

# Anthropogenic Change and the Process of Speciation

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Anthropogenic impacts on the environment alter speciation processes by affecting both geographical contexts and selection patterns on a worldwide scale. Here we review evidence of these effects. We find that human activities often generate spatial isolation between populations and thereby promote genetic divergence but also frequently cause sudden secondary contact and hybridization between diverging lineages. Human-caused environmental changes produce new ecological niches, altering selection in diverse ways that can drive diversification; but changes also often remove niches and cause extirpations. Human impacts that alter selection regimes are widespread and strong in magnitude, ranging from local changes in biotic and abiotic conditions to direct harvesting to global climate change.

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Altered selection, and evolutionary responses to it, impacts early-stage divergence of lineages, but does not necessarily lead toward speciation and persistence of separate species. Altogether, humans both promote and hinder speciation, although new species would form very slowly relative to anthropogenic hybridization, which can be nearly instantaneous. Speculating about the future of speciation, we highlight two key conclusions: (1) Humans will have a large influence on extinction and “despeciation” dynamics in the short term and on early-stage lineage divergence, and thus potentially speciation in the longer term, and (2) long-term monitoring combined with easily dated anthropogenic changes will improve our understanding of the processes of speciation. We can use this knowledge to preserve and restore ecosystems in ways that promote (re-)diversification, increasing future opportunities of speciation and enhancing biodiversity.

Our current epoch is characterized by human domination of the global landscape, with impacts on the environment and climate increasing in scope and speed (Curtzen and Stoermer 2000; Canfield et al. 2010; Lewis and Maslin 2015). Many organisms on earth have had to contend with major human-induced perturbations for hundreds of thousands of years (Roebroeks and Villa 2011), but the magnitude, extent, and pace of these perturbations have accelerated at an alarming rate over the past ~200 years (Ellis and Ramankutty 2008; Lewis and Maslin 2015). Anthropogenic impacts on organisms have led to dramatic and widespread biodiversity loss (Barnosky et al. 2011). Human activities have, inadvertently or purposefully (e.g., Table 1), further altered geographic ranges, population dynamics, and selection regimes for a vast number of the persisting taxa (e.g., Ainouche et al. 2004; Antonovics 2006; Isaksson 2018; Kennedy et al. 2020). As a consequence of these effects on the evolutionary trajectories of many species, human influences are likely to have non-trivial effects on the process of speciation (Fig. 1).

Anthropogenic disturbances often involve environmental changes that can affect evolutionary processes associated with speciation, including both increases and decreases in RI between lineages. Geographic context and selection represent some of the most important factors that influence speciation (e.g., Coyne and Orr 2004). Human activities include global movement of organisms and modification of geographical barriers, as well as diverse changes in selection. We focus here on sexually reproducing species and RI, with a specific interest in anthropogenic im-

pacts on speciation processes (i.e., evolutionary increases and decreases in RI), rather than lineage persistence over longer timescales, which is extremely challenging to predict. Although the evolution of fully reproductively isolated species is expected to be slow, partial RI can evolve during human lifetimes in a variety of taxa (Table 1) and is arguably a more common stable end point than complete RI (Servedio and Hermisson 2019). Since both geographic isolation and episodes of secondary contact can be important contributors to speciation (e.g., Anderson and Weir 2022), it is important to understand the impact humans have on these processes.

Widespread anthropogenic impacts on evolutionary dynamics not only have the potential to alter speciation processes, but also provide a remarkable opportunity for the study of speciation. Modern anthropogenic global change is distinct from prior time periods in many ways that make it an exceptional context for uncovering how speciation processes occur, at least over relatively short timescales. More precisely, many anthropogenic activities are (1) repeated at various geographic, taxonomic, and temporal scales, meaning that the effects of these activities on speciation processes can be studied in a replicated manner, (2) strong and multifaceted, with disparate ecological changes of high magnitude often acting on diverging species simultaneously, and (3) occurring almost instantaneously in geological time and, importantly, can often be precisely dated. Human impacts on evolutionary processes are present everywhere and must therefore be considered when seeking to understand contemporary evolution and speciation. Just as the prior



**Table 1.** Examples of the impacts of different human activities on divergence and hybridization

Category	Driver	Effect on reproductive isolation	Estimated start date	Generation time	Type of barrier affected	Taxon	Citation
Physical environment	Habitat modification	Decreasing	1800s	2–5 yr	Premating	Gray wolves ( <i>Canis lupus</i> ) and coyotes ( <i>Canis latrans</i> )	Lehman et al. 1991
	Habitat fragmentation	Increasing	1904–1914	2–13 yr	Premating (spatial)	Geoffrey’s tamarin ( <i>Saguinus geoffroyi</i> )	Díaz-Muñoz 2012
	Human-created structures	Increasing	1368	Annual, long-lived perennial	Premating	Grass ( <i>Cleistogenes caespitosa</i> [Poaceae]); Siberian elm ( <i>Ulmus pumila</i> [Ulmaceae]); blue knoll ( <i>Heteropappus hispidus</i> [Asteraceae]); jujube ( <i>Ziziphus jujuba</i> [Rhamnaceae]); Chinese chaste tree ( <i>Vitex negundo</i> [Verbenaceae]); apricot ( <i>Prunus armeniaca</i> [Rosaceae])	Su et al. 2003
Pollution		Increasing	1863–1939	2–4 wk	Premating (breeding site choice)	House mosquito ( <i>Culex pipiens</i> )	Byrne and Nichols 1999; Haba and McBride 2022
	Water flow regime	Both	1800–1980	1–2 yr	Premating (spatial isolation + ecological isolation)	Freshwater sculpin ( <i>Cottus</i> )	Nolte et al. 2005
	Metals/inorganics	Increasing	Mid- to late 1800s	Short-lived perennial	Premating (flowering time) + postmating (greater self-fertility)	Sweet vernal grass ( <i>Anthoxanthum odoratum</i> )	Antonovics 2006
	Synthetic organic compounds	Decreasing	1988–1997	4–8 mo	Premating (chemical signaling)	Swordtail fishes ( <i>Xiphophorus malinche</i> and <i>Xiphophorus birchmanni</i> )	Fisher et al. 2006
	Nutrients, suspended particles	Decreasing	1920s–1960s	~3 yr	Premating	Cichlids (Haplochromines, <i>Neochromis</i> , <i>Nyererei</i> complex, <i>Paralabidochromis</i> )	Seehausen et al. 1997

