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Behavioural responses to human-induced environmental change

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ABSTRACT

The initial response of individuals to human-induced environmental change is often behavioural. This can improve the performance of individuals under sudden, large-scale perturbations and maintain viable populations. The response can also give additional time for genetic changes to arise and, hence, facilitate adaptation to new conditions. On the other hand, maladaptive responses, which reduce individual fitness, may occur when individuals encounter conditions that the population has not experienced during its evolutionary history, which can decrease population viability. A growing number of studies find human disturbances to induce behavioural responses, both directly and by altering factors that influence fitness. Common causes of behavioural responses are changes in the transmission of information, the concentration of endocrine disrupters, the availability of resources, the possibility of dispersal, and the abundance of interacting species. Frequent responses are alterations in habitat choice, movements, foraging, social behaviour and reproductive behaviour. Behavioural responses depend on the genetically determined reaction norm of the individuals, which evolves over generations. Populations first respond with individual behavioural plasticity, whereafter changes may arise through innovations and the social transmission of behavioural patterns within and across generations, and, finally, by evolution of the behavioural response over generations. Only a restricted number of species show behavioural adaptations that make them thrive in severely disturbed environments. Hence, rapid human-induced disturbances often decrease the diversity of native species, while facilitating the spread of invasive species with highly plastic behaviours. Consequently, behavioural responses to human-induced environmental change can have profound effects on the distribution, adaptation, speciation and extinction of populations and, hence, on biodiversity. A better understanding of the mechanisms of behavioural responses and their causes and consequences could improve our ability to predict the effects of human-induced environmental change on individual species and on biodiversity.

Key words: adaptation, behaviour, biodiversity, climate change, conservation, fitness, human disturbance, phenotypic plasticity, reaction norms, trade-offs.

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I. INTRODUCTION

Environments are currently changing at an unprecedented rate and scale due to human activities. Most animals have been subjected to environmental perturbations during their evolutionary history, but the higher speed of human-induced changes poses a challenge for many species. Urbanization, deforestation and habitat fragmentation are examples of anthropogenic effects animals have to adapt to on a very short timescale. The initial response of animals to human-induced disturbance is often behavioural, such as altered habitat selection or vigilance. This influences in turn the survival, reproductive success and distribution of the individuals and thereby the dynamics of the population, which ultimately will influence biodiversity.

Behavioural responses to environmental change can be beneficial if they prevent individuals from suffering high fitness losses under the new conditions, due to a higher probability of survival or enhanced reproductive success. This can prevent extinction of the population and give additional time for genetic adaptation (Pigliucci, 2001). As a result, populations that survive rapid environmental changes often consist of individuals that can adjust their behaviour rapidly to new conditions (Price, Qvarnström & Irwin, 2003; West-Eberhard, 2005; Kinnison & Hairston, 2007). However, if behavioural responses are maladaptive and reduce the fitness of the individuals, then the responses could cause population declines, which, under a worst-case scenario, could result in extinction of the population (Badyaev, 2005). Maladaptive responses are likely when populations encounter conditions that they have not encountered during their evolutionary history (Ghalambor *et al.*, 2007).

The ability of individuals to adjust their behaviour to changing conditions and adapt *in situ* influences their need to search for more favourable conditions. Behavioural responses can therefore have a major impact on the distribution of species and on biodiversity in different areas. Changes in behaviour can also influence evolutionary processes, by determining which individual will survive and reproduce under the changed conditions, and thereby alter selection acting on traits. These changes can in turn have long-term effects on the viability and evolution of populations, and eventually result in speciation, or, alternatively, cause hybridisation and the loss of species and biodiversity (Seehausen, van Alphen & Witte, 1997; Taylor *et al.*, 2006).

Changes in the behaviour of single species often influence other species through species interactions, such as predation, parasitism, competition and mutualism. This can alter the abundance of different species, and even cause the extinction of populations. Moreover, species with a high degree of behavioural plasticity, which are able to adjust to a range of conditions, often become invasive. These species fare well in disturbed environments, where populations of native species are declining, and frequently have a large impact on biodiversity by causing further declines in the abundance of native species (Leprieur *et al.*, 2008).

Thus, behavioural responses to human-induced environmental changes can have profound effects on the persistence and evolution of populations and, hence, on biodiversity. The links between environmentally induced behavioural responses and biodiversity are schematically illustrated in Fig. 1. The environment changes both naturally and due to human activities, which induces behavioural responses. The responses depend on the reaction norms of the individuals, which can vary among individuals and evolve over generations, depending on heritability (Pigliucci, 2001, 2005). The behavioural responses cause changes in species interactions, population dynamics and evolutionary processes, which in turn induce modifications of behaviour and evolution of the reaction norms, resulting in feedback loops between the processes. Alterations in population dynamics and evolutionary processes ultimately determine population persistence and speciation and, thus, biodiversity.

An example of the complexity of the interactions illustrated in Fig. 1 is the influence of human activities on the behaviour and abundances of black vultures (*Coragyps atratus*) and Andean condors (*Vultur gryphus*) (Carrete *et al.*, 2010). The larger Andean condor dominates over the smaller black vulture when feeding at carcasses, which until recently segregated the two species geographically. During the last decades, black vultures have learnt to exploit food resources associated with human development, and their populations have grown and expanded geographically. Black vultures are

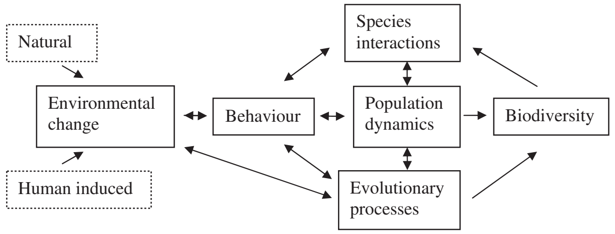

Fig. 1. The feedback system between environment, behaviour and biodiversity. Changes in environmental conditions induce behavioural responses, according to the reaction norm of the individual, which in turn affects species interactions, population dynamics, evolutionary processes and, ultimately, biodiversity. Changes in population dynamics, evolutionary processes and species interactions in turn affect behaviour, resulting in a complex network of feedback loops.

highly social and aggressive birds, and their higher abundance has changed the competitive scenario between the species. This is now threatening Andean condors, who are not as efficient as black vultures in utilizing resources provided by humans (Carrete *et al.*, 2010). This illustrates how changes in the behaviour of one species, due to human activities, can affect the population dynamics of both the species itself and of other species and thereby potentially influence biodiversity.

The importance of the links between environmental change, behaviour, population dynamics and evolutionary processes have repeatedly been stressed (Buchholz, 2007; Caro, 2007), but surprisingly little has been done to bridge these areas (Angeloni *et al.*, 2008). Here, we review the causes and the mechanisms of behavioural responses to rapid human-induced environmental changes, and discuss the consequences that the responses may have for populations and for biodiversity. Relatively little empirical research has been carried out on population consequences of behavioural responses and their evolutionary implications. We hope our review will inspire more work into this important research field. We start with examining the major environmental causes of behavioural responses, such as changes in the sensory environment and in habitat connectivity, and then proceed to discuss the determinants of the behavioural responses, i.e. the reaction norms of individuals and their evolution. We review how responses occur at different time scales, from immediate behavioural responses of individuals, over innovations and the social transmission of new behaviours within and between generations, to the evolution of behaviour across generations. We discuss how these processes depend on a range of factors, such as the speed and stage of the change and on species respective individual differences. Finally, we consider the consequences that altered behaviour of individuals may have for the dynamics and viability of populations, through effects on adaptation, speciation and extinction, and, thus, its eventual effect on biodiversity. Whether populations are able to adapt to new conditions, phenotypically and genetically, and perhaps evolve to new species, depends to a high degree on their behavioural reaction norms and the genetic variation in the norms. A better understanding of the mechanisms of behavioural responses and their causes and consequences could improve our ability to predict the effects of human-induced environmental change on populations and on species diversity.

