



Global biodiversity: Extinctions and originations

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ABSTRACT

Most claims of global biodiversity loss, while they appear to be reasonable, suffer from the problem of scale. Reliance is placed on data from islands and other restricted localities and extrapolated to the size of the entire globe. It is possible to avoid the scale effect by relying on direct information about extinctions, rather than indirect approximations as indicated by habitat decline, the species-area curve, and invasive species. Aside from isolated islands or space-restricted freshwater habitats, there is a lack of evidence indicating an abnormal loss of species diversity on the Earth's continents and oceans. Instead, speciation apparently continues to provide the world with gains in biodiversity, leaving little justification for claims of unusual global losses. The world's major conservation problem is not the loss of species, it is the plight of thousands of threatened populations, remnants of larger ones that have been over-exploited or restricted by loss of habitat. This means that our conservation attention needs to be shifted from alarm over unsubstantiated global biodiversity loss, to the current problem of the rescue of small populations that are under threat.

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KEYWORDS

Global biodiversity;
Marine diversity;
Terrestrial diversity;
Extinction;
Speciation.

INTRODUCTION

Biodiversity, as a term and a concept, has been a remarkable event in recent cultural history^[1]. It was born as "BioDiversity" during the National Forum on BioDiversity held in Washington, D.C., in September, 1986. The proceedings of the forum were published in 1988 under the title *BioDiversity* and soon became a best-seller for the National Academy Press. Although ecologists usually agree that "biodiversity", as it is now spelled, refers to all levels of organization from genes to species to communities to ecosystems, in practice it is most commonly used as synonym for "species richness" or "species diversity." In this paper, and in almost all

others that focus on conservation needs, biodiversity is equivalent to species richness. When it became known that the tropical forests contained most of the world's terrestrial species, and those forests were being destroyed at a rapid rate, many eminent ecologists envisioned large-scale species extinctions resulting in a major decline in global biodiversity. During the 1980s, numerous estimates of extinction rate indicating the loss of thousands species per year were made^[2].

By 1992, E.O. Wilson^[1] had determined that 27,000 rain forest species were becoming extinct each year, or 24 each day, and 3 each hour. Similar evidence, put forth by many other ecologists, indicating that enormous losses were taking place, had a strong

impact and resulted in biodiversity decline being recognized as the world's greatest conservation problem. Estimates of extinction taking place, not only in rain forests but in a wide variety of natural habitats, have continued to the present time. In the recent literature, there are a number of multi-authored articles calling attention to a current global biodiversity loss and predicting its continuing increase. There has been little consideration of evidence for gains in biodiversity^[3]. Obviously, global biodiversity trends, if they are accurate, provide information critical for future human welfare. In order to insure accuracy, one must pose two questions. First, what is the evidence for the large numbers of current extinctions? Second, is the world's sixth mass extinction already underway?

The following examples illustrate recent global projections that have been especially influential: (1) Nineteen coauthors collaborated on an article^[4] that predicted global biodiversity scenarios for the year 2100. Significant biodiversity decreases were based on data from terrestrial and freshwater organisms. (2) In 2005, a Millennium Ecosystem Assessment, a United Nations project involving 1360 scientists from 95 countries, was published^[5]. The assessment constituted a biodiversity synthesis which concluded that large percentages of terrestrial species were threatened and the current extinction rate was up to 1,000 times greater than indicated by the fossil record. (3) Twenty four coauthors participated in a scenario for global biodiversity in the 21st century^[6] and predicted that terrestrial, freshwater and marine biodiversity will continue to decline. (4) Forty four coauthors^[7] found several causes of predicted biodiversity declines. (5) One hundred eighty coauthors^[8] discussed the conservation status of the world's vertebrates and found species extinction rates that exceeded normal background rates by two or three orders of magnitude. (6) Others^[9] found recent biodiversity loss to be 13 times greater than the normal background rate. (7) Another group^[10], using data on amphibians, birds, and mammals, obtained results showing a roughly proportional species extinction rate commensurate with area loss. (8) A recent global synthesis^[11] revealed that terrestrial species loss was a major driver of ecosystem change that greatly outpaced background rates in the fossil record. (9) Finally,^[12] it was found that among terrestrial plants the impacts of biodiversity loss escalated through time.

