






Opinion

Sexual selection and speciation in the Anthropocene

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Anthropogenic change threatens global biodiversity by causing severe ecological disturbance and extinction. Here, we consider the effects of anthropogenic change on one process that generates biodiversity. Sexual selection (a potent evolutionary force and driver of speciation) is highly sensitive to the environment and, thus, vulnerable to anthropogenic ecological change. Anthropogenic alterations to sexual display and mate preference can make it harder to distinguish between conspecific and heterospecific mates or can weaken divergence via sexual selection, leading to higher rates of hybridization and biodiversity loss. Occasionally, anthropogenically altered sexual selection can abet diversification, but this appears less likely than biodiversity loss. In our rapidly changing world, a full understanding of sexual selection and speciation requires a global change perspective.

Bridging the nexus between sexual selection, speciation, and anthropogenic change

Sexual selection is a powerful evolutionary force widely thought to play an important role in diversification and speciation [1,2]. Recent theory [3] shows that the ‘ecological stage’ in which mating competition and mate choice play out can have far-reaching consequences for divergence among populations in signal and preference traits, reproductive isolation, and, therefore, the possibilities and mechanics of speciation.

Anthropogenic change (see [Glossary](#)) affects biodiversity in part through its ecological impacts but also by altering evolutionary processes that give rise to diversity itself [4–6]. Sexual selection depends strongly on the environment [4,5], making it a powerful force in generating new species but rendering it vulnerable to anthropogenic change. We focus here on how anthropogenic alterations to sexual selection could either hinder or promote speciation, and we describe the mechanisms by which this might occur ([Figure 1](#)). Empirical evidence demonstrates that anthropogenic change alters sexual selection and that sexual selection influences speciation, yet there are almost no studies directly connecting these three processes. We argue that understanding causal pathways linking anthropogenic change to sexual selection and speciation is critical to predicting the fate of biodiversity in the Anthropocene.

Sexual selection and its environmental dependence

Not only are sexually selected traits evolutionarily labile, their expression is highly sensitive to conditions in which an individual develops and/or currently lives, thus showing phenotypic plasticity [7]. Sexual traits are strongly influenced by ecological conditions in part because mating interactions are altered by ecology [7], which changes trait expression and how selection acts on sexual traits [3]. Therefore, anthropogenic change is likely to affect both the

Highlights

The ecological stage of mating interactions has crucial implications for trait divergence and speciation; the novel environments created by humans can undermine the speciation process.

Sexually selected traits and the fitness benefits of mating interactions are often finely attuned to the environments in which they evolved; anthropogenic change alters signal–receiver dynamics and mating decisions, thereby often increasing hybridization.

Hybridization can undermine biodiversity. Occasionally it can have a creative function by increasing potentially adaptive genetic diversity, allowing for adaptive introgression, or enhancing mating trait evolution. Yet, these outcomes are uncertain and may not fully compensate for biodiversity loss.

We inject a much-needed global change perspective for understanding sexual selection as a driver of the speciation process in a rapidly changing world.