II. CAUSES OF BEHAVIOURAL RESPONSES

Changes in abiotic and biotic environmental conditions due to human activities can influence the behaviour of individuals either directly (such as new food sources that attract individuals due to sensory drive) or by influencing factors that determine fitness and induce behavioural responses (such as reduced prey availability). The behavioural responses can be adaptive and improve individual fitness, or maladaptive and cause fitness losses, depending on the adaptiveness of the behavioural reaction norms under the new conditions. Common behavioural responses include changes in foraging, vigilance, dispersal, migration, reproductive behaviour and social behaviour (Table 1).

Environmental changes frequently influence behaviours through the second pathway, by affecting factors that determine the fitness of individuals, such as the ability to find food, avoid predation, acquire mates, provide parental care and interact with other individuals, both conspecifics and heterospecifics. Most often, environmental changes have a negative effect on fitness, such as habitat destruction that reduces survival and reproductive success of a large number of species. This forces individuals to alter their behaviour to maintain a high fitness. For a restricted number of species, environmental changes increase fitness or open up new ways to increase fitness through behavioural alterations, often at the expense of other species.

The alternative pathway, with environmental change triggering behavioural responses according to the reaction norm of the individuals, although their fitness is not affected by the change, may result in adaptive, neutral or maladaptive behavioural changes. The outcome depends on the adaptiveness of the individual reaction norms, which have evolved under past conditions.

Environmental changes often induce behavioural responses through several pathways. Urbanization, for instance, influences a multitude of factors, such as habitat structure, food resources, noise levels and the concentrations of different chemicals, all of which can cause behavioural responses, both immediate responses and the social transmission of novel behavioural patterns. The changes can also induce evolution of the behavioural reaction norms. Moreover, environmental changes frequently affect behaviours both directly and indirectly, through other species. Logging, for instance, influences the behaviour of animals directly, through the removal of nesting sites and shelters against predators, and indirectly through effects on other species, such as the density of predators or the number of competitors for food. This implies that the effects of environmental change on animal behaviour can be complex and difficult to predict.

Table 1. Examples of behavioural responses to human disturbance and their consequences for populations.

Environmental change		Behavioural response	Consequence	Species	Reference
Sensory environment and the transfer of information	Visibility	Altered mate choice	Hybridisations	Cichlids	Seehausen *et al.* (1997)
		Altered mate choice and mate competition	Relaxed selection on visual traits. Increased expenditure of time and energy	*Gasterosteus aculeatus*	Candolin *et al.* (2007)
		Altered mate choice	Relaxed selection on male body size	*Pomatoschistus minutus*	Järvenpää & Lindström (2004)
	Noise	Altered calling rate	Masking of mating calls	Several anuran species	Sun & Narins (2005)
		Increased response latency, changed orientation	Masking of mating calls	*Hyla chrysoscelis*	Bee & Swanson (2007)
	Olfaction	Altered mate choice	Hybridisation	*Xiphophorus birchmanni*	Fisher *et al.* (2006)
Disruption of physiological processes	Direct disturbance	Increased vigilance	Reduced resource use	*Rana iberica*	Rodriguez-Prieto & Fernandez-Juricic (2005)
		Changed social behaviour and habitat use	Changes in reproductive performance	*Cebuella pygmaea*	De La Torre *et al.* (2000)
		Increased vigilance	Reduced foraging	*Calidris alba*	Thomas *et al.* (2003)
	Temperature changes	Changed feeding rate	Changed growth	*Nucella ostrina*	Yamane & Gilman, 2009
	Heavy metals	Reduced burrowing speed, reduced feeding rate	Poorer condition	*Nereis diversicolor*	Kalman *et al.* (2009)
	Endocrine disrupting chemicals (EDCs)	Altered mate choice	Relaxed selection on male size	*Pomatoschistus minutes*	Saaristo *et al.* (2009)
	Pesticides	Reduced activity	Amplified negative effects of predators	*Hyla versicolor*	Relyea & Mills (2001)
Habitat characteristics	Habitat loss	Increased ranging	Relocation	*Tringa totanus*	Burton & Armitage (2008)
	Habitat fragmentation	Inbreeding avoidance	Maintenance of outbreeding	*Egernia cunninghami*	Stow & Sunnucks (2004)
		Avoidance of roads	Negative demographic and genetic effects	*Sistrurus catenatus*, *Terrapene carolina*, *Terrapene ornata*	Shepard *et al.* (2008)
	Habitat structure	Changes in mate-location strategies	Changed habitat use	*Salamis parhassus*	Bonte & Van Dyck (2009)
		Changed habitat choice, decreased flight distance	Increased population growth	*Odocoileus virginianus clavium*	Harveson *et al.* (2007)
Species interactions	Predation	Antipredator behaviour	Improved survival	Several larval anurans	Relyea (2001)

Here, we give an account of some of the major causes of behavioural responses, focussing on environmental changes that have a profound effect on individual fitness. We start with inspecting environmental factors that usually influence only a few processes that impact on fitness: the sensory environment and physiological processes. We then examine environmental factors that influence a multitude of processes that impact on fitness: the size, structure and connectivity of habitats and the abundance of other species.

(1) Changes in the sensory environment

The sensory environment, in the form of light conditions, acoustic properties and chemical compounds, determines the transmission and perception of information regarding the surroundings, such as the availability of food, the risk of predation and the identity of mates. Human activities are presently altering the sensory environment, such as traffic that changes noise levels. Since behavioural responses depend on the information that individuals acquire regarding their surroundings, changes in the sensory environment can have profound effects on the behaviour of individuals and, consequently, on their fitness.

(*a*) *Visual environment*

Humans influence the visual environment in two main ways; through the production of artificial light and by changing natural light conditions and visibility. The production of artificial light influences the orientation of individuals that rely on visual cues for movements (Longcore & Rich, 2006). Sea turtle hatchlings (*Caretta caretta* and *Chelonia mydas*), for example, move towards human settlements instead of the ocean during nights when artificial lights are brighter than the horizon over the ocean (Tuxbury & Salmon, 2005). Similarly, migratory birds are attracted to artificial lights and collide with tall, brightly lit buildings and radio towers during their migrations (Longcore & Rich, 2004). Moreover, many insect species are attracted to artificial lights, such as streetlamps, which in turn attracts insectivorous frogs, bats and birds (Longcore & Rich, 2006).

Artificial light also alters activity levels. Male green frogs (*Rana clamitans melanota*), for instance, produce less advertisement calls and move more frequently under artificial light than in ambient light (Baker & Richardson, 2006). Similarly, many bird species change the timing of singing under artificial light, such as American robins (*Turdus migratorius*) that initiate their morning chorus during the night if disturbed by artificial light (Miller, 2006). Light pollution also influences community interactions, such as competition and predator-prey interactions, by influencing activity patterns and reaction distances of predators and prey (Longcore & Rich, 2004).

The second pathway along which humans alter the visual environment is by altering natural light conditions. A growing problem in aquatic environments is eutrophication and increased turbidity. This deteriorates the visual environment and influences foraging, predator avoidance and mate-choice behaviour of organisms that rely on vision (Candolin, 2009). High turbidity levels, for instance, reduce the reactive distance of visual predators to their prey, which reduces their foraging efficiency and food intake rate, as documented for brown trout (*Salmo trutta*) (Stuart-Smith, Richardson & White, 2004) and Eurasian perch (*Perca fluviatilis*) (Radke & Gaupisch, 2005; Ljunggren & Sandström, 2007). Similarly, hampered visibility due to eutrophication impairs mate assessment in cichlids (Seehausen *et al.*, 1997; Maan, Seehausen & van Alphen, 2010), three-spined sticklebacks (*Gasterosteus aculeatus*) (Candolin, Salesto & Evers, 2007; Wong, Candolin & Lindström, 2007) and pipefish (Sundin, Berglund & Rosenqvist, 2010). On the other hand, turbidity has positive effects on species that are not dependent on good visibility, who benefit from lowered predation risk or increased feeding rate under poor visual conditions (Gregory, 1993).

