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Hybridisation and two potential consequences: speciation and reverse speciation

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Hybridisation and two potential consequences: speciation and reverse speciation

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TABLE OF CONTENTS

TABLE OF CONTENTS	p. 1
INTRODUCTION	p. 2
SPECIATION BY MEANS OF HYBRIDISATION	p. 4
REVERSE SPECIATION	p. 6
NATURALLY OCCURRING HYBRIDISATION	p. 8
ANTHROPOGENIC FACTORS INFLUENCING HYBRIDISATION	p. 9
CONCLUSION	p. 15
ACKNOWLEDGEMENTS	p. 16
LITERATURE CITED	p. 17

INTRODUCTION

The definition of the term “species” has for a long time been an object of debate and a controversial topic, with different proposals brought out (Coyne & Orr, 2004). One common species concept is the biological definition, according to which species are “groups of actually or potentially interbreeding natural populations which are reproductively isolated from other such groups” (Mayr, 1942).

During the speciation process, by which new species arise, the first barriers to evolve are usually the premating ones. The premating barriers are followed only later by extrinsic postmating barriers and eventually by intrinsic postmating barriers. In sticklebacks, for example, it has been shown that habitat isolation and sexual selection are essential reproductive barriers (Lackey & Boughman, 2017). Similarly, in the genus of freshwater fish *Etheostoma*, it has been demonstrated that sexual selection evolved faster than hybrid inviability (Mendelson, 2003). However, there are exceptions to this common pattern. One of them is represented by fruit flies, in which the two species *Drosophila suboccidentalis* and *D. occidentalis* have developed incomplete reproductive isolation, due to a prezygotic barrier, namely an asymmetrical sexual selection (Arthur & Dyer, 2015). Nonetheless, other research on hybridisation without speciation was conducted in the two closely related Adriatic pipefish species *Syngnathus typhle* and *S. taenionotus*. Pipefish are indeed characterised by male pregnancy: males brood and females provide them with eggs into the male’s brood pouch (Wilson & Orr, 2011). Moser & Wilson (2020) found no clear preference of *S. taenionotus* males towards what species the potential partner was belonging to, whereas *S. typhle* males exhibited a strong preference for conspecifics. The formation of prezygotic barriers in the Adriatic pipefish was thus partial, while postzygotic barriers between the two species were always strong, since the offspring was not viable (*S. typhle* males) or no eggs were ever detected (*S. taenionotus* males).

Hybridisation can be defined as reproduction between members of genetically distinct populations, and it takes place in hybrid zones (Barton & Hewitt, 1985). This process is of great interest, as it can hamper speciation, impeding the formation of new species. However, the spread of genes of one species into the genome of another species due to hybridisation, known as introgressive hybridisation, has also been shown to be a stage in the process of species formation itself (Dobzhansky, 1941).

Natural selection plays a key role in promoting divergence between populations (Endler, 1986; Schluter, 2000). The strength of divergent selection relative to gene flow

determines the possible success of the former in causing speciation (Hendry *et al.*, 2002; Rundle & Nosil, 2005). The time for speciation to become irreversible has to be long enough so that the environmental conditions that promote speciation can persist until the end of the process, up to more than one million years (Coyne & Orr, 2004). Before that happens, hybridisation can be responsible for speciation in reverse (also called reverse speciation), which is the merger of the two parental species into a hybrid species (Seehausen, 2006a; Taylor *et al.*, 2006).

On the other hand, it is not certain that the outcome of hybridisation is going to be reverse speciation. A standstill, in which there is no progression towards neither ordinary nor reverse speciation, is possible (Nosil *et al.*, 2009). Alternatively, barriers to gene exchange may increase and a larger proportion of the genome may acquire protection from introgression, by accumulation of linkage disequilibrium (LD) between barrier *loci* (Wu, 2001; Servedio & Noor, 2003; Via, 2009).

Environmental factors can play a role in the promotion of speciation and hybridisation. Northern latitude lakes are populated by fish species whose speciation processes are often still ongoing (Scribner *et al.*, 2001). In recent years, a parallel increase of the temperature and the turbidity of northern latitude lakes has been going on. This increase is supposedly human-induced (Whitehead *et al.*, 2009; Dokulil, 2014), and is predicted to continue in the future, together with the intensification of precipitations (Weyhenmeyer *et al.*, 2016). One of the main causes for the increase in turbidity is the increase of organic matter in lakes (Roulet & Moore, 2006; Monteith *et al.*, 2007; Larsen *et al.*, 2011; Solomon *et al.*, 2015). It has been shown that such environmental changes can influence sexual selection in fish communities (Seehausen *et al.*, 1997a; van Doorn *et al.*, 1998; Järvenpää & Lindström, 2004; Genner & Turner, 2005; Fisher *et al.*, 2006). This can happen because the reduced visual conditions can impair mate choice (Luyten & Liley, 1985, 1991; Seehausen *et al.*, 1997a; Seehausen & van Alphen, 1998; Candolin, 2004; Järvenpää & Lindström, 2004; Heubel & Schlupp, 2006; Candolin *et al.*, 2007, 2008; Engström-Öst & Candolin, 2007; Wong *et al.*, 2007). This, in turn, can increase the hybridisation rate, with potential risk for reversing the speciation process (Gilman & Behm, 2011).

In the next paragraph, we will briefly discuss the main forces by which hybridisation can enhance and speed up speciation, with particular reference to coupling and reinforcement. In the following paragraphs, we will analyse mechanisms by which hybridisation can hamper the speciation process. Examples will be provided.

SPECIATION BY MEANS OF HYBRIDISATION

Pivotal to understand the mechanism by which hybridisation can boost, or, sometimes, even trigger hybridisation, is the concept of coupling. Coupling is defined as the phenomenon by which an individual inherits two dominant alleles that are linked on the same chromosome. Incompletely isolated populations can progress towards speciation by means of association between different *loci* (Bierne *et al.*, 2011; Smadja & Butlin, 2011). It is possible that LD between barrier *loci* builds up and accumulates between different lineages. However, in spite of playing an important role, the concept of LD itself is not enough to fully understand and explain coupling (Barton, 2013). In this sense, the coincidence of the different barrier effects, is crucial. Without that happening, there would be simple accumulation of reproductive isolation, but not coupling (Barton & de Cara, 2009). An example of this is provided by the lepidopteran *Ostrinia nubilalis*, the European corn borer, where double forms of voltinism, pheromone signalling and host-plant association are present. However, since different populations do not share the same form for all the characters, no strong barriers to gene flow have developed (Dopman *et al.*, 2010; Orsucci *et al.*, 2016).

Strictly related to the concept of coupling is reinforcement (Dobzhansky, 1970), in which natural selection promotes reproductive isolation between two species. It does so by negatively selecting hybrids, with lower fitness. If the hybrid population is not viable, the individuals of the two parental species who only mate with members of the same species will have an evolutionary advantage. This will go in the direction of premating isolation and consequently enhanced divergence between the two species (Servedio & Noor, 2003; Schuler *et al.*, 2016). To some extent, reinforcement can be thought of as a particular form of coupling, in which a postzygotic barrier is the cause for the formation of a prezygotic barrier later on. Nonetheless, Butlin & Smadja (2018) argued that any barrier that actually promotes the evolution of a second barrier effect should be included, independently of their nature. However, the barriers that occur earlier are stronger than the ones occurring later in the reproductive sequence (Coyne & Orr, 2004).

