It is not an Anthropocene; it is really the Technocene: names matter in decision making under planetary crisis. Frontiers in Ecology and Evolution 8, 214.
- LOWRY, M. S., CONDIT, R., HATFIELD, B., ALLEN, S. G., BERGER, R., MORRIS, P. A., LE BOEUF, B. J. & REITER, J. (2014). Abundance, distribution, and population growth of the northern elephant seal (*Mirounga angustirostris*) in the United States from 1991 to 2010. *Aquatic Mammals* 40(1), 20–31.
- MACE, G. M. (1994). Classifying threatened species: means and ends. *Philosophical Transactions of the Royal Society B* 344, 91–97.
- MACLEOD, N. (2014). The geological extinction record: history, data, biases, and testing. In Volcanism, Impacts, and Mass Extinctions: Causes and Effects. Geological Society of America Special Paper 505 (eds G. Keller and A. C. Kerr), pp. 1–28. Geological Society of America, Boulder.
- Malhi, Y. (2017). The concept of the Anthropocene. Annual Review of Environment and Resources 42, 77–104.
- MALHI, Y., DOUGHTY, C. E., GALETTI, M., SMITH, F. A., SVENNING, J.-C. & TERBORGH, J. W. (2016). Megafauna and ecosystem function from the Pleistocene to the Anthropocene. Proceedings of the National Academy of Sciences of the United States of America 113(4), 838–846.
- MANNE, L. L., BROOKS, T. M. & PIMM, S. L. (1999). Relative risk of extinction of passerine birds on continents and islands. *Nature* 399, 258–261.
- MASOOD, E. (2018). Battle over biodiversity. An ideological clash could undermine a crucial assessment of the world's disappearing plant and animal life. *Nature* 560, 423–425.
- MATEO, P., KELLER, G., PUNEKAR, J. & SPANGENBERG, J. E. (2017). Early to late Maastrichtian environmental changes in the Indian Ocean compared with Tethys and South Atlantic. *Palaeogeography, Palaeoclimatology, Palaeoecology* 478, 121–138.
- MATISOO-SMITH, E. & DAUGHERTY, C. (2012). Africa to Aotearoa: the longest migration. Journal of the Royal Society of New Zealand 42(2), 87–92.
- MAWDSLEY, N. A. & STORK, N. E. (1995). Species extinctions in insects: ecological and biogeographical considerations. In *Insects in a Changing Environment* (eds R. Harrington and N. E. Stork), pp. 322–369. Academic Press, London.
- McCallum, M. L. (2007). Amphibian decline or extinction? Current declines dwarf background extinction rate. Journal of Herpetology 41(3), 483–491.
- McCallum, M. L. (2015). Vertebrate biodiversity losses point to a sixth mass extinction. *Biodiversity and Conservation* 24, 2497–2519.
- McKinney, M. L. (1999). High rates of extinction and threat in poorly studied taxa. Conservation Biology 13(6), 1273–1281.
- MEINE, C. (2018). Biodiversity conservation. In Encyclopedia of the Anthropocene Volume 2 (eds D. A. DellaSala and M. I. Goldstein), pp. 205–214. Elsevier, Oxford.
- Meiri, S., Bauer, A. M., Allison, A., Castro-Herrera, F., Chirio, L., Colli, G., Das, I., Doan, T. M., Glaw, F., Grismer, L. L., Hoogmoed, M., Kraus, F., Lebreton, M., Meirte, D., Nagy, Z. T., et al. (2018). Extinct, obscure or imaginary: the lizard species with the smallest ranges. *Diversity and Distributions* 24, 262–273.
- MERCKX, V. S. F. T., HENDRIKS, K. P., BEENTJES, K. K., MENNES, C. B., BECKING, L. E., PEIJNENBURG, K. T. C. A., AFENDY, A., ARUMUGAM, N., DE BOER, H., BIUN, A., BUANG, M. M., CHEN, P. P., CHUNG, A. Y. C., DOW, R., FEIJEN, F. A. A., *et al.* (2015). Evolution of endemism on a young tropical mountain. *Nature* 524, 347–350.
