

17 Anthropogenic footprints on biodiversity

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Introduction

One of the most concerning issues to modern ecology and society is the ongoing loss of biodiversity. Ecosystems are now losing species at rates only seen in previous mass extinction events (Hails, 2008; Barnosky *et al.*, 2011) with rates of extinction between 100 and 1000 times higher than pre-human levels (Pimm *et al.*, 1995). This loss, in turn, is impairing the functioning of ecosystems (Worm *et al.*, 2006; Mora *et al.*, 2011a) and their capacity to deliver goods and services to mankind (Díaz *et al.*, 2006). The sharp contrast between the declining “supply” of the Earth’s services and the rising “demand” from a growing human population indicates that such services will increasingly fall short, leading to the exacerbation of hunger, poverty, and human suffering (Campbell *et al.*, 2007; Mora & Sale, 2011).

There is relatively good consensus that biodiversity loss is being driven directly or indirectly by human stressors such as overexploitation, habitat loss, invasive species, and climate change (Myers, 1995; Sala *et al.*, 2000; Novacek & Cleland, 2001; Gaston *et al.*, 2003; Jackson, 2008; Weidenhamer & Callaway, 2010). The relative role of such stressors, however, has been a focus of controversy as all threats do provide rational mechanisms to explain biodiversity loss and unfortunately most threats co-occur in natural conditions, making it difficult to isolate their individual effects (Myers, 1995; Sala *et al.*, 2000; Novacek & Cleland, 2001; Mora *et al.*, 2007). Since the cost of mitigating specific stressors could be considerable but disproportionate among different sectors of the economy (e.g., industries vs. fishers, fishermen vs. tourism developers, etc.), this uncertainty over the relative effect of anthropogenic stressors is often used as an argument to prevent the implementation of mitigation policies (e.g., Schiermeier, 2004; Worm & Myers, 2004; Grigg & Dollar, 2005). A counter-argument, however, is that any stressor at play, if proven to have a considerable effect on biodiversity, should be mitigated regardless of its effect relative to other stressors. This would, of course, require demonstrating the significance of the stressor(s) at play. In this review, we provide an overview of the current biodiversity crisis and the role of anthropogenic stressors. The evidence is considerable and although some uncertainties remain and will probably never be answered, there is considerable knowledge to suggest that a lack of policy action

should not be further justified on the basis of a lack of knowledge (see similar pledge by Worm & Myers, 2004; Jackson, 2008; Knowlton & Jackson, 2008). Our assessment is focused on the effect of anthropogenic factors on interrelated patterns of abundance, evolution, distribution, and extinction. Note that a deterring stressor could trigger a cascade of responses starting with changes in abundance (e.g., new colonization, population increase or decline) and adaptation, and this in turn can lead to changes in geographical distribution ranging from expansion to extinction.

To obtain some insight into the comparative effect of anthropogenic drivers, we complemented our literature review with an analysis of the factors that have been associated with the extinction and critical endangerment of species in recent times. For this analysis, we collected the list of species classified as “extinct” and “critically endangered” in the IUCN Red List of Species and the threats leading to that classification (IUCN, 2012). Information on threats leading to the extinction of species was available for 266 species of animals and 27 species of plants; information on the threats leading to the critical endangering of species was available for 1743 species of animals and 877 species of plants. Threats were broadly categorized as habitat loss (i.e., the alteration of habitats into ones no longer suitable for species, including deforestation, pollution, infrastructure development, etc.), invasive species, overharvesting, and climate change.

Technical considerations

It will be almost impossible to determine the geographical position of all individuals of a given species, even those of decimated species because the rarer they become the harder they are to detect (Dulvy *et al.*, 2004). Consequently, assessing changes in the distribution of species relies on multiple extrapolation and simplifying sources of data. Some common sources of information include the geographical range or extent of occurrence (i.e., the outermost boundary within which individuals of a particular species have been recorded), the area of occupancy (i.e., the inhabited parts of the extent of occurrence), and spatial patterns of abundance throughout the geographical range of species (Gaston, 2003). These types of data provide different strengths and weaknesses. The extent of occurrence, for instance, is easy to quantify but overestimates the actual geographical distribution because individuals are not found everywhere within such an area (Gaston, 2003; Jetz *et al.*, 2008); in turn, this can cause underestimation of extinction risk (Jetz *et al.*, 2008), flawed conservation decisions about the size and position of protected areas (Rondinini *et al.*, 2006), and failure to identify actual changes in species' distributions (Burgman & Fox, 2003). Similarly, the area of occupancy fails to capture variations in abundance within occupied areas, which may lead to inappropriate decisions about the most effective placement of protected areas (Gaston, 2003) and to inappropriate conservation action for species undergoing range contractions (Channell & Lomolino, 2000). Finally, spatial patterns in abundance could be more precise to identify distributional changes but they require substantially more sampling (Gaston, 2003).

