Chapter 2

Characteristics of Collapsing Ecosystems and Main Factors of Collapses

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Additional information is available at the end of the chapter

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Abstract

The synergistic effects of direct human perturbations and climate change have been causing the mass extinction of species. Here, I present the deterministic factors of collapses in present ecosystems. I captured and synthesized the key deterministic traits and processes before a collapse in the peer-reviewed literature. The results of the literature review show that deterministic factors can be used as early warning signals of collapses. The literature also suggests that we have entered the middle stage of global mass extinction, which may be irreversible.

Keywords: climate change, human perturbation, collapse, mass extinction, biodiversity loss, early warning signals, positive feedback

1. Introduction

The synergistic effects of direct human perturbations and climate change have been causing the mass extinction of species. The current extinction rate is about 100–1000 times the background rate. The local biodiversity intactness in terrestrial ecosystems is perhaps already beyond the planetary boundary on more than half of the world's land surface [1]. About 70% of the forests are within 1 km of the forest edges, which reduces biodiversity by 10–70% [2]. According to the IUCN Red List of Threatened Species [3], 10–30% of the world's amphibian, bird and mammal species are threatened by extinction. Wilson [4] suggests that half of the species will face an extinction by 2100. Nonlinearities, positive feedbacks, abrupt collapses and regime shifts are being observed globally. The rate of temperature increase, ocean acidification, sea level rises, anoxic ocean dead zones and extinctions make the recent mass extinction comparable with the “Big Five“, even with the greatest End Permian extinction event, which wiped out 90% of species [5].

It is essential to explore all the phenomena and processes, which define the recent mass extinction to detect vulnerable ecosystems and predict the tipping points of collapses. It would be important to determine the stages of the extinction to make better predictions. Here, I present the deterministic factors of extinctions which characterize the first stage of mass extinctions. I identify the deterministic factors and their effects in recent ecosystems based on peer-reviewed literature. The results suggest that the effects of deterministic extinction traits are manifold and cascading. They represent the starting point of extinctions hence they can be used as early warning signals of collapses.

2. Triggers of recent mass extinction

The triggers of extinction can be classified into two groups, namely direct and indirect human effects. Indirect human effects usually refer to the ongoing anthropogenic climate change. The first stage of recent mass extinction is dominated by mainly direct human effects, however, climate change is becoming a contributor of sudden collapses as well.

2.1. Direct human effects

Direct human effects such as deforestation, hunting, pollution, alter the environment directly through human activities. They can be traced back to as early as the Upper Paleolithic (50–10 ka) when modern humans expanded their ranges throughout Eurasia and started to exert a great impact at a larger scale. At that time their social groupings, artifacts, tools, communication skills became much more sophisticated and specialized than before. These changes made humans more effective hunters. The increased human pressure probably contributed even to the great Pleistocene megafaunal collapse (14.8–13.7 ka) as well [6]. Development and population growth have always reinforced each other throughout the whole history. The main corner steps of this process were the appearance of agriculture (approx. 10 ka), the age of discovery (fifteenth to eighteenth century) followed by the industrial revolution (1760–1840). The global population is now over 7 billion and it is increasing by more than 80 million per year [7]. This huge pressure is manifested as direct human effects which have triggered a global mass extinction. Species and their habitats are disappearing leading to a great biodiversity loss and homogenized landscapes. Tylianakis et al. [8] pointed out that habitat modifications can alter the food web structure, decreases the evenness of interaction frequencies and increases the abundance of parasitoids. Habitat alteration and fragmentation induce processes which would not happen under normal circumstances. For instance, habitat alteration can enhance hybridization. Just to give an illustrative example, in the USA male wolves have difficulties in finding conspecific mates because of deforestation. Therefore in deforested areas they tend to pair with female coyotes which are abundant there. The genetic transfer of coyote mitochondrial DNA into wolves can give rise to a new species but it can also cause the collapse of gray wolves [9] which are critical keystone species. Without their top-down control, biodiversity starts to decline. Overhunting also affects biodiversity and biomass. It modifies the trophic structure and the species interactions. Sudden collapses and delayed extinctions are present in the ecosystems at the same time as a result of direct human perturbations.

