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Adaptation, speciation and extinction in the Anthropocene

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Humans have dramatically altered the planet over the course of a century, from the acidity of our oceans to the fragmentation of our landscapes and the temperature of our climate. Species find themselves in novel environments, within communities assembled from never before encountered mixtures of invasives and natives. The speed with which the biotic and abiotic environment of species has changed has already altered the evolutionary trajectory of species, a trend that promises to escalate. In this article, I reflect upon this altered course of evolution. Human activities have reshaped selection pressures, favouring individuals that better survive in our built landscapes, that avoid our hunting and fishing, and that best tolerate the species that we have introduced. Human-altered selection pressures have also modified how organisms live and move through the landscape, and even the nature of reproduction and genome structure. Humans are also shaping selection pressures at the species level, and I discuss how species traits are affecting both extinction and speciation rates in the Anthropocene.

1. A human-modified world

The human population has grown from 1.8 billion a century ago to 7.6 billion today (averaging approx. 1% increase per annum [1,2]). Population growth tells only part of the story. Alongside demographic growth, the ecological impacts per person have risen. Venter *et al.* estimated the *per capita* growth in human footprint on the landscape at approximately 0.52% per year (from 1993 to 2009) [3]. The product of the two—population size and *per capita* demand—has thus grown exponentially faster than either on its own.

The burgeoning demand on the resources of the planet has altered threequarters of Earth's ice-free surface [4]. Timber and other resource extraction, agricultural expansion and an increasing incidence of fire have reduced the intact forested landscape at a rate of 0.57% per year [5]. Harvesting has caused the global biomass of predatory fish to decline by two-thirds over the last century [6]. Human land use has led to an estimated loss of 10¹⁴ kilograms of organic carbon from the Earth's topsoil (approx. 8% of the top 2 m of used land), reducing productivity and contributing to CO₂ emissions [7]. One-quarter of the terrestrial surface is now considered degraded due to the combined effects of erosion, pollution, compaction and salinization [8]. Over the past century, temperatures have increased by 0.85°C, sea levels have risen by 0.2 m, and oceans have become 26% more acidic due to anthropogenic climate change [9]. The resulting pressures on natural populations have caused a 60% decline in the population size of vertebrate wildlife between 1970 and 2014, based on a meta-analysis of long-term data from 4005 species [10]. The global scale of geochemical, climatological and biological changes caused by humans has led scientists to propose a new epoch, the Anthropocene, to signify the stratigraphically distinct and pervasive impact of humans on the planet [11].

Beyond the numbers, the world's biological diversity is changing, through evolutionary change at both the within and between species levels. In this essay, I reflect upon the myriad impacts that humans have had on evolution. The nature of selection faced by species across the planet has changed, as



Figure 1. Human-altered selective forces. (*a*) Selection in built environments: feathers left on a window illustrate the high death toll of birds colliding with buildings and automobiles [12], selecting against migratory behaviour [13] and for manoeuvrability [14]. (*b*) Selection to avoid hunting or harvesting: humans target individuals with preferred traits, selecting against traits such as long ivory tusks [15]. (*c*) Selection in novel communities: both abiotic and biotic selection pressures are reshaped when humans bring together species in new assemblages, as found in cardinals nesting in introduced honeysuckles [16]. (*d*) Selection on dispersal: fragmented landscapes select for individuals that can remain in hospitable environments, favouring non-dispersing seeds in *Crepis sancta* [17]. (*e*) Selection on inheritance systems: rapid evolution associated with human cultivation can alter the genome, with increased recombination rates and polyploidy found in many domesticated plants, such as oats [18]. Photographs: (*a*) Alan Hensel; (*b*) Sarah Otto; (*c*) Jeff Whitlock; (*d*) Susan Lambrecht; (*e*) Henrik Sendelbach.

organisms are favoured that best tolerate the land development, harvesting, species introductions and environmental changes caused by humans. Species are at a greater risk of extinction than pre-human levels, causing selection at the species level due to the loss of species that are large-bodied, specialist or otherwise vulnerable to human activities. Although less well understood, humans have also altered the processes that lead to the formation of new species, and again this impact is not affecting all of the world's species equally. I argue that humans have altered the course of evolution to a degree that is unprecedented for a single species in a single century and close by discussing why this matters.