Continued

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Table 1. Continued

Category	Driver	Effect on reproductive isolation	Estimated start date	Generation time	Type of barrier affected	Taxon	Citation
		Decreasing	1930s–1940s to 1971–1979	10–15 d	Unknown	<i>Daphnia</i> ( <i>Daphnia galeata</i> and <i>Daphnia hyalina</i> )	Brede et al. 2009
Temperature	Climate change	Decreasing	1995–2003	1 yr	Premating (spatial)	Southern and northern flying squirrel ( <i>Glaucomys volans</i> and <i>Glaucomys sabrinus</i> )	Garroway et al. 2010
		Decreasing	1970–1982	1 yr	Premating	Red-breasted and red-naped sapsucker ( <i>Sphyrapicus ruber</i> and <i>Sphyrapicus nuchalis</i> )	Billerman et al. 2019
	Urban heat island	Increasing	~1900	5–15 yr	Premating (local adaptation)	Acorn ants ( <i>Temnothorax curvispinosus</i> )	Diamond et al. 2017
Biotic interactions	Altered predation/parasitism/pathogens	Decreasing	1997	1 yr	Premating (mate choice)	Small and medium tree finch ( <i>Camarhynchus parvulus</i> and <i>Camarhynchus pauper</i> )	Kleindorfer et al. 2014
	Species introductions, range expansions	Decreasing	1950s	1–3 yr	Premating/also postzygotic?	Benthic and limnetic threespine stickleback ( <i>Gasterosteus aculeatus</i> )	McPhail 1992; Taylor et al. 2005; Gow et al. 2006
		Both	Mid-1900s	30–60 d	Premating (ecological isolation) + postmating (local adaptation)	Ancestral and derived ecotypes of red-shouldered soapberry bug ( <i>Jadera haematoloma</i> )	Carroll and Boyd 1992; Carroll et al. 1998; Cenzer 2016
		Increasing	1690–1710	Short-lived perennial	Premating (ecological isolation) + postmating (sorting of intrinsic genetic incompatibilities)	Oxford ragwort ( <i>Senecio squalidus</i> )	Nevado et al. 2020

Continued



Table 1. Continued

Category	Driver	Effect on reproductive isolation	Estimated start date	Generation time	Type of barrier affected	Taxon	Citation
Close association with humans		Decreasing	1970s	Perennial, flowers annually	Premating (spatial)	Smooth and California cordgrass ( <i>Spartina alterniflora</i> and <i>Spartina foliosa</i> )	Ainouche et al. 2004
		Increasing	Late 1800s	Perennial, flowers annually	Postzygotic (hybrid sterility)	Smooth and small cordgrass ( <i>S. alterniflora</i> and <i>S. maritima</i> )	Ainouche et al. 2004
	Agriculture	Increasing	Mid-1800s	1 yr	Premating (ecological isolation)	Apple maggot ( <i>Rhagoletis pomonella</i> ) apple and haw ecotypes	Filchak et al. 2000
	Food addition	Increasing	Early 20th century	1 yr	Premating (ecological + behavioral isolation)	House finch ( <i>Carpodacus mexicanus</i> ) house and desert ecotypes	Badyaev et al. 2008
	Domestication	Both	14–40 kya	~1–4 yr	Premating (spatial, behavioral, possibly mate choice)	Dogs and wolves ( <i>Canis</i> sp.)	Bergström et al. 2022
		Both	~9 kya	~1 yr	Premating (spatial, behavioral, possibly mate choice)	Wild and domestic cats ( <i>Felis</i> sp.)	Beaumont et al. 2001
		Both	~8 kya	~6 mo	Premating (spatial, behavioral, possibly mate choice)	Wild and Domestic/feral chicken ( <i>Gallus</i> sp.)	Gering et al. 2017
		Both	~10 kya	~5–6 mo	Premating (spatial, behavioral, possibly mate choice)	Wild boar and domestic pigs ( <i>Sus</i> sp.)	Ai et al. 2015
	Increasing	170–83 kya	1–21 d	Premating (ecological isolation), possibly postzygotic	Body and head louse ( <i>Pediculus humanus corporis</i> and <i>Pediculus humanus capitis</i> )	Toups et al. 2011; for review, see Veracx and Raoult 2012	

