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## Introduction

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# Human influences on evolution, and the ecological and societal consequences

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Humans have dramatic, diverse and far-reaching influences on the evolution of other organisms. Numerous examples of this human-induced contemporary evolution have been reported in a number of 'contexts', including hunting, harvesting, fishing, agriculture, medicine, climate change, pollution, eutrophication, urbanization, habitat fragmentation, biological invasions and emerging/disappearing diseases. Although numerous papers, journal special issues and books have addressed each of these contexts individually, the time has come to consider them together and thereby seek important similarities and differences. The goal of this special issue, and this introductory paper, is to promote and expand this nascent integration. We first develop predictions as to which human contexts might cause the strongest and most consistent directional selection, the greatest changes in evolutionary potential, the greatest genetic (as opposed to plastic) changes and the greatest effects on evolutionary *diversification*. We then develop predictions as to the contexts where human-induced evolutionary changes might have the strongest effects on the population dynamics of the focal evolving species, the structure of their communities, the functions of their ecosystems and the benefits and costs for human societies. These qualitative predictions are intended as a rallying point for broader and more detailed future discussions of how human influences shape evolution, and how that evolution then influences species traits, biodiversity, ecosystems and humans.

This article is part of the themed issue 'Human influences on evolution, and the ecological and societal consequences'.

## 1. Introduction

Humans might be the 'world's greatest evolutionary force' [1,2], frequently driving what is now called 'rapid evolution', 'contemporary evolution' or 'evolution on ecological time scales'. Indeed, even the earliest putative examples of contemporary evolution often had clear anthropogenic drivers, including pollution [3–6], commercial fishing [7], species introductions/invasions [8–10], antibiotic treatments [11,12], weed control in agriculture [13,14], zoonotic and enzootic parasites [15] and others. These early examples helped spread awareness of contemporary evolution [16,17] to the point that we have since had an ever-accelerating accumulation of additional and diverse examples. Now that contemporary evolution is known to be all around us—and, indeed, driven by us—recent research and discussion has increasingly emphasized the potential eco-evolutionary consequences for population dynamics, community structure, ecosystem function and human societies [18–22]. This special issue seeks to understand this diversity of human-to-evolution-to-ecology-to-human influences, through both reviews and novel empirical studies.

The present special issue is organized around different 'contexts' for human influences, specifically pollution, eutrophication, urbanization, habitat fragmentation, climate change, domestication/agriculture, hunting/harvesting (including fishing), invasion/extinction, medicine and emerging/disappearing diseases

**Table 1.** A summary of the reviews and empirical studies in this special issue.

human-induced context	reference	type of manuscript	key insight(s)
pollution	[23]	review/empirical	strong selection imposed by human-released chemical pollution can be mitigated by physiological adaptations such as enzymatic metabolic adaptations that could be costly in non-polluted conditions
eutrophication	[24]	review/empirical	eutrophication often leads to homogenization of both phenotype and genotype and to a loss of ecological specialization, which can have cascading effects at the community and ecosystem levels
urbanization	[25]	review	the type of urban disturbance can have different effects on adaptive traits of organisms in urban environments, which can affect ecosystem processes and thus eco-evolutionary dynamics
urbanization	[26]	empirical	consideration of both changes in community responses and evolutionary responses is important in understanding community trait changes resulting from urbanization, and trait change depends on the spatial scale at which urbanization is considered
habitat fragmentation	[27]	review	anthropogenic fragmentation generates selection at multiple scales; dispersal and associated traits are likely to adapt and evolve interactively; and these adaptations might not be enough for 'rescue' at the meta-population level
habitat fragmentation (and urbanization)	[28]	empirical	fragmentation predicted trait variation better than did urbanization, and reproductive and dispersal traits were altered as a result of adaptation to urban environments
climate change	[29]	review/empirical	the role of life-history plasticity and evolution in response to shifts in competition could help us to understand how climate change induced competition might affect local communities and biodiversity
domestication/agriculture	[30]	review	agriculture and domestication can drive evolution in wild species that can have large socio-economic ramifications on ecosystem services. An understanding of these processes can help inform how to mitigate the impacts
domestication/agriculture	[31]	empirical	a comprehensive, phylogenetically controlled meta-analysis found that domestication influences the evolution of herbivore resistance, though the magnitude is highly variable. Furthermore, the evolution of plant defence traits was highly variable in direction and magnitude
hunting/harvesting	[32]	review	contrasting aquatic and terrestrial harvesting, the evolution of system-specific traits can negatively affect populations, but these effects can be mitigated through reduction of harvest intensity
hunting/harvesting	[33]	empirical	single versus multi-locus controlled traits can respond differently when subject to harvesting-induced selective pressures, and a lack of phenotypic adaptation does not mean evolution has not occurred
invasions/extinctions	[34]	review	invasive and endangered species experience comparable eco-evolutionary challenges, but important differences exist, which could help explain the differential responses of invasive (persistence) and endangered (extinction) species
invasions/extinctions	[35]	empirical	adaptation and evolution to novel environments can affect the establishment and persistence of invasive species
medicine	[36]	review	the evolution and subsequent increase of antibiotic resistance often ignores bacterial interactions, which can have large implications in eco-evolutionary feedbacks concerning bacterial communities and with whom they interact
medicine	[37]	empirical	low-levels of antibiotics can affect the ecological and evolutionary outcomes of microbial communities (e.g. bacteria–phage interactions) through unexpected interactions
emerging/disappearing diseases	[38]	review	through a variety of mechanisms, humans can alter the interactions and evolutionary trajectories of hosts and parasites, with widespread implications for disease emergence and disappearance
emerging/disappearing diseases	[39]	empirical	bat populations with extended exposure to white-nose syndrome are evolving resistance, and not tolerance, to the fungal pathogen; fitted models demonstrate growth rate of the pathogen decreases as fungal loads increase