In addition to extrapolation limitations, identifying changes in the distribution of species can also be affected by the resolution of data. As an example, the use of areas

of occupancy with geographical coordinates at a precision of 0.1° can lead to errors of ± 11 km (i.e., at the tropics, 1° equals ~ 111 km, thus a precision of 0.1° will equal ± 11 km; the error at other latitudes should be within that range). As a result of data precision, range shifts will remain undetected if the precision of available data is smaller than the shift itself (Gaston, 2003; Thomas *et al.*, 2006). An analogous bias is related to sampling effort. Because of the strong relationship between range size and abundance (Gaston, 2003), similar sampling efforts could considerably underestimate the distribution of range-restricted species. Consequently, it is common to see records of range expansions which are difficult to differentiate between prior lack of sampling and a causal mechanism (e.g., Mora *et al.*, 2000; Botts *et al.*, 2012); similarly, many species are difficult to accurately define as extinct due to the lack of sampling (Dulvy *et al.*, 2004).

The issue of species classifications is also important. On the one hand, synonyms (i.e., multiple names for the same species) will underestimate the distribution of species whose ranges are fractioned under different names for the same species. On the other hand, homonyms (i.e., the same name for different species) will overestimate the distribution of species whose ranges are actually the concatenation of the ranges of several species. Unfortunately, both of these issues are considerable: within reviewed taxonomic groups synonyms can account for up to 50% of named species (Alroy, 2002); in turn, new genetic developments in the identification of species are ramping up the number of new species due to the discovery of cryptic species (i.e., individuals reproductively isolated from each other, but whose morphology is virtually identical) (e.g., Fouquet *et al.*, 2007; Vieites *et al.*, 2009).

Magnitude of the biological crisis

In spite of limitations in the quality of data and accuracy in the metrics that describe the distribution of species, there is great certainty that species have undergone considerable changes in their geographical distribution due to human activities. Evidence of such an effect is clear even in the fossil record, which has revealed the extinction of multiple species in the wake of human arrival in previously uninhabited regions of the world. Burney and Flannery (2005), for instance, tracked human migrations from the Australian continent some 50 000 years, to the New World by the end of the Pleistocene, to remote islands in recent centuries and show how each of those new arrivals were followed by the collapse of several species in relation to factors such as overkilling, biological invasions, habitat transformation, disease and their aggravation with climatic change. Evidence of the human footprint on biodiversity is also evident and more severe in recent times. According to the IUCN Red List of Species (IUCN, 2012), 712 species of animals and 89 species of plants have been documented to have gone extinct in modern times and for evaluated groups such as scleractinian corals, amphibians, birds and mammals between 20 and 43% of their species are currently threatened with extinction. On average, monitored populations of some 1700 vertebrate species across all regions of the world have declined by nearly 30% over the past 35 years (Hails, 2008). These numbers, however, may be serious underestimates because we lack data on the status of most

species and because most species have not yet been formally described. Of the ~1.2 million species that have been described and compiled in a central database (Mora *et al.*, 2011b), only ~25 000 have complete information of their distributions, population trends and threats (IUCN, 2012). The extent to which local and global extinctions are probably passing unnoticed is further illustrated by the fact that the ~1.2 million species currently named and catalogued represent only ~14% of the species estimated to exist on Earth (Mora *et al.*, 2011b). Modeling the number of species as a function of area with a power-law relationship (i.e., $S = cA^z$, where S is the number of species, A is area, and c and z are constants) it has been possible to quantify that some 27 000 species could go extinct each year due to deforestation alone (Sax & Gaines, 2008, but see He & Hubbell, 2011). According to Barnosky *et al.* (2011), if the ongoing loss of species is to continue, the current rate of extinction could resemble levels seen in prior mass extinctions in which over 75% of all species went extinct.

Human footprints on the biodiversity crisis

Introduced species

The globalization of the economy and trade, combined with an increasing trade in wildlife, is directly and indirectly leading to the introduction of species into foreign areas. While most species introductions are unsuccessful or benign, some are devastating. The probability of successfully establishing alien populations is low (in general about 1 in 10; Williamson & Fitter, 1996) depending on the number of individuals released, the number of release events (Kolar & Lodge, 2001), the time of such events (Gertzen *et al.*, 2011), reproductive strategy (Kolar & Lodge, 2001), history of prior colonizations (Kolar & Lodge, 2001), speed of genetic adaptation to novel environments (Prentis *et al.*, 2008), and avoidance of genetic bottlenecks (e.g., purging deleterious alleles) associated with initial low genetic diversity (Frankham, 2004), etc. Of the species that make the cut of becoming successful residents, about 9 in 10 will have negligible effects (Williamson & Fitter, 1996); the remaining few, however, often have devastating ecological consequences. Invasive species have been responsible for 32% of extinctions of animal species, principally on islands, although only 5% of currently critically endangered species are threatened by invasive species (Figure 17.1). Among plants, no extinction has been related to the unique effect of invasive species and less than 2% are currently endangered for this reason alone (Figure 17.1).