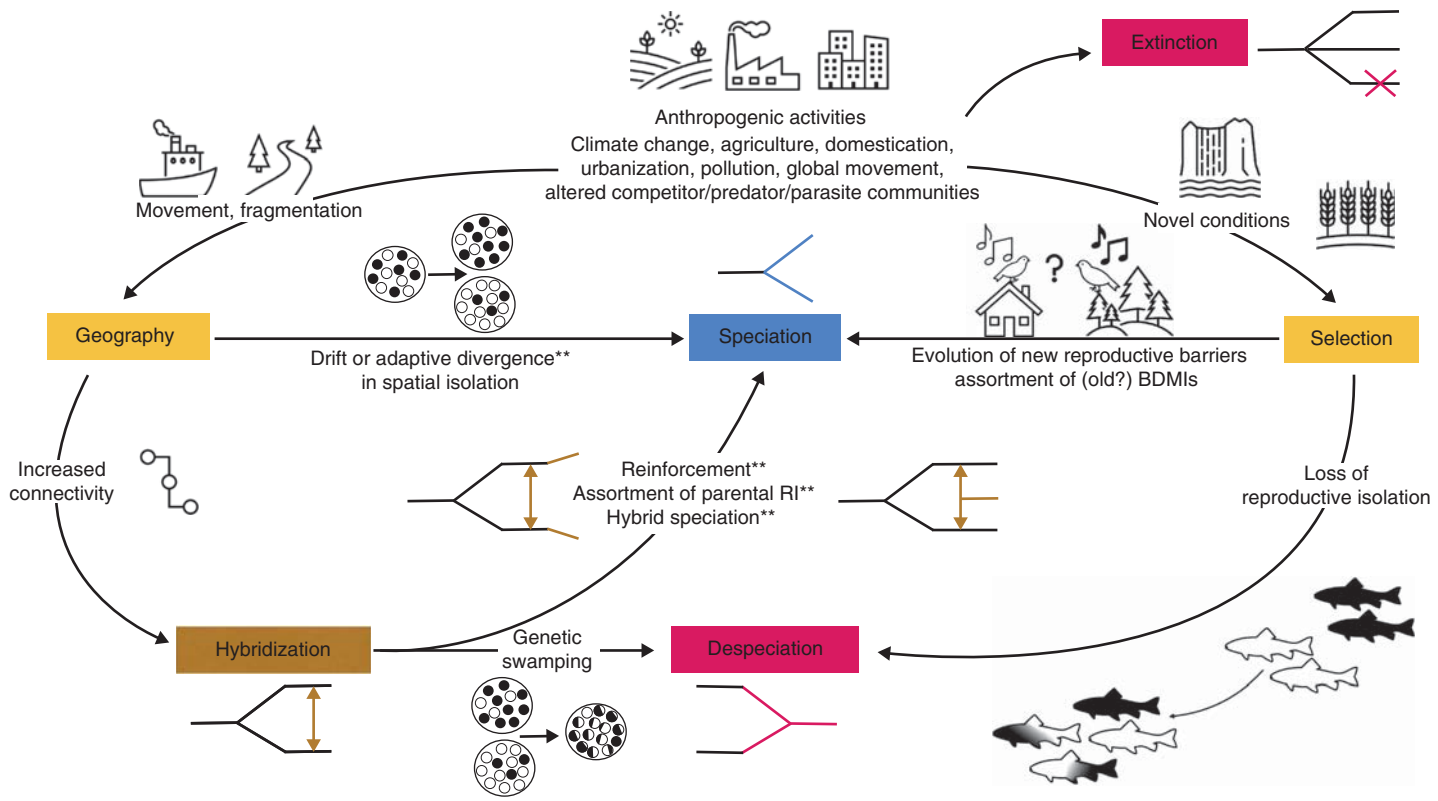
Continued



Table 1. Continued

Category	Driver	Effect on reproductive isolation	Estimated start date	Generation time	Type of barrier affected	Taxon	Citation
		Increasing	11–6 kya	1 yr	Premating (spatial, behavioral, possibly mate choice)	House sparrow ( <i>Passer domesticus</i> )	Ravinet et al. 2018
	Genetic modification	Both	2002	Perennial	Possibly postzygotic	Creeping bentgrass ( <i>Agrostis stolonifera</i> ) and annual beardgrass ( <i>Polypogon monspeliensis</i> )	Watrud et al. 2004; Zapiola and Mallory-Smith 2012

We broadly define reproductive isolation (RI) as increasing if studies showed higher genetic divergence or identified stronger isolating mechanisms in human-modified environments or time periods, and decreasing if gene flow or isolating mechanisms were reduced in human-modified environments or time periods. Estimated start date refers to the start of the specific human activity impacting that example (e.g., the construction of the Panama Canal occurred between 1904 and 1914, creating spatial isolation between populations of Geoffrey's tamarin). Generation times, when not provided in references, were drawn from the broader literature.



**Figure 1.** Schematic describing the general ways anthropogenic activities can influence the formation and loss of species by changing the geography, selection, and rates of hybridization between lineages. \*\*Indicate indirect changes in selection due to changed geography or via hybridization. (RI) Reproductive isolation, (BDMIs) Bateson–Dobzhansky–Muller incompatibilities.



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view of evolution as a slow, gradual process largely unobservable during human lifetimes has been dramatically transformed in the face of empirical evidence to the contrary, we similarly need to investigate speciation in the context of anthropogenic activities to better understand the modern pace of speciation.

In this perspective piece, we review the impact of anthropogenic change on geography and selection, two central factors in speciation processes. We highlight anthropogenic hybridization, which can act to dissolve previously distinct lineages but can also impose new patterns of selection on hybrids and parental species. We proceed with an outlook on the future of speciation, where we first ask whether speciation mechanisms may change in some way compared to their historical frequency, magnitude, or rate, and then, second, consider how we might take advantage of the ongoing occurrence of anthropogenic change to better understand processes of speciation. We argue future efforts should work toward preserving and restoring natural environments in a way that promotes diversification and future formation of new species. While most relevant studies on these topics to date have not focused on speciation per se, here we interpret prior results on the effect of human activities on evolution in the context of speciation. There is not (yet) a large literature on contemporary speciation. However, burgeoning studies on human-caused environmental change and contemporary evolution suggest that the processes of speciation should also be profoundly affected. Moreover, the recognition that RI and lineage dynamics (including extinction and hybridization) can occur on short timescales suggest we have much to gain by not ignoring modern speciation processes.