Another way by which hybridisation can promote speciation is hybrid speciation. Hybrid speciation may occur when a hybrid swarm originates. If that is the case, the hybrid population might have a lower fitness compared to the parental species in their respective ecological niches. However, not only can that same hybrid population be more adapted to novel environments, but it might also carry enough genetic variation, so that natural selection can give rise to a new species (Meier *et al.*, 2017; Selz & Seehausen, 2019). Hence, hybridisation can considerably hasten the partial or complete formation of reproductive

isolation between species, as it has been shown in Darwin's finches. A single immigrant of *Geospiza conirostris* to Daphne Major, an island, in the Galápagos archipelago (Ecuador), inhabited by *G. fortis*, was responsible for the establishment of a hybrid genetic lineage. This lineage, despite the high level of inbreeding, showed a high level of fitness, and became completely reproductively isolated from the parental species in just three generations (Grant & Grant, 2014a; Lamichhaney *et al.*, 2018). Other examples of hybrid speciation come again from birds. One of them is the hybrid speciation that occurred between the myrtle warbler (*Dendroica coronata*) and the black-fronted warbler (*D. nigrifrons*), which gave origin to the Audubon's warbler (*D. auduboni*) (Brelsford *et al.*, 2011). Another example is the Italian sparrow (*Passer italiae*), which is of hybrid origin too, where the house sparrow (*P. domesticus*) and the Spanish sparrow (*P. hispaniolensis*) are its parental species (Hermansen *et al.*, 2011). Other cases of hybrid speciation are also known in other vertebrate classes, such as in the pupfishes belonging to the genus *Cyprinodon*, in the Bahamas islands. It has been shown that, in these organisms, multiple sources of genetic variation gave their contribution to shaping their current biodiversity, especially for what trophic mechanisms are concerned (Richards & Martin, 2017).

When we consider the possible origin of a new hybrid *taxon*, the amount of extreme novel trait values that are present in hybrids, but not in parental species, is known as transgressive segregation. This is related to the genetic distance between the parental species themselves. Transgressive segregation has been thought to be a key factor for selection to act and to give rise to new species in novel environments (Slatkin & Lande, 1994; Rieseberg *et al.*, 1999, 2003). One of the most remarkable characteristics of transgressive segregation is that phenotypic traits can exceed both parental phenotypes. Examples of this can be found in plants (Schwarzbach *et al.*, 2001), in *Drosophila* (Ranganath & Aruna, 2003), and in cichlid fishes (Stelkens *et al.*, 2009).

In specific circumstances, hybridisation has proven to be helpful to avoid complete population eradication from particular areas. This happened on the Macquarie island (Australia), which lies in the Southwestern Pacific Ocean. On this island, as a result of hunting pressure, the local fur seal population became extinct in the 19th century. Starting from 1948, the island was colonised by three different species of fur seal, which hybridised together. Since then, the fur seal population on the island remained viable, with the three species being present, together with a consistent hybrid population (17-30% of all pups) with some degree of reproductive success. It was due to hybridisation that fur seals on Macquarie Island did not die out again (Lancaster *et al.*, 2006).

REVERSE SPECIATION

Since species diversity can evolve in response to ecological opportunities, the regression of ecological conditions can drive the extinction of a species that has previously been formed (Vonlanthen *et al.*, 2012). This can happen because the time it takes for two species to develop reproductive barriers between each other is much longer than the time required for speciation itself (Schluter, 2000; Coyne & Orr, 2004). In this case, one of the possible outcomes of interspecific hybridisation is reverse speciation. The phenomenon of hybridisation between species that have developed sympatrically has been documented since long (Wiegand, 1935). It is widely known that this phenomenon itself has played an important role in the evolution of current species, not only in plants (Stebbins, 1950), but also in animals (Dowling & Secor, 1997). Whenever hybridisation happens, it is useful to investigate its origin, together with the causes that have triggered or promoted it. Allendorf *et al.* (2001) have proposed a set of guidelines that help to distinguish between natural and human-induced hybridisation and to adopt the most suitable conservation measures, according to each case (Fig.1).

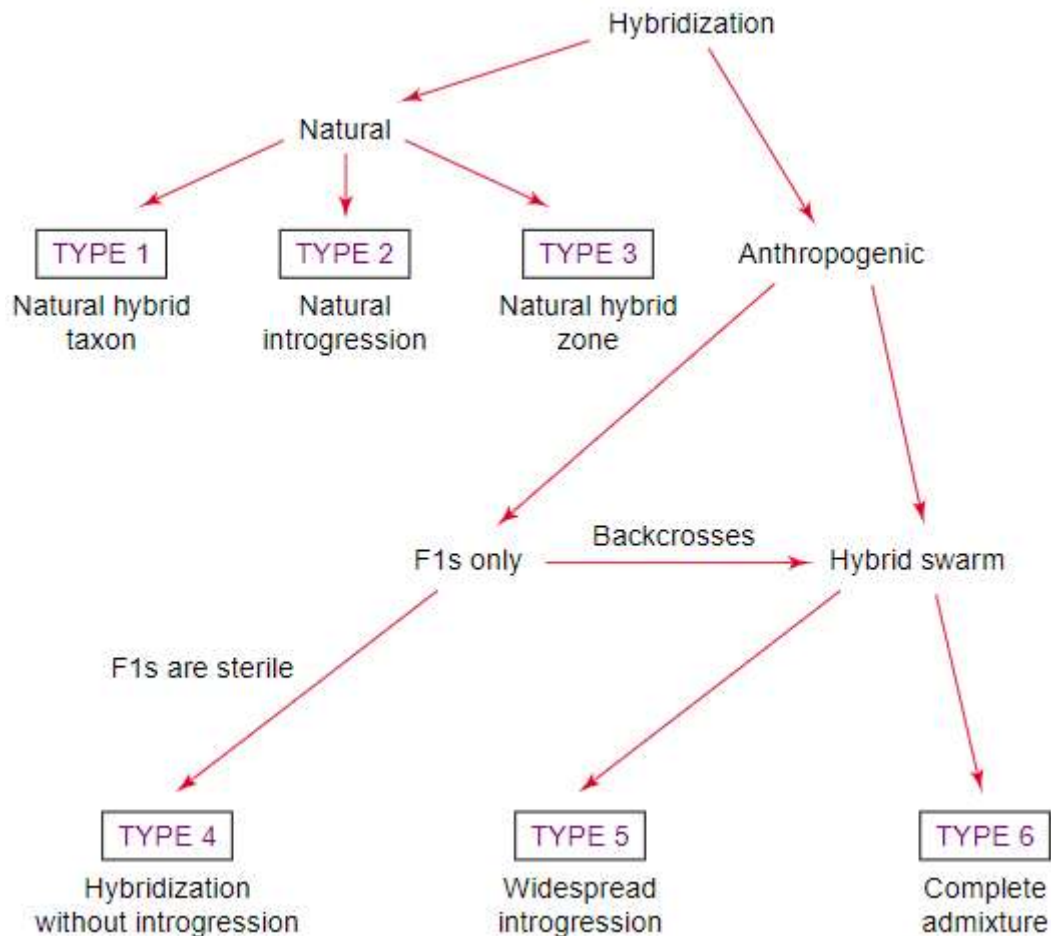


Fig. 1. Categorisation of hybridisation. Types 1-3 occur naturally, and can be object of conservation measures, while Types 4-6 are of anthropogenic origin, and should be prevented. Type 1: Hybrid populations occur naturally. Type 2: Different species can occasionally interbreed, leading to the exchange of neutral and advantageous alleles between the two species. Type 3: Two species are reproductively isolated, but, nonetheless, hybridise in a specific, limited geographical area. Type 4: F1 hybrids are sterile. Therefore, wasted reproductive effort is the main disadvantage of this kind of hybridisation, since it does not bring to genetic mixing. Type 5: A species has suffered from widespread hybridisation with another one. Still, pure populations remain, together with a hybrid population. Type 6: A species has severely suffered from widespread hybridisation with another one, to the point that almost no pure individuals remain. The hybrid population is the only one remaining, and selection against hybrids is almost absent. Adapted from Allendorf *et al.* (2001).