2.2. Indirect human effects

Indirect human effects usually refer to the ongoing anthropogenic climate change. Indirect human effects are, actually, the consequences of direct human activities and they are almost as old as direct effects if we accept the hypothesis that Paleolithic humans were one of the main triggers of the Late Pleistocene megafaunal extinction as the extirpation of mega-herbivores had an effect on the climate via vegetational and atmospherical changes [10]. Later, the spread of agriculture and the industrial revolution accelerated climate change dramatically. Agriculture modifies the climate in many ways. It is a great emitter of greenhouse gases, it increases radiative forcing through landcover alteration and it contributes to desertification. However, industrialization catalyzes the anthropogenic climate change even more. Since the mid-nineteenth century, the CO_2 level has risen from 280 to 400 ppm. By 2100, CO_2 may reach 700–800 ppm which means 3–4°C temperature increase [11]. Climate change creates feedback loops. As a result of temperature increase and ice-albedo feedback mechanism, the Arctic ice is melting. Such events usually indicate mass extinction boundaries between geologic eras according to the paleological records. Climate change increases the number of extreme events, such as severe droughts, extreme precipitation, floods, heat waves and probably hurricanes. The changes are so rapid that the wildlife may not be able to adapt and in the end it will collapse. It is important to note that direct and indirect effects act synergistically reinforcing the positive feedback loops. Direct effects decrease biodiversity and biomass. They weaken the connections in ecosystems. Hence, they increase the overall proneness to stochastic events.

3. Deterministic factors of extinctions

The deterministic factors of extinctions initiate collapses, which suggests that they could be used as early indicators of dramatic changes. Species with several deterministic factors are under the greatest threat. These species are often adapted to specific circumstances therefore they are severely hit by climate change. Their extinction brings about disrupted species interactions, ecosystem functions and trophic structure. Vulnerability, co-extinctions, homogenization and positive feedback loops are the main consequences. Here, I review the deterministic factors of collapses based on literature. I also investigate the severity of their effects in recent ecosystems.

3.1. Environmental factors

Climatic changes and pollution create unfavorable environmental conditions which make species prone to collapses.

3.1.1. Climate

Climate change alters the whole physical environment. It changes the precipitation pattern, increases the number of extreme weather events (fires, droughts, tsunamis and tropical cyclones). Climate change affects biogeochemical cycles and intensifies positive feedbacks [12]. Sea ice extent decreases, glaciers retreat, sea level rises. Ice cover retreating can increase volcanism and the number of intense earthquakes [13, 14]. Oceans suffer from extreme heat events, acidification, perhaphs slowing thermoline circulation [15] and oxygen depletion. All these changes reduce fitness and fertility. Climate change affects abundance, species richness and it can even drive genetic changes [16]. At local scale, vulnerable species respond to climatic changes with quick collapses [17].

3.1.2. Pollution

Pollution is also a main contributor of extinctions. Air, water and soil pollution severely affect the wildlife. Agriculture, industry, transportation and the commercial sector emit harmful materials, noise and excess light. Even everyday people produce an immense amount of waste. EU statistics show that a single person generates half a ton of municipal waste per year and only 50% of the waste is recycled [18]. Chemicals are getting more and more potent, but also more destructive in many cases. Pollution significantly alters the physical and chemical characteristics of the environment. Local pollution can easily turns into regional disaster. Air, water and soil communicate with each other, which means that soil contaminants can get into the water and the air, and from the air toxic contaminants can deposit in the soil and water again making pollution a large-scale problem. The consequences of pollution are manifold. It causes ozone depletion, acid rain, algal bloom, anoxic marine dead zones, waste accumulation and soil depletion. Contaminated plants and animals show reduced fitness, fertility and shortened lifespan. Pollution damages ecosystems and disrupt their functions. Unfortunately, the rate of pollution will probably keep increasing because of global population growth and short-term economic interests [18].