- MELTZER, D. J. (2020). Overkill, glacial history, and the extinction of North America's ice age megafauna. Proceedings of the National Academy of Sciences of the United States of America 117(46), 28555–28563.
- MESIBOV, R. (2004). Spare a thought for the losers. Australian Zoologist 32(4), 505–507.
 MIDDLETON, D (2017). The Carbon-Fed "Sixth Mass Genesis" An Anthropocene Success Story! Electronic file available at https://wattsupwiththat.com/2017/07/14/the-carbon-fed-sixth-mass-genesis-an-anthropocene-success-story/. Accessed 21 09 2018
- MOLDOVAN, O. T., IEPURE, S., BRAD, T., KENESZ, M., MIREA, I. C. & NĂSTASE-BUCUR, R. (2020). Database of Romanian cave invertebrates with a Red List of cave species and a list of hotspot/coldspot caves. *Biodiversity Data Journal* 8, e53571.
- MOLINA, E. (2015). Evidence and causes of the main extinction events in the Paleogene based on extinction and survival patterns of Foraminifera. *Earth-Science Reviews* 140, 166–181.
- MOLLUSCABASE EDITORS (2021). MolluscaBase. Electronic file available at http://www.molluscabase.org Accessed 13.10.2021.
- MONTE-LUNA, P., DEL, LLUCH-BELDA, D., SERVIERE-ZARAGOZA, E., CARMONA, R., REYES-BONILLA, H., AURIOLES-GAMBOA, D., CASTRO-AGUIRRE, J. L., GUZMÁN DEL PRÓO, S. A., TRUJILLO-MILLÁN, O. & BROOK, B. W. (2007). Marine extinctions revisited. Fish and Fisheries 8(2), 107–122.

- MOORE, R. (2014). In Search of Lost Frogs. Firefly Books, Richmond Hill.
- Mora, C., Tittensor, D. P., Adl, S., Simpson, A. G. B. & Worm, B. (2011). How many species are there on Earth and in the ocean? *PLoS Biology* **9**(8), e1001127.
- MURPHY, M. P., ADAMS, A. & AUSTIN, A. D. (2009). Independent colonization and extensive cryptic speciation of freshwater amphipods in the isolated groundwater springs of Australia's Great Artesian Basin. *Molecular Ecology* 18, 109–122.
- Myers, N. (2003). Biodiversity hotspots revisited. BioScience 53(10), 916–917.
- MYERS, N., MITTERMEIER, R. A., MITTERMEIER, C. G., DA FONSECA, G. A. & KENT, J. (2000). Biodiversity hotspots for conservation priorities. *Nature* 403(6772), 853–858.
- MYERS, R. A. & WORM, B. (2003). Rapid worldwide depletion of predatory fish communities. Nature 423, 280–283.
- NATIONAL PARK SERVICE (2018). Bachman's Warbler Searches at Congaree National Park. Electronic file available at https://www.nps.gov/rlc/ogbfrec/bachmans.htm. Accessed 21.04.2021.
- New, T. R. (1997). Neuroptera of Australia: faunal elements, diversity and relationships. Deutsche Entomologische Zeitschrift 44, 259–265.
- NIEMINEN, P., RYÖKÄS, E. & MUSTONEN, A.-M. (2015). Experiential thinking in creationism—a textual analysis. *PLoS One* **10**(3), e0118314.
- OLSON, S. L. & JAMES, H. F. (1991). Descriptions of thirty-two new species of birds from the Hawaiian Islands: part I. Non-Passeriformes. Omithological Monographs 45, 1–88.
- ORIHUELA, J., VIÑOLA, L. W., VÁZQUEZ, O. J., MYCHAJLIW, A. M., DE LARA, O. H., LORENZO, L. & CENTENO, J. A. (2020). Assessing the role of humans in Greater Antillean land vertebrate extinctions: new insights from Cuba. *Quaternary Science Reviews* 249, 106597.
- PAULY, D. (1995). Anecdotes and the shifting baseline syndrome of fisheries. Trends in Ecology and Evolution 10(10), 430.