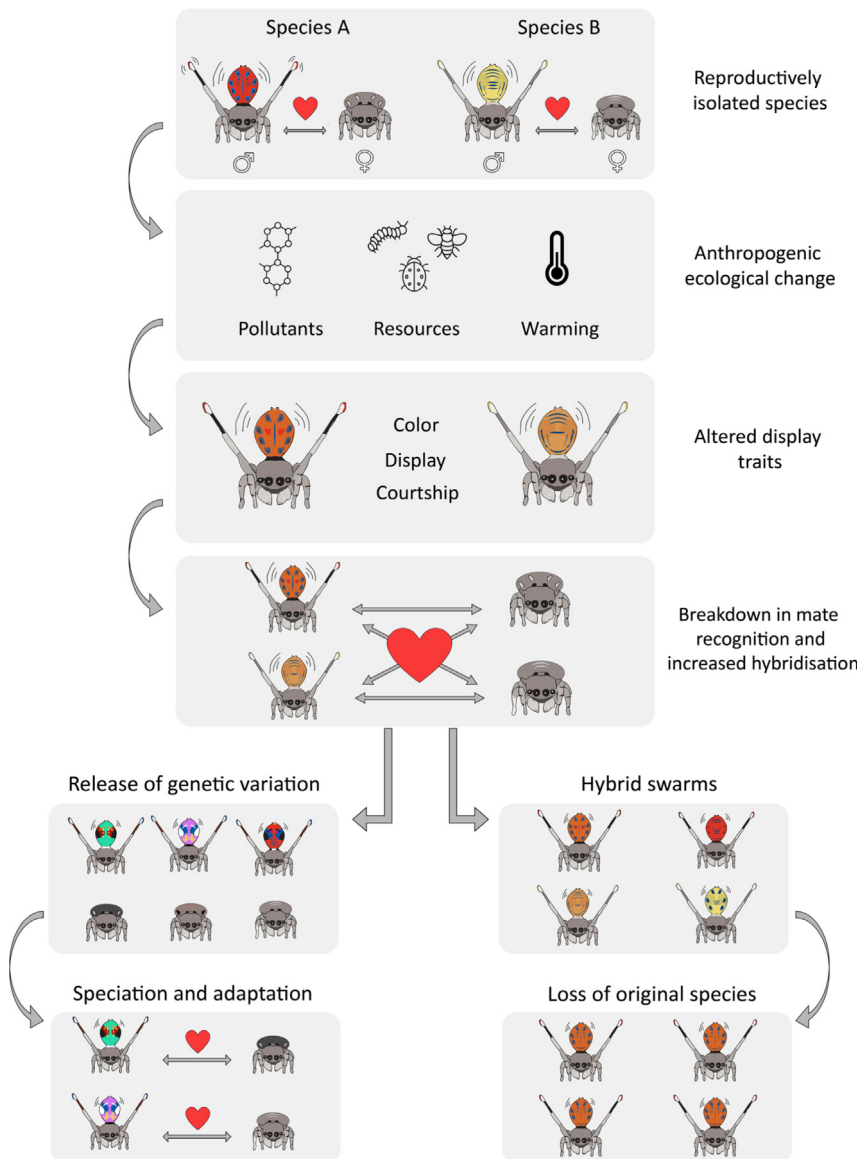
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Figure 1. Anthropogenic environmental change can disrupt sexual selection and the speciation process. This hypothetical example involves two reproductively isolated spider species that have distinct displays and preferences (color and courtship behavior), which are subject to sexual selection and play an important role in conspecific mate recognition, thus generating pre-mating reproductive isolation. We illustrate how anthropogenic ecological changes can lead to plastic changes in the development of display traits, reducing their differentiation between species. This can lead to a breakdown in conspecific mate recognition, elevating the likelihood of mate acceptance between species, thus increasing hybridization and ultimately causing genetic evolution. The consequences may enhance or diminish species diversity. Diversity can be enhanced if hybridization releases genetic variation or leads to adaptive introgression, facilitating adaptation to novel environments or generating novel sexual selection, thus potentially giving rise to new species (as shown on the bottom left). Diversity can be diminished if hybridization leads to hybrid swarms and a loss of multiple original species (as shown on the bottom right).

expression and evolution of sexual traits [8] over ecologically relevant timeframes (Box 1). Much research on environmental dependence of sexual displays concerns **condition-dependent traits** because these are likely to evolve under selection favoring reliable signaling of the benefits a mate can offer (Box 2).

Preferences for condition-dependent traits can evolve via both direct and indirect selection. Direct selection occurs when the chooser's own fitness is enhanced, whereas indirect selection occurs when offspring fitness is enhanced by alleles inherited from the chosen mate. Traits important in same-sex contests also evolve heightened condition dependence if increased investment in formidability or weapon size enhances performance in mating competition [9].

Both direct and indirect benefits of mate choice involve a component of environmental dependence. The direct benefit must elevate fitness in the chooser's current environment for the preference to be adaptive. Likewise, an indirect benefit must equip offspring with genes that elevate fitness in the world in which they develop and live. Therefore, changes in the environment can potentially erase both kinds of mate choice benefits, but especially indirect benefits due to their multigenerational nature. This is the case whether the changes are 'natural' (e.g., new habitat or altered predation regimes) or human induced (e.g., climate warming, urbanization, and agriculture). Environmental changes might therefore alter the benefits of mate choice by affecting the expression of sexual signals and also the covariance between the signal and the receiver's fitness [8]. For example, a sexual display that signals parasite resistance (e.g., diet-derived carotenoid coloration) will lose its salience if parasite abundance declines. Consequently, evolutionary models predict that preference strength would weaken or that preferences would evolve instead for a display that does indicate benefits [3].

Human activities have altered environments around the globe, and extensive research has revealed their far-reaching ecological and evolutionary consequences [10, 11]. Given how strongly many aspects of sexual selection depend on the environment, human-induced ecological changes are likely to affect the evolution of both preferences and displays. In turn, these alterations can affect the evolution of reproductive isolation between diverging taxa and thus speciation. Yet, many questions remain unanswered. We develop these ideas more fully below with the aim of promoting future research.

