



WILDLIFE EXPLOITATION OF ANTHROPOGENIC CHANGE: INTERACTIONS AND CONSEQUENCES

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ABSTRACT

Anthropogenic environmental change is continuing to accelerate globally and has important ecological consequences for virtually all life on Earth. There is extensive knowledge of the costs of anthropogenic change across many taxa, but there are also disparate examples of animals exploiting these changes and increasing their fitness. Species may benefit from novel or enhanced resources, variation in physical conditions, or from shifting biotic interactions arising from anthropogenic impacts. Here, we explore the breadth of examples, drawn from different biomes and fields of research, of animals that exploit anthropogenic change. We highlight the potential for interactions between anthropogenic impacts and explore how long benefits are likely to last. Finally, we discuss the potential costs that can arise from differential shifts in species success, and the important management implications that arise when certain species are able to exploit change. Understanding not only which species suffer but also which species benefit from anthropogenic change is critical knowledge for management of biodiversity, food sources, and disease transmission in a world increasingly impacted by humans.

INTRODUCTION

ANTHROPOGENIC change is a pervasive, accelerating threat to life on Earth. Species living in artificially modified environments are affected by multiple stressors, including habitat alteration and loss, climate change, pollution, and invasive species (Dirzo et al. 2014; Sánchez-Bayo and Wyckhuys 2019). Anthropogenic impacts are not a new phenomenon: humans have influenced the environment for a long time, such as the use of fire to alter habitat structure (Bonta et al. 2017), mass production of food through agriculture (Foley et al. 2011), or the effects of hunting on species abundances and hence species interactions (Lyons et al. 2004). Each biological discipline takes different approaches to understanding the effects of anthropogenic stressors (Orr et al. 2020), and ecological research generally focuses on declines in ecosystem health or species abundances (Dirzo et al. 2014; Sánchez-Bayo and Wyckhuys 2019; Iglesias-Carrasco et al. 2020). However, this largely ignores the fact that many species can thrive under novel conditions, even in highly disturbed habitats (Balée 1998; Lowry et al. 2013). This knowledge gap regarding potential beneficiaries reduces our understanding of the breadth of ecosystem-level consequences of anthropogenic change. Here, we define “exploiters” as those species that benefit from novel or enhanced resources or changes in physical conditions, or gain advantages from shifting biotic interactions arising from anthropogenic impacts.

These exploiters of anthropogenic change can be broadly categorized into two groups.

First, individuals may benefit directly from novel or enhanced resources and conditions (Table 1). Habitat modification changes the resources available to animals, and the capacity of animals to exploit these resources in disturbed areas is a key determinant of their success (Shochat et al. 2006; Oro et al. 2013; Sanders and Gaston 2018). Such beneficiaries are usually associated with generalist diets and habitat use, and neophilic behaviors (Tuomainen and Candolin 2011; Lowry et al. 2013; Sol et al. 2016; Sánchez-Bayo and Wyckhuys 2019). Second, individuals may benefit indirectly through changes in the dynamics of biotic interactions (Table 2). Under this scenario, changes to the environment and their effects on the habitat use, behavior, and physiology of individuals can also alter the nature of interactions, such as competition, predation, and parasitism, and this translates to different outcomes for different species (Petren et al. 1993; Ballejo et al. 2018; Sanders and Gaston 2018).

In this review, we highlight a range of ways in which different animal species benefit from anthropogenic change. Responses range from individual-level shifts in metabolism and activity patterns through to broadscale alterations in community structure and dynamics. These responses to anthropogenic change have implications for pest and crop dynamics, disease transmission, and the biodiversity and health of ecosystems across all realms. The breadth of benefits animals gain from exploiting anthropogenic change is outlined through a series of recent exemplar studies (see Figure 1; Tables 1 and 2). Our

intent here is to consolidate studies into key areas and present a highlighted snapshot of how and where animals may benefit. Below, we explore the potential differences between short- and long-term benefits, and how this may be driven by the shifting nature and severity of anthropogenic change over time. Throughout, we highlight the interacting nature of different impacts, and outline the need for comprehensive fitness measures in future studies. We begin by identifying how changing conditions can influence the success of species in anthropogenic habitats, then discuss the broader costs and long-term consequences related to these benefits, such as biotic homogenization and evolutionary change. We conclude by describing the potential future for ecosystems determined by which species suffer and which species prosper in our changing world.

EXPLOITATION OF NOVEL RESOURCES AND CONDITIONS

FOOD AND NUTRIENT SOURCES

Modified environments provide a major advantage for many animal species due to an overabundance or concentration of food, including crops, roadkill, livestock carrion, fisheries discards, and rubbish (Oro et al. 2013). These advantages are ancient, as seen in the exploitation of human food stores by rodents for millennia (Fleming and Bateman 2018). Exploiting these food sources can increase body mass, survival, and productivity, translating to increased population sizes and resilience (Oro et al. 2013). These fitness advantages can be driven by the stability of anthropogenic food sources, resulting in benefits such as increased provisioning of offspring (Lowry et al. 2013) and/or buffering during key periods of resource limitation (Ma et al. 2004; Waite et al. 2007). For example, white storks (*Ciconia ciconia*) nesting near rubbish dumps are afforded a more stable food source, and hence experience greater reproductive success than storks nesting further away (Tortosa et al. 2002). Urban predators may benefit more indirectly: urban green spaces provide a rich source of plants for herbivores (especially generalist species) that feed on both

native and exotic plants (Hanley and Goulson 2003; Tsurim et al. 2008; Goulson et al. 2012; Langemeyer et al. 2016), thus increasing their abundance and availability as prey for predators (Suri et al. 2017). Intentional wildlife food provisioning, such as feeding stations for birds and mammals, can increase reproductive success and abundance, although negative effects such as increased predation risk are sometimes observed (Cox and Gaston 2018). This intentional provisioning of food has been used by Indigenous peoples to attract species in order to hunt them (Bonta et al. 2017). Predators may gain further benefits if the impact results in increased clustering of prey, as is the case for artificial lighting, certain methods of waste disposal, and composting that all promote the aggregation of invertebrates (Lore and Flannelly 1978; Rayor and Uetz 1990; Sanders and Gaston 2018). Composting also facilitates insect breeding, so prey are both clustered and more plentiful for their predators (Lore and Flannelly 1978; Rayor and Uetz 1990). The high volume and stability of such urban food sources can increase population sizes and buffer against periods when natural food sources are scarce. This is seen, for instance, in urban-living monkeys that are more resilient to drought if they are provisioned with food by commensal human populations (Waite et al. 2007; Oro et al. 2013), and in hyenas that hunt donkeys when meat discards from humans are reduced during religious fasting periods (Yirga et al. 2012). These examples highlight the significance of dietary plasticity in allowing species to exploit anthropogenic food sources.

