



Wildlife hybrids: Insights into the European approach

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ABSTRACT

Anthropogenic hybridization is a main driver of wildlife population dynamics and evolution. However, the phenomenon is poorly addressed in international legislation and is managed in different ways at country level. There is still a lack of clear and consistent regulations on hybrids. The present article explores the legal framework for wildlife hybrids in Europe and the uncertainties surrounding their legal status, focusing on wolf-dog hybrids and Italy as case studies. Remarks are proposed regarding the evolution of the approach to the management of hybrids, considering different scenarios, including the (questionable) entrusting of a wolf-dog hybrid animal to a private individual.

1. Introduction

Hybridization and the introgression of foreign genes into wild populations are phenomena that increasingly threaten the conservation of biodiversity [1]. In fact, hybrids are specimens generated by individuals from two different lineages through genetic mixing, which can result in the loss of parental species identity and genetic uniqueness [1,2]. While natural hybridization is a process that is now widely recognized as being of evolutionary importance [3–10], anthropogenic hybridization, or human-mediated gene flow, is a major conservation concern because it is considered to be one of the main drivers of (un)natural population dynamics and evolution in many wild species, with a range of consequences that can lead to forms of decline in wildlife taxa (species, subspecies and locally adapted populations), including genetic extinction [1,11–15].

Despite its seriousness and the fact that it affects many species, the impact of “unnatural” hybridization is not fully addressed by policies and legal instruments. EU legislation as well as national legislation offer neither clear statements nor detailed guidelines regarding hybrids, ranging between ensuring the protection of parental species and permitting the protection of wild-born hybrid specimens. The term “hybrid” is not even well defined in law and when it is explicitly considered in the Official Notes on Interpretation of the Rules laid down in the EU Regulations on the Protection of Species of Wild Fauna and Flora (Commission Regulation (EU) 2023/966 [16]), no proper definition is given, but rather a description that refers to its inclusion or exclusion from the purposes of the Regulations themselves.

An effective comprehensive strategy on how to manage

hybridization and hybrids still lacks, and even standardized genetic methods are still needed [17,18]. Furthermore, despite some discouraging recommendations (see Recommendation No. 173/2014 of the Standing Committee of the Bern Convention on wolf-dog hybrids [19]), the law does not clearly state whether a hybrid animal may be kept by private individuals as an alternative to licensed rescue centers.

This article examines the situation in Europe, exploring how the phenomenon is being tackled at the European level, with a focus on the Italian legal framework, and the need to strengthen specific policies. Based on a case that occurred in Italy and was decided by the Italian Council of State, the situation of the possession of a hybrid animal as a companion animal is presented, after an analysis of the relevant legal framework. Remarks are proposed on the need to deepen the reflection on the current conservation policies and the desirability of their evolution, not forgetting, where necessary, the thoughtful consideration of individual animals and not only populations.

2. Materials and methods

This article proposes an assessment of the legal frameworks that address the issue of hybridization at the European level, with particular reference to the European Union’s Habitats Directive [20], the Bern Convention on European Wildlife and Natural Habitats [21], and the European Regulations on the Protection of Species of Wild Fauna and Flora, which implement the principles of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) [22].

On this basis, the legal status of hybrids in Europe has been examined

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in order to find guidance on the definition of “hybrid”, taking into account the position of the Standing Committee of the Bern Convention, through its relevant recommendations on hybridization of wild animals, and of the CITES Conference of the Parties (COP), which provides a definition of hybrid for the purposes of the CITES Convention.

In addition, the Convention on Biological Diversity (CBD) [23] and the position of the International Union for the Conservation of Nature (IUCN) have been considered in order to address the position of hybrids more comprehensively in relation to the objectives of species conservation.

The issue of hybridization and species protection was addressed, highlighting its unresolved characteristics and the fact that it is also linked to the need to interpret the current legal provisions. To this end, the existence of relevant European jurisprudence and relevant European Commission guidelines was explored.

The technical challenges and limitations still faced by science in the study of hybridization have been considered in relation to the difficulty of dealing with the legal definition of hybrids and the management of hybridization, assuming that both the legal meaning of “what is a hybrid” and the rules and methods chosen to manage hybridization suffer from the technical difficulties of defining the results of analytical procedures and their interpretation; and also raise ethical challenges. Consider, for example, how the different conceptual frameworks used to identify hybrids affect their categorization and decisions about whether and how to target them for management. While, in terms of management, how different are the consequences for animals of reactive management versus measures designed to prevent hybridization.

The Italian legal framework and the issue of wolf-dog hybridization have been selected as case studies, considering an emblematic case of Italian administrative jurisprudence decided by the Italian Council of State, in order to make the analysis more concrete.

3. Results and discussion

3.1. Anthropogenic hybridization

Human activities that cause disturbances and habitat loss have impacted natural resource conservation and pose new challenges to species conservation and management [24,25]. From hunting to human population growth, from global climate change to land use and land cover change, from farming and livestock production to commercial trade, anthropogenic actions are threatening wildlife species and populations around the world [26–28]. This is particularly challenging when it comes to risks posed to the conservation of the intraspecific genetic diversity of species that have evolved and adapted to local ecosystems over thousands of years [25]. In fact, anthropogenic hybridization is a result of unnatural admixture, translocation and anthropogenic environmental change, which causes human-induced gene flow when different populations with heritable traits interbreed [29]. This leads to the erosion of the genetic integrity of species and potentially drives native species to extinction through lasting impacts on locally adapted populations or native species [11].

A direct human contribution to hybridization is the intentional and unintentional introduction of non-native organisms into areas and habitats where they have never occurred naturally [30–32]. This is at the root of interbreeding between genetically distinct species and subspecies, which promotes the disruption of genetically adapted complexes and raises concerns about the survival of entire evolutionary units [30,32,33]. Furthermore, anthropogenic hybridization has been frequently reported as a form of interbreeding between domesticated populations and their wild relatives [34,35].

Hybridization is therefore a challenging issue to address, from the complexity of distinguishing between anthropogenic and natural hybridization, to the diversity of situations that need to be managed through legal and conservation efforts.

3.2. The legal status of hybrids in Europe

The issue of hybridization concerns the conservation of biodiversity. It would therefore be expected that the legal instruments governing biodiversity would address this phenomenon.

Indeed, there are few regulations in Europe that deal specifically with the status of hybrid animals.

In fact, the two most important documents concerning the preservation of the quality of the environment and providing a comprehensive framework for the protection of wild fauna - namely the Convention on the Conservation of European Wildlife and Natural Habitats (Bern Convention), European Treaty Series no. 104 [21], and the Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora (Habitats Directive) [20], which implements the Bern Convention within the EU - don't contain any provisions directly addressing the position of hybrids or the obligations of Member States with regard to hybridization.

Nevertheless, it is worth noting that they provide a basis for the development and implementation of relevant conservation policies at both international and national levels across Europe [36].

In addition, the issue of hybridization is being addressed by the Bern Convention Standing Committee, the governing body that makes recommendations on measures to be taken to achieve the objectives of the Convention and improve its effectiveness.

On 5 December 2014, the Standing Committee adopted Recommendation No. 173/2014 [19] on hybridization between wild gray wolves (*Canis lupus*) and domestic dogs (*Canis lupus familiaris*), taking into account the objectives of the Convention for the conservation of wild fauna and their natural habitats. This document recalls the challenges posed by hybridization to the conservation status of a species. Referring to a specific species (the gray wolf), the Standing Committee outlined the possibility of taking “adequate measures to monitor, prevent and mitigate hybridization” and to ensure the government-controlled removal of hybrids. The issue of keeping hybrids by private individuals (particularly wolf-dog hybrids) was also addressed, with a recommendation to ban or restrict them.

Similarly, and with a greater sense of urgency, another Recommendation was adopted in 2020 (Recommendation No. 209/2020 [37]) on the eradication of the ruddy duck *Oxyura jamaicensis* (native to the Americas and becoming an invasive species in continental Europe) from the Western Palearctic by 2025, in order to protect populations of *Oxyura leucocephala* (white-headed duck) from the threat of hybridization with this alien species. This recommendation follows a series of previous ones with the same objective (Recommendation No. 48 of the Standing Committee on the conservation of European Globally Threatened Birds, adopted on 26 January 1996 [38]; Recommendation No. 61 (1997) [39] on the Conservation of the White-headed Duck (*Oxyura leucocephala*); Recommendations No. 149 (2010) [40] and No. 185 (2016) [41] of the Standing Committee, on the Eradication of the Ruddy Duck (*Oxyura jamaicensis*) in the Western Palearctic).

More recently, Commission Regulation (EU) 2023/966 [16], amending Council Regulation (EC) No. 338/97 on the protection of species of wild fauna and flora by regulating trade therein, implementing the principles of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) [42], has addressed the issue of hybrids from the perspective of their legal trade and possession, while consolidating the interpretation of the Annexes, as follows:

“Hybrids may be specifically included in the Appendices but only if they form distinct and stable populations in the wild. Hybrid animals that have in their previous four generations of the lineage one or more specimens of species included in Annexes A or B shall be subject to this Regulation just as if they were full species, even if the hybrid concerned is not specifically included in the Annexes.”

Thus, a degree of protection is given to hybrids, albeit under specific

conditions. Furthermore, Article 2(1)(t) of Regulation (EC) No 338/97 [42] explicitly states that:

“A specimen will be considered to be a specimen of a species listed in Annexes A to D if it is, or is part of or derived from, an animal or plant at least one of whose ‘parents’ is of a species so listed. In cases where the ‘parents’ of such an animal or plant are of species listed in different Annexes, or of species only one of which is listed, the provisions of the more restrictive Annex shall apply”.