The boundaries between speciation and speciation reversal are not always so sharp and clear. An example of this comes from the fish banded darter (*Etheostoma zonale* group). Halas & Simons (2014) studied these darters in the Central Highlands in North America. In parallel with some degree of divergence detected between different populations, they detected a cryptic species in the Tennessee River. This cryptic species seems to have successfully hybridised with the species group, leading to a phenomenon of reverse speciation.

To understand to what extent current biodiversity might be prone to speciation reversal, Seehausen (2006a) proposed to compare the fraction of species whose existence is

dependent on the maintenance of a balance between selection and gene flow with the older species that are not anymore dependent on that. In sticklebacks, the number of species which evolved postglacially is six times more than the species that evolved before the last glaciation (McKinnon & Rundle, 2002). The number of postglacial species of whitefishes (*Coregonus*) is five times higher than the older ones (Bernatchez *et al.*, 1991; Hudson *et al.*, 2007), and similar proportions can be found in cichlid fishes (Seehausen, 2006b).

NATURALLY OCCURRING HYBRIDISATION

Hybridisation is a natural process that is pivotal for the evolution of biodiversity as we know it today. This process has historically received more attention in plants (Rieseberg, 1997; Arnold, 2015) than in animals. However, recent evidence in animals, as new whole-genome data are made available, is showing how crucial hybridisation is to create the genetic novelty which is necessary for selection to work on (Barton, 2013).

One of the fields that shed light on how important hybridisation was in shaping current biodiversity is paleogenomics, thanks to which genetic admixture has been shown, for instance, between the brown bear (*Ursus arctos*) and the polar bear (*Ursus maritimus*). The two species came into contact during the last glacial minimum, when the range of the polar bear was more expansive than today (Cahill *et al.*, 2018). Ancient hybridisation has been proved to have occurred between humans and Neanderthals as well (Sankararaman *et al.*, 2014; Harris & Nielsen, 2016).

Whole-genome studies on extant species have also been able to show signs of previous hybridisation between different *taxa*. One example of this is the hybridisation phenomenon that occurred in North America between the eastern wolf (*Canis lupus lycaon*) and the red wolf (*Canis lupus rufus*), but it is not the only one. The grey wolf (*Canis lupus*) and the coyote (*Canis latrans*) have been shown to hybridise as well (vonHoldt *et al.*, 2016). Moreover, the red wolf itself seems to have originated from the hybridisation between the coyote and the grey wolf (Roy *et al.*, 1996).

It is nowadays widely accepted that hybridisation is at the basis of many species radiations. Among them, probably the most remarkable example are the cichlid fishes in many African lakes (Smith *et al.*, 2003; Seehausen *et al.*, 2008a; Nevado *et al.*, 2009). In these organisms, ancient introgression is considered to be the main speciation engine (Genner & Turner, 2012). Other examples come from sailfin silversides in the Malili Lakes in Sulawesi (Indonesia) (Herder *et al.*, 2006), and from Darwin's finches on the Galápagos

islands (Grant *et al.*, 2005), where, similarly, hybrid speciation is the main process responsible for the current biodiversity.

It is believed that abundance of ecological opportunities is one of the major mechanisms responsible for promoting rapid radiations by means of introgressive hybridisation (Schluter, 2000). This would explain why cichlid fishes show a huge variety of morphologies in Lake Victoria and Lake Malawi, and why their morphology diversity is much lower in African rivers (Joyce *et al.*, 2005). A similar form of sympatric radiation in cichlids, although it resulted in not as many species as in Africa, happened in lakes Apoyo and Xiloá in Nicaragua (Barluenga *et al.*, 2006; Kautt *et al.*, 2016).

In insects as well, hybridisation can be pivotal to the maintenance of biodiversity. This occurs, for instance, in the *Drosophila simulans* clade, which is composed of the three species *D. simulans*, *D. mauritiana* and *D. sechellia*. These species show a considerable level of reproductive isolation, but data studies have shown that gene flow has occurred among them as well (Garrigan *et al.*, 2012).

Since it is usually the female which is responsible for mate choice, in most cases in which hybridisation occurs, it is usually sexually unidirectional. For example, when there are males of both species, females prefer conspecific males. If, instead, there are only allospecific males, these can have some chances of mating. This results in females of a rare species to hybridise with males of a common species, but not vice versa (Wirtz, 1999).

ANTHROPOGENIC FACTORS INFLUENCING HYBRIDISATION

Human intervention can trigger hybridisation processes, following a variety of different pathways. Among vertebrates, fishes present the wider set of examples. For instance, it has been shown that introductions of non-native species can play a role in promoting hybridisation (Rhymer & Simberloff, 1996). This was the case in Lake Michigan (USA), where the eight cisco species (*Coregonus* spp.) which were present there either disappeared or collapsed into a hybrid swarm, after the introduction of allochthonous predators (Smith, 1964; Todd & Stedman, 1989). In ciscoes, a more detailed mechanism by which the sudden introduction of new predators might be responsible for the species collapse process has been shown by Seehausen *et al.* (1997a) and by Seehausen (2006a). In their studies, Seehausen and co-workers found that the eutrophication caused by the new predator led to a fast increase in water turbidity, making mate choice both costlier and less effective.

The loss of sexual selection has been mentioned itself for being responsible for triggering reverse speciation, especially when environmental change is at its basis (Lackey & Boughman, 2017).

An important case of admixture between different species comes from the Enos Lake and other adjacent lakes in British Columbia (Canada), where a species pair of threespine sticklebacks has been studied (McPhail, 1994; Kraak *et al.*, 2001; McKinnon & Rundle, 2002; Seehausen, 2006a). In this system, it has been highlighted how a significant increase in the percentage of hybrids coincided with the introduction of the signal crayfish, *Pacifastacus leniusculus*, and the subsequent destruction of aquatic vegetation and increase in water turbidity. Before the introduction of the predator, sticklebacks of the two species exhibited different morphologies, but, after the signal crayfish was introduced, no differences were possibly detected (Taylor *et al.*, 2006) (Fig. 2). Although in Enos Lake the fitness of the hybrids was lower than the fitness of the parental species in most environmental conditions, between the 1950s and the 1970s, the species pair went close to collapsing into a hybrid swarm, due to the fluctuating water level caused by intensified quarry-mining (Gow *et al.*, 2006). Other studies, performed on Enos Lake sympatric limnetic-benthic stickleback species pairs, showed that in modern populations there was a significant reduction in terms of selection against intermediate phenotypes, thus compromising postmating isolation and allowing hybrids to fully replace the parental species (Behm *et al.*, 2010). More recently, it has been shown that interspecific hybridisation has caused the two stickleback species in Enos Lake to completely collapse into a hybrid swarm (Fig. 2). This was clear when analysing both different morphological traits and different microsatellite DNA *loci* (Taylor & Piercey, 2018).

