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Principles of Natural Resource Management Facilitate Mammalian Hybridization: A Review and Look to the Future

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Abstract

Hybridization is threatening many endangered, indigenous and rare mammal species worldwide. At the same time, wildlife managers are forced to make management decisions with scarce data and limited resources. Anthropogenic-driven landscape change is expanding at an exponential rate and may play a significant role in increasing hybridization rates. Understanding the ecological context in which hybridization occurs is crucial to increasing conservation and management effectiveness on both regional and global scales. This review explores the biological and spatial means by which anthropogenic landscape disturbances, often resulting from management practices, affect mammalian hybridization rates. We caution that the literature provides evidence that shifts in habitat characteristics may be attributed to accelerating anthropogenic disturbance, and is especially problematic for closely related mammalian species that recently diverged, and therefore have the potential to hybridize when ecological conditions are favorable. While direct impacts lead to the expansion or contraction of the distribution of wild species, indirect impacts result in expansion of the distribution of non-native species.

Additionally, management and conservation guidelines strongly depend on the degree to which anthropogenic-driven landscape change alters ecological processes and the time scale at which hybridization occurs; anthropogenic activities induce hybridization by directly and indirectly changing species composition in a given landscape. Therefore, we suggest that conservationists and wildlife decision-makers should approach hybridization as a global threat to biodiversity with site-specific solutions following our suggested guidelines. We provide a summary of the impact of various management practices on hybridization and put forward a decision tree for management. Effective management and conservation objectives should focus on reducing anthropogenic drivers that promote hybridization and introgression rates. Integrating the implications of ecological shifts due to anthropogenic landscape change into species conservation and landscape management guidelines has the potential to increase conservation and management effectiveness in light of increasing environmental change and degradation worldwide.

Keywords: Biodiversity; Conservation hybridization; Decision making; Suitable habitat; Wildlife management

Introduction

Hybridization is a Driving Force for Speciation and Extinction

Hybridization is a significant force in speciation and species extinction [1-5]. It may occur as a function of either natural or anthropogenic processes [6-9]. While natural hybridization is driven by natural selection and is considered an evolutionary process, anthropogenic hybridization is a result of human-influenced biological and/or spatial alteration [10-13]. Hybridization is especially problematic for rare and endangered endemic species that overlap with relatively abundant species because of anthropogenic landscape disturbance [14]. Hybridization can contribute to species decline and eventual extinction whether offspring are sterile or fertile [6,15]. In cases of sterile offspring, hybridization results in loss of reproductive potential (i.e., recruitment) and thus may result in the extinction of parental taxa by reducing population growth below the rate needed for replacement. In cases of fertile hybrids, genetically distinct populations may be lost through genetic mixing.

The Ecological Role of Hybrids

The harmful effects of hybridization ultimately caused the extinction of many plant and animal taxa [8,16]. Hybrids have multiple ecological roles within ecosystems at various temporal and spatial scales. Such roles primarily depend on whether hybridization is driven by natural or non-natural (i.e., anthropogenic) processes [14,17]. While it is clear that a hybrid's genetic resemblance to its parents is case specific, hybridization generally jeopardizes genetic integrity and results in reduced finessed (i.e., fertility or viability) [18-21]. While natural hybridization has played significant roles in the establishment and extinction of species, accelerating its rate may prove dangerous and undesired. Outcrossing depression, genetic assimilation, genetic drift, and genetic displacement can occur very rapidly and even a single locus can result in drastic fitness differences [1].

Anthropogenic-Driven Hybridization

Wiegand [22] was the first to report that introgressive hybridization is observed most frequently in habitats modified by humans. While natural processes might favor hybridization in evolutionary time, anthropogenic environmental change enables evolution to proceed at its "maximum rate" [7]. Because hybridization often has negative ecological results, forces that accelerate hybridization may threaten ecosystem integrity [4,9,23]. As such, anthropogenic-induced hybridization should be viewed as an evolutionary force that has a primary role in the extinction and formation of species [24]. Thereby, informed and effective conservation strategies should address the probability of it occurring and its ecological implications [13,24,25]. Thus, distinguishing between hybridization processes is critical when establishing conservation and management guidelines [24,26]. A clear understanding of the relationship between anthropogenic landscape change and hybridization rates is crucial in making informed conservation and management decisions.

Moreover, the decline in economic profitability following anthropogenic-driven hybridization is significant, primarily because hybridization causes decreased variance in desired traits in livestock such as canine litter size [20,21,27]. Leroy [26] found that one percent inbreeding in livestock leads to inbreeding depression, which corresponds to a decrease of 0.137% of the mean of a trait in a given population, and that this may have significant economic implications. [23] points out that conservation programs that address inbreeding and outbreeding concerns should be rigorously evaluated and adapted because of such economic implications. As such, population monitoring programs should determine whether allelic variation is due to genetic drift or imposed hybridization should be implemented.

Importance of Habitat Suitability Alterations

The delicate interplay among landscape characteristics that determines habitat suitability for a given species should be considered in management practices [25,28]. Landscape conversion or modification by humans has altered landscape characteristics at increasing rates over the past two centuries. Consequently, shifts in local resources and species composition have occurred [29]. Fragmentation may also induce changes in local species composition. Patchy environments, which increase under fragmentation, result in geographically isolated populations and promote hybridization due to rarity of mates [30-32]. All three processes (i.e., conversion, modification, and fragmentation) enable species that were formerly geographically and/or ecologically isolated to overlap and produce offspring. Hybrid populations possess a unique combination of heritable characteristics derived from crossbreeding, which can be traced to parental taxa [1,33]. The process of gene flow between populations whose individuals' hybridize is referred to as introgression (17) and is achieved when hybrids backcross to one or both parental populations or mate with one another. The degree of introgression will determine if hybrid individuals will give rise to a distinct taxon [34].

Viable and fertile hybrid offspring may become reproductively isolated from both parental forms and, given time, come to represent distinct entities; hybridization followed by inbreeding could increase mutation rates in offspring, leading to increased divergence from parental forms, especially where the recombinant population is geographically isolated [7,27]. Anthropogenic landscape fragmentation may accelerate this process by increasing geographic isolation. Additionally, hybrid swarms are populations in which considerable introgression has occurred (i.e., backcrossing to one or both parental taxa throughout a number of generations, in addition to mating among the hybrid individuals themselves) [8,14,25]. Extensive hybridization and introgression are often associated with habitats disturbed by anthropogenic activity [12]. Therefore, conservation strategies oriented toward avoiding hybrid swarms should incorporate guidelines to avoid introgression. Such guidelines will be most effective if they lead to landscape development and conversion that will be least disruptive to ecological conditions and geographic continuity.