2. Anthropogenic selection pressures

In the first two chapters of *The Origin of Species*, Charles Darwin contrasted selection upon variation under domestication and under nature. The distinction is becoming increasingly blurred, with humans selecting for variants

across all species that best tolerate the environmental conditions that we impose. Here, I discuss several unintended selection pressures that are altering the evolutionary trajectory of life on Earth (intended selection pressures, e.g. through antibiotic application or selective breeding, are not discussed). My goal is not to give an exhaustive list, but to highlight the range, potency and idiosyncrasy of selection pressures induced by humans (figure 1; see also [19] and references therein).

(a) Selection to survive in built landscapes

While urban areas and similarly artificial human-dominated landscapes only comprise approximately 1% of Earth's surface [8,20], the selective pressures induced in cities and other built landscapes are often intense and multifarious [21]. Building strikes and domesticated cat predation are now major mortality sources for birds and other flying animals, with tallies of 800 million collision deaths and 2.4 billion cat predation events annually in the USA [12]. Such high mortality levels can induce strong selection pressure to alter behaviour

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(e.g. flying speed, perch height), morphology (e.g. wing shape) and life-history strategies (e.g. age at first reproduction). While not fully documented, the evidence is accumulating for wide-spread evolutionary responses to these selection pressures. For example, the proportion of sedentary individuals within great bustard (*Otis tarda*) populations increased from 17% to 45% over a 15-year period, with collisions being the major source of death for migrating individuals [13]. The wing span of cliff swallows has evolved to be shorter near roads, with road-killed swallows having longer wings, consistent with selection for increased manoeuverability in the face of traffic [14].

While urban evolution has received less attention than urban ecology, cities are increasingly recognized as highly altered selective landscapes, providing the opportunity to study evolutionary shifts that occur in a replicated fashion across cities [20]. For example, mosquitoes of the molestus form of Culex pipiens have repeatedly taken advantage of the increasing availability of subways and other urban underground areas with readily available human hosts to transition to an underground life history [22]; the evolution of biting preferences for humans over birds has concomitantly evolved independently in Europe [23] and North America [24]. Urban bird feeders provide an artificial food subsidy, selecting for shifts in beak size and bite forces in urban house finches (Carpodacus mexicanus), with correlated changes in bird song [25]. White clover (Trifolium repens L.) has evolved greater tolerance to freezing within three of four northeastern North America cities, a response ascribed to the higher incidence of freeze-thaw cycles within the urban environment compared to surrounding non-urban areas [26]. The altered thermal environment of cities has also been invoked to explain shifts in migratory behaviour in urban blackbirds, which are more sedentary than paired rural populations [27].

Even the presence of human activity can induce fear and behavioural shifts in wildlife. In a meta-analysis of 72 studies, Gaynor *et al.* showed a 36% increase in nocturnality among mammals, essentially a human-avoidance mechanism, with an even stronger effect in cities, but whether genetic changes have occurred causing (or responding to) this shift towards nocturnality is unknown [28]. In other cases, genetic differences underlying behavioural shifts in response to humans have been implicated. For example, a study of black swans (*Cygnus atratus*) found that more wary individuals avoided cities and differed genetically at a dopamine receptor gene associated with fear in animals (DRD4), compared to more human-tolerant urban swans [29].

(b) Selection to avoid hunting or harvesting

Humans typically hunt or harvest in a selective manner, leading to 'unnatural selection' in the terminology of Allendorf & Hard [30], which often drives traits in exactly the opposite direction preferred by humans. Hunting pressures have long been studied for the selective pressures induced, including an early analysis by Haldane [31] documenting the decline in foxes of the silver coat variant, which was highly prized by trappers. From reductions in tusk size among elephants [15] to horn size among bighorn sheep [32], hunting selects for those traits that keep animals out of the cross-hairs [30].