In the above examples, most of the data indicating biodiversity loss is in reference to species extinction, although in some cases there is also reference to decreases in population size. The problem with the data indicating losses from extinction has been one of scale. As Pautasso^[13] has pointed out, it is risky to extrapolate from small scale data to large scale applications, as in the case from small islands to large continents or the entire globe. To avoid this problem, as well as to depend on direct instead of indirect data, it seems advisable to utilize information from documented extinctions, including the use of surrogate taxa.

There has developed an unfortunate tendency to use the term "extinction" in reference to the absence of a species from a particular locality. But this creates confusion because, in its traditional scientific use, extinction of a species indicates that it has entirely disappeared from the earth, i.e., there are no more living examples. Despite this concise definition, the term has been used in different ways for various purposes. Exaggerations and misrepresentations have been used to "get the message across"^[14].

The most frequently used predictions of species extinction are largely based on the species-area relationship (SAR) whereby the species number is related to the size of the habitat: as the habitat area declines, species are supposed to be lost^[15]. This concept had its origin in MacArthur and Wilson's work on island biogeography^[16]. The SAR remains popular due to inertia and, until recently, the lack of information about the time and locations of actual extinctions. The publications already cited (numbers 1-9), plus many opinion articles that previously appeared on the internet and the print media, resulted in the general and scientific public being convinced that plant and animal species are becoming extinct at a rapid rate and will continue to do so. We are told that the world is now undergoing its sixth mass extinction^[17,18]. Why should one be skeptical in the face of such an overwhelming expert analysis? The data on extinctions utilized in most works on global biodiversity come from applications of the SAR, as well as reports of habitat destruction and fragmentation, species invasions, and over-exploitation. As a result, it may be seen that prognostications about extinctions and biodiversity loss are based on theoretical projections instead of factual data. There are also contrasts in reports of documented extinctions between the marine and terrestrial

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environments indicating that each should be examined separately.

MARINE ENVIRONMENT

Most evaluations of global biodiversity are based on changes in the terrestrial environment, yet the oceans cover about 71% of the Earth's surface. It should be apparent that global biodiversity predictions need to be based, at least equally, on information from the sea. In the marine environment, biodiversity "losses" occur but these losses are either confined to local situations such as harbors and estuaries^[19], where populations have been severely reduced or extirpated due to overfishing, pollution, and habitat alteration, or to populations of oceanic species that have collapsed due to overfishing^[20]. But such losses are not due to species extinctions. Species whose populations have been greatly reduced lose ecological function but still exist in lesser numbers. This information points to the difference between the data from land and sea. In the first instance, there have been, in the early years of island exploration by humans, many real extinctions of endemic species, but in the second, known extinctions have been exceedingly few. The Holocene began 12,000 years ago, and a total of 20 marine extinctions have been recorded from that time until 2008^[21]. Over the same time, many hundreds of terrestrial species became extinct.

When the losses of 20 marine species (four mammals, eight birds, four molluscs, three fishes, one alga) are compared to a total marine diversity of about 2.21 million eukaryotic species^[22], the rate of extinction is exceedingly low. Furthermore, there have been no recorded marine species extinctions for the past 30 years. Although it is often assumed that invasive species are responsible for native extinctions, none of the 20 marine extinctions has been due to competition from exotic invaders^[23]. In fact, there is now good evidence that invasive species function to increase rather than decrease biodiversity. In locations where large numbers of exotic species are being introduced, such as the eastern Mediterranean Sea^[24] and in many harbors and estuaries^[19], the invaders are accommodated by the native species resulting in local biodiversity increases. Information from fossil invasions^[25-27] demonstrates that large numbers of invaders eventually speciate, thus adding to global biodiversity. It has been concluded that, in

the marine environment, invader species are a dynamic, diversity-creation force with a circum-global influence^[28].

Why are there so few marine extinctions? The fossil record tells us that the overall rate of marine species extinction is about 2.5 per year^[29]. However, this average is not useful for most comparative purposes because marine extinctions do not occur gradually but are concentrated into pulses as the result of rapid environmental changes. The most recent pulse, or a series of regional pulses, took place at the beginning of the Pleistocene about 1.5 million years ago. These extinctions are generally taken to represent a culling of species unable to cope with the onset of rapid climatic changes typical of that epoch^[30]. Since then, we have been living in a time where extinctions are low and biodiversity is increasing.