Purpose and Goals

Better understanding of the relationship between anthropogenic activities and hybridization rates will increase conservation and management effectiveness, particularly in light of environmental change and degradation [10,35-37]. The purpose of this paper is to synthesize conceptual issues which will stimulate further consideration of anthropogenic influences on hybridization. The overall goal of this paper is to identify and link specific management practices with hybridization occurrences. We hold that wildlife managers and ecosystem conservationists may benefit from suggested methods by which management effectiveness may be increased. The following two questions guided our analysis:

- Which anthropogenic management decisions induce mammalian hybridization?
- What biological and spatial information should be considered in landscape management and species conservation plans in order to decrease hybridization probability?

Methods

We conducted a search on Google scholar and web of science utilizing keywords such as hybridization, mammals, biological interventions, founder populations, and conservation implications. Papers that were cited in an exceeding number in future papers were included. Additionally, we researched specific cases and published correspondences between authors in order to get an updated comprehension of the literature. We teased out common threads concerning anthropogenic landscape changes and hybridizing species. We synthesized case studies with respect to three aspects:

- Their site-scale,
- Biological or spatial anthropogenic intervention, and
- Linkage of specific land management interventions to anthropogenic-driven hybridization.

Human-induced landscape changed is clustered into two groups: spatial (i.e., primary habitat conversion, geographic fragmentation, and peri-urban expansion), and biological (i.e., shifts in prey availability and population composition). In order to illustrate the findings developed from this synthesis, we examined case studies from five continents: Africa, Australia, Europe, North America, and South America. The paper is divided into five components. First, we briefly provide w working species definition and reference so that hybridization can be discussed within context. Second, we conducted a comprehensive review of the relationship between anthropogenic activities and hybridization induction; we summarize such affects in tables. The third section links specific spatial and biological management interventions to anthropogenic-driven hybridization (i.e., primary habitat conversion, geographic fragmentation, and peri-urban expansion), and utilizes case studies to construct a matrix to serve as a decision tool that provides clarity about activities and their implications on hybridization occurrences and induces informed decision-making. Next, we propose guidelines to be considered by management prior to policy implementation based on case studies and research gaps, and put forward a decision tree to provide assistance for interim conservation strategies. Lastly, we identify informational gaps and research needed.

Hybridization Within the Context of a Working Species Definition

Defining species affects what may be defined as a hybrid; how we define species affects what we think of as a hybrid. In order to appropriately address and recommend management guidelines, a working definition of the species concept should be outlined. We refer to the biological species concept; a species is defined as a species if it is unable to reproduce with individuals from other grouped species. However, we acknowledge that there is a working challenge concerning Mayrs [38] species concept that stems from such reproductive isolation; species are reproductively isolated entities and yet hybridization can occur. This is due to the short evolutionary time of their evolutionary divergence. Given that speciation is a complex dynamic process which unfolds through time, it is important to remember that species are not static and that a snap shot in time without context may be misleading [9]. We emphasis the concept of reproductive isolation as the basis for evolutionary diversification [9,39]. And as such, we suggest that management guidelines stress that the integrity of a species may be preserved by species boundaries and the lack of gene flow amongst them.

Current Knowledge

Anthropogenic Activities Induce Hybridization Through Spatial and Biological Alteration

Population fluctuations in the Pleistocene led to genetic subdivisions of species into ecoregions, shaping modern geographic biodiversity patterns. Since then, natural selection has been the driving force of speciation in tension zones, where stability of hybrid zones is dependent on a balance between selection against hybrids and continuous dispersal of parental genotypes [10]. Over the past century, extensive introgressive hybridization has occurred in many species as a result of habitat disturbance driven by anthropogenic activity by directly and indirectly changing species composition in a given landscape (7). We divided these into three main categories:

- shifts in habitat suitability attributed to primary habitat conversion, geographic fragmentation, or peri-urban expansion [17,26,35]
- founder events, predator control programs, and overstocking, resulting in population density shifts due to changes in competition and predation [21,36,40], and
- introduction of non-native species, resulting in shifts in local species composition [19].

Any of these influences may increase the degree of sympatry among species that previously were isolated geographically, ecologically, or both, thereby altering ecosystem dynamics, and increasing interspecies encounter rates and the probability of interspecies mating. Increased encounters among wild and domestic species are a heightened concern during the planning for biological introductions and relocations [37]. We emphasize shifts in habitat suitability and additionally clustered these into the following:

- primary habitat conversion, resulting in spatial habitat shifts,
- geographic fragmentation, resulting in population isolation, and
- peri-urban expansion, resulting in both spatial and biological shifts.

These landscape disturbances increase the rate at which species distribution expands or contracts. Furthermore, spatial shifts alter local species composition following the overlap of previously ecologically or geographically distinct species. Often, the direct result of such shifts in local species composition is increased hybridization rates [13,28].

Anthropogenic Activities Induce Hybridization and May Promote Genetic Admixture Via Hybrid Zones

Anthropogenic landscape change may result in hybrid zones; regions where two species are sympatric and hybridize and there is a spatial gradient corresponding to the frequency of a favored, neutral, and deleterious allele varies [1,10,17]. These zones are a balance between dispersal of parental taxa and selection against hybrids [39]. The expansion and contraction of species distribution can result in the breakdown of ecological and geographic barriers causing species to become sympatric (typically at the edge of two species' distributions) [40,41]. Population density fluctuations serve as hybrid zone barriers that are maintained by interactions among genes (10). Additionally, clinal trends (i.e., gradients in gene frequency) are narrow relative to species dispersal ranges and vary more in their spatial distribution within a hybrid zone. Therefore, hybrid zones enable us to analyze the variance among parental and offspring characteristics expressed within a spatial gradient, and provide opportunities to measure gene exchange between diverging taxa [10]. We focus on the creation of hybrid zones as a result of human landscape change.

Additionally, competition theory predicts that two competing species can coexist in a stable environment if provided with an adequate degree of resource separation [40]. Landscape change alters mammals' natural prey availability and abundance, which often results in shift in local adaptation and competition (e.g., sympatry of competitors in the same ecological niche) [40]. As a result, one species may eliminate or significantly reduce the numbers of the other [28]. In such cases, anthropogenic landscape disturbance act as drivers for shifts in pray-predator and competition dynamics, thereby fostering conditions ideal for hybridization.