Impacts of anthropogenic environmental change on sexual selection

Evidence is mounting that anthropogenic change can have substantive consequences for sexual selection [5] (Box 3), especially when displays signal the extent of **local adaptation** and are indicators of **mate quality** and targets of mate choice [3] (Figure 1). For instance, through its effects on metabolism and behavior, temperature change can directly affect condition as well as the expression and costs of mating signals in both ectothermic and endothermic species [12]. For example, the darkness of African lion (*Panthera leo*) manes indicates male condition and is known to influence lioness mate choice. However, when ambient temperatures are high, dark-maned males also suffer higher body temperature, sperm abnormalities, and lower food intake, potentially increasing the cost of dark manes under anthropogenic climate change [13].

Sexual trait expression can be reduced or enhanced independently of condition by chemical pollution such as endocrine disruptors. For example, the expression of sexually selected ornaments and courtship behavior was compromised in male dark-edged splitfin fish (*Girardinichthys multiradiatus*) exposed to environmentally realistic concentrations of a common insecticide [14]. Similarly, polychlorinated biphenyls impaired larynx development in African clawed frogs

Glossary

Anthropogenic change:

environmental change caused by humans (either directly or indirectly), including habitat destruction and modification, pollution, harvesting, and climate change.

Condition: the pool of metabolic resources that an individual is able to accumulate for investment in survival, reproduction, and trait expression.

Condition-dependent trait: a trait, such as a costly sexual signal, whose expression depends on the pool of resources an individual is able to acquire. The expression of condition-dependent traits thus reflects both genetic effects of resource acquisition ability and plastic effects of environmental resource abundance.

Eutrophication: enrichment of water bodies by excess nutrients leading to increased amounts of plant and algal growth that can reduce visibility in the water column.

Introgression: the transfer of genetic material from one species into the gene pool of another mediated by hybridization and repeated backcrossing with one of the parent species.

Local adaptation: when populations are more suited to the particular ecological conditions of their local environment than are other populations from other environments.

Mate quality: the net benefits an individual can provide to their mate, including direct benefits (e.g., food, nesting sites, and territory) that elevate the mate's personal fitness and the genetic benefits it can confer on offspring.

Operational sex ratio (OSR): the ratio of males to females that are ready to mate.

Resource acquisition genes: genes that affect an individual's capacity to acquire resources from its environment, thereby influencing its condition.

Resource allocation genes: genes that determine the pattern of resource allocation among different traits and functions (e.g., strongly vs. weakly condition-dependent traits).

Sexual conflict: conflict arising from differences in the evolutionary interests of males and females, including harm imposed by one sex on another or when selection on a locus acts in opposite ways for males and females.

Signal honesty: signals that reliably convey information about the signaler to the receiver.

Box 1. Timescales. Can anthropogenic environmental changes have both rapid and lasting effects on sexual selection and speciation processes?

Anthropogenic changes are considered to be major drivers of global ecological change and biodiversity loss and are persistent enough to influence evolutionary processes. Human activities are pervasive and have profoundly affected the environment over the past several thousand years. Climate warming, pollution, the growth of cities, the spread of agriculture and invasive species, and exploiting wild populations for food – none of these are going away soon, and their impacts are broad. For example, researchers have found pollutants in ice cores dating back to pre-Roman times, marking the intensification of both agriculture [57] and metal production [58,59]. Since the start of the industrial revolution ~250 years ago, the scale and pace of these early environmental changes have further magnified [57,59]. Compounding the problems of these legacy effects are many new and emerging threats, such as the more than 900 different pharmaceutical products that have now been detected in aquatic systems worldwide [60]. Despite recent efforts to curb the effects of human activities on the environment, evidence suggests that the consequences of anthropogenic changes can persist even when ecosystems are restored. In the context of sexual selection, for example, epigenetic changes to mate preferences in rats were reported three generations after exposure to endocrine-disrupting pollutants [61]. Such results highlight that anthropogenic change need not be permanent to have lasting effects.

Furthermore, evolutionary processes can take place over ecological timescales [62–64], meaning that speciation via sexual selection can occur surprisingly rapidly. Research showed that the reshuffling of standing genetic variation gave rise to novel plumage coloration in the Iberá seedeater (*Sporophila iberensis*), causing premating isolation between them and the tawny-bellied seedeater (*Sporophila hypoxantha*) to arise quickly [65]. Importantly, such processes can be affected by anthropogenic change, such as seen when chemical pollution disturbed olfactory cues important in species recognition in Mexican swordtails (*Xiphophorus malinche* and *Xiphophorus birchmanni*) and was associated with the rapid collapse of premating barriers. Genetic evidence suggested that hybrids replaced the parental species in as little as 7 years, highlighting the rapid pace at which speciation processes can be disrupted [66] (Figure 1).