This means that a hybrid produced from an animal listed in one of the Annexes to the Regulation and another animal not listed in one of the Annexes is equivalent for all legal purposes to an animal listed in the Annexes and is therefore fully subject to all the consequences of such listing.

A description similar to that of Commission Regulation (EU) 2023/966 [16], which provides guidance on what is a “hybrid” for the purposes of a practical management of these animals, is contained in a Resolution on hybrids adopted by the CITES Conference of the Parties (COP) to fill a legal gap in the framework established by the Convention on International Trade of Endangered Species of Wild Fauna and Flora to protect species from the adverse effects of international trade [43], and to ensure the effective protection of the wild species included in the system of protection. This Resolution states that “trade in hybrids of species included in the Appendices should be controlled” and that “hybrid animals that have in their recent lineage one or more specimens of species included in Appendix I or II shall be subject to the provisions of the Convention just as if they were full species, even if the hybrid concerned is not specifically included in the Appendices” (part. b)). A guideline for the interpretation of the words “recent lineage” is provided by the Resolution itself, which states that they “shall generally be interpreted to refer to the previous four generations of the lineage” (part e)). In this way, the COP offers its definition of hybrid and its idea of the recommended treatment of hybrid specimens, which is essentially the same as the statement in Commission Regulation (EU) 2023/966 [16].

It should be noted that where the legislator has intended to allow specific derogations in respect of hybrids, it has done so explicitly: thus in Article 7(1)(b)(iii) of Regulation (EC) No 338/97: “In the case of artificially propagated plants, the provisions of Articles 4 and 5 may be derogated from in accordance with the special rules laid down by the Commission concerning [...] (b) [...] (iii) trade in hybrids”.

However, it is worth noting, both from a legal and practical management perspective, that the generic species protection provisions of the Bern Convention and the Habitats Directive are designed to protect pure species.

Furthermore, in the light of the above-mentioned recommendations of the Standing Committee of the Bern Convention, stricter control, without exceptions and without reference to lineage, is required in the case of hybridization with non-native species listed as invasive alien species of EU concern. See, inter alia, the Goal and Aims of Recommendation No. 209 (2020) [37], which sets out an action plan for the eradication of the ruddy duck in the Western Palearctic, 2021–2025, focusing on: “Ruddy ducks and hybrids of ruddy ducks and white-headed ducks stop being a threat to the white-headed duck” (Goal) and “Ruddy ducks and hybrids of ruddy ducks and white-headed ducks are eliminated in the wild in the Western Palearctic. No ruddy ducks are held in captivity in the Western Palearctic, and no new introductions to the wild occur in the interim” (Aims). In this respect, EU Regulation No. 1143/2014 [44] on the prevention and control of the introduction and spread of the invasive alien species is a relevant legislative instrument in the legal framework that defines the legal status of hybrids when it comes to determining which type of hybrid would fall under which rules.

Another reference to the term “hybrid”, which is not primarily associated with the idea of “conservation”, comes from the Convention on Biological Diversity [23], which requires signatories to maintain the genetic integrity of the biological diversity within their own territories, and identifies anthropogenic hybridization and introgression as major

threats to species conservation.

Similarly, the International Union for the Conservation of Nature (IUCN), the world’s main authority on wildlife conservation, not only excludes hybrids of species from the Red List of Threatened Species [45] but also considers the effects of hybridization on the basis of taxa reduction, in the same line of pathogens, pollutants, competitors or parasites (Criterion A [46]). Hybridization is also included in the IUCN Threats Classification Scheme as a direct threat to the survival of species ([47]). No mention is made of the need to quantify specific impacts.

Thus, despite the inherent complexity of the phenomenon, hybridization is addressed in a not homogeneous and comprehensive manner at European level.

3.3. Hybridization and species conservation: an open question

As anthropogenically-induced hybridization is considered to have a negative impact on the viability of wild parental populations [1], effective management and monitoring activities are required to deal with specimens derived from such a phenomenon.

To this end, three types of intervention are generally envisaged, involving preventive, proactive, and reactive strategies [17]. The implementation of such interventions concerns anticipating the event, taking action by causing a change, and reacting to a change when it occurs. This means taking both passive and active measures to prevent and mitigate hybridization.

The former consist of a system of prohibitions and exceptions, while the latter are usually part of species conservation plans. The need for such measures will vary depending on the species concerned and the circumstances, but nevertheless they should reflect advances in understanding of ecology and evolution while encompassing the welfare of individual animals.

It is important to remember that species are not fixed entities but are constantly evolving. This means that we can’t underestimate the fact that some hybridization is part of the evolutionary process, although in many cases the causes (anthropogenic, or natural) cannot be documented and are difficult to disentangle when the anthropized and natural contexts are not clearly defined. Examples of the difficulty and complexity of defining hybridization types include the need for large genome-wide panels of molecular markers and genetic datasets, or the need for projection models to manage uncertainty by stimulating hybridization dynamics under different biological and ecological scenarios [48–51]. Furthermore, genomic technologies have made it possible to find traces of genetic admixture even in “supposedly purebred” populations where it was unexpected [24].

Thus, quantify hybridization thresholds and outlining the minimum data required to identify a hybrid is challenging [1,52–54].

This should be considered when deciding on conservation efforts using a “pure species” approach”.

In this respect, the case of the Przewalski’s horse (*Equus ferus przewalskii*) is emblematic, where the degree of hybridization with the domestic horse (*Equus caballus*) is prevalent in all populations but has not been opposed to its legal protection. In fact, despite the hybridization, this wild horse is listed in CITES Appendix I and on the IUCN Red List as a separate, wild living taxon [55–57].

This may seem at odds with the application of prevention and mitigation measures for conservation purposes, which often include the detection and removal of hybrids. However, the fact that wild animals that have lost a significant amount of their original genetic diversity are still protected as endangered as their founder population means that specimens of hybrids of other species born in the wild may also be eligible for protection in countries where their parental species is intended to be protected [36].

Another interesting case in the “wild x domestic” category in Europe is hybridization between wolf (*Canis lupus*) and dog (*Canis lupus familiaris*), which has been detected in several wolf populations [58]. Under the Bern Convention and the 1992 EU Habitats Directive, wolves enjoy

'strict protection' status in most of Europe, with the possibility of derogations (Appendix S1 – Table 1). As a result, legislative and administrative measures are in place to conserve wolves, although these may vary between signatory countries (EU members and members of the Council of Europe) that have availed themselves of the opportunity to submit a reservation for such species, including Bosnia and Herzegovina, Bulgaria, Estonia, Finland, Latvia, Lithuania, Montenegro, Romania, Ukraine [59]. The resulting patchwork of legislation, together with the fact that both the Bern Convention and the Habitats Directive do not clearly state that wild-born hybrid specimens are to be regarded as failing under the strict protection regime applicable to wolves where this is provided for, means that it is not certain that all hybrids are included within the scope of the strict protection requirements.

In particular, the question arises as to whether or not they should be considered to benefit the prohibition on killing and capture, and what their fate outside the wild. This is crucial from both a legal and practical management point of view, although it suffers from the different legal status accorded to the wolf and the consequent different reservations and derogations in the Member States, resulting in different protection regimes.

With regard to the interpretation of the main EU legislation in the field of species protection, the European Court of Justice has not explicitly addressed the issue of hybrid specimens and therefore provides no case law that can be used as guidance.

Similarly, the European Commission's general guidance document on the strict protection of animal species under the Habitats Directive [60] does not provide any guidance.

Furthermore, since the Convention allows countries a degree of discretion in determining the "requisite measures" to ensure adequate and necessary (special) protection for the species concerned, the extent to which such measures should be implemented will vary depending on the species and on the different contexts.

In addition to their legal status, a non-secondary aspect concerns the legal definition of hybrids, which in turn depends on the degree of certainty with which hybrids can be identified. At present, the scientific study and detection of hybridization are not easy tasks and pose technical challenges. Meaningful results still require thorough study design and careful data analysis, which need to be interpreted with caution, especially for species recognized as long-distance dispersers, i.e. capable of exhibiting dispersal behaviour that leads them to move outside their resident home range into non-adjacent areas and gain connectivity with other populations, including the opportunity to breed [61,62].

Despite the availability of methodological procedures and reliable tools for the genetic analysis of biological samples, the boundaries between species are often not clearly discernible [63,64,65].

In this context, it is worth highlighting that the LCIE (Large Carnivore Initiative for Europe), in its Guidelines for Population Level Management Plans for Large Carnivores [66], with reference to the state of the art, "acknowledges that it will probably be impossible to ensure that wolf populations are 100 % free from domestic dog genes", and therefore wild-born wolf-dog hybrids should "receive the same legal status as wolves" in order to "close a potential loophole for the irregular killing of wolves". These statements, together with the above-mentioned CITES COP Resolution on hybrids, are relevant in determining whether and when wolf-dog hybrids should be subject to conservation measures, given the current state of scientific knowledge.

It is clear that new tools are needed to address the phenomenon of hybridization. In addition to the desirable prospect of a more thorough understanding of evolutionary relationships [67], a broader acquisition of new knowledge could improve solutions in the future, ranging from advances in genetic and genomic methods to the importance of conducting a deep analysis of the hybrid population to determine the actual causes and consequences of hybridization, from clarifying how to implement environmental policies to considering the fate of hybrids.

3.4. Hybrid identification, between progress and persistent limitations

In the case of conservation concerns due to hybridization, where a parental species is considered to be endangered, the identification of hybrids is essential in determining potential management actions [1, 68].

Decisions on how to manage a species can be made in the light of the results of hybridization detection. Morphological identification is one of the methods available for this purpose, but it faces difficulties of interpretation, is rather ambiguous and can lead to significant biases [69,70]. Genetic studies, on the other hand, are more reliable and can provide substantial information on both recent and ancient hybridization events and forms of genetic admixture, although they are far from easy to perform and have variable discriminatory power (possible errors of inclusion and omission) [71].

