

Broken barriers: Human-induced changes to gene flow and introgression in animals

An examination of the ways in which humans *increase* genetic exchange among populations and species and the consequences for biodiversity

Erika Crispo^{1)*†}, Jean-Sébastien Moore^{2)†}, Julie A. Lee-Yaw²⁾, Suzanne M. Gray³⁾ and Benjamin C. Haller³⁾

We identify two processes by which humans increase genetic exchange among groups of individuals: by affecting the distribution of groups and dispersal patterns across a landscape, and by affecting interbreeding among sympatric or parapatric groups. Each of these processes might then have two different effects on biodiversity: changes in the number of taxa through merging or splitting of groups, and the extinction/extirpation of taxa through effects on fitness. We review the various ways in which humans are affecting genetic exchange, and highlight the difficulties in predicting the impacts on biodiversity. Gene flow and hybridization are crucially important evolutionary forces influencing biodiversity. Humans alter natural patterns of genetic exchange in myriad ways, and these anthropogenic effects are likely to influence the genetic integrity of populations and species. We argue that taking a *gene-centric* view towards conservation will help resolve issues pertaining to conservation and management.

Keywords:

■ biodiversity; climate change; dispersal; hybridization; reproductive isolation

Introduction

Biodiversity loss is occurring at a rapid rate due to anthropogenic changes to the natural environment [1, 2]. The impacts of human activities are seen at all levels of biodiversity, from the drastic modification of ecosystems to the extinction of species and the loss of genetic diversity. Mitigation of the biodiversity crisis requires not only identification of these losses, but also an understanding of the processes underlying the links between human activities and their consequences.

In this review, we examine the links between human activities and changes to patterns of gene flow and introgression among wild animal populations and species. Humans have the potential to alter natural patterns of these genetic exchanges in two main ways. First, genetic exchange between groups of individuals requires that their breeding ranges overlap. Human alterations of the physical landscape and species' distributions can thus affect gene flow and introgression by influencing the degree of contact between groups of individuals. Second, genetic exchange relies on successful breeding among groups of individuals. Thus, humans can also alter rates of gene flow and introgression through any activity that affects the integrity of reproductive barriers. Focusing on how human activities modify geographic distributions and reproductive barriers is necessary to understand how such activities

DOI 10.1002/bies.201000154

¹⁾ University of Calgary, Department of Biological Sciences, Calgary, Alberta, Canada

²⁾ University of British Columbia, Department of Zoology, Vancouver, British Columbia, Canada

³⁾ McGill University, Department of Biology, Montreal, Quebec, Canada

[†] Contributed equally to the work and should both be considered first authors.

*Corresponding author:

Erika Crispo
E-mail: erika.crispo@mail.mcgill.ca

disrupt both the fitness and the genetic integrity of populations and species.

Several reviews have touched upon the large body of literature documenting decreases in population connectivity as a consequence of anthropogenic habitat fragmentation or alteration [3–5]. The implications of such fragmentation for biodiversity are usually negative because population isolation leads to a loss of genetic diversity and an increased likelihood of extinction [6, 7]. Also of interest, however, are the cases in which human activities *increase* genetic exchange between populations (gene flow; Box 1) and distinct taxa (introgression; Box 1). Thus, while acknowledging the many studies that document decreased gene flow due to human activities, we dedicate most of this review to a discussion of human activities that may *increase* gene flow and only briefly mention situations in which genetic exchange is reduced. The first section of this review discusses various ways in which human activities increase genetic exchange among populations and species either through increased contact between formerly allopatric/parapatric taxa or by contributing to the breakdown of reproductive barriers. In the second section, we discuss the potential implications of increased genetic exchange for biodiversity (Fig. 1). In the third section, we outline ways in which future studies can make use of genetic tools to advance our understanding of human impacts on gene flow and introgression.

How human activities can lead to increased genetic exchange in animals

Bringing previously isolated groups into contact

In order for genetic exchange to occur among groups of spatially separated individuals, dispersal (Box 1) must first

occur. It follows that anything that influences the movement of individuals or gametes among breeding sites has the potential to impact genetic exchange. Several human activities, highlighted below, have directly or indirectly altered patterns of contact between populations within and among species.

Habitat alteration

Some of the biggest impacts of humans on natural patterns of population connectivity stem from alterations to the physical landscape. Dispersal, upon which gene flow depends, is greatly influenced by the landscape, and thus alterations to the landscape can drastically affect levels of gene flow among populations. For instance, it is well established that the geographical (Euclidean) distance between suitable habitat patches affects the number of individuals moving between them [8]. Specifically, populations in habitat patches that are close together (relative to the dispersal capabilities of a focal species) exchange more individuals than populations in habitat patches that are further apart. The conversion of habitat for human use alters the average physical distance among populations [9]. The consequences of such changes for gene flow are often species specific [10, 11]. For example, while the conversion of forest to agricultural fields eliminates populations and increases the average distance between populations for forest species, such conversion adds habitat and potentially allows for the establishment of new populations for species that are human commensals or that thrive in open field habitats [12, 13]. Therefore, human modification of landscapes can contribute to colonization and thus increased potential for gene flow for some species [14].

In addition to the physical arrangement of habitats, the extent to which populations exchange individuals depends on a number of species-specific responses to the landscape.

Box 1

Glossary

Adaptive genetic divergence: Genetic differences among populations occupying different environments or niches, and entailing a fitness advantage to individuals in their native environment or niche (see Box 3).

Biodiversity: Used here to refer to diversity in species and genes in nature.

Dispersal: The movement of individuals, seeds, or gametes among geographically separated populations.

Gene flow: The movement of alleles (genetic exchange) among populations as the result of successful mating between individuals from different populations.

Genomic extinction: The loss of unique combinations of genes or alleles characteristic of groups of individuals (i.e. species or populations).

Hybridization: Reproduction involving two individuals of different species.

Introgression: Genetic exchange that occurs between species (rather than between populations of a single

species). Introgression occurs when hybridization leads to the creation of fertile offspring, which can then back-cross with one or both parental species.

Invasion: The establishment of introduced individuals in a new geographic locality, usually with negative consequences for native taxa.

Migration load: The reduction in mean fitness of a population due to the introduction of maladaptive alleles through gene flow from other populations.

Migrational meltdown: The reduction in size or growth rate, potentially leading to extirpation, of a population experiencing migration load.

Population: Used here to refer to groups of individuals having at least partially divergent gene pools, whether in allopatry, parapatry, or sympatry.

Reproductive isolation: Barriers to mating and genetic exchange among groups of individuals.

Transgressive segregation: The production, in hybrids, of phenotypes that are extreme relative to the range of phenotypes observed in either parental group.