### ALTERED GEOGRAPHY

Geography is a long-recognized, important feature of speciation that greatly influences the evolution of RI (Mayr 1963; Bush 1975; Coyne and Orr 2004; Bolnick and Fitzpatrick 2007; Nosil 2012). Geographical arrangement of organisms affects gene flow between populations and species, and the magnitude and frequency of gene

flow can critically influence several mechanisms involved in speciation. For instance, gene flow affects the probability and rate of the evolution of RI via genetic drift, similar selection, and divergent selection (Nosil and Flaxman 2011; Nosil 2012; Langerhans and Riesch 2013). Human activities have substantially altered geographical context (see examples in Table 1), and these effects are likely to continue or accelerate in the future. On the one hand, anthropogenic activities can create new barriers that separate previously continuous populations or species, thereby reducing gene flow (e.g., Su et al. 2003). On the other hand, humans increase connectivity by bringing incipient species together, increasing the likelihood of hybridization (van Hengstum et al. 2012). Globally, this can lead to shifts in evolutionary trajectories, affecting both speciation and extinction rates, as well as the risk of species merging together. In the latter process, distinct lineages can fuse together via hybridization—termed “despeciation” herein—resulting in the loss of biodiversity (Seehausen 2006; Vonlanthen et al. 2012).

There is broad evidence that human-constructed barriers and environmental change often increase population fragmentation in terrestrial and aquatic taxa (Templeton et al. 2001; Fuller et al. 2015; Dobbs et al. 2017; Johnson and Munshi-South 2017; Littleford-Colquhoun et al. 2017; Langerhans and Kern 2020). For example, common drivers of fragmentation involve roads, agricultural fields, power line easements, dams, and cities (Trombulak and Frissell 2000). Such fragmentation is widespread and has driven convergent signatures of reduced connectivity in many species by reducing movement between populations, therefore reducing opportunities for mating (e.g., Smith et al. 2009; Mathner et al. 2015; Benjamin et al. 2016; Lourenço et al. 2017; Miles et al. 2018). Reduced gene flow can facilitate the evolution of RI through the accumulation of neutral differences, divergent evolutionary responses to either similar or divergent selection, and even through one-allele mechanisms of RI such as the evolution of reduced migration. Among the oldest examples of human-induced fragmentation is the Great Wall of China, which has significantly reduced gene





flow between plant populations since its construction began in 1368, apparently due to limiting both wind- and insect-dispersed pollen (Su et al. 2003). Over shorter timescales, intensive development and intervening roadways in the Los Angeles metropolitan area are associated with repeated patterns of reduced gene flow in birds, lizards, bobcats, and coyotes (Riley et al. 2006; Delaney et al. 2010).

Human barriers that split previously panmictic populations can rapidly result in population divergence in traits associated with RI, especially when fragmentation coincidentally results in strong environmental change, thereby inducing both reduced gene flow and divergent selection. For example, dams dramatically alter aquatic flow regimes and not only reduce connectivity, but often result in rapid phenotypic shifts in fishes (Haas et al. 2010; Franssen 2011; Franssen et al. 2013). Road construction across tidal creeks in The Bahamas not only fragmented populations of three Bahamian mosquitofish species (*Gambusia* spp.), but also led to diverse trait changes over ~35–50 years, including genital and body morphology, male coloration, and brain morphology (Heinen-Kay et al. 2014; Giery et al. 2015; Riesch et al. 2015; Jenkins et al. 2021). Human-induced fragmentation can also tip the balance between selection and gene flow, especially for species with limited dispersal. For instance, the construction of a parking lot dividing previously connected populations of walking stick insects (*Timema cristinae*) restricted gene flow between populations using two different host plants. This reduction in gene flow was apparently sufficient for adaptive divergence of genetically based cryptic coloration to emerge on the two hosts in <6 yr (Nosil 2009). Thus, human-caused fragmentation can play an important role in the earliest steps of speciation—we still have much to learn about the potential persistence of newly divergent lineages spawned by such anthropogenic impacts.

Humans also regularly transport organisms into new areas in which they are nonnative (Bullock et al. 2018). This can reduce intraspecific gene flow between populations in their native and introduced ranges and cause fast evolutionary changes in introduced populations, especial-

ly when the new distribution differs in ecology or climate from their native range (Mooney and Cleland 2001; Prentis et al. 2008; Whitney and Gabler 2008; Buswell et al. 2011). For example, the common reed (*Phragmites australis*) diverged between its native European and introduced North American range over the last 150 years as a result of both geographic distance and environmental differences (Guo et al. 2018). Salmon introduced to Lake Washington evolved RI after fewer than 13 generations (Hendry et al. 2000). Selection likely plays a major role in most cases of rapid divergence related to species introductions (see below), but altered geography provides a key context for the divergence.

Other anthropogenic infrastructure and activity, such as channels, bridges, and maritime traffic, instead create artificial corridors of dispersal (Crispo et al. 2011; Miles et al. 2018, 2019) that can increase gene flow between populations and species. For instance, human-driven maritime translocation is credited for genomically localized introgression tracts detected between Pacific and Atlantic species of *Ciona* tunicates, which now co-occur along the heavily shipped corridors of the English Channel (Le Moan et al. 2021). This type of consistent, human-aided gene flow increases the success and impacts of invasive species both through creating disturbed ecosystems conducive to invasion, as in the fire ant *Solenopsis invicta* (Resasco et al. 2014), and through allowing the spread of adaptive alleles between invading populations, as in Asian long-horned beetles (Javal et al. 2019). Human-caused corridors, accidental or purposeful relocation, and climate-change induced shifts in geographical range can additionally bring species into contact with closely related species, sister taxa, or incipient lineages. This could lead to hybridization and reinforcement of RI through selection against interpopulation/interspecific mating (Butlin and Smadja 2018), but high rates of hybridization can also reduce RI by causing selection against incompatibilities and despeciation (see below; Thompson et al. 2023).