3.1.3. Habitat destruction

Pimm and Raven [19] suggest that habitat destruction is the primary reason for species extinction. Anthropogenic activities (agriculture, industry and urbanization) are the main causes of habitat destruction. Biodiversity hotspots which are the most species-rich regions on Earth are declining rapidly. Tropical forests once covered about 14% of the Earth [20]. Today they occupy less than half of the original area. About 70% of species live in tropical forests [21]. According to Myers [22], 66% of plant species and almost 69% of bird species will disappear if Amazonian forests are restricted to only parks and reserves as a result of deforestation. Deforestation also affects carbon balance. According to Baccini et al. [23], tropical forests are becoming a net carbon source as a result of deforestation and from reductions in carbon density, and this way they cannot dampen the effects of climate change any more. Wetlands which provide vital ecosystem services are also threatened. They are one of the most biologically diverse ecosystems. They clean fresh water by filtering pollutants and neutralizing harmful bacteria, and they prevent devastating floods. They serve as carbon sink and shoreline stabilizer, as well. More than one-third of wetlands have been lost globally [24]. Europe has suffered the greatest loss: more than 60% of European wetlands have been destroyed [25].

Coral reefs are also one of the most diverse ecosystems on Earth. They harbor 25% of marine species [26]. They offer several important ecosystem services, such as tourism, fisheries and shoreline protection. Coral reefs are vulnerable to climate change, fishing and pollution. As of 2005 data, about 20% of coral reefs have been lost so far [27]. However, not only direct habitat destruction, but also indirect disturbances can lead to disturbed habitats and species loss [28, 29]. Ecosystems are melting globally. Main consequences are the loss of biodiversity, the loss of valuable ecosystem services, landscape degradation, increased vulnerability to stochastic events, altered carbon cycles and disrupted climate regulation.

3.2. Geographical factors

The literature suggests that the extinction rate decreases with increasing elevation under the effect of human pressure.

3.2.1. Lower elevations

Due to ongoing climate change and human pressure, a lot of marine and terrestrial habitats have become vulnerable to extinction. Species distribution has changed a lot during the modern historical period. The lower elevations are the most accessible to the ever-growing human population. As a result, many species which are targets for overhunting and/or have poor environmental tolerance have already disappeared from these regions [30]. Lomolino and Channell [31, 32] explain these changes in geographical distribution with their 'contagion model'. They suggest that anthropogenic disturbances spread like a 'contagion' and only populations which live along the edges of historical ranges can survive. The remnant populations with a small number of individuals are at a great risk of extinction as they probably live under suboptimal conditions and they usually have no potentials to migrate to optimal habitats because they are poor dispersals or they have narrower environmental tolerance [30].

3.2.2. Mid and high elevations

Species living at higher altitudes may be at risk too because they have small geographical ranges and they have nowhere to migrate [30]. Upward shifting of other species also puts pressure on them. The changing climate is becoming unfavorable as well. Warm and/or dry conditions can cause stress and shifts in phenology [16, 33] and the spread of pathogens [34]. Though recent studies suggest that middle-elevation species are affected more than the ones living at high-altitude because pathogens thrive at higher temperatures [34, 35]. Lowland species pressure, direct human effects and climate change-induced pathogens altogether jeopardize the more accessible mid-elevation regions.

3.2.3. Latitudes

The poleward shifts of species have been observed as a result of climate change during the recent decades [16]. The high latitudes are under great pressure. Tundra is warming twice as fast as the global average [11, 36] resulting in intense permafrost thaw, carbon release and woody encroachment which make them extremely vulnerable [36]. Climate warming, the greenhouse gas release of permafrost, shrub expansion create a positive feedback loop which turns tundra into boreal forest [37]. Low latitudes are also mentioned as vulnerable regions in the literature several times because of direct (overhunting, logging and pollution) and indirect effects (climate change-related heat susceptibility) [17, 28, 38]. Regime shifts, such as coniferous to a deciduous boreal forest, forest to savannas, steppe to tundra can be expected in the future [37, 39, 40].

3.2.4. Edges

It is a long-debated question if edge populations are more vulnerable to environmental changes than central populations. According to Merriam and Wegner [41], ecotones show higher extinction rates than core regions. Recent studies show that climate change may affect the core populations as well. Bennett et al. [42] created a model based on the observation of seaweeds and concluded that both central and edge populations can show the signs of heat susceptibility under recent climate change. They considered the thermal-safety margins of the populations and not the absolute temperature tolerances. According to their results, both core and edge populations displayed similar thermal stress anomaly. They pointed out that range contractions reflect the anomaly and not the variation in the absolute temperatures. Peres et al. [43] raise the question whether the core regions of Amazonia include intact forests or they are already disturbed. Indirect effects (e.g. selective logging and hunting) weaken the core regions and make them vulnerable to stochastic events.

