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Interspecies gene flow is a key evolutionary process for the adaptation of long-lived species to new environmental conditions

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RESUMEN

La especiación por hibridación y la hibridación introgresiva entre especies del mismo género se reconocen cada vez más como un mecanismo que contribuye a la generación de novedades evolutivas y a la promoción de amplitud de nicho ecológico. En especies de larga vida caracterizadas por una evolución lenta, el flujo génico interespecífico puede constituir un proceso adaptativo más eficiente que la fijación de mutación. Este supuesto se evalúa a partir de una gran muestra de estudios de casos sobre hibridación natural en las denominadas plantas y animales Matusalén. La longevidad favorece las variables del comportamiento de apareamiento a largo del tiempo y según las condiciones locales, puede explicar las altas tasas de hibridación observadas regularmente en estas especies. En raras ocasiones, la hibridación da como resultado la creación de especies híbridas poliploides y homoploides compuestas por individuos que muestran segregación transgresiva de los rasgos parentales. Se ha demostrado que mediante hibridación introgresiva, se transfieren frecuentemente grandes conjuntos de nuevos alelos de una especie a otra, a veces codificantes para caracteres adaptativos importantes, aumentando así el potencial evolutivo de las poblaciones afectadas sin alterar la integridad de las especies, haciendo que la hibridación introgresiva sea el mecanismo evolutivo más efectivo para responder a los principales cambios ambientales en especies de larga vida. Se aportan sugerencias para mejorar las estrategias de conservación de estas especies mediante la evaluación del potencial evolutivo de las zonas híbridas y la identificación de las poblaciones capaces de responder al rápido cambio climático.

Palabras clave: Flujo génico interspecifico, adaptación, especie de largo ciclo de vida.

Recibido/Received: 2/10/2017; Aceptado/Accepted: 10/12/2017; Publicado en línea/Published online: 20/12/2017

ABSTRACT

Hybrid speciation and introgressive hybridization between congeneric species are being increasingly recognised as important contributors to the generation of evolutionary novelty and to the promotion of niche-width expansion. In long-lived species characterized by slow evolution, interspecific gene flow may constitute a more efficient adaptive process than mutation fixation. This assumption is evaluated from a large survey of case studies regarding natural hybridization in Methuselah plants and animals. Longevity which favours variable mating behaviours over time and according to local conditions may explain the high hybridization rates observed regularly in these species. On rare occasions, hybridization resulted in the creation of polyploid and homoploid hybrid species composed of individuals showing transgressive segregation of parental traits. More frequently, large sets of new alleles, sometimes coding for important adaptive characters, were shown to be transferred from one species to another through introgressive hybridization, thus increasing the evolutionary potential of the concerned populations without altering species integrity, making introgressive hybridization the most effective evolutionary mechanism to respond to major environmental changes in long-lived species. Suggestions are made to improve the conservation strategies for these species by evaluating the evolutionary potential of hybrid zones and identifying the populations able to respond to rapid climate change.

Key words: Interspecies gene flow, adaptation, long-lived species.

INTRODUCTION

It is generally accepted that species' survival depends directly on their ability for adaptive evolution that is also a key component of range expansion (Pfennig *et al.*, 2016). In each species, populations survive environmental change due to the production of alleles and epialleles for traits that are adaptive to the new environment. These may arise by mutation or from gene flow from conspecific populations or related taxa. This phenomenon of interspecies hybridization is now considered to be widespread in plants and animals (Abbott *et al.*, 2013). It generally occurs according to the scenario schematised in Figure 1. First generation hybrid individuals (F1) are produced from the initial cross between two parental species. In the absence of polyploidization which may create an immediate reproductive isolation between the hybrids and their parent species, the F1 individuals usually backcross to parent genotypes at a much higher frequency than hybrid individuals (Yakimowski & Rieseberg, 2014). Continued mating of the fittest genotypes (*i. e.*, those with the highest fecundity) with parental genotypes is recognised as an important process for interspecific gene exchange (Yakimowski & Rieseberg, 2014; Canestrelli *et al.*, 2016). If genome stabilisation occurs after a few backcross generations, homoploid hybrid species may arise, providing they develop sufficient reproductive isolation and/or they can colonise niches unavailable to their parents. Extensively repeated backcrossing, a phenomenon known as introgressive hybridization, may ultimately result in the transfer of new alleles and epialleles, and/or novel gene combinations between the hybridising species, and increase genetic variation that can then be selected to augment fitness.