On land, logging and deforestation caused by humans have profound effects on light conditions. Deforestation is expected to influence the behaviour of animals that rely on visibility, particularly predator-prey and mate-choice behaviours, but the topic has so far received little attention. A recent study shows that the deterioration and fragmentation of tropical cloud forests causes an Afrotropical forest butterfly (*Salamis parhassus*) to change its mate-location strategy from perching to patrolling, which results in a faster occupancy of light gaps in the forests (Bonte & van Dyck, 2009).

The above-mentioned studies indicate that individuals often respond to changes in visibility with behavioural alterations that influence their fitness, such as altered activity time or mate-choice behaviour. This is likely to have consequences for the viability and distribution of the populations and for evolutionary processes and, thus, for the diversity of species.

(*b*) *Auditory environment*

Acoustic pollution from anthropogenic sources interferes with detection and discrimination of acoustic signals. This hampers many fitness-related behaviours, such as mate attraction and predator avoidance. For instance, acoustic pollution often masks predator arrival and associated alarm calls and thereby impedes predator detection, which reduces the individuals' probability of survival (Slabbekoorn & Ripmeester, 2008). Urbanization and traffic are common sources of noise that affect an increasing number of species. Common responses to increased noise are changes in vocalisations to prevent masking, and reductions in the investment into acoustic communication. Many anuran species, for instance, increase their calling activity when the noise from traffic is high or, alternatively, decrease calling (Sun & Narins, 2005; Lengagne, 2008).

In aquatic environments, where sound propagates better than light, noise from ship traffic and different commercial, research and military activities has increased over the past century (Tyack, 2008). This has resulted in changes in the vocalisations and behaviours of many marine mammals, such as beluga whales (*Delphinapterus leucas*) (Lesage *et al.*, 1999), manatees (*Trichechus manatus*) (Miksis-Olds & Miller, 2006) and right whales (*Eubalaena glacialis*, *E. australis*) (Parks, Clark & Tyack, 2007). The calls of killer whales, for instance, are longer in the presence of noise from whale-watching boats, probably to compensate for the acoustic pollution (Foote, Osborne & Hoelzel, 2004), while humpback whales (*Megaptera novaeangliae*) increase the repetition of phrases in their songs when exposed to low-frequency sonar (Miller *et al.*, 2000). Similarly, several dolphin species change their behaviour and vocalisation in the presence of boat sound (see for instance Buckstaff, 2004; Constantine, Brunton & Dennis, 2004; Ribeiro, Viddi & Freitas, 2005; Sini *et al.*, 2005; May-Collado & Wartzok, 2008; Miller, Solangi & Kuczaj, 2008; Tosi & Ferreira, 2009).

On land, urbanization has increased loud and low-pitched noise (Warren *et al.*, 2006). The most common response to such noise, in both humans and other animals, is to raise signal amplitude. For instance, urban great tits (*Parus major*) sing with a higher minimum frequency in noisy areas to prevent their songs from being masked by low-frequency noise (Slabbekoorn & Peet, 2003; Slabbekoorn & den Boer Visser, 2006). Other responses are temporal shifts in singing activity and avoidance of areas associated with high levels of noise (Berger & Abs, 1997; Fuller, Warren & Gaston, 2007; Slabbekoorn & Ripmeester, 2008). Thus, animals attempt to prevent fitness losses in acoustically polluted areas by changing the components of their vocalisations, such as the amplitude or the temporal activity pattern. For some species, this helps maintain viable populations in areas subjected to human acoustic pollution.

(*c*) *Olfactory environment*

Many species rely on olfactory cues for communication, navigation, predator detection, location of food and social recognition. The current release of chemicals into the environment is disrupting the transfer of olfactory cues. This hampers the reception of information regarding the environment and hinders communication among individuals, which can induce maladaptive responses in both senders and receivers (Lurling & Scheffer, 2007). Pesticides, for example, impair sexual pheromonal communication in red spotted newts (*Notophthalmus viridescens*), which disrupts their mate-choice behaviour (Park, Hempleman & Propper, 2001). Another example is the ubiquitous contaminant, 4-nonylphenol, which impairs social recognition and, hence, social organisation in fishes (Ward *et al.*, 2008).

The transfer of olfactory cues influences not only intraspecific communication but also inter-specific interactions, such as species recognition. Since species recognition is important in preventing hybridisations, chemical pollution is currently increasing hybridisations between species. For instance, the olfactory signalling system that allows female swordtail fish (*Xiphophorus birchmanni*) to recognise mates through olfactory cues is hindered in streams exposed to agricultural runoff and sewage effluents. This hampers the recognition of conspecific males, which results in an increase in the number of hybrids between *X. birchmanni* and a congener, *X. malinche* (Fisher, Wong & Rosenthal, 2006). Thus, the current increase in chemical pollution may have far-reaching consequences for the viability of populations, both by disrupting the reception of information regarding the environment and by hampering the transfer of information among individuals, both within and between species.

(2) Disrupters of physiological processes

Changes in environmental factors that regulate physiological processes also influence behavioural processes. For instance, changes in abiotic factors that affect neural and hormonal processes, such as temperature and the concentration of chemical compounds, influence a range of behaviours (Zala & Penn, 2004; Kearney, Shine & Porter, 2009). A currently growing human-induced problem is increasing temperatures due to climate change and altered habitat structures. Changed temperature influences the behaviour of animals both directly, through physiological processes, and by inducing avoidance behaviours (Huey & Tewksbury, 2009). Animals may, for example, shuttle between sun and shade to maintain an optimal body temperature to avoid negative effects on physiology (Kearney *et al.*, 2009).

Of particular concern today are endocrine-disrupting chemicals, EDCs, such as dichlorodiphenyltrichloroethane (DDT) and other organochlorine chemicals, which act as hormones in the endocrine system. They have become ubiquitous in the environment due to human activities, and are found today in the tissues of humans and wildlife, with adverse effects on social behaviour, reproductive behaviour and cognition (Zala & Penn, 2004). Tree swallows (*Tachycineta bicolor*), for instance, living in polychlorinated biphenyl (PCB)-contaminated sites build lower quality nests and are more likely to abandon or bury their eggs than birds living in cleaner areas (McCarty & Secord, 1999*a*, *b*). Similarly, DDT and PCBs have negative effects on reproductive behaviour of mice (*Mus musculus*) and rats (*Rattus norvegicus*) (Mably *et al.*, 1992; Eroschenko *et al.*, 2002; Palanza *et al.*, 2002).

EDCs frequently influence activity levels. Tadpoles (*Hyla versicolor*), for instance, reduce their swimming activity after exposure to the pesticide carbaryl (Relyea & Mills, 2001), while juvenile rainbow trout (*Oncorhynchus mykiss*) exposed to 4-nonylphenol, a surfactant used in industrial and sewage-treatment processes, show decreased shoaling tendency and are less successful in competition for food resources (Ward, Duff & Currie, 2006). In three-spined sticklebacks, increased concentrations of waterborne ethinyl estradiol, a common ingredient of contraceptive pills, cause males to become more aggressive (Bell, 2001).

EDCs also influence learning and the development of behavioural reactions during an individual's ontogeny (Zala & Penn, 2004). Impaired learning ability can hinder the spread of favourable behavioural reactions in populations and hamper the adjustment to changed conditions. For instance, mammals that are exposed to PCBs during development suffer impaired learning and memory, which influences a range of behaviours, from migration to reproduction (Schantz, Levin & Bowman, 1991; Schantz, Moshtaghian & Ness, 1995; Rice & Hayward, 1997, 1999; Rice, 2000). Thus, a growing number of studies suggest that changes in factors that affect physiological processes also influence fitness-related behaviours, which can have far-reaching consequences for the viability of populations.

(3) Changes in habitat size, structure and connectivity

Many human activities, such as deforestation and urbanisation, change the size, structure and connectivity of habitats. These changes influence a multitude of factors that determine fitness, such as the possibility of dispersal, the availability of resources and the risk of predation. Alterations in these factors often have profound effects on the survival and reproductive success of individuals and, consequently, induce behavioural responses according to the reaction norms of the individuals.