3.3. Biotic factors at species level

Extinction traits have been studied for a long time. McKinney [44] suggests based on fossil and modern data that specialization is a main factor in extinction. He mentions *adaptation to narrow range of temperature, specialized diet, large body size, low fertility, slow maturation, long lifespan, complex morphology and behavior, limited mobility and migration* as individual extinction traits. Many of them are typical characteristics of K-selected species. The list can be extended by general drought/heat susceptibility and hidden failures based on recent literature on climate change.

3.3.1. K-selected species traits

Numerous studies of recent mass extinction focus on the ongoing loss of large-bodied species. At this point of extinction, the main driving factors of their extinction are direct human perturbations, such as overhunting and habitat destruction. Most ecosystems, both terrestrial and marine systems are affected, which gives rise to concerns. Large animals usually have an important role in ecosystems. Many of them are keystone species and ecosystem engineers providing important ecosystem services. They maintain biodiversity whether they are apex predators or mutualistic seed dispersals. The loss of large-bodied species initiates the disappearance of positive species interactions. Climate change also affects large animals. Climate change-induced body size shrinkage has already observed in terrestrial and marine systems as well [16]. The main problem is that large animals cannot be replaced by small ones [45], and this way important ecosystem functions will disappear for good [46].

One of the most affected large-bodied animals is megaherbivores which are keystone species in terrestrial ecosystems [47]. Historical and modern data and models show that the loss of megaherbivores causes altered ecosystem structures and functions [6, 48, 49], and even a collapse [50]. Megaherbivores are threatened by several factors acting synergistically, such as hunting, habitat loss via human overpopulation, agricultural land use and deforestation [51]. Climate change also has a negative effect on large-bodied herbivores. Woody encroachment ceases their habitats, decreases their biodiversity and biomass in the long term [49]. Disappearing herbivores means decreasing environmental heterogeneity [52], which can make the ecosystems more vulnerable to stochastic events and it can also brings about the collapse of carnivores [49, 50].

The loss of large apex consumers has an effect on the herbivory intensity, and thus the abundance and the composition of plants, which can result in a regime shifts [53]. Without top-down control, the patterns of invasion, diseases, wildfire, biogeochemical processes and carbon sequestration alter [54]. Nevertheless, it is important to note that carnivores are not strong keystone species anymore because of their low abundance in terrestrial ecosystems, therefore their positions in food webs are already replaced by other species in many cases [47]. This fact also suggests that large carnivores solely cannot be used as effective early warning signals of vertebrate collapse [55]. However, de Thoisy et al. [55] also concluded that apex predators can be effective bioindicators of a forest collapse but only combined with forest structure, phenology and vertebrate community.

As a result of human pressure, large-bodied animals are becoming rare. The populations of large-bodied species are getting smaller and smaller mainly because of overhunting. Some rare and large-bodied species are experiencing collapse through hybridization. Kleindorfer et al. [56] observed that female individuals of rare, large-bodied tree finch species paired with smaller and common finch species in the Galápagos Archipelago. They suspect that the population of large-bodied species collapsed under the conditions of hybridization. They also assume that the hybrids gained fitness benefits. Vaz Pinto et al. [57] studied human-induced interbreeding between large-bodied, sympatric antelopes in Angola. Hybridization between sympatric species never happens under normal circumstances, therefore it is a strong sign of a decline. As a result, parental species almost collapsed and the hybrids also showed reduced viability and fertility.

3.3.2. *Specialized diet*

Recent studies show that specialized diet can lead to an extinction cascade even if the consumers can shift their diet. Gilljam et al. [58] modeled predator-prey co-extinctions with network model based on antagonistic natural and computer-generated food webs. They concluded that it is an effective short-term survival strategy for specialized predators to switch to a new prey after the extinction of the only previous prey. However, it can lead to the overexploitation of the novel prey in the long term, for example, if the predator is more mobile and the prey is rare. Gilljam et al. [58] noted that some external stochastic factor is also needed besides predation to trigger prey extinction. According to the authors, climate change-induced extreme weather events affect preys more than predators. Switching diet can improve the survival prospects but only in the short term [52]. In the long term, climate change affects negatively most specialized species, therefore diet shift only postpone the extinction of species.