Perhaps the most common impact of human activity is the reduction of both population size and genetic diversity as a result of habitat loss (e.g., Lu et al. 2001; Wei et al. 2015), fragmenta-

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tion (e.g., van der Valk et al. 2019), and/or degradation (e.g., Wisely et al. 2008; Sievers et al. 2018). Reduced population size not only increases the probability of extinction, but also decreases the efficacy of evolutionary responses to selection by reducing available genetic variation (Charlesworth 2009), which may be particularly critical in the context of adapting to, and persisting under, rapidly changing conditions (see next section). A small population size may, however, increase the probability of quick divergence and evolution of RI in the case of strong selection for local adaptation (Gavrilets 2003). Furthermore, population size asymmetry between species at secondary contact greatly affects the probability and dynamics of hybridization (Qvarnström et al. 2023).

To predict the lasting impacts of altered geographic context on speciation, we need to understand the persistence of both human-caused environmental changes and diverging lineages. Humans have a net negative influence on species number, as the rates of anthropogenic despeciation and extinctions outpace the rate at which new species may be formed. It is nevertheless also relevant to understand when and how humans interfere with processes of speciation over short and long timescales. Understanding how altered geographic contexts affect even transient divergence between populations or processes operating within incipient species in real time can prove quite consequential, as these can have long-lasting effects on both ongoing and future speciation processes. This may be especially important if anthropogenic activity increases the frequency of early-stage divergence followed by extinction.

### ALTERED SELECTION

Most speciation events probably involve selection, and RI typically evolves faster in response to selection than other mechanisms (Schluter 2009). Human activities that modify biotic and abiotic features are now well known for altering selection and adaptation (Brady et al. 2009; Darimont et al. 2009; Murúa et al. 2010; Hendry et al. 2017; Thompson et al. 2019). Anthropogenic drivers of selection are numerous and vary in

magnitude, geographic scale, and novelty (Isaksson 2018; Price 2022); we need only look around us to see the footprint of direct selection (e.g., domestication; Larson and Fuller 2014), the built environment (Alberti et al. 2017; Szulkin et al. 2020), pollution (Loria et al. 2019), altered ecological communities (Strauss et al. 2006), and climate change (Franks and Hoffmann 2012) to name a few. Altogether, these varied impacts on selection that characterize human activities may generate ecological opportunity for resilient taxa that persist in human-altered environments (Wellborn and Langerhans 2015; Isaksson 2018; Ravinet et al. 2018; Campbell-Staton 2020).

How do human-induced changes to selective landscapes affect speciation processes? Selection can influence the evolution of RI through three major mechanisms, and all are affected by human activities: divergent selection (ecological speciation), similar selection (mutation-order speciation), and reinforcement (selection against interpopulation mating after secondary contact) (Langerhans and Riesch 2013). In each scenario, which are not mutually exclusive, human-caused selection can alter traits that influence RI. Anthropogenic sources of divergent selection have received the most attention to date, while few studies have examined similar selection or reinforcement in this context. This is unfortunate, as these mechanisms may commonly occur, and the strongest evidence from the wild that responses to selection actually influence RI come from cases of reinforcement selection (because selection directly favors RI).

Many traits evolving in response to human activity have the potential to directly impact RI, like the timing and duration of reproduction (Alberti et al. 2017; Sirkiä et al. 2018), song frequency, timing, and composition (e.g., Reichard et al. 2020; Kunc and Schmidt 2021), mate-choice modality (de Jong et al. 2018), genital morphology (Heinen-Kay et al. 2014), and male color signals (Giery et al. 2015; Koneru and Caro 2022). Impacts of climate change on sexual selection are also likely to affect premating and postmating prezygotic and postzygotic reproductive barriers (Pilakouta and Ålund 2021; Garlovsky et al. 2023). Of course, adaptation



does not imply speciation, and responses to selection can also reduce RI (e.g., Owens and Samuk 2020). Evidence is accumulating that anthropogenic impacts can indeed influence RI in both positive and negative manners, often involving selection (Table 1). With the growing evidence for human-induced selection and contemporary adaptation, it would be surprising if anthropogenic selection did not influence speciation. But currently less clear is how exactly this occurs, whether promoting or hindering RI is more common, where we should focus our efforts to understand it, and how to assess the potential for lineage persistence after early stages of divergence.

Anthropogenic activities often generate divergent selection, with anthropogenic environments representing novel niches far removed from ancestral environments (e.g., Isaksson 2018; Szulkin et al. 2020, Santangelo et al. 2022). When novel divergent selection pressures are paired with the movement of genes between formerly isolated areas, this can contribute to the rapid appearance of novel habitat specialists. For example, the common house mosquito (*Culex pipiens*) colonized the London Underground transit system about 100 years ago, leading to changes in breeding environment that, in turn, contributed to RI between surface- and subway-dwelling populations (Byrne and Nichols 1999). However, these lineages did not arise in situ. Instead, previously existing genotypes, likely originating from human-adapted *Culex pipiens molestus* in the Middle East, underwent spatial reorganization and have since colonized multiple subway systems (Haba and McBride 2022).

One striking example of a human-induced divergence event is that of a derived ecotype of the hawthorn fruit fly, which emerged along the Eastern coast of North America within the last 200 years (Walsh 1867). Here the anthropogenic introduction and proliferation of domesticated apples facilitated a host shift from their native host, hawthorne (Bush 1992). Because hawthorne and apple differ in the timing of their fruiting, allochronic isolation between sympatric populations was possible; and, much like subway mosquitos, the genes underlying allochronic RI already existed in another part of

the *Rhagoletis* range in Mexico (Feder et al. 2003). The movement of these genes northward, paired with multiple divergent selection pressures and larval host fidelity, contributed to both olfactory preference for the derived host and genetic differentiation between ecotypes (Feder et al. 1988, 1994; Linn et al. 2003; Egan et al. 2015). This host plant shift induced by human-mediated species introductions triggered local population divergence in the hawthorne flies and the emergence of a possible new lineage—the apple maggot fly (Tait et al. 2016).