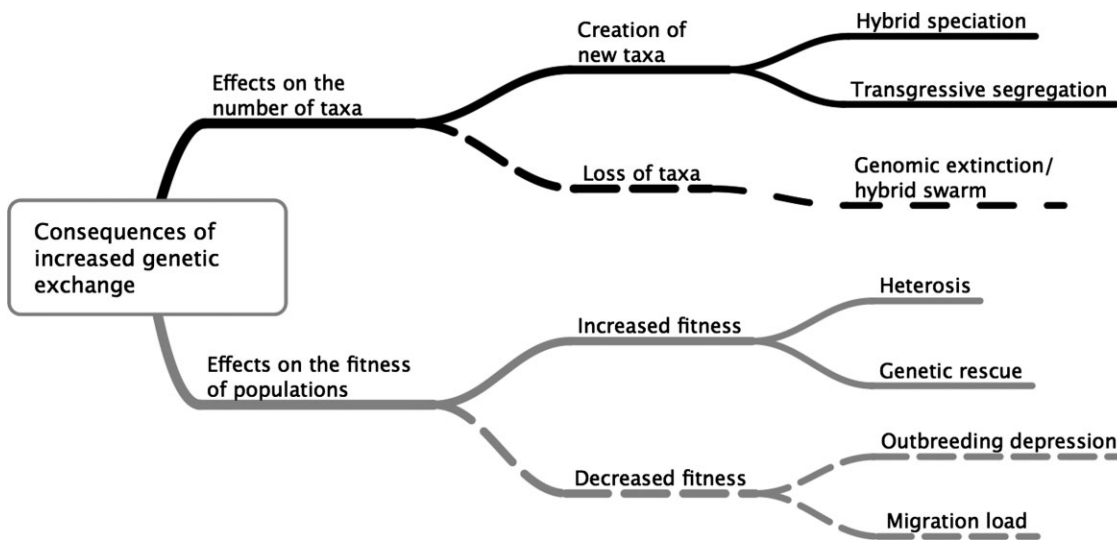


Figure 1. Flow diagram summarizing the potential consequences of increased genetic exchange. The black underlines examples in which gene flow affects the number of taxa, and the grey underlines examples in which gene flow affects the fitness of populations. Dotted lines show cases in which gene flow has negative consequences for biodiversity, while the continuous lines show cases in which gene flow has positive consequences for biodiversity.

Dispersal is influenced by the behaviour of individuals [15, 16], the dispersal capabilities of species [17, 18], and the probability of survival [19] in different habitats [20, 21]. Responses are readily observed when habitats are modified. Roads, for example, serve as a strong barrier to gene flow for many species that are either sensitive to gaps [22] or that suffer high mortality during road-crossing attempts [5]. However, the disturbed habitat associated with roads can provide resources and serve as corridors for some species, potentially increasing the rate of encounter between groups of individuals that would otherwise not be connected. For instance, roadside ditches are thought to provide ideal landing sites for fertilized female western harvest ants following the nuptial flight [23]. Similarly, invasive cane toads in Australia use roads as corridors [24, 25], possibly because of the decreased physical resistance to movement offered by these structurally simple surfaces [24]. In both cases, the role of roads in promoting range expansion has been highlighted, but it is not difficult to envision how roads may similarly increase contact between discrete populations.

Ultimately, then, while landscape change is expected to lead to greater population isolation for most species, some species may actually experience increased gene flow between populations as a result of human modifications of the landscape. These species are generally expected to be those that have close associations with humans or that thrive in disturbed habitats [26]. To anticipate the downstream consequences of increased gene flow in such species, it is necessary to consider the impact of these species on ecosystems, and the interaction between this impact and the level of gene flow. For instance, in the case of an invasive

species which thrives in disturbed areas, if increased gene flow eventually leads to improved population fitness (see “Consequences of increasing genetic exchange” below), human-augmented gene flow may increase the invasiveness of the species.

Climate change

In addition to direct modification of the landscape, many human activities have indirect impacts on species’ distributions. Of particular concern is the response of biodiversity to climate change. While climate change may cause a myriad of ecological and evolutionary responses, we focus on the shifting of ranges to track changing temperatures [27].

Species’ ranges may shift as a consequence of dispersers having increased establishment success in previously unsuitable habitats as climatic conditions change. In other cases, individuals may actively seek out environmental conditions to which they are adapted (e.g. *habitat matching* [15, 28]). In addition to natural range changes, the potential extinction of less mobile taxa has led some managers to propose the translocation of individuals of threatened taxa to new locations where environmental conditions are expected to be more suitable for survival (i.e. *assisted colonisation* or *managed relocation* [29, 30]). Whether taxa move to new areas on their own or are intentionally introduced through assisted migration, range changes as a result of climate change fundamentally result in the introduction of species into places where they were previously absent [31].

Both latitudinal and altitudinal shifts in species’ ranges are expected under climate change models [27, 32, 33]. One of the potential outcomes of taxa reshuffling may be contact between formerly allopatric species, creating the potential for hybridization (Box 1). A contemporary example of hybridization following range expansion is that of grizzly (*Ursus arctos*) and polar bears (*Ursus maritimus*) [34]. At least two cases of hybridization between grizzly and polar bears have been documented following the northward expansion of the grizzly bear’s range [34, 35]. Similarly, range shifts in two species of flying squirrels (*Glaucomys sabrinus* and *Glaucomys volans*) as

a result of climate change have increased the amount of overlap between these two species, and genetic analysis has confirmed that hybridization occurs between these species [36].

While it is difficult to predict the outcome of new species interactions, it seems intuitive that genetic exchange among closely related lineages could be common. Examining the outcome of contact between lineages that colonised previously glaciated areas supports this prediction. For example, species of hare (*Lepus* spp.) experienced periods of range expansion and contraction in the Iberian Peninsula and Eurasia during the Pleistocene as temperatures alternately warmed and cooled. Three species currently from Iberia were found to have mitochondrial haplotypes characteristic of a fourth hare species (*Lepus timidus*) that is currently restricted to boreal and Arctic regions [37]. Genetic data thus indicate that the ranges of these species at one time overlapped, leading to gene introgression. Given these results, and given that climate change is currently occurring at a faster rate than has been documented historically, anthropogenic climate change may have important consequences for the genetic integrity of populations and species.

Direct introductions

Humans additionally alter contact among taxa through the direct movement of individuals between locations. Both accidental and intentional introductions have been demonstrated

to have a variety of evolutionary impacts on native taxa [38–41], one of which is invasion-mediated hybridization leading to genetic exchange between native and introduced taxa [42, 43].

Invasion-mediated hybridization between native and introduced species has been widely studied [42]. Examples in animals come from a variety of taxa: insects [44], crustaceans [45], fish [46, 47], amphibians [48], birds [49, 50], and mammals [51, 52]. Invasions can be a particularly potent force increasing genetic exchange between closely related, but formerly *allopatric*, taxa in particular. Formerly allopatric taxa may lack pre-zygotic barriers to reproduction because reinforcement would not have had the opportunity to evolve (Box 2).

While introductions are an important cause of increased gene exchange, increased genetic exchange can in turn contribute to the fitness of the introduced taxa [53]. For example, the introduced barred tiger salamander (*Ambystoma mavortium*) readily hybridizes with the native California tiger salamander (*Ambystoma californiense*), and individuals of mixed ancestry exhibit increased fitness, likely contributing to the success of the invasion [48].

Invasions are generally thought to be the movement of a non-native species into a new region. However, humans also introduce individuals from populations with non-native genotypes into local populations within species. Human-mediated introductions of non-native genotypes, sometimes referred to as *cryptic invasions* [54, 55], could be common but have received little attention. The majority of examples

Box 2

Are formerly allopatric taxa at increased risk of hybridization?

Reinforcement is a process by which pre-zygotic barriers to reproduction evolve as a consequence of selection against maladaptive interspecific matings when ranges overlap. Because natural selection does not have the opportunity to select against such matings when taxa are allopatric, the theory of reinforcement predicts that the strength of pre-zygotic isolation will be greater in sympatry than in allopatry. While support for this idea has waxed and waned over the years [61], a large body of theory and a number of empirical studies now suggests that reinforcement is a fairly common process [107].