3.3.3. Heat/drought susceptibility

Considering climate warming, sternothermy, which is the adaptation of species to a narrow range of temperature, can be an *Achilles' heel of susceptible species. It is projected that the sea surface temperature may rise by 3°C by the end of this century. Marine organisms living near the Equator, especially sessile species, are under great threat as they are adapted to a very narrow range of temperature* [59]. Perry and Morgan [17] observed the extinction of the most abundant reef-building species on the southern Maldives reefs. This species was the less tolerant to the changes in temperature, thus the most vulnerable to warming events. The mass mortality of the fast-growing, most abundant species brought about the secondary extinction of other species and a complete collapse. However, mobile tropical species are also jeopardized. Rummer et al. [59] conducted an experiment to test the thermal tolerance windows of tropical fish species. They pointed out that even relatively small temperature rise (2–3°C) can lead to local extinctions. They also suggest that species slow in adaptation will move to higher latitudes.

Climate change-driven seasonal changes in precipitation and temperature affect several ecosystems all around the world. Brookshire and Weaver [60] investigated biomass decline of grasslands in the Greater Yellowstone Ecosystem for 40 years. According to their results, the grassland production decreased by more than 50%, mainly because of a drop in late summer rainfall. Even drought-resilient forest types produce canopy collapse due to extreme drought and heat events [61]. Mortality as a result of heat susceptibility is not a stand-alone phenomenon. It can trigger co-extinction especially if keystone species, symbiotic species are involved. Kikuchi et al. [62] carried out an experiment on a pest insect and its heat-susceptible bacterial symbiont. They pointed out that mid-summer extreme heat can cause a significant decline in the insect population because of the collapse of its symbiont vulnerable to heat stress.

3.3.4. Hidden failures

Species might have some hidden failures which are revealed only when the environmental conditions change significantly. Torres-Ruiz et al. [63] reported on the hydraulic failure of tropical trees in the Amazonia. The synergistic effect of highly vulnerable xylem tissues and the more frequent and extreme droughts because of climate change results in forest dieback.

3.3.5. Endemic or relict species with weak dispersal capacity

Species restricted to geographic locations are threatened by both direct and indirect human effects as they have nowhere to migrate. Sandel et al. [64] investigated the relationship between Late Quaternary climate change velocity and the presence or absence of endemic species. They found that endemics, especially weakly dispersing amphibians, disappeared in high-velocity regions. Areas with low-velocity preserved small-ranged species. Sandel et al. [64] modeled future climate change and found discrepancies between the patterns of past and future climate change, which suggests that past low-velocity areas with a high number of endemic species may become high-velocity regions. For example, the western part of Amazonia and Central Africa which hosts many endemic and rare species may face great climatic changes in the future, according to the authors. Bergstrom et al. [35] observed the rapid collapse of a Sub-Antarctic alpine ecosystem after the loss of keystone endemic cushion plant. Climate change-modified climatic conditions. It decreased summer water availability, increased wind speed, sunshine and evaporation, which increased stress in cushion plants. Bergstrom et al. [35] suspect that the increased environmental stress made the plants more susceptible to pathogens.

3.4. Biotic factors at population level

3.4.1. Abundance

Significant changes in abundance traits are typical signs of extinction. Small ranges as a result of hunting, deforestation and fragmentation, low abundance, decreased population growth rates [16], seasonal population aggregation [43] can increase extinction proneness. Although the global overall aboveground biomass has increased during the recent years [65], a decrease in the abundance at local and regional scales can be experienced. The main drivers are still direct human disturbances; however, climate change-related abundance changes have also been reported.

Common species are becoming rare [66], which decreases resilience and increases the vulnerability to collapse. Barbosa et al. [67] conducted a field experiment to test the effects of reducing the abundance of a common species in an association of arthropods and an abundant shrub. The species richness and the abundance of other species did not change during the experiment; however, they experienced higher parasitism, lower connectance, interaction evenness and robustness. Winfree et al. [68] modeled plant-pollinator networks and they concluded that abundance is one of the most important drivers of extinction, and abundant species are the most persistent. Abundance is even more important factor than diet breadth. They also simulated what happens if an abundant species disappear first. They experienced a quick secondary extinction. Perry and Morgan [17] also pointed out that climate change can affect abundant species badly. They observed climate change-driven bleaching which caused a collapse on the southern Maldives reefs. The mass mortality of the fast-growing, most abundant species brought about the secondary extinction of other species and a complete collapse. The most abundant species was the most vulnerable to warming events, so the less tolerant to changes in temperature.