Anthropogenic pollutants can also affect the nutrients available for, and hence support the growth and fitness of, different species. Roadside air pollution high in nitrogen dioxide (NO_2 ; a chemical pollutant) increases the protein content and thus nutritional quality of plants making them a more attractive resource (Bolsinger and Flückiger 1987). More strikingly, chemical pollutants in the form of nutrient-rich agricultural runoff into aquatic habitats can promote algal growth, dramatically increasing its abundance resulting in cascading biological consequences (Weber et al. 2010). There has been a strong focus

TABLE 1

Examples of organisms benefiting from their exploitation of anthropogenic changes in resources and habitats

Anthropogenic change	Benefit	Example animals	References	
Food and nutrient sources	Novel food sources	Increased abundance, reproductive success and resilience, reduced mortality	Birds (<i>Ciconia ciconia</i> , <i>Coragyps atratus</i> , <i>Accipiter melanoleucus</i>)	Ballejo et al. (2018); Tortosa et al. (2002); Suri et al. (2017)
			Mammals (<i>Procyon lotor</i> , <i>Semnopithecus entellus</i>)	Bateman and Fleming (2012); Waite et al. (2007)
			Bees (<i>Bombus</i> spp.)	Hanley and Goulson (2003); Goulson et al. (2012)
Food and nutrient sources	Aggregated food sources	Increased predation success	Birds (various species)	Oro et al. (2013); Ballejo et al. (2018)
			Mammals (various bats, <i>Rattus norvegicus</i> , <i>Rattus rattus</i> , <i>Felis catus</i>)	Rydell (2006); Schoeman (2016); Lore and Flannelly (1978); Fleming and Bateman (2018)
			Reptiles (<i>Hemidactylus frenatus</i>)	Petren et al. (1993)
			Spiders (various species)	Rayor and Uetz (1990); Heiling and Herberstein (1999); Lowe et al. (2016); Willmott et al. (2019)
Food and nutrient sources	Increased nutrients	Increased growth, reproduction, and range	Common carp (<i>Cyprinus carpio</i>)	Weber et al. (2010)
			Agricultural pests, e.g., aphids (<i>Aphis fabae</i>)	Saunders et al. (2016); Bolsinger and Flückiger (1987)
Novel habitats and conditions	Artificial habitat	Breeding/foraging sites, increased abundance/diversity	Many urban species (e.g., <i>Columba livia domestica</i>)	Johnson and Munshi-South (2017); Tsurim et al. (2008)
			Coral reef fish assemblages	Arena et al. (2007); Fowler and Booth (2012)
			Monoculture pests	Sánchez-Bayo and Wyckhuys (2019)
	Artificial waterbodies	Breeding and foraging sites, reduced stress, expanded range	Amphibians (<i>Rhinella marina</i>)	Letnic et al. (2014)
			Mammals (<i>Macropus giganteus</i>)	Dawson et al. (2006)
			Various waterbirds	Ma et al. (2004)
Irrigation	Expanded range, huge abundance, increased growth	Mosquitoes (many, including <i>Aedes aegypti</i>)	Hanford et al. (2019)	
		Agricultural pests and other animals	Saunders et al. (2016)	
Habitat structure modifications	Expanded range, huge abundance, increased growth	Sap-feeding insects	Huberty and Denno (2004)	
		Increased survival and biomass, reduced competition	Trout (<i>Salvelinus fontinalis</i>), crayfish (<i>Cambarus bartoni</i>), mink (<i>Mustela vison</i>)	Burgess and Bider (1980)

TABLE 1
Continued

Anthropogenic change	Benefit	Example animals	References
Increased temperature	Increased growth, reduced winter mortality, expanded range	Ground beetles (Carabidae), orb-weavers (Araneidae)	Lövei et al. (2006); Miyashita et al. (1998)
		Spiders (<i>Trichonephila plumipes</i>)	Lowe et al. (2014)
		Insects (<i>Atalopedes campestris</i>)	Crozier (2004); Deutsch et al. (2008)
		Mammals (<i>Trichechus manatus</i> , <i>Pteropus poliocephalus</i>)	Laist and Reynolds (2005); Parris and Hazell (2005)
		Marine biota (many species)	Barnes (2002)
		Insects (Collembola)	Phillips et al. (2017)
Artificial light at night	Reduced competition for light-tolerant species	Bats (various species)	Rydell (2006); Schoeman (2016)
		Lizards (<i>Hemidactylus frenatus</i>)	Petren et al. (1993)
		Spiders (<i>Araneus diadematus</i>)	Heiling and Herberstein (1999)
Migration and transmission	Increased dispersal and range	Marine biota (many species)	Barnes (2002)
		Livestock, pets, game animals, biological control species	Letnic et al. (2014); Henriksson et al. (2016); Lockwood et al. (2019)
	Increased dispersal and range	Global invasives/urban invaders (rats, pigeons, cellar spiders, etc.)	McKinney (2006); Alirol et al. (2011); Aplin et al. (2011); Sol et al. (2012); Letnic et al. (2014); Henriksson et al. (2016); Langemeyer et al. (2016)
		Livestock and urban parasites	Marano et al. (2007); Fox et al. (2015)
Artificial materials	Mate attraction	Birds (<i>Ptilonorhynchus violaceus</i>)	Coleman et al. (2004)
	Territory signaling, nest structure	Birds (<i>Milvus migrans</i> , <i>Lanius excubitor</i>)	Canal et al. (2016); Antczak et al. (2010)
	Reduced parasite load	Birds (<i>Passer domesticus</i> , <i>Carpodacus mexicanus</i>)	Suárez-Rodríguez et al. (2013)
	Reduced predation pressure	Octopuses Spiders (<i>Phonognatha</i> spp.)	Anecdotal evidence N. J. Willmott, pers. obs.