The importance of invasive species for extinction has been a topic of debate. For instance, among oceanic islands there is a strong correlation between the number of exotic predatory mammal species established after European colonization and the magnitude of bird extinctions (Blackburn *et al.*, 2004). Yet the rate of mammal invasions was also correlated with the magnitude of habitat loss (Didham *et al.*, 2005), and this collinearity complicates determining whether bird extinctions were caused by the loss of their habitat or by mammal invasions (Didham *et al.*, 2005). Another debate has been related to the role of invasive species on species currently threatened (Gurevitch &

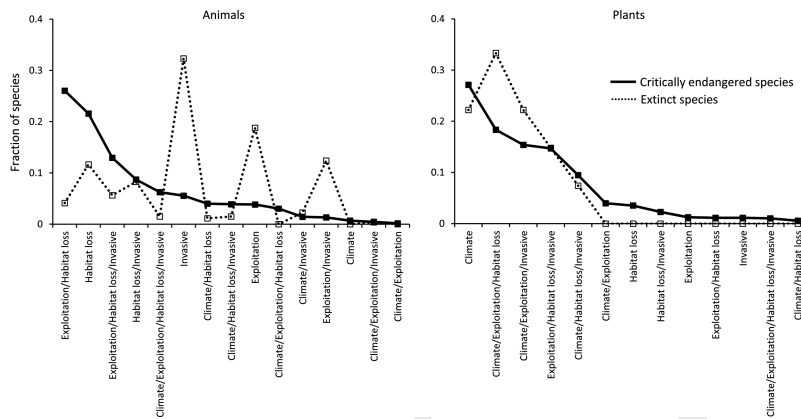


Figure 17.1. Frequency distribution of extinct and critically endangered animal and plant species according to their most likely threats. Data from IUCN (2012).

Padilla, 2004; vs. Ricciardi, 2004; Clavero & García-Berthou, 2005); this debate clarified that while documented extinctions were greatly linked to invasive species, such effect is minor among species currently at risk of extinction: species most vulnerable to invasive species have already gone extinct (this is confirmed in Figure 17.1).

Among animal species, the mechanism through which invasive species drive other species to extinction or affect their geographical distribution is most likely related to predation, often of eggs or young (Sax & Gaines, 2008) and indirectly through the loss of ecosystem functions (e.g., the loss of birds can lead to the decline of plant populations in relation to the reduction of pollination, seed dispersal and increases in insect populations that feed on plants; Pearson & Callaway, 2003). Among invasive plants, the process of impact is mediated by competitive exclusion through allelopathy or “novel weapons”, and indirectly by altering nutrient cycles through litter and root exudates; at times the use of herbicides to control invasive plants may also affect ecosystems overall (Weidenhamer & Callaway, 2010). Of the documented extinctions caused by invasive species, predation alone (i.e., in the absence of other factors) is listed as being responsible for 30% of extinct animal species (Sax & Gaines, 2008), whereas competition has never been listed as the sole factor responsible for species extinctions (Sax & Gaines, 2008). Predation by invasive species, in concert with other factors, is believed to account for 98% of all animal extinctions (Sax & Gaines, 2008).

Overexploitation

Overexploitation can be defined as a human-induced source of mortality beyond natural levels of replenishment. Since the loss of individuals is larger than the gain, populations decline. The reasons for human exploitation of certain species are multiple and include supplying an increasing demand for food (e.g., ~15% of the animal protein consumed by humans is directly or indirectly derived from fisheries; FAO, 2011), cultural reasons (e.g., ornaments and jewels derived from animal parts such rhino horns, fur, etc; Loveridge *et al.*,

2012), medicines and remedies (e.g., penises of tigers, shark fins, etc.; Loveridge *et al.*, 2012), recreational purposes (e.g., hunting and fishing; Loveridge *et al.*, 2012), and limiting human fatalities and livestock losses (e.g., Michalski *et al.*, 2006; Loveridge *et al.*, 2012; Marchini & Macdonald, 2012) to name a few. As a single threat, overexploitation has been the second leading cause of extinction among animals, accounting alone for 18% of extinct animal species; in contrast, no plant species has gone extinct due to the unique effects of overexploitation; only 4% and 1% of animal and plant species, respectively, currently at risk of extinction are so by the unique effect of overexploitation (Figure 17.1).