The availability and affordability of genetic data facilitates the documentation of population demography and genetic contamination and, in practice, supports the assessment of hybridization at the population scale and the convenient definition of targeted interventions [72–74].

Since the beginning of the 2000s, a number of sensitive genetic tools have been developed, and have become essential to elucidate the eventual need for management actions in a more consistent manner than drawing conclusions based on phenotypic and morphological traits that are difficult to interpret [70,75,76], and indeed individual phenotypic and genetic indicators of hybridization often differ [75,54,77].

Nevertheless, as hinted above, one aspect that should be considered in this framework is that a degree of inherent uncertainty often still affects the identification of wild-domestic hybrids, as well as the classification of individuals as parental or mixed, especially when hybrids are detected using a limited number of genetic markers (e.g. when analyses are based on poor quality DNA samples) [71,76,78–80]. Even the more recent use of genomics in conservation is still mostly limited to a few specific cases due to certain application-specific issues (e.g. cost, availability of genomic resources, technical and infrastructural competence) [81].

As a result, it is not always easy to determine the genetic lineage of wild-domestic hybrids and to distinguish between F1, F2 or later generations, especially in populations where admixture has been ongoing for multiple generations, resulting in complete "hybrid swarms" (e.g. Scottish wildcat) [54]. This problem contributes to the lack of systematic and coordinated management of wolf-dog hybrids across in Europe.

3.4.1. The normative challenge of hybrid definition

Defining hybrids with reliable scientific information is relevant for legal and conservation management [82,76]. Since it involves determining the level at which individuals should be protected by wildlife and habitat legislation, it is probably the most important normative challenge facing conservation management policy [24,70,54].

To stay with the case of the wolf-dog hybrid and the European legal framework, although hybridization is not specifically mentioned in either the Bern Convention or the Habitats Directive, these documents provide some form of protection for wild wolf-dog hybrids [36].

The point is that, while activities such as monitoring the phenomenon and adopting preventive and mitigating measures to deal with hybridization are envisaged, it is not clearly described when hybrids need to be actively controlled. This highlights the difficulty of identifying hybrids and detecting backcrossing, and emphasizes the need to ensure good integration of legal and genetic considerations, so that conservation management regulations are consistent with categories that can realistically be achieved by genetic analysis. Overall, characterizing the genetic nature of wolves and their hybrids continues to be an important aspect of conservation of the species and the integrity of wild populations.

It is worth noting that the CITES guidelines also include wolf-dog hybrids with wolf ancestry within the last four generations under the

protection of wolves although this level of ancestry can be difficult to detect even with advanced methods and high-quality biological samples [70,83]. Harmoinen et al. [84] even state that it is currently impossible to apply management and regulatory requirements to the number of hybrid generations because it is not possible to accurately identify every individual with wolf ancestry within the last four generations. This limits the effectiveness of conservation decisions by creating a mismatch between legal obligations and their practical implementation. It is clear, therefore, that increasingly reliable and convenient genetic tools for defining the proportion of admixture and the thresholds for detecting hybrids as well as the establishment of a standardized genetic evaluation system are crucial for practical decisions.

On the other hand, the relevant legal instruments should be improved in order to mitigate hybridization effectively and in a humanely acceptable manner. In particular, clear guidance should be provided on how to categorize hybrids and how to deal with threats from hybridization in the wild. This should include the possibility to apply for adequate and justified derogations from full species protection for conservation purposes.

3.5. The ethical challenge of hybridization management

The ethical perspective through which hybridization management should be viewed is another relevant issue to consider. Indeed, the options for intervention mainly involve invasive practices, including possible sterilization, trapping, captivity or even lethal control of the spread of hybrid animals (the latter solution is only legal in a few EU countries, e.g. those that have made exceptions or reservations to the strict protection of wolves and allow culling in special cases, such as Austria, Croatia, Norway and Romania), in order to advance conservation goals and mitigate the effects of hybridization. Regardless of the type of intervention approach, the intervention itself has ethical implications that require a prior assessment of the justifiability and feasibility of practical decisions [17]. These characteristics need to be assessed on technical, economic, and social grounds, bearing in mind the importance of the availability of adequate resources and facilities, which are crucial for achieving meaningful results. In addition, public opinion on hybrids should not be underestimated, as emotional issues affecting society can strongly influence decision-making processes. Addressing all these fundamental matters involves considering specific solutions tailored to specific conservation contexts, local legal frameworks, but also public attitudes, and after analysing of all available options [17,24,80,85–87].

Applied to the case of wolf-dog hybrids, for which there is still no standard management practice and which is often highly emotionally controversial, this means that a meaningful discussion, supported by accurate scientific research, is needed to establish significant and broadly supported conservation measures [17].

To this end, efforts should involve interdisciplinary collaboration, as the concerns to be balanced range from technical and ecological to legal and ethical, not to mention that the problem to be addressed is one of anthropogenic consequence rather than a natural evolutionary process. With regard to wolf x dog hybridization, it is mainly due to anthropogenic factors, linked to the presence of free-roaming dogs (both owned and stray), for which proper management practices by private individuals or public administrations (e.g. municipalities or regions) are complex, often inadequate or even lacking. In addition, the presence of the wolves has been gradually spreading across Europe over the last few decades, favoured by more anthropized areas where they are more likely to encounter dogs [65]. As von Essen and Allen [88] point out, humans are solely responsible for the existence of wolf-dog hybrids, and it would therefore be “unconscionable” to forget this premise and not to take it into account when deciding on their management. This consideration might be rejected by practitioners and managers dealing with practical issues as neither appropriate nor practical in dealing with reality. However, from an ethical point of view it should be seen as essential in

considering what course of action might produce an outcome that is not only practically but also morally acceptable.

3.6. Dealing with hybridization: towards new perspectives?

3.6.1. Wolf-dog hybrids and Italy as case studies

According to the EU publication “The situation of the wolf (*canis lupus*) in the European union. An in-depth analysis”, Italy is the European country where the highest rates of wolf-dog hybridization have been found [89].

The national wolf survey carried out in the Italian peninsula from October 2020 to September 2021 revealed that of the 513 wolf individuals identified, 11,7 % showed signs of recent hybridization with domestic dogs, 15,6 % of older hybridization while in 72,7 % of the specimens no genetic signs of recent or older hybridization were found. “Older hybridization” was intended as backcrossing of hybrids into the wolf population more than approximately three generations in the past (<https://www.isprambiente.gov.it/it/attivita/biodiversita/monito-raggio-nazionale-del-lupo/risultati>).

These results follow a study carried out by Salvatori et al. [18] at a local scale, in which they found a 30,6 % proportion of admixed individuals and highlighted the widespread occurrence of admixed individuals from older generations of backcrossing, concluding that this raises serious conservation concerns for wolves in unmanaged landscapes.

BOX 1 - The taxonomic status of wolf-dog hybrids in Italy

According to the taxonomic classification of Linnaeus (1758) [90], the dog and the wolf belong to the same class of mammals, to the same order *Carnivora*, to the same family *Canidae*, to the same genus *Canis* and to the same species *Canis lupus*. The dog is also a subspecies “*familiaris*” in *Canis lupus familiaris*.

In fact, according to the most widely accepted hypothesis of the dog’s origin, *Canis lupus familiaris* is a domesticated form of the wolf *Canis lupus* [91–98].

According to research performed by Nowak and Federoff [99], the Italian wolf warrants recognition as the subspecies *Canis lupus italicus*. Their conclusions were extended and confirmed by Montana et al. [100].

Thus, both dogs and wolves belong to the same taxonomic entity (*Canis lupus*).

From a management perspective, the taxonomic framework of wolves and dogs (BOX 1) provides an element of consideration, as it makes it important to consider the legal status of the two subspecies as well as their hybrids.

In this respect, a fundamental difference between dogs and wolves is their interaction with humans; wolves are wild creatures, whereas dogs are dependent on human resources and care. Normally, hybrids also have an independent and viable life as wild animals. They should therefore be subject to the same laws and have a legal status that is essentially equivalent to that of wild animals.

However, as mentioned above, in Europe there is no uniform international and national legal framework for hybrids and their management, which is linked to their ancestry.

Furthermore, the question of whether the conservation status of species should be considered at the level of European Member States or at the population level has not yet been resolved.

3.6.1.1. Focus on Italian legislation concerning hybrids. The Italian Law No. 150/1992 [101], which implements the CITES Convention, states that a wild specimen is an animal of wild origin or a specimen resulting from a birth in captivity limited to the first generation.

It is therefore unclear if hybrids are included.

Likewise, Article 2 of Law No. 157/1992 [102] states that the wild animals covered by the law itself include “species of which there are populations living permanently or temporarily in a state of natural

freedom within the national territory". There is nothing in the law to suggest that hybrid species are among the protected species specifically mentioned.

Therefore, the animal resulting from a crossbreeding with a domestic species does not fall within the definitions provided by this legislation.

The subsequent Legislative Decree no. 135/2022 [103], which implements Regulation (EU) 2016/429 (Animal Health Law) [104], introduced a definition of the hybrid as an "individual resulting from the crossing of parents belonging to different species. The term is currently also used for individuals resulting from the crossing of different subspecies (geographical breeds) of the same species or of wild species with domestic breeds from which they originate". Moreover, when specifically dealing with "Species dangerous to health, public safety or to biodiversity" (Art. 4) this decree provides for the extension of the concept of hybrids to all animals derived from a cross between protected species and other wild or domestic taxa, regardless of the number of generations since the original crossing. The decree also sets out a series of prohibitions relating to live specimens of wild species and their hybrids: from importing and keeping to trading and breeding such live animals, removed from their natural habitat.