Many anthropogenic impacts that are replicated across the globe can influence speciation by selection mechanisms in ways that partially depend on geography. If impacted areas are geographically isolated (whether naturally or through human modification), divergent selection between impacted and unimpacted populations could lead to parallel divergence and contribute to the evolution of RI. For instance, urban environments have been shown to act as parallel niche-space for the cosmopolitan legume *Trifolium repens*, wherein city ecosystems tend to share more similarities to one another than with the adjacent surrounding environment regardless of geographic location (Santangelo et al. 2022). If gene flow is facilitated between impacted areas, it could lead to only one primary divergence event, such as in cosmopolitan or commensal species. Moreover, if anthropogenic impacts induce similar selection across multiple geographically isolated populations, RI could evolve between independent cases of the same anthropogenic driver via adaptive responses to similar selection. That is, different populations may evolve different traits in response to the same selection regime (i.e., mutation-order speciation), and consequently result in elevated RI between populations, such as cases of intragenomic conflict (e.g., cytoplasmic male sterility, meiotic drive), sexual conflict, sexual (or social) selection for arbitrary traits, and alternative adaptive solutions to selection via competition, predation, parasitism, etc. (Price 2008; Schluter 2009; Martin and Mendelson 2012; Langerhans and Riesch 2013). We currently know little about how these processes may unfold in an anthropogenic context.

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Some anthropogenic effects are ubiquitous and homogenize environments, making niches less distinct. In the case of anthropogenic climate change, homogenizing effects on abiotic conditions have been demonstrated in coastal estuaries (Ferrarin et al. 2014), high arctic tundra (Stewart et al. 2018), coral reefs (Richardson et al. 2018), and others. These cases can reduce the likelihood of divergent selection between environments, but adaptation to these homogeneous environments could still increase RI. This could occur if natural geographic isolation among populations remains unchanged, or if human actions increase geographic isolation, as responses to similar selection could promote RI among different cases of these similar environments. However, if gene flow is moderate, or especially if human activities increase gene flow, there would be little chance for these mutation-order processes as adaptive alleles could easily spread throughout populations and prevent the accumulation of RI. Perhaps adaptation in the absence of RI is more likely in these scenarios, but more research is needed.

### ALTERED HYBRIDIZATION

Hybridization can dissolve distinct evolutionary lineages (despeciation), but can also promote diversification through reinforcement and generation of new hybrid lineages (Mallet 2007; Arnold and Kunte 2017; Ottenburghs 2018; McFarlane and Pemberton 2019). The frequency of interspecific hybridization can increase due to the breakdown of geographic and ecological barriers, both heavily impacted by human activities (reviewed in Grabenstein and Taylor 2018; Grabenstein et al. 2023). These two processes likely often interact, for example, when species are transported to a new locality and when environmental change in situ alters hybridization frequency (Guo 2014; McFarlane and Pemberton 2019).

First, globalization has led to a drastic increase in the frequency and magnitude of direct species introductions via activities including horticulture, agriculture, aquaculture, shipping, and the pet trade (Lewis and Maslin 2015; Price 2022). Among birds, the extensive introduction

of the mallard duck (*Anas platyrhynchos*) to multiple locations worldwide led to the establishment of several hybrid populations with a variety of other duck species (Rhymer et al. 1994; Muñoz-Fuentes et al. 2007; Čížková et al. 2012; Ford et al. 2017; Lawson et al. 2021). In the sea, the Mediterranean mussel *Mytilus galloprovincialis* has been introduced worldwide by maritime traffic and aquaculture and formed anthropogenic admixture zones with its sister species *Mytilus trossulus* in California (Saarman and Pogson 2015) and Japan (Brannock et al. 2009), *Mytilus planulatus* in Australia (Popovic et al. 2020), *Mytilus edulis* in the English Channel (Simon et al. 2020), and *Mytilus platensis* in Argentina (Zbawicka et al. 2018).

Second, human-aided range expansions (e.g., via climate change) can also result in the secondary contact of previously isolated species, involving a simultaneous breakdown of geographic and ecological barriers (Lehman et al. 1991; Chunco 2014; reviewed in Taylor et al. 2014). For example, the range of southern flying squirrels (*Glaucomys volans*) has recently expanded northward into the range of northern flying squirrels (*Glaucomys sabrinus*), leading to hybridization (Garroway et al. 2010, 2011) and in some cases competitive exclusion (Wood et al. 2016). While ecological overlap between these two species in their new ranges is not entirely clear (O'Brien et al. 2021), the rapid movement of southern flying squirrels could potentially introduce novel parasites or diseases to the northern flying squirrel via hybridization, leading to population level threats in addition to competition or hybridization (Krichbaum et al. 2010; but see O'Brien et al. 2022).

Third, human-induced environmental change can alter the probability of hybridization and the fitness of hybrids by disrupting preexisting selective regimes (e.g., through eutrophication: Seehausen et al. 1997; Vonlanthen et al. 2012; Dokulil 2014; see also Box 1 for a detailed example) or by creating novel, often very strong selective regimes favoring hybridization and/or adaptive introgression (e.g., in the case of pesticide or pollutant resistance: Oziolor et al. 2019; Le Corre et al. 2020; Valencia-Montoya et al. 2020). A special case of secondary contact is





### BOX 1. PATTERNS AND CONSEQUENCES OF HYBRIDIZATION DUE TO ANTHROPOGENIC CHANGE IN WHITEFISH-ADAPTIVE RADIATION IN PERI-ALPINE LAKES

Anthropogenic ecological change can result in a breakdown of selection regimes that maintain ecological and genetic divergence and, thus, cause increased gene flow and a reduction in divergence and diversity. One example for this process are the consequences of eutrophication on adaptive radiations of *Coregonus* whitefish in peri-Alpine lakes.