Many of the human activities described here put formerly allopatric taxa in contact. If reinforcement is a common evolutionary process, we would expect those taxa to be at increased risk of hybridization compared to taxa that are naturally sympatric. One possible example is the case of hybridization between the native westslope cutthroat trout (*Oncorhynchus clarki lewisi*, WCT) and introduced rainbow trout (*O. mykiss*, RBT) [108]. In many areas where RBT were artificially introduced, populations of WCT are threatened with genomic extinction through introgressive hybridization with RBT. However, in the few areas where WCT and RBT are naturally sympatric, the two

species appear to segregate spatially and temporally, thus limiting interspecific matings. Furthermore, an additional sub-species of cutthroat trout (coastal cutthroat trout; *O. clarki clarki*) is naturally sympatric with RBT throughout most of its range, and the two species appear to coexist with limited hybridization (see [108] for references). Evidence of selection against hybrids in areas of natural sympatry between CCT and RBT exists and provides one of the necessary conditions for reinforcement [61], although whether existing pre-zygotic isolation reflects reinforcement requires further investigation.

Mechanisms other than reinforcement are expected to lead to patterns where reproductive isolation is stronger in sympatry than in allopatry (for example, isolation can be a simple by-product of ecological character displacement). Testing for a role of reinforcement in cases such as the trout example would seem useful to gain a better understanding of the mechanisms that promote human-induced hybridization. Such tests typically involve mate preference trials. Reinforcement theory predicts that populations of females that evolve in sympatry with heterospecific males will show more discrimination than populations of females that evolve in allopatry. Further, males should discriminate less than females because the fitness costs associated with mating with the wrong species is higher for females [61]. Such differences in behaviour between sexes are not expected if stronger pre-zygotic isolation in sympatry was a by-product of ecological character displacement.

come from the plant literature (e.g. [55, 56]), but a few examples have been documented in animals. An example of a cryptic invasion is that of the ascidian (*Clavelina lepadiformis*), which occurred when ship hull transport resulted in the introduction of individuals from the Atlantic clade into the range of the well-differentiated Mediterranean clade [57].

Another threat to the genomic integrity of native species comes from interbreeding with domesticated taxa that have been artificially selected to perform in environmental conditions that are different from those faced by their wild relatives [58]. Interbreeding between native and domesticated taxa is common, with high-profile examples from domesticated birds and mammals [59], as well as cases of domesticated salmonids escaping from fish farms and interbreeding with declining wild stocks [58, 60]. While the process of interbreeding between native and domestic taxa shares many features with introgression from invasive taxa (e.g. introduction of locally maladaptive alleles), some features of domesticated taxa can make such introgression particularly detrimental. For instance, the often extremely low genetic diversity of domestic populations could lead to a reduction in the genetic diversity of wild populations. Artificial selection in domestic animals also selects for traits that may be malad-

aptive in the wild or only adaptive in human-modified environments. Genetic exchange with domestic animals may thus lead to outbreeding depression or reduced local adaptation in the wild (Box 3).

Disrupting reproductive barriers

Barriers to reproduction prevent interbreeding among groups of individuals whose ranges overlap. Several types of isolating barriers are involved in the evolution and maintenance of biodiversity [61]. We review two barriers that are influenced by human activities. First, behavioural, pre-mating isolating barriers can be affected by changes in the sensory environment that influence mate recognition or preference. Second, ecologically dependent post-zygotic isolating barriers can be affected by changes in the selective environment that influence the fitness of hybrids.

Changing the sensory environment

In animals, the sensory *scene* is the environmental interface for communication amongst individuals [62]. The sensory scene is therefore crucial in the finding and choosing of mates. The sensory environment experienced by organisms can be altered by humans in many ways. For example, urban and underwater noise masks auditory signals [63–66], pollutants in the air and water alter transmission (and potentially reception) of chemical signals [67], electrical noise (e.g. from hydroelectric dams or power lines) might inhibit electrosensory communication [68], and turbidity alters the intensity and colour of light underwater, interfering with visual signals [69, 70]. Such alteration of the sensory environment can cause increased genetic exchange among taxa that have not built up other forms of reproductive isolation (Box 1), resulting in a loss of biodiversity.

A now classic example of habitat degradation leading to the loss of biodiversity through hybridization is the *reverse speciation* of Lake Victoria (East Africa) haplochromine cichlid fishes through a breakdown of pre-mating isolating barriers [71, 72]. Reproductive isolation between sympatric cichlid species in Lake Victoria is driven by mate choice based largely on male nuptial colouration. Lake Victoria has suffered drastic environmental changes over the last 100 years [73], leading to increased eutrophication and turbidity that has decreased and altered the spectrum of available light underwater [70, 74]. Laboratory experiments showed that females prefer conspecifics over heterospecifics under broad spectrum illumination, but that preference is lost when the illumination is manipulated to mimic the effects of turbidity [71].

On the other hand, if animals respond to degradation of the sensory environment by altering their signals (changing amplitude or spectrum, or using a different sensory modality), it could lead to a *reduction* in genetic exchange between populations in disturbed versus undisturbed environments. For example, urban environments are noisy, especially in the low-frequency end of the sound spectrum, which is the preferred frequency range of many bird species [75]. In response, some bird species have altered the frequency and pitch of their songs in order to be heard above the urban cacophony (e.g. Great Tits, *Parus major* [75]; European Blackbirds, *Turdus*

Box 3

Interactions between gene flow and adaptation

Gene flow is the movement of genes between populations (Box 1) [109, 110]. If populations are geographically separated, gene flow first requires the dispersal of individuals, seeds, or gametes between the populations. If populations are not separated, such dispersal is not necessary. In either geographical scenario, gene flow is here defined as occurring if mating takes place between individuals of the two populations and if the hybrid offspring successfully backcross into a parental population, although some definitions do not require these steps [111].

The term “adaptive genetic divergence” refers to genetic differences between populations that arise from differential selective pressures between environments [112] or disruptive selection within a single environment [89]. Gene flow is often seen as opposing this process of adaptation, since it introduces alleles suitable to opposing environmental conditions (e.g. maladaptive to the environment in question) into a population [81]. However, gene flow can also promote adaptive divergence in some cases (see “Consequences of increasing genetic exchange”) and so its net effect may depend upon many factors [88, 110]. There is some evidence that gene flow may be less important in constraining adaptive divergence than is often supposed [113], perhaps because gene flow may be more limited than expected in many situations and may thus often be overridden by the selective regime [114].

merula [76]). Individuals with altered songs may no longer be recognized as potential mates by individuals outside of urban areas where songs remain unchanged, possibly leading to the genetic isolation of urban birds, although this remains to be tested explicitly.

Whether sensory scene degradation increases or decreases genetic exchange might be a matter of scale (e.g. within vs. between habitats, respectively). For example, if habitat degradation homogenizes an environment [72], or reduces the spectrum of available signalling space within an environment [68], we might expect a weakening of mate preferences and a breakdown of reproductive isolating barriers within the degraded habitat. At larger scales, however, between-habitat variation may lead to reduced gene flow. Most studied cases of sensory scene alteration have focused on within-habitat degradation and thus support the former effect [68]. However, as for any situation where gene flow is reduced, the latter scenario may also represent an important challenge for some populations and species. In both cases, the consequences for biodiversity remain unclear and future studies are needed to examine the fate of hybrids when sensory scene alteration leads to the breakdown of barriers, and of populations when it leads to the isolation of groups of individuals.