It is worth noting that the European Animal Health Law does not cover hybrids, so the Italian decree seems to partially fill such a legal loophole on hybrids, on the Italian territory. In particular, the provision broadening the concept of hybrid, while overcoming the technical limitations of identifying crossings up to the fourth generation, introduces an innovation that is in line with the objective of clarifying the legal definition of hybrids and can help policy makers to take into account hybridization and to refine strategies and conservation legislation in the future with regard to any system that has experienced gene flow. The subsequent operational decrees, which will fully implement the decree and define the prohibitions on possession of hybrids themselves, have yet to be approved. It is expected that existing loopholes will be addressed, as part of the objectives of the Decree itself.

However, at present, no provision is made for the management of these specimens. Furthermore, this law does not contain any provisions that would classify hybrids as protected species and does not clarify which obligations (protection or control obligations) apply to them. Therefore, the implementation of the Italian legislation could be difficult and could lead to aporia.

3.6.1.2. Focus on Italian jurisprudence concerning hybrids. Italian jurisprudence has established an approach according to which animals adapted to wild living conditions, comparable to those of the actual wild fauna, may fall within the scope of the rules on the protection of wild fauna (see Court of Cassation, Section III, 26 January 2004, n. 2598) [105].

This is in line with Law No. 157/1992 on the protection of homoeothermic fauna and hunting [102], which considers animals that live and reproduce independently of humans (non-domesticated) to be equivalent to wild fauna, regardless of their zoological classification.

On the other hand, animals are only considered domesticated when all aspects of their lives, such as housing, feeding and breeding are completely under human control.

Thus, the Court of Cassation concluded that the legal distinction between wild animals and domestic animals does not correspond to the classification used in zoological science, but that their living conditions are relevant, and that, from this point of view, hybrids must be given the possibility of being treated as wild or domestic animals, depending on the situation in which they live or have lived.

A similar approach was also taken by the Italian Council of State in relation to a wolf-dog hybrid [106], which ruled on the revocation of the keeping of a live hybrid specimen of *Canis lupus italicus* by a private individual. Again, the condition of the animal was decisive and it was established that in the case of animals whose living conditions are similar to those of wild animals, the protection of the animal in its

accustomed condition must prevail. Therefore, the rules for the protection of hybrids apply if the condition of the animal is indeed comparable to that of wild fauna.

In order to determine whether wildlife protection legislation could apply, the abovementioned sentence also considered the merits of the definition of hybrid.

In the situation examined, a dog-wolf hybrid had been entrusted by the competent authority to a private individual, who had expressed a willingness to keep the animal as a companion animal. Against this situation, the Italian Ministry for the Environment, Land and Sea Protection, together with the CITES Office, recalling the Annex to Regulation (EC) 338/97, point 11, objected that the dog-wolf hybrid should be considered as a "full species" up to the fourth generation of the lineage and therefore could only be kept by an authorized structure.¹ The Council of State considered these questions of interpretation and application of the existing legislation on wild animals and recalled that the case of the dog-wolf hybrid living in a domestic environment is not directly regulated by the existing legislation, nor is there any need to reconcile the hybrid characteristics of the animal with the dangers it poses for the protection of wild species. Furthermore, the judgement stated that the genetic analysis of the hybrid nature of the animal did not add any significant elements to the possible double legal treatment. In support of this argument, the judges referred to a scientific assessment according to which "the data obtained from the analysis of the mitochondrial DNA sequence regarding the matrilineal origin does not mean that the subject's mother is a wolf, since the mitochondrial data can remain unchanged for many generations and it is not possible to determine whether the female has retained the mitochondrial haplotype characteristic of the wolf population even after several crossings" [106].

It should be noted that such a conclusion could have been challenged by genetics experts, given the availability of extensive additional data from nuclear DNA that could have clarified the generation to which the hybrid itself belonged. This observation reminds us of the potential pitfalls in the analysis of genetic test results, associated with misinterpretation, misunderstanding, or even misreading of the genetic report, which are even more challenging when the data are managed by non-specialists unfamiliar with genetic concepts. These pitfalls can further complicate a regulatory framework that gives hybrids an uncertain legal status. However, this sentence stated that the analysis carried out by ISPRA (Higher Institute for Environmental Protection and Research) confirming the hybrid nature of the animal was not sufficient, nor was the matrilineal nature of the DNA - nor was the number of intervening generations specified, and the final decision was founded on this basis.

It was also pointed out that Law No. 150 of 7 February 1992 [101] on the trade in and possession of specimens of endangered fauna and flora, as amended by Law No. 59 of 13 March 1993 [107], also provides only for wild fauna and animals born in captivity, limited to the first generation.

In addition, the Council of State noted that "there are also legally recognized dog breeds derived from recent hybridization with wolves". In the light of these premises, it stated that the arguments for considering a hybrid animal as a species necessarily protected by European and Italian legislation were therefore lacking.

This is relevant when it comes to deciding whether a specimen of dog-wolf hybrid that needs to be removed from the wild habitat must be recovered in an authorized wildlife rescue center, or whether it can even be kept as a companion animal.

The Council of State, with decision No. 4639/2014 [106], introduced a clear principle of interpretation of the current legislation, stating that, in case of doubt, the interpretive criterion of the prevalence of the protection of the effectiveness of the condition of natural freedom must

¹ It should be noted that the above rule implies that only in the fifth generation are animals whose parents are listed in the Annexes to the Regulation exempted from the Regulation therein.

be applied.

Interestingly, the jurisprudence has added a criterion to help define “hybrid” in relation to the law.

In this perspective, the hybrid living in domestic conditions - according to the same rationale - falls outside the scope of the legislation and can be treated differently from the one living in the wild. Such a hybrid can therefore be kept by a private individual, and the Court has ruled accordingly.

This is an interesting jurisprudential approach based on scientific and legal evidence, even if it presents aspects that conflict with at least one of the requirements of Recommendation No. 173/2014 of the Standing Committee of the Bern Convention on wolf-dog hybrids [19], which favours “the prohibition or restriction of the keeping of wolves and wolf-dog hybrids as pets”.

It should also be noted that the genealogical element is of great importance and must be taken into account and carefully demonstrated. This last aspect underlines the complications that characterize it, since the genetic and genomic methods used to detect hybrids and define their lineage are complex and vary widely between laboratories within and between countries. For this reason, the term “hybrid” itself is often ambiguous and lacks a solid basis to inform effective management strategies [58].

This framework suggests that the issue of hybrids (such as, but not limited to, dog x wolf hybrids) is multifaceted and that decisions about them require a comprehensive assessment, including aspects that may vary from case to case, and does not exclude inedited solutions.

This is also important from the point of view of respecting the welfare of individual animals allowing for the management of admixed individuals taking into account their “cultural function” [108–110], while interpreting existing rules.

3.7. Remarks

Anthropogenic hybridization is a broad issue that currently still lacks a resolving policy [24,36,111].

This scenario suggests the need for improved management, which in turn would benefit from the standardization of reliable technical methods for detecting admixed individuals. Consensus on the definition of hybrids, also from a legal point of view, should also be sought in order to provide concrete guidance useful for establishing a clear legal framework. On this basis, more appropriate normative criteria and management protocols could be established, ensuring guidance and tools for the implementation of appropriate preventive, reactive and proactive interventions, which could also be more respectful of the ethical and social relevance of the issue of hybridization.

In this context, in addition to the need for more in-depth scientific studies aimed at generating more evidence to promote specific knowledge and support more effective and feasible approaches, a look at the (albeit limited) jurisprudential approach offers the opportunity to highlight the importance of taking evidence-based decisions, which may vary from case to case.

Interestingly, this can open a window to unexpected solutions that are critically needed to provide answers in specific situations.

If the main recommendation to be addressed to the European legislator is to adopt a clear and common definition of a hybrid animal and to indicate with equal clarity its legal status, it still seems important not to underestimate the fact that hybrids are not only a “category” but also individuals. The latter, in a cultural-historical period such as the present one and in a geographical-political area such as Europe, where the recognition of animals as sentient beings is now established both culturally and legally, should be a fundamental aspect of the guidelines and regulations for managing the effects of hybridization on wild species.

Italian jurisprudence has shown that it is possible and even appropriate to take into account aspects of the lives of hybrid animals that relate to respect for their interests.

The case of the wolf-dog hybrid examined by the Italian Council of State presents characteristics that distinguish it from the generality of hybrids living in the wild. It should also be emphasized that caution should be exercised in generalizing the principle that an individual with a proportion of wild ancestry can be kept as a companion animal in a domestic environment. In fact, it could encourage cases of illegal activities leading to such conditions or even adversely affect the wildlife trade scenario by encouraging illegal harvesting. It should be remembered that the issue of wildlife conservation always arises when dealing with hybrids, and therefore the potential future perverse ‘market demand’ would be detrimental, as it could even stimulate an illegal trade in wild animals for the purpose of breeding hybrids as pets, which could be another insidious source of anthropogenic hybridization.

Another aspect that should not be underestimated is the additional complex needs of a wild hybrid compared to a normal pet, which owners will simply not be able to meet. This could lead to animal suffering and even the risk of abandonment, again with potential negative impacts on the natural environment of wild specimens.

However, it is important to emphasize the value of the sentence under consideration as a case study that is useful in demonstrating that addressing the issue of anthropogenic hybridization means confronting a multitude of elements, the validity of which can be extrapolated from the individual contingency, thus as a piece of the whole puzzle of its environmental framework.

These elements are: the availability of hybridization detection techniques and their relative sensitivity and reliability, the assessment of the living conditions of the specimen(s), the risks to conservation and to the animal(s) concerned, and, above all, the ability to interpret the regulations in force.