TERRESTRIAL ENVIRONMENT

Is the terrestrial environment completely different from the marine in terms of species extinctions? It has been observed that well-known surrogate taxa can be used as biodiversity indicators^[31]. Birds and mammals are good surrogates for vertebrates because the species are the best known and their recent extinction rates have been recorded. The records and the geographical locations of the extinctions, based upon evidence in the IUCN Red List and the CREO List at the American Museum of Natural History, have been analyzed^[32]. Extinctions during the past 500 years demonstrate an enormous difference between islands and continents. On all continents, only three mammals are recorded as having gone extinct. The remaining mammal extinctions (58 or 95%) took place on islands (Australia, due to its history of isolation, was classified as an island). Of 128 extinct bird species, 122 (95.3%) were island extinctions and only six were on continents. Human hunting, egg gathering and introduced predators were apparently responsible for the great majority of the extinctions.

Another discovery^[32] was that no continental bird or mammal was documented to have gone extinct solely because of habitat reduction. Early prehistoric waves of extinction, in America around 12,000 years BP, were also not due to habitat alteration but largely because of hunting and other exploitation^[33]. For many years, habi-

tat reduction, especially tropical deforestation, had been regarded as the primary cause of species loss. Numerous estimates were made using the SAR. As noted, many of these estimates produced very high extinction numbers. Stork^[34] provided an up-to-date list of 20 studies that made similar high estimates and noted the lack of empirical data to support them. Furthermore, there has been criticism about the usefulness of the SAR^[35,36]. An important contribution is a recent paper by Wearn et al.^[37] on the Brazilian Amazon, who found that losses of vertebrate species have been minimal (1%) and that 80% of the losses projected by habitat decline are still to come.

The foregoing terrestrial data have been derived from works on the vertebrates, mainly mammals and birds, because their species are well known and most of them have been studied over many years. But the Zoological Society of London has published the world's first study of global invertebrate biodiversity^[38]. This report, produced in conjunction with the IUCN and its Species Survival Commission, concluded that about 80% of the world's species were invertebrates and about 20% of them were threatened with extinction. Of the world's terrestrial invertebrates, about 90% are insects. According to the IUCN Red List, only 59 insect species out a total of about two million have become extinct since the year 1500.

As noted, the mammals and birds have been used as surrogates to indicate the extinction rate of terrestrial vertebrates. In the same manner, one can utilize the two best known insect groups, the butterflies and the tiger beetles, as surrogates for extinction in terrestrial invertebrates. Both groups are widely distributed except for the pole regions and almost all the species are well known. The world total of butterfly species is about 17,280^[39] and the 2012 IUCN Red List includes three that have become extinct during the past 500 years. There are about 2,300 species of tiger beetles^[40] and, although several are listed as endangered, none has become extinct. As the total insect extinctions (59 out of approximately two million) and the three surrogate losses (3 out of 19,580) demonstrate, very few insect species have been lost and the extinction rate appears to be even less than that of the vertebrates.

Global projections of biodiversity loss generally include extinctions due to invasive species^[11], and many other writers blame exotic species for native biodiversity

loss^[41,42]. The internet continues to carry a message^[43] claiming that almost half of America's species are threatened by invaders and that native species loss caused by invaders is second only to habitat destruction. However, the study^[32], based on factual evidence of extinctions rather than theoretical forecasts, found no evidence that habitat destruction was an important factor. Furthermore, the same study did not implicate invasive species in the extinction of continental natives. This information served to substantiate works^[44,45] that also did not find evidence that continental extinctions had been caused by exotic invaders. In fact, human introductions for agricultural and ornamental purposes, along with natural invasions, have produced substantial gains in continental plant biodiversity^[46]. The many endemic species that became extinct on oceanic islands and restricted freshwater habitats were primarily the victims of predation by humans and animals they introduced, instead of competition by natural invaders^[47,48].