Altering patterns of natural selection

Divergent populations or species have often evolved to fill different ecological niches. In many cases, hybrid individuals exhibit intermediate phenotypes and suffer reduced fitness relative to parental types, thus contributing to the maintenance of distinct taxa. However, the alteration of habitats may change the niche space, thereby influencing reproductive isolation through altered selection against hybrids (a type of post-zygotic isolation).

Studies on the effects of human activities on post-zygotic isolating mechanisms are scarce. While several studies document the collapse of incipient species, these usually concern a breakdown in pre-mating barriers (see above). A potential example of human activities reducing post-zygotic isolation comes from Darwin's finches on the Galápagos Islands. Beak size bimodality occurs in many populations of the Medium Ground Finch (*Geospiza fortis*), with larger-beaked individuals adapted for feeding on harder seeds and smaller-beaked individuals adapted for feeding on softer seeds [77]. In a population located near a large human settlement, however, bimodality has decreased over time [78]. A possible reason for the observed loss of beak size bimodality is human-augmented food availability for the birds, such that all individuals are able to easily acquire food regardless of beak size. This change in the distribution of resources eliminates selection against individuals with intermediate beak phenotypes and thus may be contributing to the breakdown of post-zygotic isolation between large and small beaked birds in this area [78]. This example supports theoretical models highlighting the ease with which post-zygotic barriers can be interrupted [72], and demonstrates how anthropogenic alterations of genetic exchange can contribute to the loss of taxa or at least of phenotypic diversity.

Consequences of increasing genetic exchange for biodiversity

The potential impacts of human activities on gene flow and introgression are varied. The great majority of the literature focuses on situations in which genetic exchange between groups is reduced. In the present review, we have highlighted the flip side of the coin: the potential for human activities to increase gene flow. The consequences of this side of the story for biodiversity are difficult to predict. We identify two ways in which human-induced increases in genetic exchange can have direct consequences on biodiversity. First, increased rates of genetic exchange can impact the fitness of populations and species and can therefore influence their persistence. Second, as alluded to above, increased genetic exchange can result in the loss or creation of entire taxa (Fig. 1).

Population fitness can be affected negatively and positively by gene flow. *Negative* effects occur when gene flow between locally adapted populations results in decreased adaptation due to the introduction of locally maladaptive alleles and the swamping out of locally beneficial alleles, a consequence referred to as migration load [79] (Box 1, Box 3, Fig. 1). Theory suggests that if the migration load on a population is strong enough, the reduction in fitness can lead to reduced population growth and eventually to the extirpation of the population, a process referred to as migrational meltdown [80] (Box 1). Gene flow between locally adapted populations can also lead to outbreeding depression when adaptive combinations of alleles (i.e. co-adapted gene complexes) get broken down [81] or when genetically incompatible alleles are recombined into the same genome [82]. The last two effects may be particularly difficult to detect because they often are only expressed after the second (or subsequent) generation of interbreeding after the two parental genomes recombine [82].

Positive effects of gene flow on population fitness can include the rescue of small populations from the loss of genetic diversity due to drift [83, 84] and from the perils of inbreeding [85, 86] (Fig. 1). Gene flow also allows the exchange of beneficial mutations among gene pools [87]. These effects promote biodiversity by preventing extinction and increasing genetic variation upon which natural selection, and thus the response to environmental change, is dependent. Such positive effects are expected when gene flow between populations is moderate [88]. However, the effects of gene flow on fitness are poorly understood, and the relative importance of positive and negative effects in nature remains an open question [88, 89].

In addition to affecting population fitness, gene flow or introgression between species can lead to the extinction or creation of entire species. A common outcome of hybridization is the creation of hybrid swarms in which unique combinations of alleles in the parental genomes are lost as genomes get mixed, an outcome called *genomic extinction* [90] (Box 1, Fig. 1). The creation of hybrid swarms is facilitated when there are no mating barriers in place and no selection against hybrids. The many examples of genomic extinctions following hybridization with invasive species serve as an example of this process [42] as does the classic case of the Lake Victoria cichlids discussed above.

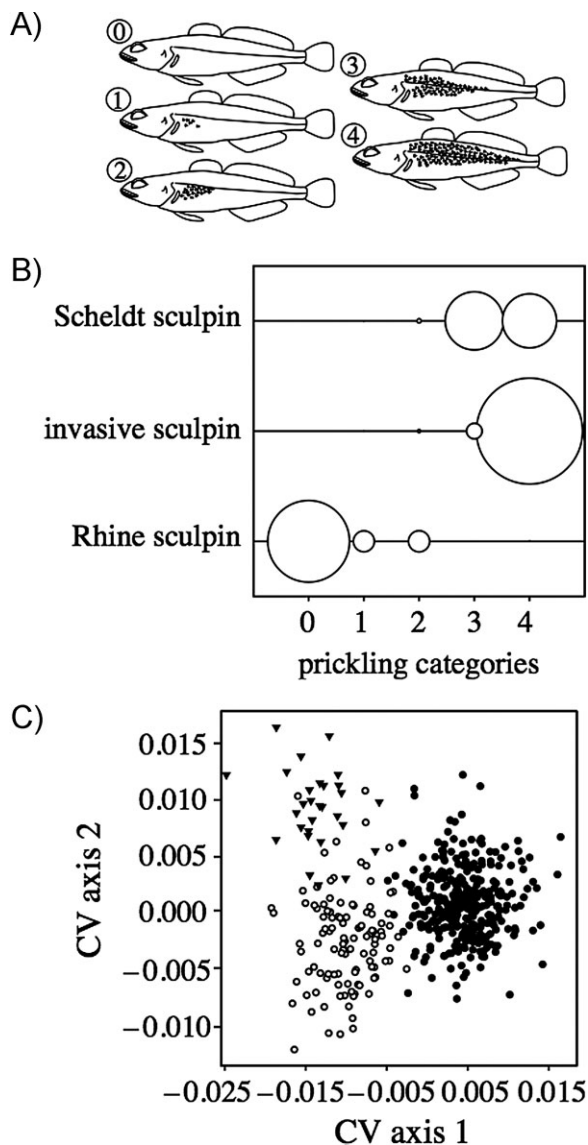


Figure 2. An example of transgressive segregation leading to increased invasiveness. The Scheldt and the Rhine sculpins are two lineages of *Cottus gobio* that have been isolated for up to 1 Myr. Hybridization, potentially anthropogenic, between the two lineages has led to the creation of a new hybrid taxon that was subsequently able to colonize stretches of the Rhine River previously free of sculpins. **A:** The five prickling categories used to determine the phenotype of sculpins. **B:** Bubble plots showing the frequency of the five prickling categories among the two parental groups and the hybrid taxa. Note that hybrid sculpins tend to have more prickles than either of the parental taxa. **C:** Results of a canonical variates analysis (CVA) of sculpin body shape using geometric morphometric methods. The hybrid sculpins (open circles) exhibit morphology that is distinct from, rather than intermediate to, the two parental lineages (black triangles = Scheldt sculpins; filled circles = Rhine sculpins). Modified from [115] and reprinted with permission of the Royal Society.

As alluded to earlier, human-mediated hybridization can also lead to the generation of new hybrid taxa [91]. Such taxa may be reproductively isolated from the parental species, or may interbreed freely but be maintained by natural selection.