A growing problem associated with human activities is the fragmentation of habitats. This often reduces the density of individuals within the patches, due to a decline in the amount or diversity of resources within each patch (such as food or breeding sites), more efficient predators, or the avoidance by individuals of small patches with a low density of conspecifics (Bender, Contreras & Fahrig, 1998; Connor, Courtney & Yoder, 2000; Fletcher, 2009). Reduced density decreases encounter rates between individuals, which can alter both social behaviour and mate-choice behaviour and, thus, the fitness of individuals (Banks *et al.*, 2007). Alternatively, habitat fragmentation may raise population density, through the shrinking of suitable habitats, which similarly can influence interactions among individuals (Debinski & Holt, 2000; MacDonald *et al.*, 2004). Habitat fragmentation, for instance, increases the densities of Eurasian badgers (*Meles meles*) and meadow voles (*Microtus pennsylvanicus*) within the fragmented patches, which strengthens competition for limited resources and causes aggressive encounters between individuals (Boonstra & Boag, 1992; MacDonald *et al.*, 2004).

Between patches, fragmentation reduces dispersal. This lessens gene flow and increases genetic drift and inbreeding, which can reduce genetic diversity and increase the risk of extinction (Frankham, Ballou & Briscoe, 2002). Extinction of populations causes selection at the population level, favouring populations consisting of individuals with behavioural responses that reduce the risk of inbreeding. In support of this, southern hairy-nosed wombats (*Lasiorhinus latifrons*) and agile antechinuses (*Antechinus agilis*) avoid breeding with close relatives in fragmented habitats (Parrott, Ward & Temple-Smith, 2007; Walker, Sunnucks & Taylor, 2008).

Changes in habitat structure often also alter the availability of resources, such as nesting sites and shelters against predators. To prevent the loss of fitness, animals are then forced to change their behaviour and accept novel resources. For instance, the building of cities has removed traditional nesting sites and shelters for a large number of species, which has forced animals to either accept novel sites or search for habitats with more favourable conditions (Tratalos *et al.*, 2007).

Thus, an increasing number of studies show that changes in habitat characteristics, such as connectivity and resource abundances, induce behavioural responses that influence the fitness of individuals. This affects the viability and distribution of populations, and the evolution of behavioural reaction norms, and, eventually, biodiversity.

(4) Changes in the abundance of heterospecifics

Environmental changes that alter the presence or relative abundance of single species also influence interspecific interactions, such as predator-prey relationships, parasite-host interactions, mutualism and competition. Moreover, differences in responses among species can result in mismatches between species in phenologies and dispersal patterns and constrain the ability of single species to adjust to environmental change (Berg *et al.*, 2010). For example, the response of parasitoids to environmental change is constrained by that of their hosts, since parasitoids are dependent on the ecology of their hosts (Hance *et al.*, 2007). Such multi-species interactions imply that predicting the consequences of environmental change for individual species requires knowledge on species interactions.

Specialised species often suffer more from human activities than do generalists. A reduction in the number of specialists can therefore result in the competitive release of generalist species that are behaviourally flexible (Slabbekoorn & Halfwerk, 2009). Omnivorous predators, for instance, are less negatively affected by habitat change than specialist predators and increase their predation rate when competition from specialists declines (Ryall & Fahrig, 2006). Feral predators and predators in edge-habitats, in particular, are favoured by human disturbances and benefit through increased predation success (Kareiva, 1987; Chalfoun, Thompson & Ratnaswamy, 2002; Ries *et al.*, 2004).

An anthropogenic disturbance with a major impact on multi-species interactions is habitat fragmentation, since it usually alters the density and diversity of species. For instance, the fragmentation of forest landscapes depresses the breeding success of black grouse (*Tetrao tetrix*) and capercaillie (*Tetrao urogallus*), most likely due to an increase in the density of generalist predators and a higher rate of nest predation (Kurki *et al.*, 2000). Habitat fragmentation also impairs the ability of species to protect themselves against predators. Fragmentation through logging, for example, reduces forest cover and the protection of the nests of many songbirds, which increases predation by predatory species, such as gray jays (*Perisoreus canadensis*) (Thompson, Warkentin & Flemming, 2008).

The responses of interacting species to environmental change depend on the initial ecological conditions. For example, the effect of habitat fragmentation on the distribution of the ectoparasitic deer tick (*Ixodes scapularis*) on small rodents varies among areas; in some areas, parasite prevalence increases with fragmentation, while in others it decreases (Allan, Keesing & Ostfeld, 2003; Wilder & Meikle, 2004). Similarly, the effect of temperature changes on host-parasite interactions varies widely depending on genotype-by-genotype-by-environment interactions (Thomas & Blanford, 2003). This complexity of interactions among species, and their dependence on environmental conditions, emphasizes the importance of considering the community of species and their interactions when evaluating the effect of human-induced environmental changes on the viability of populations and on species diversity.

III. MECHANISMS AND PATTERNS

In the preceding section, we discussed the major causes of behavioural responses to human-induced environmental change. We now turn to the mechanisms of the responses, the behavioural reaction norms, and the factors that influence the responses, such as physiological processes, the rate and stage of change, species characteristics and individual differences. To predict which species will be able to withstand rapid human-induced environmental changes and which will not, we need a good understanding of the mechanisms of the behavioural responses and their dependence on extrinsic and intrinsic factors.

At the population level, behavioural responses take place at three different time scales: first, through immediate individual responses, whereby individuals adjust their behaviour to the environment according to their individual reaction norm, then, by innovations and the social transmission of new behaviours within and across generations, and, finally, by the evolution of the behavioural reaction norms over generations. Herein, we will mostly concentrate on immediate individual responses, the first response to sudden human-induced environmental changes, since these determine if the population will survive the initial change.

Immediate behavioural responses to environmental change depend on the reaction norm of the individuals, i.e. the phenotypes that a single genotype can produce depending on environmental conditions. We start with examining these reaction norms and their evolution, and then move to inspect the factors that influence the responses.

(1) Behavioural reaction norms

The behavioural responses of an individual to different environmental conditions can be described with a reaction norm (Pigliucci, 2001). The responses can be fixed and invariant or more or less plastic and depend on extrinsic and intrinsic conditions. The reaction norm and its plasticity is genetically determined and, consequently, a product of past evolutionary processes. This has two major implications, first that past ecological and evolutionary processes determine the reactions of individuals under prevailing conditions and, thus, the ability of individuals to adjust to changed conditions, and second, that behavioural reaction norms can evolve and become better adapted to new conditions, depending on genetic variation and constraints.

Behavioural responses can change over time through innovations and the social transmission of new behavioural patterns, and through evolutionary changes of the reaction norm (Fig. 2). The ability to adopt new behaviours through innovations and learning is genetically determined and under selection, with environmental conditions influencing the process. The evolution of behavioural reaction norms is constrained by the amount of genetic variation, the magnitude of gene flow, allometric relationships, environmental covariances, phylogenetic history and trade-offs between traits (Auld, Agrawal & Relyea, 2010).

The degree of plasticity in behavioural responses is predicted to depend on the heterogeneity of the environment in which the behaviours evolved: plastic behaviours are favoured in heterogeneous or fluctuating environments, but lost in stable environments, where directional selection favours canalized traits and more fixed behaviours (van Tienderen, 1991; Pigliucci, 2001; Sultan & Spencer, 2002). Animals from environments that are temporally or spatially variable are therefore more likely than animals from stable environments to encompass favourable reaction norms, which would allow them to cope behaviourally with new conditions (Carey, 2009).

If the environment differs much from what the species has experienced during its recent history, then adaptive reaction norms that allow the species to adjust to new conditions may not exist. Adjustment then hinges on the adoption of new behaviours, through innovations and learning, and on the contemporary evolution of the behavioural reaction norms. Empirical studies show that the evolution of reaction norms can be rapid (Callahan, Maughan & Steiner, 2008; Buskirk & Steiner, 2009). For instance, phototactic behaviour in *Daphnia* spp. populations, which is a predator-avoidance strategy related to diel vertical migration, evolves rapidly under different levels of fish predation (Cousyn *et al.*, 2001).