(table 1). In this introductory paper, we seek to facilitate integration across these contexts by suggesting generalities and exceptions for how they shape evolutionary dynamics and how they thereby have downstream ecological and societal consequences. From the standpoint of evolutionary changes, in §2 we ask: In which contexts will ...

- (a) ...directional selection be the strongest and most consistent?
- (b) ...evolutionary potential be the most dramatically altered?
- (c) ...genetic, as opposed to plastic, responses be most likely?
- (d) ...evolutionary diversification be most altered?

Then, from the standpoint of ecological and societal consequences, in §3 we ask: In which contexts will human-induced evolution most alter ...

- (a) ...population dynamics?
- (b) ...community structure?
- (c) ...ecosystem function?
- (d) ...human societies?

Two conceptual frameworks help to guide this integration: the phenotypic adaptive landscape and eco-evolutionary dynamics. The phenotypic adaptive landscape is a multidimensional surface relating mean population fitness to mean phenotypes [40–42]. These surfaces are expected to have peaks that correspond to high-fitness phenotypes and valleys that correspond to low-fitness phenotypes (figure 1). Selection thus favours populations phenotypically ‘climbing’ the slopes towards the fitness peaks. Human activities can alter these dynamics by changing the number, position, elevation and gradient of the peaks (figure 1; [43]), and also by changing the distribution of phenotypes across the surface (e.g. through gene flow, hybridization, mutation and plasticity). Eco-evolutionary dynamics then asks how these changes in phenotype/fitness influence the dynamics of the evolving population (e.g. population size, population growth, age structure), the structure of the community in which it is embedded (e.g. numbers and diversity of species, food web structure), and various ‘functions’ of the overall ecosystem (e.g. primary productivity, decomposition, nutrient cycling). Any of these eco-evolutionary effects could then impact human societies and feed back to further influence evolutionary change (figure 2).

When considering human effects on evolution and the potential consequences, it is sometimes useful to draw a distinction between how humans interact with their ‘enemies’ (or ‘adversaries’) versus their ‘friends’. In the case of enemies—such as weeds, pests and pathogens—we typically want to decrease their abundance and impact [30,36,38], which we attempt through various control measures, such as weeding, herbicides, pesticides, antibiotics or culling. Not surprisingly, the resulting selection favours resistance/tolerance to our control efforts, which can reduce their efficacy [30,36,38]. Of course, these direct interactions between humans and their enemies can spillover to influence non-target species [44], which can have a variety of cascading consequences. In the case of friends—most obviously crops and natural resources, but also biodiversity in

general—we typically want to increase properties such as abundance, productivity and stability [30,45]. Here we hope for—and sometimes facilitate—adaptive evolution that benefits the target species, such as by enhancing adaptive potential in endangered species [46–48], as well as any ecosystem services key species might provide. Of course, the categories ‘friend’ and ‘enemy’ are not always mutually exclusive, such as when ‘frenemies’ have both benefits and costs depending on the time or context. One example would be pathogenic bacteria evolving to influence other pathogens [49]. Finally, we could have organismal ‘neighbours’ that we frequently see and encounter; and, although they could be enemies or friends, are perhaps more often ‘just there’.

