Hybridization due to changing species distributions: adding problems or solutions to conservation of biodiversity during global change?

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ABSTRACT

Background: Due to increasing global change, the rate of hybridization appears to be increasing.

Question: Is hybridization adding problems or solutions to the effects of global change on biodiversity?

Methods: We divided ourselves into two independent groups. Each group listed topics it thought appropriate. We then compared and combined the lists, extracting a natural structure of the topics. We next divided ourselves into three specialized subgroups and discussed the topics in more depth. In a final plenary meeting, we brought ideas together, discussed open topics, identified consensus or differences of opinion, and prepared a preliminary report.

Results: Our lists of topics were highly similar, suggesting that we missed only a few topics. We agreed that it is important to consider hybridization in both its genetic and ecological context and with explicit attention paid to phylogenetic and biogeographic history. It is also necessary to distinguish between underlying processes and resulting consequences. Knowledge of the consequences of hybridization is more developed in genetics than in ecology. We suggest that hybridization adds problems (loss of biodiversity, ecosystem degradation) as well as solutions (new adaptive variation, ecosystem robustness) to global change challenges. Which

of these applies in a given case depends on its evolutionary and environmental context, and on the objectives of conservation management. We provide five groups of questions to stimulate further research.

INTRODUCTION

A major goal in conservation is to maintain current biodiversity and the conditions and processes that support it. In a world that is rapidly changing due to human actions, this is an increasingly challenging task. Loss and alteration of habitats, climate change, eutrophication, and the introduction of exotic species are some of the greatest current anthropogenic threats to biodiversity. One relatively underappreciated way in which these factors can impact biodiversity, and the one that is the focus of this paper, is by hybridization.

Hybridization involves the combination of evolutionarily divergent gene pools (e.g. populations, ecotypes or species). While some view hybridization as a nuisance (Mayr, 1942), upsetting the natural order of things, it is in fact a natural process that may have been common in the evolutionary history of many organisms. Darwin (1859) had pointed to those intermediate forms as being relevant to the study of evolution, but it was not until the twentieth century that the role of interspecific hybridization in evolution became a topic of research (Anderson and Stebbins, 1954), and the suggestion was made that hybridization can make an important contribution to novel evolutionary trajectories (Lewontin and Birch, 1966). However, global change may be accelerating the rate and impact of hybridization in an unprecedented way, by changing species distributions and the fate of hybrids. For example, introduced exotic species may come into contact with closely related species with which they hybridize. Alteration of habitat may also cause 'hybridization of the environment' where ecologically segregated species come into greater contact, facilitating hybridization, and may create novel habitats in which hybrids thrive (Anderson, 1948; Anderson and Stebbins, 1954). There is great potential for ongoing hybridization between domestic species and wild progenitors or other related species, and for weedy hybridized relatives of crops to cause considerable agricultural losses and rapidly gain genes with useful traits such as herbicide resistance from their domestic relatives. And finally, climate change may cause changes in species distributions followed by novel contact and hybridization between previously isolated species.

Hybridization can affect biodiversity in many different ways, including the disappearance of one or both parental species, the introgression of beneficial adaptive genetic variation from one species to another, and the generation of novel hybrid species (Abbott *et al.*, 2013). Hence, hybridization can be seen to cause additional problems to the challenges for biodiversity conservation posed by global change, but also to provide partial solutions. The extent and consequences of hybridization will vary with the length of divergent evolutionary history between the hybridizing species and spatial factors, necessitating consideration of the phylogeographic relationships and levels of relatedness as part of the study of process and outcome of hybridization. Hybridization generates novel interactions from genetic through to ecosystem levels and triggers a range of interacting processes leading to multiple ecological and evolutionary outcomes. Therefore, it is important to understand the different

contexts in which hybridization occurs and impacts on biodiversity and, where possible and desired, to take appropriate actions to manage the resulting consequences at the individual, population, species, community, and ecosystem level.

Ecologists, evolutionary biologists, conservation biologists, and policy-makers should benefit from a broader understanding of how human impacts are changing the frequency, forms, and outcomes of hybridization and its ecological and evolutionary impacts in natural systems. The aim of this paper is to increase attention to and understanding of these issues, especially how global change impacts hybridization and its consequences on biodiversity generation and conservation. We also highlight how the evaluation of the conservation impacts of hybridization depends on who is doing the evaluation and the criteria being used.

We first introduce the processes involved in hybridization. We then look at the consequences that hybridization can have. Next, we discuss the effects that different viewpoints and objectives can have on our perception of hybridization and its importance, and end by listing a number of open research questions. We look at processes and consequences in three different contexts: a genetic one, one of space and time, and an ecological one. In this way, we attempt to convey the breadth, richness, and complexity surrounding hybridization, as well as the challenges that lie ahead in studying and understanding the importance of hybridization in response to global change.