- PAULY, D., WATSON, R. & ALDER, J. (2005). Global trends in world fisheries: impacts on marine ecosystems and food security. *Philosophical Transactions of the Royal Society B* 360, 5–12.
- Penz, C., Simonsen, T. J. & Devries, P. (2011). A new *Orobrassolis* butterfly (Nymphalidae, Brassolini): a casualty of habitat destruction. *Zootaxa* **2740**, 35–43.
- PETERS, H., O'LEARY, B. C., HAWKINS, J. P., CARPENTER, K. E. & ROBERTS, C. M. (2013). Conus: first comprehensive conservation Red List assessment of a marine gastropod mollusc genus. PLoS One 8(12), e83353.
- PIMM, S. L., JENKINS, C. N., ABELL, R., BROOKS, R. M., GITTLEMAN, J. L., JOPPA, L. N., RAVEN, P. H., ROBERTS, C. M. & SEXTON, J. O. (2014). The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344(6187), 1246752.
- PIMM, S. L., MOULTON, M. P. & JUSTICE, L. J. (1994). Bird extinctions in the central Pacific. *Philosophical Transactions of the Royal Society, London, B* **344**, 27–33.
- Pacific. Philosophical Transactions of the Royal Society, London, B 344, 27–33.
 PIMM, S. L. & RAVEN, P. H. (2000). Biodiversity: extinction by numbers. Nature 403(6772), 343–845.
- PIMM, S. L. & RAVEN, P. H. (2019). The state of the World's biodiversity. In *Biological Extinction: New Perspectives* (eds P. DASGUPTA, P. H. RAVEN and A. L. McIVOR), pp. 80–112. Cambridge University Press, Cambridge.
- PIMM, S., RAVEN, P., PETERSON, A., ŞEKERCIOĞLU, Ç. H. & EHRLICH, P. H. (2006). Human impacts on the rates of recent, present, and future bird extinctions. Proceedings of the National Academy of Sciences of the United States of America 103(29), 10941–10946.
- PIMM, S. L., RUSSELL, G. J., GITTLEMAN, J. L. & BROOKS, T. M. (1995). The future of biodiversity. Science 269, 347–350.
- PLATT, J. R. (2019). Rise of the extinction deniers. Electronic file available at https:// blogs.scientificamerican.com/extinction-countdown/rise-of-the-extinction-deniers/ . Accessed 3.10.2021.
- PLOTNICK, R. E., SMITH, F. A. & LYONS, S. K. (2016). The fossil record of the sixth extinction. *Ecology Letters* **19**, 546–553.
- POINAR, G. O. Jr. (1993). Insects in amber. Annual Review of Entomology 38(1), 145-159.
- PONDER, W. F. & CLARK, G. A. (1990). A radiation of hydrobiid snails in threatened artesian springs in western Queensland. Records of the Australian Museum 42(3), 301–363.
- PORCH, N. & SMITH, T. R. (2017). New Pycnomerus Erichson (Coleoptera: Zopheridae: Pycnomerini) from Rimatara, French Polynesia. Zootaxa 4237(1), 154–166.
- Prathapan, K. D., Pethiyagoda, R., Bawa, K. S., Raven, P. H., Rajan, P. D., Acosta, L. E., Adams, B., Adl, S., Ahyon, S. T., Anderson, R., Arango, C. P., Arnedo, M. A., Arbruster, J. W., Avila, L. J., Azevedo, C. O., et al. (2018). When the cure kills CBD limits biodiversity research. Science 360(6396), 1405–1406.
- Pyron, R. A. (2017). We don't need to save endangered species. Extinction is part of evolution. The Washington Post, 22 November 2017. Electronic file available at https://www.washingtonpost.com/outlook/we-dont-need-to-save-endangered species-extinction-is-part-of-evolution/2017/11/21/57fc5658-cdb4-11e7-a1a3-0d1e45a6de3d_story.html?utm_term=.c21c77675200. Accessed 23.08.2018.
- RBG Kew (2016). The State of the World's Plants Report 2016. Royal Botanic Gardens, Kew.