Primarily examples of implications of human-induced landscape change concerns the most endangered canid population, the Ethiopian wolf *(Canis simensis);* densities are decreasing due to primary habitat destruction and fragmentation, associated with agriculture [36]. This is primarily because alpine landscapes are increasingly subjected to overgrazing by livestock [41]. Moreover, peri-urban expansion results in encounters with domestic dogs and human prosecution. Overgrazing results in increased competition for food resources, favoring free ranging dogs [22,36]. Similarly, population declines in the formerly widespread Italian wolf (*Canis lupus*) were concomitant with a decline in populations of their natural ungulate prey and an increase in the numbers of free-ranging dogs, which are their competitors for food [41,42]. Reduction in prey abundance is additionally responsible for the prominent decline of the endangered African wild dog [29].

Benjamin-Fink [14] question the role of state owned reserves in the facilitation of hybridization and genetic admixture of the endemic black wildebeest and the more common blue wildebeest in South Africa. In which the overlap of both subspecies is induced by the practice of translocation. Thereby, poising a significant threat to the genetic integrity of the black wildebeest, which has successfully recovered from two bottle necks in the past [25,42]. Mitchell and Banks [40] attribute declining dingo numbers to shifts in food resources that favor the competing foxes. In turn, increasing fox numbers result in increased competition and provide dingo populations with additional pressure. Furthermore, Gipson and Sealander [43] suggest that a **c**hange in the food habits of wild canids in Arkansas induced hybridization rates between coyotes and feral dogs**,** and Stronen et al., [24] suggest that such changes facilitated coyote-wolves admixed individuals, which are found in Canada (their classification is based on a combination of ancestry and admixture percentage).

Additional mammalian species undergoing human-driven hybridization include the following: Mexican howler monkeys (*Alouatta palliata* and *Alouatta pigra*) [43]; African Cercopithecince monkeys [44]; wolves and dogs across Europe [45]; European wildcats (*Felis silvestris*) and domestic cats in Europe [27,46]; races of house mice (*Mus musculus domesticus*) in Portugal and in Italy [47,48]; martens (*M. caurina* and *M. americana*) on Kuiu Island, Alaska; wild canids (i.e**.,** coyotes, gray wolves and red wolves) and dogs in eastern North America [24,37]; Canada lynx (*Lynx canadensis*) and bobcats (*Lynx rufus*) in North America ; dingos and foxes or dogs in Australia [40]; Ethiopian wolves (*Canis simensis*) and domestic dogs in Ethiopia; African wildcats (*Felis lybica*) and domestic cats in Africa [27]; and wild dogs (*Lycaon pictus*) and domestic dogs in Africa [36,46].

Spatial and Biological Management Interventions

Primary Habitat Conversion

The conversion of primary habitat to secondary habitat can lead to the mixing of previously distinct gene pools between two native species or between a native and an introduced species, thereby increasing hybridization worldwide [19,47-49]. Perhaps the most studied example of hybridization induced by primary habitat conversion is that between gray wolves and coyotes which originated during the extensive agricultural cultivation of the southern United States by European settlers and has continued in more recent years [50-53]. The demographic dynamics of gray wolves and coyotes have changed dramatically in North America over the last two centuries. Gray wolves once inhabited all of North America except for coastal areas of Mexico [54]. However, due to agriculture expansion westward and northward, wolves declined rapidly due to habitat destruction, loss of large game, and direct exploitation by humans [55].

As large, highly mobile predators, wolves require extensive, uninterrupted forested tracts in which to hunt ungulates (33). In contrast, the historical habitat of coyotes primarily consisted of plains and deserts [54]. The coyote's smaller body size and flexible social behavior enables it to persist in relatively small habitat patches and on relatively small prey. In addition, predator control programs were largely targeted at gray wolves rather than coyotes, resulting in relatively high coyote numbers. As such, the differences in population size and genetic variability of gray wolves and coyotes reflect their contrasting recent histories [56,57]. This rapid expansion was coincident with a precipitous decrease in the abundance and geographic range of gray wolves. Escalating human populations, in conjunction with deforestation, resulted in converting forest landscapes to agricultural landscapes, thereby creating a hybrid zone in which coyote numbers increased [54]. Because of such primary habitat conversion coupled with predator control programs, coyote populations increased and expanded their range to include all of North America, whereas gray wolf populations decreased.

As more forested landscapes are converted to farmland, opportunistic coyotes invade and increase their contact with wolves. Mitochondrial DNA (mtDNA) analyses of wolves and coyotes throughout North America document such changes and provide evidence for hybridization in Minnesota and southeastern Canada, areas where coyotes have recently increased in abundance and where gray wolf numbers have declined [52]. Moreover, Lehman et al. [54] found that tested wolves did not have coyote alleles in areas of sympatry where conversion to agriculture is slow or nonexistent, such as Alaska and Montana. This finding is not surprising, because these two species are ecological competitors; under stable ecological conditions, encounters usually result in coyotes being killed by wolves [55]. However, diminishing wolf populations enable coyote's abundant populations in agriculturally developed areas that share edges with wolf habitat [54]. Hybridizing sympatric or near-sympatric populations of coyotes and gray wolves have existed in Minnesota and Quebec for only about 90 years [52,54]. However, the dimensions of the hybrid zone, and thereby hybridization rates, may increase given time and continued change in habitat structure [56].

The degree of hybridization between gray wolves and coyotes is of particular interest to conservationists. There is a debate within the scientific community about whether the red wolf originated as a hybrid between gray wolves and coyotes. This debate has the power to determine major conservation actions (17), such as those concerning the future of the red wolfs' listing and programs [57,58]. The answer is closely dependent on the temporal scale used in asking the question; hybridization between gray wolves and coyotes has occurred only within the last 100 years, and has been confined to the region in which the western red wolves' distribution overlaps with the southeastern part of the coyotes' range [59]. The red wolf territory is larger than gray wolf-coyote hybrid territory; pre-1940 red wolf DNA samples are from the southwestern US, an area in which hybridization between gray wolves and coyotes did not occur, thereby indicating that red wolves could have originated from gray-wolf-coyote hybrids. Such information is important when establishing guidelines for species recovery plans that emphasize the importance of the origin of founder individuals [57].