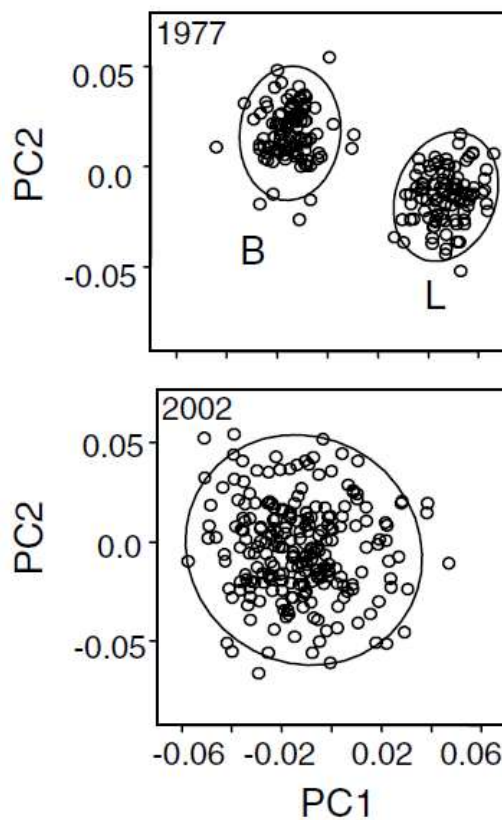


Fig. 2. Specimens of threespine sticklebacks from Enos Lake plotted along the first two axes of morphological variation in 1977 and in 2002, respectively before and after the introduction of the signal crayfish, *Pacifastacus leniusculus*. Before the introduction of the signal crayfish, the differences between the benthic and the limnetic species were evident, whereas after the predator was introduced, the two species collapsed into a hybrid swarm. Key: B, benthic; L, limnetic. Adapted from Taylor *et al.* (2006).

In Lake Victoria, the introduction of a predator led to an increased level of eutrophication, and to a consequent higher degree of turbidity. The deterioration of the visual conditions coincided with the appearance of intermediate cichlid phenotypes, likely due to the increased costs of mate choice and to random mating becoming more effective in terms of fitness. This is understandable if we consider that sexual selection in these species is strongly based on colouration, and reduced visual conditions make recognising conspecifics more difficult and costlier (Seehausen *et al.*, 1997a; Seehausen & van Alphen, 1998). As a consequence, in just three years, between 1984 and 1987, more than 200 endemic cichlid species were lost in Lake Victoria (Seehausen *et al.*, 1997b).

The strong focus on visual cues as a mate selection criterion is common in freshwater fish species, and has been demonstrated in other contexts as well, where hybridisation is not directly involved, as in Trinidad guppies. Female guppies, in clear headwater streams, assess

males on the basis of frequency of display and bright colouration, but, in lowland turbid streams, female cooperation is not needed, as males thrust their gonopodium toward the female's genital pore (Luyten & Liley, 1985, 1991).

However, eutrophication and turbidity do not necessarily arise as a consequence of an introduced predator. Increased eutrophication levels in shallow coastal waters are influencing the breeding behaviour of the threespine stickleback, *Gasterosteus aculeatus*. Where the growth of filamentous algae is higher, the variation in number of eggs between nests is lower (Candolin, 2004; Candolin *et al.*, 2007). This happens because of the lower variation in male mating behaviour, which, in turn, is probably due to the relaxed sexual selection, considering the poorer visual conditions (Candolin, 2004; Candolin *et al.*, 2007). In turbid waters, stickleback courtship effort is reduced as well (Wong *et al.*, 2007). Females spend significantly more time in assessing potential males in clear waters, although the final decision seems to be independent of the water turbidity (Wong *et al.*, 2007). This would suggest that other cues, not only visual, are involved in mate choice (Engström-Öst & Candolin, 2007). On the other hand, male sticklebacks exhibit less aggressive behaviour towards other males when visual conditions are poor, making their parental care more efficient, as they can devote more energy to it. Moreover, better oxygen conditions in the presence of an artificially increased amounts of phytoplankton mean that the egg hatching rate is higher (Candolin *et al.*, 2008).

In another fish of a bisexual-unisexual species complex, male sperm from *Poecilia latipinna* is used by females of the species *P. formosa* to trigger embryogenesis (i.e. sexual parasitism). Reproduction for *P. latipinna* males can either be with conspecifics or with heterospecific females. The time males spent in assessing their potential partner is significantly reduced in conditions of turbid water, but did not influence the rate of the costly heterospecific matings (Heubel & Schlupp, 2006).

An experimental study by Sundin *et al.* (2010) on the broad-nosed pipefish (*Syngnathus typhle*) brought further evidence that an increase in water turbidity was related to a decrease in the time that males used to spend assessing females before mating. This suggests that the disturbance factor may impair the possibility for visually based mate choice (Sundin *et al.*, 2010).

In the sand goby, *Pomatoschistus minutus*, in conditions of clear water larger males have much higher mating chances. However, in turbid waters, sexual selection operated by females is more relaxed, and mating success is more independent of the dimensions of males

(Järvenpää & Lindström, 2004). This experiment, despite not being directly related to a case of hybridisation, is interesting in showing the effects of eutrophication on a mating system.

Another key factor which is worth mentioning is the loss of environmental heterogeneity. One of the possible outcomes of this phenomenon is that two species, previously geographically or ecologically isolated, come into contact and potentially hybridise (Seehausen *et al.*, 2008b). This loss of ecological opportunities can have eutrophication among its causes, as in the case of the European whitefish in Swiss lakes. Environmental homogenisation is thus pivotal for reverse speciation to take place (Vonlanthen *et al.*, 2012).

The examples cited above showed that eutrophication and water turbidity are certainly among the main factors responsible for increased hybridisation rates in aquatic environments. However, two species of swordtail fish *Xiphophorus birchmanni* and *X. malinche* started hybridising during the 1990s, as a result of human-induced hormonal disruption. The newly formed hybrid population exhibited strong assortative mating under certain circumstances, but, under other conditions, reproductive isolation was compromised, suggesting plasticity of reproductive barriers of certain hybrid *taxa* (Rosenthal, 2013; Schumer *et al.*, 2017). In particular, the preference for conspecifics was lost in conditions of presence in water of high levels of humic acid, due to the presence of sewage effluents and agricultural drainage water. It is therefore believed that the pollutant can interfere with the chemical communication system of swordtail fish (Fisher *et al.*, 2006).

Examples of hybridisation are present in other classes of vertebrates as well. Among amphibians, in northern Spain, Perez's frog (*Pelophylax perezi*) commonly hybridises with the green frog (*P. esculentus* complex), but in central Spain the latter does not occur naturally. This represents a natural geographical reproductive barrier, and thus the subsequent introduction of the green frog in central Spain is a major cause for concern for hybridisation in an area where it does not occur naturally (Arano *et al.*, 1995).

Among birds, the white-headed duck (*Oxyura leucocephala*) went through a conspicuous reduction of its range during the 20th century. It is currently recovering, however, still classified as "endangered" by the International Union for Conservation of Nature (Green & Hughes, 2001). Furthermore, the North American ruddy duck (*O. jamaicensis*) managed to escape from breeding facilities, in the United Kingdom, and reached Spain, where the white-headed duck is present. There, the two species have been shown to hybridise. Hence, the presence of the North American ruddy duck in Spain currently

constitutes a threat to the genetic integrity of the white-headed duck (Muñoz-Fuentes *et al.*, 2007).

