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Linking animal behavior to ecosystem change in disturbed environments

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Environmental disturbances often cause individuals to change their behavior. The behavioral responses can induce a chain of reactions through the network of species interactions, *via* consumptive and trait mediated connections. Given that species interactions define ecosystem structure and functioning, changes to these interactions often have ecological repercussions. Here, we explore the transmission of behavioral responses through the network of species interactions, and how the responses influence ecological conditions. We describe the underlying mechanisms and the ultimate impact that the behavioral responses can have on ecosystem structure and functioning, including biodiversity and ecosystems stability and services. We explain why behavioral responses of some species have a larger impact than that of others on ecosystems, and why research should focus on these species and their interactions. With the work, we synthesize existing theory and empirical evidence to provide a conceptual framework that links behavior responses to altered species interactions, community dynamics, and ecosystem processes. Considering that species interactions link biodiversity to ecosystem functioning, a deeper understanding of behavioral responses and their causes and consequences can improve our knowledge of the mechanisms and pathways through which human activities alter ecosystems. This knowledge can improve our ability to predict the effects of ongoing disturbances on communities and ecosystems and decide on the interventions needed to mitigate negative effects.

KEYWORDS

anthropogenic disturbances, climate change, environmental change, food webs, keystone species, phenology, species interactions, trophic interactions

Introduction

Environments around the world are rapidly changing mainly because of human activities. Habitat destruction, climate change, pollution, invasion of foreign species, and harvesting are drastically altering the living conditions for species (Ceballos *et al.*, 2015; Blowes *et al.*, 2019). The changes influence species directly as well as indirectly through interactions with other affected species and altered abiotic conditions

(Tylianakis et al., 2008; Gilman et al., 2010). These direct and indirect impacts influence in turn population dynamics and thereby ecosystem structure, function, and stability (i.e., the ability of the ecosystem to resist change or return to the original state following a perturbation) (Ives and Carpenter, 2007).

The impact that environmental changes have on populations is often mediated by behavioral responses of individuals, particularly at the early stage of environmental change before evolutionary changes have occurred (Tuomainen and Candolin, 2011; Sih, 2013; Wong and Candolin, 2015). The behavioral responses can be direct reactions to the environmental change, such as when animals move away from a disturbed area, or a consequence of changes in physiology or life history traits, such as higher stress levels or reduced size at maturity. These behavioral responses influence in turn other species in the community and can cause cascading effects that ripple through the community *via* the network of species interactions (Tylianakis et al., 2008; Hoover and Tylianakis, 2012; Palkovacs and Dalton, 2012; Bartley et al., 2019). These cascading effects increase the pathways through which an environmental change reaches a species, and they can have a larger impact on species than the direct impact of the environmental change (Ockendon et al., 2014). The impact of the behavioral responses can be further altered by feedbacks among species and time lags, and result in complex changes to the species community.

The impact that behavioral responses of individuals have on community structure and ecosystem function depends on the traits and abundance of the species, with some species have a larger impact than others, such as keystone species (Paine, 1966; Power et al., 1996), dominant species (Avolio et al., 2019), foundation species (Ellison, 2019), and ecosystem engineers (Jones et al., 1994; Wright and Jones, 2006). Such species have been termed 'biotic multipliers' (Zarnetske et al., 2012; Urban et al., 2017). Focusing research on these species and their behavioral responses can provide essential information of the effects that environmental disturbances have on ecosystems and the underlying mechanisms (Urban et al., 2017).

Here, the aim is to give an overview of our current knowledge of how changes in the behavior of ecologically central species influence species interaction networks and thereby ecosystem structure, function, and stability. We provide a conceptual framework that links behavioral responses to species interactions, communities, and ecosystems, and discuss the factors that influence these links (Figure 1). We begin by explaining the central role that behavioral responses of biotic multipliers have in mediating impacts of environmental change on ecosystems. We then sketch out the impact that various environmental changes have on the behavior of species, and how these behavioral responses in turn influence species interactions and community composition. Next, we explain how changes in the behavior of individuals and species interactions influence

ecological processes, such as biogeochemical cycles, biodiversity, and ecosystem stability and services. We end by outlining key avenues and priorities for future research.

