

Forum

Why don't all species overexploit?



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Overexploitation of natural resources is often viewed as a problem characteristic of only the human species. However, any species could evolve a capacity to overexploit its essential resources through natural selection and competition, even to the point of resource collapse. Here, we describe the processes that potentially lead to overexploitation and synthesize what is known about overexploitation limiters in other species. We propose that there are five pathways that counteract the evolutionary drive towards overexploitation and/or mitigate its consequences: top-down trophic control, interference, cost-efficiency tradeoffs, resource trait evolution, and spatial heterogeneity. These mechanisms constrain the number of exploiters and/or lower the rate of the resource usage at the individual level. We hypothesize that in ecosystems with reasonable functional diversity, coevolution strengthens this limiter network, preventing overexploitation, and thus argue that diversity begets stability via evolution. Violent population cycles in species-poor northern ecosystems and eruptions of invading alien species are exceptions that confirm this rule, because these ecosystems either lack functional diversity or there has not been enough time for coevolution to play out its stabilizing role. We propose that the overexploitation by our own species could be prevented via a network of socio-economical limiters that act in an analogous way.

Keywords: evolutionary suicide, exploitation, green world hypothesis, trophic cascades

Synthesis

Natural selection can drive species to increase their exploitation of resources – so, why aren't all species overexploiting? In this paper, we synthesize knowledge of mechanisms that limit overexploitation. We present five pathways that counteract the evolutionary drive towards increased exploitation and mitigate its consequences: top-down trophic control, interference, cost-efficiency tradeoffs, resource trait evolution, and spatial heterogeneity. Functional diversity and coevolution appear to strengthen these limiters, and thus we argue that diversity begets stability via evolution. A network of analogous socio-economical limiters could also mitigate overexploitation by humans.



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Introduction

Amid the current environmental crisis, humanity is faced with the great challenges of how to stop utilizing resources faster than they renew, and how to prevent land, water and geosphere usage that degrades the quality of our habitat. The problem of destructive use of environment has been addressed by politics and numerous fields of sciences, yet, greenhouse emissions accumulate (IPCC 2019), the 6th mass extinction continues, and ecosystem services and functioning are threatened across the globe (Pimm et al. 2014, Díaz et al. 2019). However, these challenges are not unique in the biosphere. We are surrounded by millions of species that have already faced the danger of destructive resource exploitation during their evolutionary histories (Vuorinen 2018).

The danger of destructive exploitation arises from the basic principles of evolution. Natural selection leads to the increase of genes that promote their own propagation, resulting in individuals that prioritize their own survival and reproduction (Dawkins 1976, Okasha 2006) over sustainable resource use for the common good (Rankin and López-Sepulcre 2005, Kokko and Heubel 2011, Rankin et al. 2011, Morris et al. 2016). Selection at higher levels, such as between groups, species, or eco-energetic networks (Wynne-Edwards 1962, Patten and Odum 1981) is rare and weak, and hardly ever capable of overriding individual selection (Okasha 2006, Jeler 2018). Pursuit of immediate individual gain can be expected to result in 'laissez-faire' exploitation, generating scramble competition where individual fitness is maximized by maximal ability to depress limiting resources while still surviving and reproducing (MacArthur 1972, Tilman 1982).

Destructive resource use, caused by increase of individual exploitation capacity and the consequent population growth, could thus be expected to be the baseline for all organisms – not an anomaly encountered only in human species.

In laissez-faire exploitation systems, the consequences of an exploiter evolving higher exploitation capacity mimic the consequences of enrichment (Rosenzweig 1971). Initially, increasing the attack rate of the exploiter increases the productivity of the resource and the equilibrium density of the exploiter. When the point of maximum sustainable resource yield (the resource density yielding the highest possible sustainable catch, Sutherland 2001) is reached, the equilibrium density of the exploiter starts to decrease (Abrams 2019). Simultaneously, the exploiter–resource equilibrium approaches a bifurcation point where a locally stable equilibrium is replaced by limit cycle dynamics. The ensuing cycles are characterized by periodic, severe resource depressions, followed by precipitous crashes in exploiter numbers, creating an acute extinction risk (Rosenzweig 1971, Getz 1998, Turchin 2003). Such situations will here be referred to as overexploitation, as opposed to prudent exploitation, where the equilibrium is stable and resource renewal rate is high. Trophic exploitation thus forms a gradient where increasing exploitation capacity is first advantageous both for individual exploiters and for the species. At some point along this gradient, however, the situation changes dramatically: what is good for an individual exploiter becomes an extinction risk for the species.

Trophic exploitation and cascades that result from it are indeed widespread in the biosphere (Terborgh et al. 2001, Estes et al. 2011, Ripple and Beschta 2012, Letnic and Ripple

Table 1. Examples of organisms with self-detrimental exploitation patterns and the resources they exploit. Only species with documented cases (see the references for details) are included.

Organism	Exploited resource	Self-detrimental exploitation patterns	References
Bacteria that manipulate host reproduction, e.g. certain lineages of <i>Wolbachia</i> bacteria	Host insect population	Eliminates male insects to drive reproduction, and thus endangers the existence of the host population.	Hurst et al. 2002, Dyson and Hurst 2004
Edible frog <i>Pelophylax klepton esculentus</i>	Parental species population	Outcompetes the population of parental species that is essential for edible frog in hybridogenetic reproduction system (sexual parasitism).	Anholt et al. 2003, Hoogesteger et al. 2014
Amazon molly <i>Poecilia formosa</i> females	Relative species population (e.g. <i>P. mexicana</i>)	Outcompetes the population of relative species that is essential for Amazon molly in gynogenetic reproduction system (sexual parasitism).	Heubel et al. 2009, Kokko and Heubel 2011
Canada lynx <i>Lynx canadensis</i>	Snowshoe hare – prey	Collapses the prey population.	Korpimäki et al. 2004, Krebs et al. 2014
Norwegian lemming <i>Lemmus lemmus</i>	Bryophytes – forage	Diminishes the forage.	Korpimäki et al. 2004, Olofsson et al. 2012
Plants with nitrogen-fixing bacteria	Nitrogen-poor soil	Enriches the soil with nitrogen and thus brings competitive disadvantage to itself.	Townsend et al. 2003
Common lizard <i>Lacerta vivipara</i> males	Common lizard females	Kill females in reproduction competition.	Kokko and Brooks 2003, Rankin et al. 2011
Carboniferous forest trees	Atmospheric carbon	Absorbed carbon into the plant structures that accumulated in swamps and accelerated carbon-requiring soil weathering by deep rooting, thus contributing to climatic cooling.	Beerling and Berner 2005, Cleal and Thomas 2005, DiMichele et al. 2009, Montañez et al. 2016