- REDDING, D. W. & MOOERS, A. Ø. (2006). Incorporating evolutionary measures into conservation prioritization. *Conservation Biology* **20**(6), 1670–1678.
- RÉGNIER, C., FONTAINE, B. & BOUCHET, P. (2009). Not knowing, not recording, not listing: numerous unnoticed mollusk extinctions. *Conservation Biology* 23, 1214–1221.

- RÉGNIER, C., ACHAZ, G., LAMBERT, A., COWIE, R. H., BOUCHET, P. & FONTAINE, B. (2015a). Mass extinction in poorly known taxa. Proceedings of the National Academy of Sciences of the United States of America 112(25), 7761–7766.
- RÉGNIER, C., BOUCHET, P., HAYES, K. A., YEUNG, N. W., CHRISTENSEN, C. C., CHUNG, D. J. D., FONTAINE, B. & COWIE, R. H. (2015b). Extinction in a hyperdiverse endemic Hawaiian land snail family and implications for the underestimation of invertebrate extinction. *Conservation Biology* 29(6), 1715–1723.
- REJMÁNEK, M. (2018). Vascular plant extinctions in California: a critical assessment. Diversity and Distributions 24(1), 129–136.
- RENNE, P. T., DEINO, A. L., HILGEN, F. J., KUIPER, K. F., MARK, D. F., MITCHELL, W. S. III, MORGAN, L. E., MUNDIL, R. & SMIT, J. (2013). Time scales of critical events around the Cretaceous-Paleogene boundary. *Science* 339, 684–687.
- RICCIARDI, A. & RYAN, R. (2018a). Invasive species denialism revisited: response to Sagoff. Biological Invasions 20, 2731–2738.
- RICCIARDI, A. & RYAN, R. (2018b). The exponential growth of invasive species denialism. *Biological Invasions* 20, 549–553.
- RICHLING, I. & BOUCHET, P. (2013). Extinct even before scientific recognition: a remarkable radiation of helicinid snails (Helicinidae) on the Gambier Islands, French Polynesia. Biodiversity and Conservation 22, 2433–2468.
- RIETH, T. M., HUNT, T. L., LIPO, C. & WILMSHURST, J. M. (2011). The 13th century Polynesian colonization of Hawai'i [sic] Island. *Journal of Archaeological Science* 38, 2740–2749.
- Říhová, D., Janovský, Z., Horsák, M. & Juričková, L. (2018). Shell decomposition rates in relation to shell size and habitat conditions in contrasting types of Central European forests. *Journal of Molluscan Studies* 84(1), 54–61.
- RIPPLE, W. J., WOLF, C., NEWSOME, T. M., GALETTI, M., ALAMGIR, M., CRIST, E. & 15,364 SCIENTIST SIGNATORIES FROM 184 COUNTRIES (2017). World scientists' warning to humanity: a second notice. *BioScience* 67(12), 1026–1028.
- ROBERTS, C. M. & HAWKINS, J. P. (1999). Extinction risk in the sea. Trends in Ecology and Evolution 14(6), 241–246.
- ROBERTS, D. L. & JARIĆ, I. (2016). Inferring extinction in North American and Hawaiian birds in the presence of sighting uncertainty. *PeerJ* **4**, e2426.
- ROCHA-ORTEGA, M., RODRIGUEZ, P. & CÓRDOBA-AGUILAR, A. (2021). Geographical, temporal and taxonomic biases in insect GBIF data on biodiversity and extinction. *Ecological Entomology* **46**(4), 718–728.
- RODRIGUES, A. S. L., PILGRIM, J. D., LAMOREUX, J. F., HOFFMANN, M. & BROOKS, T. M. (2006). The value of the IUCN Red List for conservation. *Trends in Ecology and Evolution* 21(2), 71–76.
- ROLSTON, H. III (2018). Endangered species and biodiversity. In *Encyclopedia of the Anthropocene. Volume 2* (eds D. A. DellaSala and M. I. Goldstein), pp. 199–203. Elsevier, Oxford.
- ROSENBERG, G. (2014). A new critical estimate of named species level diversity of the Recent Mollusca. American Malacological Bulletin 32, 308–322.