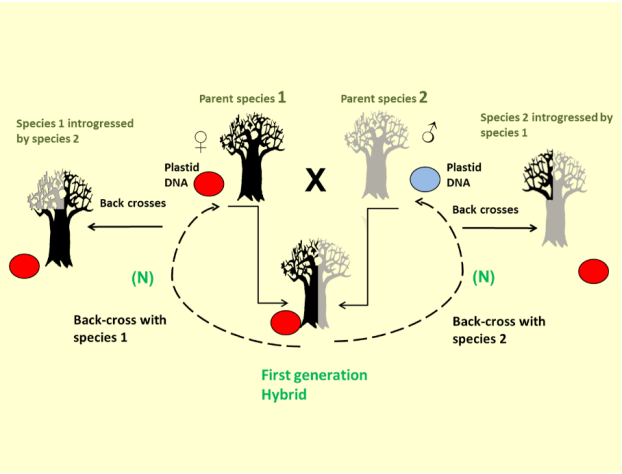

Figure 1. Schematic scenario showing initial hybridization and subsequent multiple (N) back-cross generations between species. In this scenario, maternal plastid DNA inheritance is assumed.

According to theoretical predictions (Orr & Unckless, 2008), local adaptation to environmental change, more particularly at the range edge, is unlikely to result from mutations because of the considerable time necessary for the occurrence and the spread of favourable mutations in the concerned populations. Conversely, local adaptation is theoretically expected and has indeed been found to result mostly from admixture, more particularly from the hybridization of congeneric species (Abbott *et al.*, 2013; Stelkens *et al.*, 2014). In recent years, interspecific admixture involving repeated introgression in contact areas has been shown to be a facilitator of species range expansion by creating genetic variation that allows populations to adapt to selective pressures, either through the transfer of specific adaptive alleles, the selection of novel gene-combinations facilitating evolutionary innovation, or through the local increase of genetic and epigenetic diversity that allows the persistence of threatened populations (or species) and/or the creation of the conditions for further adaptation (Bräutigam *et al.*, 2013; Pfennig *et al.*, 2016).

In plants as in animals, most long-lived species are large organisms characterized by slow rates of evolution, when compared to species with faster generation turnover (Smith & Donoghue, 2008; Thomas *et al.*, 2010). In addition to genetic inertia due to low replacement rates in the populations, the slow molecular evolution observed in long-lived species has been mainly attributed to the accumulation of lethal mutations during life (Zhong *et al.*, 2014). Interspecies gene flow through hybridization could therefore be expected to be crucial for adaptation to rapid environmental changes in these species.

In the present review, this assumption is evaluated from a large survey of case studies in long-lived plants and animals. More specifically, the review addresses the following questions: (1) Is interspecies hybridization frequent and widespread in these species? (2) What are the main evolutionary outcomes of hybridization in terms of speciation and genetic introgression?, (3) How effective are interspecific isolation barriers with respect to hybridization?, (4) What do we know about the adaptive effect of interspecific gene flow in long-lived species, and (5) What are the impacts of human-induced environmental disturbances and climate change on natural interspecific hybridization on these species? The final objective is to inventory current scientific knowledge regarding the natural evolution of long-lived species in order to guide their conservation, while preserving and making the best use of their adaptive potential, particularly in view of their survival in the context of changing climate.

IS INTERSPECIES HYBRIDIZATION FREQUENT AND WIDESPREAD IN LONG-LIVED SPECIES?