2017, Batten et al. 2018, Fisher et al. 2021). But why should the process stop at prudent exploitation when natural selection should, in principle, favor further increase in exploitation capacity? And why should organisms refrain from other kinds of behaviours that increase individual fitness at the cost of long-term survival prospects of the populations and species, such as twisting sex ratios of host species or altering the composition of the soil or the atmosphere? (Table 1) Given that only the payoffs for individuals count, it can be argued that a drive towards evolutionary suicide should be common in nature (Webb 2003, Heubel et al. 2009, Rankin et al. 2011, Parvinen and Dieckmann 2013).

Despite the self-destructive tendencies discussed above, documented cases of evolutionary suicides are absent from the literature. Moreover, violent density oscillations, accompanied by high risk of local extinction, are mainly found in species-poor high latitude ecosystems (Hanski et al. 1991, Klemola et al. 2002, Oksanen et al. 2008), and in ecosystems invaded by alien species (Strayer et al. 2017, Larson et al. 2019). The lack of documented evolutionary suicides and the relative rarity of oscillatory dynamics indicates that along the above described exploitation gradient, most species are in the realms of weak to prudent exploitation. We are unaware of any cogent explanation for why such situation should prevail.

In this article, we will first review mechanisms that are known to reduce the intensity of exploitation. These mechanisms are widely known in biology, but are usually discussed in isolation from each other. In nature, however, they operate together in multispecies food webs and in different time scales, which creates interactions between ecological and evolutionary processes. We have therefore found it useful to bring these mechanisms together under the concept overexploitation limiter. To our understanding, these limiters may emerge from five different directions: from the actions of organisms at higher trophic levels, to be referred to as top-down limiters; from interactions within the exploiter population or the same trophic level, to be referred to as interference limiters; from tradeoffs of the exploiter organism in question, to be referred to as cost-efficiency limiters; from responses of resources, to be referred to as resource trait limiters; and from landscape usage of the organisms, to be referred to as spatial heterogeneity limiters. We propose that in ecosystems with reasonably high functional diversity and a co-evolved species community, these overexploitation limiters form a network of density-dependent negative eco-evolutionary feedbacks that counteracts overexploitation (Neutel et al. 2007), thus stabilizing exploiter–resource interactions even in complex food webs that would otherwise be highly unstable (Barabás et al. 2017). This process might also provide clues on how human-kind could resolve its overexploitation problems.

Top–down limiters

As described in the introduction, increases in exploitation capacity increase the density of the exploiter within a wide range of parameter values. Therefore, an efficient exploiter

thus becomes an attractive resource for organisms higher in the food chain – predators, parasites and pathogens – i.e. the exploiter will become the exploited. This can limit exploiter numbers and/or curb its exploitation capacity before the sustainable yield of its resource starts diminishing. This process is density-dependent in evolutionary time scale, because the rewards depend on the density of the exploiter. In ecological time scales, density dependence is created e.g. via search image development and the positive impact of high density on parasite and pathogen transmission. Predators can thus prevent herbivores from depleting plants, accounting for the Green Worlds where plant biomass is abundant (Hairston et al. 1960, Estes et al. 2011, Oksanen et al. 2020). Similarly, predation on decomposers may contribute to the existence of the Brown World, i.e. to the abundance of organic matter in soil (DeSouza et al. 2009, Sitvarin et al. 2016). However, while preventing the overexploitation of one trophic level, laissez-faire top–down control creates a risk of severe overexploitation one step higher in the food chain.

The overall risk of overexploitation in the food web can, however, be reduced if the exploitation capacity of exploiters is reduced by sub-lethal parasites or pathogens (Tompkins et al. 2002). Another mechanism reducing the overall risk of overexploitation is functional diversity of the predator guild, combined with high food web connectivity, i.e. that there is a web of weaker trophic interactions within the top trophic level, referred to as food web omnivory or intraguild predation (Polis et al. 1989, Neutel et al. 2007). Functionally diverse predator guilds usually include mesopredators, specialized on the basal prey and apex predators, preying both on the basal prey and on mesopredators (Prugh et al. 2009, Newsome et al. 2017). As most mesopredators are efficient exploiters of basal prey, intraguild predation usually mitigates the total exploitation pressure in the community (Neutel et al. 2007, Jiménez et al. 2019, Cunningham et al. 2020). Moreover, intraguild predation counteracts the destabilizing impacts of enrichment (Rosenzweig 1971), via reduction or elimination of the efficient mesopredators that could otherwise overexploit the basal prey (Diehl and Feissel 2001, Aunapuu and Oksanen 2003, Amarasekare 2008, Aunapuu et al. 2010).

In exploiters with large intra-species size variation, adults frequently prey on juveniles of their own species, which is likely to generate bottlenecks that promote self-limitation (Claessen et al. 2000). Cannibalism and infanticide are common in other predators, too, creating density-dependency and thus reducing the risk of overexploitation (Janssen et al. 2002, Hager and Johnstone 2004).

Interference limiters

Within exploiter guilds, individual selection can favour various forms of interference, as such behavior increases the individual's share of the resource pool. The population and community level consequence of interference is reduced intensity of exploitation competition and thus also reduced

risk of overexploitation. Moreover, the stability of the exploiter–resource equilibrium is enhanced (Murdoch and Oaten 1975).