on harmful algal blooms that release toxins or block sunlight into the water (Chislock et al. 2013). However, smaller algal blooms can provide extra food and hence fitness benefits for species at higher trophic levels,

particularly species that are tolerant of poorer water quality, such as the invasive common carp (*Cyprinus carpio*; Weber et al. 2010). The widespread use of fertilizers results in nutrient-rich soils, which can greatly expand

TABLE 2

Examples of how anthropogenic changes lead to positive outcomes in biotic interactions for certain species

Anthropogenic change	Benefit	Example animals	References		
Competition	Competitor exclusion	Less competition for food and breeding sites	Bats (various species) Birds (various species) Fish (various species)	Rydell (2006); Schoeman (2016) Sol et al. (2012) Clavel et al. (2011)	
	Altered habitat	Less competition for food and habitat	Lizards (<i>Hemidactylus frenatus</i>) Mammals (<i>Rattus norvegicus</i>)	Petren et al. (1993) Rowland (2009)	
	Increased abundance due to anthropogenic food	Outcompete other species for food, increased range	Birds (<i>Coragyps atratus</i>)	Ballejo et al. (2018)	
	Reduced abundance of competitors due to toxins	Less competition for food, higher growth/abundance	Zooplankton (<i>Moina micrura</i> , rotifers) Dung-breeding flies (Ceratopogonidae and Psychodidae) Agricultural insects	Hanazato (2001) Iwasa et al. (2005) Nicholls and Altieri (1997)	
	Benefits for prey	Predator exclusion	Decreased mortality due to predation, increased reproductive success	Birds that nest in noisy habitats Rodents Nocturnal insects (Coleoptera) <i>Daphnia magna</i>	Francis et al. (2009) Gaston et al. (2013) Cravens et al. (2018) Hanazato (2001)
Benefits for predators		Aggregation of prey	Increased predation success, increased abundance and fecundity	Nocturnal insectivores	Sanders and Gaston (2018); Wakefield et al. (2015); Svensson and Rydell (1998); Schoeman (2016)
		Prey more visible		Intertidal predators	Underwood et al. (2017); Chan et al. (2010); Saaristo et al. (2018)
	Antipredator disruption	Introduced predators	Crowder and Snyder (2010)		
Benefits for hosts	Separation from parasites	Reduced parasitic load, increased survival	Freshwater predators	Saaristo et al. (2018); Cox and Lima (2006)	
	Exclusion of parasites		Birds (<i>Falco tinnunculus</i>), mammals (<i>Felis catus</i>)	Fleming and Bateman (2018)	
Benefits for parasites/ parasitoids	Separation from parasites	Increased transmission, range, and abundance	Birds (<i>Accipiter melanoleucus</i> , <i>Passer domesticus</i> , <i>Carpodacus mexicanus</i>)	Suri et al. (2017); Suárez-Rodríguez et al. (2013)	
	Exclusion of parasites		Introduced species	Clavel et al. (2011)	
	Increased host abundance		Avian parasites (<i>Schistocephalus solidus</i> , <i>Trichobilharzia ocellata</i>)	Macnab and Barber (2012); Lafferty and Kuris (1999); Epstein et al. (2006)	
	Aggregation of hosts				
	Weakened host immunity				

TABLE 2
Continued

Anthropogenic change	Benefit	Example animals	References
		Urban mammal parasites	McCleery (2010); Werner and Nunn (2020)
		Parasitoid wasps and flies	Baker and Potter (2020); Kruidhof et al. (2015)
		Varroa mites	Sánchez-Bayo et al. (2016)
		Livestock parasites	Fox et al. (2015)

the geographic ranges of some plant species, support the animals that live in or feed on them (McKinney 2008). This is one of many examples where changes in the resources available in novel habitats can facilitate colonization by certain species.

NOVEL HABITATS AND CONDITIONS

Human modifications to habitats include changes in both habitat structure and abiotic

conditions. This can improve habitat suitability and provide resources that facilitate settlement by certain species, and alter physiological and ecological dynamics within these systems. As described above, habitat modification can increase the availability of resources for certain species. For example, agricultural practices increase the range and density of a small proportion of crops and livestock, and this has provided bountiful resources for animals that have been able to utilize them for thousands of years

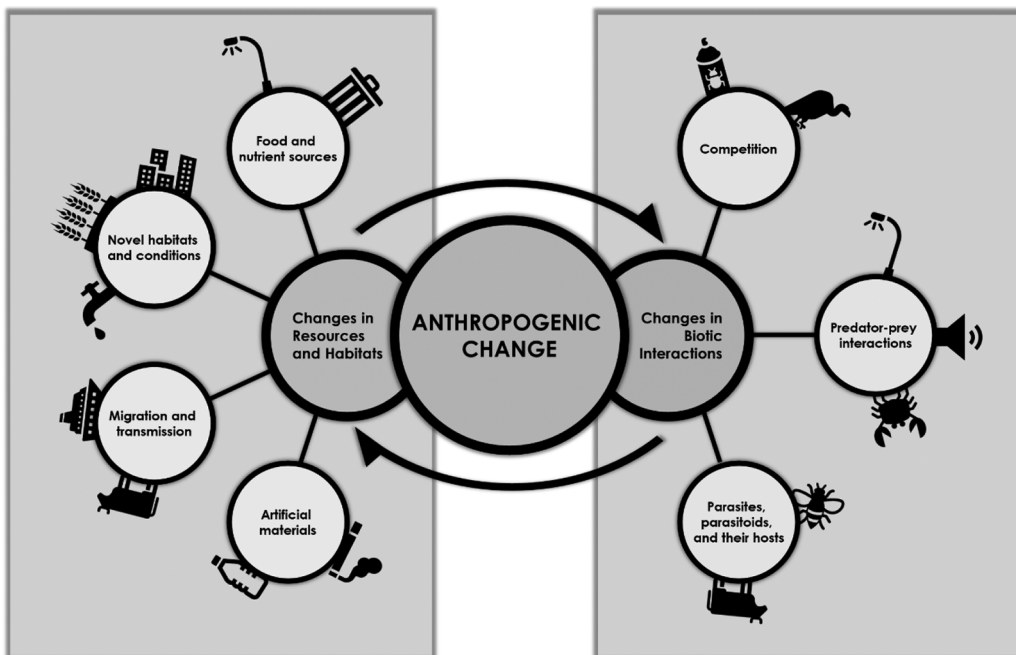


FIGURE 1. BROAD CATEGORIES DESCRIBING THE TYPES OF ANTHROPOGENIC CHANGE THAT ANIMALS ARE ABLE TO EXPLOIT

The circles on the left-hand side refer to cases where human modifications to the environment directly affect animals, while the circles on the right-hand side describe examples of shifts in interactions between species as a result of anthropogenic change. See the online edition for a color version of this figure.