The factors that restrict the evolution of plastic behaviours are poorly known. Most empirical studies have found insignificant or weak costs of plasticity, and more investigations on the evolution of behavioural responses are currently needed (Buskirk & Steiner, 2009). Increased knowledge about the evolution and expression of plasticity could improve our ability to predict behavioural responses of species to environmental change, which could, eventually, help us forecast potential changes in biodiversity.

(2) Physiological processes

Human disturbances frequently influence the behaviour of animals through physiological processes or, alternatively, by inducing behavioural avoidance responses to prevent harmful physiological changes (Dell'Omo, 2002; Amiard-Triquet, 2009). Physiological processes, like metabolism and neuroendocrine processes, control functions that determine fitness, such as the immune system, reproductive functions and body growth, and changes in them can have profound effects on behavioural responses. For instance, noise and increased concentrations of chemical compounds frequently cause neuroendocrine responses, which influence a range of behaviours, such as migration and parental care, (Wingfield, 2008). The responses are often used as behavioural biomarkers of exposure to stress or chemical pollutants (Dell'Omo, 2002; Amiard-Triquet, 2009).

An increasing number of studies find human-induced environmental change to cause physiological stress and thereby induce behavioural alterations. For instance, direct disturbance by humans increases stress-related behaviours in

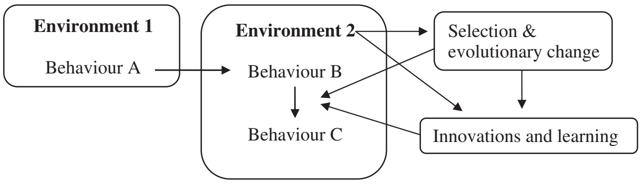

Fig. 2. The dependence of behaviour on environmental conditions and evolutionary processes. Changes in environmental conditions cause individuals to change their behaviour from A to B according to their genetically determined reaction norm. Selection on the reaction norm and the adoption of new behaviours cause the behaviour to change from B to C. The ability to adopt new behaviours through innovations and learning is genetically determined and influenced by environmental conditions and can evolve.

marsh harriers (*Circus aeruginosus*), such as alarm calls, chases against other intruding birds and increases in time spent flying, which decrease their nest-directed behaviour (Fernandez & Azkona, 1993). Similarly, the presence of tourists causes stress responses in Humboldt penguins (*Spheniscus humboldti*), such as higher heart rate and increased energy expenditure, which increase the probability that the birds will desert their nests (Ellenberg *et al.*, 2006). In bearded vultures (*Gypaetus barbatus*), human disturbances reduce nest attendance, which increases the probability of breeding failure (Arroyo & Razin, 2006).

Animals attempt to avoid stressful conditions by moving away from the disturbance or by changing their temporal pattern of activity (Clotfelter, Bell & Levering, 2004; Scott & Sloman, 2004). A polychaete worm (*Nereis diversicolor*), for instance, avoids toxic chemicals by reducing its burrowing speed in contaminated estuaries (Mouneyrac, Perrein-Ettajani & Amiard-Triquet, 2010). Similarly, many aquatic organisms avoid areas that have become anoxid due to human-induced eutrophication (Kidwell *et al.*, 2009). For instance, brown shrimps (*Farfantepenaeus aztecus*) and Atlantic croakers (*Micropogonias undulatus*) in the northern Gulf of Mexico move away from hypoxia areas and congregate along the edge of hypoxic zones (Craig, Crowder & Henwood, 2005).

(3) Influence of the rate and stage of change

The rate at which the change occurs has a major impact on behavioural responses, at both the individual and the population level. When the environment changes rapidly, animals have to react fast (Hairston *et al.*, 2005). Deforestation, for instance, forces individuals immediately to change nesting sites, switch to new food sources or adopt novel anti-predator strategies. Populations consisting of too few individuals with adaptive reaction norms for the maintenance of viable populations will then go extinct (Ghalambor *et al.*, 2007). If the environmental change is drastic, only a few species may be able to cope with the change and survive. These few species will then encounter lowered resource competition and benefit from the rapid change, resulting in a species-poor community with a few successful species (Poloczanska *et al.*, 2008). On the other hand, environmental changes that occur slowly allow animals to adjust their behaviour gradually to the new conditions. This provides time for experience to accrue and for learning of new behavioural reactions. Slowly progressing changes can also give time for the emergence of favourable genotypes through mutations and gene flow, and allow evolutionary responses through selection. For example, the gradual progress of climate change has allowed many species to adjust to the changes that so far have occurred, particularly through changes in the timing of migration and breeding, although it is not always known if the responses are due to plasticity or to evolutionary changes (Reusch & Wood, 2007; Charmantier *et al.*, 2008; Gienapp *et al.*, 2008).

The initial response of animals to environmental change is usually plastic alterations of behaviour, according to the genetically determined reaction norm. If the initial response is adaptive and reductions in fitness are prevented, then no further changes in phenotypes and genotypes are needed. However, if the initial behavioural response is incomplete and does not maximise individual fitness, then further changes are required (Ghalambor *et al.*, 2007). An incomplete behavioural response can be due to limits of plasticity, which prevent individuals from behaving optimally (Price *et al.*, 2003), or to costs of plasticity that cause individuals with highly plastic behaviour to have a lower fitness than individuals with less plastic behaviour (Auld *et al.*, 2010).

Responses at later stages of environmental change can be due to the social transmission of new behavioural reactions and to genetic alterations of the behavioural reaction norms. If the environment continues to change, animals may be forced to alter their behaviour continuously. Changes in behaviour through innovations and the social transmission of new behavioural patterns have been suggested to help individuals adjust to environmental change and facilitate evolutionary adaptation (Lefebvre, Reader & Sol, 2004; Sol *et al.*, 2005; van der Post & Hogeweg, 2009). In support of this, avian species with larger relative brains, which enhances their innovation propensity, are more successful at establishing themselves in novel environments (Sol *et al.*, 2005).

Genetic alterations of behavioural reaction norms occur over generations and become apparent at later stages of adjustment. They depend on the existence of genetic variation in the right direction and can, at least under some conditions, be fast (Reznick *et al.*, 1997). An example of a genetic change is the alteration in migration behaviour of the Glanville fritillary butterfly (*Melitaea cinxia*); during the colonization of new habitats, highly dispersive individuals dominate at the settlement stage while genetically determined sedentary individuals increase in frequency over time (Hanski *et al.*, 2004; Saastamoinen, 2008). However, little empirical attention has so far been paid to the relative importance of plastic and genetic responses at different stages of human-induced environmental change, and more work, particularly empirical work, is currently needed.

(4) Influence of life histories, specialisation and individual differences

Behavioural responses to environmental change depend on life histories and the degree of habitat specialisation of the species. Life histories are major determinants of behavioural responses, since they determine the allocation between present and future effort. For instance, animals confronting disturbances have to decide whether to stay or leave the area, and may then be forced to balance the value of current offspring against future reproductive opportunities. The outcome of this trade-off varies among species; long-lived species that produce only a few young over their lifetime value current offspring higher than iteroparous species that produce several broods over their short life-span (Magnhagen, 1991; Roff, 2002). Iteroparous species are therefore more likely to desert their offspring under environmental change.

Species also differ in their degree of habitat specialisation and, hence, in their sensitivity to habitat change. Habitat generalists are usually less sensitive to human disturbance than specialists and often survive changes better (Bonier, Martin & Wingfield, 2007; Hamer & McDonnell, 2008; Colles, Liow & Prinzing, 2009). A well-known example is the rat (*Rattus norvegicus*), a habitat generalist that can adjust its behaviour to a range of environments (McKinney, 2002). In addition, special characteristics of the environment may determine who survives. The common frog (*Rana temporaria*), for instance, has survived urbanisation in south-east England better than the large common toad (*Bufo bufo*), probably due to common frogs being able to use garden ponds in urban and suburban areas, while toads are not (Carrier & Beebee, 2003).