An especially efficient form of interference is territoriality (Bazykin 1974, Turchin 2003), which can readily emerge via individual selection if exploiters have full control over their resources against all potential competitors (Pulliam 1988, Hinsch and Komdeur 2017, O’Neil et al. 2020). Territoriality creates density-dependence through despotic (Fretwell 1972) or pre-emptive (Pulliam 1988) habitat selection. However, the condition of full control over resources is unlikely to be met if the resources are exploited by qualitatively different types of exploiters, such as mammals and birds or vertebrates and insects. The potential of territoriality to act as an overexploitation limiter in terrestrial nature is thus greatest among large predatory mammals, because both they and their prey are invulnerable to avian predation. Even for large predators, however, territoriality is unlikely to be as rigid as assumed by Bazykin (1974), because the costs of territorial defense increase with increasing exploiter density (Fretwell 1972, Both and Visser 2003). Accordingly, wolf pack territoriality (Cassidy 2013, O’Neil et al. 2020) appears to be strong enough to prevent wolf–ungulate cycles (Vucetich and Peterson 2004), but wolves nevertheless profoundly depress the densities of their ungulate prey (Ripple and Beschta 2012).

In addition to excluding competitors, exploiters can directly interfere with each other’s foraging activities (Beddington 1975, Rankin 2007). However, the density-dependence thus created is weak and only results in a modest increase in equilibrium resource density (Free et al. 1977, Oksanen et al. 1995). A more powerful form of density dependence is generated by behavioral responses of prey to perceived predation risk, such as alertness and hiding, resulting from presence of other predators (Brown et al. 1999). This indirect form of feeding interference is dependent on predator density and can substantially reduce the hunting success of predators (Brown et al. 1999, Gaynor et al. 2019), thus increasing equilibrium prey density and re-enforcing stability. In species with large intraspecific size differences, exploitation competition between size classes can create density dependence in a way analogous to intraspecific interference (de Roos 2020).

Cost-efficiency limiters

Natural selection does not blindly award increasing exploitation capacity but is an optimization process where highest fitness is obtained through a proper balance between different fitness components (Levins 1968). Increased exploitation capacity is often associated with diminishing returns. Moreover, the traits that increase exploitation capacity may reduce the capacity to perform other functions, such as maintaining secondary sex characteristics important in sexual selection, or impose other tradeoffs. For example, increased speed and agility might be accompanied by an increased risk of bone break. These tradeoffs may eventually override

the advantages of increased capacity to exploit the preferred resource (Abrams 1986). For parasites and pathogens, there is a tradeoff between virulence and transmission success, often leading to evolution towards relatively mild virulence (Tompkins et al. 2002).

There are also tradeoffs between different aspects of the feeding niche. Traits that improve the capacity to exploit the preferred resource and to survive and to reproduce at low resource density (e.g. small size, which deprives the resource its safe hideouts and reduces the energy requirements of the exploiter) may also limit the capacity to exploit alternative resources and/or increase the risk of intraguild predation. Depending on the supply of alternative resources and the abundance of intraguild predators, natural selection may thus favour more generalized feeding habits and relatively large body size (even at the cost of lower attack rate on preferred prey and higher energy requirements), because this provides access to a wider size-range of prey and protection against intraguild predation. This reduces the risk of overexploitation and creates an exploiter guild where most exploiters are capable of switching between alternative resource types, potentially resulting in the predominance of a stabilizing type III functional response (Hanski et al. 1991, Oksanen et al. 2001, van Baalen et al. 2001). Cost–efficiency limiters may thus have a strong stabilizing impact and can effectively counteract overexploitation. According to our reasoning, however, their potential depends on community structure, which shows profound latitudinal variation (Mendoza and Araújo 2019).

Resource–trait limiters

The dynamical consequences of increasing exploitation capacity in the exploiter can be reduced or annulled by counter-adaptations of the resource. Intense exploitation implies apparent competition (Holt 1977) among resource organisms. Their fitness is thus determined by the ratio of the intrinsic rate of population growth to the attack rate of the exploiter for the species in question (i.e. r_i/a_i). (For plants, r_i must be interpreted as the rate of module or biomass production.) Reduced values of a_i counteract overexploitation and enhance the stability of the system (Murdoch and Oaten 1975), whereas increased values of r_i will only increase the equilibrium density of the exploiter (Rosenzweig 1971, Turchin 2003).

Plants can reduce the attack rate of herbivores by prostrate growth and by mechanical, phenological and/or chemical defences (L. Oksanen 1990, Strömberg et al. 2013). Herbivores can respond by counteradaptations (Strömberg et al. 2013) and can therefore decimate plant biomass even in communities dominated by well defended plants (Oksanen et al. 2010, Estes et al. 2011, Ripple and Beschta 2012). Nevertheless, the equilibrium biomass of plants is normally higher if plants are well defended or physically difficult to obtain (L. Oksanen 1990). Hence plant defences usually increase the ‘greenness’ of ecosystems characterized by strong herbivore–plant interactions. Moreover,

the protected or hidden parts of the vegetation create a relative refugium, resulting in a stabilizing type III functional response (Murdoch and Oaten 1975, Nath et al. 2019). Also the Brown World of soils might be partly explained by the complexity of the soil carbon compounds that are beyond most organisms' decomposing capabilities (Allison 2006).