(Saunders et al. 2016; Fleming and Bateman 2018; Sánchez-Bayo and Wyckhuys 2019). Comparable benefits are observed for the pests of species grown in aquaculture (Forrest et al. 2009; Ward et al. 2020). It is important to note, however, that these practices can harm other species. The establishment of agricultural land involves the destruction of natural habitats, so native species are often excluded or harmed (Saunders et al. 2016; Sánchez-Bayo and Wyckhuys 2019); whereas aquaculture releases waste, antibiotics, and nutrients into surrounding waters, which can have variable and deleterious effects on wildlife (Forrest et al. 2009; Ward et al. 2020). For the species that do benefit, as with anthropogenic food sources, artificial habitats are often less ephemeral than natural habitats. For example, artificial water sources, such as irrigation and ponds, provide relatively reliable sources of water (Tsurim et al. 2008), and so artificial water bodies facilitate colonization by a number of species. These water sources can: promote breeding for aquatic insects (Hanford et al. 2019); potentially reduce metabolic costs associated with water stress (Shochat et al. 2004); improve the quality of plants as a food source for herbivores (Huberty and Denno 2004); supplement natural habitats during harsh periods (Ma et al. 2004); and allow the establishment of species that might otherwise desiccate (Letnic et al. 2014).

The physical structure itself of artificial habitats can support certain species, and increasing evidence suggests that preadaptation to certain habitat structure is a predictor of the success of an individual in novel environments (Johnson and Munshi-South 2017). For instance, impervious surfaces in urban environments simulate the rocky surfaces on which pigeons naturally nest, thereby providing a high quantity of good nesting sites (Johnson and Munshi-South 2017). These surfaces and the crevices within them similarly provide excellent scaffolding for spider species, including the now extremely abundant black house spider (*Badumna* spp.), which naturally constructs webs in the crevices of hard structures such as rocks and rough tree bark (Main 2001). Interestingly, artificial habitats are often constructed or

modified specifically to improve outcomes for animal communities. One example is the establishment of novel marine habitats, such as sunken vessels providing structure for coral reefs (Box 1). These structures support similar (Fowler and Booth 2012) or higher (Arenas et al. 2007) fish biodiversity and population sizes compared with nearby natural reefs. More subtle changes such as improvements in water flow and creation of shelter in freshwater systems can reduce predation risk and increase habitat suitability, thus expanding the biomass of some species (Burgess and Bider 1980). However, manipulation of habitat shape can also have unintended consequences for different species. For example, habitat fragmentation disadvantages some species by creating more habitat edges but is beneficial for edge-dwelling species (Miyashita et al. 1998; Lövei et al. 2006).

Changes to other abiotic conditions such as temperature or light cycles can also be biologically beneficial. Increasing temperatures, associated with climate change, places some species beyond their thermal tolerance, but can allow more heat-tolerant species to move into and occupy new habitats (Deutsch et al. 2008; Madeira et al. 2012). Temperature increases at both local and landscape scales can also accelerate development and expand growth and survivorship (Crozier 2004; Lowe et al. 2014), leading to increases in population size and range (Crozier 2004; Deutsch et al. 2008). Developmental acceleration and subsequent larger body size in urban areas is observed in the golden orb-weaving spider (*Trichonephila plumipes*) resulting in urban individuals producing more offspring compared to their counterparts in natural habitats (Lowe et al. 2014). Increased urban temperatures have also facilitated the establishment of the grey-headed flying fox (*Pteropus poliocephalus*) outside its natural range by reducing the severity of previously inhospitable winter frosts (Parris and Hazell 2005). Artificial light at night (from streetlights, cars, and other urban light sources) fragments local habitat into light and dark patches. This typically benefits light-tolerant species, which experience reduced competition in light patches due to the loss of light phobic species, and gain access to prey

BOX 1

Management decisions informed by exploitation of anthropogenic change

The cane toad (*Rhinella marina*), native to South and Central America, was introduced to Australia beginning in 1935 to control the native grey-backed cane beetle (*Dermolepida albobirtum*) and French's beetle (*Lepidiota frenchi*), which were considered pests of sugar cane crops (Shine 2010). The toads were ineffective as pest control, and have instead rapidly spread along the northern and eastern coasts of Australia, causing significant ecological damage (Shine 2010). Although attempts to control the toads have largely been unsuccessful, an understanding of how cane toads benefit from human alterations to the environment may prove useful. The spread of cane toads through semi-arid areas, which constitute large swaths of their potential range, is facilitated by their use of artificial waterbodies for hydration and reproduction. Hence, the construction of toad-proof barriers around these pivotal water sources may prove to be an effective means of limiting their spread (Letnic et al. 2015).

Many marine habitats, such as coral reefs, are threatened by anthropogenic processes, including development and climate change. In an attempt to reverse this damage, artificial habitats are being designed and constructed to support optimal marine biodiversity. However, this requires detailed knowledge of how habitat structure influences the success of different species. For example, sunken vessels can support higher fish abundance and species richness compared with natural reefs, but with strongly differing trophic structure (Arena et al. 2007). More detailed studies of how well species can exploit different habitat types, such as seagrass meadows, breakwater units, or objects of high vertical relief, can inform how the construction of marine habitats will support those species. This could, in turn, allow the construction of habitats to support key fisheries species or to maximize biodiversity (Morris et al. 2018).

aggregating around lights (Sanders and Gaston 2018). Artificial lighting in caves can similarly promote the establishment of algae, mosses, and ferns, providing food and nutrient sources for cave-dwelling heterotrophs (Johnson 1979). Although examples for these effects are found across a variety of habitats, detailed knowledge remains restricted to a small number of biomes, a research bias that deserves significant future attention.