The mechanism through which overexploitation affects the distribution of species is directly through mortality (e.g., killing of adults, collection of eggs). In principle, overexploitation should be self-regulated because declining populations will increase the cost of harvesting beyond profitability, at which point harvesting pressure should decrease. Unfortunately, there are multiple reasons why this is not the case and harvesting is continued despite the ongoing decline of exploited species. First, in some instances the declining supply of overexploited species can also lead to an increase in their market price (Courchamp *et al.*, 2006). This process is known to trigger exploitation vortices, in which smaller populations enhance further exploitation as rarer individuals become increasingly more valuable (Courchamp *et al.*, 2006). A similar mechanism results from access roads which open new markets for trade and add value to the exploitation of certain species (e.g., Macdonald *et al.*, 2012). A second reason promoting exploitation of declining species is economic subsidies. Here governments grant different types of aids to compensate the monetary loss associated with declining stocks, thus preventing social turmoil but further intensifying exploitation (Sumaila *et al.*, 2008; Mora *et al.*, 2009; Mora & Sale, 2011).

Habitat loss

Habitat loss could be defined as the process by which the area inhabited by a species is rendered functionally unsuitable to further sustain individuals of the species. The causes of habitat loss are diverse and include the expansion for agriculture and urban areas (Short & Burdick, 1996; Gaston *et al.*, 2003), climate change (Thomas *et al.*, 2004), sea-level rise and sedimentation (Valiela *et al.*, 2001), pollution (Short & Burdick, 1996), roads (Rytwinski & Fahrig, 2012), and excessive tourism (Schlacher & Thompson, 2012), among others. As a reference, the expansion of agricultural land has been associated with a 25% decline of the world's bird numbers since pre-agricultural times (Gaston *et al.*, 2003), whereas ongoing climate change is expected to make certain areas inhospitable "committing to extinction" between 15 and 37% of the world's birds by 2050 (Thomas *et al.*, 2004). Individually, habitat loss is the third leading cause of extinction in animals, being the sole factor in the extinction of 11% of extinctions and accounting for the current vulnerability of 21% of threatened animal species. Yet of the documented plant extinctions not one occurred for this reason alone and only ~4% are currently threatened by the sole effect of habitat loss (Figure 17.1). Habitat loss is considered the most pervasive driver of current biodiversity change (Sala *et al.*, 2000) with an estimated 27 000 species extinct each year due to deforestation alone (Sax &

Gaines, 2008, but see He & Hubbell, 2011). Many of these extinct species are likely not to have been described yet (Mora *et al.*, 2011b).

The mechanism through which habitat loss increases extinction risk is probably related to the maintenance of populations in metapopulation systems (i.e., a group of spatially separated populations interlinked by dispersal). Three characteristics of habitats are critical to the maintenance of such systems: size, isolation, and habitat quality (Hill *et al.*, 1996; Griffen & Drake, 2008). Size will influence directly the number of individuals that can be supported and the probability of immigration (Hill *et al.*, 1996; Griffen & Drake, 2008); additionally, depending on the area/perimeter ratio, it could also trigger edge effects, which may cause changes in populations due to drastic environmental shifts and susceptibility to negative interactions with other species (Murcia, 1995). Isolation can create genetic bottlenecks and increase the probability of extinction by haphazard phenomena (Hill *et al.*, 1996) whereas habitat quality can influence the amount and resilience of individuals in the population and reduce the chance of recolonization of previously occupied patches (Griffen & Drake, 2008). An important aspect of metapopulation dynamics and habitat loss is the existence of extinction debts (i.e., delayed extinction triggered by the loss of habitats; Tilman *et al.*, 1994). According to this idea, isolation, reduced amount and quality of habitats and accentuated ecological interactions arising from habitat loss can lead to transient/un-sustainable populations; because extinction may occur long after habitat loss, such extinctions represent a debt of current habitat loss (Tilman *et al.*, 1994).