In ecosystems with strong predator–herbivore interactions, larger-bodied herbivores experience lower attack rates from predators (lower values of a_i) (Hopcraft et al. 2010) as do more agile species and populations with diet specialization on high quality forage (Oksanen 1992). Combined with behavioural responses, such as hiding or herd formation, these herbivore traits constrain the exploitation capacity of predators (Brown et al. 1999, ter Hofstede and Ratcliffe 2016, Wilson et al. 2018). In this context, the arms' race analogy (Dawkins and Krebs 1979) has limited applicability (Abrams 1986). Resource-limited exploiters are by definition engaged in intense resource competition. Hence, traits that increase their exploitation capacity also increase their fitness regardless of the traits of the resource, until optimal cost–gain balance is reached. This cost–gain balance need not be influenced by the anti-exploitation strategies of the resource (Abrams 1986). The logic is the same for parasitism, too. (For parasites in Table 1, Hurst et al. 2002, Heubel et al. 2009, Lehtonen et al. 2013.)

Moreover, there is also a tradeoff between increasing intrinsic rate of population growth r_i and reducing attack rate a_i . Plants cannot have both high growth rate and costly defence. Therefore, high investments in chemical defences can only be expected in nutrient-poor environments, where plants often have a surplus of reduced carbon (L. Oksanen 1990). For herbivores, there is a tradeoff between the risks and rewards of reproduction, where the outcome can depend on small differences in external conditions (Oksanen and Lundberg 1995, Fuelling and Halle 2004). However, even organisms that opt for high r_i can be expected to use all methods by which a_i can be reduced without sacrificing high r_i (e.g. thorns and silica in plants; Strömberg et al. 2013). We can therefore expect that the evolution of the resource will reduce the probability of overexploitation, but the strength of this impact will vary between different ecosystems, depending whether the r_i/a_i ratio can be more efficiently increased by increasing the value of r_i or by reducing the value of a_i .

Spatial heterogeneity limiters

Heterogeneity of the environment may prevent overexploitation in multiple ways, depending on the size and distances between patches. In a fine grained environment, the impact of spatial heterogeneity is mediated via differences in attack rate (Turchin 2003) between different habitats (Savino and Stein 1989, Kauffman et al. 2007). The more the resource density gets depressed by exploitation, the greater fraction of the resource population will be found in the safest habitats. The relative resource refugium thus created generates a stabilizing type III functional response in exploiters, boosting

the likelihood of a locally stable exploiter–resource equilibrium (Rosenzweig and MacArthur 1963, Murdoch and Oaten 1975).

If the patches are large enough to be recognized by the exploiter, it is likely to practice optimal patch use (Charnov 1976), resulting in aggregation of exploiters to patches with highest resource density. With this grain size, spatial heterogeneity will thus create a situation where exploiters have greater impact on the resource density experienced by other exploiters than on the absolute resource density, averaged over the landscape (for the underlying details, Hassel and Varley 1979, Free et al. 1977). These effects are referred to as pseudo-interference (Free et al. 1977) as they mimic the impacts of true interference between exploiters, increasing the chances of stability and reducing the risk of overexploitation (Pacala et al. 1990). However, the evolutionary stability of such systems requires that high quality patches are few and located far apart (van Baalen and Sabelis 1993).

In landscapes where the sizes of habitat patches exceed the sizes of exploiters' territories or home ranges, optimally behaving exploiters choose habitats on the basis of the inherent quality of each habitat and the density of competitors (Fretwell 1972). With ideal free habitat selection, they will depress the resource to the same level in all habitats, and the resulting dynamics will not differ from dynamics within a homogeneous landscape (Oksanen et al. 1995). Predators can, however, be expected to use their capacity to inflict injury also against conspecifics and to have ideal despotic or ideal preemptive habitat selection (Fretwell 1972, Pulliam 1988), creating source–sink dynamics which reduce the risk of overexploitation in the best habitats and enhance stability (Holt 1985, T. Oksanen 1990). Small predators, in turn, may find refugium in low quality habitats when physically stronger competitors abound in better ones (Aunapuu and Oksanen 2003).

If habitat patches are big enough to support an entire exploiter population, exploiter metapopulations are formed. Provided that between-patch dispersal rates are sufficiently high to allow recolonization but sufficiently low to prevent landscape-level synchronization, landscape-level overexploitation can be avoided, even if exploiters were driving themselves to extinction locally (Huffaker 1958, Holyoak and Lawler 1996, Hwang and Kuang 2003, Sabelis et al. 2005). Metapopulation level stability is further enhanced if the exploiter responds to local population peaks by long-distance emigration (Kalela 1949, Fryxell and Lundberg 1993, Ruxton and Rohani 1999, Heino and Hanski 2001). Moreover, movements between patches also tend to decrease the amplitude of oscillations within individual patches (Jansen 1995).

Synthesis

Across the evolutionary time scale, exploitation systems are governed by two counteracting forces: those that enhance exploitation, and others that suppress it. Inter- and intra-specific resource competition, generated by *laissez-faire*

exploiter resource interactions, reward the ability to depress limiting resources to the lowest level (MacArthur 1972, Tilman 1982). The consequent increase in exploitation capacity first increases the equilibrium density of the exploiter, but with further increases in exploitation capacity, the equilibrium density of the exploiter starts to decrease (Abrams 2019), and the equilibrium will be destabilized, creating cyclic or chaotic dynamics, accompanied by a high risk of exploiter extinction (Rosenzweig 1971). This destructive force is counteracted by five pathways, referred to as overexploitation limiters: top-down control, interference, cost-efficiency tradeoffs, resource traits, and spatial heterogeneity, all hindering laissez-faire resource use in the ecological time scale. The strengths of most of these forces, in turn, are determined by evolution, which ultimately settles whether the outcome is limit cycles with recurrent resource and exploiter collapses, prudent exploitation where the resource is regulated safely above its maximum sustainable yield density, or something in between (Fig. 1). This leaves us with several open questions: Are the existing ecosystems constructed in such a way that the forces counteracting overexploitation dominate over the forces enhancing exploitation, and if so, why? Are there differences between ecosystems in the strengths of the overexploitation limiters? And if there are, what is the causal background of these differences?