In the present survey, case studies reporting natural interspecies hybridization identified or confirmed by using molecular data were considered in millenary and centenary species, except in those characterized by exclusive or very predominant clonal reproduction. For animals, case studies regarding species living 50 years or more were also included (Table 1). For vertebrate species, lifespans refer to Carey & Judge (2000). As the species concept is not uniform in plants as in animals, in a few cases indicated with asterisks in the table 1, hybridization between long-lived subspecies or ecotypes were added to the list, as they clearly share many characteristics with species, such as genetic and ecological differences, as well as assorting mating. A good example is provided by genus *Orcinus* (killer whales) that formally comprised a single cosmopolitan species including several well differentiated ecotypes which were considered to be distinct species by several authors (Morin *et al.*, 2010; Riesch *et al.*, 2012). Finally, the numerous case studies regarding human-mediated contacts between species (e. g. controlled crosses or unintentional introduction of non-native species) were not considered in the survey.

Table 1. Total number of millenary (M), centenary (C), and long-lived animal species (L) involved in interspecific hybridization as inferred from molecular analysis, with their genus and organism type. In each genus, the number of new allopolyploid and homoploid species resulting from hybridization, introgressive hybridization cases, and evidence for adaptive variation (+) are also shown (see the text for details).

Genus	Life span	Species No	Polyploid species	Homoploid species	Introgressive hybridization	Adaptive variation	Reference
Osmunda (fern)	C	5	1	3 (e)	1	-	[1-3]
Polysticum (fern)	C	4	-	-	2	+	[4-5]
Araucaria (conifer)	C	4	-	-	2	-	[6]
Taxus (yew / conifer)	M	3	-	-	2	-	[7]
Cupressus (cypress/ conifer)	C /M	2	-	-	2	-	[8]
Juniperus (juniper/ conifer)	C	21	-	-	9	-	[9-14]
Larix (larch/ conifer)	C/M	5	-	-	3	-	[15-16]
Abies (fir / conifer)	C	10	-	-	4	-	[17-22]
Picea (spruce/ conifer)	C	10	-	1(a)	6	+	[23-30]
Pinus (pine/ conifer)	C	20	-	3(a)	8	+	[31-41]
Adansonia (baobab)	M	4	-	1(a)	4	+	[42]
Platanus (plane tree)	M	3	-	-	2	-	[43]
Ficus (fig tree)	C/M	9	-	-	4	-	[44-46]
Olea (olive tree)	C/M	4*	1	-	1	-	[47-48]
Fraxinus (ash tree)	C	2	-	-	1	+	[49-52]
Fagus (beech tree)	C	2*	-	-	1	-	[53-54]
Quercus (oak tree)	C	42	-	2(b)	22	+	[55-73]
Betula (birch tree)	C	5	1	-	3	-	[74-75]
Eucalyptus (eucalyptus)	C	42	-	-	31	+	[76-81]
Populus (poplar tree)	C/M	13	-	-	8	+	[82-92]
Yucca (agave)	C	4*	-	1(b)	1	-	[93-94]
Opuntia (cactus)	C	20	10	-	-	-	[95-96]
Strongylocentrotus (urchin)	L	2	-	-	1	-	[97-98]
Bathymodiolus (mussel)	L	4	-	-	2	+	[99-101]
Anguilla (eel)	L	2	-	-	1	-	[102-103]
Sebastes (rockfish)	L	15	-	-	8	-	[104-111]
Acipenser (sturgeon)	L /C	20	11	-	-	-	[112]
Somniosus (shark)	C	2	-	-	1	-	[113]
Crocodylus (crocodile)	L	2	-	-	1	-	[114]
Chelonoidis (giant tortoise)	C	2	-	-	1	-	[115-116]
Chelonia/*Eretmochelys* (turtle)	L	4	-	-	3	-	[117-118]
Emys (terrapin)	L	4 +2*	-	-	3	-	[119-120]
Trachemys (terrapin)	L	10	-	-	4	-	[121]
Larus (gull)	L	3	-	-	2	-	[122-123]
Phoebastria (albatross)	L	2	-	-	1		[124]
Amazona (parrot)	L	2*	-	-	1	-	[125]
Psittacus (parrot)	L	2*	-	-	1	-	[126]
Balaenoptera (whale)	L/C	2	-	-	1	-	[127]
Globicephala (pilot whale)	L	2	-	-	1	-	[128-129]
Orcinus (killer whale)	L/C	2**	-	-	1	-	[130-131]
Stenella (dolphin)	L	2	-	1(c)	1	-	[132]
Loxodonta (elephant)	L	2	-	-	1	-	[133]
Ursus (bear)	L	2	-	-	1	-	[134]
Pan (chimpanzee)	L	2	-	-	1	-	[135]
Homo (human)	L/C	2	-	-	1	+	[136-138]

* Subspecies, ** Ecotypes (see the text for details). Origin of reproductive isolation between homoploid hybrid and parent species: habitat divergence (a), temporal divergence (b), assortative mating behaviour (c), geographic isolation (d), unknown (e).