DISCUSSION

It is now possible to make a realistic assessment of global biodiversity trends without having to depend on estimates of habitat destruction, species invasions, or other abstract and possibly subjective factors. For the past 500 years, there have been few documented extinctions in the oceans and on the continents, with the exception of some restricted freshwater habitats. This does not imply an absence of unobserved extinctions. Even when estimates of such extinctions are included, it has been observed that contemporary extinctions have not been as high as generally predicted^[49], and that less than 1% of all organisms could have become extinct within the past 400 years^[34]. In summary, the available data suggest that biodiversity has held up very well. In fact, there are good indications that, during the Holocene, there have been gains in global biodiversity. The losses of endemics on islands and other restricted habitats, while regrettable, were a sideshow. That is, they were isolated and did not, with very few exceptions, contribute to the genetic diversity that promoted evolutionary adaptation in other parts of the world. The island status of Australia may be questioned, but it was effectively isolated from the other parts of the terrestrial world during the latter half of the Cenozoic. In a modern biogeographic sense, Australia, Madagascar, and

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New Zealand are big islands isolated from the rest of the terrestrial world. Despite the early losses of endemics, oceanic islands have shown biodiversity gains in recent years^[47].

Most historical accounts, based on fossil materials, demonstrate a long-term rise in biodiversity despite some setbacks caused by mass extinction. It has been proposed^[50] that the growth of marine and continental biodiversity through the Phanerozoic can be represented by a hyperbolic curve, created by a positive feedback between diversity growth and community structure. Hyperbolic growth suggested to the authors that “co-operative” interactions between taxa can play an important role in evolution and that biodiversity gain is a self-accelerating process. As communities become more diverse and stable, the native species facilitate additional species entering the community. This theory foretold evidence that invasive species did increase biodiversity because they were accommodated by native species^[51].

In addition to the global biodiversity increase indicated by the speciation of invader species, it seems apparent that speciation is still taking place in other ways. Examination of the speciation process through molecular methods has revealed numerous cases of rapid adaptive divergence. Such cases, suggesting the occurrence of ecological speciation, have been demonstrated in plants, invertebrates, and vertebrates^[52]. Specific examples have been reported in mammals^[53], echinoderms^[54], and plants^[55]. Deforestation and other human-caused habitat changes often separate populations that were once continuous. Each population effectively separated embarks on its own evolutionary course, another cause of biodiversity increase. It now seems apparent that speciation is indeed taking place in contemporary time and is adding to global biodiversity. How does one compare these indications of biodiversity gain to the claims of biodiversity loss made by so many? As noted, most of the loss claims are based on theory while the gains are based on specific examples.

Considering the evidence now available, I suggest that it is questionable science to publish articles lamenting an escalating loss of biodiversity caused by a rising tide of extinctions, and it is inaccurate to claim that the Earth is in the midst of its sixth mass extinction. In addition, it is no longer possible to blame invasive species for the loss of biodiversity. Extinctions are not increas-

ing and invasive species, both naturally occurring and human-introduced, do not subtract but add to biodiversity. However, so many papers have been published asserting just the opposite that various government and conservation agencies have been misled. The United Nations published a book^[56] giving guidelines for the prevention of biodiversity loss due to biological invasion. While considerable remedial work has been necessary to control the spread of destructive invaders, agricultural pests in particular, most objections to the exotics were based on assumptions that they were doing great harm by eliminating native species. For example, a recent publication was devoted to global indicators of biological invasion^[42]. The authors said the IUCN Red List Index demonstrated that invasive species pressure was driving declines in species diversity, with overall impact apparently increasing.

Although the Red List has proved to be useful in identifying extinctions and calling attention to rare species in need of conservation, it represents the opinions of experts as to which species are threatened (in danger of becoming extinct). As more species are placed on the Red List, the threat appears to be growing but this does not mean that more species are actually becoming extinct. Many species are rare because they have always been so. Large numbers of threatened continental mammals may not be significant *as yet* considering that only three have become extinct in the past 500 years. But it does mean that threatened species need to be protected. Populations of many species have become smaller but extinctions have not greatly increased. In evaluating threat, is it not more important to rely upon what has actually happened in recent history rather than trust opinions as to what might have happened?

Based on the Red List of species under threat and other indirect evidence, the United Nations Environmental Programme has emphasized a negative impact of invasive species on biodiversity^[42]. Leadership by the UN gave rise to an International Convention on Biological Diversity, followed by legislative action in many nations. Numerous meetings have taken place and goals were set for the control of invasive species and biodiversity loss. It seems incredible that such a large and expensive campaign could be fueled by questionable data on the existence of biodiversity loss and the supposed involvement of invader species. Certainly,

some invasive species have negative effects on human endeavors, sometimes they may reduce the abundance of native populations, and there is occasional interbreeding, but they do not cause the extinction of native species and do increase species diversity.