Habitat change in the Chatman Islands was deemed to be responsible for an expansion of the range of the red-fronted parakeet (*Cyanoramphus novaezelandiae*) into the range of the yellow-crowned parakeet (*C. auriceps*). This, in turn, provoked an increase of the hybridisation rate between the two species (Cade, 1983).

In the Galápagos Islands, the recent disappearance of the large tree finch (*Camarhynchus psittacula*) and evident signs of hybridisation between the medium tree finch (*C. pauper*) and the small tree finch (*C. parvulus*), have been associated with the establishment of a human settlement on the island, just before Charles Darwin's visit in 1835 (Grant & Grant, 2014b).

Among mammals, the coyote and the grey wolf have been found to hybridise in areas which were previously forested, but were later devoted to agriculture. The grey wolf is usually found in forests, while the coyote prefers prairies and open environments. This probably indicates that the hybrid swarm that has originated is more adapted to the new changing environment (Lehman *et al.*, 1991; Wayne *et al.*, 1998). Also, the African savannah elephant (*Loxodonta africana*) and the African forest elephant (*L. cyclotis*) have shown signs of introgressive hybridisation, both during the Holocene, and, more recently, as a consequence of deforestation in the transition areas between their environments (Roca *et al.*, 2005). In both cases, environmental change and homogenisation were the origin of the hybridisation events.

Finally, an example of how climate change can increase hybridisation rates between allopatric species comes from insects. The distribution ranges of the eastern swallowtail (*Papilio glaucus*) and the Canadian tiger swallowtail (*P. canadensis*) only overlap to a small extent. Lately, as a consequence of climatic change, the eastern swallowtail range expanded northwards into the Canadian tiger swallowtail's range. The result was the formation of a hybrid *taxon* characterised by a delayed adult emergence phenotype (Scriber & Ordning, 2005; Scriber *et al.*, 2008). The late flight of the adult hybrids happens when the flight of the parental species has ended. This helps the hybrid populations to maintain their reproductive isolation (Mercader *et al.*, 2009).

CONCLUSION

Hybridisation is a widespread phenomenon that occurs naturally and can have different consequences, from enhancing speciation mechanisms, to maintaining species diversity, to promoting reverse speciation. Nonetheless, human activities are contributing, through different mechanisms, to an artificial increase of hybridisation rates between different species in different ecosystems, and this is particularly prevalent in freshwater environments.

A first challenge in conservation biology is to understand the causes of hybridisation events, and to distinguish between the ones that occur spontaneously, and the ones that are a response to anthropogenic factors. In the first case, conservation measures should be enforced to protect the ecosystem equilibria, whereas, in the second case, attempts to mitigate the effects of human activities should be made (Allendorf *et al.*, 2001).

In freshwater environments, most of the hybridisation examples reported in literature were due to increased levels of eutrophication and turbidity. In the light of this consideration, the recent increment of these two parameter values should be considered, and greater efforts should be put into practice to prevent eutrophication.

Among vertebrates, the class from which more cases of naturally occurring hybridisation have been reported, is fish. Therefore, considering that fishes might be more prone than other organisms to mating with heterospecifics, a concern should be raised about the introduction of non-native species of fish that has been carried out extensively worldwide, and that might be, in many unstudied ecosystems, pivotal to forms of non-natural hybridisation (Campton, 1987; Smith, 1992).

Environmental homogenisation is going on, together with the transition from natural to managed systems. The loss of biodiversity is ongoing, and is challenging to stop. Therefore, together with efforts aimed at maintaining genetic diversity, it is of fundamental importance that conservationists put into practice concrete actions aiming at the maintenance of the “ecological mechanisms that generate and maintain species diversity at the evolutionary front” (Seehausen, 2006a).

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LITERATURE CITED

- ALLENDORF F.W., LEARY R.F., SPRUELL P. & WENBURG J.K. (2001). The problems with hybrids: setting conservation guidelines. *Trends in Ecology & Evolution*, 16: 613-622.
- ARANO B., LLORENTE G., GARCÍA-PARIS M. & HERRERO P. (1995). Species translocation menaces Iberian waterfrogs. *Conservation Biology*, 9: 196-198.
- ARNOLD M.L. (2015). Divergence with genetic exchange. Oxford University Press, Oxford, England, United Kingdom.
- ARTHUR N.J. & DYER K.A. (2015). Asymmetrical sexual isolation but no postmating isolation between the closely related species *Drosophila suboccidentalis* and *Drosophila occidentalis*. *BMC Evolutionary Biology*, 15: 38.
- BARLUENGA M., STÖLTING K.N., SALZBURGER W., MUSCHICK M. & MEYER A. (2006). Sympatric speciation in Nicaraguan crater lake cichlid fish. *Nature*, 439: 719-723.
- BARTON N.H. (2013). Does hybridization influence speciation? *Journal of Evolutionary Biology*, 26: 267-269.
- BARTON N.H. & DE CARA M. (2009). The evolution of strong reproductive isolation. *Evolution*, 63(5): 1171-1190.
- BARTON N.H. & HEWITT G.M. (1985). Analysis of hybrid zones. *Annual Review of Ecology, Evolution, and Systematics*, 16: 113-48.
- BEHM J.E., IVES A.R. & BOUGHMAN J.W. (2010). Breakdown in postmating isolation and collapse of a species pair through hybridization. *American Naturalist*, 175: 11-26.
- BERNATCHEZ L., COLOMBANI F. & DODSON J.J. (1991). Phylogenetic relationships among the subfamily Coregoninae as revealed by mitochondrial DNA restriction analysis. *Journal of Fish Biology*, 39(Suppl. A): 283-290.
- BIERNE N., WELCH J., LOIRE E., BONHOMME F. & DAVID P. (2011). The coupling hypothesis: why genome scans may fail to map local adaptation genes. *Molecular Ecology*, 20: 2044-2072.
- BRELSFORD A., MILÁ B. & IRWIN D.E. (2011). Hybrid origin of Audubon's warbler. *Molecular Ecology*, 20: 2380-2389.
- BUTLIN R.K. & SMADJA C.M. (2018). Coupling, reinforcement, and speciation. *The American Naturalist*, 191: 155-172.
- CADE T.J. (1983). Hybridization and gene exchange among birds in relation to conservation. In: Schonewald-Cox C.M., Chambers S.M., MacBryde B. & Thomas L. (eds.). Genetics and conservation: a reference manual for managing wild animal and plant populations. Benjamin/Cummings Publishing Co. Inc., Menlo Park, California, United States of America, 288-309.
- CAHILL J.A., HEINTZMAN P.D., HARRIS K., TEASDALE M.D., KAPP J., SOARES A.E.R., STIRLING I., BRADLEY D., EDWARDS C.J., GRAIM K., KISLEIKA A.A., MALEV A.V., MONAGHAN N., GREEN R.E. & SHAPIRO B. (2018). Genomic evidence of widespread admixture from polar bears into brown bears during the last ice age. *Molecular Biology and Evolution*, 35: 1120-1129.
- CAMPTON D.E. (1987). Natural hybridization and introgression in fishes: methods of detection and genetic interpretations. In: Ryman N. & Utter F. (eds.). Population genetics and fishery management. University of Washington Press, Seattle, Washington, United States of America, 161-192.
- CANDOLIN U. (2004) Effects of algae cover on egg acquisition in male three-spined stickleback. *Behaviour*, 141: 1389-1399.