One possible outcome is that the above-discussed overexploitation limiters are too weak to overcome the positive feedbacks, leading to overexploitation. Under this scenario, individual selection would continuously create self-destructive lineages (Muroya 2004, Zu et al. 2015), but the majority of these lineages would have, by definition, destroyed themselves (Webb 2003, Jablonski 2008). For example, pronounced natural variation in the numbers of the Rocky Mountain locust *Melanoplus spretus* seems to have contributed to its extinction (Gaston and Fuller 2008). It is also possible that androgenesis (Lehtonen et al. 2013) and plant dioecy (Vamosi and Otto 2002) are rare in the biosphere because they introduce a risky evolutionary drive towards sex imbalances. Carboniferous forests, exploiting the CO₂ supply in the air, likely enhanced the climate cooling that contributed to the collapse of these forests (Beerling and Berner 2005, Cleal and Thomas 2005, DiMichele et al. 2009, Montañez et al. 2016). Thus, it can be hypothesized that overexploitation is rare in the current biosphere simply because the development from prudent exploitation to overexploitation and extinction proceeds rapidly and can thus seldom be observed.

The hypothesis outlined in the Introduction provides a more optimistic explanation for the relatively low prevalence of self-destructive exploitation dynamics in the biosphere: that exploitation systems have a general tendency to evolve mechanisms that prevent overexploitation. Recall that the path to overexploitation goes via efficient but prudent exploitation, resulting in high abundance of the exploiter. The more abundant an exploiter species is and the more efficient it is in exploiting its preferred resource, the greater evolutionary

pressure there is: 1) for other species to evolve an ability to exploit the exploiter; 2) for the emergence of interference between the exploiters; 3) for tradeoffs that make it beneficial to refrain from further increases in the capacity to exploit the preferred resource; 4) for counter-adaptations in the resource, and; 5) for the evolution of density-dependent dispersal behaviours. According to our hypothesis, these overexploitation limiters act analogously to the negative density-dependencies in the ecological time scale, and, in functionally diverse ecosystems, are able to stabilize the system in evolutionary (and ecological) time scales before it drifts from prudent exploitation to overexploitation. Our hypothesis is thus a modification of Van Valen's (1973) Red Queen theme: If one species starts to be ahead of others and gain dominance, stabilizing forces will emerge and stop or reverse the process.

Discussion

Preconditions for the emergence of the efficient overexploitation limiters outlined above are reasonably high functional diversity, food web connectivity and shared evolutionary history of the species. Dynamically significant intraguild predation (food web omnivory) requires a diverse predator guild, where larger predators are adapted to exploit smaller ones. The stabilizing role of cost-efficiency limiters is maximized if there are several alternative resource types and the exploiter has evolved an ability to monitor changes in their abundances, and to switch to the abundant ones. The stabilizing impacts of spatial heterogeneity are maximized if organisms are adapted to utilize the options thus emerging. While high diversity and connectivity in food webs are destabilizing per se (Pimm 1979, Thébault and Fontaine 2010, May 2019), we argue that in food webs consisting of coevolved organisms, diversity and connectivity are vital for avoidance of overexploitation, as they are accompanied by non-random and highly stabilizing patterns in linkage strength (Neutel et al. 2007, Ulanowicz et al. 2014). Thus, diversity begets stability, as proposed by MacArthur (1955), Elton (1958) and Hutchinson (1959).

As terrestrial communities vary profoundly with respect to diversity (Mendoza and Araújo 2019), also the strengths of different overexploitation limiters vary between different exploitation systems (Fig. 2). In many high-latitude ecosystems, the preconditions of high functional diversity and food web connectivity are not satisfied. Consequently, high latitude food webs are characterized by violently oscillatory dynamics, where periodic, severe resource overexploitations are followed by exploiter crashes severe enough to make local extinctions probable. A striking example is the interaction between Norwegian lemmings *Lemmus lemmus* and the Fennoscandian tundra vegetation (Turchin et al. 2000, Ims et al. 2011, Olofsson et al. 2012, Hoset et al. 2014, Ehrich et al. 2020). Equally devastating interactions are displayed between geometrid moths and subarctic mountain birch forests (Tenow et al. 2007, Jepsen et al. 2008), and between small predators and small rodents in boreal and low