FUTURE PROSPECTS

As global warming continues it will reach a point where the climatic and associated changes will bring about a major extinction event. When this occurs, it will result in the loss of many species that already have a precarious existence. Predictions for extensive terrestrial extinctions under continued global warming have been made^[6,57]. For the marine environment, I have estimated there are presently about one thousand or more small populations of fishes and invertebrates that are the collapsed remnants of species that have been overfished^[58]. These remnants are now found over all the oceans, from the tropics to the poles to the deep sea^[21]. They have exhibited a remarkable ability to hang on despite handicaps such as the loss of genetic diversity, depensation (Allee effect), and inbreeding depression. Those handicaps have decreased the ability of small-population species to resist environmental changes. Therefore, they collectively constitute an extinction debt to be paid when more global warming takes its toll.

On the continents, many species will be able to adjust to increased warming by migrating to more suitable locations, but others may be trapped by an inability to move due to habitat alteration. Island and high altitude species will be especially vulnerable. Arctic and Antarctic species will find it difficult to survive unless they can make rapid evolutionary adjustments to temperature change and the influx of predators from warmer regions^[59]. The first global study on the impact of climate warming on marine biodiversity was published in 2009^[60]. It projected the distributional ranges of a sample of 1066 exploited fish and invertebrates for 2050. The projections indicated that climate change may lead to numerous local extinctions in the sub-polar regions, the tropics and semi-enclosed seas. Species migration from lower latitudes was projected to be most intense in the Arctic and the Southern Ocean. Together, the projections resulted in a dramatic species turnover of more than 60% of present biodiversity. Unless steps can be taken to reduce the progression of global warming, there

will be an enormous biodiversity loss for both land and sea.

CONSERVATION

The world's greatest conservation problem lies with thousands of species that were once widespread but are now represented only by very small populations. They are the remnants of species that were almost destroyed by human over-exploitation, habitat destruction, and pollution. These populations are threatened with extinction unless they are protected to the extent that they can begin to increase in numbers. The conservation plan, initiated by the World Wildlife Fund and supported by the Zoological Society of London, The Global Footprint Network, and the European Space Agency, is promising. Their Living Planet Index for 2012 provided information on the status of 9,014 vertebrate populations belonging to 2,688 species^[61]. The Index reported that the subject populations had undergone a 28% global loss since 1970; the greatest decline was in the tropics where the loss was 60%. This kind of empirical research, carried on over many years, is essential in order to identify the species whose populations are at the greatest risk. The Living Planet Index needs to be extended to include invertebrates and plants. The fact that so many threatened populations still exist, provides numerous conservation opportunities for those who wish to participate in their rescue and maintenance.

CONCLUSIONS

An extensive series of works on global biodiversity, published during the past 40 years, have decried an apparent continuing loss of species and have predicted increased losses. Both the conclusions on the present state and the future projections are suspect because they seldom utilize the facts on species extinctions but instead rely upon indirect evidence. Estimates using the species-area curve, the amount of habit destroyed, species invasions, and the ICUN Red List of threatened species have been popular. But, such estimates encounter a serious scale problem in trying to extrapolate from extinctions in small areas to the entire globe. The Red List has been especially influential because as more species are added to the List, the greater the apparent danger of extinction. It is now evident that exceedingly few

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marine species are known to have become extinct in the last 12,000 years. A recent evaluation of terrestrial vertebrate biodiversity, based on documented extinctions of birds and mammals for the past 500 years, has been published. These sources, and the dearth of recorded invertebrate losses, show that extinction rates in the oceanic and continental world (aside from isolated habitats) have been very low, meaning that so far there have been no unusual global biodiversity losses. Less than 1% of all organisms may have become extinct during the past few centuries. Instead, human-caused and natural invasions by exotic species, and their accommodation in native ecosystems, have increased local biodiversity, while speciation among past invaders has resulted in a buildup of global biodiversity. In addition to invasion effects, molecular research indicates that contemporary species formation is contributing to global biodiversity increases.