Indeed, hybrids may contain beneficial combinations of alleles previously isolated in the parental genomes [87, 92], making them better suited to occupy the geographic range of one or both parental species. Alternatively, hybrid taxa can fill niches that were not previously used by the native genotypes (e.g. the *bounded-hybrid superiority model* [93]). For instance, hybridization can result in transgressive segregation [94, 95], the creation of extreme phenotypes outside the phenotypic limits observed in both parental species (Box 1, Fig. 1). Such extreme phenotypes may be able to colonize areas previously unoccupied by either parental species. For instance, the sculpin *Cottus gobio* was absent from the lower reaches of the Rhine River until approximately 20 years ago. Sculpins have recently expanded their range into this previously sculpin-free habitat, and the sculpins inhabiting those new habitats have been shown to be hybrids between two isolated ancestral lineages. This population expansion is thought to have been facilitated by transgressive segregation, in which the hybrids have increased numbers of spine-like scales on their body and a body shape outside the phenotypic limits of either parental species (Fig. 2).

Hybrid swarms leading to genomic extinctions are likely to be a more common outcome of human-induced hybridization than hybrid speciation. As transgressive segregation and hybrid fitness occur under relatively few genetic and environmental conditions, only a fraction of hybridization events will lead to the creation of distinct hybrid taxa that are reproductively isolated from the parental taxa [96]. In contrast, all hybridization events that generate fertile hybrids have the potential to create hybrid swarms (unless there is strong selection against those hybrids) and thus it is easier for hybridization to result in the formation of hybrid swarms than to result in the generation of hybrid species.

Genetic tools for conservation: Future directions

Thus far, we have reviewed several ways in which human activities alter natural patterns of gene flow and introgression and the consequences these alterations could have on biodiversity. In this section, we highlight new genetic methods that allow investigation of the processes underlying some of these consequences.

First, genetic markers can help us understand the extent to which different types of habitat impede or facilitate gene flow and how human activities disrupt natural patterns of population connectivity. The burgeoning field of landscape genetics [3, 97, 98], and associated methodologies, represents one of the most promising developments towards this goal. Investigators in this field combine molecular markers and geographical information systems (GIS) data to test hypotheses regarding the relationship between gene flow and landscape heterogeneity. Such tests have the potential to reveal important factors that govern the effects of habitat change on population connectivity. One example describes population connectivity in response to natural fire disturbance and anthropogenic tree harvesting in the Rocky Mountain tailed frog (*Ascaphus montanus*). Despite the similarities between natural and anthropogenic disturbance (i.e. the removal of

trees), frogs were able to maintain high levels of population connectivity across previously burned areas [99], whereas timber harvesting restricted gene flow to stream corridors [99]. The authors attributed this difference to variation in the availability of woody debris, which facilitates amphibian dispersal and is often removed under current timber harvesting practices. The study thus highlights how genetic tools, combined with other data, can suggest changes to existing practices that might mitigate some impacts of human activities.

Second, genetic studies can reveal the extent of progress towards genomic extinction in cases when human activities lead to introgression between taxa. The conservation value of hybrid taxa is a contentious topic; when at-risk species hybridize with non-endangered species, it is unclear how much admixture should be tolerated before considering the resulting hybrids unworthy of conservation efforts [100]. We echo the call of Petit [54] in proposing a shift toward a more gene-centric approach to the study of human-mediated introgression.

Currently, homogeneity at a few neutral molecular markers is used as a criterion to determine whether genomic extinction has occurred [100]. However, neutral markers are expected to flow freely between hybridizing taxa, unless they are closely linked to selected alleles [101, 102]. In contrast, areas of the genome under divergent selection may remain differentiated, such that populations currently deemed hybrid swarms may in fact maintain critical adaptive differences. The current use of molecular markers to designate taxa does not recognize the potential for hybrid individuals to be repositories of these valuable differences.

A gene-centric approach, in contrast, would make use of genome scans and related methods to survey the genome with hundreds of markers [103]. In this way, regions of the genome under selection between habitats can be identified (Fig. 3). The number, size, or ecological importance of the alleles harboured in such regions of elevated divergence would constitute a better criterion for determining the appropriate conservation status of an introgressed population than homogeneity at a few neutral markers. Genome scans are now commonly performed in non-model organisms and evidence suggests that natural selection does maintain some islands of genomic divergence in naturally occurring hybrids [90]. More research is needed to explore whether similar genomic signatures persist in the case of human-induced hybridization events.

Another interesting question that can be answered using a more gene-centric approach to human-mediated genetic exchange regards the direction of genetic transfer between native and invading taxa. It has been suggested that genes under selection are more likely to move from the native species to the invading species [104], a tendency that has been called *inheritance from the rare species* [105]. A review of empirical studies identified introgression from the native to the invading genome in 82% of examined cases, and genomic extinction was common [106]. If this tendency is indeed as common as that evidence suggests, native species may maintain their genomic integrity in the face of hybridization more often than currently believed. Regardless, appraisal of the direction of genetic transfer may save scarce conservation resources in cases in which the native gene pool is not threatened (although this does not negate the other detrimental ecologi-

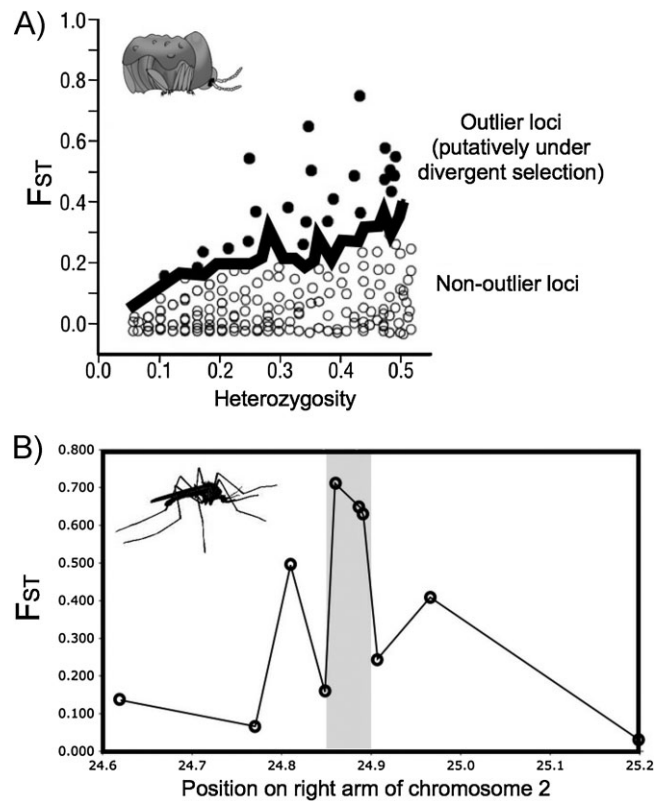


Figure 3. Two examples of genome scans. **A:** The use of amplified fragment length polymorphism to show heterogeneous genome differentiation between two ecotypes of the leaf beetle *Neochlamisus bebbianae* with different host plants (willow and maple). Gene flow causes homogeneity throughout most of the genome, but natural selection maintains significant amounts of differentiation at several loci. The black line shows the maximum level of genetic divergence expected under neutrality, determined using simulations. The loci that fall above this threshold are inferred to be under divergent selection. Modified from [116] and reprinted with permission from the Society for the Study of Evolution. The drawing of the beetle is courtesy of Christopher Brown. **B:** A fine-scale analysis of differentiation along a portion of the right arm of chromosome 2 for two incipient species of the mosquito *Anopheles gambiae*. In this case, the authors followed up on a previous genome scan study by sequencing loci that were identified as outliers [117]. Natural selection maintained differentiation in only a narrow portion of the genome (shown by the grey area). Modified from [117] and reprinted with permission from the Society of Molecular Biology and Evolution. The mosquito drawing is a royalty-free image from iStockphoto.

cal consequences of invaders, and that eradication may still be necessary even if introgression into native taxa appears unlikely). Taking a more gene-centric view of hybridization may thus help resolve current conservation and management dilemmas regarding the status of introgressed populations.