PROCESSES INVOLVED IN HYBRIDIZATION

In its broadest sense, hybridization can be defined as reproductive interactions between individuals representing lineages that show some degree of evolutionary divergence. Within this broad definition, hybridization occurs at many different levels of divergence in terms of evolutionary time, phenotypic distinctiveness, and the genomic regions showing divergence. For example, two subspecies of *Antirrhinum* snapdragon flowers (*A. majus pseudomajus* and *A. m. striatum*) hybridize in the Pyrenees and show narrow hybrid zones for distinctive flower colours controlled by a few genes under selection, but are hardly differentiated across the rest of the genome (Whibley *et al.*, 2006). At the other extreme, some fish species that diverged up to 20 million years ago (mya) can still hybridize (Bolnick and Near, 2005). Below we examine: (1) genetic processes affecting the genomes of hybridizing populations; (2) the role that the amount of genomic divergence, evolutionary time (or time since hybridization), and geographical space have on determining which of these genetic processes will occur; and (3) the ecological effects of hybridization that can extend towards all directly or indirectly interacting populations and species.

Genetic context

Evaluating the effects of hybridization in a genetic context is fundamental because interactions between genomes of hybridizing taxa can make for a range of different outcomes. These are reviewed briefly in Box 1. Studies of local adaptation and hybridization include challenges of distinguishing neutral and adaptive genetic variation and finding evidence for fitness effects at both the individual and population level. Which of these genetic processes will occur depends on the extent of adaptive and overall genomic divergence between hybridizing taxa and the effects of time and space.

Box 1

Heterosis is the fitness gain frequently observed in hybrids as a result of increased heterozygosity after combining alleles from both parents, reversing the effects of inbreeding depression due to the accumulated load of mildly deleterious alleles (Hochholdinger and Hoecker, 2007). Heterosis can also result from deregulation of gene expression leading to enhanced growth (Syed and Chen, 2004; Song *et al.*, 2010). In most cases, heterozygosity and heterosis rapidly dissipate in later generation hybrids; however, if hybridization is recurrent, hybrid populations can maintain elevated heterosis for longer. Alternatively, heterozygosity and associated heterosis can be 'fixed' in hybrid individuals that undergo polyploidization or reproduce asexually.

Hybrid speciation can occur when hybrid offspring are or become reproductively isolated from both parental species. The occurrence of allopolyploidy or chromosomal inversions, by creating a barrier to gene exchange, may facilitate hybrid speciation. In addition, hybrids may differ pheno-typically and ecologically from the parental forms and even show traits that lie outside the range of their parents [*transgressive segregation* (Rieseberg *et al.*, 1999; Stelkens and Seehausen, 2009)]. This can add behavioural or ecological reproductive barriers to intrinsic genetic reproductive barriers when present (Selz *et al.*, 2014). Moreover, it provides evolutionary novelty that could enable adaptation to new niches (Gross and Rieseberg, 2005; Tobler and Carson, 2010). In the case of allopolyploid hybrid speciation, the effect of heterosis could be fixed, which could benefit the hybrid species.

Adaptive introgression occurs when genetic variation that is moved from one species to another by hybridization increases individual fitness. In such a situation, selection is extremely efficient at promoting gene flow even across strong reproductive barriers (Arnold and Martin, 2009; Dasmahapatra *et al.*, 2012). This process could be relatively important for adaptation, as occasional hybridization between taxa that are phylogenetically and geographically sufficiently close might be more common than the occurrence of rare new adaptive mutations within taxa. Introgression is particularly advantageous in the case of complex adaptations that are either multigenic or require multiple changes within genes, and which are even less likely to evolve *de novo* (Kim *et al.*, 2008). The common view that evolution occurs by selection on newly arising mutations might be biased if it is easier to detect adaptation involving novel changes within taxa than adaptation involving introgression of standing variation between close relatives

Outbreeding depression occurs when the hybrids are less fit than the parental forms and develops as populations become locally adapted, and offspring produced by parents from different populations have reduced ecological performance and associated fitness. Gene flow is crucial in determining the extent of local adaptation that can build across populations (Lenormand, 2002): local adaptation tends to be compromised by gene flow because of the potential introduction of maladaptive genetic variation (but see Edelaar *et al.*, 2008; Edelaar and Bolnick, 2012). Local adaptation can be considered a mild form of reproductive isolation whose persistence depends on the balance between divergent selection and gene flow.

Hybrid breakdown or *hybrid incompatibility* frequently results following hybridization between more divergent taxa and is of great biological interest because it reflects the processes of speciation in action (Feder *et al.*, 2012; Abbott *et al.*, 2013). Multi-locus incompatibilities such as Bateson-Dobzhansky-Muller (BDM) incompatibilities between different interacting sets of co-adapted genes steadily accumulate between diverging species (Coyne and Orr, 1997; Bolnick and Near; 2005, Matute *et al.*, 2010; Moyle and Nakazato, 2010; Stelkens *et al.*, 2010; Singhal and Moritz, 2013). Chromosomal rearrangements also facilitate the isolation of genomes and divergent evolution in hybridizing systems because the rearranged regions cause unbalanced genomic representation and incompatibility when this region recombines in hybrids, thus protecting small genomic regions from recombination (Kirkpatrick and Barton, 2006; Feder and Nosil, 2009). Hybrid breakdown or intrinsic low hybrid fitness can be asymmetric depending on the direction of the cross (Turelli and Moyle, 2007), or occur in later generations after F1 hybrid formation, allowing introgression even if hybrids are highly unfit.