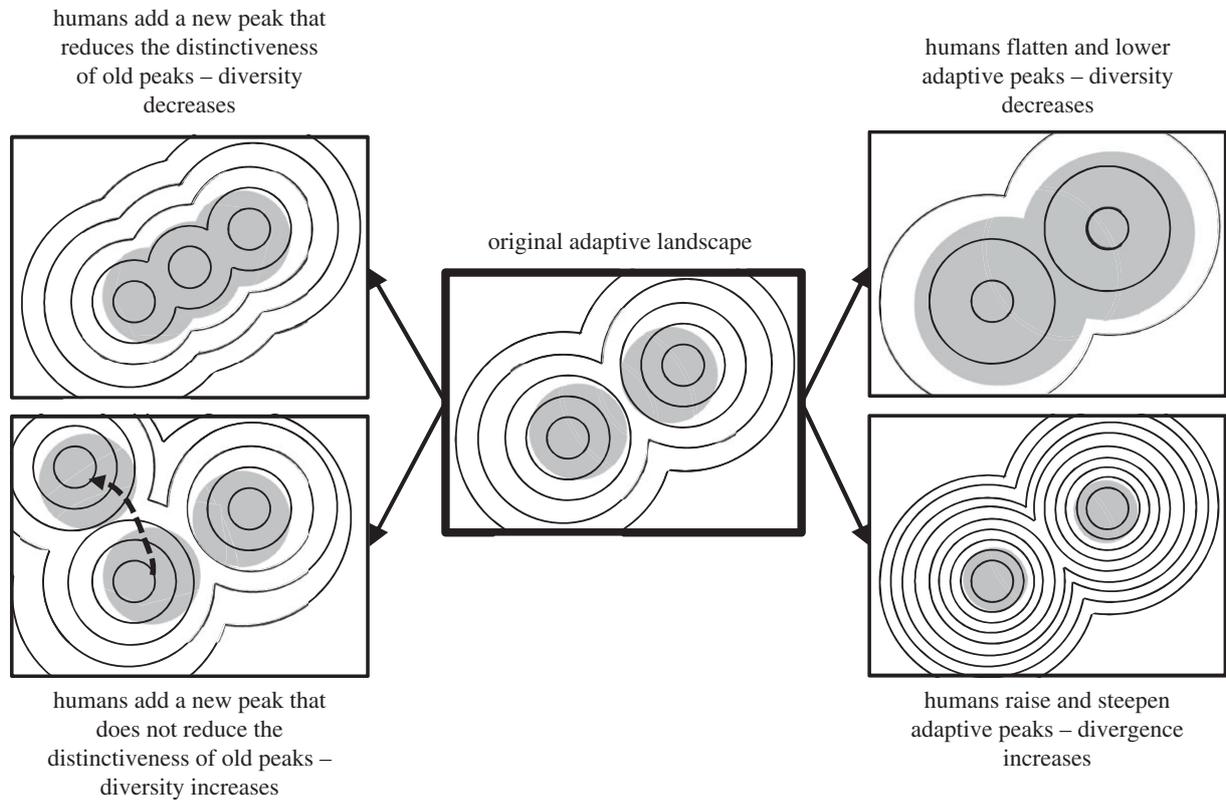
In the sections that follow, we suggest some answers to the above questions—in each case starting with a paragraph on general predictions and following with a paragraph overlaying those predictions onto the above human contexts. It was not possible to be comprehensive or definitive, partly owing to space constraints and partly owing to incomplete information. Instead, we seek to suggest some particularly strong associations while making an implicit ‘all else being equal’ assumption. Although we sometimes note interesting exceptions, it is important to acknowledge that many other points and examples and exceptions can be advanced. Thus, we intend these sections as a ‘draft’ of ideas that we hope will ferment further work and discussion.

## 2. Human influences on evolution (figure 3)

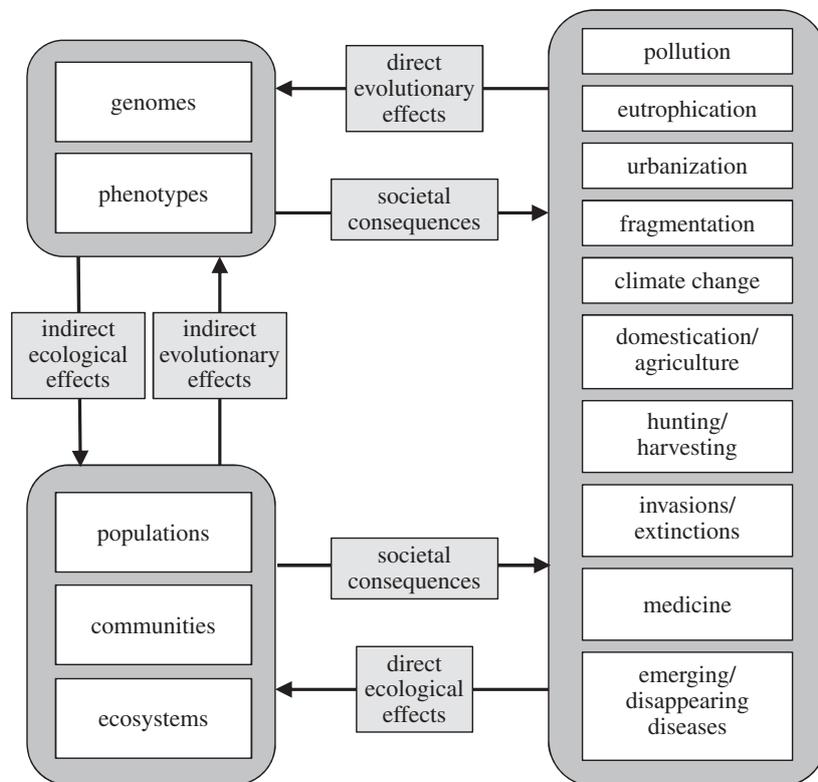
### (a) In which contexts will directional selection be the strongest and most consistent?