Sperm competition: the process that arises when the sperm of two or more males compete to fertilize the same eggs.

Transgressive: extreme phenotypes seen in hybrid populations compared with those found in the parental species.



Figure 1. Impact of chemical pollution on hybridization between two sympatric swordtail species, *Xiphophorus birchmanni* and *Xiphophorus malinche*. Photo credit: Daniel Lee Powell (*X. birchmanni*), Juan Miguel Artigas Azas (*X. malinche*), and Gaston Jofre Rodriguez (hybrid).

(*Xenopus laevis*), thus affecting their ability to produce advertisement calls [15]. Insecticide exposure also altered cuticular hydrocarbon profiles of leaf beetles (*Phaedon cochleariae*), disrupting intersexual chemical communication during mating [16,17]. By contrast, exposure to endocrine

disruptors caused male European starlings (*Sturnus vulgaris*) to produce more complex songs that females preferred [18].

Anthropogenic environmental changes can alter resources, affecting the expression of condition-dependent traits. For example, male guppies (*Poecilia reticulata*) from experimental populations with low food availability reduced courtship display and developed smaller patches of orange ornamentation [19]. More generally, anthropogenic changes that alter resource availability (e.g., pollution, urbanization, agriculture, and overfishing) can potentially affect condition-dependent displays (Box 2).

Environmental disturbances can also influence the opportunity for sexual selection by altering the magnitude of differences in trait expression between low- and high-condition mates [4]. For example, anthropogenic noise has a disproportionate effect on poor-condition European eels (*Anguilla anguilla*) [20], and low-condition common mussels (*Mytilus edulis*) accumulate more metal toxicants than high-condition conspecifics [21]. Such examples reveal that human-induced environmental change can enhance quality differences between individuals, which, in turn, can reinforce **signal honesty**.

Conversely, anthropogenic change can potentially attenuate signal differences between individuals, leading to a mismatch between condition and indicator traits. Research shows that nutrient

Box 2. How does the environment shape the development of sexual traits?

Costly traits such as sexual signals typically exhibit heightened condition dependence, enabling individuals to optimize investment in such traits given the quantity of metabolic resources that they can acquire. This pool of metabolic resources, called **condition**, is expected to reflect both resource abundance in the developmental environment and the quality of the individual's **resource acquisition genes**. A separate set of **resource allocation genes** is assumed to regulate relative allocation to various traits [67,68] (Figure 1A). Condition dependence thus involves a kind of plasticity that links trait expression and evolution to the environment.

Condition is conventionally regarded as a single pool of resources whose size determines the expression of all costly traits. Variation in environmental factors, such as resource abundance and stress, has therefore been assumed to shift trait expression along a single axis of condition (Figure 1A). However, recent empirical findings suggest instead that trait expression can be affected differently by environmental versus genetic quality [69–71] and that environmental factors can have trait-specific effects [72,73]. These findings suggest that condition comprises multiple separate resource pools that regulate different traits (i.e., that condition is multidimensional; Figure 1B).

In addition to condition-dependent effects outlined above, some anthropogenic factors appear to exert condition-independent effects on trait expression (Figure 1C). Such plastic effects can involve endocrine-disrupting pollutants that dysregulate allocation genes in males, thereby altering or feminizing male sexual morphology or behavior [15]. Such substances can also alter mate preferences by disrupting brain development [74].

The mechanisms of developmental plasticity that link environmental factors to the expression of signals and preferences could determine how anthropogenic changes might impact signaler–receiver systems. If anthropogenic changes in resources or stress merely shift trait expression along a single ‘condition’ axis, condition-dependent traits could continue to signal local adaptation as long as signal honesty is maintained. But if changes in environmental factors alter allocation among traits or dysregulate development in a condition-independent way, then such changes could disrupt existing signals or even create novel signals that convey different information. Such plastic changes may, in turn, affect the maintenance of existing species or promote speciation by altering signaler–receiver systems.

More generally, the plasticity of trait development can alter the genetic covariance between phenotype and fitness and thereby influence the rate and course of genetic evolution. Plasticity can shield alleles from selection, thus slowing the rate of adaptive evolution. However, this process could also lead to a build-up of cryptic genetic variation that, if later expressed in a novel environment, might facilitate adaptive evolution. Plasticity is therefore likely to influence or mediate many evolutionary responses to anthropogenic environmental change, a broad topic that we cannot address comprehensively in this paper. Rather, we focus primarily on one specific role for plasticity, whereby plastic changes in the expression of sexual traits lead to the disruption of existing signaler–receiver systems and thereby influence sexual coevolution and speciation.