Brookshire and Weaver [59] studied a native C3 grassland in the Greater Yellowstone Ecosystem using historical records (1969–2012) to investigate the effects of climate change. They documented a more than 50% decrease in the above-ground net primary production. They blamed the decreased late-season precipitation and higher temperatures for the drought-driven production decline. They noted that CO_2 fertilization could not counterbalance the negative effects of droughts. They also pointed out that drought affects some species more seriously [59, 69]. Perennial forbs showed a greater drought susceptibility, which resulted in local extinctions with no recovery. The increased drought also caused a long-term oscillation of higher frequency in production.

3.4.2. Population cycles

Cornulier et al. [70] reported on the dampening of small herbivore cycles in several European ecosystems because of decreased winter population growth. Small herbivores provide important ecosystem functions, thus their population collapses are worrying. The authors blame climatic drivers for the increased frequencies of low amplitudes.

Barnes et al. [71] observed the local extinction of echinoid *Paracentrotus lividus* after a cycle collapse. *Paracentrotus lividus* is a keystone species which maintains trophic and food web structure as well as biodiversity. They graze algae, and thus they keep coral reefs healthy. The loss of keystone species results in regime shift and homogenization. The population showed an increased level of fluctuation since the 1920s before its collapse during the 1980s. During the collapse, old individuals became dominants. About 20 years after the collapse no individuals were found. The reason for the collapse is likely to be an increased variation of sea surface temperature with episodes of great increase which inhibited spawning.

3.4.3. Strong Allee effects

Pollinators are suffering in many ways under climate change. Dennis and Kemp [72] modeled a hive collapse due to a strong Allee effect. They concluded that strong Allee effect combined with environmental stressors (climate change, pathogens, pesticide and mites) can lead to the collapse of hives.

3.5. Biotic factors at community level

3.5.1. Positive species interactions

Facilitation or positive species interactions promote species co-existence. Facilitation maintains biodiversity and provides important ecosystem functions. It increases resilience and works as a buffer under stress [73]. Intensive direct human perturbations and climate change susceptibility of species lead to disrupted positive species interactions. The loss of positive species interactions are the signs of large-scale extinction [74].

According to the stress-gradient hypothesis, the frequency of facilitation increases with stress in plant communities. He and Bertness [75] emphasize that facilitation is enhanced and not competition under increasing physical and biological stresses. Exceptional cases are weak stress, non-limiting sources, stresses outside the niche, simultaneous multiple stresses and temporally dependent effects. Typically, dispersal-limited invertebrates and plants use facilitation to expand their species ranges. As direct human perturbations and climate change act synergistically, positive species interactions are under great threat.

Different life histories may affect the responses given to stress. Michalet et al. [76] reviewed literature on plant responses in water-stress ecosystems. They pointed out that getting closer to a tipping point, facilitation either collapses or switches to competition in plant-plant interactions. More specifically, switching from facilitation to competition is the strategy of beneficiary species due to increasing environmental stress, while nurse plant species experience the collapse of facilitation.

In many cases, extinction traits and drivers act synergistically accelerating extinction processes. For instance, a large body is considered as a main determinant factor in mass extinctions in the literature [43]. In plant-animal mutualistic relationships, large-bodied animals are frequent interacting partners. They are threatened by overhunting worldwide, thus their ecosystem functions are also jeopardized. Large-bodied, seed-dispersing species are keystone species in tropical forests [27], hence their extinction brings about ecosystem degradation. Several studies show that the overhunting of large-bodied seed-dispersing species in the Amazonian forests generates long-term biomass depletion and biodiversity decrease because of the disrupted plant-animal mutualistic interactions [27, 28, 77, 78]. Large-bodied, seed dispersals cannot be replaced by small ones [27, 44, 74], because the large seeds of neotropical trees physically cannot be consumed by smaller species. Tropical giant trees are disappearing partly because of the indirect effects of seed dispersal extinction and partly because of the direct effects of logging. As a result, giant trees are replaced by pioneers, which along with other factors are triggering a positive feedback loop and regime shifts in tropical forests [79]. Without large animals, seed dispersal distances reduce and ecosystem functions degrade [45]. However, it is very difficult to detect the degradation of species interactions, especially in a seemingly intact forest. Pérez-Méndez et al. [77] suggest that reduced 'seed dispersal distances' can be used as an early warning signal of the collapsing mutualistic plant-animal relationships.