MIGRATION AND TRANSMISSION

Human activities have contributed significantly to the spread of wildlife into new habitats through transmission via human transport and introductions (intentional or accidental), complemented by other anthropogenic factors that have facilitated subsequent invasion. Intentional introductions, including game animals for recreational hunting (Henriksson et al. 2016), agricultural and aquaculture (Andow 1983; Forrest et al. 2009), and the global

pet trade (Lockwood et al. 2019) can have catastrophic consequences. An infamous example of the negative impacts of intentional introductions followed the importation of cane toads (*Rhinella marina*) to Australia to control several sugar cane beetle species (Letnic et al. 2014). Due to favorable environmental conditions, including the presence of more permanent and geographically widespread artificial waterbodies (Box 1), and a lack of natural enemies, these highly toxic toads have dramatically increased their range, while causing local extinctions of populations of native species (Letnic et al. 2014). Accidental biotic introductions can also occur directly via human transport (Alirol et al. 2011; Aplin et al. 2011), such as the classic historical example of black rats (*Rattus rattus*) being transported on ships, which has resulted in their now worldwide distribution but an associated increased transmission of disease (Aplin et al. 2011). Importantly, accidental transmission of animals can be exacerbated by other anthropogenic changes acting simultaneously.

Cointrroductions can increase the success of invasive species, such as the global spread of the accidentally introduced grey house spider (*Badumna longinqua*) that was facilitated by the dispersal of eucalyptus plantations worldwide (Simó et al. 2011). Similarly, livestock parasites inevitably spread wherever the livestock are farmed (Fèvre et al. 2006; Marano et al. 2007). Effects may be exacerbated if high temperatures, due to climate change, suppress livestock immune function, thereby increasing parasite transmission (Fox et al. 2015). The density of urban exploiters (including people) also facilitates transmission of pathogens within and between habitats, such as the spread of *Schistosoma* blood flukes, which are particularly prevalent in large cities with high immigration rates (Alirol et al. 2011). Artificial light at night (Tasciotti 2017) and water availability (Hanford et al. 2019) are further linked with increasing the transmission of such mosquito-borne diseases. Anthropogenic pollutants can also incidentally facilitate migration in marine environments. A variety of marine larvae have increased their migration capacity by attaching to drifting plastic debris, allowing them to settle in new regions and expand their range. Although dispersal into the polar regions is currently limited by low polar temperatures, polar warming associated with climate change may increase the dispersal capacity of certain species (Barnes 2002). Similarly, polar warming appears to facilitate the spread of invasive terrestrial species from research stations, posing a biosecurity threat to polar habitats (Phillips et al. 2017). Thus, although benefits for species due to human influences on migration can depend strongly on the species and multiple anthropogenic factors, there can be important consequences when species benefit from these processes.

ARTIFICIAL MATERIALS

Some animals exploit the presence of anthropogenic pollutants by actively incorporating artificial materials for signaling or defense. The avian literature has several examples where a species actively uses artificial litter. Black kites (*Milvus migrans*) are known

to add white plastics or paper to increase the conspicuousness of their nests, acting as an honest signal to conspecifics of the viability, territory quality, and conflict dominance of the signaler (Canal et al. 2016). Similarly, male bowerbirds (Ptilonorhynchidae) incorporate brightly colored plastics in their bowers, increasing their attractiveness to younger females (Coleman et al. 2004). In neither case, however, were the health consequences of the plastics tested. In the great grey shrike (*Lanius excubitor*), the use of plastics increases nest stability, but it can also entangle hatchlings and adults leading to a reduction in fitness (Antczak et al. 2010). Overall, the incorporation of plastics into nests and bowers correlates with their availability in the environment, but an understanding of their relative costs and benefits is unknown and the taxonomic and ecological breadth is currently limited. Although examples are rare, some nonavian species appear to use plastics for defense. Leaf-curling spiders (*Phonognatha* spp.) construct shelters in their webs out of various plastics (N. J. Willmott, pers. obs.) and octopuses use marine pollution such as bottles or plastics as armor against predators (Sigurdsson 2019). These examples all involve the use of artificial resources to alter biotic interactions, but further research is needed to quantify actual fitness costs and benefits across contexts.

CHANGES IN BIOTIC INTERACTIONS

COMPETITIVE ADVANTAGES

Anthropogenic change can alter competition for food and breeding sites or differentially impact species because some competitors are less resistant to change, all of which can have considerable fitness consequences. Species that can exploit locally available, novel food resources may benefit through increased population sizes, but this may shift or even reverse the outcome of previous density-dependent interspecific competition. For example, black vulture (*Coragyps atratus*) populations that feed on rubbish in urbanized habitats have increased abundance to the point where they currently outcompete the larger, and formerly dominant, Andean

condor (*Vultur gryphus*) for access to carrion, often from livestock (Ballejo et al. 2018). Similarly, the simplification of habitat and aggregation of insects around artificial lights allows the bigger, more aggressive common house gecko (*Hemidactylus frenatus*) to defend food patches and outcompete native geckos on multiple Pacific islands (Petren et al. 1993). Species that have long been associated with humans also provide useful insights into the impacts of changing stressors. For example, black rats (*R. rattus*) were likely displaced by brown rats (*R. norvegicus*) in cooler regions and urban areas because brown rats are larger and more aggressive, and better suited to the bricked and tiled human houses that became dominant (Rowland 2009). Additionally, brown rats have broader dietary niches and are more resistant to weather extremes (Traweger et al. 2006; Aplin et al. 2011). Pesticides can favor pesticide-resistant species over normally competitively dominant (but less pesticide-resistant) species. In freshwater systems, pesticide runoff can suppress the dominant *Daphnia*, allowing numerous smaller species to reach higher abundances (Hanazato 2001). In some extreme cases, anthropogenic disturbances can remove competition altogether. For instance, agricultural pesticides can render livestock dung pats inhospitable to native dung beetle larvae, reducing competition for breeding resources, and increasing offspring emergence rates in some fly families (Iwasa et al. 2005). Removal of competition can also occur through geographic exclusion, as can be the case for introduced species that, in their new environment, are freed from their coevolved natural competitors (Clavel et al. 2011). Although competitive dominance over native species is often a key component of invasion success, introduced species are not always competitively superior (Sol et al. 2012). Invasive species are often better able to exploit novel urban niches than native species and so end up thriving in the absence of competition (Sol et al. 2012).