In regard to the present state of research on global biodiversity, we live in a strange time. Conservation biologists are split in two groups: one, the largest, is convinced that biodiversity is being lost at a rapid rate, while the other sees a buildup of species diversity almost everywhere (continents, islands, and seas). This paper presents evidence for the latter view, but this should not be taken as good news because there will be a drastic decline if climate warming continues and if threatened species are not given better protection. Species most likely to disappear will be those represented by small endemic populations on islands and other restricted habitats, and those that exist as remnants of much larger ones in continental and oceanic areas. The longer a population exists in a reduced state, the more likely it is to suffer from genetic loss, inbreeding and depensation. In general, species represented by the smallest populations should receive conservation priorities. However, it is the small populations of newly formed species in high diversity centers of origin (terrestrial and marine) that deserve the most attention. They, more than any others, contain within their genes the evolutionary future of the biotic world.

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REFERENCES

- [1] E.O.Wilson; *The Diversity of Life*, Harvard University Press, Cambridge, (1982).
- [2] N.E.Stork; Measuring global biodiversity and its decline, In L.Reaka-Kudla, D.E.Wilson, E.O.Wilson, (Eds); *Biodiversity II*, Joseph Henry Press, Washington, DC, 41-68 (1997).
- [3] D.F.Sax, S.D.Gaines; *Trends in Ecology and Evolution*, **18**, 561-565 (2003).
- [4] O.E.Sala, F.S.Chapin, J.J.Armesto, et al.; *Science*, **287**, 1770-1774 (2000).
- [5] Island Press; Millennium ecosystem assessment, in *Ecosystems and Human Well-being: Synthesis*, Island Press, Washington, DC, (2005).
- [6] H.M.Pereira, P.W.Leadley, V.Proença, et al.; *Science*, **330**, 1496-1501 (2010).
- [7] S.H.M.Butchart, M.Walpole, B.Collen, et al.; *Science*, **328**, 1164-1168 (2010).
- [8] M.C.Hoffmann, C.Hilton-Taylor, A.Angulo, et al.; *Science*, **330**, 1503-1509 (2011).
- [9] A.D.Barnosky, N.Matzke, S.Tomyia, et al.; *Nature*, **471**, 51-57 (2011).
- [10] D.Storch, P.Keil, W.Jetz; *Nature*, **488**, 78-81 (2012).
- [11] D.U.Hooper, E.C.Adair, B.J.Cardinale, et al.; *Nature*, (2012).
- [12] P.B.Reich, D.Tilman, F.Isbell, et al.; *Science*, **336**, 589-592 (2012).
- [13] M.Pautasso; *Ecological Letters*, **10**, 16-24 (2007).
- [14] R.J.Ladle, P.Jepson; *Conservation Letters*, **1**, 111-118 (2008).
- [15] N.E.Stork; *Biodiversity and Conservation*, **19**, 357-371 (2010).
- [16] R.H.MacArthur, E.O.Wilson; *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ, (1967).
- [17] G.A.Ceballos, A.Garcia, P.R.Ehrlich; *Journal of Cosmology*, **8**, 1821-1831 (2010).
- [18] J.Chase; *PLoS Biology*, **10**(3), (2012).
- [19] J.C.Briggs; *Marine Ecology Progress Series*, **449**, 297-302 (2012).
- [20] B.Worm, E.B.Barbier, N.Beaumont, et al.; *Science*, **314**, 787-790 (2006).
- [21] N.K.Dulvy, J.K.Pinnegar, J.D.Reynolds; *Holocene extinctions in the sea*, in S.T. Turvey, (Ed); *Holocene Extinctions*. Oxford University Press, Oxford, 129-150 (2009).
- [22] C.Mora, D.P.Tittensor, S.AdL, A.G.B.Simpson B.Worm; *PLoS Biology*, **9**(8), (2011).
- [23] J.C.Briggs; *Journal of Biogeography*, **34**, 193-198