- CANDOLIN U., ENGSTRÖM-ÖST J. & SALESTO T. (2008). Human-induced eutrophication enhances reproductive success through effects on parenting ability in sticklebacks. *Oikos*, 117: 459-465.
- CANDOLIN U., SALESTO T. & EVERS M. (2007). Changed environmental conditions weaken sexual selection in sticklebacks. *Journal of Evolutionary Biology*, 20: 233-239.
- COYNE J.A. & ORR H.A. (2004). Speciation. Sinauer Associates Inc., Sunderland, Massachusetts, United States of America.
- DOBZHANSKY T. (1941). Genetics and the origin of species. Columbia University Press, New York City, New York, United States of America, 350.
- DOBZHANSKY T. (1970). Genetics of the evolutionary process. Columbia University Press, New York City, New York, United States of America.
- DOKULIL M. (2014). Impact of climate warming on European inland waters. *Inland Waters*, 4(1): 27-40.
- VAN DOORN G.S., NOEST A.J. & HOGEWEG P. (1998). Sympatric speciation and extinction driven by environment dependent sexual selection. *Proceedings of the Royal Society B: Biological Sciences*, 265: 1915-1919.
- DOPMAN E.B., ROBBINS P.S. & SEAMAN A. (2010). Components of reproductive isolation between North American pheromone strains of the European corn borer. *Evolution*, 64: 881-902.
- DOWLING T.E. & SECOR C.L. (1997). The role of hybridization and introgression in the diversification of animals. *Annual Review of Ecology, Evolution, and Systematics*, 28: 593-619.
- ENDLER J.A. (1986). Natural selection in the wild. Princeton University Press, Princeton, New Jersey, United States of America.
- ENGSTRÖM-ÖST J. & CANDOLIN U. (2007). Human-induced water turbidity alters selection on sexual displays in sticklebacks. *Behavioral Ecology*, 18: 393-398.
- FISHER H.S., WONG B.B.M. & ROSENTHAL G.G. (2006). Alteration of the chemical environment disrupts communication in a freshwater fish. *Proceedings of the Royal Society B: Biological Sciences*, 273: 1187-1193.
- GARRIGAN D., KINGAN S.B., GENEVA A.J., ANDOLFATTO P, CLARK A.G., THORNTON K.R. & PRESGRAVES D.C. (2012). Genome sequencing reveals complex speciation in the *Drosophila simulans* clade. *Genome Research*, 22: 1499-1511.
- GENNER M.J. & TURNER G.F. (2005). The mbuna cichlids of Lake Malawi: a model for rapid speciation and adaptive radiation. *Fish and Fisheries*, 6: 1-34.
- GENNER M.J. & TURNER G.F. (2012). Ancient hybridization and phenotypic novelty within lake Malawi's cichlid fish radiation. *Molecular Biology and Evolution*, 29: 195-206.
- GILMAN R.T. & BEHM J.E. (2011). Hybridization, species collapse, and species reemergence after disturbance to premating mechanisms of reproduction isolation. *Evolution*, 65: 2592-2605.
- GOW J.L., PEICHEL C.L. & TAYLOR E.B. (2006). Contrasting hybridization rates between sympatric three-spined sticklebacks highlight the fragility of reproductive barriers between evolutionarily young species. *Molecular Ecology*, 15: 739-752.
- GRANT P.R. & GRANT B.R. (2014a). 40 years of evolution: finches on Daphne Major island. Princeton University Press, Princeton, New Jersey, United States of America.
- GRANT P.R. & GRANT B.R. (2014b). Evolutionary biology: speciation undone. *Nature*, 507(7491): 178-179.
- GRANT P.R., GRANT B.R. & PETREN K. (2005). Hybridization in the recent past. *The American Naturalist*, 166: 56-67.

- GREEN A.J. & HUGHES B. (2001). White-headed duck *Oxyura leucocephala*. In: Parkin D.B. (ed.). BWP Update: the journal of birds of the Western Palearctic. Oxford University Press, Oxford, England, United Kingdom, 3: 79-90.
- HALAS D. & SIMONS A.M. (2014). Cryptic speciation reversal in the *Etheostoma zonale* (Teleostei: Percidae) species group, with an examination of the effect of recombination and introgression on species tree inference. *Molecular Phylogenetics and Evolution*, 70: 13-28.
- HARRIS K. & NIELSEN R. (2016). The genetic cost of Neanderthal introgression. *Genetics*, 203: 881-891.
- HENDRY A.P., TAYLOR E.B. & McPHAIL J.D. (2002). Adaptive divergence and the balance between selection and gene flow: lake and stream stickleback in the Misty system. *Evolution*, 56: 1199-1216.
- HERDER F., NOLTE A.W., PFAENDER J., SCHWARZER J., HADIATY R.K. & SCHLIEWEN U.K. (2006). Adaptive radiation and hybridization in Wallace's dreamponds: evidence from sailfin silversides in the Malili Lakes of Sulawesi. *Proceedings of the Royal Society B: Biological Sciences*, 273: 2209-2217.
- HERMANSEN J.S., SÆTHER S.A., ELGVIN T.O., BORGE T., HJELLE E. & SÆTRE G.P. (2011). Hybrid speciation in sparrows I: phenotypic intermediacy, genetic admixture and barriers to gene flow. *Molecular Ecology*, 20: 3812-3822.
- HEUBEL K.U. & SCHLUPP I. (2006). Turbidity affects association behaviour in male *Poecilia latipinna*. *Journal of Fish Biology*, 68: 555-568.
- HUDSON A.G., VONLANTHEN P., MÜLLER R. & SEEHAUSEN O. (2007). Review: the geography of speciation and adaptive radiation in coregonines. *Advances in Limnology*, 60: 111-146.
- JÄRVENPÄÄ M. & LINDSTRÖM K. (2004). Water turbidity by algal blooms causes mating system breakdown in a shallow-water fish, the sand goby *Pomatoschistus minutus*. *Proceedings of the Royal Society B: Biological Sciences*, 271: 2361-2365.
- JOYCE D.A., LUNT D.H., BILLS R., TURNER G.F., KATONGO C., DUFTNER N., STURMBAUER C. & SEEHAUSEN O. (2005). An extant cichlid fish radiation emerged in an extinct Pleistocene lake. *Nature*, 435: 90-95.
- KAUTT A.F., MACHADO-SCHIAFFINO G. & MEYER A. (2016). Multispecies outcomes of sympatric speciation after admixture with the source population in two radiations of Nicaraguan crater lake cichlids. *PLOS Genetics*, 12(6): e1006157.
- KRAAK S.B.M., MUNDWILER B. & HART P.J.B. (2001). Increased number of hybrids between benthic and limnetic three-spined sticklebacks in Enos Lake, Canada; the collapse of a species pair? *Journal of Fish Biology*, 58: 1458-1464.
- LACKEY A.C. & BOUGHMAN J.W. (2017). Evolution of reproductive isolation in stickleback fish. *Evolution*, 71(2): 357-372.
- LAMICHHANEY S., HAN F., WEBSTER M.T., ANDERSSON L., GRANT B.R. & GRANT P.R. (2018). Rapid hybrid speciation in Darwin's finches. *Science*, 359(6372): 224-228.
- LANCASTER M.L., GEMMELL N.J., NEGRO S., GOLDSWORTHY S. & SUNNUCKS P. (2006). Ménage à trois on Macquarie Island: hybridization among three species of fur seal (*Arctocephalus* spp.) following historical population extinction. *Molecular Ecology*, 15: 3681-3692.
- LARSEN S., ANDERSEN T.O.M. & HESSEN D.O. (2011). Climate change predicted to cause severe increase of organic carbon in lakes. *Global Change Biology*, 17(2): 1186-1192.
- LEHMAN N., EISENHAWER A., HANSEN K., MECH L.D., PETERSON R.O., GOGAN P.J.P. & WAYNE R.K. (1991). Introgression of coyote mitochondrial DNA into sympatric North American gray wolf populations. *Evolution*, 45: 104-119.