Fishing also induces selection pressure on body size, life history and morphology often in a manner that makes fish less catchable and/or less desirable. In an analysis of 143 time series, Sharpe & Hendry found rapid decreases in fish length at 50% maturity and earlier maturation, changes that were strongly correlated with the intensity of fishing pressures [33]. Fishing not only selects on size but also shape and behaviour. For example, recreational hook-and-line fishing has selected for smaller mouth gapes [34], while gillnet fishing has selected against a more active, bold and aggressive genotype in rainbow trout [35]. These evolutionary responses generally reduce catch value per unit effort.

Across a broad spectrum of harvested species, rates of evolutionary change induced by human culling were found to be three times higher than in natural systems [36]. Reflecting upon harvesting in general, Sharpe & Hendry [33] concluded that 'exploitation is a very strong selective force, probably outside the normal intensities of selection in most natural populations'.

(c) Selection in novel communities

Beyond altering the physical environment, humans are altering the biotic environment faced by species across the planet. Most obviously, communities are altered through the introduction of non-native species but also when species' ranges shift at different rates in response to anthropogenic habitat alteration and climate change. Bumblebees in North America and Europe, for example, are not spreading poleward in response to warming at their northern range edges as much as expected based on contractions at their southern range edges [37]. Thus, plants whose ranges are shifting poleward will probably face different communities of pollinators.

When humans bring species together into novel assemblages, strong evolutionary and co-evolutionary selective pressures can result, especially if the species within a new community had little to no prior contact. Strauss et al. [38] reviewed 31 well-documented cases of altered evolutionary responses to introduced species, including insects evolving in response to novel host plants, plants evolving in response to novel herbivores, fish evolving in response to novel competitors and predators, and resistance evolving in response to novel diseases. Responses involved morphological and/or physiological changes (21 cases), behavioural changes (11 cases) and life-history changes (3 cases). As a striking example, cardinals in high condition (as indicated by bright red coloration) prefer to establish territories within an introduced honeysuckle, where their nests are more heavily predated; the net result is a reversal in the direction of selection for bright plumage [16]. Altogether, these diverse examples illustrate the variety of ways that humans indirectly alter selection by changing the biological community within which species live and reproduce. Metaphorically, the Red Queen must run faster and in new directions to keep her place within newly assembled communities.

Beyond altered biotic selection pressures, changes to the community can affect how species respond to abiotic changes in their environment. In Kleynhans *et al.* [39], we found that the grass *Poa pratensis* evolved increased fitness in response to 14 years of elevated CO_2 supplementation in the field, but only when plants remained in the same community context in which selection had occurred. Our results suggest that the realized selection pressures induced by anthropogenic environmental changes are reshaped by the surrounding community (essentially altering the direction and magnitude of selection experienced in multivariate trait space). Consequently, adaptation to abiotic changes, such as elevated CO_2 ,

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may be quite sensitive to variation over time and space in the surrounding community.

(d) Selection on dispersal

While the above examples focused on trait responses to selection, human-induced selection pressures can also shape how species live and move through their environment. In increasingly fragmented and exploited landscapes, dispersal and migratory behaviour are subject to different selection pressures in the Anthropocene.

Theoretically, we expect reduced dispersal rates to evolve within fragmented but stable patches so that organisms can remain in hospitable environments [40]. For example, we found that selection to avoid fishing pressures is expected to select for fish that remain in marine protected areas, potentially improving the efficacy of marine reserves over the span of decades [41]. Empirically, selection against dispersal has favoured heavy non-dispersing seeds relative to lighter dispersing seeds of the weedy hawksbeard (*Crepis sancta*) in Montpellier, France, where the soil is patchily distributed among the built environment [17]. Similar changes in dispersal propensity and distances moved have been observed in several systems (see citations in [42]).

While reduced dispersal protects local populations in the short term, dispersal is critical over the long term for recolonizing patches after local extinction events and for facilitating genetic exchange and the maintenance of variation. With increasing patch extinction rates, theory predicts that higher dispersal rates can be favoured, allowing faster recolonization [43]. Consistent with these expectations, a greenhouse experiment with Arabidopsis thaliana found that plants evolved to disperse three times farther across fragmented habitats in only six generations [44]. Yet increasing dispersal through unsuitable habitats is risky. To reduce these risks, selection can favour dispersal behaviours that are more leptokurtic (either staying put or dispersing far) or more targeted to suitable habitats [42]. A study of the butterfly Proclossiana eunomia in Belgium found, indeed, that individuals were more likely to stay within their natal patch in the most fragmented of the landscapes studied, were more likely to die if they dispersed, but when they dispersed they flew faster and straighter through inhospitable habitats [45,46], although the extent to which this represents a recently evolved trait is uncertain.