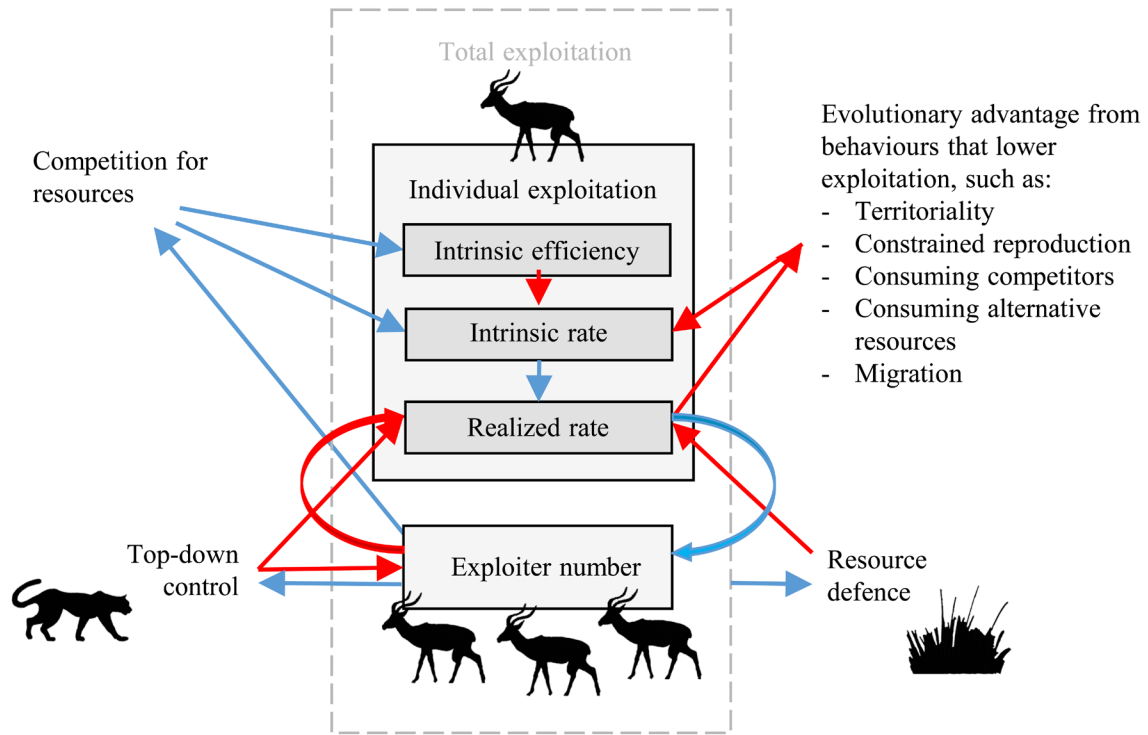


Figure 1. Schematic illustration of the general structure of exploitation dynamics, applicable for any species. Positive (increase) effects are marked with blue, negative (decrease) effects with red. Individual resource usage consists of intrinsic exploitation rate, affected by intrinsic exploitation efficiency, resulting into the realized exploitation rate. Increased competition pressure increases both realized exploitation rates of the individual, which increases exploiter number, leading to increased competition in a positive feedback loop. Increasing exploitation efficiency cannot overcome this self-amplifying circle because ultimately, increased exploitation efficiency simply allows for increased number of individuals in the population or increased individual exploitation rate, likely keeping the total exploitation constant. However, realized individual-level exploitation rate reflects into the number of individuals, which, in turn, reflects to individual exploitation rate in a negative feedback loop. Exploiter number is further controlled by top-down control and resource defences. Competition for resources increases with exploiter number, which affects intrinsic efficiency and intrinsic rate at individual level. Additional factors are evolutionarily beneficial behaviours that lower exploitation rate, such as territoriality or consumption of alternative resources.

arctic ecosystems (Hanski et al. 2001, Korpimäki et al. 2004, Krebs et al. 2014). In these ecosystems, the persistence of exploiters appears to primarily depend on spatial heterogeneity limiters, allowing survival at the metapopulation level. This is enhanced by the strong dispersal behaviour of exploiters during population peaks (Kalela 1949, Oksanen 1992; Fig. 2A), and by outbreak cropping by invading predators (Oksanen et al. 2013).

Towards lower latitudes, species diversity increases, and so does the connectivity of terrestrial food webs. The feeding niches of predators become broader, creating possibilities for stabilizing type III functional responses, prey switching, and intraguild predation (food web omnivory) (Erlinge et al. 1983, Hanski et al. 1991, Klemola et al. 2002). Recall that the ability to exploit a diverse set of resources is inevitably associated with comparatively low efficiency to exploit any single resource type. Thus, when simple food chains intertwine into complex food webs, exploitation connections between individual species are weakened (Yodzis 1981, Neutel et al.

2007, Rooney and McCann 2012, Mendoza and Araújo 2019, Oksanen et al. 2020). The crucial stabilizing feature is that while the energetically dominating trophic interactions are few, species rich food webs also have lots of weak trophic links (Neutel et al. 2007, Ulanowicz et al. 2014), often representing intraguild predation, which mitigates the exploitation pressure imposed on basal prey. Moreover, these food webs contain links that are sensitive to prey density, and can therefore curb developing outbreaks at an early stage (Hanski and Parviainen 1985, Hanski et al. 1991, Klemola et al. 2002).

In evolutionary timescales, such stabilising trophic links are likely to emerge due to the Red Queen principle (Van Valen 1973): If a species embedded in an interconnected food web starts to evolve high exploitation capacity, it also gains numerical dominance at an early stage of the process, when the yield of its resource is high and overexploitation has not yet realized. Therefore, other parts of the food web will respond and counteract this, also changing the evolutionary tradeoffs of the exploiter. Food webs with high diversity and

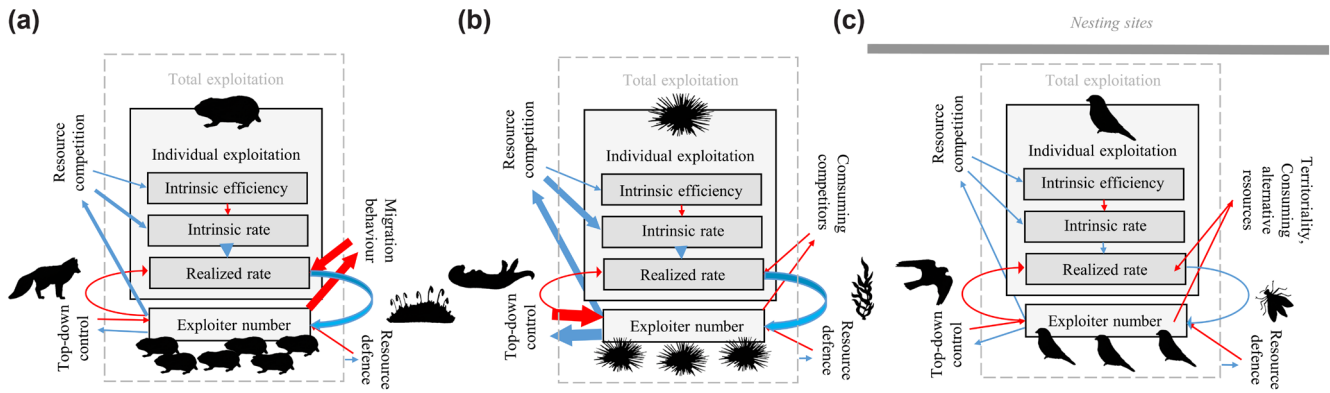


Figure 2. Schematic illustration of the structure of exploitation dynamics in three systems with differing key limiter mechanisms: (a) migration behaviour, (b) top-down predation and (c) available nesting sites. Positive (increase) effects are indicated with blue arrows, negative (decrease) effects with red. The thickness of the arrows represents the strength of each pathway in the exploitation dynamics. Norwegian lemmings in the Scandinavian tundra do not have constant effective limiter mechanisms, and thus they express temporal overshoots; however, migration behaviour prevents global extinction, and predation dampens the exploitation peaks (a). Sea urchins are strongly limited by sea otter predation at the Pacific coasts of North America, holding the exploiter number and total exploitation below sustainable threshold (b). The number of small passerine birds is often constrained by the number of nesting holes, and the role of the limiter pathways is thus negligible (c).