Biotic multipliers of disturbances

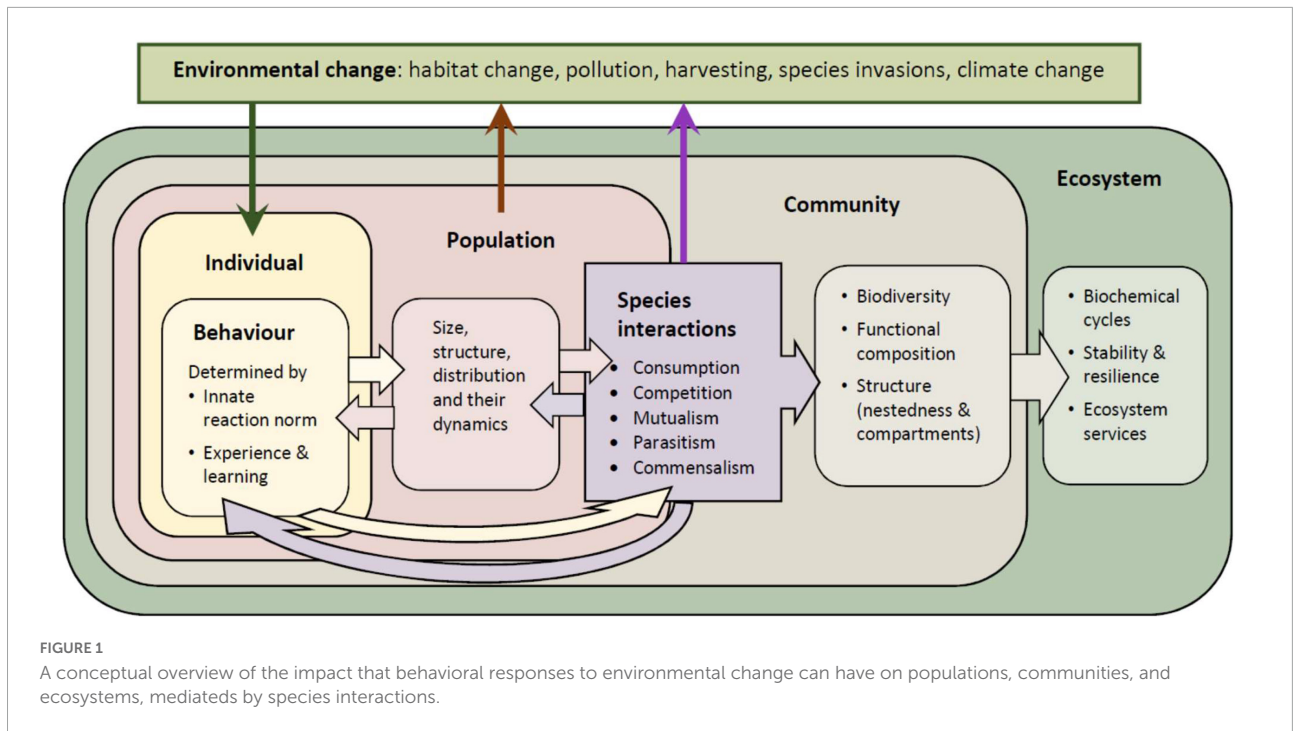
Biotic multipliers are ecologically important species that regulate or influence the abundance and function of a range of other species, directly or indirectly (Zarnetske et al., 2012). Changes in their behavior can initiate a cascade of effects through species interaction networks. Such species are keystone species, ecosystem engineers, and dominant species. These concepts partly overlap as a species can have multiple functions and belong to several groups (de Visser et al., 2013).

Keystone species

Keystone species are those with a disproportionately large effect on the ecosystems relative to their low biomass (Paine, 1966; Power et al., 1996). They have low functional redundancy, with no other species being able to fill their ecological niche should they disappear from the ecosystem. Thus, without them, the ecosystem would be dramatically different. Typical keystone species are top predators that regulate the abundance and distribution of several prey species and, hence, cause top-down effects that can be transmitted down to primary producers. A classic example is wolves (*Canis lupus*) that control the abundance of herbivores (if wolf populations are allowed to grow large enough and are not decimated by humans). These keystone predators are not necessarily large, or even at the top of the food web, as demonstrated by the sea star *Pisaster ochraceus*, which was the first species to be assigned a keystone role in regulating the biodiversity of intertidal plains (Paine, 1966). Similarly, pollinators can be keystone species as they are vital for plant reproduction and diversity.

Ecosystem engineers

Ecosystem engineers are species that modify the habitat and directly or indirectly modulate the availability of resources to other species (Jones et al., 1994). Typical examples are beavers (*Castor* sp.) and earthworms (*Lumbricus* sp.). They cause physical changes to biotic and abiotic components of the environment, either *via* their own physical structures, which can be living or dead (autogenic engineers), or by transforming living or non-living materials from one state to another by mechanical or other means (allogenic engineers). Foundation species, which create conditions required for the persistence of other species, are a subgroup of ecosystem engineers (Jones et al., 1994).