These are all crucial to the development of ideas about hybrid animals that can help not only to better understand such a category, but also to promote the development of better perspectives on how hybrid animals should be represented and treated, although on the background of the need of preventive, proactive or reactive conservation actions.

Rather than being seen solely as a threat and a form of genetic pollution to be combated, hybridization could become the subject of new arguments and less rigid approaches, perhaps precisely because of a willingness to dwell on the evaluation of individual cases. Moreover, the scientific literature is already suggesting new ways of looking at hybridization as a conservation tool that may (paradoxically) have positive implications. This may be because it can increase the adaptive potential of a population, for example to survive changing conditions or inbreeding depression (e.g., in case of small and isolated populations) or even because it can provide a reservoir of (at least some) parental genetic material when a population or species is at risk of extinction [112–121].

We do not want to pave the way for the possible disappearance of all pure breeds. In actual fact, in addition to the known biological risks, the unclear legal status of hybrids and the current official conservation policies do not allow unnatural hybridization to be considered a positive evolutionary phenomenon per se.

However, it should not be forgotten that humans themselves, as *Homo sapiens* - modern humans - are in part a product of the hybridization that led to their evolution [122].

The fact that in many cases it is not possible to morphologically recognize most hybrid individuals should give rise to reflections on their “unacceptability”.

Certainly, human-induced hybridization has implications for conservation goals.

However, it can also provide food for thought about the role of humanity as an evolutionary force, making the need to manage anthropogenic hybridization more flexibly, including the opportunity to consider hybrid organisms as living, sentient individuals whose “place in the world” deserves to be valued.

4. Conclusion

The present analysis shows that anthropogenic hybridization is still an unresolved issue that needs to be addressed in a thorough and evolved manner, just as hybrids are evolution-in-progress. Management decisions should address the potential role of hybridization implementing policies and taking into account conservation concerns, but also the role of hybrid organisms per se, without excluding case-by-case solutions and the inherent value of individuals.

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Supplementary materials

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Data availability

No data was used for the research described in the article.

References

- [1] F.W. Allendorf, R.F. Leary, P. Spruell, J.K. Wenburg, The problems with hybrids: setting conservation guidelines, *Trends Ecol. Evol.* 16 (2001) 613–622, [https://doi.org/10.1016/S0169-5347\(01\)02290-X](https://doi.org/10.1016/S0169-5347(01)02290-X).
- [2] S.S. Schneider, L.J. Leamy, L.A. Lewis, G. DeGrandi-Hoffman, The influence of hybridization between African and European honeybees, *Apis mellifera*, on asymmetries in wing size and shape, *Evolution (N Y)* 57 (2003) 2350–2364.
- [3] E. Mayr, *Systematics and the Origin of Species*, Columbia University Press, New York, NY, 1982.
- [4] T. Dobzhansky, *Genetics and the Origin of Species*, 3rd Ed, Columbia University Press, New York, NY, 1951, p. 1942.
- [5] B.D. DeMarais, T.E. Dowling, M.E. Douglas, W.L. Minckley, P.C. Marsh, Origin of *Gila seminuda* (Teleostei: cyprinidae) through introgressive hybridization: implications for evolution and conservation, *Proc. Natl. Acad. Sci. USA* 89 (1992) 2747–2751, <https://doi.org/10.1073/pnas.89.7.2747>.
- [6] B.R. Grant, P. Grant, Hybridization and speciation in Darwin's finches: the role of sexual imprinting on a culturally transmitted trait, in: D.J. Howard, S. H. Berlocher (Eds.), *Endless Forms: Species and Speciation*, Oxford University Press, New York, NY, 1998, pp. 404–422.
- [7] J. Mavárez, C.A. Salazar, E. Bermingham, C. Salcedo, C.D. Jiggins, M. Linares, Speciation by hybridization in Heliconius butterflies, *Nature* 441 (2006) 868–871, <https://doi.org/10.1038/nature04738>.
- [8] P.A. Larsen, M.R. Marchán-Rivadeneira, R.J. Baker, Natural hybridization generates mammalian lineage with species characteristics, *Proc. Natl. Acad. Sci. USA* 107 (25) (2010) 11447–11452, <https://doi.org/10.1073/pnas.1000133107>. Epub 2010 Jun 2. PMID: 20534512; PMCID: PMC2895066.
- [9] R. Abbott, D. Albach, S. Ansell, J. Arntzen, S. Baird, N. Bierne, J. Boughman, A. Brelsford, C. Buerkle, R. Buggs, R. Butlin, U. Dieckmann, F. Eroukhanoff, A. Grill, S. Cahan, J. Hermansen, G. Hewitt, A. Hudson, C. Jiggins, J. Jones, B. Keller, T. Marczewski, J. Mallet, P. Martinez-Rodriguez, M. Möst, S. Mullen, R. Nichols, A.W. Nolte, C. Parisod, K. Pfennig, A.M. Rice, M.G. Ritchie, B. Seifert, C.M. Smadja, R. Stelkens, J.M. Szymura, R. Väinölä, J.B.W. Wolf, D. Zinner, Hybridization and speciation, *J. Evol. Biol.* 26 (2) (2013) 229–246, <https://doi.org/10.1111/j.1420-9101.2012.02599.x>. PMID: 23323997.
- [10] E.H.C. de Oliveira, A.J.B. Gomes, A.F. Costa, R. Emin-Lima, C.R. Bonvicino, M. C. Viana, L.M.A. Reis, M.D. Vidal, M.V.G. Cavalcanti, F.L.N. Attademo, F.O. Luna, S. Siciliano, Karyotypical Confirmation of Natural Hybridization Between Two Manatee Species, *Trichechus manatus* and *Trichechus inunguis*, *Life* 12 (5) (2022) 616, <https://doi.org/10.3390/life12050616>.
- [11] J.M. Rhymer, D. Simberloff, Extinction by hybridization and introgression, *Annu. Rev. Ecol. Syst.* 27 (1996) 83–109.
- [12] M. Pilot, C. Greco, B.M. vonHoldt, E. Randi, W. Jedrzejewski, V.E. Sidorovich, M. K. Konopiński, E.A. Ostrander, R.K. Wayne, A.S. Macdougall, K.S. McCann, G. Gellner, R. Turkington, Diversity loss with persistent human disturbance increases vulnerability to ecosystem collapse, *Nature* 494 (2013) 86–89, <https://doi.org/10.1038/nature11869>.
- [13] R. Abbott, N.H. Barton, J.M. Good, Genomics of hybridization and its evolutionary consequences, *Mol. Ecol.* 25 (2016) 2325–2332.
- [14] A. Miraldo, S. Li, M.K. Borregaard, A. Flórez-rodríguez, S. Gopalakrishnan, M. Rizvanovic, Z. Wang, C. Rahbek, K.A. Marske, Nogués-Bravo D. An Anthropocene map of genetic diversity, *Science* 353 (2016) 24–27, <https://doi.org/10.1126/science.aaf4381>.
- [15] A.P. Hendry, K.M. Gotanda, E.I. Svensson, Human influences on evolution, and the ecological and societal consequences, *Philos. Trans. R Soc. B Biol. Sci.* 372 (2017) 20160028, <https://doi.org/10.1098/rstb.2016.0028>.
- [16] Commission Regulation (EU) 2023/966 of 15 May 2023 amending Council Regulation (EC) No 338/97 to reflect the amendments adopted at the 2022 19th meeting of the Conference of the Parties to the Convention on International Trade in Endangered Species of Wild Fauna and Flora. <http://data.europa.eu/eli/reg/2023/966/oj>.
- [17] V. Donfrancesco, P. Ciucci, V. Salvatori, D. Benson, L.W. Andersen, E. Bassi, J. C. Blanco, L. Boitani, R. Caniglia, A. Canu, C. Capitani, G. Chapron, S. D. Czarnomska, E. Fabbri, M. Galaverni, A. Galov, O. Gimenez, R. Godinho, C. Greco, M. Hindrikson, D. Huber, P. Hulva, W. Jedrzejewski, J. Kusak, J.D. C. Linnell, L. Llanaea, J.V. López-Bao, P. Männil, F. Marucco, H. Mattioli, P. Milanese, C. Milleret, R.W. Myslajek, A. Ordiz, V. Palacios, H.C. Pedersen, C. Pertoldi, M. Pilot, E. Randi, A. Rodríguez, U. Saarma, H. Sand, M. Scandura, A. V. Stronen, E. Tsingarska, N. Mukherjee, Unravelling the scientific debate on how to address wolf-dog hybridization in Europe, *Front. Ecol. Evol.* 7 (2019) e175, <https://doi.org/10.3389/fevo.2019.00175>.
- [18] V. Salvatori, R. Godinho, C. Braschi, L. Boitani, P. Ciucci, High levels of recent wolf dog introgressive hybridization in agricultural landscapes of central Italy, *Eur. J. Wildl. Res.* 65 (2019) 73, <https://doi.org/10.1007/s10344-019-1313-3>.
- [19] Recommendation N° 173 on hybridisation between wild grey wolves (*Canis lupus*) and domestic dogs (*Canis lupus familiaris*), Standing Committee of the Convention on the Conservation of European Wildlife and Natural Habitats, 2014. Strasbourg 5 December.
- [20] Council Directive 92/43/EEC of 21 May 1992 on the Conservation of Natural Habitats and of Wild Fauna and Flora (Habitats Directive) <http://data.europa.eu/eli/dir/1992/43/oj>.
- [21] Council of Europe Convention on the conservation of European Wildlife and Natural Habitats (Bern Convention), Bern, 19 September 1979, in force 1 November 1983, European Treaty Series - No. 104 <http://data.europa.eu/eli/convention/1982/72/oj>.
- [22] Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), 1973. <http://data.europa.eu/eli/convention/2015/451/oj>.
- [23] United Nations, Convention On Biological Diversity (with annexes), United Nations, New York, 1993, pp. 143–382. Concluded at Rio de Janeiro on 5 June 1992. No.30619 (United Nations Treaty Series, 1760(I-30619)).
- [24] R.K. Wayne, H.B. Shaffer, Hybridization and endangered species protection in the molecular era, *Mol. Ecol.* 25 (2016) 2680–2689, <https://doi.org/10.1111/mec.13642>.
- [25] A. Taylor-Brown, R. Booth, A. Gillett, E. Mealy, S.M. Ogbourne, A. Polkinghorne, G.C. Conroy, The impact of human activities on Australian wildlife, *PLoS One* 14 (1) (2019) e0206958, <https://doi.org/10.1371/journal.pone.0206958>.
- [26] C. Cîmpianu, E. Corodescu, Landscape dynamics analysis in Iași Metropolitan Area (Romania) using remote sensing data, *Cinç Continents* 3 (7) (2013) 18–32. Available online, http://www.cinçcontinents.uv.ro/3/3_7_Cimpianu.pdf.
- [27] A.S. MacDougall, K.S. McCann, G. Gellner, R. Turkington, Diversity loss with persistent human disturbance increases vulnerability to ecosystem collapse, *Nature* 494 (7435) (2013) 86–89, <https://doi.org/10.1038/nature11869>. PMID: 23389543.
- [28] M. Mimura, T. Yahara, D.P. Faith, E. Vázquez-Domínguez, R.I. Colautti, H. Araki, F. Javadi, J. Núñez-Farfán, A.S. Mori, S. Zhou, P.M. Hollingsworth, L.E. Neaves, Y. Fukano, G.F. Smith, Y.I. Sato, H. Tachida, A. Hendry, Understanding and monitoring the consequences of human impacts on intraspecific variation, *Evol. Appl.* 10 (2017) 121–139, <https://doi.org/10.1111/eva.12436>.
- [29] M.L. Arnold, *Natural Hybridization and Evolution*, Oxford University Press, New York, 1997.
- [30] C.C. Muhlfeld, S.T. Kalinowski, T.E. McMahon, M.L. Taper, S. Painter, R.F. Leary, F.W. Allendorf, Hybridization rapidly reduces fitness of a native trout in the wild, *Biol. Lett.* 5 (2009) 328–331, <https://doi.org/10.1098/rsbl.2009.0033>.
- [31] M. Todesco, M.A. Pascual, G.L. Owens, K.L. Ostevik, B.T. Moyers, S. Hübnér, S. M. Heredia, M.A. Hahn, C. Caseys, D.G. Bock, Hybridization and extinction, *Evol. Appl.* 9 (2016) 892–908, <https://doi.org/10.1111/eva.12367>.
- [32] J. Huisman, L.E.B. Kruuk, P.A. Ellis, T. Clutton-Brock, J.M. Pemberton, Inbreeding depression across the lifespan in a wild mammal population, *Proc. Natl. Acad. Sci. U.S.A.* 113 (2016) 3585–3590, <https://doi.org/10.1073/pnas.1518046113>.
- [33] H.V. Senn, G.M. Swanson, S.J. Goodman, N.H. Barton, J.M. Pemberton, Phenotypic correlates of hybridisation between red and sika deer (genus *Cervus*), *J. Anim. Ecol.* 79 (2010) 414–425, <https://doi.org/10.1111/j.1365-2656.2009.01633.x>.
- [34] P. Saetre, J. Lindberg, J.A. Leonard, K. Olsson, U. Pettersson, H. Ellegren, T. F. Bergström, C. Vila, E. Jazin, From wild wolf to domestic dog: gene expression changes in the brain, *Mol. Brain Res.* 126 (2004) 198–206, <https://doi.org/10.1016/j.molbrainres.2004.05.003>.