Under disturbed conditions in North America, hybridization between wolves and coyotes is more common and more extensive than between wolves and their much closer relative, the domestic dog [53,54,57]. However, wolf-dog hybrids are more common in Europe [50,55]. Massive forest clearing throughout central Europe and the Alps has resulted in the decline and geographical isolation of the formerly widespread Italian wolf population [50]. Wolves declined concomitantly with their natural ungulate prey and the increasing numbers of free-ranging feral dog packs. Competition for food and space and interbreeding with dogs are considered prominent threats to wolf conservation in Italy and worldwide [55].

Altering landscape management practices results in a change in local canine composition. An additional example concerns the USA; agriculture practices in Arkansas have shifted from small-scale to large-scale farming. Over the past two centuries, this shift has included large-scale timber clear-cutting. Large-scale clearing favors coyotes, whose habitat overlaps with that of feral dogs. As a result, the abundance of feral dog-coyote hybrids increased, which led to the local extinction of the more specialized red wolf, a change that was documented within a period of 35 years [43]. Shifts in distribution patterns increase hybridization rates, thereby posing additional survival pressure on endemic populations by altering the fragile ecosystem equilibrium through favored adaptive behavior [43]. Landscape modifications are likely to negatively affect specialized species by favoring generalists [60]. Frequently those generalists are non-native species whose range has expanded.

Additional examples of sympatric species hybridizing due to primary habitat conversion include Canada lynxs (*Lynx canadensis*) and bobcats (*Lynx rufus*) in North America [61], Gray wolves and coyotes in Europe and the Near east [53], Ethiopian wolves *(Canis simensis)* and domestic dogs in Ethiopia [62], dingos (*Canis lupus dingo*) and domestic dogs or foxes in Australia [63], European wildcats (*Felis silvestris*) and domestic cats in Europe [64], African wildcats (*Felis lybica*) and domestic cats in Africa [27] and house mice (*Mus musculus domesticus*) in Portugal [48]. In these cases, hybridization may reduce the efficiency of conservation strategies by jeopardizing genetic integrity.

Anthropogenic landscape change may result in geographical shifts in habitats and thus shifts in species distribution. Habitat loss, degradation, and alterations are the main reasons for such distribution shifts. Previously ecologically and geographically distinct species overlap in a given habitat after alteration. Human landscape disturbance induces species sympatry that may lead to increased intensity of competition between ecological competitors and hybridization between rare and common species.

The latter is mainly due to the difficulty in encountering mates in the resulting reduced population. Anthropogenic landscape change creates environments in which the ecological balance among competitors is altered. Under such conditions, the ecological structure is broken by anthropogenic landscape change. A primary example of such ecological alteration is the sympatry of gray wolves and coyotes [52,65]. These two species are ecological competitors [66]. In natural landscapes, encounters likely result in coyotes being killed by wolves [54]; in human altered landscapes, the interaction results in hybridization [36,55]. Such hybridization is attributed to a shift in local species composition that results in significantly high interspecies mating encounters (Figure 1). Similarly, European (*Felis silestris*) and African wildcats (*Felis lybica*) compete with domestic cats (*Felis silvestris catus*) for food and vegetative cover. Because wildcats are rare in any habitat, encounters may result in hybridization rather than death [50]. Similarly, Gottelli et al. [62] attribute the decline in Ethiopian wolf (*Canis simensis*) populations to a breakdown in their ecological barrier with domestic dogs (*Canis familiaris*), who are their main food competitors. These examples illustrate why landscape managers should consider such breakdowns in ecological interspecies relationships that might result from implementing ill-informed landscape management plans.

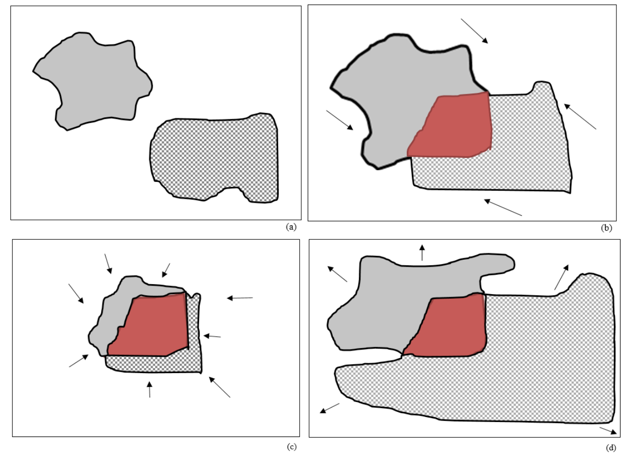

Figure 1: Conceptual shifts in species` abundances due to human-induced landscape alterations and consequential formation of hybridization grounds and hybrid zones. Gray area illustrates species` 'a' land occupancy, checkers area illustrates species` 'b' land occupancy, and the red zone indicates hybridization grounds and hybrid zones. area **(a)** the natural state of species 'a' and species `b` homerange. **(b)** homerange range expansion due to artificially improved carrying capacity (and thus, suitable habitat) creates sympatry between species which allows for interspecies mating encounters and hybridization. **(c)** given time, stochasticity and external forces (e.g., restoration projects, droughts, decreased carrying capacity, increased competition with additional species, etc`) will operate to shrink the distribution of species 'a' and 'b', thereby facilitating the creation of a hybrid zone. **(d)** given time, external forces (increased carrying capacity and decreased competition) will cause distribution expansion of species 'a' and 'b', while stochastic variables maintain the core interbreeding zone and as such, facilitate the creation of a hybrid zone.

The boreal forests of Canada and Alaska serves as core habitat for lynx, while bobcats are widespread in southern Canada and the contiguous United States. Although lynx and bobcats do not typically co-occur, the peripheries of their ranges overlap in a hybrid zone in Minnesota, due to primary habitat conversion (i.e., deforestation) [61]. As a result of such habitat overlap, lynx and bobcats hybridize. Lynx have a threatened status [67] and the primary conservation plan is reintroduction of lynx into the wild. However, hybridization potentially limits the distribution and recovery of lynx [61]. Similarly, two species of marten hybridize on Kuiu Island in southern Alaska; *Martes caurina* are endemic to Kuiu Island while *M. americana* was restricted to the mainland. The species currently overlap on Kuiu Island. Half of the Kuiu Island population possesses *M. americana* characteristics that are common to nearby island and mainland populations while the other half have *M. caurina* characteristics unique to Kuiu Island. The shift in *M. americana* distribution is attributed to the extensive logging of the mature temperate forest that once supported *M. americana* subspecies; the clearance acts as a hybrid zone that favors hybrid individuals. As more forests are cleared, hybridization poses a threat to the endemic *M. caurina*.