Genetic homogenization or swamping can occur when hybrids are fitter than the parental species, but also when they are equally fit or even less fit. If there are no strong barriers to hybridization (e.g. assortative mating by habitat, time or mating preference or selection against hybrids), then the proportion of hybrids can increase with each generation as new F1 hybrids and hybrid backcrosses to the parental species are produced until, over time, no non-hybrid parental genotypes are left (Hegde *et al.*, 2006). If one of the two species is numerically dominant, then the final hybrid population will genetically resemble that species more. If one of the two hybridizing species (e.g. a non-native invading species) continuously receives genetic input from non-hybridizing conspecific populations, then the genetic homogenization will have a directional component and over time leave little obvious trace of the second parent involved in the hybridization [*swamping* (Prentis *et al.*, 2007)].

Spatial and temporal context

Taxa differ in the rate of potential hybridization and introgression in response to changes in species distributions or in habitat conditions. Hybridization takes place in a spatio-temporal context that reflects the evolutionary history of the hybridizing parental populations/ species. Thus, hybridization can occur among closely related sympatric or parapatric taxa within adaptive radiations, allopatric sister species that have experienced extensive divergence, or distantly related (non-sister) species (Fig. 1). The time since populations began diverging and the extent and cause of divergence will have a large impact on the outcome of any hybridization event. Hybridization among younger taxa is more likely to lead to adaptive introgression or the formation of hybrid swarms, as intrinsic genetic incompatibilities may be absent or rare. Here, reproductive barriers likely depend more on ecological aspects such as resource or habitat use, such that hybridization happens after habitat alteration. If species have closely occurring geographical distributions, then natural hybridization could occur after contact is established (in secondary sympatry or primary hybrid zones), such as after natural range expansions due to historic changes in climate (Fig. 1). As species become spatially more separated, the lower the probability that natural range expansions or long-distance colonization events will bring species into contact, and thus the lower the probability that these species will hybridize. Similarly, the longer two populations have diverged, the lower the probability that hybridization will be successful, and the greater the probability that hybridization will lead to reproductive interference, or even that reproductive interactions no longer occur at all and genetic co-existence is possible (Fig. 1). The likelihood and tempo of this decrease in hybridization varies widely between different groups of organisms. For example, allopolyploid plants most likely arise between species pairs that diverged between 4 and 8 mya, as this is the window between hybrid sterility and cross-incompatibility of progenitors (Levin, 2012, 2013), whereas fish often hybridize down to 20 mya without polyploidization of hybrids (Bolnick and Near, 2005). Most taxa are probably naturally subject to episodes of hybridization and introgression in their evolutionary history. The critical question is to what extent humans are changing the frequency and/or distribution (taxonomic, geographical) of such episodes?

Ecological context

Hybridization affects ecosystem biodiversity and functioning through the production of a hybrid population or even a novel hybrid species, or because of changes in genetic differentiation and numbers (even extinction) of the hybridizing parental species. These
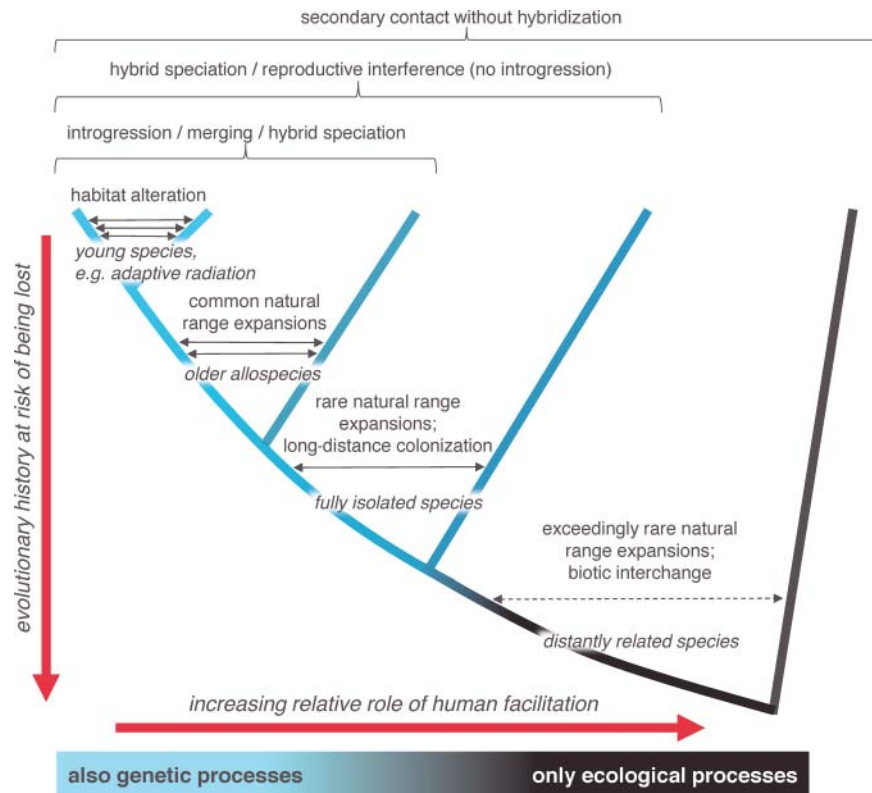
Fig. 1. Placing aspects of hybridization in a phylogenetic context. A schematic phylogeny indicates the types of potentially hybridizing taxa, and how the likelihood of natural events that may drive hybridization diminishes with phylogenetic depth. Phylogenetic relatedness impacts on ecological and evolutionary outcomes of hybridization (top and bottom). Red arrows indicate how human facilitation of hybridization increases with phylogenetic depth, while at the same time increasing the evolutionary history at risk of being lost.