- LUYTEN P.H. & LILEY N.R. (1985). Geographic variation in the sexual behaviour of the guppy, *Poecilia reticulata* (Peters). *Behaviour*, 95: 164-179.
- LUYTEN P.H. & LILEY N.R. (1991). Sexual selection and competitive mating success of males guppies (*Poecilia reticulata*) from four Trinidad populations. *Behavioral Ecology and Sociobiology*, 28: 329-336.
- MAYR E. (1942). Systematics and the origin of species. Columbia University Press, New York City, New York, United States of America.
- McKINNON J.S. & RUNDLE H.D. (2002). Speciation in nature: the threespine stickleback model systems. *Trends in Ecology and Evolution*, 17: 480-488.
- McPHAIL J.D. (1994). Speciation and the evolution of reproductive isolation in the sticklebacks (*Gasterosteus*) of southwestern British Columbia. In: Bell A.M. & Foster S.A. (eds.). The evolutionary biology of the threespine stickleback. Oxford University Press, Oxford, England, United Kingdom, 400-437.
- MEIER J.I., MARQUES D.A., MWAICO S., WAGNER C.E., EXCOFFIER L. & SEEHAUSEN O. (2017). Ancient hybridization fuels rapid cichlid fish adaptive radiations. *Nature Communications*, 8: 1-11.
- MENDELSON T.C. (2003). Sexual isolation evolves faster than hybrid inviability in a diverse and sexually dimorphic genus of fish (Percidae: *Etheostoma*). *Evolution*, 57(2): 317-327.
- MERCADER R.J., AARDEMA M.L. & SCRIBER J.M. (2009). Hybridization leads to host-use divergence in a polyphagous butterfly sibling species pair. *Oecologia*, 158: 651-662.
- MONTEITH D.T., STODDARD J.L., EVANS C.D., DE WIT H.A., FORSIUS M., HØGÅSEN T., WILANDER A., SKJELKVÅLE B.L., JEFFRIES D.S., VUORENMAA J., KELLER B., KOPÁČEK J. & VESELY J. (2007). Dissolved organic carbon trends resulting from changes in atmospheric deposition chemistry. *Nature*, 450(7169): 537-540.
- MOSER F.N. & WILSON A.B. (2020). Reproductive isolation following hybrid speciation in Mediterranean pipefish (*Syngnathus* spp.). *Animal Behaviour*, 161: 77-87.
- MUÑOZ-FUENTES V., VILA C., GREEN A.J., NEGRO J.J. & SORENSON M.D. (2007). Hybridization between white-headed ducks and introduced ruddy ducks in Spain. *Molecular Ecology*, 16(3): 629-638.
- NEVADO B., KOBLMÜLLER S., STURMBAUER C., SNOEKS J., USANO-ALEMANY J. & VERHEYEN E. (2009). Complete mitochondrial DNA replacement in a Lake Tanganyika cichlid fish. *Molecular Ecology*, 18: 4240-4255.
- NOSIL P., HARMON L.J. & SEEHAUSEN O. (2009). Ecological explanations for (incomplete) speciation. *Trends in Ecology and Evolution*, 24: 145-156.
- ORSUCCI M., AUDIOT P., POMMIER A., RAYNAUD C., RAMORA B., ZANETTO A., BOURGUET D. & STREIFF R. (2016). Host specialization involving attraction, avoidance and performance, in two phytophagous moth species. *Journal of Evolutionary Biology*, 29: 114-125.
- RANGANATH H.A. & ARUNA S. (2003). Hybridization, transgressive segregation and evolution of new genetic systems in *Drosophila*. *Journal of Genetics*, 82(3): 163-177.
- RHYMER J.M. & SIMBERLOFF D. (1996). Extinction by hybridization and introgression. *Annual Review of Ecology and Systematics*, 27(1): 83-109.
- RICHARDS E.J. & MARTIN C.H. (2017). Adaptive introgression from distant Caribbean islands contributed to the diversification of a microendemic adaptive radiation of trophic specialist pupfishes. *PLOS Genetics*, 13(8): e1006919.
- RIESEBERG L.H. (1997). Hybrid origins of plant species. *Annual Review of Ecology and Systematics*, 28: 359-389.

- RIESEBERG L.H., ARCHER M.A. & WAYNE R.K. (1999). Transgressive segregation, adaptation and speciation. *Heredity*, 83: 363-372.
- RIESEBERG L.H., RAYMOND O., ROSENTHAL D.M., LAI Z., LIVINGSTONE K., NAKAZATO T., DURPHY J.L., SCHWARZBACH A.E., DONOVAN L.A. & LEXER C. (2003). Major ecological transitions in wild sunflowers facilitated by hybridization. *Science*, 301: 1211-1216.
- ROCA A.L., GEORGIADIS N. & O'BRIEN S.J. (2005). Cytonuclear genomic dissociation in African elephant species. *Nature Genetics*, 37: 96-100.
- ROSENTHAL G.G. (2013). Individual mating decisions and hybridization. *Journal of Evolutionary Biology*, 26: 252-255.
- ROULET N. & MOORE T.R. (2006). Environmental chemistry: Browning the waters. *Nature*, 444(7117): 283-284.
- ROY M.S., GEFFEN E., SMITH D. & WAYNE R.K. (1996). Molecular genetics of pre-1940 red wolves. *Conservation Biology*, 10: 1413-1424.
- RUNDLE H.D. & NOSIL P. (2005). Ecological speciation. *Ecology Letters*, 8: 336-352.
- SANKARARAMAN S., MALLICK S., DANNEMANN M., PRÜFER K., KELSO J., PÄÄBO S., PATTERSON N. & REICH D. (2014). The genomic landscape of Neanderthal ancestry in present-day humans. *Nature*, 507: 354-357.
- SCHLUTER D. (2000). The ecology of adaptive radiation. Oxford University Press, Oxford, England, United Kingdom.
- SCHULER H., HOOD G.R., EGAN S.P. & FEDER J.L. (2016). Modes and mechanisms of speciation. *Reviews in Cell Biology and Molecular Medicine*, 2(3): 60-93.
- SCHUMER M., POWELL D.L., DELCLÓS P.J., SQUIRE M., CUI R., ANDOLFATTO P. & ROSENTHAL G.G. (2017). Assortative mating and persistent reproductive isolation in hybrids. *Proceedings of the National Academy of Sciences of the United States of America*, 114(41): 10936-10941.
- SCHWARZBACH A.E., DONOVAN L.A. & RIESEBERG L.H. (2001). Transgressive character expression in a hybrid sunflower species. *American Journal of Botany*, 88(2): 270-277.
- SCRIBER J.M. & ORDING G.J. (2005). Ecological speciation without host plant specialization; possible origins of a recently described cryptic *Papilio* species. *Entomologia Experimentalis et Applicata*, 115: 247-263.
- SCRIBER J.M., ORDING G.J. & MERCADER R.J. (2008). Introgression and parapatric speciation in a hybrid zone. In: Tilmon K.J. (ed.). *Specialization, speciation, and radiation: the evolutionary biology of herbivorous insects*. University of California Press, Berkeley, California, United States, 69-87.
- SCRIBNER K.T., PAGE K.S. & BARTRON M.L. (2001). Hybridization in freshwater fishes: a review of case studies and cytonuclear methods of biological inference. *Reviews in Fish Biology and Fisheries*, 10: 293-323.
- SEEHAUSEN O. (2006a). Conservation: losing biodiversity by reverse speciation. *Current Biology*, 16: 334-337.
- SEEHAUSEN O. (2006b). African cichlid fish: a model system in adaptive radiation research. *Proceedings of the Royal Society B: Biological Sciences*, 273(1597): 1987-1998.
- SEEHAUSEN O. & VAN ALPHEN J.J.M. (1998). The effect of male coloration on female mate choice in closely related Lake Victoria cichlids (*Haplochromis nyererei* complex). *Behavioral Ecology and Sociobiology*, 42: 1-8.
- SEEHAUSEN O., VAN ALPHEN J.J.M. & WITTE F. (1997a). Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science*, 277: 1808-1811.