- (2007).
- [24] B.S.Galil; *Marine Pollution Bulletin*, **55**, 314-322 (2007).
- [25] G.J.Vermeij; *Science*, **253**, 1099-1104 (1991).
- [26] G.J.Vermeij; Invasion as expectation, in D.F.Sax, J.J.Stachowicz, S.D.Gaines, (Eds); *Species Invasions*, Sinauer, Sunderland, MA, 315-339 (2005a).
- [27] G.J.Vermeij; *Paleobiology*, **31**, 624-632 (2005b).
- [28] J.C.Briggs, B.W.Bowen; *Journal of Biogeography*, **40**, (2013).
- [29] J.J.Sepkoski; *Proceedings Royal Society*, **B353**, 315-326 (1998).
- [30] D.Jablonski; *Proceedings National Academy of Science USA*, **105**(1), 11528-11535 (2008).
- [31] T.M.Caro, G.O'Doherty; *Conservation Biology*, **13**, 805-814 (1999).
- [32] C.Loehle, W.Eschenbach; *Diversity and Distributions*, **18**, 84-91 (2012).
- [33] W.Ripple, B.Van Valkenburgh; *BioScience*, **60**, 516-526 (2010).
- [34] N.E.Stork; *Biodiversity and Conservation*, **19**, 357-371 (2010).
- [35] O.T.Lewis; *Philosophical Transactions Royal Society, B*, **362**, 163-171 (2006).
- [36] F.He, S.P.Hubbell; *Nature*, **473**, 368-371 (2011).
- [37] O.R.Wearn, D.C.Reuman, R.M.Ewers; *Science*, **337**, 228-232 (2012).
- [38] B.Collen, M.Böhm, R.Kemp, E.M.Baillie; *Spineless: Status and Trends of the World's Invertebrates*, Zoological Society of London, UK, (2012).
- [39] O.Shields; *Journal Lepidopterists Society*, **45**, 178-183 (1989).
- [40] D.L.Pearson; *The evolution, ecology, and diversity of the cincindelids*. Cornell University Press, Cornell, NY, (2001).
- [41] H.A.Mooney, R.J.Hobbs; *Invasive species in a changing world*. Island Press, Washington, DC, (2000).
- [42] M.A.McGeoch, S.H.M.Butchart, D.Spear, et al.; *Diversity and Distributions*, **16**, 95-108 (2010).
- [43] D.Simberloff; *Introduced species: the threat to biodiversity & what can be done*, www.actionbioscience.org/simberloff.html (accessed 4/12/2012; online 7/22/13), (2000).
- [44] J.Gurevitch, D.K.Padilla; *Trends in Ecology and Evolution*, **19**, 470-474 (2004).
- [45] M.A.Davis; *Invasion Biology*. Oxford University Press, Oxford, (2009).
- [46] E.C.Ellis, E.C.Antill, H.Kreft; *PLoS ONE*, **7**(1), (2012).
- [47] D.F.Sax, S.D.Gaines; *Proceedings National Academy of Science USA*, **105**, 11490-11497 (2008).
- [48] A.Ricciardi, H.J.MacIssac; *Impacts of biological invasions on freshwater ecosystems*, in D.M.Richardson, (Ed); *Fifty Years of Invasion Ecology*. Wiley-Blackwell, London, 211-224 (2011).
- [49] M.J.Costello, R.M.May, N.E.Stork; *Science*, **339**, 413-416 (2013).
- [50] A.V.Markov, A.V.Korotaev; *Zhurnal Obshchei Biologii*, in Russian, **69**, 175-194 (2008).
- [51] J.C.Briggs; *Marine Biology*, **157**, 2117-2126 (2010).
- [52] A.P.Hendry, P.Nosil, L.H.Rieseberg; *Functional Ecology*, **21**, 455-464 (2008).
- [53] K.C.Rowe, K.P.Aplin, P.R.Baverstock et al.; *Systematic Biology*, **60**, 188-203 (2011).
- [54] J.B.Puritz, C.C.Keever, J.A.Addison, et al.; *Proceedings Royal Society B*, 1343 (2012).
- [55] J.P.Foxe, J.Slotte, E.A.Stahl, et al.; *Proceedings National Academy of Science USA*, **106**, 5241-5245 (2009).
- [56] IUCN; *Guidelines for the Prevention of Biodiversity Loss due to Biological Invasion*. The World Conservation Union, Gland, Switzerland, (2000).
- [57] C.D.Thomas, A.Cameron, R.E.Green et al.; *Nature*, **427**, 145-148 (2004).
- [58] J.C.Briggs; *Marine Biology*, **158**, 485-488 (2011).
- [59] R.B.Aronson, S.Thatje, A.Clarke, et al.; *Annual Review of Ecology, Evolution and Systematics*, **38**, 129-154 (2007).
- [60] W.W.L.Cheung, V.W.Y.Lam, J.L.Sarmiento, K.Kearney, R.Watson, D.Pauly; *Fish and Fisheries*, **10**, 235-251 (2009).
- [61] *Living Planet Index*; www.livingplanetindex.org (accessed 2/14/13; online 7/22/13), (2012).