Directional selection favouring evolutionary change is expected to be the strongest and most consistent when population phenotypes rest persistently on the slopes of steep adaptive peaks (figure 1). This state can arise when the elevations and gradients of peaks are the greatest, and when their displacement from current phenotypes is the farthest, fastest and most sustained. One confluence of these conditions occurs when selection consistently favours the most extreme trait values (e.g. the largest body sizes) independent of the specific distribution of trait values. Another confluence occurs in antagonistic coevolution, where the evolution of one species (e.g. a parasite) to better exploit another species (e.g. a host) leads to the evolution of countermeasures and, hence, the continual evolution of both species [50–54]. These coevolutionary arms races come in two general forms [54]: escalating arms races [55] and cyclical Red Queen dynamics [56]. Both forms of antagonistic coevolution can impose strong directional selection, but escalating arms races might more often lead to consistent directional change.

Strong and consistent directional selection might arise in any of the human-disturbance contexts, but we specifically wish to highlight hunting/harvesting, climate change and certain agricultural and human health situations. For hunting/harvesting, selection can actively target and disproportionately remove the largest individuals each generation, regardless of average body size [32]. Strong directional selection for smaller size thus should persist even as evolution proceeds. Matching this expectation, phenotypic changes in wild populations are greatest when humans act as predators



**Figure 1.** Hypothetical adaptive landscapes showing mean population fitness (contours) with respect to mean phenotype for two traits ( $x$  and  $y$  axes). Grey circles show potential distributions of phenotype. The starting (original) adaptive landscape is in the central thick box and has two fitness peaks that are each occupied by its own reasonably well-adapted population. The left-hand panels depict two forms of a potential human-caused increase in the number of peaks. The right-hand panels depict two forms of human-caused changes in the heights of peaks and the gradients around peaks. This figure is modified from [43].



**Figure 2.** Graphical representation of how eco-evolutionary dynamics interact with human influences. Human activities (at right) can have direct ecological effects on the dynamics of a focal species (populations), the structure of its community (communities) and the function of its ecosystem (ecosystems). These direct ecological effects can influence the traits (phenotypes) and genetic properties (genomes) of species, thus leading to indirect evolutionary effects of human activities. Human activities can also directly influence the phenotypes and genomes of species that can then influence population dynamics, community structure, and ecosystem function. Changes in any of these evolutionary or ecological parameters can then feedback to have important consequences for human activities, and human societies.

	directional selection	evolutionary potential reduced population size → increased population size	genetic response, not plastic response	evolutionary diversification decreased diversity → increased diversity
pollution		abiotic stressors leading to reduced population size mutagen enhancement leading to increased population size	often 'novel' selective pressures	decreased diversification due to strong selection from the creation of novel environments
eutrophication		abiotic stressor(s) leading to reduced population sizes of species of interest abiotic stressors(s) leading to an increase in non-desirable species (e.g. algal blooms)	often 'novel' selective pressures	
urbanization		habitat loss leading to reduced population sizes		decreased diversification due to strong selection from homogenization of environments increased diversification due to strong selection from novel environments creating heterogeneity
habitat fragmentation		fragmentation leads to smaller population sizes and reduced gene flow		decreased diversification from strong selection and increased evolutionary independence increased diversification from increased speciation rates
climate change	optimum trait values, especially phenology, shift in response to ongoing environmental change such as global warming			
domestication and agriculture	efforts to control 'enemies' such as pests and weeds impose strong selection and result in the evolution of tolerance and/or resistance		intensive attempts at weed and pest control leads to increasing genetic changes	
hunting and harvesting	targetted removal of (usually) the largest individuals, no matter mean population size	direct harvesting leading to reduced population size		
invasions and extinctions		invasive predators or parasites leading to reduced native species population size 'enemy release' or increased hybridization leading to increased invasive population size		decreased diversification through altered distinctiveness of environments and gene flow increased diversification through novel selection and new 'environments'
medicine	evolution of tolerance and/or resistance in response to attempts to control 'enemies' such as pathogens		intensive attempts at pathogen control leads to increasing genetic changes	
emerging and disappearing diseases	evolution of tolerance and/or resistance in response to attempts to control 'enemies' such as diseases	emerging diseases leading to reduced population size disappearing diseases leading to increased population size		

**Figure 3.** A schematic outlining some expectations for which human-disturbance contexts might most strongly influence evolutionary dynamics. These suggestions are not meant to be definitive but rather a starting point, or a template, for discussion and further work. For this reason, a number of context-by-question cells do not have predictions—and are therefore empty. Stated another way, we have here only highlighted a number of potential expectations—many others are possible. And, of course, exceptions are certain to occur in every instance.