- [35] E. Popova, D. Zlatanova, Living a dog's life: a putative gray wolf in a feral dog group, *Mammalia* 84 (2020) 115–120, <https://doi.org/10.1515/mammalia-2019-0010>.
- [36] A. Trouwborst, Exploring the legal status of wolf-dog hybrids and other dubious animals: international and EU law and the wildlife conservation problem of hybridization with domestic and alien species, *RECIEL* 23 (2014) 111–124.
- [37] Recommendation No. 209 (2020) of the Standing Committee, adopted on 4 December 2020, on the eradication of the ruddy duck (*Oxyura jamaicensis*) in the Western Palaearctic by 2025, Standing Committee of the Convention on the conservation of European wildlife and natural habitats.
- [38] Recommendation No. 48 of the Standing Committee, adopted on 26 January 1996, on the conservation of European globally threatened birds, Standing Committee of the Convention on the conservation of European wildlife and natural habitats.
- [39] Recommendation No. 61 of the Standing Committee, adopted on 5 December 1997, on the conservation of the White-headed Duck (*Oxyura leucocephala*), Standing Committee of the Convention on the conservation of European wildlife and natural habitats.
- [40] Recommendation No. 149 of the Standing Committee, adopted on 9 December 2010, on the eradication of the Ruddy Duck (*Oxyura jamaicensis*) in the Western Palaearctic, Standing Committee of the Convention on the conservation of European wildlife and natural habitats.
- [41] Recommendation No. 185 of the Standing Committee, examined on 18 November 2016, on the eradication of the Ruddy Duck (*Oxyura jamaicensis*) in the Western Palaearctic by 2020, Standing Committee of the Convention on the conservation of European wildlife and natural habitats.
- [42] Council Regulation (EC) No 338/97 of 9 December 1996 on the protection of species of wild fauna and flora by regulating trade therein. Consolidated Version 20/05/2023. Accessed July 2024. <http://data.europa.eu/eli/reg/1997/338/oj>.
- [43] CITES Resolution Conf. 10.17 (Rev. CoP14) on Animal Hybrids (1997).
- [44] Regulation (EU) No 1143/2014 of the European Parliament and of the Council of 22 October 2014 on the prevention and management of the introduction and spread of invasive alien species <http://data.europa.eu/eli/reg/2014/1143/oj>.
- [45] IUCN (2024a). The IUCN Red List of Threatened Species. Version 2024-1. <https://www.iucnredlist.org> Accessed July 2024.
- [46] IUCN, Standards and Petitions Committee, 2019. Guidelines For Using the IUCN Red List Categories and Criteria. Version 14, Prepared by the Standards and Petitions Committee, 2024. Available online at: <http://www.iucnredlist.org/> (accessed July 2024).
- [47] IUCN (2024c). Threats Classification Scheme (Version 3.2) [WWW Document]. Available online at: <https://www.iucnredlist.org/resources/threat-classification-scheme> (accessed July 2024).
- [48] R.J. Fredrickson, P.W. Hedrick, Dynamics of hybridization and introgression in red wolves and coyotes, *Conserv. Biol.* 20 (2006) 1272–1283.
- [49] J. Malukiewicz, V. Boere, L.F. Fuzessy, A.D. Grativol, J.A. French, I.O. Silva, L.C. M. Pereira, C.R. Ruiz-Miranda, Y.M. Valença, A.C. Stone, Hybridization effects and genetic diversity of the common and black-tufted marmoset (*Callithrix jacchus* and *C. penicillata*) mitochondrial control region, *Am. J. Phys. Anthropol.* 155 (2014) 522–536, <https://doi.org/10.1002/ajpa.22605>.
- [50] J. Malukiewicz, V. Boere, L.F. Fuzessy, A.D. Grativol, I. de Oliveira e Silva, L.C. M. Pereira, C.R. Ruiz-Miranda, Y.M. Valença, A.C. Stone, Natural and anthropogenic hybridization in two species of eastern Brazilian marmosets (*Callithrix jacchus* and *C. penicillata*), *PLoS One* 10 (2015) e0127268, <https://doi.org/10.1371/journal.pone.0127268>.
- [51] L.R. Nathan, N. Mamoozadeh, H.R. Tumas, S. Günselman, K. Klass, A. Metcalfe, C. Edge, L.P. Waits, P. Spruell, E. Lowery, E. Connor, A.R. Bearlin, M.J. Fortin, E. Landguth, A spatially-explicit, individual-based demogenetic simulation framework for evaluating hybridization dynamics, *Ecol. Modell.* 401 (2019) 40–51.
- [52] R. Oliveira, E. Randi, F. Mattucci, J.D. Kurushima, L.A. Lyons, P.C. Alves, Toward a genome-wide approach for detecting hybrids: informative SNPs to detect introgression between domestic cats and European wildcats (*Felis silvestris*), *Hereditas* (Edinb) 115 (2015) 195–205, <https://doi.org/10.1038/hdy.2015.25>.
- [53] A.M. van Wyk, D.L. Dalton, S. Hoban, M...W. Bruford, I.M. Russo, C. Birss, P. Grobler, B.J. van Vuuren, A. Kotzé, Quantitative evaluation of hybridization and the impact on biodiversity conservation, *Ecol. Evol.* 7 (1) (2016) 320–330, <https://doi.org/10.1002/ece3.2595>.
- [54] H.V. Senn, M. Ghazali, J. Kaden, D. Barclay, B. Harrower, R.D. Campbell, D. W. Macdonald, A.C. Kitchener, Distinguishing the victim from the threat: sNP-based methods reveal the extent of introgressive hybridization between wildcats and domestic cats in Scotland and inform future in situ and ex situ management options for species restoration, *Evol. Appl.* 12 (2019) 399–414, <https://doi.org/10.1111/eva.12720>.
- [55] Ryder O.A. Genetic Studies of Przewalski's Horses and Their Impact on Conservation. In Przewalski's Horse: The History and Biology of an Endangered Species. Boyd L., Houpt K.A., Eds., The State University of New York Press; Albany, NY, USA; 1994, pp. 75–92.
- [56] Clark E.L., Javzansuren M. (compilers) Mongolian Red List of Mammals. Regional Red List Series Vol. 1. Dulamtsuren S., Baillie J.E.M., Batsaikhan N., Samiya R., Stubbe M. Eds. Zoological Society of London, London; 2006.
- [57] S.R.B. King, L. Boyd, W. Zimmermann, B.E. Kendall, *Equus Ferus*, The IUCN Red List of Threatened Species, 2015 e.T41763A97204950, <https://doi.org/10.2305/IUCN.UK.2015-2.RLTS.T41763A45172856.en>. Available online at Accessed July 2024.