Conclusion

Human activities have a variety of demonstrated effects on natural patterns of genetic exchange between populations and species, including cases of increased genetic exchange.

Previous studies have clearly shown that increased genetic exchange can lead to genomic extinction through the formation of a hybrid swarm, or alternatively, that it can lead to the creation of new taxa through hybrid speciation. Examples of genomic extinction following anthropogenic hybridization appear more common than examples of hybrid speciation, and it could thus be concluded that genomic extinction is a more likely end result of hybridization (barring any publication bias). In comparison, there has been little empirical work regarding the effects of changes in fitness resulting from gene flow. We are still mostly unable to predict changes in fitness following a given increase or decrease in genetic exchange, and we are even further from an empirical understanding of how such a change in fitness would influence population persistence. It is our opinion that such effects will tend to be species-specific and truly general predictability will remain elusive. Despite this, the field would greatly benefit from more empirical data from a variety of taxa, documenting the causal chain beginning with human alterations to the environment, through changes to the rate of gene flow and introgression, on to the resulting effects on hybridization and population fitness, and ending in outcomes such as genomic extinction, hybrid speciation, and changes to population persistence. This empirical work will be aided by the use of new molecular tools that will allow a much more in-depth understanding of the underlying processes affected by anthropogenic changes to gene flow.

Acknowledgments

E. Crispo was funded by a Postdoctoral Fellowship from the Natural Sciences and Engineering Research Council of Canada (NSERC). J.-S. Moore was funded by a Bourse de Doctorat en Recherche from the Fond Québécois de Recherche sur la Nature et les Technologies. J. Lee-Yaw was funded by an NSERC Canada Graduate Scholarship, The Pacific Century Graduate Scholarship, and a University of British Columbia 4-year fellowship for PhD students. S. Gray was funded by an NSERC Visiting Fellowship in a Government Lab. B. Haller was supported under a National Science Foundation Graduate Research Fellowship. We thank C. Blair, G. Conte, A. Hendry, A. Moore, M. Yau, and an anonymous reviewer for comments that greatly improved earlier versions of the manuscript.

References

- Vitousek PM, Mooney HA, Lubchenco J, Melillo JM. 1997. Human domination of Earth's ecosystems. *Science* **277**: 494–9.
- Thomas CD, Cameron A, Green RE, Bakkenes M, et al. 2004. Extinction risk from climate change. *Nature* **427**: 145–8.
- Storfer A, Murphy MA, Spear SF, Holderegger R, et al. 2010. Landscape genetics: where are we now? *Mol Ecol* **19**: 3496–514.
- Debinski DM, Holt RD. 2000. A survey and overview of habitat fragmentation experiments. *Conserv Biol* **14**: 342–55.
- Holderegger R, Di Giulio M. 2010. The genetic effects of roads: A review of empirical evidence. *Basic Appl Ecol* **11**: 522–31.
- Keyghobadi N. 2007. The genetic implications of habitat fragmentation for animals. *Can J Zool* **85**: 1049–64.
- Reed DH. 2004. Extinction risk in fragmented habitats. *Anim Conserv* **7**: 181–91.
- Wright S. 1931. Isolation by distance. *Genetics* **28**: 139–56.
- MacArthur RH, Wilson EO. 1967. *The theory of island biogeography*. Princeton, NJ: Princeton University Press.
- Darvill B, O'Connor S, Lye GC, Waters J, et al. 2010. Cryptic differences in dispersal lead to differential sensitivity to habitat fragmentation in two bumblebee species. *Mol Ecol* **19**: 53–63.
- Watanabe K, Monaghan MT, Takemon Y, Omura T. 2010. Dispersal ability determines the genetic effects of habitat fragmentation in three species of aquatic insect. *Aquat Conserv* **20**: 574–9.
- Suarez AV, Bolger DT, Case TJ. 1998. Effects of fragmentation and invasion on native ant communities in coastal southern California. *Ecology* **79**: 2041–56.
- Gobeil JF, Villard MA. 2002. Permeability of three boreal forest landscape types to bird movements as determined from experimental translocations. *Oikos* **98**: 447–58.
- Nève G, Barascud B, Descimon H, Baguette M. 2008. Gene flow rise with habitat fragmentation in the bog fritillary butterfly (Lepidoptera: Nymphalidae). *BMC Evol Biol* **8**: 84.
- Edelaar P, Siepielski AM, Clobert J. 2008. Matching habitat choice causes directed gene flow: A neglected dimension in evolution and ecology. *Evolution* **62**: 2462–72.
- Forschler MI, del Val E, Bairlein F. 2010. Extraordinary high natal philopatry in a migratory passerine. *J Ornithol* **151**: 745–8.
- Hellberg ME. 1996. Dependence of gene flow on geographic distance in two solitary corals with different larval dispersal capabilities. *Evolution* **50**: 1167–75.
- Hoehn M, Sarre SD, Henle K. 2007. The tales of two geckos: Does dispersal prevent extinction in recently fragmented populations? *Mol Ecol* **16**: 3299–312.
- Cosentino BJ, Schooley RL, Phillips CA. 2011. Connectivity of agroecosystems: dispersal costs can vary among crops. *Land Ecol* **26**: 371–9.
- Baguette M, Van Dyck H. 2007. Landscape connectivity and animal behavior: Functional grain as a key determinant for dispersal. *Land Ecol* **22**: 1117–29.
- Knowlton JL, Graham CH. 2010. Using behavioral landscape ecology to predict species' responses to land-use and climate change. *Biol Conserv* **143**: 1342–54.
- Tremblay MA, St Clair CC. 2009. Factors affecting the permeability of transportation and riparian corridors to the movements of songbirds in an urban landscape. *J Appl Ecol* **46**: 1314–22.
- DeMers MN. 1993. Roadside ditches as corridors for range expansion of the western harvester ant (*Pogonomyrmex occidentalis* Cresson). *Land Ecol* **8**: 93–102.
- Brown GP, Phillips BL, Webb JK, Shine R. 2006. Toad on the road: Use of roads as dispersal corridors by cane toads (*Bufo marinus*) at an invasion front in tropical Australia. *Biol Conserv* **133**: 88–94.
- Seabrook WA, Dettmann EB. 1996. Roads as activity corridors for cane toads in Australia. *J Wildl Manag* **60**: 363–8.
- Leu M, Hanser SE, Knick ST. 2008. The human footprint in the west: A large-scale analysis of anthropogenic impacts. *Ecol Appl* **18**: 1119–39.
- Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**: 37–42.
- Clobert J, Le Galliard JF, Cote J, Meylan S, et al. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol Lett* **12**: 197–209.
- Hoegh-Guldberg O, Hughes L, McIntyre S, Lindenmayer DB, et al. 2008. Assisted colonization and rapid climate change. *Science* **321**: 345–6.
- Richardson DM, Hellmann JJ, McLachlan JS, Sax DF, et al. 2009. Multidimensional evaluation of managed relocation. *Proc Natl Acad Sci USA* **106**: 9721–4.
- Ricciardi A, Simberloff D. 2009. Assisted colonization is not a viable conservation strategy. *Trends Ecol Evol* **24**: 248–53.
- Walther GR, Post E, Convey P, Menzel A, et al. 2002. Ecological responses to recent climate change. *Nature* **416**: 389–95.
- Parmesan C. 2006. Ecological and evolutionary responses to recent climate change. *Annu Rev Ecol Syst* **37**: 637–69.
- Doupé JP, England JH, Furze M, Paetkau D. 2007. Most northerly observation of a grizzly bear (*Ursus arctos*) in Canada: Photographic and DNA evidence from Melville Island, Northwest territories. *Arctic* **60**: 271–6.
- Kelly B, Whiteley A, Tallmon D. 2010. The Arctic melting pot. *Nature* **468**: 891.
- Garroway CJ, Bowman J, Cascaden TJ, Holloway GL, et al. 2010. Climate change induced hybridization in flying squirrels. *Global Change Biol* **16**: 113–21.