[2,57] and when fishing intensity is strongest [58]. For climate change, one might similarly assume that, because warming is ongoing, optimal trait values should continue to shift in the same direction, with a clear example being the advancement of spring phenology [29,59]. However, year-to-year climate variation can exceed the overall warming trend, and so selection should be variable from year to year [60]. Of course, directional selection will not be eternal in either context, because harvesting often ceases when fish get too small or rare, and because phenology cannot advance indefinitely. Hence, we instead expect the strongest and most consistent directional selection to arise when humans instigate or intensify escalating arms races, such as when we kill or control our enemies (weeds, pests, pathogens), which then evolve resistance, which thus necessitates newer or stronger control measures—and so on [30,36,38]. Even here, directional selection might stop—or at least weaken—if, for example, enemies evolve tolerance instead of resistance [39,54,61], if they evolve to become friends or neighbours (e.g. domestication of wild animals or plants [62,63]), or if we wipe them out.

### (b) In which contexts will evolutionary potential be the most dramatically altered?

Evolutionary potential is determined by the distribution of genetic (co)variance across the adaptive landscape, with greater variance and better alignment with the direction of selection both expected to speed evolution [64]. Any perturbation that alters genetic (co)variance can thus influence evolutionary dynamics on a given adaptive landscape. In some cases, genetic variation can *increase*, including through greater gene flow, hybridization or mutation. Such increases can be beneficial if enough of the new variation is adaptive versus detrimental if too much of it is maladaptive. In other cases, genetic variation can *decrease*, most obviously through strong selection or reduced population size (which might or might not be coupled: [65–67]), with the latter increasing genetic drift and inbreeding. Such decreases could be beneficial (e.g. if they reflect precise adaptation) or detrimental (e.g. if they limit future responses to selection).

We suggest that the greatest *increases* in genetic variation will attend contexts where population sizes increase most dramatically, such as for introduced species experiencing ‘enemy release’ [35,68] and for native species benefiting from ‘disappearing diseases’ [38]. Increases are also expected when diverse source populations are brought together in new locations [34,69,70] and in the case of exposure to mutagens (e.g. pollution [71,72]). We suggest that the greatest *decreases* in genetic variation will attend contexts where selection is strong and consistent, and/or when population sizes decrease dramatically. Some contexts that generate strong selection were discussed in §2a, especially hunting/harvesting and some coevolutionary arms races. However, even exceptionally strong selection does not always deplete relevant genetic variation [73,74], especially when the selection is variable in time and space. Some contexts that can greatly reduce population size include habitat loss (e.g. urbanization [27]), strong abiotic stressors (e.g. pollution [23,24]) and strong biotic stressors (e.g. invasive predators/parasites [34] and emerging diseases [38]). Additionally, genetic variation within populations can decrease owing to fragmentation that reduces gene flow [72].

### (c) In which contexts will genetic (as opposed to plastic) responses be most likely?

When environments change, organisms can respond adaptively by moving to new locations, by altering their phenotypes as individuals (plasticity), or by evolving as populations (genetic change). Focusing on the latter two possibilities, many instances are known where populations have persisted through dramatic environmental shifts, and where adaptive phenotypic change appears to have played a key role [28,31,75]. In these cases, a fundamental question is whether the phenotypic changes were plastic or genetic, which is often hard to conclusively establish—especially in the contexts of climate change [76–78] and hunting/harvesting [33]. In general, genetic change is expected to be more important when populations are larger (because standing genetic variation and mutational inputs are greater), when generation times are shorter (because even small per generation changes can achieve larger per year changes), when the altered environmental conditions are novel (because existing *adaptive* plasticity would be less likely) and when the environmental change is greater (because the scope for plasticity is limited).

These considerations suggest that genetic responses should be greatest in the contexts of human health and agriculture, although evolution certainly also has been documented in the other contexts. The reason we emphasize health and agriculture is that humans are there trying to control their enemies (e.g. weeds, pests, pathogens), which tend to be abundant and have relatively short generation times. Moreover, control measures are often novel and selection is often continual. The evolution of such enemies is correspondingly very common, rapid and dramatic [79–84]. Another context where genetic changes might be especially important is pollution—because the selection pressures often involve novel chemicals for which existing adaptive plasticity is unlikely [3,23]. Regardless of the context, the relative contributions of plasticity and genetic change should vary through time. Plasticity could allow rapid immediate responses and therefore should be especially important at the outset of a disturbance, as suggested in the ‘Baldwin Effect’ (reviewed in [85]). However, plasticity is limited and can be costly, thus favouring subsequent genetic changes, including the evolution of plasticity [86,87].