effects can extend towards all directly or indirectly interacting populations and species. To assess the likely higher-level impacts of hybridization in multi-species systems (communities, food webs, mutualistic networks, ecosystems), it is necessary to consider at least three bodies of ecological theory: food web or network theory (trophic interactions, competition, and mutualisms), theory on biodiversity-ecosystem functioning (primary and secondary production, nutrient cycling, resilience of community and ecosystems), and theory on ecosystem services (Fig. 2). Ultimately, these will need to be combined with evolutionary and metacommunity theories to incorporate the spatial, temporal, and genetic components, and the resulting eco-evolutionary dynamics to improve our currently limited understanding (Leitch *et al.*, 2014). The focus of hybridization studies to date has mostly been on isolated nodes in the network (e.g. 'what are population consequences for the parents and hybrids?'), rather than on the interactions or the system as a whole (e.g. how do the hybrids operate within the 'rewired' food web?) (Fig. 3).
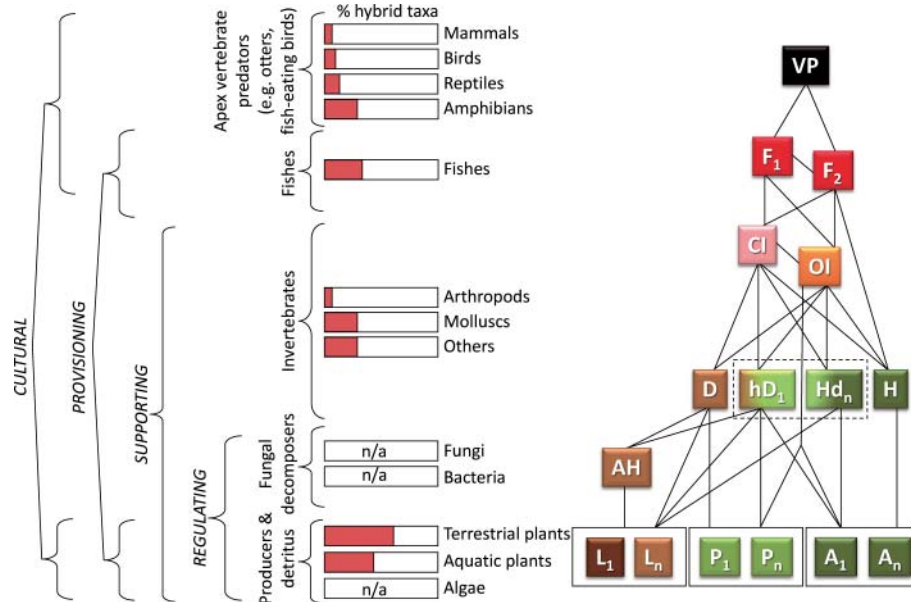
Fig. 2. Schematic of a food web from a generic freshwater ecosystem, mapping hypothetical propensity of hybridization (horizontal bars; n/a = groups where the species concept is often not applicable) onto ecosystem services (left), taxonomy (centre), and trophic position (right). VP = vertebrate predator, F = fish, CI = carnivorous invertebrate, OI = omnivorous invertebrate, D = detritivore, hD/Hd = herbivore-detritivore, H = herbivore, AH = aquatic hyphomycete, L = leaf-litter, P = plant, A = algae. Ecosystem service delivery within the food web is indicated in italic text. In this schematic, cultural and provisioning services may be provided by both top predators (e.g. ornithological ecotourism, recreational angling, and fisheries production) and primary producers (aesthetically valuable water plants of conservation concern), whereas regulatory services (e.g. carbon sequestration, water purification, and toxicant degradation) tend to be restricted primarily to the lower trophic levels.