With climate warming, the availability of resources in the spring is shifting earlier in many parts of the world, with the timing of migration moving forward by an estimated 2.3 days per decade [47]. Although the mechanisms are often unknown, evidence for at least some genetic response to selection is mounting. For example, a study of pink salmon in Alaska found that migration back into streams occurred two weeks earlier than 40 years ago, accompanied by a three-fold decrease in a genetic marker associated with late dispersal [48].

Migratory behaviour can also be affected by anthropogenic shifts in resource availability. The popularity of bird feeders and a warming climate has made for more hospitable winters for birds in Britain over the past century [49]. In response, a sub-population of blackcap warblers (*Sylvia atricapilla*) has evolved a new migratory route to Britain, with offspring raised in captivity showing different flight orientation preferences than related birds that migrate to Spain [50]. Successful dispersal also requires successful breeding in a new environment. As a consequence, we may expect features that enhance reproductive assurance, include selfing, asexuality and perenniality, to evolve when novel sites are being colonized (Baker's rule [51]). Indeed, some annual plants are more self-compatible in their invasive range than where they are native (*Echium plantagineum*) and where weedy than non-weedy (*Centaurea solstitialis*) [52].

(e) Selection on inheritance systems

The very nature of inheritance can also be shaped by humanaltered selection pressures. During periods of rapid environmental change, selection favours increased mutation rates, particularly within clonal organisms where mutator alleles can hitchhike along with the beneficial mutations that they generate. Mutator strains are repeatedly observed in microbes following exposure to antibiotics but also in response to selection on virulence and transmissibility (see [53] for examples).

To reduce selective interference among loci, the rates of sexual reproduction and recombination are also expected to rise following periods of intense selection. Evidence for the impact of humans on recombination rates has been found in both domesticated mammals (see triangles in fig. 1 of [54]) and plants [18].

Plants living in human-disturbed habitats were found to inbreed more than in undisturbed habitats, altering patterns of inheritance in many species [55]. In their review, Eckert *et al.* [55] attribute this rise in inbreeding to pollen becoming more limited in disturbed areas, due to either a reduced abundance of pollinators and/or a lower density of plants. While these shifts in the mating system cause genetic changes (e.g. higher homozygosity), how they alter selective pressures is not yet known. Eckert *et al.* provide several predictions for how selection probably shifts in response to pollen limitation, calling for empirical work linking human disturbance to floral and mating system evolution.

Genome size has also been inadvertently shaped by human selective pressures. In many crop species, genome doubling (polyploidization) has an effect on agriculturally valuable traits, such as fruit size, with humans selecting and propagating polyploid varieties of many crops (e.g. blueberries, wheat, sugar cane, coffee and cotton [56]). Structural changes in the genome, including gene loss/duplication and chromosomal loss/duplication, also represent one of the fastest routes by which organisms adapt to an altered environment. In an experiment with yeast adapting to high copper concentrations [57], which is often used in wine grape cultivation, we found both gene duplications and aneuploidy arose repeatedly and rapidly (in the course of two weeks) [57]. Similarly, Gallone et al. [58] found 'staggering' levels of copy number variants and genomic structural changes in domesticated strains of yeast used in brewing.

While not exhaustive, these examples highlight the dramatic ways in which human-imposed selection pressures are altering organisms, down to the very way that they reproduce their genomes.

4. Extinction in the Anthropocene

In addition to altering the selective forces shaping evolution within species, humans are also imposing selection at the species level. Most alarmingly, humans have increased the rate at which

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species are going extinct and strongly determine which species are at risk of extinction.

Pre-humans, the background rate of extinction, estimated from lineage-over-time plots, is 1000 times lower than in the Anthropocene [59]. Over one in five species of vertebrates [60], invertebrates [61] and plants [62] are now at risk of extinction. While currently a minor risk factor, continued climate change is projected to rival habitat loss as the primary threat to species at risk by the end of this century [63].