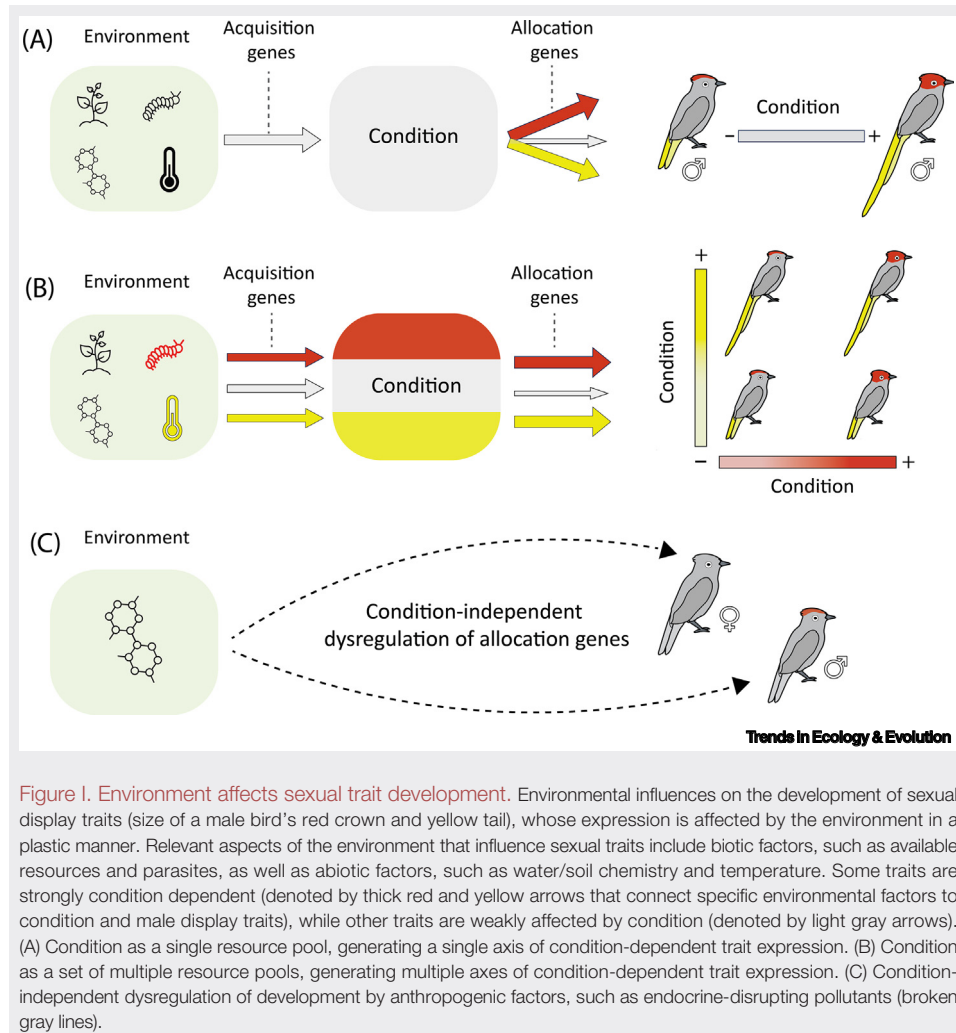


Figure 1. Environment affects sexual trait development. Environmental influences on the development of sexual display traits (size of a male bird's red crown and yellow tail), whose expression is affected by the environment in a plastic manner. Relevant aspects of the environment that influence sexual traits include biotic factors, such as available resources and parasites, as well as abiotic factors, such as water/soil chemistry and temperature. Some traits are strongly condition dependent (denoted by thick red and yellow arrows that connect specific environmental factors to condition and male display traits), while other traits are weakly affected by condition (denoted by light gray arrows). (A) Condition as a single resource pool, generating a single axis of condition-dependent trait expression. (B) Condition as a set of multiple resource pools, generating multiple axes of condition-dependent trait expression. (C) Condition-independent dysregulation of development by anthropogenic factors, such as endocrine-disrupting pollutants (broken gray lines).

pollution may allow all potential mates within a population, irrespective of genetic quality, to gain access to formerly limited resources, reducing variation among individuals in condition-dependent displays, decreasing signal honesty, and relaxing sexual selection [22].