Dominant species

Dominant species are abundant species whose effects on the community and ecosystem is proportional to their abundance (Avolio et al., 2019). They are linked to many species and are main contributors to ecosystem function, such as bioturbation and carbon storage and flows (Dangles and Malmqvist, 2004; Solan et al., 2004; Taylor et al., 2006). Thus, they underpin the provision of many ecosystem services to people. Some dominant species are also ecosystem engineers and foundation species. Changes in their abundance and behavior can significantly impact ecosystem functioning. Examples of dominant species are large bodied zooplankton in lakes without fish predators.

experiences of earlier generations can additionally influence responses through transgenerational effects (Bell and Hellmann, 2019)(Figure 1).

Behavioral responses can be adaptive or maladaptive, much depending on the similarity of the new conditions to the past ones; responses are more likely to be adaptive when the environmental change extends earlier encountered conditions, such as a rise in temperature, than when it results in completely new conditions, such as exposure to traffic noise. Yet, the extension of earlier encountered conditions can also result in maladaptive responses, especially when non-linear responses are required to improve fitness. For instance, an animal that linearly increases its activity with increasing temperature may suffer from reduced fitness if the adaptive response would be decrease activity when temperature rises above a certain threshold.

Influence of environmental change on behavior

Mechanisms behind behavioral responses

Human activities that alter abiotic or biotic components of an ecosystem often cause behavioral changes in animals either directly or indirectly through the responses of other individuals or species. How animals respond depends on their genetically determined innate reaction norms, and their experiences and learning possibilities during lifetime (Tuomainen and Candolin, 2011; Sih, 2013; Wong and Candolin, 2015). In some species,

Behavioral responses to disturbances

Animals may respond to environmental change immediately or after a time lag, depending on whether physiological modifications or learning is needed, and whether the change affects them directly (such as higher temperature) or indirectly through interactions with other affected organisms. In addition, the phenotype of an animal influences responses, such as age, sex, body condition, personality, and social dominance (Sih, 2013; McCallum et al., 2021).

Response can be modified over time, depending on the responses of other individuals and species, and on gradual changes in environmental conditions

(Tuomainen and Candolin, 2011). In addition, feedback among biotic and abiotic components can modify the responses, as can other environmental disturbances (Jackson et al., 2021). Thus, individuals in a population can show large individual, as well as spatial and temporal variation, in responses.

In the following, we outline the main responses of animals to ongoing human-induced disturbances. We describe their underlying mechanisms and consequences, drawing on theoretical predictions and empirical examples from the literature.

Harvesting

The removal of individuals from a population can influence the behavior of remaining individuals, either by inducing direct behavioral responses or through the selective removal of individuals with particular characteristics, such as bolder individuals (Diaz Pauli and Sih, 2017; Palkovacs et al., 2018; Sbragaglia et al., 2021b). For instance, fisheries that remove the individuals most vulnerable to the specific fishing techniques used alter the composition and behavior of the remaining population (Sbragaglia et al., 2021a).

Harvesting can also alter social interactions, such as aggression, mate choice, and parental care, through effects on the density, structure, or distribution of the population. These changes in social interactions can have further implications for population characteristics, through effects on birth and death rates and dispersal (Diaz Pauli and Sih, 2017; Palkovacs et al., 2018). Similarly, changes in population characteristics, such as its size or age structure, can influence interspecific interactions and influence the dynamics of the involved populations (Hoover and Tylanakis, 2012).

Correspondingly, the decimation of other species, or changes in their populations structure, can alter both intra- and interspecific behavior, such as competition for resources both within and between populations.

Habitat change

Changes in habitat characteristics - through modification, fragmentation, and destruction of the habitat - are common causes of behavioral modifications. For instance, the removal of shielding vegetation causes predators to alter their predatory tactics to prevent prey from detecting them too early in the hunting process (Michel and Adams, 2009). Behavioral responses that influence birth or mortality rates, or dispersal, can in turn influence population characteristics and thereby both intra- and interspecific interactions, as discussed for harvesting.

The responses of other species to changes in the habitat can similarly influence behavior. For instance, the disappearance of

prey because of altered vegetation structure may force predators to alter their prey selection (Michel and Adams, 2009).

Pollution

Pollution takes many forms, such as noise, light, and chemical pollution. It creates novel conditions that influence the behavior of individuals, such as their habitat choice and activity (Swaddle et al., 2015; Shannon et al., 2016). Pollution that influences physiological processes, often through hormonal changes, can induce a range of behavioral modifications, from altered activity to reduced investment in reproductive behaviors (Zala and Penn, 2004; Wingfield, 2013; Candolin, 2019a; Candolin and Wong, 2019).

In addition to the direct effects of pollution, indirect effects through species interactions cause behavioral modifications (Willems et al., 2022). In particular, the trophic transmission of chemical pollutants can influence species not directly exposed to the pollutant (Arnot and Gobas, 2006; Previsic et al., 2021). Many compounds, such as heavy metals, pesticides, pharmaceuticals, and microplastics, accumulate in the tissue of organisms, with the concentration increasing for each trophic level (Gall et al., 2015; Puckowski et al., 2016).