- ROSKOV, Y., OWER, G., ORRELL, T., NICOLSON, D., BAILLY, N., KIRK, P. M., BOURGOIN, T., DEWALT, R. E., DECOCK, W., NIEUKERKEN, E. VAN & PENEY, L., EDS. (2019). Species 2000 & ITIS Catalogue of Life, 2019 Annual Checklist. Species 2000: Naturalis, Leiden. Electronic file available at www.catalogueoflife. org/annual-checklist/2019
- ROSSINI, R. A., FENSHAM, R. J., STEWART, B., GOTCH, K. T. & KENNARD, M. J. (2018). Biogeographical patterns of endemic diversity and its conservation in Australia's artesian desert springs. *Diversity and Distributions* 24, 1199–1216.
- Rózsa, L. & Vas, Z. (2015). Co-extinct and critically co-endangered species of parasitic lice, and conservation-induced extinction: should lice be reintroduced to their hosts? Onv 49(1), 107–110.
- RUBINOFF, D. (2017). Hawaiian Lepidoptera represent remarkable diversity that is disappearing before it can be discoverered [sic]. News of The Lepidopterists' Society 59(4), 202–204.
- RULL, V., VEGAS-VILARRÚBIA, T., HUBER, H. & SEÑARIS, C. (2019). Biodiversity of Pantepui: The Pristine "Lost World" of the Neotropical Guiana Highlands. Academic Press, London.
- RUTJENS, B. T., VAN DER LINDEN, S. & VAN DER LEE, R. (2021). Science skepticism in times of COVID-19. Group Processes & Intergroup Relations 24(2), 276–283.
- RYBICKI, J. & HANSKI, I. (2013). Species—area relationships and extinctions caused by habitat loss and fragmentation. *Ecology Letters* 16, 27–38.
- SALLAN, L. C. & COATES, M. I. (2010). End-Devonian extinction and a bottleneck in the early evolution of modern jawed vertebrates. Proceedings of the National Academy of Sciences of the United States of America 107, 10131–10135.
- SALTRÉ, F., CHADOEUF, J., PETERS, K. J., McDOWELL, M. C., FRIEDRICH, T., TIMMERMANN, A., ULM, S. & BRADSHAW, C. J. A. (2019). Climate-human interaction associated with southeast Australian megafauna extinction patterns. *Nature Communications* 10, 5311.
- SANDOM, C., FAURBY, S., SANDEL, B. & SVENNING, J. C. (2014). Global late Quaternary megafauna extinctions linked to humans, not climate change. Proceedings of the Royal Society B 281(1787), 20133254.
- SARTORI, A. F., GARGOMINY, O. & FONTAINE, B. (2013). Anthropogenic extinction of Pacific land snails: a case study of Rurutu, French Polynesia, with description of eight new species of endodontids (Pulmonata). Zootaxa 3640, 343–372.

SARTORI, A. F., GARGOMINY, O. & FONTAINE, B. (2014). Radiation and decline of endodontid land snails in Makatea, French Polynesia. *Zootaxa* 3772(1), 1–68.

- SCHEFFERS, B. R., JOPPA, L. N., PIMM, S. L. & LAURANCE, W. F. (2012). What we know and don't know about Earth's missing biodiversity. *Trends in Ecology & Evolution* 27, 501–510.
- SELLMAN, S., SÄTERBERG, T. & EBENMAN, B. (2016). Pattern of functional extinctions in ecological networks with a variety of interaction types. Theoretical Ecology 9, 83–94.
- SEPKOSKI, J. J., Jr. (1996). Patterns of Phanerozoic extinction: a perspective from global data bases. In Global Events and Event Stratigraphy in the Phanerozoic (ed. O. H. WALLISER), pp. 35–51. Springer, Berlin, Heidelberg.
- SHEEHAN, P. M. (2001). The Late Ordovician mass extinction. Annual Review of Earth and Planetary Science 29, 331–364.
- SHI, H., SINGH, A., KANT, S., ZHU, Z. & WALLER, E. (2005). Integrating habitat status, human population pressure, and protection status into biodiversity conservation priority setting. Conservation Biology 19(4), 1273–1285.