Besides direct human effects, climate change also influences mutualistic relationships. For example, climate change causes irregularities in flowering time, which evokes failures in pollination [16, 80]. Pollination is a key ecosystem function, therefore pollinator collapses bring about the loss of an important ecosystem service [81]. Pollinators usually peform an abrupt and great biodiversity loss, which is explained by nestedness [73]. As a result of climate change, droughts are becoming more extreme in some regions. Heat susceptibility can be a weak point of mutualistic relationships. Kikuchi et al. [61] carried out an experiment and pointed out that heat-susceptible symbionts can drive symbiotic relationships into a collapse.

As we can see, mutualistic relationships are threatened by both direct and indirect interactions globally [73], which results in collapses and positive feedback loops worldwide. It is important to assess the tipping point of mutualistic communities to be able to estimate the resilience of ecosystems. When tipping points are crossed, systems give abrupt, nonlinear responses, which eventually lead to a quick collapse. Close to tipping points, ecosystems tend to slow down (usually referred to as 'critical slowing down'). Dakos and Bascompte [82] suggest that capturing this phenomenon by statistical signals can help to predict tipping points. They propose that increasing variance and autocorrelation are the best statistical indicators to assess the tipping points of mutualistic communities.

3.5.2. Negative species interactions

3.5.2.1. Competition

Positive interactions decrease competition and maintain biodiversity [83]. While positive species interactions promote co-existence, competition usually triggers an extinction. Biodiversity decrease caused by human perturbations can increase competitiveness [84]. Recent mass extinction is the result of direct and indirect human perturbations ,which act synergistically. As human pressure does not reduce and global temperature is increasing, ecosystems are under the pressure of several factors, which suggests that positive interactions are facing a great decline globally. If this tendency continues, Earth will become a homogenized system dominated by mainly negative species interactions.

It is important to note that competition is not always something 'destructive' but also has an important role in maintaining communities, even in the light of climate change. For example, increasing temperature can be beneficial for some pathogens and parasites which extend their species ranges under more favorable climatic conditions. Having non-host competitors in a community provides a dilution effect and reduces the number of infected host-species at a local scale [85].

The literature suggests that positive interactions collapse first if species cannot switch to competition [76]. Considering competitors, strong competitors have more chance to survive in most cases and they collapse later during extinction. Matusick et al. [61] conducted a field investigation and aerial survey in a Mediterranean-type eucalypt forest in southwestern Australia. The canopy collapsed in patches in the observed forest as a response to extreme water stress. The less competitive mid-story tree species collapsed first and they did not show any signs of re-sprouting.

However, stronger competitors can also fail if they perform well only under very specific environmental circumstances. Yu et al. [86] observed the collapse of a key species in a Mongolian semi-arid grassland during a long-term disturbance prevention. The species adapted the best to a narrow environmental niche that outcompeted other species within a community. However, long-term environmental changes hit this species first. In this case, the dominant key species was replaced by less competitive subdominant species.

In ecosystems which maintain high species richness, invaders are less competitive and less abundant [87]. Fragmentation as a direct human effect increases competition which in turn leads to biodiversity loss [87]. Decreased biodiversity and resilience foster the spread of invaders, generalized pathogens which are often strong competitors.

3.5.2.2. Predation

Predators, especially marine top predators are declining globally [88]. Predators have an important controlling role in healthy ecosystems. They maintain biodiversity and stabilize landscape, especially keystone species. Re-introducing wolves in the Yellowstone National Park greatly increased the resilience and re-balanced the whole ecosystem [89]. Sharks are also keystone predators. Without their strong top-down control, marine ecosystems would alter and shift to a homogenized system [88]. Predators literally keep diseases away as they can reduce the effectiveness of pathogens. Khalil et al. [85] studied a vole population, its non-host competitors and its predator in northern Sweden. They highlighted that the presence of competitors and the predator decreased the number of infected vole individuals within the population.