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As shown in Table 1, interspecific hybridization involves a large range of plant and animal species and is particularly high in genera *Juniperus, Abies, Picea* and *Pinus* (conifers), *Quercus, Eucalyptus* and *Populus* (hardwood trees), *Opuntia* (cactus), *Sebastes* and *Acipenser* (fish genera) and *Trachemys* (terrapin). All these genera include numerous long-lived species. The number of species indicated in Table 1 is probably an underestimate owing to the large number of interspecific hybridizations reported in the past, exclusively on the basis of morphology, e. g. in oaks (Rushton, 1993). Moreover, in long-lived plant and animal species, e. g. in oaks (Staudt *et al.*, 2004) and in geoemydid turtles (Fujii *et al.*, 2014), natural hybridization between exotic and congeneric native or naturalised species has often been reported

to occur relatively rapidly after the known time of introduction, indicating a favourable aptitude for hybridization.

Theory predicts that, besides species intrinsic properties regarding pre-zygotic barriers and post-zygotic isolation forces (see Vallejo-Marin & Hiscock, 2016, for a review), interspecies hybridization depends on environmental factors, more specifically the habitat and climate conditions, determining the relative abundance of species and the relative frequency of gametes involved in intra- and interspecific reproduction (Cannon & Lerdau, 2015; Klein *et al.*,2017). In long-lived species predominantly consisting of large primarily outcrossing organisms with slow replacement rate (see above), under unfavourable environmental conditions, individual's survival is generally favoured over their reproductive investment (Bromham, 2011). As reported by Morris *et al.* (2008), the presence of a persistent adult stage should allow long-lived species to better tolerate yearly fluctuations in reproduction, including local or occasional fecundity decrease, which may result from inter-species hybridization in contact areas. In addition, longevity should increase the opportunity to produce interspecific hybrids from highly compatible parental individuals.

OUTCOMES OF HYBRIDIZATION IN LONG-LIVED SPECIES

As also reported for shorter-lived organisms (Mallet, 2008), hybridization rarely leads to speciation in long-lived species (Table 1). Speciation by allopolyploidy is restricted to very few species of ferns of the genus *Osmunda* (Sigel, 2016) and hardwood trees, namely in *Olea* (Besnard *et al.*, 2008) and *Betula* (Tsuda *et al.*, 2017), but is generalised in *Opuntia* (cactus) (Majure *et al.*, 2012). In animals, this mode of speciation is found exclusively in sturgeons where it has been confirmed for most the species of the *Acipenser* genus (Mable *et al.*, 2011 and references therein). Fish are generally reported to be prone to form reproductively successful hybrids and, except in Salmonidae, the allopolyploid origin of numerous species, specifically those that reproduce in freshwater environments, has been confirmed and was attributed to environmental variability during the breeding season that should increase the production of unreduced gametes (Mable *et al.*, 2011).