At the individual level, large differences in behavioural responses to novel conditions often occur (Dingemanse *et al.*, 2010). Individuals differ in traits such as boldness and temperament, that is, in personality, which can influence their responses to human disturbance (Koolhaas *et al.*, 1999; Minderman *et al.*, 2009). Eastern chipmunks (*Tamias striatus*), for example, vary in their stress response to human disturbance and how they distribute themselves in relation to the disturbance (Martin & Reale, 2008). Moreover, behavioural decisions may be condition-dependent with individuals in good condition changing their behaviour either more or less than individuals in poor condition (Beale & Monaghan, 2004). For instance, individuals in poor condition may make more risky decisions and search for food in more dangerous habitats than well-fed individuals. In the rodent porcupine (*Erethizon dorsatum*), for example, nutritionally stressed individuals forage in more risky habitats where predation risk is higher (Sweitzer, 1996). Such individual differences in responses imply that results based on the observation of a restricted number of individuals can be unreliable and should be interpreted with care (see also Dingemanse *et al.*, 2010).

(5) Adaptive or maladaptive responses

The behavioural response of an individual to environmental change can be adaptive and increase its fitness, or maladaptive and decrease its fitness. If enough individuals respond adaptively, then the viability of the population may be maintained or even improved, while maladaptive responses can further reduce population viability.

(*a*) *Adaptive responses*

Adaptive behavioural responses to environmental change increase the survival and reproductive success of the individuals. Adaptive responses are most likely when the human-disturbed environment resembles environments that the species has experienced in the past, since adaptive reaction norms could then have evolved under the past conditions and still exist in the population. An example of a behavioural response that often is adaptive under human-induced environmental change is the inclusion of new food sources in the diet, such as new prey species or food provided by humans. For instance, bears (*Ursus* spp.) and small mammals in national parks have started to include food left in garbage dumps and provided by recreationists in their diet (Boyle & Samson, 1985). Similarly, several scavenging raptors have benefitted from including animals killed by vehicles along human-constructed roads in their diet (Lambertucci *et al.*, 2009).

Urban areas often place special requirements on animals by being homogenous habitats with reduced seasonality, few natural enemies, high noise levels and intense anthropogenic activity. Species that are able to cope with these conditions often show high behavioural plasticity, such as high flexibility in their use of food (McKinney, 2006; Bonier, Martin & Wingfield, 2007). In addition, urban adapters often have traits that facilitate their adjustment to urban areas, such as high levels of aggression that allow them to outcompete other species. For instance, European starlings (*Sturnus vulgaris*) and house sparrows (*Passer domesticus*) fare well in urban areas where they are aggressive competitors that exclude other species (Marzluff, 2001). Similarly, invasive species often harbour much plasticity in behaviour and encompass special behaviours that allow them to survive and reproduce in human-disturbed environments, such as plastic feeding modes, behavioural innovations and aggressive behaviour (Jeschke & Strayer, 2006).

(*b*) *Maladaptive responses*

When the environment changes to a state that the species has not experienced during its recent evolutionary history, then individuals often respond in a maladaptive manner. For instance, the introduction of a new predator may require behavioural responses that individuals do no encompass. Those individuals that do not behave in a favourable manner will then suffer reduced survival or reproductive success, which may diminish the viability of the population.

Maladaptive behavioural responses to rapid human-induced environmental changes are common. There are two main ways in which they arise; through maladaptive changes in behaviour, and through a continuation of old behavioural patterns although this is fatal under altered conditions. An example of the first possibility, maladaptive changes, is increased vigilance that incurs no fitness advantages in the form of increased survival, but reduces the time spent on other fitness-enhancing activities, such as foraging or parental care (i.e. Andersen, Linnell & Langvatn, 1996; Argue, Mills & Patterson, 2008). For instance, Amur tigers (*Panthera tigris altaica*) that hunt near roads with much human disturbance abandon their kills and eat less meat than tigers hunting in areas undisturbed by humans (Kerley *et al.*, 2002). This results in decreased survival and reproductive success of tigers in areas with much human disturbance (Kerley *et al.*, 2002). Similarly, colonial water birds abandon their nests temporarily or permanently when disturbed by humans, with fatal consequences for their offspring (Carney & Sydeman, 1999).

The other possibility, that animals continue to behave in the same way as in the old environment, although this is maladaptive and reduces fitness, is similarly common. Courting three-spined stickleback males, for instance, continue to court females vigorously and show off their bright red nuptial coloration when placed in an environment with increased algae growth and reduced visibility, even though the visual traits no longer increase mate attraction but are a waste of time and energy (Candolin *et al.*, 2007). Similarly, behaviours that ensured honest advertisement of individual quality during mate choice under past conditions may not ensure honesty under changed conditions (Candolin, 2009). In the three-spined stickleback mate-choice system, for example, male-male competition ensures that courtship activity reflects male condition, but increased turbidity of the water relaxes the social control of visual signalling, which reduces the honesty of the courtship activity as a sexual signal of condition (Wong *et al.*, 2007).

IV. CONSEQUENCES OF BEHAVIOURAL RESPONSES

In the preceding sections, we reviewed behavioural responses to human-induced environmental change, their causes and their mechanisms. We now explore the consequences of the behavioural responses for populations, considering species distributions, adaptation, population growth, speciation and extinction, that is, the processes that determine biodiversity.

(1) Species distributions

If behavioural responses and changes in behavioural reaction norms, through innovations, learning and evolutionary processes, cannot preserve a population within an area, then individuals have to move and search for more favourable habitats. The success of the search depends on the species' dispersal potential, the speed of the environmental change and the availability of new areas for colonization (Holt & Keitt, 2000). Human-induced environmental changes often alter the availability of suitable habitats and, hence, the possibility of dispersal (Walther *et al.*, 2002). Logging and urbanization, for example, cause the fragmentation of habitats, which hampers the ability of species to disperse. Currently, several amphibian species suffer from limited dispersal in urban and suburban landscapes (Hamer & McDonnell, 2008). This reduces the genetic connectivity of the populations and, hence, increases the risk of inbreeding within the populations. This can result in the loss of genetic variation and have negative demographic and genetic consequences (Brook *et al.*, 2002).

A growing environmental problem with profound effects on the distribution of species is climate change. Several studies find species to alter their habitat ranges with increasing temperatures, although it is not always clear if the range shifts are due to changes in dispersal and migration behaviour, or to changes in mortality and survival in different areas (Parmesan & Yohe, 2003; Parmesan 2006; Forister *et al.*, 2010). One of the most striking examples of range shifts fuelled by global warming, which appears to be due to changes in migration behaviour, is the distribution of the rufous hummingbird (*Selasphorus rufus*). This species migrates between breeding grounds in northwestern North America and its primary wintering grounds in Mexico. Until the 1970s, no more than 30 birds per year were spotted along the Gulf Coast in southwestern United States during the autumn and winter. Thereafter, the number of individuals has steadily increased and today the species is considered regular in this region in winter (Hill, Sargent & Sargent, 1998).

In metapopulations or metacommunities, the effect of environmental change on dispersal can vary among subpopulations and subcommunities, and influence the distribution and composition of the populations and communities (Thomas & Hanski, 2004). An example is the metacommunity of three *Daphnia* species in rockpools in Finland. During warm and dry summers, colonization rates increase for all three species, but the species-specific increases vary among communities. This leads to changes in the dynamics and composition of the whole metacommunity (Altermatt, Pajunen & Ebert, 2008).

(2) Species invasions

According to the "intermediate disturbance hypothesis", species diversity is highest under intermediate levels of disturbance, while high levels of disturbance promote the invasion of non-indigenous species at the expense of native species (Lockwood, Hoopes & Marchetti, 2007). Human disturbances are currently decreasing the diversity of native species, which favours invasions of non-indigenous species (Mooney & Hobbs, 2000; Piola & Johnston, 2008; Leprieur *et al.*, 2008; Ficetola *et al.*, 2010). Characteristics of invaders that facilitate their invasions are the ability to adjust their behaviour to new conditions, such as innovative foraging (Holway & Suarez, 1999; Sol, Timmermans & Lefebvre, 2002), and high levels of interspecific aggression, which helps invaders outcompete other species (Holway & Suarez, 1999).