- SEEHAUSEN O., TAKIMOTO G., ROY D. & JOKELA J. (2008b). Speciation reversal and biodiversity dynamics with hybridization in changing environments. *Molecular Ecology*, 17(1): 30-44.
- SEEHAUSEN O., TERA I Y., MEGALHAES I.S., CARLETON K.L., MROSSO H.D.J., MIYAGI R., VAN DER SLUIJS I., SCHNEIDER M.V., MAAN M.E., TACHIDA H., IMAI H. & OKADA N. (2008a). Speciation through sensory drive in cichlid fish. *Nature*, 455: 620-627.
- SEEHAUSEN O., WITTE F., KATUNZI E.F.B., SMITS J. & BOUTON N. (1997b). Patterns of the remnant cichlid fauna in southern Lake Victoria. *Conservation Biology*, 11: 890-905.
- SELZ O.M. & SEEHAUSEN O. (2019). Interspecific hybridization can generate functional novelty in cichlid fish. *Proceedings of the Royal Society B: Biological Sciences*, 286: 20191621.
- SERVEDIO M.R. & NOOR M.A.F. (2003). The role of reinforcement in speciation: theory and data. *Annual Review of Ecology, Evolution, and Systematics*, 34: 339-364.
- SLATKIN M. & LANDE R. (1994). Segregation variance after hybridization of isolated populations. *Genetic Research*, 64: 51-56.
- SMADJA C.M. & BUTLIN R.K. (2011). A framework for comparing processes of speciation in the presence of gene flow. *Molecular Ecology*, 20: 5123-5140.
- SMITH G.R. (1992). Introgression in fishes - significance for paleontology, cladistics, and evolutionary rates. *Systematic Biology*, 41: 41-57.
- SMITH P.F., KONINGS A. & KORNFIELD I. (2003). Hybrid origin of a cichlid population in Lake Malawi: implications for genetic variation and species diversity. *Molecular Ecology*, 12: 2497-2504.
- SMITH S.H. (1964). Status of the deepwater cisco population of Lake Michigan. *Transactions of the American Fisheries Society*, 93: 115-163.
- SOLOMON C.T., JONES S.E., WEIDEL B.C., BUFFAM I., FORK M.L., KARLSSON J., LARSEN S., LENNON J.T., READ J.S., SADRO S. & SAROS J.E. (2015). Ecosystem consequences of changing inputs of terrestrial dissolved organic matter to lakes: current knowledge and future challenges. *Ecosystems*, 18: 376-389.
- STEBBINS G.L. (1950). Variation and evolution in plants. Columbia University Press, New York City, New York, United States of America.
- STELKENS R.B., SCHMID C., SELZ O. & SEEHAUSEN O. (2009). Phenotypic novelty in experimental hybrids is predicted by the genetic distance between species of cichlid fish. *BMC Evolutionary Biology*, 9: 283.
- SUNDIN J., BERGLUND A. & ROSENQVIST G. (2010). Turbidity hampers mate choice in a pipefish. *Ethology*, 116: 713-721.
- TAYLOR E.B., BOUGHMAN J.W., GROENENBOOM M., SNIATYNSKI M., SCHLUTER D. & GOW J.L. (2006). Speciation in reverse: morphological and genetic evidence of the collapse of a three-spined stickleback (*Gasterosteus aculeatus*) species pair. *Molecular Ecology*, 15: 343-355.
- TAYLOR E.B. & PIERCEY R.S. (2018). Going, going, gone: evidence for loss of an endemic species pair of threespine sticklebacks (*Gasterosteus aculeatus*) with implications for protection under species-at-risk legislation. *Conservation Genetics*, 19(2): 297-308.
- TODD T.N. & STEDMAN R.M. (1989). Hybridization of ciscoes (*Coregonus* spp.) in Lake Huron. *Canadian Journal of Zoology*, 67: 1679-1685.
- VIA S. (2009). Natural selection in action during speciation. *Proceedings of the National Academy of Sciences of the United States of America*, 106: 9939-9946.

- VONHOLDT B.M., CAHILL J.A., FAN Z., GRONAU I., ROBINSON J., POLLINGER J.P., SHAPIRO B., WALL J. & WAYNE R.K. (2016). Whole-genome sequence analysis shows that two endemic species of North American wolf are admixtures of the coyote and gray wolf. *Science Advances*, 2(7): e1501714.
- VONLANTHEN P., BITTNER D., HUDSON A.G., YOUNG K.A., MÜLLER R., LUNDGAARD-HANSEN B., ROY D., DI PIAZZA S., LARGIADER C.R. & SEEHAUSEN O. (2012). Eutrophication causes speciation reversal in whitefish adaptive radiations. *Nature*, 482: 357-362.
- WAYNE R.K., ROY M.S. & GITTLEMAN J.L. (1998). Origin of the red wolf: response to Nowak and Federoff and Gardener. *Conservation Biology*, 12: 726-729.
- WEYHENMEYER G.A., MÜLLER R.A., NORMAN M. & TRANVIK L.J. (2016). Sensitivity of freshwaters to browning in response to future climate change. *Climatic Change*, 134(1-2): 225-239.
- WHITEHEAD P.G., WILBY R.L., BATTARBEE R.W., KERNAN M. & WADE A.J. (2009). A review of the potential impacts of climate change on surface water quality. *Hydrological Sciences Journal*, 54(1): 101-123.
- WIEGAND K.M. (1935). A taxonomist's experience with hybrids in the wild. *Science*, 81: 161-166.
- WILSON A.B. & ORR J.W. (2011). The evolutionary origins of Syngnathidae: pipefishes and seahorses. *Journal of Fish Biology*, 78(6): 1603-1623.
- WIRTZ P. (1999). Mother species - father species: unidirectional hybridization in animals with female choice. *Animal Behaviour*, 58: 1-12.
- WONG B.B.M., CANDOLIN U. & LINDSTRÖM K. (2007). Environmental deterioration compromises socially enforced signals of male quality in three-spined sticklebacks. *The American Naturalist*, 170: 184-189.
- WU C.I. (2001). The genic view of the process of speciation. *Journal of Evolutionary Biology*, 14: 851-865.

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