As a result of human perturbation, top-down control of predators either decrease or increase. Both of them can lead to biodiversity decrease. An increased top-down control usually triggers the collapse of preys. Gilljam et al. [57] created a model to investigate if a specialized predator can survive if it switches to a new prey after losing the only prey. They concluded that shifting a diet does not always help predators to survive, especially if the prey cannot escape or it is rare or the consumer is an efficient predator. Strong human perturbation can cause an increased top-down and a bottom-up control simultaneously, which leads to a long-term decline in both preys and predators [90].

3.5.3. Keystone species

Keystone species and their functions are disappearing. They are hit by both direct and indirect effects. Overhunting, hybridization and climate change [34] accelerate their extinction. Keystone species have important functions (e.g. seed-dispersing and pollination) in ecosystems. They maintain biodiversity. Their collapse, especially if they have strong top-down control, leads to regime shifts and homogenization. Megaherbivores, carnivores [46] and pollinators have key functions. Keystone species are threatened by the synergistic effects of deterministic extinction factors. For example, K-selected species traits, nestedness. Jordano [74] suggests that the disappearance of key mutualistic interactions is an early warning signal of extinctions.

4. Conclusions

Extinctions driven by deterministic factors are present in the ecosystems globally as a result of direct and indirect human effects. Both terrestrial and marine habitats are overexploited under the ever-growing human pressure. Considering environmental factors, species living at low elevations, low and high latitudes and/or in suboptimal habitats (e.g. at the peripheries of historical species ranges) are under greater threat than rest of the world. At the species level, K-selected species, especially large-bodied species, specifically large herbivores, carnivores are becoming rare mainly due to extensive hunting. Species adapted to a narrow range of temperature will probably collapse quickly, especially if they are not mobile, because of rapid climatic change. Seasonal changes in precipitation and temperature affect several ecosystems all around the world. Both grasslands and forests are suffering experiencing biodiversity and/or biomass loss and collapses [91]. Hidden failures, which are revealed only during significant changes in environmental conditions, will enhance collapses. Endemic, rare and weak dispersing species in regions with the largest and quickest climatic changes will probably die out. At the community level, positive species interactions are already melting because of the high number of species loss. Species interactions and functions are disappearing. The abundance of predators has decreased dramatically because of overhunting. Small mammal population cycles are collapsing as a result of climate change. Populations experiencing Allee effect will probably have a tendency to collapse under climate change. Common species are becoming rare, which decreases resilience and increases the vulnerability to collapse. Studies show that abundant species are one of the most persistent, except in case of specialization. The extinction of abundant species can be followed by co-extinction and rapid collapse. Literature suggests that many keystone species have deterministic species traits, which can lead ecosystems to a sudden collapse. Further consequences of human activities in the ecosystems are genetic changes, hybridization, invasion, pathogens, shorter food chains, altered trophic structure, disrupted species interactions and general homogenization.

Sudden collapses have a high priority in the literature. Frequently mentioned triggers of rapid collapses are, among others, nestedness in mutualistic communities, adaptation to a narrow range of environmental factor, keystone species with deterministic species traits. The extinction of abundant species can be followed by rapid and extensive collapse. It must be noted that deterministic factors tend to converge, which increases the probability of collapses. An ecosystem which is burdened with several deterministic extinction factors and belongs to a high-velocity region is under the greatest threat. That is why it is important to identify the early warning signals of collapses. Deterministic factors of extinctions and other factors which trigger sudden collapses are likely to be good indicators. Specialization at species level seems to be one of the most vulnerable extinction traits. According to the literature, carnivores, forest structure, phenology and vertebrate community altogether can be used as indicators of forest collapses. The collapse of mutualistic plant-animal relationships could be detected with reduced seed dispersal distances. Short-lived specialists respond to perturbation quickly, thus they can be considered as good early warning indicators, as well.

Mainly direct human effects dominate the first stage of recent mass extinction and it can be characterized by deterministic extinction factors which undermine the biodiversity and thus the resilience of ecosystems. In the next stage, which probably has already started, an increased number of stochastic events can be expected because of climate change. Stochastic events bring about the sudden collapses of the weakened ecosystems. Positive feedback loops both in climate (e.g. Arctic sea ice melting) and in ecosystems (e.g. forest collapses) are present. They are likely to indicate the onset of the middle stage of mass extinction, which may be irreversible [92].

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