The Ethiopian wolf is the world's rarest canid and is threatened by increasing rates of hybridization with free-ranging dogs. Their native habitat, the alpine zone of Ethiopia, covered 100,000 km^2 just 15,000 years ago. Alpine landscapes are increasingly subject to overgrazing due to increasing peri-urban expansion [36]. Overgrazing results in increased competition for food resources, favoring free ranging dogs [36,47]. As a result, fewer than 500 individuals occur in the Ethiopian Rift Valley, restricted to above 3000 m, where they prey exclusively on rodents [62]. At the same time, free-ranging feral dogs have become more abundant due to their generalist character [47]. This shift in species composition has resulted in increased encounters between rare (i.e., Ethiopian wolf) and common (i.e., free-ranging dog) species and thus increased interspecies mating opportunities. Thus, increasing hybridization rates are attributed to recent decreases in suitable habitat due to human activities [62]. Conservation and management plans need to consider hybridization rates at various spatial scales. The long term survival of this most threaded canids requires conserving key habitats for both the wolf and its preys`, in conjunction with full community participation [68]; incorporating community-led conservation initiatives that focus on better understanding the ecosystems complexity in addition to the interaction with indigenous people increase participation and acceptance levels.

Peri-Urban Expansion

Enacting and enforcing conservation strategies is particularly difficult in regards to hybrids between wild protected species and their domestic cousins [63] because introgression causes difficulty in distinguishing wild from domesticated or hybrid forms. Additionally, rapid displacement of native or wild species by their invasive or domesticated counterparts may occur [15]. Moreover, rare species may be particularly sensitive to hybridization where sympatry with common species occurs [61]. Hybridization may present conservation problems if it threatens the genetic integrity of endangered species [53]. Human population growth, which gives rise to peri-urbanization (the expansion of human settlements), has been found to correlate with hybridization rates. Peri-urban expansion may increase hybridization rates through one of three processes:

- Loss of suitable habitat due to habitat conversion or degradation,
- Increased encounters among domestic and wild populations due to shifts in relative population numbers, and
- Decreases in wild population size and range due to ecological shifts (e.g., food type and abundance) and predator control programs.

Rates of hybridization and introgression vary with the relative densities of wild and domestic species [47]. Hybridization between gray wolves and dogs is most frequent near human settlements, where wolves are found in low densities but feral and domestic dogs are common [53], as was documented for the Ethiopian wolf and domestic dogs (36). Domestic dog populations are significantly higher than those of the endangered Ethiopian wolf (by a ratio of 10:1) [62]. Thus, hybridization between the Ethiopian wolves and free-ranging dogs is promoted and facilitated by human-induced sympatry [47]. In addition to hybridization, domestic dogs threaten Ethiopian wolf populations because they carry diseases such as rabies and act as competitors for food (36). In Australia, domestic dogs also present a threat to dingo populations due to hybridization [63]. There are increasing numbers of domesticated dogs on private land and aboriginal camps, and dingo populations are steadily decreasing [49].

Shifts in species composition may also be due to shifts in resource availability. The wolf mother of a wolf–dog hybrid litter was observed to feed regularly at human garbage sites [47]. This suggests an ecological shift due to human presence, favoring scavengers. Such ecological shifts, in conjunction with intensive hunting pressure on wild animals, could favor crossbreeding with domestic populations through the decline of wild population size and range in conjunction with increasing domestic population size and range. Such ecological shifts may also favor hybridization between two wild species, such as in the case of wild *Canis* and coyotes. As a result of decreased wild wolf populations, encountering a conspecific mate becomes rare, in comparison to encounters with coyotes [54]. Although hybridization between wolves and coyotes is less expected because these two species normally coexist as ecological competitors [66], altering competition results in increased hybridization rates, such as in red wolf-coyote hybridization [53,56] and gray wolf-coyote hybridization [54]. In addition, predator control programs are largely targeted at gray wolves.

Additional well-documented mammalian wild-domestic hybridization examples involve cats [63]. Domestic cats are distributed worldwide and are virtually sympatric with European and African wildcats almost everywhere the latter two exist, indicating that hybridization is a global problem, albeit with site-specific solutions. Vila et al. [53] found evidence of high survival rates of wildcat-domestic cat hybrids in Romania and western Russia. In contrast, other studies suggest that despite a long period of sympatry in central Italy [50], hybridization is limited to specific areas at the geographical and ecological edges of habitats (i.e., transition zones). Increasing habitat disturbance might alter such geographic limitations and thus increase hybridization rates. And as such, there is a need to consider species` home ranges during the process of developing peri-urban expansion plans so that overlap remains minimal.

Geographic Fragmentation

Geographic fragmentation increases hybridization by increasing the size of edge zones between habitats. These intensify edge effects on small populations and the creation of transition zones (i.e., species sympatry within habitat edges). Increasing inbreeding genetic drift, due to population isolation and decline, may produce morphological divergence and reduce genetic diversity [69]. Therefore, fragmentation can jeopardize genetic integrity. Geographic fragmentation further affects hybridization rate in the same way that primary habitat modification and conversion do. Spatial shifts in habitats may result in a change in local resources such as habitat quality and size, in addition to prey availability and abundance. Consequently, species range may expand or contract, resulting in shifts in local species composition.

Anthropogenic Activities Facilitate Hybridization Through Alteration of Biological Mechanisms

An increasing number of examples of genetic exchange between species have been reported [14,69]. Three biological mechanisms serve to reduce hybridization: 1) ecological barriers, 2) behavior patterns and/ or 3) temporal and/or spatial barriers. A breakdown in any of these mechanisms may increase the probability of interspecies mating [34] through sympatry of geographically and/or ecologically isolated species. The impact of such activities is similar to actively translocation and jexo-stocking (i.e., when hybridizing species are overstocked on a given farm) of wildlife for game management [13,14]. Such changes increase encounter rates and the probability of interspecies mating [13]. In the following section, we provide examples that illustrate anthropogenic landscape change favors hybridization by altering biological mechanisms.