connectivity thus also avoid the occasional destruction of the vegetation, which happens even in productive northern ecosystems with predation-driven dynamics (Hoset et al. 2017). The importance of resource diversity for the stability of exploitation systems is illustrated by the eye opening case of sea otters that keep the kelp forests ‘green’ along the Pacific coasts of North America by regulating sea urchins (Fig. 2B; Estes and Palmisano 1974, Estes et al. 2011). Rather than being dependent on sea urchins, sea otters belong to a species-rich marine food web. This food web provides a rich supply of alternative resources, thus allowing sea otters to remain numerous even when the density of sea urchins is depressed.

Besides being diverse and highly interconnected, terrestrial food webs at lower latitude environments have also strong connections to non-collapsible biotic resources, such as fruits, seeds, nectar, and detritus (Hanski and Parviainen 1985, Tanhuanpää et al. 1999, Oksanen et al. 2020). By contributing energy into the food web, these resources have a strong stabilizing effect (Pimm 1991, Rooney and McCann 2012, Ulanowicz et al. 2014). The same holds for interactions where the limiting factor is space or solar energy. For example, the number of sessile animals of the intertidal zone may be constrained by space, and population growth of some passerine birds limited by the number of nest holes (Fig. 2C; Lohmus and Remm 2005). However, this mechanism hardly works for mobile animals at the community level, because the same food items can be exploited by other species that are not dependent on the resource in question.

Recall that the above discussion focuses on food webs consisting of coevolved organisms. The importance of coevolution in overexploitation prevention is highlighted by the rapid population increases (Strayer et al. 2017, Larson et al. 2019) and collapses (Klein 1968) of non-native species and by their contributions to resource extinctions (Doherty et al. 2016). Even though the exact mechanisms of these boom-and-bust

dynamics are often obscure (Strayer et al. 2017, Larson et al. 2019), resource destruction appears to be a plausible explanation. When the system has not had enough time to develop effective pathways that could prevent overexploitation, destructive exploiter–resource interactions readily happen until the invading exploiter gets embedded in the network of negative feedbacks.

Pathogens and resource traits used to limit the exploitation capacity of our ancestors. For example, many large mammals of Africa might have been saved from end-of-Pleistocene megafauna extinction by evolving fear of humans (Sandom et al. 2014) or by the deadly sleeping sickness transmitted to humans by tsetse flies (Hortolà and Martínez-Navarro 2013). However, the development of tools, weaponry, sanitation, and modern medicine has undermined the effectiveness of top-down and resource–trait limiters. Cultural evolution typically outpaces the biological evolution; thus *Homo sapiens* continues to be a functionally novel species, not embedded in the network of negative feedbacks, and our exploitation dynamics resembles that of the invasive species (Diamond 2005, Turchin 2009, Vuorinen 2018). As a consequence, nowadays only exceptionally fast evolving organisms, such as SARS-CoV-2 causing COVID-19, can have effects on human exploitation rates (Rugani and Caro 2020). Mobility driven by exploitation-induced resource patchiness used to be central for many hunter–gatherer and nomadic peoples (e.g. Sámi people tended to move when wood and other local resources exhausted; Lehtola 2012), but for the resources of modern society, such spatial heterogeneity limiters rarely work, as all resource populations are either under equal exploitation pressure, or extinctions of local populations override local recoveries. Although accelerated during recent decades, overexploitation by human is by no means a modern phenomenon (Diamond 2005, Turchin 2009, Dilworth 2010, Sandom et al. 2014), indicating that our species has since the Paleolithic Stone Age been only