Climate change

Increasing greenhouse gas emissions are changing the Earth's climate and biodiversity. CO₂ concentrations have increased from 280 ppm in pre-industrial times to 380 by 2000 and could reach between 550 and 800 ppm by 2100 depending on the emissions scenario (Solomon *et al.*, 2007). Since pre-industrial times and as response to the greenhouse effect of CO₂ and other human-generated gases, average global temperature has increased by 0.74°C, whereas the mixture of CO₂ with water has acidified the world's ocean by 0.1 pH units (Solomon *et al.*, 2007). Future projections indicate that temperature could rise by up to 5°C and pH decrease by 0.3 units before 2100 (Solomon *et al.*, 2007). In addition to temperature and pH, climate change may also trigger changes in rainfall, extreme weather events, and sea level rise. The magnitude of these changes would be unprecedented in the Earth's history during the last 20 million years (RSL, 2005). As a single factor, climate change is the leading factor in extinction (~22%) and imperilment (27%) of plants but has played only a minor role in the extinction and endangerment of animals (Figure 17.1); one would expect, however, an indirect effect of plant loss on animals, as the former provide critical resources for the later. Climate change has also been linked to substantial pole-ward shifts, and tropical and low-elevation retreats in multiple species (Parmesan & Yohe, 2003; Wilson *et al.*, 2005; Franco *et al.*, 2006; Devictor *et al.*, 2012). For example, range shifts have been consistent with climate change in over 80% of monitored species, averaging 6.1 km per decade (Parmesan & Yohe, 2003), ranging as high as 114 km northward over 18 years in Europe

(Devictor *et al.*, 2012). The best-documented cases of uphill displacement and tropical retreat are available for butterflies, which are moving uphill at 70 m per decade in Spain (Wilson *et al.*, 2005), ~50 m per decade in Britain (Franco *et al.*, 2006) and retreating from the tropics towards high latitudes at ~44 km per decade in Britain (Franco *et al.*, 2006). In fishes, climate change is expected to cause changes in community composition in over 60% of the world oceans by 2050 due to local extinctions and facilitation of invasions (Cheung *et al.*, 2009).

Linking changes in the distribution of species to climate change, however, has been challenging. In some instances, for example, patterns that could be explained by temperature could alternatively be explained by a covariant of temperature. Gaylord and Gaines (2000), for example, documented that while many boundaries in the distribution of marine organisms with pelagic larvae are coincident with abrupt changes in temperature, these same places coincide with changes in the directions of currents, which prevent the dispersal and settlement of populations up-current. Likewise, transplant experiments have indicated that while in some cases species fail to survive in more poleward locations, in other cases they thrive, highlighting the complexity of generalizing patterns of expansion solely from temperature changes (Gaston, 2003). The existence of source-sink populations has also been implied to yield errors on projection of climate change effects as species could persist in some places only because individuals disperse into them from elsewhere (Davis *et al.*, 1998). Additionally, climate change may unbalance ecological interactions, and thus local extinctions or population increases could be caused by the latter but not the former (Davis *et al.*, 1998). Conversely, there may also be a lag in response to the effects of climate change, in which species track changes in temperature at a rate slower than the rate of change in temperature; and this may underestimate actual responses to climate change (Devictor *et al.*, 2012).

The mechanisms through which climate change affects the distribution of species are diverse, including changes in the suitability of habitats, influencing physiological processes, increasing exposure and susceptibility to pathogens, affecting the timing, extent, direction and even propensity to migrate, etc. (Parmesan & Yohe, 2003; Fabry, 2008; Hoegh-Guldberg & Bruno, 2010; Devictor *et al.*, 2012). Climate change has also been related to changes in other geophysical processes and biological responses such as ocean acidification impacting calcification (Fabry, 2008), oxygen depletion and the growing expansion of dead zones in the world oceans (Stramma *et al.*, 2010) and iron enrichment and ocean productivity (Shi *et al.*, 2010). The great variety of physiological processes that are mediated by temperature, pH, oxygen, and nutrients highlights the broad spectrum of processes potentially influenced by climate change. Among coral and reef fish species, it is often argued that these changes are happening too fast for species to adapt, although this has been topic of debate (e.g., Mora & Ospina, 2001; Baird & Maynard, 2008; Hoegh-Guldberg & Bruno, 2010; Pandolfi *et al.*, 2011).

Interaction among drivers

A major unknown about projections of biodiversity change is the extent to which anthropogenic threats interact and potentially accelerate the risk of extinction (Myers,

1995; Sala *et al.*, 2000; Mora *et al.*, 2007; Brook *et al.*, 2008; Mora, 2008). Around 70% of the animal and plant species currently critically endangered are so by the effects of two or more anthropogenic factors (Figure 17.1). Although it is often said that anthropogenic stressors interact in a synergistic manner (i.e., causing a larger effect than the individual effects combined), a recent meta-analysis indicated that cases of synergies are rarer than simple additive or antagonistic effects (Darling & Côté, 2008). Examination of 57 experimental studies combining the effects of multiple stressors indicated that synergistic interactions occurred in 36% of the cases, whereas non-synergistic responses were reported in the remaining 64% of the cases (i.e., 42% and 22% reported antagonistic and additive effects, respectively). These results, however, need to be considered within context. For instance, Mora *et al.* (2007) showed that the interacting effects of habitat loss and overharvesting were additive whereas the interaction of either habitat loss or overharvesting with warming led to synergistic declines in population size in either case.