- [58] M. Hindrikson, J. Remm, M. Pilot, R. Godinho, A.V. Stronen, L. Baltrūnaitė, S. D. Czarnomska, J.A. Leonard, E. Randi, C. Nowak, M. Åkesson, J.V. López-Bao, F. Álvares, L. Llana, J. Echegaray, C. Vilà, J. Ozolins, D. Rungis, J. Aspi, L. Paule, T. Skrbineš, U. Saarma, Wolf population genetics in Europe: a systematic review, meta-analysis and suggestions for conservation and management, *Biol. Rev. Camb. Philos. Soc.* 92 (3) (2017) 1601–1629, <https://doi.org/10.1111/brv.12298>. Epub 2016 Sep 28. PMID: 27682639.
- [59] Bern Convention Standing Committee 42nd Meeting report T-PVS/Inf(2022)45, 2022. Strasbourg 28 November – 2 December.
- [60] European Commission, Directorate General for Environment, Guidance Document On the Strict Protection of Animal Species of Community Interest Under the Habitats Directive 92/43/EEC, European Commission, 2007. Final version, February 2007.
- [61] A.V. Stronen, J. Aspi, R. Caniglia, E. Fabbri, M. Galaverni, R. Godinho, L. Kvist, F. Mattucci, C. Nowak, A. von Thaden, J. Harmoinen, Wolf-dog admixture highlights the need for methodological standards and multidisciplinary cooperation for effective governance of wild x domestic hybrids, *Biol. Conserv.* 266 (2022) 109467, <https://doi.org/10.1016/j.biocon.2022.109467>.
- [62] S. Mancinelli, P. Ciucci, Beyond Home: preliminary Data on Wolf Extraterritorial Forays and Dispersal in Central Italy, *Mamm. Biol.* 93 (2018) 51–55.
- [63] R. Lorenzini, R. Fanelli, G. Grifoni, F. Scholl, Fico R. Wolf-dog crossbreeding, "Smelling" a hybrid may not be easy, *Mamm. Biol.* 79 (2014) 149–156, <https://doi.org/10.1016/j.mambio.2013.07.080>.
- [64] M.A. Supple, B. Shapiro, Conservation of biodiversity in the genomics era, *Genome Biol* 19 (2018) 131.
- [65] V. Salvatori, V. Donfrancesco, A. Trouwborst, L. Boitani, J.D.C. Linnell, F. Álvares, M. Åkesson, V. Balys, J.C. Blanco, S. Chiriac, D. Cirovic, C. Groff, M. Guinot-Ghestem, D. Huber, I. Kojola, J. Kusak, M. Kutsal, Y. Iliopoulos, O. Ionescu, A. Majic Skrbineš, P. Mannil, F. Marucco, D. Melovski, R. W. Myslejek, S. Nowak, J. Ozolins, G. Rauer, I. Reinhardt, R. Rigg, L. Schley, T. Skrbineš, L. Svensson, A. Trajce, I. Trbojevic, E. Tzingarska, M. von Arx, P. Ciucci, European agreements for nature conservation need to explicitly address wolf-dog hybridisation, *Biol. Conserv.* 248 (2020), <https://doi.org/10.1016/j.biocon.2020.108525>.
- [66] LCIE Guidelines for Population Level Management Plans for Large Carnivores, European Commission, Directorate-General for Environment, 6 May 2024.
- [67] M.L. Morrison, B.G. Marcot, R.W. Mannan, *Wildlife-habitat relationships: Concepts and Applications*, 3rd edition, Island Press, Washington, D.C., USA, 2006.
- [68] F.W. Allendorf, R.F. Leary, Conservation and distribution of genetic variation in a polytypic species, the cutthroat trout, *Conserv. Biol.* 2 (1988) 170–184.
- [69] J. Mallet, Hybridization as an invasion of the genome, *Trends Ecol Evol* 20 (5) (2005) 229–237, <https://doi.org/10.1016/j.tree.2005.02.010>. PMID: 16701374.
- [70] M. Galaverni, R. Caniglia, L. Pagani, E. Fabbri, A. Boattini, E. Randi, Disentangling Timing of Admixture, Patterns of Introgression, and Phenotypic Indicators in a Hybridizing Wolf Population, *Mol. Biol. Evol.* 34 (2017) 2324–2339, <https://doi.org/10.1093/molbev/msx169>.
- [71] S.E. McFarlane, J.M. Pemberton, Detecting the true extent of introgression during anthropogenic hybridization, *Trends Ecol. Evol.* 4 (2019) 315–326.
- [72] J.R. Adams, B.T. Kelly, L.P. Waits, Using faecal DNA sampling and GIS to monitor hybridization between red wolves (*Canis rufus*) and coyotes (*Canis latrans*), *Mol. Ecol.* 12 (8) (2003) 2175–2186.
- [73] E.M. Gese, P.A. Terletzky, Using the 'placeholder' concept to reduce genetic introgression of an endangered carnivore, *Biol. Conserv.* 192 (2015) 11–19.
- [74] B.M. vonHoldt, J.P. Pollinger, D.A. Earl, H.G. Parker, E.A. Ostrander, R.K. Wayne, Identification of recent hybridization between gray wolves and domesticated dogs by SNP genotyping, *Mamm. Genome* 24 (2013) 80–88.
- [75] J. Kusak, E. Fabbri, A. Galov, T. Gomerčić, H. Arbanasić, R. Caniglia, M. Galaverni, S. Reljić, D. Huber, E. Randi, Wolf-dog hybridization in Croatia, *Vet Arh* 88 (2018) 375–395, <https://doi.org/10.24099/vet.arhiv.170314>.
- [76] A. Dzięch, Identification of Wolf-Dog Hybrids in Europe – An Overview of Genetic Studies, *Front. Ecol. Evol.* 9 (2021) 760160, <https://doi.org/10.3389/fevo.2021.760160>.
- [77] K.M. Cairns, K.D. Newman, M.S. Crowther, M. Letnic, Pelage variation in dingoes across southeastern Australia: implications for conservation and management, *J. Zool.* 314 (2021) 104–115.
- [78] N.L. Santostasi, P. Ciucci, R. Caniglia, E. Fabbri, L. Molinari, W. Reggioni, O. Gimenez, Use of hidden Markov capture-recapture models to estimate abundance in the presence of uncertainty: application to the estimation of prevalence of hybrids in animal populations, *Ecol. Evol.* 9 (2019) 744–755.
- [79] F. Mattucci, M. Galaverni, L.A. Lyons, P.C. Alves, E. Randi, E. Velli, L. Pagani, R. Caniglia, Genomic approaches to identify hybrids and estimate admixture times in European wildcat populations, *Sci. Rep.* 9 (2019) e11612, <https://doi.org/10.1038/s41598-019-48002-w>.
- [80] R. Caniglia, M. Galaverni, E. Velli, F. Mattucci, A. Canu, M. Apollonio, N. Mucci, M. Scandura, E. Fabbri, A standardized approach to empirically define reliable assignment thresholds and appropriate management categories in deeply introgressed populations, *Sci. Rep.* 10 (2020) 2862.
- [81] K. Ghildiyal, S.S. Nayak, D. Rajawat, A. Sharma, S. Chhotaray, B. Bhushan, T. Dutt, M. Panigrahi, Genomic insights into the conservation of wild and domestic animal diversity: a review, *Gene* 30 (11) (2023), <https://doi.org/10.1016/j.gene.2023.147719>, 886:147719Epub 2023 Aug 18. PMID: 37597708.
- [82] A. Amorim, F. Pereira, C. Alves, O. García, Species assignment in forensics and the challenge of hybrids Forensic, *Sci. Int. Genet.* 48 (2020) e102333, <https://doi.org/10.1016/j.fsigen.2020.102333>.
- [83] M. Pilot, C. Greco, B.M. vonHoldt, E. Randi, W. Jędrzejewski, V.E. Sidorovich, M. K. Konopiński, E.A. Ostrander, R.K. Wayne, Widespread, long-term admixture between grey wolves and domestic dogs across Eurasia and its implications for