Apart from effects on display traits, anthropogenic change can also alter sexual selection by changing mate preferences, including through direct effects on mate choice. For example, female guppies exposed to an endocrine-disrupting pollutant were less sexually responsive and less choosy than unexposed females [23]. This was exacerbated because pollutant-exposed males increased their sneak copulations, further bypassing female mate choice [24]. Environmental changes can also affect mate choice indirectly by undermining the capacity to properly evaluate and discriminate between potential suitors. For instance, female preference for high-quality male songs in field crickets (*Gryllus bimaculatus*) was disrupted by anthropogenic noise [25]. Moreover, disturbances that undermine the link between signal value and signaler quality can potentially reduce the benefit of preference for indicator traits or increase the cost. This could reduce variance in mating success within a sex irrespective of quality, as exemplified by threespine sticklebacks (*Gasterosteus aculeatus*) in response to human-induced **eutrophication** [26]. This, in

Box 3. Anthropogenic effects on other aspects of sexual selection

While we have primarily focused on how anthropogenic change might influence mating displays and mate choice, human-induced environmental change can affect the strength and direction of sexual selection through other pathways, with potential consequences for speciation. For instance, many anthropogenic changes can affect survival both directly (e.g., overfishing) and indirectly (e.g., habitat loss) [75,76], thereby altering the density and distribution of individuals within populations. These effects likely change mate encounter rates and influence mate competition, thus altering mating systems and the strength of sexual selection [77].

Anthropogenic change can also influence sexual selection by changing the **operational sex ratio** (OSR). For example, OSR can be altered when anthropogenic changes have sex-specific effects on organismal survival [78,79]. Global warming has also been shown to alter OSR in species with temperature-dependent sex determination [80]. Moreover, endocrine-disrupting pollutants are known to affect sexual development in multiple taxa [81,82], highlighting the potential for these chemicals to influence OSR and the opportunity for sexual selection in wild populations.

Anthropogenic change could also alter mating systems via effects on male–male competition [77]. Indeed, exposure to an androgenic steroid pollutant resulted in increased aggression and male–male competition in guppies [83]. Furthermore, climate change has altered the costs and benefits of competition in male Californian sea lions (*Zalophus californianus*). Typically, male sea lions monopolize mating opportunities by defending a breeding territory and resident females from rival males. However, high temperatures induce males to spend more time in the water to keep cool, reducing the ability of dominant individuals to defend their territories, likely resulting in a more equal distribution of mating success among males [84].

Sexual selection generated by **sperm competition** and fertilization dynamics might be especially vulnerable to anthropogenic disturbance. Sperm production and quality are sensitive to temperature as well as nutrition, pollutants, and other environmental factors [85–87]. Moreover, some of these factors could induce transgenerational effects on male fertility [88].

Anthropogenic change could also alter the nature and intensity of **sexual conflict** [89,90]. Stressful environmental conditions, such as those caused by climate change, tend to weaken sexually antagonistic selection in natural populations [91]. Likewise, experimental studies on *Drosophila melanogaster* suggest that high ambient temperatures reduce the costs to females of male harm associated with male-biased OSR and polyandry [12,92]. Theory suggests that such changes in sexual conflict intensity could either promote or impede diversification and speciation [93–95], warranting further work on these questions.

turn, may also increase the utility of other cues if they improve mate quality assessment under the altered conditions.

A recent meta-analysis supported these ideas by finding that anthropogenic change reduced variance in relative fitness and the opportunity for selection, lowering overall selection strength [27]. Anthropogenic effects on mating traits can instead be amplified by demographic changes associated with human activities, such as in small or fragmented populations [28]. The pervasiveness and rate of human impacts may cause extensive changes to sexual selection, many of which probably remain to be discovered. Such alterations could have important consequences for population fitness and the ability to adapt to the changing world [29] as well as the process of speciation, as we show in the next section.

Consequences for speciation

Eroding diversity

Anthropogenic changes to sexual selection can undermine recognition of conspecific mates, leading to species diversity loss through hybridization [11]. This can occur because human-altered sexual selection may reduce differentiation or detectability of differences in display traits among closely related species, similar to reduced display variation among high- and low-condition mates. Hampered capacity to assess displays would make it harder to distinguish conspecific and heterospecific mates [30,31]. Furthermore, anthropogenic changes that directly alter mate preferences are also likely to hinder mate choice for high-condition conspecific mates, leading to fitness losses, as shown when field crickets call in noisy urban environments [25]. When display no longer functions to indicate local adaptation, theory predicts a weakening of

preference divergence [3] and strength. Weakened sexual selection may lead to less elaborate display and preference. Research shows that reduced choosiness leads to higher acceptance of heterospecific mates [32]. All of these alterations could increase hybridization, potentially causing species merging and loss [2,33].