In long-lived plant species, homoploid hybrid speciation was reported in several genera, with a single hybrid species identified in most of them, except in ferns, pines and oaks, where a maximum of three homoploid species were formally identified (Table 1). In long lived animals, a single case of homoploid speciation has been documented in a dolphin genus (Amaral *et al.*, 2014). Homoploid hybrid speciation is considered to be rare both in plants and animals, likely because it requires several restrictive conditions, *i.e.*, the arising of a stable, fertile and reproductively isolated hybrid lineage without change in chromosome number (Vallejo-Marin & Hiscock, 2016). Reproductive isolation between parental and hybrid taxa may be achieved by diverse evolutionary processes. Habitat divergence was identified as the isolating factor in several homoploid hybrid species, e.g., in *Picea purpurea* Mast. (Sun *et al.*, 2014), *Pinus densata* Mast. (Wang *et al.*, 2011), *P. funebris* Kom., *P. takahasii* Nakai (Ren *et al.*, 2012), and in *Adansonia alb*a Jum. & H. Perr. (Leong Pock Tsy *et al.*, 2013). A change in flowering phenology compared to the parental species was observed in *Quercus afares* Pomel (Mir *et al.*, 2006) and *Yucca gloriosa* L. (Rentsch & Leebens-Mack, 2012), whereas ethological isolation was suggested for *Stenella clymene* Cray (the clymene dolphin) (Amaral *et al.*, 2014) (Table 1). As reported by Mavárez & Linares (2008), detecting hybrid species still remains a challenge despite the numerous genetic resources available for testing their occurrence, including the possibility of analysing DNA from fossils, and in spite of the effective statistical methods developed recently to distinguish hybridization from incomplete lineage sorting (Wen *et al.*, 2016). Hybrid species are lineages with mixed ancestry and their identification depends on the use of diagnostic markers whose rate is expected to increase with divergence between the parental hybridizing species while the probability of successful interspecific cross increases with species' genetic relatedness. Moreover, identifying the source of reproductive isolation of homoploid species needs coordinated multidisciplinary approaches combining genetic, morphological, geographical

and eco-physiological data, which explains why few groups of long-lived organisms have been the subject of such detailed investigation to date.

Introgressive hybridization is by far the most common outcome of hybridization in long-lived species and it involves a large range of plant and animal genera (Table 1). In several case studies reported recently, e.g., in the genera *Araucaria* (Gaudeul *et al.*, 2014), *Picea* (Halmilton & Aitken, 2013), *Anguilla* (Wielgos *et al.*, 2014) and *Phoebastria* (albatross) (Rohwer *et al.*, 2014), introgressive hybridization was either revealed or confirmed decisively by using high-resolution cytoplasmic and nuclear molecular markers (e. g. DNA sequencing in very recent years) in the analysis of the same individuals, in combination with their morphological variation and geographic distribution. Introgressive hybridization was often observed in secondary contacts between congeneric species and was associated with past or current range expansions during which gene introgression is theoretically expected to occur, predominantly from the resident species to the invading one (Currat *et al.*, 2008). By using cytoplasmic markers, this prediction was verified in several long-lived taxa, namely between *Phoenobastria nigripes* Audubon and *P. immutabilis* Rothschild (Rohwer *et al.*, 2014), *Quercus suber* L. and *Q. ilex* L. (Lumaret & Jabbour-Zahab, 2009 and references therein), in three pairs of *Eucalyptus* species (Mc Kinnon *et al.*, 2004a, 2004b), and between *Populus fremontii* S. Watts. and *P. angustifolia* James (Currat *et al.*, 2008 and references therein). In their genetic analysis of hybrid zones between two spruce species, Du *et al.* (2011) reported that introgression was very significant and occurred from *Picea likiangensis* (franch.) E. Pritz (the resident species) into *P. purpurea* Mast. (the expanding species) for the maternally inherited mitochondrial (mt) DNA characterized by low gene flow via seeds. However, bidirectional and more limited introgression was identified for chloroplast (cp) DNA paternally inherited and transmitted at a higher rate, thus suggesting that the extent of introgression varies according to the rate of intraspecific gene flow. For nuclear markers, the prediction of Currat *et al.* (2008) was verified in several empirical studies regarding long-lived species, e.g. between *Anguilla anguilla* L. and *A. rostrata* Lesueur (Wielgos *et al.*, 2014), between *Populus fremontii* S. watts. and *P. angustifolia* James (Currat *et al.*, 2008 and references therein), or between *Betula pubescens* Ehrh (a tetraploid invading species) and two diploid resident species, *B. nana* L. and *B. pendula* Roth (Zohren *et al.*, 2016). In oaks, similar rates of bidirectional nuclear introgression were obtained on average between Quercus suber L. and *Q. ilex* L. when the species were analysed over their whole range, but substantial variation was identified according to *loci* and contact areas (Lumaret & Jabbour-Zahab, 2009). The direction of introgression between *Quercus robur* L. and *Q. petrae* (Matt.) Liebl. which are sympatric European oak species was also found to match the theoretical prediction but exclusively at *loci* influenced by selection (outlier *loci*). These would therefore be more appropriate to make inferences about past demographic processes than non-outlier *loci* (Guichoux *et al.*, 2013).