### (d) In which contexts will evolutionary diversification be most altered?

Biodiversity evolves through adaptation to (i) different environments (i.e. different peaks on an adaptive landscape) and (ii) similar environments in different locations (i.e. the same peak on different adaptive landscapes) [41]. Thus, human influences that change the number, type and distinctiveness of environments and locations will effectively change the number, position and shape of adaptive peaks, which will thereby influence the evolution of biodiversity (figure 1) [88]. These effects could arise in three basic ways. First, humans can change how populations in different locations experience divergent selection by, for example, translocating species into new locations [89] or altering habitats in some locations [90–92]. Second, humans can modify the number and distinctiveness of alternative environments in a given location, thereby altering disruptive selection [93]. Third, humans can modify the evolutionary independence of populations and species by altering hybridization, gene flow and introgression

[94]. In each case, the effects can be 'positive' by facilitating the evolution of *increased* biodiversity (reviewed in [95]) or 'negative' by causing the evolution of *decreased* biodiversity [94].

Each of the contexts for human influence could have the above ramifications; yet they seem particularly to converge for species introductions that lead to biological invasions. Specifically, introduced species often experience novel selective pressures, especially new biotic interactions, and have considerable evolutionary independence from source populations in the native range. In addition, introduced species can provide new 'environments' for adaptation by native species, with an exemplar being new insect host races—and their associated species—on introduced plants [10,96,97]. Alternatively, or additionally, species introductions can cause the *evolution* of decreased biodiversity by altering the distinctiveness of natural environments, with an exemplar being new food types for birds that diminish the distinctiveness of native food types [93]. Introductions can also increase or decrease biodiversity by altering patterns of gene flow, hybridization and gene flow within and among species [94,98]. Other contexts that merit special mention are fragmentation, which imposes strong selection and increases evolutionary independence [27,91], and urbanization and pollution, which create especially novel environments [3,23,25,99].

### 3. Ecological and societal consequences (figure 4)

#### (a) In which contexts will human-induced evolution most alter population dynamics?

Humans have direct effects on species that alter aspects of their population structure ranging from age distributions to overall abundance. Beyond these direct demographic effects, humans can indirectly modify species' population dynamics by influencing their *evolution*. For instance, environmental change should render many populations maladapted, leading to decreased individual fitness, which should decrease population size—potentially causing extirpation or extinction. Yet this maladaptation should also generate selection, which should promote adaptation that increases individual fitness, which should increase population size—potentially allowing 'evolutionary rescue' (reviewed in [20,100,101]). However, these potential evolutionary benefits are not inevitable, nor are they necessarily sufficient for recovery. First, evolutionary rescue depends on sufficient adaptive genetic variation, which might or might not be present (see §2a). Second, strong selection can impose a mortality cost (i.e. 'hard' selection) that dramatically reduces population size, which can decrease genetic variation and increase inbreeding, drift and stochastic extinction [19,20,102,103]. As an additional effect, human activities can lead to the *evolution* of increased (or decreased) carrying capacity in particular species, such as through adaptation to new environments or resources.

Evolution occurring in any of the contexts for human influence could alter species' population dynamics, with several effects being especially clear. First, the negative effects of pollution (e.g. toxic chemicals) should often impose hard selection that can influence population size [104]. Second, attempts to reduce or eliminate enemies in agriculture and medicine are specifically designed to decrease the target's absolute fitness and should therefore also impose hard selection. With respect to the evolution of carrying capacity, several other human

activities seem likely to be particularly potent. For instance, humans often generate novel environments (e.g. urbanization [27] and agriculture [30]) and novel species interactions (e.g. invasions/extinctions [34] and emerging/disappearing diseases [38]) that can provide opportunities for evolutionary niche expansion. Putative examples might be mosquitoes adapting to the London Underground [105] and—again—new insect host races on introduced plants [10,96,97]. In all of these scenarios—and others—the *evolution* caused by human activities can substantially alter the abundance, age structure and population growth rate.

#### (b) In which contexts will human-induced evolution most alter community structure?

As was the case for population dynamics (§3a), humans often have direct demographic influences on community structure, whereas we are here interested in the evolutionary effects. We distinguish two main scenarios. First, human activities can have broad effects that simultaneously influence the evolution of many species, thus providing multiple points of entry for influence on a given community. Second, human activities can have strong effects on the evolution of particular 'important' species, which can then have cascading effects on the broader community [37]. These cascading effects could be a direct result of trait change in the important species; that is, trait-mediated effects of an evolving species on the community in which it is embedded. Alternatively or additionally, the evolution of an important species could alter its population dynamics, which could thereby influence the rest of the community.