Although the effect of interacting factors is likely to be case specific, empirical studies highlight multiple mechanisms through which co-occurring factors interact and add to the decline of wild populations (Figure 17.2). In the marine realm, for instance, climate change can accelerate the development of pelagic larvae, which in turn reduces the potential for dispersal. Simultaneously, climate change is reducing the suitability of habitats, therefore increasing their isolation. This combination of reduced dispersal capabilities and increasing isolation of habitats adds to the species' risks of extinction (Mora & Sale, 2011). Another example is the ongoing decline in wild frog populations, which appears to be linked to an interaction between global warming and disease. Some suggested mechanisms include an upward extension of fungal pathogens to encompass virtually all high-elevation anuran

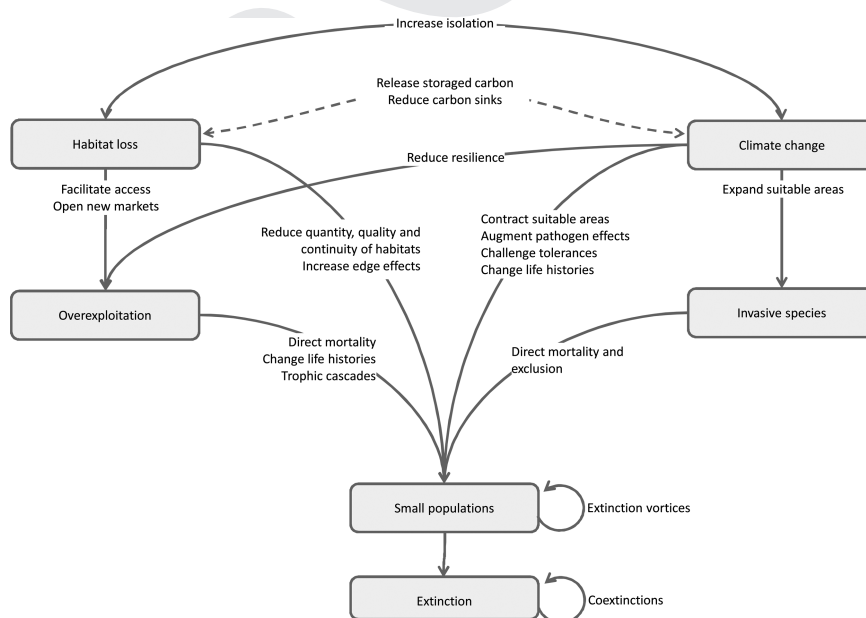


Figure 17.2. Independent and interacting effects of anthropogenic stressors on species.

habitats (Seimon *et al.*, 2007) and a shift in environmental conditions that are optimum for the growth of pathogens, thus encouraging outbreaks (Pounds *et al.*, 2006). A similar situation has been reported for coral species, where ongoing exposure to stressors such as warming and pollution appear to have undermined their resilience, making them particularly vulnerable to mortality by diseases (Bruno *et al.*, 2007; Mora, 2009; Rogers, 2009). In general climate change might facilitate invasions by non-indigenous species that act as novel competitors, predators or pathogens (Brook *et al.*, 2008) and such effects may be exacerbated if invasions occur simultaneously with the loss and deterioration of habitats (Didham *et al.*, 2005). Another interesting mechanism involving the interaction of stressors is how roads and associated habitat loss grant access to new grounds for exploitation and trade of species (Macdonald *et al.*, 2012).

Intrinsic characteristics and resilience to stressors

The extent to which anthropogenic factors will result in changes in the distribution of species depends to a large degree upon life history characteristics or intrinsic attributes of species. For example, the contrasting effect of anthropogenic stressors in animals and plants (Figure 17.1) is very likely to be due to different life histories offering different levels of resilience. More specifically, for instance, the expansion and/or collapse of species subjected to excessive fishing appears to be strongly mediated by behavioral aggregations which increase their rate of harvest, body size which makes them particularly targeted, and longevity and fecundity which affect their rate of recovery (Pauly *et al.*, 1998; Worm & Tittensor, 2011). Likewise the resilience to habitat loss appears to be undermined in species that are rare (in abundance), specialized (in habitat and food), have little dispersing capabilities, high population variability and high trophic position (Davies *et al.*, 2000; Tschardtke *et al.*, 2002; Öckinger *et al.*, 2010). Resilience to climate change may also vary among species depending upon their abilities to disperse (Dolman & Sutherland, 1995; Warren *et al.*, 2001; Parmesan & Yohe, 2003; Franco *et al.*, 2006; Lawler *et al.*, 2010), ability to alter migration routes (Dolman & Sutherland, 1995), physiological tolerance (Mora & Ospina, 2001; Jiguet *et al.*, 2007) and the timing and frequency of reproduction to maximize recovery and chances of adaptation through mutations (Mora *et al.*, 2007) to name some. It should be noted, however, that some traits of resilience may not be sufficient to withstand widespread and intensifying anthropogenic stressors. For instance, abundant and widespread species are markedly underrepresented in the extinction record, indicating their resilience to extinction, perhaps due to possessing these traits (McKinney, 1997; Şekercioğlu *et al.*, 2012), yet a number of species that are currently highly threatened or have recently become extinct due to anthropogenic factors were at some point considered common and widespread (Gaston & Fuller, 2007).