CONSEQUENCES OF HYBRIDIZATION

Genetic context

Restoring heterosis to combat inbreeding depression and improve population viability can be a potential tool for the conservation of critically endangered species. As such, controlled hybridization of the rare Florida panther *Puma concolor coryi* and the related Texas cougar *P. c. couguar* was implemented to increase the genetic diversity of the former, leading to a rapid demographic recovery (Hedrick, 1995). This process seems also to occur naturally; for example, alleviation of locally expressed inbreeding depression is thought to favour introgression from mainland sparrows into Mandarte Island sparrows (*Melospiza melodia*) in British Columbia (Keller *et al.*, 1994). Allopolyploidy is frequent in plants because it both restores meiotic function (homologous chromosome pairing) and fixes heterosis in new hybrids, which could confer fitness advantages over parental species. A number of successfully established allopolyploid plant species have arisen during the last century following accidental or deliberate human-mediated introductions of parental species, including new *Tragopogon* species in North America derived from introduced European parental species
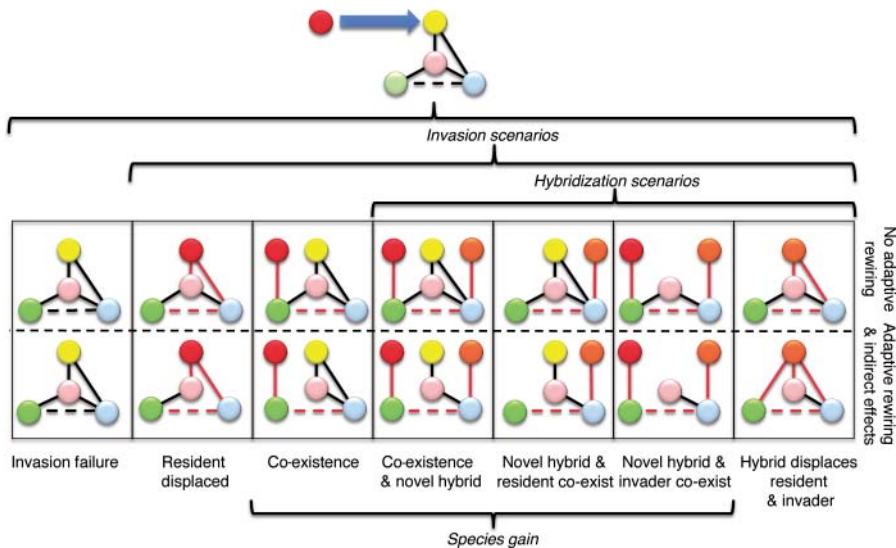
Fig. 3. Potential changes to species interaction networks in response to invasion and hybridization. Boxes show different examples of potential outcomes of invasion and hybridization in a schematic food web. Species are indicated by coloured dots, while interactions between species are separated as direct (solid lines) or indirect (dashed lines), and as pre-existing (black) or new (red). The invading species (dark red) and the novel hybrid (dark orange) exhibit a similar ecology to a native species (pale yellow) at the top level in the interaction network. Invasion outcomes range from invasion failure to establishment of the new species, co-existence, hybridization, and species replacement. This may lead to increased biodiversity, or species turnover with no change in biodiversity, and a range of possible indirect effects, such as altered apparent competition among prey that share predators. Note that additional scenarios can arise where the invader and hybrids cause species extinctions by removing prey nodes from the network, but these other more extreme conditions are not shown here. In addition, the invader will have different effects depending on its trophic position. Here we have highlighted a top predator invasion as an example because these can have especially powerful cascading effects, via top-down control.

(Soltis *et al.*, 2004), and *Senecio cambrensis* and *Spartina anglica* in the UK both due to hybridization between native and introduced parental species (Abbott and Lowe, 2004; Ainouche *et al.*, 2009). North American *Helianthus* sunflowers are a classic case of multiple hybrid speciation events. Some of these events are hundreds of thousands of years old predating human interference, while others are recent and probably have a human component to them, such as alteration of habitats or introductions of domesticated sunflower across North America bringing species into contact (Rieseberg *et al.*, 1999; Gross and Rieseberg, 2005). Hybrid asexual races of *Leuciscus* minnows in Iberia (Alves *et al.*, 2001) and *Poeciliopsis* minnows in South America (Vrijenhoek, 1993) are analogous examples in animals. Heterosis as a process promoting hybridization and introgression will have important impacts on biodiversity, in some cases decreasing it when hybrids with superior fitness replace parents and other ecosystem components (see 'Ecological context', below), and in other cases increasing it due to the emergence of new hybrid taxa.

   Adaptive introgression has occurred naturally, probably as a common natural process. Its historic presence can be inferred from evolutionary signatures, for example *Heliconius*

butterfly mimetic wing colour supergenes show signals of elevated gene flow between species (Dasmahapatra *et al.*, 2012). By its very nature, adaptive introgression can also be detected as a response to current conditions. For example, strong selection has been implicated in the spread of warfarin pesticide resistance alleles from the Algerian mouse, *Mus spretus*, to domestic mouse, *M. musculus domesticus* through introgression (Song *et al.*, 2011). Because adaptive introgression could increase the viability of individuals and happen over just a few generations, in a world of increasing global change and hybridizing contact there may be more and more examples of introgression following hybridization as an adaptive response to altered selection pressures. For some species, adaptive introgression might be one way by which decline towards extinction could be reversed, as a form of evolutionary rescue. For example, in the past, *in-situ* survival of endemic species through periods of climate change appears to have been facilitated by hybridization (Becker *et al.*, 2013). Introgression can be cryptic where the phenotypic appearance of the original taxa is maintained leading to underestimates of the evolutionary importance of hybridization (Ward *et al.*, 2012).