HOW EFFECTIVE ARE THE INTERSPECIFIC ISOLATING BARRIERS IN LONG-LIVED SPECIES?

In several recent studies, both intrinsic and extrinsic factors acting as either pre-zygotic or post-zygotic barriers were shown to contribute to the maintenance of long-lived species boundaries, although their respective strength may vary between the first- and later generation hybrids. For instance, a strong assortative mating pattern acting as a prezygotic barrier was discovered in first-generation hybrids between *Pinus pumila* and *P. parviflora*, as the combined result of flowering time differences and cross incompatibility (Ito *et al.*, 2008). Genetic introgression between the two species was the consequence of a breakdown of these prezygotic barriers and the occurrence of unselective mating in the subsequent generations through backcrossing between hybrids and parental species (Ito *et al.*, 2008). In oaks, as compared to post-zygotic barriers (germination rate and early survival), prezygotic barriers (specifically gametic incompatibility), were shown to be predominantly responsible for reproductive isolation between the species (Lepais *et al.*, 2013). Conversely, in poplars and eucalypts, intrinsic post-zygotic

barriers were revealed to be strong and persistent in advanced-generation hybrids, accounting for most reproductive isolation in these tree species (Larcombe *et al.*, 2016; Christe *et al.*, 2016). In animals, reproductive isolation is mostly due to prezygotic barriers, more particularly to geographical isolation which increases genetic differentiation (Faure *et al.*, 2009; Pujolar *et al.*, 2014), habitat segregation, as observed in rockfishes (Buonaccorsi *et al.*, 2011), and mating behaviour, as revealed in the gulls of the *Larus* complex (Sonsthagen *et al.*, 2016). In these last species, the reinforcement of prezygotic barriers was identified as being the result of past episodes of hybridization inducing the selection of protective barriers against hybridization.

IS HYBRIDIZATION AN EFFICIENT PROCESS FOR THE GENERATION OF ADAPTIVE VARIATION IN LONG-LIVED SPECIES?

As a consequence of a mixture between very different parental genomes, large amounts of genetic variation and new genetic combinations potentially of functional significance are expected to occur in the genomes of early-generation hybrids. As admixed populations return to equilibrium, this genetic variation decreases substantially and stabilizes through the fixing of chromosomal blocks, leading to genomes characterized by stable admixed ancestry over subsequent generations (see Ungerer *et al.*, 1998 for details). During the process, the transgressive segregation of parental traits may promote the development of characters outside the parental phenotypic range in hybrid populations/species that allow them to thrive in new environments.

In long-lived species, the transgressive segregation of parental characters was invoked to explain the extreme morphological characteristics of the hybrid dolphin species *Stenella clymene* Gray (Amaral *et al.*, 2014), and the unique ecological traits and the extreme habitats of *Pinus densata* Mast. In this last species, ecological divergence was considered to be a more important driver than geographical isolation (Mao & Wang, 2011). When grown in a common garden and analysed for several metabolic functions (volatile terpene emissions, freezing tolerance), *Quercus afares* Pomel, a deciduous oak species derived from hybridization between an evergreen species, *Q. suber* L., and a deciduous species, *Q. canariensis* Willd. (Mir *et al.*, 2006), was revealed to possess extreme physiological traits indicative of better adaptation to cold conditions as compared with its parental species (Cavender-Bares *et al.*, 2005; Welter *et al.*, 2012). Moreover, the species was reported to be more sensitive to excessive soil moister than *Q. canariensis* Willd., its deciduous parent species (Teissier *et al.*, 1994). The hybrid species currently grows in the lowest part of the altitudinal distribution of *Q. canariensis* L., which occupies many upper sites characterised by low temperatures and very high precipitation rates, specifically in early spring (Messaoudène *et al.*, 2007). Thus, in *Q. afares* Pomel, the transgressive segregation of parental traits for cold adaptation likely did not contribute to reproductive isolation which is currently provided by an intermediate flowering time of the hybrid species between those of its parents. The transgressive traits observed in *Q. afares* Pomel may constitute an evolutionary potential to thrive in colder and drier environments in the event of climate change.