Behavioral Patterns

The differences in the degree of introgression of dog genes into gray wolf and Ethiopian wolf populations may reflect differences in the mating system of the two species [53]. The breeding season of the latter is very short and females disperse from their natal pack to copulate with males from neighboring territories [62]. Additionally, Ethiopian wolf hybrids usually are found in areas where Ethiopian wolves are significantly outnumbered by free-ranging domestic dogs (36). Thus, female wolves encounter male dogs at a higher frequency than male wolves, and therefore often mate with the dogs. After mating, females return to their natal pack to give birth and get assistance from pack members in raising their young. Consequently, hybrid pups are socialized as Ethiopian wolves and easily integrate into their population, and the high survival rate of Ethiopian wolf-dog hybrids increases further.

In contrast, female dispersing gray wolves do not return to their natal pack because the reproducing alpha pair holds dominance over reproduction. Because male dogs do not assist in rearing their young, offspring of gray wolf-dog matings rarely survive in the wild. Thus, introgression is less likely to occur in gray wolf-dog hybrids than in Ethiopian wolf-dog hybrids. However, landscape alteration such as fragmentation may result in isolated populations in which the previously reproductively dominant alpha pair is missing. Thus, the wolf social fabric might be compromised by human activities. Such findings suggest that altering pack behavior and population dynamics may change hybrid introgression rates. Such information is vital when designing strategies to decrease hybridization rates, especially when funding is limited and human landscape change is accelerating.

Temporal Patterns

Natural interspecific breeding rates may be low due to differences in breeding seasons and physiological characteristics among species. However, shifts in local environmental conditions may result in shifts in biotic and micro-abiotic factors. Abiotic conditions and food availability are the main variables correlated with breeding seasons. Shifts in those variables may alter breeding seasons, physiological characteristics, or both. In such cases, coupled with shifts in local species composition, hybridization probability increases. Additionally, landscape changes may favor introgression and hybrid establishment, increasing the extinction probability of relatively less fit or rare species. While coyotes are well adapted to blizzards and low temperatures, Mengel [70] suggested that the physiology of coydogs (coyotes × domestic dogs) is not adapted to harsh winter weather and therefore the latter are at a disadvantage when competing with established coyotes [70]. In such examples, environmental conditions result in hybrid disadvantages that prevent introgression. However, shifts in environmental conditions (e.g., peri-urban expansion that increases shelter and food availability), result in conditions that favor hybrids and promote introgression.

Hybridization has the potential to produce morphological, physiological, and behavioral changes. Due to species and sex-specific body size differences, there is a strong directionality of interspecific mating. Female coyotes mate with male wolves [55], female Canada lynx (*Lynx canadensis*) hybridize with male bobcats (*Lynx rufus*) (Schwartz et al., 2004); male Australian, African, and European wildcats mate with female domestic cats [27]; and female wolves mate with male dogs [50]. Backcrossing is frequent in such cases, threatening each species' genetic integrity. Estrus cycles are physiological differences that further distinguish dogs from wild wolves and wolf-like canids. Female wolves have a single estrus per year, and males exhibit seasonally elevated testosterone levels. Dogs do not follow this pattern; female dogs can produce two litters per year and males continuously maintain high testosterone levels.

Consequently, male dogs can mate with female wolves during the wolves' peak receptivity whereas the reverse mating may not often occur. Ecological balances preclude dogs from mating with wolves within stable ecosystems. However, anthropogenic landscape change alters this ecological balance and may result in the introgression of domestic genes. Such introgression threatens the integrity of wild canid gene pools [36]. Canid and wildcat populations are threatened in Australia, Africa, Europe, and the North America by their crossbreeding with feral or free-ranging dogs and domestic cats, respectively [49,63]. Thus, a shift in the breeding season of hybrids may restrict their chances to backcross into parental populations and therefore increase the probability of hybrid taxa becoming established [13,16].

Hybridization can pose a threat to small populations and rare species even if gene pools do not mix [8]. Small populations and rare species are often limited by the number of reproductively fertile females. In such cases, sterile hybrids pose additional pressure due to decreased recruitment opportunities [8]. In addition, common species and rare–common hybrid individuals increase the intensity of ecological competition against rare species. Knowledge about such patterns may serve as the foundation of informed conservation and management decisions.

Lessones Learned: Conservation Implications and Future Steps

Management for hybridization has two basic components: (1) is the management practice causing a direct or indirect shift in species distribution (i.e., altering intraspecies and interspecies dynamics by age, gender, range, competition, or altering habitat suitability characteristics by landscape conversion, modification, or fragmentation). The goal of conservation management is usually to maintain current species diversity with carrying capacity in mind. To do this, we conducted a crossboard synthesis of management interventions that resulted in hybridization and outlined methods to achieve efficient management guidelines. We offer a structured decision analysis and path in order to maximize currently employed, and future, management plans (Figure 2). We then present a serious of guidelines to be considered prior to management intervention.

Conservation Implications

Extensive hybridization is often associated with habitats disturbed by anthropogenic activity. If we are to succeed in managing hybridization, we must recognize its growing magnitude and its threats, especially to rare and endangered endemic species. That need is crucial in light of accelerating environmental change. Underlying anthropogenic forces that induce hybridization rates vary among geographic locations. That variation means that conservation and landscape management guidelines must be case-specific. Development of such guidelines should begin by identifying the specific type of anthropogenic landscape disturbance that threatens to facilitate the hybridization in question [i.e., model the relationship between landscape and the taxa in question, following the process outlined in (Figure 2)]. Once such an analysis has been completed, the manager may develop conservation guidelines around the temporal and spatial scales of concern in that specific case.

Better understanding of the ecological context in which hybridization occurs may increase the effectiveness of long-term conservation and management strategies. Managers may establish objectives focused upon decreasing the degree to which anthropogenic forces promote hybridization and introgression. The following section offers guidance for developing such objectives and for future research.