Negative outcomes will ensue where hybridization disrupts local adaptation resulting in maladapted hybrids and outbreeding depression. For example, ibex from southern latitudes have a different reproductive timing compared with ibex from more northern latitudes, and the introduction of southern individuals to a northern population led to the production of hybrids that reproduced at sub-optimal times and the extinction of the northern population (Turcek, 1951). Hybrid incompatibilities that have evolved *in situ* can make species resistant to introgression with co-occurring relatives, particularly if reinforcing selection against hybridization then occurs (Servedio and Noor, 2003). However, hybridization frequency due to human environmental disturbance might cross a threshold beyond which hybridizing barriers are ineffective and taxa rapidly converge (Seehausen *et al.*, 2008; Gilman and Behm, 2011; Vonlanthen *et al.*, 2012). Equally, environmental change can alter adaptive landscapes and erode pre-existing local adaptation, up to the point that local populations become more vulnerable to introgression and are swamped. When a non-native species is numerically dominant over a native species, hybridization can result in the genetic dilution and eventual extinction of the native species, even when certain reproductive barriers are in place. In fact, even if no introgression occurs because of complete sterility of F1 hybrids, hybridization can still lead to population declines and extinction (Prentis *et al.*, 2007). Producing sterile hybrids is a form of the Allee effect, as this kind of hybridization can be viewed as wasted reproductive output with greater negative effects on the more rare hybridizing species (Huxel, 2004). A dramatic example of extinction despite hybrid incompatibility is provided by a moving hybrid zone in Spain whereby diploid annual mercury plants, *Mercurialis annua*, are taking over the range of hexaploid annual mercury due to pollen swamping (Buggs and Pannell, 2006).

Spatial and temporal context

As outlined above, the spatio-temporal context of hybridization affects the outcomes of hybridization (Fig. 1). Similarly, this context determines which aspects of global change might play a role in increasing hybridization between which kinds of species. Habitat alteration by human activities can be expected to be more relevant in promoting hybridization among younger taxa, which are not yet separated by strong genetic incompatibilities. Habitat alteration can bring taxa with previously overlapping geographic distributions together in a disturbed habitat, or enable range expansion that brings previously allopatric taxa into contact. Human-induced climate change can also lead to geographic distribution

changes, causing previously isolated taxa to come into contact. Natural long-distance colonizations or large-scale range expansion are typically rare, but human activities (accidental transport, deliberate introduction) are now greatly increasing the movement of taxa, resulting in the establishment of non-native and invasive species, and enhanced probabilities for hybridization among evolutionarily more divergent taxa. Finally, human-mediated introductions can also lead to introductions of hybrid material to new areas/environments leading to the origin of new taxa, as in the case of the recently originated homoploid hybrid species *Senecio squalidus* (Abbott *et al.*, 2009).

Investigations of clades showing adaptive radiations are particularly informative about the impacts of human disturbance and consequent changes in hybridization frequency on patterns of biodiversity. Recent ecological radiations such as those of fish in postglacial lake systems show predominantly extrinsic post-zygotic and pre-zygotic reproductive isolation based on divergent ecological adaptations and are thus sensitive to changes in niche structure and new species introductions (Vonlanthen *et al.*, 2012). Range shifts in response to climate change or human introductions can bring species into hybridizing contact that have not evolved effective hybridizing barriers, in which cases rampant introgression is both expected and observed (Rosenfield *et al.*, 2004; Muñoz-Fuentes *et al.*, 2007). In other cases, deliberate introductions of relatively evolutionarily divergent species into systems that contain pairs of reproductively isolated sympatric species can promote merging of otherwise isolated sympatric taxa, as has occurred following stocking of trout, *Salmo trutta*, from recently recolonized glaciated northern Europe to refugial southern Europe that contained a greater diversity of hitherto reproductively isolated trout species (Giuffra *et al.*, 1994; Keller *et al.*, 2012; O. Seehausen, unpublished data).

Hybridization between introduced and native species can generate novel biodiversity on extremely short time and spatial scales when favoured by selection. New ecotypes of hybrid sculpins in the Rhine–Scheldt river systems are a good example of evolutionary novelty in response to human disturbance. Canals now link parental drainage systems and a novel hybrid ecotype has emerged that has invaded highly disturbed, warm and oxygen-poor waters of the main channel of the Rhine when both parental species are restricted to small hillside streams (Nolte *et al.*, 2005). Allopolyploid speciation can be an extremely rapid adaptive consequence of hybridization such as the new allopolyploid *Tragopogon* goatsbeard species described above that have established successfully in North America where the introduced progenitors hybridized, but not in Europe where the same native progenitors co-exist in a stable ecological context (Soltis *et al.*, 2004). Historical examples also exist such as the Hawaiian silversword radiation (endemic genera: *Argyroxiphium*, *Dubautia*, and *Wilkesia*) during the last 5–6 million years, which has arisen from early hybridization between North American immigrants (Barrier *et al.*, 1999). Another striking example of historic hybridization following long-distance dispersal is between *Senecio flavus* (Namibia) and *S. glaucus* (North Africa) that led to the origin of the allopolyploid *S. mohavensis* within the last 1 million years (Coleman *et al.*, 2001, 2003).