Although introgressive hybridization is relatively common in long-lived species, its adaptive significance has been demonstrated in a restricted number of case studies and rarely in animals (Table 1). Most of the early studies were based on the finding of true diagnostic alleles between two ecologically divergent hybridizing species and required extensive sampling from both species' natural ranges. Therefore, many early analyses of hybrid zones between long-lived species were conducted with a restricted number of genetic markers and, most often, without linkage information. In these studies, e. g. in ferns (Kenter *et al.*, 2000), spruces (Hamilton *et al.* 2013), poplars (Vanden Broek *et al.*, 2005 and references therein), ash tree species (Gerard *et al.*, 2013), mussels (Faure *et al.*, 2009), eucalypts (Mc Kinnon *et al.*, 2010) and pine species (Cullingham *et al.*, 2012), parallel morphological and genetic clines showing variation according to loci and indicative of allele filtering were obtained in replicated transects along environmental gradients, suggesting an important role for extrinsic selection in the genetic structuring and maintenance

of hybrid zones between long-lived species. In recent years, the development of genetic mapping of species differences and the application of novel analytical techniques to molecular data have provided access to a genome wide panel of codominant nuclear markers. As a consequence, the detection of adaptive genetic variation in hybrid zones was substantially improved with the possibility to identify large numbers of candidate loci for local adaptation (outlier loci), including markers sourced from expressed sequence tags (EST-derived markers) coding for known functional traits. Thus, in a secondary contact between two recently diverged North American poplar species, combined genomic and functional approaches were performed on pure and admixed populations. Evidence of adaptive introgression was obtained from the direct association between the introgression of a *Populus balsamifera* L. (balsam poplar) DNA fragment containing alleles for local adaptation into *P. trichocarpa* Torr. & A. Gray (black cottonwood) and the simultaneous expression of the corresponding adaptive traits in the latter species (Suarez-Gonzalez *et al.*, 2016). Moreover, J. Degner presented the results from a recent study of genomic clines in a mosaic hybrid zone between *Picea engelmannii* Parry and *P. glauca* (Moench) Voss in Western Canada (Holliday *et al.* (2017). Disproportionate introgression of single nucleotide polymorphism markers (SNPs) related to climate variables were found in hybrid individuals and, in a given environment, these hybrids possessed disproportionately introgressed alleles from the parental species that best matched their habitat. For genus *Homo*, complex statistical methods were recently developed to identify archaic introgressed fragments in the genome sequences of modern humans. Strong evidence of the adaptive genetic introgression of Neanderthal DNA sequences into the modern human gene pool was obtained for several genes involved in various metabolic functions, e. g., defence against pathogens, pigmentation, response to hypoxia at high elevations and lipid catabolism (see Racimo *et al.*, 2015 for a review). Despite recurrent gene exchanges within contact zones, specific genomic regions remain refractory to interspecies gene flow so that the genetic differences characterizing parental species identity are maintained, as shown by detailed investigations in several case studies, e. g., in poplars (Christe *et al.*, 2016), oaks (Ortego *et al.*, 2017), rockfishes (Buonaccorsi *et al.*, 2011) and gulls (Sonsthagen *et al.*, 2016).

IMPACTS OF HUMAN-INDUCED ENVIRONMENTAL DISTURBANCES AND CLIMATE CHANGE ON INTERSPECIFIC HYBRIDIZATION.

Beyond introductions of exotic species (not considered in this review), different forms of anthropogenic disturbance (land-use alterations, habitat disturbance) and climate change have been shown to facilitate the formation of hybrids in long-lived species by eroding premating reproductive isolating barriers, in accordance with the Anderson & Stebbins' (1954) disturbance hypothesis. For instance, in oaks, Ortego *et al.* (2017) found a significant increase in hybridization between *Quercus durata* Jeps. and *Q. berberidifolia* Liebm. with increasing wildfire frequency. Recent forest destruction was also considered to be responsible for higher hybridization between the forest elephant (*Loxodonta cyclotis* Matschie) and the savannah elephant (*L. Africana* Cuvier) (Ishida *et al.*, 2011), and between several sea turtle species due to the warming of their nesting beaches and that caused drastic local population collapses (Vilaça *et al.*, 2012). During past and current global warming episodes, several cases of hybridization occurred between the polar bear (*Ursus maritimus* Phipps) and the grizzly bear (*U. arctos* L.) following the northward expansion of the grizzly bear's range (Cahill *et al.*, 2015). Recent sea warming was also considered to be responsible for an increase in introgressive hybridization in rockfish (Sahat *et al.*, 2017) and in pilot-whales by creating overlaps between the species' habitats during the reproduction season (Miralles *et al.*, 2016).