Simultaneous multispecies evolutionary effects (scenario 1) seem possible in many contexts, but especially so for wholesale alterations of the environment. One such context is climate change, which is reshaping the phenology (and other traits) of large sets of interacting species [59], which thereby alters relative species abundances and the structure of food webs [106]. Wholesale environmental alterations are also typical in urbanization, fragmentation, pollution and agriculture [106,107]. Cascading effects of an important species (scenario 2) seem most likely when humans influence the evolution of particular 'keystone' species, 'foundation' species, 'niche constructing' species, 'ecosystem engineers', 'strong interactors' and so on. These important species could be those having very large effects as individuals (e.g. beavers, elephants and sea otters) or large effects owing to their high abundance (e.g. weeds, pests, pathogens and migratory species). We suggest that the community consequences of evolution in important species such as these are particularly likely for hunting/harvesting and human health, where humans often directly target specific large-effect friends or enemies. The same should be true when climate change or the bioaccumulation of toxins influences the evolution of apex predators [108,109].

#### (c) In which contexts will human-induced evolution most alter ecosystem function?

Human influences on evolution (§§2a–d) that then have consequences for the dynamics of populations and species (§3a) and the structure of communities (§3b) might thereby alter various aspects of ecosystem function, such as primary productivity, nutrient cycling, decomposition rates and carbon sequestration [19,110]. In parallel to our above suggestions for community

	population dynamics impose hard selection alter carrying capacity	community structure important species evolution multi-species evolution	ecosystem function important species evolution multi-species evolution	human societies enemies friends
pollution	effects can be density independent and prone to imposing hard selection novel environments lead to niche expansion increasing carrying capacity		wholesale environmental change causes evolution of several species which affects ecosystem services	decreased presence or abundance of useful species (e.g. pollinators)
eutrophication	effects can be density independent and prone to imposing hard selection novel environments lead to niche expansion increasing carrying capacity			noxious blooms are enemies to human societies
urbanization	novel environments lead to niche expansion increasing carrying capacity	wholesale environmental alterations	wholesale environmental change causes evolution of several species which affects ecosystem services	increasing contact with humans
habitat fragmentation		wholesale environmental alterations		loss of apex predators
climate change		evolution of phenology in multiple species alters species abundance and food webs	wholesale environmental change causes evolution of several species which affects ecosystem services	severe alterations to ecosystem services
domestication and agriculture	reducing enemies (pests) leads to decreased absolute fitness resulting in hard selection novel environments from agricultural development lead to niche expansion increasing carrying capacity	wholesale environmental alterations	single species evolution can have cascading effects on ecosystem services wholesale environmental alterations	weeds and pests are enemies to human society domestication of plants and animals is friendly to human society
hunting and harvesting		removal of ecologically important species has cascading effects on community	single species evolution can have cascading effects on ecosystem services, and external abiotic factors might not be an obscuring factor	hunting and harvesting are friendly to human society
invasions and extinctions	novel species interactions alter carrying capacity		external abiotic factors might not be an obscuring factor on evolutionary effects	invasive species are enemies to human society
medicine	reducing enemies (pathogens) leads to decreased absolute fitness resulting in hard selection	highly abundant pathogens can be ecologically important	single species evolution can have cascading effects on ecosystem services	pathogens are enemies to human society
emerging and disappearing diseases	reducing enemies (diseases) leads to decreased absolute fitness resulting in hard selection novel species interactions alter carrying capacity	highly abundant diseases can be ecologically important	single species evolution can have cascading effects on ecosystem services	emerging diseases are enemies to human society

**Figure 4.** A schematic outlining some expectations for which human-disturbance contexts might initiate the most important ecological and societal effects of human-induced evolution. For further explanations and caveats, see the caption for figure 3.

structure, these effects could arise through wholesale environmental manipulations that influence the evolution of many species, or through effects on the evolution of specific important species, which could then have trait- or density-mediated effects on ecosystems. Additionally, the evolutionary effects on community structure considered in the previous question could cascade to have ecosystem consequences (figure 2). Finally, any evolutionary influences on a particular ecosystem function could have cascading influences on other ecosystem functions, including through feedbacks that influence community structure, population dynamics and trait evolution [19] (figure 2).

The most important contexts for human-caused evolutionary effects on ecosystem function might be similar to those described above for community structure. First, wholesale environmental change that causes the evolution of many species that together have important ecosystem effects seems particularly likely for climate change, urbanization, pollution and agriculture. Second, cascading effects of the evolution of important species seem particularly likely for hunting/harvesting, agriculture and human health. Although evolutionary effects on ecosystem function could be strong (e.g. for plant size affecting nutrient and carbon cycling [111]), theory and empirical assessments have suggested that such effects might be weaker at the ecosystem level than at the community level [19,110]. The hypothesized reason is that additional external variables are expected to strongly influence ecosystem processes, and thereby swamp, or at least obscure, the effects of contemporary evolution. As examples, potential ecosystem effects of evolution might be swamped for climate change by the direct abiotic effects of varying temperature and precipitation, for agriculture by the direct effects of fertilizer and irrigation and for eutrophication by the direct effects of nutrients. Thus, we might expect the effects of evolution on ecosystems to be strongest, or at least the most obvious, in contexts where external drivers are not changing dramatically at the same time. Two such contexts might be introduced/invasive species and hunting/harvesting, where changes in biotic conditions could be more important than changes in abiotic factors. Of course, it is also possible for altered biotic interactions to swamp or obscure underlying eco-evolutionary dynamics.