PREDATOR-PREY DYNAMICS

The redistribution of resources and shifts in predatory and antipredatory behaviors

due to anthropogenic disturbance can modify predator-prey interactions. For example, the presence of artificial night lighting alters interactions between insects and insectivores (Sanders and Gaston 2018), often enhancing predation success for nocturnal insectivores. This is driven by several mechanisms: night lighting can aggregate insect prey (Sanders and Gaston 2018); make prey more visible to predators (Cravens et al. 2018; Sanders and Gaston 2018); and, in the case of mercury vapor and LED lights, disrupt antipredatory behavior (e.g., moths: Svensson and Rydell 1998; Wakefield et al. 2015; dogwhelks: Underwood et al. 2017). Noise pollution from boats and chemical pollution are linked to similar interspecific disruptions: boat noise, for instance, reduces the approach distance at which hermit crabs will hide from predators, reducing capture difficulty for predators (Chan et al. 2010); and chemical pollutants disrupt antipredator defenses in a number of freshwater systems enhancing predator foraging success (Saaristo et al. 2018). Despite increasing evidence of behavioral change, actual fitness effects for predators and long-term community effects are rarely measured. Aside from direct benefits, predators can indirectly benefit if the disturbance excludes competing predators (Schoeman 2016; Ballejo et al. 2018). Invasive species are typically generalists and thus are conferred higher predation success both in terms of the diversity of prey available to them but also because native prey often lack coevolved defenses (Crowder and Snyder 2010; Clavel et al. 2011). Predator success is often facilitated by their ability to exploit novel prey, such as cats (*Felis catus*) feeding on rodents around human food stores up to 9500 years ago (Fleming and Bateman 2018). These beneficial relationships may require the development of novel hunting strategies, as seen in European kestrels (*Falco tinnunculus*)—these birds are usually flight hunters, but will use sit-and-wait techniques above ventilation channels to catch bats and common swifts (Fleming and Bateman 2018). However, responses can vary across contexts: freshwater prey, for example, can be especially vulnerable to introduced predators because these species show greater naivety than terrestrial prey to novel predators (Cox and

Lima 2006). These sorts of biome-specific differences can arise due to different levels of connectivity between and within habitat types (Cox and Lima 2006), again highlighting the importance of anthropogenic impacts on habitat structure for species persistence.

Conversely, anthropogenic changes can benefit prey species by disrupting predation or excluding predators. In the presence of night lighting, some beetle species benefit through reduced predation pressure from bats, because bats switch their foraging focus to moths, whose antipredator defenses are disrupted (Minnaar et al. 2015; Cravens et al. 2018). Artificial night lighting also enhances the visual environment making predators easier for potential prey to detect thus hindering the specialized low-lighting nocturnal predator vision (Gaston et al. 2013) and reducing predation pressure. Comparable disruptions to predator-prey dynamics driven by species-specific differences in response are evident for noise and chemical pollution. In particular, if predators avoid noisy areas, prey species that are able to live in these environments may have lower mortality and higher reproductive success (Francis et al. 2009). Chemical pollutants such as acetylcholine-inhibiting pesticides disrupt muscle control in predators, rendering them less adept at capturing their prey, thus reducing predation pressure (Saaristo et al. 2018). Finally, human-driven declines in mammalian predator populations relieve predation pressures for lower trophic-level predators, increasing their abundance (Ripple and Beschta 2012; Gibb et al. 2021).

PARASITES AND PARASITIDS

Changes in habitat structure and physical conditions can dramatically alter parasite-host dynamics. For a host, geographical separation from their parasites or disruption to the parasite life cycle can be advantageous. Urban sparrowhawks have fewer *Leucocytozoon* blood parasites than in natural habitats because the life cycle of the intermediate vector, the black fly (Simuliidae), requires flowing fresh water, a resource that is reduced in urban areas (Suri et al. 2017). Introduced species

may also benefit if their natural parasites are unable to similarly adapt to the new habitat, and they may be further advantaged as native species will still experience pressure from their coevolved parasites (Clavel et al. 2011). Alternatively, species may actively use a pollutant to protect against parasites. Anecdotally, crows have been observed bathing in smokestacks, and this may work to clean parasites off their feathers (Kennedy 2018), although the fitness implications of this behavior are yet to be demonstrated experimentally. Birds that incorporate nicotine cigarettes in their nests confer a reduced parasite load for their growing chicks (Suárez-Rodríguez et al. 2013), but research suggests they may pay a significant fitness cost as the nicotine is linked to DNA damage in chicks (Suárez-Rodríguez and Garcia 2014).

In contrast, many parasites benefit from anthropogenic change. Climate warming and urban heat can increase parasite growth rates and reproductive fitness (Macnab and Barber 2012). The bird tapeworm *Schistocephalus solidus* exploits this by altering the behavior of its host, the three-spined stickleback, to seek out warmer habitats (Macnab and Barber 2012). Similarly, chemical pollution can increase the density of intermediate vectors, such as eutrophication increasing the population sizes of freshwater snails that transmit avian blood fluke (Lafferty and Kuris 1999). Urban green areas can also increase host densities, benefiting their parasites (Goulson et al. 2012). This can increase parasite transmission in urban birds (Epstein et al. 2006) and mammals (McCleery 2010). For example, urban striped field mice (*Apodemus agrarius*) carry higher densities of ectoparasites including ectoparasite species normally specific to cats and dogs (McCleery 2010). A reduction in habitat complexity due to agriculture also makes it easier for parasitoids, such as wasps and flies, to find their more concentrated hosts (Kruidhof et al. 2015). Additionally, parasites benefit when pesticides weaken host defenses, particularly when those pesticides have weaker effects on parasites, as seen in bees attacked by varroa mites (Sánchez-Bayo et al. 2016). Immune function can also be suppressed by exposure to artificial light at night (Durrant et al. 2015)

and by increasing temperatures (Fox et al. 2015), and these combined stressors can greatly increase parasite transmission (Kernbach et al. 2018).