Non-native species

Human activities are promoting the spread of species and their possibility of successfully invading new areas (Pysek et al., 2020). These invaders influence the behavior of native species as novel predators, prey, competitors, parasites, and mutualists (Simberloff et al., 2013). Native species may respond with adaptive or maladaptive behavioral responses, which may cause further changes to their population dynamics and species interactions (Simberloff et al., 2013; Pysek et al., 2020).

Non-native species that outcompete native species in resource acquisition often force native species to alter their behavior, such as habitat choice, activity, or aggression (Ricciardi et al., 2013). Similarly, the appearance of a new predator often induce behavioral changes (Sih et al., 2010), as does new parasites by altering the body condition of the species they infect (Barber, 2007). Indirect effects of invaders, through effects on other species, are especially common, given that invaders often alter the structure of food webs and species interactions (Candolin et al., 2018).

Climate change

Global warming and linked effects on the climate, such as altered precipitation and wind patterns, influence the behavior of species, particularly through effects on habitat

quality and physiological processes (Buchholz et al., 2019). The impact is often mediated by altered resource availability and quality (Rosenblatt and Schmitz, 2016). For instance, changes in temperature and water availability alters the nutrient content of plants, which influence the foraging behavior of herbivores. If the alteration in behavior influences birth and death rates, or dispersal, the characteristics of the population may change and induce further behavioral modifications (Pelletier and Garant, 2012).

Climate change that alters metabolic rate is another common cause of behavioral modifications, especially in ectothermic species. Warming and enhanced metabolism often increase feeding rate through faster locomotion, more frequent encounters with prey, or faster prey capture, handling time, or ingestion (Rall et al., 2012; Rosenblatt and Schmitz, 2016). On the other hand, if energetic demands increase faster than feeding rates, climate change may eventually lead to starvation and population decline, with further consequences for behavior (Boukal et al., 2019).

Climate change also influences the timing of life-history events, such as the timing of reproduction and migration, given that these are often sensitive to abiotic conditions (Both et al., 2009; Buchanan and Partecke, 2012). Changes in the timing can in turn have implications for population dynamics and species interactions (Kharouba et al., 2018).

Plastic or evolutionary responses?

Animals often respond to a change in the environment with an immediate plastic modification of their behavior (Candolin and Wong, 2012). With time, evolutionary (genetic) changes may take place and result in behaviors that are better adapted to the new conditions. The possibility of genetic adaptation depends, however, on a range of factors, such as the generation time of the species, the presence and nature of genetic variation in the behavior, the rate at which new mutations arise, the size of the population, and the dispersal of individuals and gene flow (Hoffmann and Sgro, 2011; Bell, 2017).

Adaptive behavioral responses can facilitate genetic adaptation by preventing rapid population decline and thereby providing more time for genetic changes (Tuomainen and Candolin, 2011). Behavioral responses can also expose genetic variation that selection can then act on (Candolin and Jensen, 2021). Maladaptive behavioral responses, on the other hand, can have the opposite effect, eventually resulting in population decline and even extinction.

Species with a central role in regulating communities are often larger species with longer generation times. These are unlikely to be able to adapt genetically to rapid human-induced environmental changes, but have to rely on phenotypic plasticity and earlier evolved behavioral reaction norms. Species with shorter generation times and large genetic diversity,

often combined with large population sizes, are more likely to adapt genetically to rapid environmental changes (Bell, 2017). Thus, many ecologically important species, such as many top predators with longer generation times, have to rely on behavioral reaction norms that evolved before the environment changed, which increases the probability of maladaptive responses.

The transmission of effects through species interaction networks

Mechanisms

Behavioral alterations by one species influence other species *via* the network of species interactions (Figure 2). Behavioral responses can also alter the disturbance itself. For instance, increased foraging activity by some consumers in an anthropogenically eutrophied habitat binds nutrients into biomass, which mitigates the impact of eutrophication on other species (Candolin, 2019b).

The impact that behavioral responses have on linked species can be trait or density-mediated, respectively (Abrams, 1995; Werner and Peacor, 2003; Schmitz and Trussell, 2016). Trait-mediated effects arise when the behavioral response of a species directly influences other species. Density-mediated effects arise when the behavioral response alters the density of the species itself, through impact on birth, death, or dispersal rates, and this influences other species (Carpenter and Kitchell, 1988; Lima and Dill, 1990). These trait- and density-mediated effects can result in cascades of effects that ripple through the species interaction network, through top-down, bottom-up, and lateral effects, as well as through changes in nutrient recycling and abiotic conditions (Leroux and Loreau, 2010; Heath et al., 2014).