37. Melo-Ferreira J, Boursot P, Randi E, Kryukov A, et al. 2007. The rise and fall of the mountain hare (*Lepus timidus*) during Pleistocene glaciations: Expansion and retreat with hybridization in the Iberian Peninsula. *Mol Ecol* **16**: 605–18.
38. Vellend M, Harmon LJ, Lockwood JL, Mayfield MM, et al. 2007. Effects of exotic species on evolutionary diversification. *Trends Ecol Evol* **22**: 481–8.
39. Olden JD, LeRoy Poff N, Douglas MR, Douglas ME, et al. 2004. Ecological and evolutionary consequences of biotic homogenization. *Trends Ecol Evol* **19**: 18–24.
40. Mooney HA, Cleland EE. 2001. The evolutionary impact of invasive species. *Proc Natl Acad Sci USA* **98**: 5446–51.
41. Cox GW. 2004. *Alien Species and Evolution: The Evolutionary Ecology of Exotic Plants, Animals, Microbes, and Interacting Native Species*. Washington: Island Press.
42. Rhymer JM, Simberloff D. 1996. Extinction by hybridization and introgression. *Annu Rev Ecol Syst* **27**: 83–109.
43. Largiadèr CR. 2007. Hybridization and introgression between native and alien species. In: Nentwig W, ed. *Biological Invasions*. New York: Springer Publishing, p 275–292.
44. Schneider SS, Hoffman GD, Smith DR. 2004. The African honey bee: Factors contributing to a successful biological invasion. *Annu Rev Entomol* **49**: 351–76.
45. Perry WL, Feder JL, Lodge DM. 2001. Implications of hybridization between introduced and resident *Orconectes* crayfishes. *Conserv Biol* **15**: 1656–66.
46. Rubidge E, Corbett P, Taylor EB. 2001. A molecular analysis of hybridization between native westslope cutthroat trout and introduced rainbow trout in southeastern British Columbia, Canada. *J Fish Biol* **59**: 42–54.
47. Walters DM, Blum MJ, Rasleigh B, Freeman BJ, et al. 2008. Red shiner invasion and hybridization with blacktail shiner in the upper Coosa River, USA. *Biol Invas* **10**: 1229–42.
48. Fitzpatrick BM, Shaffer HB. 2007. Hybrid vigor between native and introduced salamanders raises new challenges for conservation. *Proc Natl Acad Sci USA* **104**: 15793–8.
49. Mank JE, Carlson JE, Brittingham MC. 2004. A century of hybridization: Decreasing genetic distance between American black ducks and mallards. *Conserv Genet* **5**: 395–403.
50. Kulikova IV, Zhuravlev YN, McCracken KG. 2004. Asymmetric hybridization and sex-biased gene flow between Eastern Spot-billed Ducks (*Anas zonorhyncha*) and Mallards (*A. platyrhynchos*) in the Russian Far East. *Auk* **121**: 930–49.
51. Abernethy K. 1994. The establishment of a hybrid zone between red and sika deer (genus *Cervus*). *Mol Ecol* **3**: 551–62.
52. Thulin CG, Tegelström H. 2002. Biased geographical distribution of mitochondrial DNA that passed the species barrier from mountain hares to brown hares (genus *Lepus*): An effect of genetic incompatibility and mating behaviour? *J Zool* **258**: 299–306.
53. Schierenbeck KA, Ellstrand NC. 2009. Hybridization and the evolution of invasiveness in plants and other organisms. *Biol Invas* **11**: 1093–105.
54. Petit RJ. 2004. Biological invasions at the gene level. *Divers Dist* **10**: 159–65.
55. Saltonstall K. 2002. Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. *Proc Natl Acad Sci USA* **99**: 2445–9.
56. Petit RJ, Bodénès C, Ducouso A, Roussel G, et al. 2004. Hybridization as a mechanism of invasion in oaks. *New Phytol* **161**: 151–64.
57. Turon X, Tarjuelo I, Duran S, Pascual M. 2003. Characterising invasion processes with genetic data: An Atlantic clade of *Clavelina lepadiformis* (Ascidiacea) introduced into Mediterranean harbours. *Hydrobiology* **503**: 29–35.
58. Hutchings JA, Fraser DJ. 2008. The nature of fisheries-and farming-induced evolution. *Mol Ecol* **17**: 294–313.
59. Randi E. 2008. Detecting hybridization between wild species and their domesticated relatives. *Mol Ecol* **17**: 285–93.
60. Hindar K, Ryman N, Utter F. 1991. Genetic effects of cultured fish on natural fish populations. *Can J Fish Aquat Sci* **48**: 945–57.
61. Coyne JA, Orr HA. 2004. *Speciation*. Sunderland, MA: Sinauer Associates.
62. Fay RR, Popper AN. 2000. Evolution of hearing in vertebrates: The inner ears and processing. *Hearing Res* **149**: 1–10.
63. Popper AN, Hastings MC. 2009. The effects of human-generated sound on fish. *Integr Zool* **4**: 43–52.
64. Slabbekoom H, Ripmeester EAP. 2008. Birdsong and anthropogenic noise: Implications and applications for conservation. *Mol Ecol* **17**: 72–83.
65. Slabbekoom H, Bouton N, van Opzeeland I, Coers A, et al. 2010. A noisy spring: The impact of globally rising underwater sound levels on fish. *Trends Ecol Evol* **25**: 419–27.
66. Laiolo P. 2010. The emerging significance of bioacoustics in animal species conservation. *Biol Conserv* **143**: 1635–45.
67. Smadja C, Butlin RK. 2009. On the scent of speciation: the chemosensory system and its role in premating isolation. *Heredity* **102**: 77–97.
68. van der Sluijs I, Gray S, Amorim M, Barber I, et al. 2011. Communication in troubled waters: The evolutionary implications of changing environments on fish communication systems. *Evol Ecol* **25**: 623–40.
69. Candolin U, Salesto T, Evers M. 2007. Changed environmental conditions weaken sexual selection in sticklebacks. *Evol Biol* **20**: 233–9.
70. Utne-Palm AC. 2002. Visual feeding of fish in a turbid environment: Physical and behavioural aspects. *Mar Fresh Behav Physiol* **35**: 111–28.
71. Seehausen O, van Alphen JJM, Witte F. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* **277**: 1808–11.
72. Seehausen O, Takimoto G, Roy D, Jokela J. 2008. Speciation reversal and biodiversity dynamics with hybridization in changing environments. *Mol Ecol* **17**: 30–44.
73. Hecky RE, Mugidde R, Ramlal PS, Talbot MR, et al. 2010. Multiple stressors cause rapid ecosystem change in Lake Victoria. *Fresh Biol* **55**: 19–42.
74. Lythgoe JN. 1979. *The ecology of vision*. Oxford, UK: Clarendon Press.
75. Slabbekoom H, Peet M. 2003. Birds sing at a higher pitch in urban noise: Great tits hit the high notes to ensure that their mating calls are heard above the city's din. *Nature* **424**: 267.
76. Ripmeester EAP, Mulder M, Slabbekoom H. 2010. Habitat-dependent acoustic divergence affects playback response in urban and forest populations of the European blackbird. *Behav Ecol* **21**: 876–83.
77. Herrel A, Podos J, Huber SK, Hendry AP. 2005. Bite performance and morphology in a population of Darwin's finches: Implications for the evolution of beak shape. *Funct Ecol* **19**: 43–8.
78. Hendry AP, Grant PR, Grant BR, Ford HA, et al. 2006. Possible human impacts on adaptive radiation: Beak size bimodality in Darwin's finches. *Proc R Soc B* **273**: 1887–94.
79. Bolnick DI, Nosil P. 2007. Natural selection in populations subject to a migration load. *Evolution* **61**: 2229–43.
80. Ronce O, Kirkpatrick M. 2001. When sources become sinks: Migrational meltdown in heterogeneous habitats. *Evolution* **55**: 1520–31.
81. Mayr E. 1963. *Animal Species and Evolution*. Cambridge, MA: Harvard University Press.
82. Edmands S. 2007. Between and rock and a hard place: Evaluating the relative risks of inbreeding and outbreeding for conservation and management. *Mol Ecol* **16**: 463–75.
83. Hogg JT, Forbes SH, Steele BM, Luikart G. 2006. Genetic rescue of an insular population of large mammals. *Proc R Soc B* **273**: 1491–9.
84. Tallmon DA, Luikart G, Waples RS. 2004. The alluring simplicity and complex reality of genetic rescue. *Trends Ecol Evol* **19**: 489–96.
85. Hedrick PW, Kalinowski ST. 2000. Inbreeding depression in conservation biology. *Annu Rev Ecol Syst* **31**: 139–62.
86. Ebert D, Haag C, Kirkpatrick M, Rieck M, et al. 2002. A selective advantage to immigrant genes in a *Daphnia* metapopulation. *Science* **295**: 485–8.
87. Holt RD, Gomulkiewicz R. 1997. How does immigration influence local adaptation? A reexamination of a familiar paradigm. *Am Nat* **149**: 563–72.
88. Garant D, Forde SE, Hendry AP. 2007. The multifarious effects of dispersal and gene flow on contemporary adaptation. *Funct Ecol* **21**: 434–43.
89. Dieckmann U, Doebeli M, Metz JAJ, Tautz D, eds. 2004. *Adaptive Speciation*. Cambridge, UK: Cambridge University Press.
90. Nosil P, Funk DJ, Ortiz-Barrientos D. 2009. Divergent selection and heterogeneous genomic divergence. *Mol Ecol* **18**: 375–402.
91. Mallet J. 2007. Hybrid speciation. *Nature* **446**: 279–83.
92. Arnold ML. 1997. *Natural Hybridization and Evolution*. Oxford, UK: Oxford University Press.
93. Moore WS. 1977. Evaluation of narrow hybrid zones in vertebrates. *Quart Rev Biol* **52**: 263–77.
94. Bell MA, Travis MP. 2005. Hybridization, transgressive segregation, genetic covariation, and adaptive radiation. *Trends Ecol Evol* **20**: 358–61.
95. Rieseberg LH, Archer MA, Wayne RK. 1999. Transgressive segregation, adaptation and speciation. *Heredity* **83**: 363–72.