Extinction in the Anthropocene is non-random, which generates species-level selection against those traits that elevate extinction risk. Many of the known extinctions over the past two centuries have been caused by overexploitation, with humans hunting to extinction species such as the sea mink, Caribbean monk seal, great auk and passenger pigeon. Such extinctions permanently remove species prized by humans (e.g. for the fur of the monk seal) and whose traits make them particularly susceptible to harvest (such as the flocking behaviour of the passenger pigeon). Large body size has also increased extinction rates of species subject to hunting throughout the past 50 000 years, eliminating half of the large terrestrial mammalian species [64].

Extinction driven by overexploitation tends to be noticed. Humans pay attention to species that they hunt and fish, documenting their demise. Extinction from overexploitation can also be rapid, with *per capita* mortality remaining high even as the targeted population decreases in size if humans search farther and innovate to continue to capture the resource (e.g. [65]). An accelerating approach to extinction or 'extinction vortex' can even result if rarity increases the value of the exploited species to humans [66].

By contrast, many of the unknown extinctions from the past two centuries, as well as current extinction threats [64], are caused by habitat loss and degradation. Unlike overexploitation, extinction caused by habitat change can be a prolonged process [67], with at-risk species persisting in remaining patches of suitable habitat. Indeed, a decelerating approach to extinction is expected if habitat most desirable to humans is converted first, leaving remnant patches that are protected, hard to access or difficult to develop where species can persist.

While species with patchy ranges may persist over the short term, they are subject to declining genetic diversity and localized ecological disasters that place them at risk of extinction in the long term. As a consequence, anthropogenic habitat change is thought to have generated a substantial extinction debt (e.g. [67,68]), which may take years to millennia to realize, depending on the extent of habitat loss [67]. The extinction debt, along with the fact that anthropogenic habitat change endangers many rare species that are unknown to science [69], makes it challenging to document fully which species are going extinct and what traits are being lost.

By examining which types of taxa are most endangered, however, studies have shown that the extinction debt is not borne evenly among species. Species with small ranges are particularly threatened [69]. By contrast, widespread species, generalists, dispersive species and human commensals are, on average, less prone to extinction [70]. Other less obvious character traits have also been shown to be associated with an increased threat of extinction. By comparing the IUCN red-list status of species, Vamosi & Vamosi [71] found that plants with separate sexes (dioecy) are more likely to be at risk of extinction than hermaphroditic sister clades, potentially because pollen flow and seed dispersal are more easily disrupted when male and female functions reside in different plants. Woody plants [71] and tropical plants [72] are also more at risk. In birds, species with larger body sizes [73], lower fecundity [73] and larger testes size (an indicator of stronger post-mating sexual selection) [74] are more likely to be endangered, potentially because such species are less able to recover when driven to small population sizes.

Humans are thus reshaping the living world through non-random extinction, leading to a rise in frequency of widespread species that tolerate human activities, a fragmented environment, and an altered climate.

5. Speciation in the Anthropocene

Relative to extinction, less is known about how humans have altered the rate of speciation. Estimates of background speciation rates can also be estimated from lineage-over-time plots and from intervals between nodes in a phylogeny (especially nearer the present), suggesting that species' splits occur at roughly every 2 Myr, on average, per lineage [75]. Estimating modern speciation rates is more challenging. It is easier to document the loss of a species previously known to be present than to witness the birth of a species, especially when divergence is so recent that few characters distinguish the new species from its parent(s), leading to cryptic young taxa [76].

While the effect of humans on the rate of speciation is unknown, many examples exist of how humans have altered the speciation process [77]. The mechanisms underlying these impacts can be roughly categorized as human-altered niches, human-altered contact and human-altered selection.

(a) Human-altered niches

Human activities have altered and created novel niche space. Crop domestication and the spread of agriculture, in particular, have generated novel plant hosts for many insects and pathogens. One of the best documented cases of contemporary speciation is *Rhagoletis pomonella*, following a host switch to domesticated apples [78]. Similarly, the introduction of invasive honeysuckle (*Lonicera*) from Asia provided a novel niche that favoured the spread of a newly formed homoploid hybrid species of *Rhagoletis* (between *R. mendax* and *R. zephyria*) [79]. Host specialization onto different crops has also driven speciation in fungi, with *Rhynchosporium*, for example, diversifying into at least three pathogenic species specialized on different cereals in the past 4000 years [80].