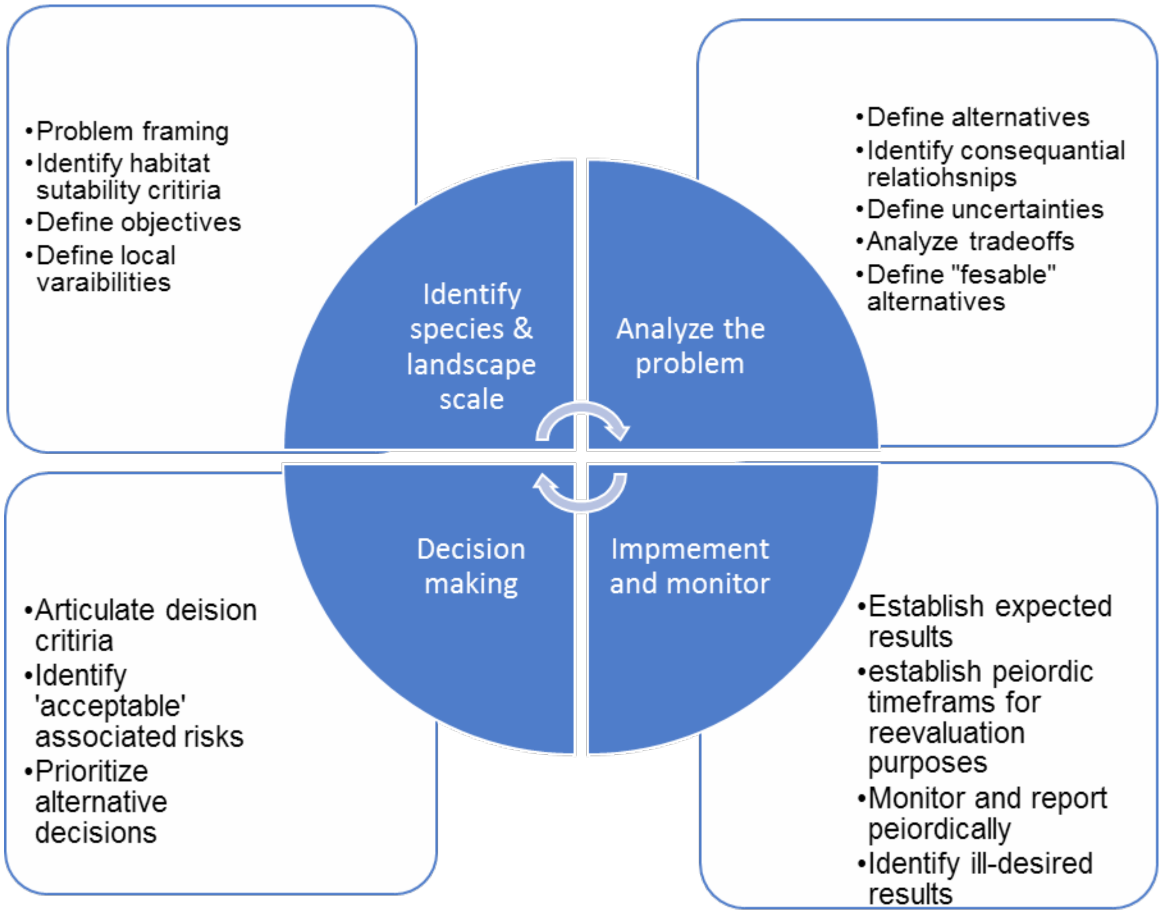

Figure 2: A structures decision analysis to promote management for hybridization. this is a sequential and region-specific process designed to better understand local variables and minimize hybridization occurrences. Key steps are highlighted in the core blue circle. Associated sub-steps are listed in corresponding blocks.

Guidelines to Be Considered by Decision Makers Prior to Management Implementation

Anthropogenic landscape changes promote hybridization rates by shifting ecological and geographical interactions A synthesis of the studies cited in this paper indicates a common pattern by which anthropogenic forces induce hybridization and introgression. This pattern follows one of three paths: (1) primary habitat conversion, (2) peri-urban expansion, or 3) geographic fragmentation. Those forces directly or indirectly result in a shift in local species composition (Figure 1). While direct impacts lead to the expansion or contraction of the distribution of wild species, indirect impacts result in expansion of the distribution of non-native species. Altering the distribution of habitat types can increase the degree of sympatry among species that previously were geographically or ecologically isolated. Those shifts in species composition alter interspecies encounters and the probability of cross-species mating, therefore hybridization (Figure 1).

In addition, anthropogenic landscape change often creates hybrid zones (Figure 1). Such relationships need to be examined with particular attention to outcomes if we are to increase conservation efficiency. Hybridization may threaten species in one of two ways: 1) given spatial and reproductive isolation, fertile hybrids may create a hybrid swam, or 2) population levels will be beneath those needed for population replacement due to sterile hybrids. Efficient conservation actions recognize human activities that increase hybridization and reduce, eliminate, or avoid those activities that cause hybridization by considering the following guidelines.

Habitat Conversion and Restoration

Conversion of primary habitat to secondary habitat will result in shifts in prey availability and cover abundance (i.e., suitable habitat). Deforestation and agricultural land expansion are examples of activities that result in the loss of suitable habitat, which in turn results in contraction of species' distributions. These losses can be avoided or mitigated by increasing or maintaining proportional habitat distribution through informed landscape development decisions, as well as through direct landscape restoration.

Peri-Urban Expansion and Control of Feral and Domestic Species

Designating landscapes for urban or semi-urban development, instituting mammal extermination programs, and introducing non-native species are all associated with peri-urban expansion. These processes shift competitive advantages to favor domestic species, causing the distribution of indigenous species to contract. In such cases, wild individuals become outnumbered by domestic and feral individuals, encounters between wild and domestic species increase, and hybridization is promoted. Therefore, if management objectives include decreasing hybridization rates, efforts should focus on reducing encounters between wild and domestic species. This can be achieved by (1) public education to reduce the number of domestic free-roaming dogs and cats, and (2) enforcement of feral species eradication programs to achieve lower wild-feral encounter rates. A low-budget alternative in many situations may be as simple as increasing the efficiency of garbage removal. Control of both wild and domestic populations reduce hybridization by decreasing the kind of competition that favors domestic species and by reducing the degree to which species composition balance is affected by peri-urban expansion.

Geographic Fragmentation and The Need for Continuity in Landscape Development Plans

Geographic fragmentation is caused by ill-informed landscape development decisions. These development plans ignore the role that landscape continuity plays in the viability of small populations (e.g., genetic drift, isolation). In such small populations, hybridization increases the threat of extinction because fragmentation often results in reproductive isolation in conjunction with isolated and degraded habitats. Attempts to reduce such problems should focus on maintaining connectivity among habitats within a given landscape. Such strategies will ensure gene flow among metapopulations and decrease threats from hybridization.

Reintroduction Programs

Given the important role of human-driven habitat modification and biological control in population reestablishment in areas of local extinction, effective reintroduction programs can reduce vulnerability to hybridization and genetic admixture by incorporation variables such as local species abundance and composition and their habitat context, in their risk assessment in order to minimize overlapping previously ecologically and/or geographically isolated species. As such, reintroduction programs will expand their focus from simply meeting habitat requirements for reintroduced populations. Considerations for the ecosystem complexity will reflect in accurate risk assessments to the success of the program.