Invaders frequently cause behavioural changes in native species, through interference and exploitative competition, and by increasing predation risk and modifying the habitat (Bertness, 1984; Fritts & Rodda, 1998; Byers, 2000). For instance, the introduction of brown trout (*Salmo trutta*) into streams in New Zealand has increased predation risk on many native species, such as mayfly nymphs and freshwater crayfish, which has caused behavioural changes in the native species (Townsend, 1996). Similarly, the spread of the toxic South American cane toad (*Bufo marinus*) throughout tropical Australia has decreased the preference of the native black snake (*Pseudechis porphyriacus*) for toads as prey (Phillips & Shine, 2006; Phillips *et al.*, 2010).

Invasions and subsequent changes in the behaviour of both invaders and native species are often associated with the rapid evolution of the invader, and sometimes also of the native species. For instance, the introduction of a cichlid fish, *Cynotilapia afra,* into Lake Malawi has resulted in the divergence of the species into genetically and phenotypically distinct northern and southern populations within two decades, most likely facilitated by diverging mate-choice behaviour (Streelman *et al.*, 2004). Another example is the toxic cane toad (*Bufo marinus*), which is spreading through Australia and appears to have undergone rapid evolution for faster migration and increased invasion rate (Phillips *et al.*, 2006). Invaders also influence mate-choice behaviour of other species and cause the merging of species, such as the coloniser *C. afra* that is hybridizing with the native *Metriaclima zebra* in parts of Lake Malawi where water clarity is low (Streelman *et al.*, 2004).

(3) Adaptation and population growth

Adaptation of populations to changed environmental conditions hinges on phenotypic plasticity and genetic changes. Plastic behavioural responses are beneficial if they improve the fitness of the individuals under the new conditions and move the phenotypic value of the population closer to the optimum, i.e. to the adaptive peak on an adaptive landscape (Ghalambor *et al.*, 2007; Crispo, 2008). If behavioural responses place the population at the optimum, then stabilizing selection can follow and no genetic differentiation is needed (Ghalambor *et al.*, 2007). If the responses result in changes in the right direction, but the population is still displaced from the optimum, then directional selection towards the optimum will follow, which could drive the population towards the peak through genetic changes. If behavioural responses move the population further from the optimum, i.e. maladaptive responses, then the viability of the population will decrease, which can increase the risk of extinction (Badyaev, 2005).

Behavioural responses that do not result in perfectly adapted phenotypes can be beneficial if they give the population additional time to adapt genetically to the new conditions, or if they expose new phenotypes to selection (Pigliucci, 2001, 2005). However, a genetic response to directional selection requires that standing genetic variation in the right direction exists, or that mutations or gene flow provide the population with beneficial alleles (Kawecki & Ebert, 2004). Since human-induced environmental changes usually are rapid, mutations may play a minor role and genetic adaptation may rely primarily on standing genetic variation and on gene flow. A problem here is that anthropogenic disturbances often reduce genetic variation, such as the fragmentation of habitats that reduces gene flow and enhances genetic drift. Genetic adaptation to human-induced environmental changes can therefore be challenging. Any facilitation of the process, such as the addition of time through behavioural responses, can then have a major impact on success.

Support for the importance of behavioural responses in mitigating fitness losses and facilitating adaptation to environmental change comes from studies on timing of breeding in birds. Many bird populations have advanced their breeding time under climate change to maximise reproductive success (Przybylo, Sheldon & Merilä, 2000; Nussey *et al.*, 2005; Parmesan, 2006; Charmantier *et al.*, 2008; 2008; Lyon, Chaine & Winkler, 2008; Schaefer, Jetz & Böhning-Gaese, 2008; Reed *et al.*, 2009). The adjustments are often so fast that plastic alteration is the most likely explanation (Gienapp *et al.*, 2008). However, the degree to which species will be able to continue to adjust their behaviour, if the changes continue, is unknown. This is due to our ignorance regarding the mechanisms of the responses, i.e. the relative role of plastic and genetic responses, and limited information on how much plasticity animals encompass in their behaviour (Gienapp *et al.*, 2008).

A growing number of studies find environment-induced behavioural responses to change the strength of selection acting on traits, which could alter evolutionary processes. For instance, exposure to an endocrine-disrupting chemical, 17α-ethinyl estradiol, influences mate-choice behaviour of sand gobies (*Pomatoschistus minutus*) and relaxes sexual selection on male size (Saaristo *et al.*, 2009). Similarly, reduced visibility due to eutrophication influences mate-choice behaviour of three-spined sticklebacks, which relaxes sexual selection on several male traits (Candolin *et al.*, 2007; Candolin, 2009). Over time, relaxed selection on some traits and strengthened selection on others is expected to result in genetic changes, depending on the existence of additive genetic variation and on constraints.

Behavioural responses that are maladaptive reduce the viability of the population. For instance, the advancement in breeding date of migratory birds due to climate change has resulted in mismatches with the seasonal availability of food for several populations, due to responses to climate change varying across trophic levels (Stenseth *et al.*, 2002; Visser & Both, 2005; Both *et al.*, 2009). An example is Dutch populations of pied flycatchers (*Ficedula hypoleuca*) that have declined by about 90% in areas where bird arrival is not matched to food abundance (Both *et al.*, 2006).

Species that are able to adjust their behaviour to suit new conditions can, on the other hand, benefit from human-induced alterations of the environment. They can increase in numbers at the expense of species that are not able to adjust (McKinney, 2002). Rats and gulls (order Laridae), for instance, can easily switch to new food sources that are provided accidentally (garbage) or intentionally (bird food) by humans (McKinney, 2002). Another example of a beneficial behavioural adjustment is the foraging behaviour of the unique dung beetle fauna of Madagascar. Before the arrival of humans, beetles were entirely dependent on lemur faeces and carrion as resources. When cattle were introduced by humans about 1000 years ago, many species colonized cattle dung and were able to extend their geographic range (Orsini, Koivulehto & Hanski, 2007). Today, cattle dung is used by about 30 endemic dung beetle species (Rahagalala *et al.*, 2009).

(4) Speciation and hybridisation

The diversity of species is the result of adaptation to heterogeneous environments. Consequently, the effect of human activities on species diversity depends, ultimately, on how humans influence habitat heterogeneity and thereby the diversity of niches. Behavioural responses often play a crucial role in mediating population divergences and speciation processes in heterogeneous habitats (Reznick, Rodd & Nunney, 2004; Hendry *et al.*, 2006; Seehausen, 2006; Candolin & Heuschele, 2008). For instance, the songs of great tits (*Parus major*), which are important in mate attraction and territory defences, have diverged between urban and forest habitats (Slabbekoorn & den Boer-Visser, 2006). Similarly, the songs of an African rainforest bird, the greenbul (*Andropadus virens*), have diverged between human-altered secondary forests and pristine forests (Smith *et al.*, 2008). Whether these divergences eventually will result in speciation is unknown, and depends on the genetic basis of the divergences.

Behavioural responses to human disturbance also can have the opposite effect and cause hybridization between distinct species (Grant & Grant, 2002) or reverse ongoing speciation (Seehausen *et al.*, 1997; Taylor *et al.*, 2006). In particular, alterations in mating behaviour and mate choosiness due to environmental disturbances can increase gene flow and the number of hybrids. Since about half of all vertebrate species are at some stage of divergence, it seems likely that the number of human-interfered speciation processes will increase in the future (Hunter, 2006). A classical example of the effect of human disturbance on mate-choice behaviour and thereby on biodiversity, comes from Lake Victoria. The diversity of cichlid fishes in the lake is maintained by assortative mating based on colour differences. Due to human activities and eutrophication, the turbidity of the water has increased, which constrains mate choice based on colour cues and promotes hybridisation. As a result, the mechanism maintaining reproductive isolation in the lake is not working properly and the diversity of fishes is threatened (Seehausen *et al.*, 1997; Maan *et al.*, 2010).