- the conservation status of hybrids, *Evol. Appl.* 11 (2018) 662–680, <https://doi.org/10.1111/eva.12595>.
- [84] J. Harmoinen, A. von Thaden, J. Aspi, L. Kvist, B. Cocchiararo, A. Jarausch, A. Gazzola, T. Sin, H. Lohi, M.K. Hytönen, I. Kojola, A.V. Stronen, R. Caniglia, F. Mattucci, M. Galaverni, R. Godinho, A. Ruiz-González, E. Randi, V. Muñoz-Fuentes, C. Nowak, Reliable wolf-dog hybrid detection in Europe using a reduced SNP panel developed for non-invasively collected samples, *BMC Genomics* 22 (1) (2021) 473.
- [85] N. Lescureux, J.D.C. Linnell, Warring brothers: the complex interactions between wolves (*Canis lupus*) and dogs (*Canis familiaris*) *Biol. Conserv.* 171 (2014) 232–245.
- [86] B.M. Fitzpatrick, M.E. Ryan, J.R. Johnson, J. Corush, E.T. Carter, Hybridization and the species problem in conservation, *Curr. Zool.* 61 (2015) 206–216.
- [87] S. Dubois, N. Fenwick, E.A. Ryan, L. Baker, S.E. Baker, N.J. Beausoleil, S. Carter, B. Cartwright, F. Costa, C. Draper, J. Griffin, A. Grogan, G. Howald, B. Jones, K. E. Littin, A.T. Lombard, D.J. Mellor, D. Ramp, C.A. Schuppli, D. Fraser, International consensus principles for ethical wildlife control, *Conserv. Biol.* 31 (2017) 753–760.
- [88] E. von Essen, M.P. Allen, A Rabble in the Zoopolis? Considering Responsibilities for Wildlife Hybrids, *J. Soc. Philos.* 47 (2016) 171–187, <https://doi.org/10.1111/josp.12150>.
- [89] European Commission, Directorate-General for Environment, J. Blanco, K. Sundseth, The Situation of the Wolf (*canis lupus*) in the European union – An in-Depth Analysis, Publications Office of the European Union, 2023. <https://data.europa.eu/doi/10.2779/187513>. Accessed July 2024.
- [90] C. Linnaeus, *Systema Naturae*, 10, 1, 1758, p. 1e824.
- [91] R.P. Coppinger, C.K. Smith, The domestication of evolution, *Environ Conserv* 10 (4) (1983) 283–292.
- [92] Clutton-Brock J. Dog. In *Evolution of Domestic Animals*. I. Mason Ed. London: Longman; 1984, 198–211.
- [93] J. Clutton-Brock, J. Serpell Ed, *Origins of the Dog: domestication and early history*. In *The domestic dog: Its evolution, Behavior and Interactions With People*, Cambridge University Press, 1995, pp. 7–20.
- [94] D.F. Morey, Size, shape and development in the evolution of the domestic dog, *J. Archaeol. Sci.* 19 (1992) 181–204.
- [95] D.E. Wilson, D.M. Reeder, *Mammal Species of the world: a Taxonomic and Geographic Reference*, 3rd ed., Johns Hopkins University Press, Baltimore, Maryland, 2005. ISBN 0-8018-8221-4.
- [96] C. Vilà, P. Savolainen, J.E. Maldonado, I.R. Amorim, J.E. Rice, R.L. Honeycutt, K. A. Crandall, J. Ludeburg, R.K. Wayne, Multiple and Ancient Origins of the Dog, *Science* 276 (1997) 1687–1689.
- [97] S.J. Crockford, A commentary on dog evolution: regional variation, breed development and hybridization with wolves, in: S.J. Crockford (Ed.), *Dogs Through time: an Archaeological Perspective*, Archaeopress, Oxford, 2000, pp. 295–312. BAR International Series 889.
- [98] R. Coppinger, L. Coppinger, *Dogs: a Startling New Understanding of Canine origin, Behavior and Evolution*, 2001. Scribner, NY.
- [99] R.M. Nowak, N.E. Federoff, The systematic status of the Italian wolf *Canis lupus*, *Acta Theriol* 47 (3) (2002) 333–338.
- [100] L. Montana, R. Caniglia, M. Galaverni, E. Fabbri, A. Ahmed, B.Č. Bolířková, S. D. Czarnomska, A. Galov, R. Godinho, M. Hindrikson, P. Hulva, B. Jędrzejewska, M. Jelencić, M. Kotal, U. Saarma, T. Skrbinšek, E. Randi, Combining phylogenetic and demographic inferences to assess the origin of the genetic diversity in an isolated wolf population, *PLoS ONE* 12 (5) (2017) e0176560, <https://doi.org/10.1371/journal.pone.0176560>.
- [101] Italian Law No. 150/1992 concerning crimes relevant to the application in Italy of the Convention on the International Trade of Endangered Species of Wild Flora and Fauna, and of the EEC Regulation No. 3626/82, and also making provisions for the trade and keeping of dangerous or harmful animals and reptiles. Last amended date 12 September 2022.
- [102] Italian Law No. 157/1992 Norme per la protezione della fauna selvatica omeoterma e per il prelievo venatorio. (Gazzetta Ufficiale no. 46 of 25/02/1992 - Ordinary Supplement no. 41).
- [103] Italian Legislative Decree No. 135/2022 concerning provisions for the implementation of Regulation (EU) 2016/429 of the European Parliament and of the Council of 9 March 2016 on trade, import, conservation of animals of wild and exotic fauna and training of animal handlers and professionals, also with a view to reducing the risk of outbreaks of zoonoses, as well as the introduction of penal provisions to punish illegal trade in protected species, pursuant to Article 14, paragraph 2, letters a), b), n), o), p), q), of Law No. 53 of 22 April 2021.
- [104] Regulation (EU) 2016/429 of the European Parliament and of the Council of 9 March 2016 on transmissible animal diseases and amending and repealing certain acts in the area of animal health ('Animal Health Law'). <http://data.europa.eu/eli/reg/2016/429/oj>.
- [105] Court of Cassation Sect. III Criminal 26 January 2004, no. 2598, available online on <https://www.ambienteditto.it/sentenze/2004/Cassazione/Cassazione%20Penale%202004%20n.%202598.htm> Accessed July 2024.
- [106] Council of State, Section III, no. 4639, of 11 September 2014. Hunting and animals. Illegality of the Revocation of the Fostering of a Live Hybrid Specimen of *Canis lupus italicus*.
- [107] Italian Law No. 59/1993 concerning conversion into law, with amendments, of Decree-Law No 2 of 12 January 1993, amending and supplementing Law No. 150 of 7 February 1992, on the trade in and possession of specimens of fauna and flora threatened with extinction.
- [108] M.J. Daniels, L. Corbett, Redefining introgressed protected mammals: when is a wildcat a wild cat and a dingo a wild dog? *Wildl. Res.* 30 (2003) 213–218, <https://doi.org/10.1071/WRO2045>.
- [109] A.S. Glen, Hybridisation between dingoes and domestic dogs: a comment on Jones (2009), *Aust. Mammal.* 32 (1) (2010) 76–77, <https://doi.org/10.1071/AM09031>.
- [110] L.M. van Eeden, C.R. Dickman, T.M. Newsome, M.S. Crowther, What should we do with wild dogs? Taxonomic tangles and the management of dingo-dog hybridisation, *Aust. Zool.* 40 (2018) 92–101, <https://doi.org/10.7882/AZ.2018.031>, 2019.
- [111] S. Pietti, H.A. Hager, C. Gerrard, Characteristics for evaluating the conservation value of species hybrids, *Biodivers. Conserv.* 24 (2015) 1931–1955, <https://doi.org/10.1007/s10531-015-0919-3>.
- [112] S. Cozzolino, A.M. Nardella, S. Impagliazzo, A. Widmer, C. Lexer, Hybridization and conservation of Mediterranean orchids: should we protect the orchid hybrids or the orchid hybrid zones? *Biol. Cons.* 129 (1) (2006) 14–23, <https://doi.org/10.1016/j.biocon.2005.09.043>.
- [113] T.A. Jones, T.A. Monaco, A role for assisted evolution in designing native plant materials for domesticated landscapes, *Front. Ecol. Environ.* 7 (2009) 541–547.
- [114] A.A. Hoffmann, C.M. Sgrò, Climate change and evolutionary adaptation, *Nature* 470 (2011) 479–485.
- [115] S.M. Carlson, C.J. Cunningham, P.A.H. Westley, Evolutionary rescue in a changing world, *TREE* 29 (2014) 521–530.
- [116] A.R. Whiteley, S.W. Fitzpatrick, W.C. Funk, D.A. Tallmon, Genetic rescue to the rescue, *TREE* 30 (2015) 42–49.
- [117] J.A. Hamilton, J.M. Miller, Adaptive introgression as a resource for management and genetic conservation in a changing climate, *Conserv. Biol.* 30 (2016) 33–41.
- [118] J.I. Meier, D.A. Marques, S. Mwaiko, C.E. Wagner, L. Excoffier, O. Seehausen, Ancient hybridization fuels rapid cichlid fish adaptive radiations, *Nat. Commun.* 8 (2017) 14363.
- [119] M.J.H. van Oppen, R.D. Gates, L.L. Blackall, N. Cantin, L.J. Chakravarti, W. Y. Chan, C. Cormick, A. Crean, K. Damjanovic, H. Epstein, P.L. Harrison, T. A. Jones, M. Miller, R.J. Pears, L.M. Peplow, D.A. Raftos, B. Schaffelke, K. Stewart, G. Torda, D. Wachenfeld, A.R. Weeks, H.M. Putnam, Shifting paradigms in restoration of the world's coral reefs, *Glo. Chang. Biol.* 23 (2017) 3437–3448.
- [120] W.Y. Chan, L.M. Peplow, P. Menéndez, A.A. Hoffmann, M.J.H. van Oppen, Interspecific hybridization may provide novel opportunities for coral reef restoration, *Front. Mar. Sci.* 5 (2018) e160, <https://doi.org/10.3389/fmars.2018.00160>.
- [121] W.Y. Chan, A.A. Hoffmann, M.J.H. van Oppen, Hybridization as a conservation management tool, *Conserv. Lett.* 12 (2019) e12652.
- [122] R.R. Ackermann, M.L. Arnold, M.D. Baiz, J.A. Cahill, L. Cortés-Ortiz, B.J. Evans, B.R. Grant, P.R. Grant, B. Hallgrímsson, R.A. Humphreys, C.J. Jolly, J. Malukiewicz, C.J. Percival, T.B. Ritzman, C. Roos, C.C. Roseman, L. Schroeder, F.H. Smith, K.A. Warren, R.K. Wayne, D. Zinner, Hybridization in human evolution: insights from other organisms, *Evol. Anthropol.* 28 (4) (2019) 189–209, <https://doi.org/10.1002/evan.21787>.