LONG-TERM CONSEQUENCES BIODIVERSITY AND EXCLUSION OF NATIVE SPECIES

A major consequence of exploitation of anthropogenic change is biotic homogenization, which is where biodiversity declines due to the exclusion of some species, while other species become much more abundant. Biotic homogenization is driven by similarities in disturbed habitats between different geographic regions, as seen in urban parks and gardens, which often include similar species and habitat structures across different cities. This lack of habitat diversity allows some species to greatly increase their range and abundance (e.g., pigeons, rats, cellar spiders; McKinney 2008; Lowry et al. 2013). Species-specific traits such as dietary or habitat preferences play a key role, but are context dependent. For example, urban exploiters are often native generalists and/or introduced species that are capable of adapting to a range of conditions (Wong and Candolin 2015; Sánchez-Bayo and Wyckhuys 2019). In contrast, in agricultural systems, specialist herbivores on crop species or parasites of livestock are usually more successful (Saunders et al. 2016). Although the introduction of exotic species often displaces native species that are unable to adapt to disturbed habitats, this is not always the case (Alvey 2006; Plowes et al. 2007). Understanding which conditions provide sanctuary for native species is essential for biodiversity management. Further, the responses of native species depend on the type of anthropogenic disturbance, such as older residential areas protecting native fire ants from their invasive congeners (Plowes et al. 2007). Additionally, there can be complex relationships between native species that are disrupted by anthropogenic change, or indeed by subsequent mitigation of these changes. Reintroductions of mammalian predators into landscapes can reduce populations of

lower trophic-level predators that had thrived in their absence (Gibb et al. 2021), which has consequences for preserving native biodiversity (Ripple and Beschta 2012). More investigation is needed to fully understand how other factors such as increasing temperatures and habitat alterations influence these outcomes, particularly as introduced species are often better able to exploit anthropogenic change (Lowry et al. 2013; Sánchez-Bayo and Wyckhuys 2019).

SPREAD OF PARASITES, PESTS, AND DISEASE

Many of the animal species that benefit from anthropogenic change are harmful (or perceived to be disruptive), including parasites and pests. The spread of these animals is largely promoted by other anthropogenic factors dramatically increasing the abundance of their hosts, human effects on migration and transmission, and shifts in interspecific interactions. The use of crop monocultures provides enormous food resources for specialists on those cultivated plants (Andow 1983), while negatively impacting species that are unable to thrive on these plants (Sánchez-Bayo and Wyckhuys 2019). The same effect is seen for livestock parasites (Marano et al. 2007) and scavengers (Ballejo et al. 2018). The effects of these homogeneous populations have been exacerbated by the historical and ongoing application of broad-spectrum pesticides. Specifically, these pesticides kill the natural enemies of pests, making it easier for pests to rapidly repopulate agricultural areas when pesticide use stops (Sánchez-Bayo and Wyckhuys 2019). Pesticide use in a rotating crop field suppresses some pests and their predators, but if pesticide-resistant pest species are also present, secondary pest outbreaks may lead to lower crop yields than if pesticides had not been used (Sánchez-Bayo and Wyckhuys 2019). Pesticide resistance allows some species to occupy pesticide-sprayed areas, experiencing less competition and predation from nonresistant species (Nicholls and Altieri 1997). The spread of pests and disease can be further exacerbated by other anthropogenic stressors such as artificial light at night suppressing immune systems or increased

temperatures promoting parasite growth. Thus, anthropogenic change, and increased connectivity between different disturbed habitats, can lead to high abundances of pests and parasites, benefiting those species but greatly reducing biodiversity (Waite et al. 2007). Understanding these processes and their interactions is also important where conditions increase the density of disease vectors (Tasciotti 2017; Hanford et al. 2019) or urban land use differentially affects the success of species (Hanford et al. 2019). Historical perspectives are useful here, as seen in the displacement of the black rat by the brown rat, contributing to the decline of the bubonic plague (Barnes 2005; Rowland 2009). This knowledge is critical for urban planning decisions to minimize disease spread, and for agricultural management to maintain biodiversity and maximize food production (Andow 1983). Further, a warming climate may accelerate reproduction and the spread of pathogens and pests that threaten agriculture and public health (Fox et al. 2015; Sánchez-Bayo and Wyckhuys 2019), showing how particular stressors can have diverse and widespread impacts beyond their immediate effects.

EVOLUTIONARY RESPONSES FACILITATING EXPLOITATION OF ANTHROPOGENIC CHANGE

Although the ability to exploit and benefit from anthropogenic change often relies on behavioral plasticity or preadaptation (Wong and Candolin 2015) to novel conditions such as anthropogenic food sources or artificial habitats, some species have exhibited evolutionary responses that improve their capacity to benefit. A well-known example is the peppered moth (*Biston betularia*) evolving darker coloration at a population level in response to pollution coating trees, and then shifting back to a lighter coloration when pollution controls were implemented (Lambert et al. 2021). Similarly, faced with pesticide exposure, some species evolve pesticide resistance, facilitating their survival in polluted habitats. Another example is seen in the use of supplementary feeders, where bill length in great tits (*Parus major*) has increased, improving their ability to utilize this novel food source (Bosse

et al. 2017). These cases demonstrate how a feedback cycle can develop, where species that are initially able to inhabit disturbed habitats are then able to adapt to those habitats, further increasing their success over subsequent generations. Behavioral plasticity is an important first step that facilitates short-term benefits as it allows animals to shift their behavior and take advantage of novel conditions (Wong and Candolin 2015). However, long-term evolutionary consequences are rarely clear (Lambert et al. 2021), so more research is required to determine how different species will respond. Evidence for adaptation has largely been limited to heat islands and chemical pollution, with relatively little attention given to other stressors (but see Hopkins et al. 2018). It will be important to consider how multiple anthropogenic stressors acting together can change selection pressures, and how these stressors are likely to change in the future according to new technologies and management policies because this will alter the selection pressures.