The frequency of dispersal events across biogeographic realms has dramatically increased with the advent of human disturbance, and the hybridizing impacts of this depend in part on the temporal and spatial context. For example, the current biota of the Mediterranean Sea predominantly reflects a continuous history of immigration and diversification since the opening of the strait of Gibraltar with the Atlantic Ocean 5 mya (Bianchi and Morri, 2000; Patarnello *et al.*, 2007; Lejeusne *et al.*, 2009). In recent times, the Mediterranean Sea has experienced a major influx of approximately 10 new species per year from the Red Sea/Indian Ocean in the

century and a half since the construction of the Suez Canal reconnected these marine systems that had been separate for the last 10 million years (Galil, 2009). Despite extensive recent migration, there have been relatively few cases of invasion with hybridization from the Red Sea because these faunas have been isolated for 10 million years. In contrast, one would expect a new wave of Atlantic invaders responding to global change to probably lead to relatively more cases of invasion with hybridization because the Strait of Gibraltar represents a more recent phylogenetic break.

Ecological context

Invasions can proceed with or without hybridization, and with or without rewiring of the food web due to adaptive responses and indirect effects, as outlined in Fig. 3. It is clear that the range of possible ecological consequences of hybridization is large, and empirical examples exist. For a hybrid population to establish, it needs to occupy or create a previously unoccupied niche or to replace a resident species: this can have positive, neutral or negative impacts on ecosystem functioning, which can be hard to predict *a priori*. A common phenomenon in biodiversity–ecosystem functioning studies is that as a system loses a species, its role is replaced by an equivalent species or group of species from within the resident species pool, usually via growth and/or density compensation. Adding a species with a new role in a previously unoccupied niche will shift ecosystem functioning, potentially enhancing overall process rates and facilitate population increase. A classic example is the North American ruddy duck, *Oxyura jamaicensis*, which reached populations numbering in the thousands within just a few decades following the escape of just seven founding individuals in the UK (Muñoz-Fuentes *et al.*, 2007). In the UK, this species was initially welcomed as a new addition to the avifauna but problems arose after it spread to Spain and started to hybridize with a distantly related allospecies, the endangered white-headed duck *O. leucocephala* (Muñoz-Fuentes *et al.*, 2007). If hybrids are simply a blend of the ecological traits of the parent species, it might be easier to predict ecosystem-level consequences; but if it has unique characteristics not found in either parent species (e.g. due to transgressive segregation), then reliable predictions become increasingly difficult, or impossible (Woodward *et al.*, 2013; Leitch *et al.*, 2014). Some cases of diversification following transgressive hybrid expression are known, but it is not yet clear whether this is the rule rather than the exception (Rieseberg *et al.*, 1999; Selz *et al.*, 2013, 2014).

One way to better understand the ecosystem consequences of hybridization could be to map the provisioning of ecosystem services and the taxonomic and functional traits of native, invasive, and hybrid taxa onto food webs to study the network context and ramifications at higher ecosystem levels that have not been considered before. This contrasts with the traditional treatment of nodes in food webs as fixed entities rather than being transmutable (Reiss *et al.*, 2009). Particular attention should be directed to hybridization in keystone species, such as top predators occupying highly connected nodes in the food web or ecosystem engineers, as these are good candidates to cause the strongest ecosystem effects. There are many examples of invasive species acting as keystones, especially where they colonize a previously isolated area such as oceanic islands or large lakes. Invasives also tend to be generalists, so they can rapidly forge many new links when colonizing a food web, and many of them are high in the food chain, exploiting a vacant niche in which they have few or no predators. While probably rare in absolute numbers compared with invaders at lower food web levels, some of these high trophic level invaders are hybrids, such as the

invasive Nile perch in Lake Victoria, which is a hybrid between *Lates niloticus* of Lake Albert and *L. longispinis* of Lake Turkana (Harrison, 1991). Clearly, invasion and hybridization at the top of the food web will have very different consequences for ecosystem processes and services than at lower trophic levels, where hybridization could be especially pronounced (Leitch *et al.*, 2014). There are several examples of invasive–hybrid consumer species at inter-mediate trophic levels, especially among vertebrates and in freshwaters. For example, in the UK hybridization between native Crucian carp *Carassius carassius* and introduced goldfish *C. auratus* is rampant, with few if any genetically pure stocks of the resident species left (Wheeler, 2000). These fishes can have powerful effects on ecosystem functioning, with the potential to trigger regime shifts from a clear-water, vegetation-rich state to a turbid-water, vegetation-poor state in shallow lakes (Richardson and Whoriskey, 1992). Native cyprinids hybridize readily in many freshwaters, with bream–roach, roach–dace, and other combinations appearing regularly, yet these have not become invasive in mainland Europe. Nonetheless, there is a potential threat from newly introduced cyprinids forming hybrids that become invasive, especially in areas where the community is not already saturated. For example, the lacustrine fish fauna of Ireland has been invaded by hybrids between introduced roach (*Rutilus rutilus*) and introduced bream (*Abramis brama*), which show overlapping trophic positions but with hybrids expressing the greatest flexibility in diet (Toscano *et al.*, 2010; Hayden *et al.*, 2011).