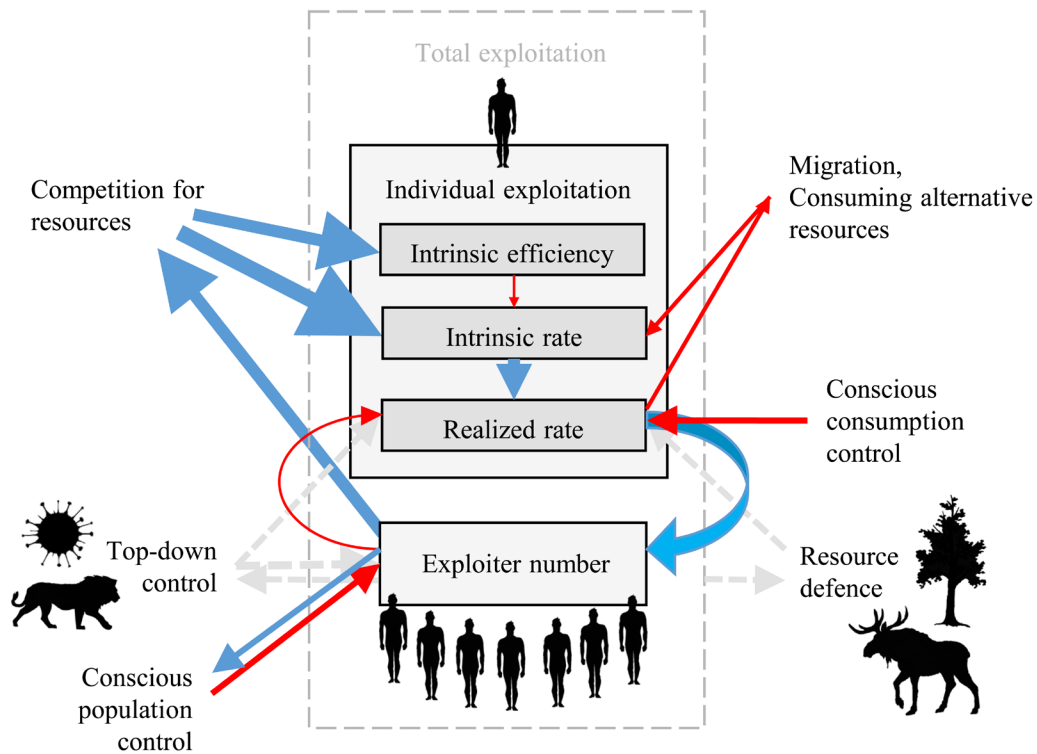


Figure 3. Schematic illustration of the structure of exploitation dynamics in present-day humans. Positive (increase) effects are indicated with blue arrows, negative (decrease) effects with red. The thickness of the arrows represents the strength of each pathway in the exploitation dynamics. Competition over resources drives increased realized consumption rates and exploiter number, only marginally counteracted by increased intrinsic efficiency, exploiter number and advantages from behaviours that lower exploitation. Top-down limiters and resource defence limiter are practically non-existent. Conscious consumption and population controls are pathways that could replace them, but are currently not applied strong enough to counteract the positive feedback loop driving overexploitation.

weakly influenced by the stabilizing networks of negative feedbacks (Fig. 3). This leaves us with the challenge of replacing the natural regulation of overexploitation with efficient but ethically acceptable socio-economic limiters.

The task of finding appropriate overexploitation limiters for our species is challenging, as in modern socio-economical system, also interference and cost-efficiency limiters are undermined. Most resource extraction is not conducted by individual humans but by capitalistic production machineries (White 2019, Blühdorn 2020). Its cost-efficiency is therefore not determined by physiological and evolutionary losses and gains of living organisms, where the principle of diminishing returns applies, but by monetary losses and gains of in economy, where there are, in principle, no physical limits on how much of a resource can be turned into profit. Interference limiters hardly help, as the majority of people do not have individual control over the natural resources they are dependent on, such as clean atmosphere or biodiversity, making these resources non-defendable against other consumers. Thus, the open-market based economy often encourages turning natural resources into profit rather than preserving and protecting them for own use, making the current global socio-economic system structurally forced to drive us towards overexploitation (Clark et al. 2018, Zink 2019). Alternative exploitation targets, especially non-collapsible ones such as

renewable energy, may provide some alleviation of the over-use of certain natural resources, assuming they are economically viable (Wiser and Millstein 2020).

The functioning principles of the overexploitation limiters provide clues on how these forces driving unsustainable overexploitation could be constrained. As a rule, the overexploitation limiters discussed above rely on limiting access to common-pool resources, preventing the tragedy of the unmanaged commons (Cox 1985, Hardin 1994). By increasing the costs of exploitation, socio-political mechanisms can be used to replace the negative exploitation feedbacks that our species has lost. Exploitation bans, environmental taxation, emissions trade and carbon pricing provide protection to resources in a similar manner as top-down trophic control, evolution of resource traits or cost-efficiency limiters. They can also be used to enhance metapopulation dynamics by forbidding exploitation in certain areas while harvesting others, which is a common practice, for example, in management of forests and global fisheries. Human overexploitation control can also arise at the grass-root level within the exploiters, analogous to interference limiters: As presented by Ostrom (1990), local groups may avoid resource collapse by diverse institutional structures that depend on mutual trust and collective-choice arrangements, allowing most resource appropriators to participate

in the decision-making. This type of collective management requires clear group boundaries and a possibility for the group members to monitor other member's behaviour for social sanctioning to avoid free-riding, i.e. ingroup principles (Harth et al. 2013). In addition, the resource must be fully controlled by the group, not exposed to outsider exploiters such as corporations. When Ostrom's (1990) conditions are met, group exploitation control works along same principles as pack territoriality. This can be enhanced, for example, by the current trend of recognizing the group rights of indigenous peoples (Oksanen 2020). In addition, our in-group tendencies may help to create social pressure towards decreased consumption (resembling interference), for example, by condemning conspicuous consumption for purely status-related reasons as morally unacceptable. All these socio-economical mechanisms form a network that may guide us towards more sustainable resource use.

Eco-evolutionary overexploitation limiters also provide hints on what type of solutions are unlikely to work for our species. For example, increasing resource usage efficiency as such has been ineffective in hindering overexploitation because efficiency gains tend to be nullified by rebound effects (Barker et al. 2009, Sorrell et al. 2009, Dilworth 2010), in a same way as increased consumption efficiency simply leads to more exploiters in natural exploitation systems (Fig. 1). In the light of biology, also relying on spontaneous voluntary exploitation abstention appears risky: refraining from consuming a common pool resource lowered the fitness of our ancestors, leading to present-day humans with short-sighted exploitation preferences (Penn 2003). We also have a biological tendency to downplay distant, collective threats, and to see our personal contribution to them as negligible (Garg 2016, Wong-Parodi and Feygina 2020).

There are major socio-economical challenges that hinder our ability to transform the societal structures to take into account the ecological and evolutionary realities, and to prevent laissez-faire resource use (White 2019, Zink 2019, Blühdorn 2020). Yet, the behaviour of our species is highly sensitive to social and economic incentives, and thus we should have all means to overcome these challenges by reconstructing our socio-economical system in an ethically acceptable way to enhance the desired behavioural patterns instead of the ones driving overexploitation. The dynamics of exploitation by other species may help us to delimit which actions are most likely to help us to solve our environmental crisis, as human species is not exempt from the universal principles of resource exploitation. By filling the knowledge gap of how and under which premises the pathways reducing the probability of severe overexploitation emerge for other species, we can both better understand the basic functions of the biosphere, and to prevent ourselves from destroying it.

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Author contributions

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