96. **Bullini L.** 1994. Origin and evolution of animal hybrid species. *Trends Ecol Evol* **9**: 422–6.
97. **Manel S, Schwartz MK, Luikart G, Taberlet P.** 2003. Landscape genetics: Combining landscape ecology and population genetics. *Trends Ecol Evol* **18**: 189–97.
98. **Storfer A, Murphy MA, Evans JS, Goldberg CS, et al.** 2007. Putting the 'landscape' in landscape genetics. *Heredity* **98**: 128–42.
99. **Spear SF, Storfer A.** 2010. Anthropogenic and natural disturbance lead to differing patterns of gene flow in the Rocky Mountain tailed frog, *Ascaphus montanus*. *Biol Conserv* **143**: 778–86.
100. **Allendorf FW, Leary RF, Spruell P, Wenburg JK.** 2001. The problems with hybrids: setting conservation guidelines. *Trends Ecol Evol* **16**: 613–22.
101. **Wu C.** 2001. The genic view of the process of speciation. *J Evol Biol* **14**: 851–65.
102. **Gavrilets S, Vose A.** 2005. Dynamic patterns of adaptive radiation. *Proc Natl Acad Sci USA* **102**: 18040–5.
103. **Storz JF.** 2005. Using genome scans of DNA polymorphism to infer adaptive population divergence. *Mol Ecol* **14**: 671–88.
104. **Excoffier L, Foll M, Petit RJ.** 2009. Genetic consequences of range expansions. *Annu Rev Ecol Syst* **40**: 481–501.
105. **Costedoat C, Pech N, Chappaz R, Gilles A.** 2007. Novelty in hybrid zones: Crossroads between population genomic and ecological approaches. *PLOS One* **2**: E357.
106. **Currat M, Ruedi M, Petit RJ, Excoffier L.** 2008. The hidden side of invasions: Massive introgression by local genes. *Evolution* **62**: 1908–20.
107. **Servedio MR, Noor MAF.** 2003. The role of reinforcement in speciation: Theory and data. *Annu Rev Ecol Syst* **34**: 339–64.
108. **Rubidge EM, Taylor EB.** 2004. Hybrid zone structure and the potential role of selection in hybridizing populations of native westslope cutthroat trout (*Oncorhynchus clarki lewisi*) and introduced rainbow trout (*O. mykiss*). *Mol Ecol* **13**: 3735–49.
109. **Endler JA.** 1977. *Geographic Variation, Speciation, and Clines*. Princeton, NJ: Princeton University Press.
110. **Slatkin M.** 1987. Gene flow and the geographic structure of natural populations. *Science* **236**: 787–92.
111. **Mallet J.** 2001. Gene flow. In: Woiwod IP, Reynolds DR, Thomas CD, eds. *Insect Movement: Mechanisms and Consequences*. Wallingford, UK: CAB International. p 337–360.
112. **Schluter D.** 2001. Ecology and the origin of species. *Trends Ecol Evol* **16**: 372–80.
113. **Nosil P.** 2008. Speciation with gene flow could be common. *Mol Ecol* **17**: 2103–6.
114. **Ehrlich PR, Raven PH.** 1969. Differentiation of populations. *Science* **165**: 1228–32.
115. **Nolte AW, Freyhof J, Stemshorn KC, Tautz D.** 2005. An invasive lineage of sculpins, *Cottus* sp. (Pisces, Teleostei) in the Rhine with new habitat adaptations has originated from hybridization between old phylogeographic groups. *Proc R Soc B* **272**: 2379–87.
116. **Egan SP, Nosil P, Funk DJ.** 2008. Selection and genomic differentiation during ecological speciation: Isolating the contributions of host association via a comparative genome scan of *Neochlamisus bebbianae* leaf beetles. *Evolution* **62**: 1162–81.
117. **Turner TL, Hahn MW.** 2007. Locus- and population-specific selection and differentiation between incipient species of *Anopheles gambiae*. *Mol Biol Evol* **24**: 2132–8.