Since the last glaciation, whitefish have colonized peri-Alpine lakes and undergone replicated adaptive radiations into ecologically and genetically differentiated species over the last 10,000–15,000 years. The >30 species can be grouped into six different ecomorph classes across all lakes that are differentiated in morphology, ecology, and breeding behavior. This includes large-bodied benthic invertebrate feeders with few widely spaced gill-rakers, which spawn in summer in shallow littoral habitats; small-bodied zooplankton feeders with many, densely spaced gill-rakers, which spawn in deeper areas in summer or winter; and, in some lakes, profundal summer-spawning species with few gill-rakers (e.g., in Lake Thun and the now extinct Kilch in Lake Constance). The various ecomorphs have evolved independently in the different lake systems and their parallel evolution is explained by a polygenic adaptive architecture, with at least one major effect loci (the *edar* gene) explaining variation in gill-raker number, with secondary contact and allele sharing among flocks (De-Kayne et al. 2022).

Whitefish diversity declined precipitously with severe eutrophication of Swiss peri-alpine lakes, in part because eutrophication homogenized niche space and undermined the diversification process (Vonlanthen et al. 2012). Environmental gradients and thus both ecological and reproductive niche diversity within lakes were eroded by the ecological alterations from eutrophication. Consequently, premating isolation and divergent selection that formerly maintained high levels of extrinsic post-zygotic RI among whitefish species were significantly weakened, leading to increased hybridization among sympatric species and despeciation (Vonlanthen et al. 2012). Eutrophication also caused anoxic conditions in deep water, leading to recruitment failure and subsequent loss of deep-spawning species (Vonlanthen et al. 2012; Frei et al. 2022, 2023). Diversity loss included losses of individual species, as well as lessened functional diversity and genetic differentiation of remaining whitefish (Vonlanthen et al. 2012).

But where humans have caused drastic ecological changes they can work to alleviate them. Thus, concerted efforts were undertaken to remediate pollution in these lakes through water treatment and reduced phosphorus inputs, which facilitated rapid recovery of many lakes to their former oligotrophic state (Smith and Schindler 2009). Following this ecological restoration, functional diversity (variation in gill-raker number) in some whitefish taxa was rapidly reinstated (Jacobs et al. 2019). Under eutrophication, hybridization included extensive introgression from species that became extinct and data suggest substantial introgression of putatively adaptive alleles that underpinned the initial diversification of whitefish in these lakes (Jacobs et al. 2019; Frei et al. 2022), likely facilitating rediversification and recolonization of the now restored deep-water habitats. These patterns highlight both the fragility of extrinsic RI when environments change, and also that hybridization may have helped to preserve variation now fueling the recovery of diversity after lakes were restored (Frei et al. 2023). However, while some functional diversity has been restored, species diversity has not recovered and deep-water species are still absent, indicating that there are constraints on what can be restored after severe disturbance.

This example of the consequences for eutrophication on peri-Alpine whitefish shows the drastic consequences of human activities on RI and functional diversity. However, it also highlights the importance of swift action and implementation of remediation measures that can restore ecological gradients and allow for at least some degree of rediversification using genetic variation that may still be present.

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the feralization of domesticated species in which humans are directly involved in both the evolution of the domesticated lineage and in its secondary contact with a nondomesticated lineage. Examples of hybridization between wild and feral species include Scottish wild and domestic cats (Senn et al. 2019), wolf and dog (Pilot et al. 2018), chicken and junglefowl (Gering et al. 2015), pig and boar (Mary et al. 2022), and maize and teosinte (Le Corre et al. 2020).

Hybridization through anthropogenic secondary contact can, under some circumstances, generate biodiversity. A classic example of homoploid hybrid speciation is the Oxford ragwort (*Senecio squalidus*), which is derived and reproductively isolated from two parental species native to Italy that were cultivated and incidentally crossed at the Oxford botanic garden in the late seventeenth century (Nevado et al. 2020). The subsequent spread of *S. squalidus* throughout much of Great Britain was aided by the development of rail and road networks, whose verges appear to mimic the lava rock in the range of the parental species (Harris 2002). Thus, human activity is directly implicated in both the formation of a species and the creation of habitat necessary for that species to establish and spread. Similarly, the human-aided introduction of the house sparrow (*Passer domesticus*) into the Mediterranean region resulted in secondary contact and hybridization with the Spanish sparrow *Passer hispaniolensis*, leading to the formation of a reproductively isolated homoploid hybrid commensal species—the Italian sparrow (*Passer italiae*) (Elgvin et al. 2017; Runemark et al. 2018). A third example is seen in dock mussels—a distinct ecotype of *Mytilus* associated with port habitats that have arisen through human-mediated hybridization between *M. edulis* and *M. galloprovincialis* and colonized multiple ports in parallel, and now constitutes a stable admixed population that can hybridize with the local parental species (Simon et al. 2020).

In summary, one consequence of human-induced breakdowns in geographic and ecological barriers is an increase in the opportunity and frequency of hybridization, especially across very long distances, in many places and across multiple species within a food web and/or ecosystem at the same time. The outcomes of an-

thropogenic hybridization are more likely to be negative than positive. While adaptive introgression (Hamilton and Miller 2016), reinforcement of preexisting barriers, and hybrid speciation (see Peñalba et al. 2023; Zhang et al. 2023) are possible outcomes, many documented cases of anthropogenic hybridization have resulted in a breakdown of RI between species (Grabenstein and Taylor 2018). It is thus very unlikely for anthropogenic hybridization to result in a positive outcome for global biodiversity.