- SIMBERLOFF, D. (1992). Do species—area curves predict extinction in fragmented forest? In Tropical Deforestation and Species Extinction (eds T. C. Whitmore and J. A. SAYER), pp. 75–89. Chapman & Hall, London.
- SMITH, D. M. & MARCOT, J. D. (2015). The fossil record and macroevolutionary history of the beetles. Proceedings of the Royal Society B 282, 20150060.
- SMITH, D. M. & MOE-HOFFMAN, A. P. (2007). Taphonomy of Diptera in lacustrine environments: a case study from Florissant fossil beds, Colorado. *PALAIOS* 22, 623–629.
- SMITH, F. A., ELLIOT SMITH, R. E., LYONS, S. & PAYNE, J. L. (2018). Body size downgrading of mammals over the late Quaternary. Science 360, 310–313.
- SMITH, M. (2019). [A]wake for 'the passions of this earth': extinction and the absurd 'ethics' of novel ecosystems. Cultural Studies Review 25, 119–134.
- SOARES, P., RITO, T., TREJAUT, J., MORMINA, M., HILL, C., TINKLER-HUNDAL, E., BRAID, M., CLARKE, D. J., LOO, J.-H., THOMSON, N., DENHAM, T., DONOHUE, M., MACAULAY, V., LIN, M., OPPENHEIMER, S. et al. (2011). Ancient voyaging and Polynesian origins. American Journal of Human Genetics 88, 239–247.
- SOULÉ, M. E. (2013). The "New Conservation". Conservation Biology 27(5), 895–897.
 STEADMAN, D. W. (1995). Prehistoric extinction of Pacific island birds: biodiversity meets zooarchaeology. Science 267, 1123–1131.
- STELBRINK, B., SHIROKAYA, A. A., FÖLLER, K., WILKE, T. & ALBRECHT, C. (2016).
 Origin and diversification of Lake Ohrid's endemic acroloxid limpets: the role of geography and ecology. BMC Evolutionary Biology 16, 273.
- STORK, N. E. (1997). Measuring global biodiversity and its decline. In *Biodiversity II. Understanding and Protecting our Biological Resources* (eds M. L. Reaka-Kudla, D. E. Wilson and E. O. Wilson), pp. 41–68. Joseph Henry Press, Washington.
- STORK, N. E. (2010). Re-assessing current extinction rates. *Biodiversity and Conservation* 10, 357–371
- STORK, N. E. (2018). How many species of insects and other terrestrial arthropods are there on Earth? *Annual Review of Entomology* **63**, 31–45.
- there on Earth? Annual Review of Entomology **63**, 31–45.

 STUART, A. J. (1991). Mammalian extinctions in the late Pleistocene of northern Eurasia and North America. *Biological Reviews* **66**, 453–562.
- Sullivan, J. M., Constant, V. & Lubchenco, J. (2019). Extinction threats to life in the ocean and opportunities for their amelioration. In *Biological Extinction: New Perspectives* (eds P. Dasgupta, P. H. Raven and A. L. McIvor), pp. 113–137. Cambridge University Press, Cambridge.
- TAN, J. L. & HUA, B. (2008). The second species of the Chinese Panorpodidae (Mecoptera), Panorpodes brachypodus sp. nov. Zootaxa 1751, 59–64.
- TASSIN, J. (2014). La grande invasion. Qui a peur des espèces invasives?. Odile Jacob, Paris.
- TEDESCO, P. A., BIGORNE, R., BOGAN, A. E., GIAM, X., JÉZÉQUEL, C. & HUGUENY, B. (2014). Estimating how many undescribed species have gone extinct. Conservation Biology 28(5), 1360–1370.
- Tenorio, M. J., Abalde, S., Pardos-Blas, J. R. & Zardoya, R. (2020). Taxonomic revision of West African cone snails (Gastropoda: Conidae) based upon mitogenomic studies: implications for conservation. *European Journal of Taxonomy* **663**, 1–89.