Top-down effects

Top consumers are important regulators of food webs. Their removal often has cascading impacts on lower trophic levels, which alters the abundance, biomass, and distribution of species (Ripple et al., 2014; Rasher et al., 2020). In particular, the current extinction and decline of top consumers – termed trophic downgrading – is triggering waves of secondary extinctions and the disassembly of communities (Estes et al., 2011; Donohue et al., 2017). For instance, mild winters have decreased the ability of wolves (*Canis lupus*) to kill moose (*Alces alces*) on Isle Royale in Michigan, which has reduced their abundance and allowed the moose population to grow (Wilmers et al., 2006).

The often profound impact that the decline of top consumers have on species communities are due their low

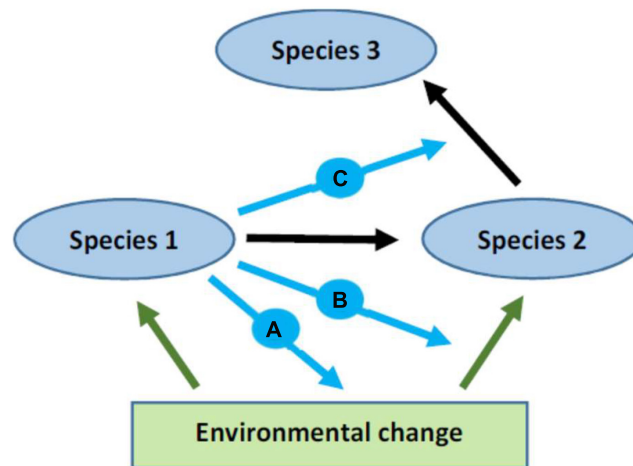


FIGURE 2

Illustration of the direct and indirect pathways through which changes in the behavior of one species can influence other species. Environmental change influences species 1 and 2 directly (green arrows), and changes in the behavior of species 1 influence in turn species 2 (black arrow), for instance through predation. Species 1 can influence species 2 also by altering the effect of the environmental change on species 2 (blue arrows a and b). Examples are (A) declining prey abundance that is amplified by the behavioural response of species 1, and (B) influence of species 1 on the distribution of species 2 and thereby on its exposure to the environmental change. Changes in species 2 influence in turn species 3 (black arrow), and the effect can be modulated by species 1 (blue arrow c), for instance by species 1 altering the environment and, thus, encounters between species 2 and 3. Feedbacks between the species can further alter the impacts of species 1 on the two other species.

diversity and functional redundancy - their loss and function cannot be compensated by other species (Duffy, 2003). Top consumers are also more sensitive to environmental changes than most species at lower trophic levels, because of their larger body size and higher metabolic demands and resource requirements (Urban et al., 2017). Thus, many human-caused ecosystem changes are mediated by the decline of top consumers.

The cascading effects that the decline of top consumers have on species interaction networks can amplify the impact of other environmental changes on communities (Shurin et al., 2012). For instance, the loss of a keystone predator, the sea otter *Enhydra lutris*, from subarctic marine ecosystems has interacted with ocean warming in eroding calcareous reefs: the loss has promoted the growth of herbivore populations, which graze on the algae that build the calcareous reefs, resulting in overgrazing and the acceleration of the negative effects of warming on the reefs (Rasher et al., 2020).

Not all consumers are negatively affected by environmental change. Some benefit and cause in turn declines in consumers. For instance, a mesocosm experiment showed that warming advances zooplankton phenology and that this causes an earlier top-down control of phytoplankton and, hence, a strong reduction in their abundance (Velthuis et al., 2017).

Top consumers that are not affected by environmental change can moderate the effect of environmental change on lower trophic levels. For instance, the freshwater sculpin *Cottus nozawae* - a dominant predator in temperate stream communities - buffers the negative effects of heatwaves

on benthic algae by reducing macroinvertebrate densities (Ross et al., 2022).

Bottom-up effects

Bottom-up effects - mediated by nutrient availability - are important regulators of community composition in ecosystems with low producer redundancy and where consumers are highly specialized in their diet (Hunter and Price, 1992). For instance, a simulation study showed that the extinction of primary producers in ecosystems with low connectance (complexity) can cause more secondary extinctions than the removal of herbivores or top consumers (Eklöf and Ebenman, 2006). Similarly, environmental changes that alter the nutrient content of plants can change the growth rates of consumers and their population dynamics, resulting in effects that can propagate upwards in the food web through altered foraging behavior of higher trophic levels (Cross et al., 2015).