THE EVOLUTIONARY TRAP

Although many species can exploit anthropogenic change, and adaptation may facilitate this exploitation, in most cases the long-term outcomes are not known. An evolutionary trap may occur where an anthropogenic change may provide short-term benefits, but ultimately result in long-term harm (Schlaepfer et al. 2002). A specific, well-researched type of evolutionary trap is the ecological trap, where an animal incorrectly perceives a habitat as beneficial (Hale and Swearer 2016). For instance, planting milkweed in gardens to facilitate monarch butterfly (*Danaus plexippus*) reproduction has significant fitness costs for the butterflies due to high urban densities of invasive parasitoid paper wasps (Baker and Potter 2020). Similarly, as urban areas heat up, some species grow larger and increase their fecundity (Lowe et al. 2014), but as temperatures surpass species-specific thermal tolerances, mortality may increase (Hamblin et al. 2017). Artificial night lighting increases foraging success for insectivores, but the combination

of intense predation pressure and physiological damage is likely destroying insect populations, so these predation benefits are unlikely to persist long term (Owens et al. 2020). Further, the benefits for urban exploiters can be equivocal even in the short term. For example, although exploiter species may consequently be more abundant, individual quality may be reduced due to inferior food quality (Johnson et al. 2012; Oro et al. 2013). Evidence from urban birds suggests this may result in a reproductive trade-off between offspring quality and quantity (Shochat 2004). Ecological traps can also result from shifts in biotic interactions. For example, olive-sided flycatchers (*Contopus cooperi*), which are adapted to early postdisturbance habitats, are more likely to nest in selectively harvested forests than naturally burned forests, but experience decreased nest success in harvested forests (Robertson and Hutto 2007). This is likely a result of a higher abundance of nest predators in harvested forests compared with postfire landscapes. Counterintuitively, reducing some environmental impacts may cause harm for species that now rely on anthropogenic processes. For example, seabirds that feed on fisheries discards may face food shortages when these discards are banned (Oro et al. 2013), and manatees (*Trichechus manatus*) that currently rely on thermal outputs from power plants for warmth during winter will be threatened when these power plants are retired (Laist and Reynolds 2005). Hence, longitudinal studies that consider plastic and evolutionary responses to anthropogenic change are vital (Sih et al. 2011).

MANAGEMENT AND RESEARCH IMPLICATIONS

MANAGING EXPLOITERS

This review has highlighted important gaps in our knowledge of the costs and benefits of anthropogenic change (Barzman et al. 2015; Fox et al. 2015). A key outcome of exploitation of human impacts identified across biomes and fields of research is that some species become highly abundant, while others decline. As conditions are often similar across

disturbed habitats, even in different parts of the world, this leads to local reductions in biodiversity and global biotic homogenization. It is clear that, in a disturbed world, successful management of biodiversity requires a detailed understanding of which species have the capacity to exploit anthropogenic change (Box 1). However, an important barrier to this is a lack of data regarding the long-term outcomes for animals. The fitness consequences for the majority of species remain largely anecdotal and unquantified (for example, the use of litter by spiders and smokestacks by crows). Further, many ostensible benefits have associated, but often unmeasured, costs (e.g., chicks reared in nests with cigarettes suffer increased DNA damage), highlighting the need for a comprehensive assessment of fitness. In doing so, attention should be given to how multiple forms of anthropogenic change function together. Increased temperatures can benefit prey predators when coupled with higher prey availability (Lowe et al. 2014), but are detrimental in the absence of foraging benefits under laboratory conditions (Johnson et al. 2019). Comparably, artificial lights increase foraging success in the field due to enhanced prey attraction and thus availability (Willmott et al. 2019), but this stressor could confer considerable fitness costs if urban conditions reduced prey availability (Willmott et al. 2018). Assessments of fitness outcomes are further complicated by variation in the timing and duration of exposure to stressors. For example, some insects may be exposed to chemical pollutants during their aquatic larval stage (Saaristo et al. 2018), while their terrestrial adults may be more exposed to artificial lights (Sanders and Gaston 2018) and encounter different introduced predators (Cox and Lima 2006).

SHIFTING ANTHROPOGENIC IMPACTS

Much of the discussion thus far, both in this review and in the literature more broadly, has focused on how animals respond to anthropogenic change in its current form. However, the properties of different forms of human impacts will change through time,

and so how animals respond will also need to adapt. Climate change, by definition, is a shifting stressor, and so provides a useful example for how variation in animal responses might be driven by a variable stressor (Benito-Garzón et al. 2014). Climate change studies highlight the value of considering differences between biomes, such as the greater impacts expected for equatorial regions and habitats such as tundra and boreal forest (Benito-Garzón et al. 2014). More recently, research into the effects of artificial light at night has been addressing the outcomes of the global transition to more energy efficient LED lights, which emit more of the physiologically harmful (blue) wavelengths compared with older lights (Gaston et al. 2013). The impact of this transition in lighting technologies is both broad and potentially catastrophic for all ecological levels—from individuals through to communities and corresponding changes in ecosystem function (Sanders and Gaston 2018). It is crucial to consider differences between biomes in this context. For example, freshwater systems will be vulnerable to the effects of climate change, but may also disproportionately benefit from reductions in pesticide usage, as many pesticides have strong effects on aquatic animals (Hanazato 2001). Likewise, terrestrial natural habitats are being quickly replaced by artificial habitats such as urban and agricultural areas, but terrestrial prey species show greater resilience to introduced predators compared with freshwater habitats (Cox and Lima 2006). Although most anthropogenic changes have the potential to benefit some species and harm others in all biomes, future management practices will require detailed consideration of the differences between biomes as human impacts shift in the future.

CONCLUSIONS

As anthropogenic change increasingly pervades the natural world, management decisions will need to consider not only which species are negatively affected, but if, and indeed how, some species are able to exploit novel conditions and resources. These changes

differentially impact species, altering the outcomes of biotic interactions, and therefore causing cascading impacts throughout an ecosystem. A holistic approach is required to make accurate predictions about the potential consequences of anthropogenic disturbance for ecosystems. However, it will be vital to develop a complete picture of fitness outcomes (Lambert et al. 2021), rather than basing conclusions on certain traits or partial fitness measures. This is especially important as pollutant-specific reviews often report equivocal results (Pekár 2012; Oro et al. 2013; Sanders and Gaston 2018). Further, no environmental stressor acts in isolation, yet to date the research understanding how multiple stressors function together is scarce. When a species is able to exploit anthropogenic change, there are sometimes associated costs, and this can reduce native biodiversity and disrupt the health of ecosystems. As a result, top-down control of pests can be reduced, and the spread of parasites and disease can be accelerated. Additionally, key ecosystem services can be lost if important species are unable to cope with anthropogenic conditions. Thus, the success of a few exploiting species can have cascading effects that compromise the health of entire ecosystems. Facilitating management decisions in this area necessitates a greater focus across taxa and biomes, and an increased emphasis on long-term fitness outcomes. Preserving a healthy, biodiverse ecological community requires knowledge of not only which species are being harmed by anthropogenic change, but also what species are benefiting and how long these benefits can last.

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