Contaminated sites, e.g. mine tailings, can also promote speciation because of the strong ecological selection for locally adapted genotypes. For example, the sweet vernal grass, *Anthoxanthum odoratum* L. has adapted to heavy metals surrounding a mine active in the mid- to late 1800s. This local adaptation has been accompanied by a shift in flowering time and an increase in selfing rate, generating substantial reproductive isolation that has been maintained over the past 40 years [81]. Adaptation to copper-heavy mine tailings has also driven both local adaptation and reproductive isolation in *Mimulus gutatus* [82].

Climate change is also opening up niches in locations that previously were inaccessible. The blackcap warblers that now migrate to the UK are beginning to show evidence of assortative mating and genetic differentiation from those that migrate to Spain [83], exhibiting the initial steps of speciation in under a century. Humans are, however, also homogenizing environments that previously were heterogeneous, eroding the potential for speciation. For example, the nesting habitats of benthic and limnetic sticklebacks in Enos Lake in western Canada were homogenized after the invasion of signal crayfish in the 1980s. As a consequence, the two young stickleback species collapsed into a single hybrid swarm [84]. Similarly, the narrowing of the visual environment in Lake Victoria due to human-caused eutrophication has led to the loss of mate preferences that maintain species, with a fourfold reduction in the number of species in the most turbid waters [85].

(b) Human-altered contact

The global mixing of species by either intentional or accidental introduction by humans is also providing novel opportunities for speciation. In particular, hybrid speciation is facilitated between species that were previously isolated. A prime example is the grass *Spartina alterniflora*, native to eastern North America and introduced by humans both to western North America and Europe [86]. Hybridization with native *S. foliosa* in California has led to a hybrid swarm, while hybridization with *S. maritima* in France and separately in England generated sterile hybrids (*Spartina × neyrautii* and *S. × townsendii*, respectively). Polyploidization of *S. × townsendii* subsequently produced *Spartina anglica*, a fertile and highly invasive species that vigourously colonizes and alters sedimentation in salt marshes [86].

Spartina illustrates the opposing effects that human introductions are likely to have on speciation. On the one hand, species brought into secondary contact by humans can collapse into a hybrid swarm when reproductive isolation is not sufficiently strong (as in western North America [86]), hindering speciation. On the other hand, crosses between more isolated species can facilitate hybrid speciation (as in Europe [86]).

Reproductive character displacement is another potential evolutionary outcome of human-caused secondary contact, where mating systems evolve to reduce gene flow between partially incompatible species when in contact. For example, mating to males of the mosquito *Aedes albopictus* effectively sterilizes females of *Ae. aegypti*, leading to population declines of the latter where they overlap in range in the Americas, where both species are introduced and invasive [87]. *Ae. aegypti* have recently evolved lower rates of interspecific mating in sympatry with *Ae. Albopictus* than in allopatry, a tell-tale sign of reproductive character displacement, reducing gene flow and allowing *Ae. aegypti* to persist [87].

In addition to increasing contact rates between previously isolated populations, humans are also decreasing contact rates between previously connected populations. Roads, dams, deforestation and other habitat alterations act as anthropogenic vicariance events. Evidence is accumulating that such human-caused isolation events have led to genetic and morphological divergence (e.g. in sticklebacks following the construction of a dam in Iceland [88]; in Geoffroy's tamarin following the construction of the Panama canal [89]; see also references in [90]). Evidence that such isolation has led to allopatric speciation is, however, lacking, likely reflecting the slower accumulation of reproductive isolating barriers in the absence of strong ecological selection. In the long-term, the fragmentation of species ranges into isolated populations may also increase the rate of speciation, for those species capable of persisting.

(c) Human-altered selection

Finally, speciation rates may be affected by the changing nature and strength of selection in the Anthropocene. With more intensive selection, adaptive mutations are expected to become fixed in different populations at a higher rate, decreasing the expected time until an incompatibility arises between populations according to the 'snowball' model of speciation [91].