Over generations, preference may evolve to favor instead a different display or sensory modality that better indicates benefits likely to be obtained from mate choice in disturbed conditions [34]. Moreover, many anthropogenic changes homogenize ecological conditions. This may induce parallel or convergent evolution if signaling systems of multiple species evolve in response to the same homogenizing anthropogenic change by the mechanisms we describe. Consequently, displays and/or preferences may converge, reducing differentiation in mating traits, thus undermining reproductive isolation and promoting hybridization [2].

In a classic example of species collapse through hybridization resulting from anthropogenic change to sexual and natural selection, invasive crayfish altered ecological conditions and mating interactions between two stickleback species [30,35]. This undermined the strong preferences females once had for the mating displays of conspecific males [30,31], which initially diverged due to sexual selection [36]. These changes to sexual selection and ecology led to heightened hybridization and a near-complete merging of the stickleback species [37].

In another example, hybridization between mountain (*Poecile gambeli*) and black-capped (*Poecile atricapillus*) chickadees is elevated in urban areas, and a putative cause is eroded pre-mating isolation due to altered song frequencies and chorus behavior [38]. Sympatric birds are in worse condition than birds in allopatric regions [39], and we suggest that worsened condition could contribute to these mating trait changes and weakened pre-mating isolation. Generally, anthropogenic ecological change is both pervasive and rapid (Box 1), and speciation is slow relative to hybridization; thus, it seems likely that these changes to sexual selection will erode species diversity.

Maintaining or enhancing diversity?

Anthropogenic change may also have positive consequences for speciation under certain conditions. While these processes are likely slower and more uncertain than the often rapid and well-documented loss of species diversity caused by anthropogenic change, we speculate about possible diversity-enhancing outcomes here. Changes in sexual signals or preferences could lead to novel evolutionary outcomes, and hybridization could generate new, distinctive populations. Moreover, mechanisms like condition dependence may, under certain circumstances, work even as the genetic and environmental basis of fitness shifts (see Figure 1A in Box 2). The complex interactions between ecological conditions, signaling, and the fitness consequences of mate choice could generate a rich diversity of behaviors, signaling strategies, and mating outcomes.

Mating trait differentiation in novel environments?

Mating traits can adapt rapidly to novel environments. Multiple studies from urban environments document differentiation in display and/or preference between urban and rural populations, despite the challenges urbanization imposes for organismal adaptation [40,41]. For example, freed partly from the pressures of predation and parasitism in forested habitats, urban-dwelling male Túngara frogs (*Physalaemus pustulosus*) produce more attractive mating calls in urban environments while retaining plasticity to produce attractive calls in forested areas, thus giving them a mating advantage over forest-dwelling frogs in both environments [42].

Differentiation in mating traits can be correlated with and sometimes facilitate adaptation. For example, in both urban and rural populations of great tits (*Parus major*), the width of a male's black 'tie' indicates both his boldness and survival chances in his respective environment [43]. Divergence of mating traits in distinct environments could actually promote population differentiation. For example, human disturbance of little greenbul (*Andropadus virens*) rainforest habitat caused song divergence among habitats that differ in the level of human disturbance [44,45]. Observed song divergence correlates to genetic differentiation among forested and disturbed populations [46]. In the long term, such divergence could enhance the chances of speciation between diverging populations.

Creative hybridization?

Changes to sexual selection can alter recognition of conspecific mates, thereby altering the incidence of hybridization. Although, as already discussed, hybridization arising from anthropogenic changes to sexual selection and ecology may reduce diversity, it can sometimes contribute to diversification. This creative force is more likely when human-induced changes generate novel ecological conditions that might be best met with novel genetic variation, which can be generated through hybridization. Sexual selection could facilitate these diversity-enhancing consequences of hybridization in several ways.

The mixing of species' genomes during hybridization increases genetic variance, including variance of mating traits. This occurs, in part, by releasing new sources of additive genetic variance as well as new dominance, epistatic, and **transgressive** effects, which can far exceed variation from mutation and migration [47]. Hybrid populations contain genetic variation from two previously distinct species, including variants favored by selection in at least one of the parent species [48], providing a large pool of genetic variation on which selection might act to promote adaptation of ecological or mating traits and/or speciation in novel environments. Hybridization can also produce novel combinations of the parental species' genomes [49,50], some of which may be especially favored in the novel conditions created by anthropogenic change. Conservation biologists recognize the 'genetic rescue' effects of introducing individuals from a different population to breed with members of a shrinking or isolated population [51]. Similarly, it may be possible for hybridization to provide genetic variants that lead to adaptation in human-altered environments.