Conserving Genetic Integrity; Hybrid Identification and Recovery Programs

Hybrid individuals have a combination of distinct parental genes, and are identified by various genetic or phenotypic characters or both. However, the extent of genetic variance is often not accounted for by morphological variance. Detection of hybrids using morphological characters assumes that hybrid individuals are phenotypically intermediate between the parental individuals. Often, however, this is not the case; hybrids may express a mosaic of parental phenotypes. Additionally, individuals from hybrid swarms that derive most of their genes from one parental taxon are often morphologically indistinguishable from that parental taxon. As a result, genetic techniques may be more reliable when attempting to distinguish hybrids from parental taxa and in attempts to gain insight about hybridization.

Morphological identification techniques also are ineffective when attempting to identify the temporal scale at which hybridization occurred (i.e., distinguishing among first generation hybrids, backcrossed individuals, and later generation hybrids). Such temporal distinctions are crucial because if a hybrid swarm has not formed and a sufficient number of parental individuals remain, it may be possible to recover the genetic integrity of the population by removing hybrids. The number of parental individuals present may determine if there is a need for captive breeding programs. Such programs need to incorporate clear guidelines to ensure genetic purity of the breeding stock. Locations where the parental taxa occur will have been subjected to differing anthropogenic landscape disturbances, so there will be variance in the degree to which locations have incorporated genetic variance. Selecting founders from a range of well-understood locations will increase genetic diversity and, if done carefully, can reduce the influences of hybridization.

Ecological changes modify behavioral relationships and reproductive interactions between wolves and dogs. Efficient conservation plans define human activities that increase hybridization rates and incorporate guidelines to decrease or avoid them. Such conservation plans may be simple, such as efficient garbage removal methods. Moreover, the need to control the expansion of wolf populations. Randi et al. (2000) further suggest that feral dog packs should be eradicated to ensure the conservation of genetic integrity of pure lineages.

Current Informational Gaps and Needed Research

Future Research and Conservation Methods

Mostly, the primary objective of wildlife managers and conservationists is to preserve habitat suitability and species` genetic integrity as much as possible. Current management practices, however, have flaws, including unintentional promotion of mammalian hybridization. Translocations with conservation objectives such as creating founder effects, managing for inbreeding and outbreeding, and combating bottlenecks have also resulted in hybridization [5,21,23,71]. Additionally, translocation activities and overstocking game animals, management practices driven by economic incentives, also increase hybridization [14].

Primary examples of a management practice that facilitated hybridization while aiming to establish founder programs in order to address conservation concerns associated with bottlenecks include bontebok (*Damaliscus pygargus pygargus*) with blesbok (*Damaliscus pygargus phillipsi*), and black wildebeest (*Connochaetes gnou*) with blue wildebeest (*Connochaetes taurinus*) in South Africa; black wildebeest were reintroduction and overlapped with blue wildebeest in Abe Bailey national reserve. The entire population consisted of backcrossed hybrids of varying degrees and was culled to preserve the genetic integrity [13,72]. Additional species and subspecies that have experienced allelic diversity loss due to the hybridization that followed translocation include Lichtenstein`s hartebeest (*Alcelaphus lichtensteinii*), common tsessebe (*Damaliscus lunatus*), blesbok (*Damaliscus pygargus phillipsi*), bushbuck (*Tragelaphus scriptus*), nyala (*Tragelaphus angasii*), giraffe (*Giraffa camelopardalis*), Burchell`s zebra (*E. burchellii*), roan antelope (*Hippotragus equinus*), sable antelope (*H. niger*), waterbuck (*Kobus ellipsiprymnus*), lechwe (*Kobus leche*), scimitar-horned oryx (*Oryx dammah*), gemsbok (*O. gazella*), Hartmann`s mountain zebra (*Equus zebra hartmannae*), Cape eland (*Taurotragus oryx oryx*), and Livingstone`s eland (*T. oryx livingstonii*) in South Africa. We have identified a number of priority areas that require research effort.

Additional Demographic and Genetic Surveys

The literature discusses the hybridization phenomenon in depth. However, the number and scope of case studies is limited. Demographic and genetic surveys of populations subjected to anthropogenic landscape alteration and likely to undergo hybridization are needed to better understand and identify the effects of landscape change on hybridization and related population declines.

Lack of Species-Level Information

There is a need to develop genetic methodologies that will indicate hybrid generation (i.e., degree of introgression). Such information may provide a temporal context in which management and conservation guidelines should be formed. For example, Randi et al. [50,55] found evidence of hybridization between wolves and dogs, and between non-native wolves and local wolves, in Italian populations. However, they downplayed the significance of such information due to the lack of evidence of introgression. They suggested that the mtDNA monomorphism they observed was possibly the outcome of random drift in the small, declining, and isolated population; and that such populations are a result of low effective population size (recruitment) during the last 100 years and continued loss of genetic variability [55].

Monitoring Populations That Include Hybrid Individuals

Certain conditions do not favor introgression and, therefore, hybridization threats to wild populations diminish. In light of accelerating anthropogenic landscape alterations, there is a need to monitor the dynamics and viability of such populations and their surrounding landscape with the aim of identifying correlations and drivers that do not favor hybridization and determine the reasons why some populations hybridize, and others do not.

Integration of Landscape Models

Landscape change is a primary driver in hybridization. As such, landscape models are relevant to hybridization-related research and should be incorporated into and discussed in them. For example, satellite images and GIS references can be used to document spatial and temporal changes in landscape cover. Integrating such information into predictive models of population dynamics will increase the accuracy of predicting the probability that hybridization will occur within landscapes subjected to anthropogenic change. This will increase informed species conservation and landscape management decision-making.

Integration of Simulation Models

A decision tree and simulation models offer a safe way to investigate the degree to which suggested, and currently enforced, management strategies may result in hybridization. we caution against the idealized reality that is simulated in and offered by such models. When acknowledging and factoring for idealized ecological processes simulation, models may become an asset and serve decision-makers that are forced to implement management strategies under limited resources and scarce data. Informed and efficient management strategies should be narrow enough to address the conservation concern at hand, and yet broad enough to adjust and adapt for its ecosystem-level implications. Our decision tree assists management by illuminating which spatial and biological processes to consider and their appropriate scale, in addition to their weight and functional structure of interactions. Decision-makers can vary functional parameters, thereby tailoring this tool to aid them in investigating the degree to which management strategies facilitated hybridization.

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