Potentially even more important than the number of substitutions is the nature of those substitutions. With strong selection induced in human-altered environments [33], genetic changes are more likely to involve large-effect mutations, which our recent research suggests is more likely to lead to speciation. Why? Large-effect mutations are more likely to have stronger deleterious side effects (either due to pleiotropy or hitchhiking) that contribute to reduced fitness of inter-population hybrids. Furthermore, the chance that offspring overshoot a fitness optimum is increased when crossing two lines carrying different large-effect beneficial mutations.

The hypothesis that strong selection is likely to shorten the time to speciation is consistent with our laboratory experiments with yeast. After only days of exposure to the fungicide nystatin, we have observed that independently adapted strains, bearing different large-effect mutations, show reduced 'hybrid' fitness (Dobzhansky–Muller incompatibilities) in 33–50% of the crosses [92]. Modelling also confirms this hypothesis. By moving a fitness optimum rapidly versus slowly, we find that large-effect mutations that accumulate in a rapidly changing environment generate stronger reproductive incompatibilities than small-effect mutations that accumulate when the environment changes slowly, even when the populations have reached the same optimum [93].

Similarly, genetic analyses of the *Mimulus gutatus* populations adapted to mine tailings show that the reproductive incompatibility with surrounding populations is associated with a major-effect mutation at the *Tol1* locus [82]. In this case, the strong selection allowed hitchhiking of a linked mutation at the *Nec1* locus that is thought to be responsible for the incompatibility.

In summary, there are good reasons to expect more rapid speciation in the Anthropocene [90], particularly in groups evolving into new niches and responding rapidly to selection. In other groups, however, human-caused secondary contact, habitat degradation and environmental homogenization are causing the collapse of what might otherwise have remained or become good species. The net impact of humans on speciation rates, even whether that impact is positive or negative, remains unknown.

6. Conclusion

Humans have altered the course of evolution. The pervasiveness of evolutionary impacts, from genome structure to dispersal rates, on species throughout the globe should make us take pause. Particularly troubling is the elevated extinction rate associated with human activities, which is disproportionately leading to the loss of large-bodied, specialist, narrow-ranged species, as well as species that are otherwise vulnerable to humans.

While the impacts of humans on extinction rates have rightfully received substantial attention, humans are also reshaping the selection pressures within species, favouring organisms 6

that are human-tolerant over those that are human-sensitive, whether sensitive to development, harvesting, anthropogenic climate change, etc. It is worth emphasizing that, in many cases, human-associated selection pressures can be strong, stronger than is typically measured in less impacted systems [36]. There are theoretical reasons to expect that strong selection imposed by humans will lead, as a side consequence, to fitness loss in other attributes of survival and reproduction, with genetic substitutions expected to reduce fitness on average by roughly half the strength of selection imposed by humans on those loci [94]. From morphological changes, such as wing shape and body size, to behavioural changes, such as biting preferences and migration routes, our world is evolving less under the pressures of natural selection and more under the pressures of anthropogenic selection.

While human activities can also facilitate speciation (e.g. to novel host plants), widespread introductions and movement of species, as well as homogenization of environments, have led to the collapse of incipient species. More research is needed to determine the net effect of humans on speciation rates. If negative, then the net loss of biodiversity is even higher than currently considered if we include species that are not forming due to human activities, adding a speciation debt to the extinction debt.

Why does it matter that humans are altering the course of evolution more intensely than has any other species? First,

we will leave a legacy to future generations that is less natural and less wild than the biological world into which we were born. This is not simply because of the loss of species but also because of the imposition of a common selective pressure to tolerate human activities. Second, by moving individuals around the world and homogenizing environments, we may well be reducing the rate of speciation. As a consequence, it will take longer for the planet to recover from the current extinction crisis, and certain classes of species may be particularly prone to loss but not recovery (e.g. large-bodied animals). Finally, evolutionary changes in response to human pressures have policy implications, as diseases and their vectors become better adapted to life within our cities, pests become better adapted to our crops and our prey become better adapted to our means of harvesting. As we have witnessed with the evolution of antibiotic resistance, humans may impose selection, but we will often not retain the upper hand.

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