- TER HALLE, A. & PEREZ, E. (2020). Plastic pollution at sea: the seventh continent. Encyclopedia of the Environment [online ISSN 2555-0950]. Electronic file available at https://www.encyclopedie-environnement.org/en/water/plastic-pollution-at-seaseventh-continent/. Accessed 21.07.2020.
- THOMAS, C. D. (2017). Inheritors of the Earth. How Nature Is Thriving in an Age of Extinction. Public Affairs, New York.
- Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., Erasmus, B. F. N., Ferreira de Siqueira, M., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A. S., Midgley, G. F., Miles, L., et al. (2004). Extinction risk from climate change. Nature 427, 145–148.
- Thomas, J. A., Telfer, M. G., Roy, D. B., Preston, C. D., Greenwood, J. J. D., Asher, J., Fox, R., Clarke, R. T. & Lawton, J. H. (2004). Comparative losses of British butterflies, birds, and plants and the global extinction crisis. *Science* **303**(5665), 1879–1881.

THOMPSON, C. J., KOSHKINA, V., BURGMAN, M. A., BUTCHART, S. H. & STONE, L. (2017). Inferring extinctions II: a practical, iterative model based on records and surveys. *Biological Conservation* 214, 328–335.

- TIAN, M. & DEUVE, T. (2007). Review of four species of the genus Brachinus Weber (Coleoptera: Caraboidea: Brachinidae) from the Philippines. Zootaxa 1546(1), 15–22.
- TILMAN, D., MAY, R. M., LEHMAN, C. L. & NOWAK, M. A. (1994). Habitat destruction and the extinction debt. *Nature* 371(6492), 65–66.
- TILMAN, D., CLARK, M., WILLIAMS, D. R., KIMMEL, K., POLASKY, S. & PACKER, C. (2017). Future threats to biodiversity and pathways to their prevention. *Nature* 546, 73–81.
- Tobias, J. (2019). Republicans aren't just climate deniers. They deny the extinction crisis, too. *The Guardian*, 23 May 2019. Electronic file available at https://www.theguardian.com/commentisfree/2019/may/23/republicans-arent-just-climate-deniers-they-deny-the-extinction-crisis-too. Accessed 5.10.2021.
- TOBIN, T. S., BITZ, C. M. & ARCHER, D. (2017). Modeling climatic effects of carbon dioxide emissions from Deccan Traps volcanic eruptions around the Cretaceous-Paleogene boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology* 478, 139–148.
- TONG, P. S. (2020). More policies and laws, is it better for biodiversity conservation in Malaysia? Conservation Science and Practice 2, e235.
- TRIANTIS, K. A., BORGES, P. A. V., LADLE, R. J., HORTAL, J., CARDOSO, P., GASPAR, C., DINIS, F., MENDONCA, E., SILVEIRA, L. M. A., GABRIEL, R., MELO, C., SANTOS, A. M. C., AMORIM, I. R., RIBEIRO, S. P., SERRANO, A. R. M., et al. (2010). Extinction debt on oceanic islands. *Ecography* 33, 285–294.
- Turvey, S. T. & Crees, J. J. (2019). Extinction in the Anthropocene. *Current Biology* 29, R982–R986.
- URBAN, M. C. (2015). Accelerating extinction risk from climate change. Science 348(6234), 571–573.
- VAN KLINK, R., BOWLER, D. E., GONGALSKY, K. B., SWENGEL, A. B., GENTILE, A. & CHASE, J. M. (2020). Meta-analysis reveals declines in terrestrial but increases in freshwater insect abundances. *Science* 368(6489), 417–420.
- Van Vuuren, D. P., Sala, O. E. & Pereira, H. M. (2006). The future of vascular plant diversity under four global scenarios. *Ecology and Society* 11(2), 25.
- VERMEULEN, J. J. & MARZUKI, M. E. (2014). 'Charopa' lafargei (Gastropoda, Pulmonata, Charopidae), a new, presumed narrowly endemic species from peninsular Malaysia. Basteria 78, 31–34.