Interplay between top-down and bottom-up effects

Top-down effects counteract bottom-up effects and their interaction determines the ultimate impact of behavioral responses on food webs. The interaction is often complex with feedbacks between trophic levels. For instance, climate change that improves the nutrient content of primary producers

and promotes the growth of consumers also increases the consumption rate of the consumers, which can feed back to influence primary producers (Rosenblatt and Schmitz, 2016). Such opposing effects of top-down and bottom-up effects can avert larger shifts in community structure, (Lynam et al., 2017). This is especially the case when ecosystems are exposed to several stressors. For instance, the influence of eutrophication on primary production is counteracted by global warming that increases foraging activity of consumers (Kratina et al., 2012).

Top-down and bottom-up effects do not always oppose each other but can also act additively (Shurin et al., 2012). For instance, nutrient enrichment that promotes primary production through a bottom-up effect can be strengthened by global warming that reduces the size of predators and their foraging pressure (Jochum et al., 2012). This can allow the biomass of primary producers to increase even further.

Generally the removal of top consumers has a larger impact on food webs than the removal of herbivores or primary producers, given that top consumers generally are more sensitive to environmental changes than species at lower trophic levels (Duffy, 2003; Voigt et al., 2003; Borrvall and Ebenman, 2006).

Lateral effects

Interactions within a trophic level, i.e., non-trophic, lateral interactions (such as competitive, mutualistic and commensalistic interactions), determine together with trophic interactions (consumptive and parasitic interactions) the structure of species interaction networks (Kefi et al., 2012). Competition, in particular, can drastically alter trophic interactions (Sih et al., 1998; Davenport and Chalcraft, 2013). For instance, the intensity of competition among freshwater insect predators for prey determines their top-down effect on the prey community, such as the composition of zooplankton (Sentis et al., 2017b).

Trophic and non-trophic (lateral) interactions often differ in their sensitivity to environmental change, with trophic interactions generally being more sensitive and, hence, more often having negative effects on communities (Sentis et al., 2017b; Vesely et al., 2019). Non-trophic, lateral interactions are more dependent on species traits, which can stabilize ecological communities by weakening disrupted trophic interactions and dampening population oscillations (Rall et al., 2008).

Phenological asynchronies

Human-induced environmental changes that alter the timing of behaviors, such as migration or reproductive behaviors, can cause mismatches with optimal abiotic and biotic conditions (Kharouba et al., 2018; Renner and Zohner, 2018).

For example, birds that breed earlier because of climate change can suffer from food shortage if the advancement differs from that of their prey, which can lead to failed reproduction (Visser et al., 2012). Such mismatches are often caused by species using cues that differ in their sensitivity to environmental conditions to time their activities.

Other common causes of mismatches in the timing of activities are differences in response rate or time lag among species, because of constraints or costs associated with the responses (Both et al., 2009; Chen et al., 2019). In addition, species may differ in their recovery rate, as higher trophic levels are generally slower in responding to environmental changes than lower levels (Thackeray et al., 2016). Phenological mismatches also occur when the environmental change occurs at a time of the year that promotes one trophic level over another (Straile et al., 2015). For, instance, higher temperature during the period when zooplankton populations start to grow increases their population sizes, but results in food limitation later in the season (Wagner and Benndorf, 2007).

Finally, abiotic factors can cause mismatches by limiting the ability of species to respond to environmental change. For example, while grazers increase their grazing pressure in response to rising temperature, primary producers may be unable to respond because of the lack of nutrients, resulting in overgrazing (Thackeray et al., 2016). This overgrazing can in turn feed back to influence the grazers and result in complex changes to the food web.

Individual variation in behavioral responses

Individuals within a population often vary in their behavioral responses to environmental change, depending on traits such as physiology, developmental stage, sex, social status, and personality (Bolnick et al., 2011; Schmitz and Trussell, 2016). This variation influences species interactions and the dynamics of populations. For instance, the impact of a predator on the prey community is smaller if only some of the individuals switch to an alternative prey when their main prey declines than if all individuals, or none of them, altered their prey selection (Toscano and Griffen, 2014; Belgrad and Griffen, 2016; Sommer and Schmitz, 2020).

Similarly, variation among individuals in responses to altered resource availability can influence competitive interactions by alter niche overlap (Violle et al., 2012). Species with more variable responses may broaden their niches more than other species and gain a competitive advantage (Hogle et al., 2022). Likewise, environmental changes that alter the frequency of specific behavioral types, for instance through the emigration of bold individuals, can influence species interactions (Pelletier and Garant, 2012). In addition, changes in the presence of individuals at different developmental

stages often influence interactions, given that ontogeny and individual development is a common cause of temporal changes in behavior both within and between species (Persson and de Roos, 2013; Toscano and Rudolf, 2021).

Restructuring of species interaction networks

Variation among species in their behavioral responses to environmental change often restructures species interaction networks. For instance, increased consumption and attack rate by consumers because of global warming augments the biomass of higher trophic levels while reducing that of lower levels (Shurin et al., 2012; Dell et al., 2014). Warming also decreases the size of individuals, which further modifies consumer-resource interactions (Horne et al., 2015; Sentis et al., 2017a). Such changes can reduce the importance of earlier dominant or keystone species in favor of other species (Tanentzap et al., 2020).