### ALTERED SPECIES TURNOVER RATES

Are we changing the predominant mechanisms leading to speciation? Geographic isolation is well documented as an important, and perhaps even necessary, step for the evolution of complete RI (Anderson and Weir 2022). As we have seen above, with increasing globalization, humans are causing geographic barriers to collapse, but also causing population subdivisions via habitat fragmentation. We are directly or indirectly altering selection regimes, with consequences for evolutionary processes known to play important roles in speciation. Anthropogenic activities are likely also increasing the speed and frequency of both early divergence between populations (i.e., potentially leading to speciation) and the collapse of recently diverged lineages (i.e., “despeciation”). Since anthropogenic extinction is orders of magnitude faster and more taxonomically wide-reaching than anthropogenic speciation, and because fewer species in turn lowers chances to speciate, the global diversification rate will likely decline in the short term. Our impact on processes of speciation will inevitably vary across taxa, with habitat fragmentation having a strong impact locally, and global movement of species acting on a totally different scale. The consequences will thus depend on a species’ dispersal ability. Are we likely to witness an increase in populations/species found in a transient stage on the speciation continuum (e.g., showing partial RI; Servedio and Hermisson 2019), compared to what was observed before human disturbances? Are we introducing new biases in patterns of diversification across taxa? It is difficult to predict which, if any, of the currently diverging lineages will result in

fully isolated species. However, incipient species showing some degree of RI do represent distinct lineages that may increase functional biodiversity, and can thus play an important role in ecosystem functioning.

Can our knowledge of past events of mass extinction and current data on the resilience of different taxa to global climate change allow us to predict how the world may look after us? On a much longer scale (millions of years), and somewhat paradoxically, the ongoing extinction crisis is likely to cause an increased speciation rate in the future. Based on evidence from the fossil record, elevated extinction rates generally trigger acceleration of speciation rates when ecological communities reestablish (Harries et al. 1996; Hallam and Wignall 1997; Foote 2023). For example, marine microfossils appear to flourish after large extinction events (Keller and Pardo 2004). While the extinction of many large vertebrates (megafauna) is a well-known example of human impact, other less visible taxa are also greatly affected by anthropogenic disturbance, such as insect habitat specialists (Wagner 2021). This is an exciting avenue for future studies.

Recent examples of ecosystem diversification (see Box 1) have shown that taking rapid action to restore habitats has a positive effect on diversity. While we will likely lose much of the biodiversity present before human activities, some of the adaptive genetic and phenotypic variation that allowed for initial diversification can be retained, thereby potentially allowing population persistence and ultimately, the formation of new taxa (Ottenburghs 2021). At the core of the diversification process is divergent selection arising from complex niche space, to which organisms adapt and diverge from one another. Therefore, conservation efforts may need to focus on preserving features that promote the diversification process *per se*, potentially allowing new species to emerge in the future.

### LONG-TERM STUDIES OF ANTHROPOGENIC CHANGE AS A TOOL TO UNDERSTAND SPECIATION

The multitude of ways that human activities alter geographic context, create new sources of selec-

tion, and induce secondary contact, combined with the fact that many such events are replicated and can be precisely dated, constitute some very exciting opportunities for researchers to study speciation. Many cases of early divergence have been identified by studying organisms that have colonized human-modified environments in parallel with their “wilder” counterparts, which allowed identifying phenotypic and genomic differentiation in these new environments (Filchak et al. 2000; Fonseca et al. 2004; Wright et al. 2013). In some cases, high levels of RI have been documented. Observing the emergence of new species is rarely possible, but documenting past collapse of species or partially diverged lineages may be relatively easy in contemporary systems (Otto 2018), provided that known young species or locally adapted population pairs are followed over time (Rosenblum et al. 2012). Famous documented examples of such collapses are only possible because of long-term studies and include threespine sticklebacks (Taylor et al. 2006), cichlids (Seehausen et al. 1997), and soapberry bugs (Carroll and Boyd 1992; Carroll et al. 1998; Censer 2016), where human-induced changes in environmental conditions caused the rapid collapse of reproductive barriers. In one case, both the collapse and re-emergence of divergent whitefish species were observed over a few decades in Alpine lakes first affected by eutrophication, but then cleaned in hopes of reversing the consequences of this anthropogenic disturbance (see Box 1), thanks to long-term monitoring of these lakes.

Hybrid zones are often referred to as “natural laboratories” (Barton and Hewitt 1985; Hewitt 1988) and anthropogenic hybrid zones provide a particular powerful framework to study speciation (Grabenstein and Taylor 2018). Anthropogenic hybrid zones offer well controlled, natural experiments as they (1) are often replicated in space (e.g., Simon et al. 2020; Westram et al. 2021), (2) have firm dates for secondary contact from written records (e.g., Calfee et al. 2020; McFarlane et al. 2020), and (3) may have precise estimates of the number of introduced individuals (e.g., Ratcliffe 1987; reviewed in Grabenstein and Taylor 2018). Additionally, because anthropogenic hybrid zones are necessarily new, there is the opportunity to understand the initial break-



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down or buildup of RI at secondary contact. This is often not possible in older hybrid zones where we study the separate question of how RI is maintained. Anthropogenic hybrid zones, particularly when studied over many decades, are thus a powerful opportunity to test theoretical predictions about speciation processes directly in the wild (Anderson and Weir 2022).

## CONCLUSION

We have described here that the ubiquity of human impacts, affecting both geography and selection, often in parallel and very rapid ways, may change the predominant mechanisms of speciation. We may be approaching an era where it is not possible to study evolution without human disturbance. The best documented examples of human-induced early lineage divergence and species collapse were detected thanks to long-term monitoring. We would like to emphasize the power of studying natural systems over several decades or even centuries, and the need for more long-term thinking in our research field. This allows not only the detection and quantification of our impact on the environment, but also the identification of ways to remediate these impacts. By preserving and restoring ecosystems in ways that promote (re-)diversification, instead of focusing on the conservation of single species, we have the power to increase future opportunities of speciation, and ultimately enhance biodiversity.

## AUTHOR CONTRIBUTIONS

All authors contributed to the conceptualization of the paper, writing of the original draft, and reviewing and editing of the final version. M.Å. and M.C. led and administered the project.

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