- VOLKMANN, L., MARTYN, I., MOULTON, V., SPILLNER, A. & MOOERS, A. O. (2014). Prioritizing populations for conservation using phylogenetic networks. PLoS One 9(2), e88945.
- WAKE, D. B. & VREDENBURG, V. T. (2008). Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proceedings of the National Academy of Sciences of the United States of America* 105(Suppl. 1), 11466—11472
- WASHINGTON, H. (2018). Denial—the key barrier to solving climate change. In Encyclopedia of the Anthropocene. Volume 2 (cds D. A. DELIASALA and M. I. GOLDSTEIN), pp. 493–499. Elsevier, Oxford.
- Wells, A., Johanson, K. A. & Dostine, P. (2019). Why are so many species based on a single specimen? Zoosymposia 14(1), 32–38.
- WEST, D., DAVID, B. & LING, N. (2014). Prototroctes oxyrhynchus. The IUCN Red List of Threatened Species 2014: e.T18384A20887241.
- WHITE, W. T., KYNE, P. M. & HARRIS, M. (2019). Lost before found: a new species of whaler shark *Carcharhinus obsolerus* from the Western Central Pacific known only from historic records. *PLoS One* 14(1), e0209387.
- WHITEHOUSE, N. J. (2004). Mire ontogeny, environmental and climatic change inferred from fossil beetle successions from Hatfield moors, eastern England. *The Holocene* 14(1), 79–93.
- WHITEHOUSE, N. J. (2006). The Holocene British and Irish ancient forest fossil beetle fauna: implications for forest history, biodiversity and faunal colonisation. *Quaternary Science Reviews* 25, 1755–1789.
- WIENS, D., SWEET, T. & WORSLEY, T. (2020). Validating the new paradigm for extinction: overcoming 200 years of historical neglect, philosophical misconception, and inadequate language. *Quarterly Review of Biology* 95(2), 109–124.
- WILLIAMS, M. (2021). Endangered and threatened wildlife and plants; removal of 23 extinct species from the lists of endangered and threatened wildlife and plants. Federal Register 86(187), 54298–54338.
- WILSON, E. O. (1999). The Diversity of Life. Belknap Press of Harvard University Press, Cambridge.
- WILSON, K. A., CABEZA, M. & KLEIN, C. J. (2009). Fundamental concepts of spatial conservation prioritization. In *Spatial Conservation Prioritization: Quantitative Methods* and Computational Tools (eds A. Moilanen, K. A. Wilson and H. Possingham), pp. 16–27. Oxford University Press, Oxford.
- Worm, B., Barbier, E. B., Beaumont, N., Duffy, J. E., Folke, C., Halpern, B. S., Jackson, J. B. C., Lotze, H. K., Micheli, F., Palumbi, S. R., Sala, E., Selkoe, K. A., Stachowicz, J. J. & Watson, R.

- (2006). Impacts of biodiversity loss on ocean ecosystem services. Science 314(5800), 787–790
- Young, R. P., Hudson, M. A., Terry, A. M. R., Jones, C. G., Lewis, R. E., Tatayah, V., Zuël, N. & Butchart, S. H. M. (2014). Accounting for conservation: using the IUCN Red List Index to evaluate the impact of a conservation organization. *Biological Conservation* 180, 84–96.
- Zeller, D. & Pauly, D. (2018). The 'presentist bias' in time-series data: implications for fisheries science and policy. *Marine Policy* **90**, 14–19.
- ZHANG, L.-J., CHEN, S.-H., YANG, L.-T., JIN, L. & KÖHLER, F. (2015). Systematic revision of the freshwater snail Margarya Nevill, 1877 (Mollusca: Viviparidae) endemic to the ancient lakes of Yunnan, China, with description of new taxa. Zoological Journal of the Linnean Society 174, 760–800.
- ZIMMERMANN, G., GARGOMINY, O. & FONTAINE, B. (2009). Quatre espèces nouvelles d'Endodontidae (Mollusca, Pulmonata) éteints de Rurutu (Iles Australes, Polynésie française). Zoosystema 31, 791–805.

(Received 28 November 2020; revised 4 November 2021; accepted 8 November 2021; published online 10 January 2022)