Similar patterns can be found in the three-spined stickleback. After the last ice age, about 10 000 years ago, the original marine form of the three-spined stickleback colonized freshwater lakes in British Columbia. This resulted in ecological divergence of the species into two distinct sympatric forms, limnetic and benthic (Schluter & McPhail, 1992). However, in some lakes, the number of hybrids is increasing rapidly, probably due to the introduction of a crayfish that increases water turbidity and, hence, hampers mate choice of sticklebacks (Taylor *et al.*, 2006).

(5) Extinction

If individuals cannot adjust to changed conditions through phenotypic flexibility and/or genetic adaptation, then individuals either have to move to other habitats or the population will face the risk of extinction (Hoffmann *et al.*, 2003; Stockwell, Hendry & Kinnison, 2003). Several animal populations are presently declining because of an inability to cope behaviourally with human-induced environmental changes. Black grouse (*Tetrao tetrix*) populations, for instance, have not been able to adjust with adaptive behavioural responses to changes in predation pressure and food availability and are declining (Ludwig *et al.*, 2006, 2008). A growing human-created problem, which causes population declines and extinctions, is the invasion of foreign species. Invasive species are often behaviourally highly flexible and outcompete native species, as discussed above.

Human-induced environmental changes are expected to have profound negative effects on the diversity of native species, since many species do not harbour enough behavioural plasticity to cope with rapid environmental changes, nor are they able to respond rapidly enough with genetic changes (Visser, 2008). These species will suffer from increased extinction risk. For instance, species in tropical forests, which represent the earth's major reservoir of terrestrial biodiversity, are threatened by anthropogenic activities, such as deforestation, overexploitation of resources and the introduction of invasive species (Myers *et al.*, 2000). Habitat specialists that cannot adjust their behaviour to changed conditions are particularly vulnerable. In Singapore, for instance, the local extinction rate for forest specialists is 33%, compared to only 7% for species that tolerate open or forest-edge habitats (Brook, Sodhi & Ng, 2003). The same vulnerability is found in endemic species that have a restricted geographical range. Madagascar, with its endemic biota, has lost about half of its forest cover since 1953. This threatens several endemic insect species with small habitat ranges, such as the endemic forest-dwelling *Helictopleurini* dung beetle that is not able to adjust to open areas and expand its range (Hanski *et al.*, 2007).

To prevent further population crashes and extinctions, more information is needed on behavioural responses of animals to environmental changes at the individual level, and the consequences that the responses may have for populations and species. This is a challenging task, since the responses of individuals depend not only on the direct effect of environmental change, but also on the responses of other species and on processes at other trophic levels.

V. OPEN QUESTIONS AND FUTURE DIRECTIONS

Theoretical and empirical work on behavioural responses to rapid environmental change suggests that behavioural responses can play a major role in improving the survival and reproductive success of individuals. Thus, behavioural responses could facilitate genetic adaptation, by providing more time for genetic changes to accrue and by exposing new phenotypes to selection (Pigliucci, 2001; Ghalambor *et al.*, 2007; Kinnison & Hairston, 2007). However, no empirical evidence exists for plastic behavioural responses facilitating genetic adaptation to human disturbance. Moreover, an increasing number of studies suggest that behavioural responses can be maladaptive and hamper adjustment to changed conditions (Candolin *et al.*, 2007; Candolin, 2009). Thus, more work on the occurrence, mechanisms and adaptiveness of behavioural responses is needed, to elucidate whether the responses facilitate or hamper adaptation to rapid environmental changes.

According to theory, the evolutionary rescue of populations under changing conditions depends on population size, additive genetic variation and how maladapted to the conditions the population is (Barret & Schluter, 2008; Orr & Unckless, 2008; Willi & Hoffman, 2009). The effects of population size and genetic variation on adaptation are currently receiving much attention, but the influence of the degree of maladaptation has attracted less interest. In particular, the influence of maladapted behavioural responses has received very little consideration. Most investigations focus on recording behavioural responses, which is an important first step, but the research needs to move to the next level, to determine the fitness consequences of the responses and their influence on evolutionary processes. Behavioural responses and environmentally induced variation in phenotypes are often seen as factors that constrain evolution, by shielding the genotypes from the effects of selection, while the potential of behavioural responses to mitigate fitness losses under rapidly changing conditions is seldom acknowledged.

Another important field that deserves more attention is the influence of past environmental conditions on the adaptiveness of behavioural reaction norms under changing conditions. Reaction norms determine the ability of populations to adjust behaviourally to changing conditions. They are the product of past ecological and evolutionary processes, which implies that past conditions dictate responses to new conditions. Thus, to predict the future we need to know the past. The evolution of reaction norms has received much theoretical attention, but the factors that restrict their evolution are still poorly known (Buskirk & Steiner, 2009; Auld *et al.*, 2010). More effort should also be put on unravelling the factors that influence the behavioural responses in the changing environment, such as the rate and stage of change, temporal and spatial variation in environmental conditions and the size and fragmentation of the population.

A further consideration that should be borne in mind is that populations are part of communities. Complex interspecific interactions, such as mutualism, competition, predation and parasitism, determine the behavioural response of single species (Berg *et al.*, 2010). To predict the response of single species to environmental change, and to determine the impact that the responses will have on communities and on biodiversity, we need to understand multispecies interactions. Considering the myriads of interactions that occur in communities, the task is daunting but important.

The contribution of behavioural information to conservation biology and the management of endangered species has so far been meagre (Caro, 2007; Angeloni *et al.*, 2008). Population dynamics depend on decisions and behaviours of individuals, and behavioural information is therefore vital for correct decision-making in conservation issues. This stresses the importance of collaboration between behavioural ecologists and conservationists. Much research is currently done on behavioural responses to environmental change, but the crucial link between behavioural responses and population viability, and how this link influences evolutionary processes is missing. More information on the topic is needed before we can efficiently use information on behavioural responses in conservation work.

VI. CONCLUSIONS

(1) The initial response of individuals to human-induced environmental change is usually alterations of behaviour. Individuals attempt to prevent fitness losses by adjusting their behaviour to the environment, such as increasing vigilance or reducing mate choosiness. The responses can influence the survival, reproductive success and distribution of individuals and, hence, have a major impact on population dynamics and biodiversity.

(2) Human activities cause behavioural alterations by disrupting physiological processes and by changing the sensory environment, the size, structure and connectivity of habitats, the availability of resources, and the abundance of heterospecifics.

(3) The behavioural response to changed conditions depends on the individual's reaction norm, i.e. the phenotypic responses that a single genotype can produce, depending on environmental conditions. Behavioural responses can be fixed or more or less plastic and depend on environmental conditions. Reaction norms have a genetic basis and evolve over generations, and can change within generations through innovations and the social transmission of new behaviours. Both extrinsic and intrinsic factors influence behavioural responses, such as the rate and stage of change, life-history trade-offs, the degree of habitat specialisation and individual differences.

(4) Behavioural responses can be adaptive or maladaptive and influence the fitness of individuals. The long-term effects of behavioural responses are often poorly known. Adaptive behavioural responses move the population closer to the phenotypic optimum, which can give the population additional time to adapt genetically to new conditions. Responses that are maladaptive can reduce population viability and increase the risk of extinction.

(5) Behavioural responses can have profound effects on the distribution of species by influencing movements and survival in the changed habitat. This can influence gene flow and the degree of inbreeding and, hence, the amount of genetic variation and population viability. Behavioural responses can also cause population divergence and speciation or, alternatively, cause reversed speciation or extinction, with consequences for biodiversity.

(6) Only a limited, homogenized set of species thrive in severely disturbed habitats. Behaviourally flexible species that can adjust to a range of environmental conditions often become invasive. These species may alter the habitat they invade and cause behavioural responses in native species.

(7) Basing conservation efforts on behavioural data could be effective, but relatively little has been done to bridge these areas. Much work is currently carried out on recording behavioural responses to changing environmental conditions, while information on the mechanisms of the responses, and their fitness consequences and evolutionary implications is lacking. This information is needed before behavioural data can efficiently be used in conservation work.

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