Restructuring also occurs when some species amplify or dampen the impact of environmental change on other species (Urban et al., 2016). For example, the negative impact of warming on the survival of a dominant tadpole species, *Hyla versicolor*, is dampened by predation by a dragonfly on a competing tadpole species, as this reduces competitive interactions between the two tadpole species (Rudolf and Roman, 2018). Correspondingly, the impact of climate change on vegetation can be amplified by the grazing activity of herbivores (Boulangeat et al., 2018).

The restructuring of species interaction networks can in turn facilitate the invasion of new species (Pysek et al., 2020). Invasion success depends on the behavior of both the invader and the native species, and changes in either because of environmental change can influence the invasion success (Chapple et al., 2012). For instance, aggressive interactions between an invading shrimp, *Palaemon elegans*, and a native fish, the three-spined stickleback, *Gasterosteus aculeatus*, reduces the ability of the shrimp to invade habitats occupied by the fish (Jakubaviciute and Candolin, 2021). However, the aggression of the fish depends on its population density, which implies that changes in its density - because of human activities - can influence the invasion success of the shrimp and, hence, its impact on the community (Candolin et al., 2018).

The invasion of new species can also introduce non-native pathogens, which can alter species interaction and affect population sizes markedly. An example is the outbreak of the Squirrelpox disease in the native red squirrel (*Sciurus vulgaris*) in the United Kingdom with the introduction of the non-native gray squirrels (*S. carolinensis*), which carries the virus. The outbreak has altered the competitive interaction between the two species, favoring the non-native gray squirrel (Chantrey et al., 2014).

Ecological consequences: Impact of behavioral responses on abiotic components, biodiversity, and ecosystem services

Biogeochemical cycles and abiotic conditions

Changes in behaviors that alter species interactions influence ecological processes, such as the flow of energy and matter through the food web and between habitats and ecosystems. These ecological effects are often mediated by consumers, including detritivores, (Ren et al., 2022). For instance, a change in the foraging behavior and top-down control of consumers influences not only the biomass of lower trophic levels, but also biogeochemical cycles, such as the cycling of nutrients, carbon, and water through the ecosystem.

If altered consumer behavior influences the biomass of primary producers, the rate of assimilation can change and further alter biogeochemical cycles (Bakker et al., 2016; Ren et al., 2022). Similarly, changes in the behavior of consumers can influence respiration rate and the carbon dissimilatory process, through changes in their own metabolism and in the abundance and activity of other species. Changes in consumer behavior can also influence decomposition and abiotic conditions, such as oxygen availability (Ren et al., 2022). For instance, reduced burial activity of polychetes in aquatic sediments (bioturbation) reduces oxygen availability for other organisms in the sediments, which in turn reduces their decomposition activity (Kristensen, 2000). Changes in the activity of terrestrial detritivores can again alter soil formation and its characteristics. For example, the ingestion of microplastics by earthworms and other detritivores increases their mortality rate, which reduces their activity, especially when combined with other contaminants, such as heavy metals (Bhagat et al., 2021).

Changes in the consumption by herbivores of vegetation can in turn alter light conditions, both within and below the vegetation. Similarly, changes in the consumption by zooplankton of phytoplankton can alter water turbidity and light penetration and, hence, assimilation in deeper water. Reduced assimilation can in turn cause hypoxia and alter the benthic community. Likewise, changes in the activity of terrestrial herbivores can change the influx of nutrients to aquatic ecosystems and affect algae blooms and light penetration. For instance, the replacement of large wildlife with livestock on the African savanna has increased the transfer of organic matter and nutrient from terrestrial to aquatic ecosystems, with further consequences for these ecosystems (Iteba et al., 2021). The impact of consumers on vegetation can also alter the climate, given that the biomass and composition of vegetation influences humidity, temperature, and the release of water vapor and cloud formation (Green et al., 2017).

The transfer of energy and matter between habitats and ecosystems is obviously also sensitive to changes in animal movements. Shifts in where animals stay, what they feed on, and where they die, alter biogeochemical processes within habitats and, thus, ecological processes and components, such as primary production and biodiversity (Peller et al., 2022).

Biodiversity and ecosystem stability

Species and their behavioral activities and interactions with other species determine biodiversity and ecological processes, which in turn influence the stability of ecosystems - the ability to resist changes or return to the original state following a disturbance (Loreau and de Mazancourt, 2013; Hautier et al., 2015). In particular, the current decline of top predators and relaxation of their top-down control is likely to destabilize ecosystems, given that predation moderates competition among species, which otherwise can cause large fluctuations in population sizes (Loreau and de Mazancourt, 2013).