Alternative equilibrium states

One of the most worrisome pieces of knowledge about the current loss of biodiversity is the possibility that such changes could be irreversible if species get locked into alternative and less desirable states. This may occur if the processes of adaptation to ongoing

and intensifying anthropogenic stressors leads to a loss of genetic diversity and the fixation of “maladaptive” traits (Walsh *et al.*, 2006; Swain *et al.*, 2007; Allendorf & Hard, 2009; Conover *et al.*, 2009; Darimont *et al.*, 2009). It should also be noted that “maladaptations” that impair demographic processes can potentially cause extinction in what has been defined as “evolutionary suicide” (Rankin & Lopez-Sepulcre, 2005). Evidence of changes in life traits induced by human stressors is diverse. For instance, overexploitation, by taking large proportions of the populations and targeting large, reproductive-aged adults, has been shown to induce particularly rapid and dramatic changes in life history traits of fishes, mammals, and plants (Allendorf & Hard, 2009; Darimont *et al.*, 2009). Experimental evidence suggests that intensified size-selective fishing induces substantial declines in mean body size, fecundity, and larval viability, which in turn detrimentally affect recruitment, yield, and biomass (Conover & Munch, 2002; Walsh *et al.*, 2006). Likewise, increasing warming has been related to reductions in body size (Sheridan & Bickford, 2011), clutch size (Winkler *et al.*, 2002), accelerated early development among marine organisms (Hoegh-Guldberg & Bruno, 2010; Mora & Sale, 2011), and mismatches between key reproductive and migratory cycles (e.g., matching reproduction to the production of early stages of zooplankton is essential to ensure sufficient food supply and larval survival in cod; Bollens *et al.*, 1992; some birds also link their reproduction to coincide with peaks in food availability, which maximize offspring survival; Visser *et al.*, 1998). Since temperature is fundamental to the biochemistry of most organisms, some physiological responses may be “inescapable” in the face of changing climate (Sheridan & Bickford, 2011). Induced evolution may also occur in response to habitat loss. For example, differential sex-mortality combined with an isolation of habitats by fences and roads has led to an increase in clutch size but a reduction in the years nesting in American prairie-chickens (*Tympanuchus pallidicinctus*); this trade-off increased the species’ susceptibility to year-to-year environmental variations and appears to explain observed population declines in the species (Patten *et al.*, 2005). Habitat loss and subsequent fragmentation may also induce genetic bottlenecks since isolation may lead to inbreeding, reduced reproductive output, and genetic drift; these responses are often associated with extinction debts in which genetic diversity is lost slowly over multiple generations (Lowe *et al.*, 2005). Even invasive species have been documented to induce morphological, behavioral, physiological, and life history changes in native species (Carroll, 2007); as a case example, some Australian snakes have evolved a reduced size of their mouth as a way to escape the lethal effect of eating poisonous invasive cane toads (Phillips & Shine, 2004).

The potential to reverse “maladaptations” depends on the degree to which such changes are genetically based and the severity of the loss of genetic diversity. Recent advances on genome-wide scanning are likely to improve our understanding of the genetic basis of phenetic changes induced by anthropogenic stressors (Dettman *et al.*, 2012). However, empirical studies have shown that many collapsed fish populations have failed to recover after a decade or more with little fishing (Hutchings, 2000; Swain *et al.*, 2007), supporting the hypothesis that induced changes are affecting the genetic makeup of species and that such changes may be irreversible (Swain *et al.*, 2007) or very hard to reverse (Allendorf & Hard, 2009). The challenge of reversing genetic changes is

supported by some models (e.g., de Roos *et al.*, 2006). If ultimately such changes lead to extinction, it is worth noting that the replacement of extinct species (i.e., through origination of new species) in prior mass extinction events has been of the order of 10s of millions of years (note that a large number of niches were probably vacant after those mass extinction events) (Kirchner & Weil, 2000).