Hybridization can also enable the capture of genes from another species through the **introgression** of adaptive alleles from one species into the other. Such introgression can facilitate adaptation while not eroding species diversity, especially when populations are far from their optimum, such as occurs in novel environments [48]. In a classic example, Gulf killifish (*Fundulus grandis*) adapted to polluted water as a result of hybridizing with congeneric Atlantic killifish (*Fundulus heteroclitus*). The resulting introgression of adaptive alleles made Gulf killifish more tolerant to toxicants [52]. Mate choice plays a key role in reproductive isolation between these species, and female *F. grandis* are more permissive, thus facilitating the introgression of alleles for toxicant resistance [53].

A particularly intriguing example of the pervasive effects anthropogenic change has on sexual selection and speciation (first eroding species diversity and then restoring it) is lake whitefish (*Coregonus* spp.) in prealpine lakes. Whitefish species were lost via hybridization when eutrophication interfered with the ability to distinguish among species during mate choice and homogenized formerly distinct niches [54]. Quick action and stringent regulations subsequently restored water clarity, once again enabling recognition of conspecific displays and partially restoring niche space. Distinct ecomorphs resembling the original species reappeared [55]. Rediversification was possible because the hybridization that took place under eutrophication provided a rich

pool of genetic variation on which selection acted when environmental conditions improved [56]. This example underscores that taking efforts to restore environmental conditions can re-establish the evolutionary processes that generate new species, allowing species recovery and even diversification.

Concluding remarks and future directions

The strong environmental dependence of sexual selection and the increasing ecological reach of anthropogenic change have the potential, in combination, to induce widespread rapid alterations to the speciation process. In many cases, such changes are likely to erode or slow the generation of species diversity. Effects that enhance species diversity are also possible but may be less widespread. Local conservation interventions to rapidly ameliorate negative effects have occasionally proven successful, and we suggest that greater understanding of how anthropogenic change alters sexual selection could be valuable for those seeking to prevent biodiversity loss or to promote biodiversity gain.

Of the many potentially informative research directions we foresee (see [Outstanding questions](#)), one important avenue to pursue is how, under various kinds of anthropogenic change, different mechanisms of sexual selection interact with each other to either promote or impede speciation. A second avenue to pursue is to understand at the mechanistic level how sexual selection alters both the incidence of hybridization and whether the outcomes erode or enhance biodiversity. Considering also that sexual selection can play a powerful role in facilitating adaptation and population persistence, and can be especially effective in novel and rapidly changing environments [29], these efforts are worthwhile both scientifically and to inform efforts to ameliorate negative anthropogenic effects on the world's biodiversity.

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Declaration of interests

No interests are declared.

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Outstanding questions

More work remains to fully address the primary question we have posed: how do anthropogenic changes alter the development and expression of sexual signals and preferences, and what are the consequences of this for speciation?

How does the interplay between different mechanisms of sexual selection or sensory modalities alter speciation? Does this vary across taxa?

Can anthropogenic changes induce nongenetic transgenerational effects on sexual trait expression in offspring? What consequences does this have for diversification?

To what extent are genetic versus plastic (e.g., learned) mechanisms involved in population responses to altered sexual selection?

How do anthropogenic environmental changes influence the intensity of sexually antagonistic selection and sexual conflict, and how do such changes in sexual conflict affect biodiversity?

Many relevant studies focus on a subset of animal taxa, such as fishes, birds, mammals, and arthropods. How can the understanding of speciation under anthropogenic change be broadened to other taxa that experience sexual selection? These could include broadcast spawners in the oceans (where the interactions are primarily among gametes) or plants (where floral traits act as signals to attract pollinators, akin to sexual signaling and mate preference in animals, and in pollen–pistil interactions, akin to sperm competition and cryptic female choice in animals).

Sexual selection can promote adaptation in changing environments, especially when sexual conflict is weak. Can this help ameliorate maladaptation caused by anthropogenic change?

When does the net result of these effects erode biodiversity (e.g., through hybridization) versus maintain or even enhance biodiversity (e.g., by promoting reinforcement of premating isolation)?

How do these effects on a few species scale up to affect whole communities

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of interacting species, with potential consequences for sexual signals and preferences, ecological interactions, and species diversity? For example, the invasion of parasitoids that find hosts using acoustic signals can have community-wide effects on acoustically communicating insects and their diversification.

Anthropogenic environmental change is occurring at such scale and with such speed that it sets up multiple opportunities for quasiexperimental testing. How can we leverage this to test both detailed mechanisms and large-scale theoretic predictions about the interactions between sexual selection and speciation?

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