Changes in the behavior of dominant and common species can similarly cause cascades of effects that alter ecosystem stability (Gaston, 2010). Common species shape their environments and are involved in a large number of biotic interactions, and behavioral changes in such species are especially likely to cause extinction cascades that reduce the stability of species interaction networks (Dunne et al., 2002).

The behavior of species and their interactions can also buffer the effects of environmental change on communities and improve ecosystem stability. This is especially likely when species show redundancy in their ecological functions, as this gives rise to an 'insurance effect' (Yachi and Loreau, 1999). Species rich communities with multiple interactions, both within and between trophic levels, are consequently expected to be most resilient against environmental perturbations (Neutel et al., 2007; Rooney and McCann, 2012; Oliver et al., 2015). Correspondingly, ecosystems with few but highly specialized interactions are more sensitive to environmental disturbances. Thus, the decline of behavioral interactions among species can reduce the ability of ecosystems to resist large-scale changes in the face of human activities.

Ecosystem services

Ecosystems provide a range of services to humans, such as food security, control of pests and parasites, clean air and water, and recreational possibilities (Pecl et al., 2017). These services depend on the behavior of species and changes in these - because of human activities - can consequently have negative ramifications for the services.

Food security, in particular, is highly dependent on the behavior of species. Many plant species, including crops, depend

on insect pollinators. Thus, the current decline of pollinators is expected to negatively affect pollination success and crop yield (Wagner et al., 2021). Similarly, the dispersal of seeds depends on animal resource use and movements, and changes in these behaviors can consequently influence the population dynamics of plants (McConkey et al., 2012).

Clear air and water are similarly dependent on the behavior of species. Plants both bind and emit volatile compounds, which implies that changes in the behavior of grazers and detritivores can alter these dynamics (Wang et al., 2018). Correspondingly, changes in the foraging behavior and resource use of consumers can influence their waste products and thereby water, air, and soil quality (Angerer et al., 2021).

Changes in behavior can also influence the dynamics of pathogens and parasites, particularly by altering encounters between individuals and species and, hence, the transmission rate of these organisms, as well as by influencing the physical condition of individuals and their ability to resist infection or recover from it (Budria and Candolin, 2014). Increased transmission or reduced resistance can promote the introduction and rapid spread of pests that destroy resources, such as crops and forest products, and allow the transmission of parasites and pathogens to humans and other animals and cause pandemics (McNeely, 2021).

Last but not least, human health and well-being depends on the recreational value of nature. Behavioral responses to human-induced environmental changes are both a cause and a consequence of the current loss of species and species interactions. Thus, human-induced behavioral responses are further boosting the impact that we humans are having on ecosystems and their use for recreation and well-being (Pecl et al., 2017).

In general, the resilience of ecosystem services to human-induced environmental changes depends on the fragility of the network of species interactions, i.e., the number of species functional traits and links between them (Ross et al., 2021). More diverse communities with many behavioral links between functionally different species are expected to provide the most robust ecosystem services (Ross et al., 2021). Thus, the current loss of biodiversity and behavioral interactions is expected to reduce the provisioning of the goods and services that we humans depend on.

Outlook and future avenues of research

Behavior underlies interactions within and between species and with the abiotic environment. Behavior consequently links biotic and abiotic factors together and determines biodiversity and ecosystem processes. Thus, changes in the behavior of animals can influence ecosystem structure, dynamics, and function. Yet, few studies on the impact of human disturbances

on communities and ecosystems consider the behavior of animals. In this review, we have shown that critical information on the mechanisms behind ecosystem changes can be gained by considering the behavior of animals. Information on the causes, mechanisms, and consequences of behavioral responses to environmental disturbances, and how the responses scale up to influence communities and ecosystems, can improve our ability to assess and predict the consequences of human activities for ecosystems, as well as to inform ecosystem management.

Unraveling the links between species and assessing their sensitivity to human activities is, however, challenging. Species are linked by a multitude of direct and indirect interactions, which can be differentially affected by environmental change. Thus, research has to concentrate on some species and their interactions. Top predators, ecosystem engineers, and dominant species are obvious candidates, given the large number of species they interact with, directly and indirectly, and the major impact they have on ecological processes. In this review, we have provided a conceptual framework for understanding the links between behavior and ecosystem processes and the factors that influence these links.

The research challenge is further complicated by the multitude of disturbances animals are exposed to. Future studies need to consider interactions among these and their combined effects. Moreover, given the multitude of pathways through which environmental disturbances influence animals and their interactions, collaboration among researchers is needed, as well as open access to data. Only through open, collaborative research can we gradually gain a deeper understanding of the pathways and mechanisms through which human activities influence ecosystems.

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Conflict of interest

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