Extinction vortices and chains of extinction

Studies into patterns of extinction have revealed that declines in abundance and distribution imposed by anthropogenic stressors can be self-accelerated (i.e., the so-called extinction vortices). In turn, the decimation and/or extinction of species may lead to the extinction of other species (i.e., the so-called “chain of extinction”; Brook *et al.*, 2008) and disruption of ecological processes (i.e., the so-called “phase shifts”, “trophic cascades” or “alternative states”; Bellwood *et al.*, 2004; Myers *et al.*, 2007; Heithaus *et al.*, 2008; Jackson, 2008). Patterns of extinction in monitored vertebrate species confirmed, for instance, that time to extinction scales to the logarithm of population size (i.e., the decline of populations is accelerated as the time-to-extinction is approached; Fagan & Holmes, 2006). It is likely that a combination of loss of genetic variation (which decreases population adaptive potential; Elam *et al.*, 2007), inbreeding depression (due to the limited number of mates to choose from, which in turn increases the expression of recessive deleterious genes and over-dominant genes; Soulé & Mills, 1998; Tanaka, 1998), Allee effects (Myers *et al.*, 1995), and environmental variability (Soulé & Mills, 1998; Tanaka, 1998) may all contribute to a general corrosion of population dynamics, causing a negative per-capita replacement rate as extinction is approached.

The consequences of a particular anthropogenic stressor may not end with the extinction of the species directly under threat, if such a species is critical to the viability of other species or ecosystem processes. In one of the most comprehensive assessments of “co-extinctions” or “chains of extinction”, Koh *et al.* (2004) analyzed coevolved interspecific systems (e.g., predator/prey, herbivore/plant and parasite/host) among species currently listed as extinct or endangered in the IUCN Red List. Their results indicate that 204 affiliate species may have become extinct historically due to the extinction of 399 host species. Likewise 9491 species currently endangered may be host to 6088 affiliate species, which thus are currently “coendangered” and likely to go extinct if their hosts become extinct. As a result of tight ecological interactions, induced changes on specific species can transcend to broader ecosystem consequences in what is named phase shifts, trophic cascades or alternative states (Bellwood *et al.*, 2004; Myers *et al.*, 2007; Heithaus *et al.*, 2008; Jackson, 2008).

Concluding remarks

Quantifying the relative role of anthropogenic drivers in the loss of biodiversity is likely to remain challenging and, if shown, such studies are likely to demonstrate that the relative role of such factors may not be generalized among and even within species. For

instance, the response of primates to forestry, agriculture, and hunting showed that the relative vulnerability of particular species to one threat does not predict its response to others, which is expected considering that different biological traits will determine the response to each type of threat (Isaac & Cowlishaw, 2004). Likewise Cardillo *et al.* (2008) showed that a global model of different types of predictors related to human and environmental impacts, species' life history traits and ecology did have a low explanatory power in determining extinction risk among mammals. These studies suggest that species responses to anthropogenic stressors are likely to be highly individualistic. However, despite this lack of generality and difficulty in quantifying the relative effect of individual drivers and mechanisms, there is overwhelming evidence to suggest that, from a cautionary and ethical perspective, threatened species should be managed as if all stressors at play were responsible for their decline. Arguably, the focus could also be shifted to what drives overexploitation, habitat loss, climate change, and invasive species in the first place. This focus will make clear that at the core of these stressors are our patterns of consumption and ongoing population growth (Mora & Sale, 2011). This focus will require a shift in conservation perspectives but could provide more definitive solutions to a broad range of stressors. The relentless loss of biodiversity and associated loss of goods and services suggest that we cannot afford much delay before choosing the right response to these stressors.

Synopsis

Humanity has taken a heavy toll on the Earth's biodiversity. Clues for such a human footprint are found ever since prehistoric times but have become considerably more evident and severe in recent times. We are now on the verge of a sixth mass extinction event whose causes are well connected to stressors such as habitat loss, overexploitation, invasive species, and climate change. While the relative effect of such stressors will remain challenging to quantify and will most likely be individualistic, there is considerable evidence to suggest that from a cautionary and ethical perspective, threatened species should be managed as if all stressors at play were responsible for their decline. Arguably, a less contentious conservation strategy could focus on what drives such stressors in the first place, which will probably reveal the role of our patterns of consumption and ongoing population growth. This new focus will require a shift in conservation perspectives but should deliver more definitive solutions to a broad range of issues. Regardless of the solution, the rapid loss of biodiversity, goods, and services suggests that we cannot afford much delay before choosing the right response to these stressors.

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