EVALUATING THE IMPACT OF HYBRIDIZATION: THE IMPORTANCE OF DIFFERENT VIEWPOINTS AND OBJECTIVES

The evaluation of the effects of hybridization depends on who is doing the evaluation, and more specifically in which context and with which objectives the effects are compared. While this is perhaps self-evident, in many cases discussions can become heated and unfocused because people are measuring impacts with different tools, scales, units, and dimensions. For example, someone who is simply documenting and studying hybridization as a genetic phenomenon might be more interested in documenting frequency and outcomes of hybridization and might not have a strong opinion on the need for managing invaders and hybrids, compared with others whose priorities are to prevent or limit the global extinction of a native species due to competition with new invasive hybrids.

We argue that in many cases, value judgements about hybridization being negative or positive should be reserved or at least placed into its proper context, especially as characteristics can be affected in contrasting directions. While one might assume that actions to conserve one species automatically benefit the rest of the ecological network in which it is embedded under the 'optimist's scenario', this is not necessarily the case when the complexity of the network is better understood (Pocock *et al.*, 2012). As another example, beefalo (hybrids between native bison, *Bison bison*, and introduced domestic cattle, *Bos taurus*) in North America represent an improved provisioning service because of increased meat production per capita, but at the same time a reduced cultural-aesthetic service being provided by a hybrid: ecotourists are willing to pay a premium to see wild bison but hybridity, especially if visibly evident, diminishes that appeal (Halbert *et al.*, 2005). This becomes increasingly important when making management decisions. For example, depending on whether the focus is on maintaining evolutionary history or ecological functioning, one might set priorities differently. We might be particularly concerned about loss of phylogenetically distinct allospecies because this means loss of a great deal of

evolutionary history: in that case, the relative importance of human impacts is greatest at larger phylogenetic/biogeographic distances (Fig. 1). If one is more concerned about the conservation of functional diversity and its relevance to ecosystem functioning, then loss of recently ecologically diverged taxa from adaptive radiations may be of more concern (Becker *et al.*, 2013). Even though distinct functional phenotypes can re-evolve, this is unlikely to happen on a timescale relevant to current human society.

Using fixed criteria to value the occurrence of hybridization is becoming increasingly difficult. For example, one could state that native species have a greater conservation value than non-native species and their hybrid progenitors, whereby non-nativeness is defined as having arrived in historic times to a region due to human activity. But what if a new species arrived because it changed its distribution in response to human-induced climate change: is that a natural range expansion making it a newly acquired, native species that should be protected, or range expansion indirectly due to human activity, making it a non-native species that should be eliminated? And what if this new species starts to hybridize with a native one and genetic material is introgressing: does that threaten the genetic integrity of the original native species, or could it be an adaptive response to the changed climate, enabling the native species to persist? Alternatively, is the presence of hybrids in a vacant niche preferable to an overall loss in diversity if a native parental species has already gone extinct? While considerable progress is being made to address these issues in individual cases, opposing solutions are often possible depending on one's background and ideas on 'how things should be'.

OPEN QUESTIONS/AREAS FOR FURTHER RESEARCH

Although we have outlined how aspects of genetics, ecology, and space and time combine to give a wide diversity of outcomes and consequences of hybridization, our knowledge on this is still very unbalanced. For example, the genetic principles of hybridization are now relatively well known, but insight into the relevance of hybridization and local adaptation for ecosystem functioning is far sketchier. We therefore conclude by identifying questions for further research:

- Is there a relationship between historical dynamics and current vulnerability to changed frequency of hybridization? In other words, can we predict differences in the resilience and negative impact of hybridization between refugial (stable) and non-refugial (unstable) species, between communities with strong or shallow co-evolutionary histories (evolutionary assembly vs. colonization assembly), or between high or low latitude? Do these factors influence how likely a hybrid is to exhibit transgressive and possibly disruptive characteristics?
- What is the rate of introgression as a function of phylogenetic and/or biogeographic distance (Fig. 1) and how are the evolutionary consequences of such introgression affected by human-mediated habitat modifications such as agro-ecosystems and aquaculture? What are the conditional probabilities of successful invasion following successful hybridization – that is, how many failures are we missing in the 'ghost of hybridization past'?
- Was introgression elevated during periods of past rapid change and can we detect the evolutionary consequences, such as diversity increases or decreases at such times and variation across biomes or latitudes? It is important to understand natural background

levels of hybridization as a baseline against which to assess the hybridization in response to rapid global change. Comparative genomics approaches could be promising in this regard if we could identify and estimate the prevalence and size of introgressed chromosome segments to measure past hybridization.

- How can we integrate the likelihood and impacts of hybridization into ecological network theory? Do hybrid invasions predominantly affect ecological network structure without affecting biodiversity, or do they tend to affect biodiversity without altering ecosystem structure? Can we identify nodes, trophic levels, or interaction types that are most vulnerable to hybridization (Figs. 2, 3)?
- How do we reconcile contrasting ecosystem services provided by new hybrids (e.g. food production vs. cultural-aesthetic values)? Given that most regulatory ecosystem services such as carbon sequestration and nutrient cycling are done by microbes at the base of the food web, should we be most concerned with identifying, predicting, and managing hybridization impacts on cultural-aesthetic, supporting or provisioning services?

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