#### (d) In which contexts will human-induced evolution most alter human societies?

We have thus far addressed how human influences on evolution can alter ecological processes at the population, community and ecosystem levels. It is now time to evaluate when these effects might have the greatest consequences for humans themselves, with respect either to services (from our friends) or disservices (from our enemies). First, some organismal traits are of specific interest to humans, such as the size of hunted/harvested animals, the concentration of useful plant chemicals, the nutrient content of agricultural products or the resistance of weeds/pests/pathogens to control measures. Second, humans can derive costs or benefits from evolutionary effects on the population dynamics of focal organisms, such as the biomass of harvested or cultivated species, the abundance of weeds/pests/pathogens, and the density and spread of undesirable invasive species. Third, evolutionary effects on communities can interact with our desire to preserve biodiversity [112,113]. Fourth, evolutionary changes can influence

emergent ecosystem properties that humans care about, such as carbon sequestration, water clarity or air quality.

The consequences of human-induced evolution for human societies are most obvious when the evolving organisms provide direct benefits as friends (e.g. hunting/harvesting and domestication) or direct costs as enemies (e.g. weeds/pests/pathogens, invasive species and emerging diseases). A less direct conduit for societal impacts occurs when humans influence the evolution of our 'neighbours', which can thereby influence our appreciation of nature or provide a mechanism for emerging enemies or friends. Importantly, all of the contexts for human-induced evolution have the potential to feedback to influence human societies through—for example—biodiversity, nutrient cycling and productivity. Stated plainly, all ecosystem services and disservices are shaped by past and future evolution, making them—more properly—EVOsystem services and disservices [113,114]. We further suggest that societal impacts will be strongly shaped by the nature and strength of feedbacks (figure 2), such as when humans cause the evolution of organisms in ways that have societal impacts, which then induces humans to further modify the evolution of those organisms. Those feedbacks could be positive (reinforcing), which will tend to destabilize eco-evolutionary systems, or negative (opposing), which will tend to stabilize eco-evolutionary systems [19,115]. An especially clear example of positive feedback is the race between organisms detrimental to humans and our attempts to control them.

## 4. Knowledge gaps and future directions

We have made a number of assertions as to the contexts where human-induced evolution is most likely to modify particular evolutionary processes (figure 3) and, thereby, alter particular ecological outcomes (figure 4). These assertions amount to intuitive predictions that now require formal empirical assessment. These assessments could be implemented through meta-analyses of intensities of selection and rates of phenotypic change in different contexts for human influence. Some analyses of this sort have already been attempted: Hendry *et al.* [75] compared the rates of phenotypic change for various types of human influence; Darimont *et al.* [57] showed that rates of change were greatest when humans acted as predators, and Westley [116] did not find consistently faster evolution in biological invasions. These databases have continued to grow, and the time seems ripe for formal analyses of predictions such as those we have here tendered. Of course, we emphasize that our predictions are merely a starting point intended to promote research and discussion in this area.

For the most part, we have emphasized links between evolutionary and ecological *change*. However, contemporary evolution might be even more important in shaping a lack of change (i.e. stability) in ecological processes [115,117]. As a result, human-induced evolution, as well as its ecological and societal consequences, could be often 'cryptic' [118]. At present, reliable methods for inferring these cryptic dynamics in nature are lacking, despite their likely prevalence and importance [118]. Increasing attention should be directed toward this difficult but critical enterprise. We have also tended to emphasize particular simple chains of causal interactions, such as from a particular human activity to the evolution of a particular species to a particular ecological response to a particular societal

consequence. However, many other interactions likely influence each particular link in any instance, and we therefore need to move beyond these ‘focal species’ approaches.

From our increasing knowledge of how humans influence evolution comes the opportunity, perhaps even the responsibility, for humans to do something about it and, indeed, we already are in a number of arenas. Assisted gene flow is used to facilitate genetic rescue of endangered populations [119,120] and assisted evolution is employed in some conservation efforts [121]. Size limits in fisheries are altered to reduce size selectivity [122]. Refuges of non-*Bt* crops are used to reduce the evolution of resistance by pests to *Bt* crops [123,124]. Mosquitoes are engineered to be more resistant to infection by malaria or dengue [125], or are targeted later in life, because selection is weaker [126]. Multiple-target drug cocktails are developed to reduce the chance (or at least speed) of resistance evolution in HIV [1,127], bacterial infections [128] and cancer [129]. In short, evolutionary thinking is already having practical applications in biodiversity, human health, agriculture and natural resource management [2,112,130–132]. The future affords even greater

opportunities to influence evolution in informed, effective, restrained and safe directions [45,112].

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