CONCLUSIONS AND OUTLOOK

For any species, phenotypic plasticity and migration constitute the most immediate responses to environmental changes, including global warming, as shown recently in European white oaks (Truffaut

et al., 2017). An effective adaptive evolutionary response or evolutionary rescue is necessary to respond to more persistent and/or drastic environmental changes and allow long-term species persistence (Gonzalez *et al.*, 2012). However, theory predicts that, even in species characterized by large populations and with minimal stochastic effects, population rescue will take a minimum of 25 generations (Bell & Gonzalez, 2009), making species with long generation times unsuitable for such evolutionary recovery (Vander Wal *et al.*, 2013) leading some authors to recommend assisted migration to facilitate gene flow in long-lived species (Carlson *et al.*, 2014). Recently, introgressive hybridization has been suggested to have the potential to generate the diversity necessary to respond more rapidly to a changing environment, and the identification, genetic study and conservation of hybridization zones was advocated as a useful management option to preserve species' evolutionary potential (Baskett & Gomulkiewicz, 2011; Hamilton & Miller, 2016).

The numerous case studies examined in the present review clearly show that natural hybridization is widespread in long-lived species, specifically in plants, although its importance is probably underestimated in animals (Hedrick, 2013). This review also indicates that interspecies hybridization rarely results in new polyploid and homoploid species but, when it does, they are often comprised of individuals showing transgressive segregation of parental traits. Much more frequently, large sets of new alleles at multiple *loci*, sometimes coding for important adaptive characters, were shown to be transferred from one species to another through introgressive hybridization, increasing the evolutionary potential of the concerned populations, without alteration of species integrity. Evolutionary change was often exhibited within a few generations, possibly making introgressive hybridization the most effective evolutionary mechanism for response to major environmental changes by long-lived species. These species are mostly comprised of large organisms that constitute ecologically and economically important species (e. g. forest and fruit trees and large animals, including several threatened species), thus justifying particular attention in conservation programs. Owing to increased rates of climate change, conservation strategies should consider, in addition to parent species, current hybridization zones, and after they have been identified by using molecular markers, all of the populations derived from past introgressive hybridization and which predominantly exhibit advanced-generation hybrids (*i. e.* cryptic genetic variation as exemplified in Fig. 2). In addition, the evolutionary potential of the populations derived from hybridization should be evaluated carefully by conducting coordinated genetic and eco-physiological studies so that the conservation of the genetic resources best able to respond effectively to major environmental changes can be prioritized. Thereby, natural, adaptive evolution of long-lived species can be facilitated and appropriate genetic resources be available for rescue operations for endangered species or for the rational management of new areas e.g., by reforestation.

Figure 2. Cryptic genetic variation in the baobabs of Madagascar: this very large, millenary tree grows in the *Adansonia rubrostipa* Jum. & H. Perrier population of the Tsimanampetsotse National Park, along the south-western coast of the island (Patrut *et al.*, 2015). By using nuclear microsatellites as markers, the tree was revealed to be one of the several second-generation hybrids between *A. rubrostipa* and *A. za* Baill. identified at the site. Both parental species are endemic to the island, have distinct geographical ranges and differ in important adaptive traits (Leong Pock Tsy *et al.*, 2013). (Photo: R. Lumaret)

ACKNOWLEDGMENTS

I am very grateful to Gregory T. Sullivan for useful comments that greatly improved the manuscript.

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Este número ha recibido una ayuda del Vicerrectorado de Investigación y Transferencia de Conocimiento de la Universidad de Alicante

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