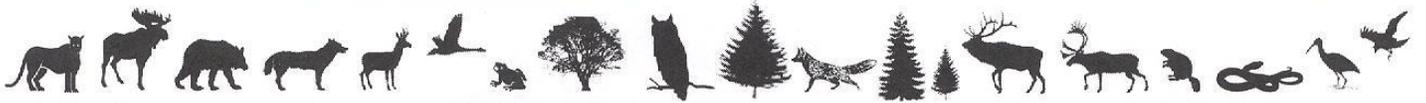


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## The *Martes* Complex: Opportunities for Developing Multi-species Management and Conservation Strategies

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### Abstract

The genera *Martes*, *Pekania*, *Gulo*, and *Eira* (the *Martes* Complex) share many life history traits and conservation challenges. In this paper, we discuss management and conservation strategies that can help address common concerns about the persistence of species in the *Martes* Complex in the face of increasing habitat loss and fragmentation, climate change, and other challenges to the sustainability of their populations and maintenance of their genetic diversity. We review management issues associated with the persistence of *Martes* populations, including productivity (e.g., management of natal and maternal dens, and resting sites), mortality factors (e.g., fur harvest, incidental trapping); refuges, and translocations. We also identify a series of measures to maintain vertical and horizontal structural complexity within forest stands, and mosaics of forest stands with varying ages and structures in forested landscapes. Additionally, we discuss various silvicultural approaches to managing cut blocks at stand and landscape scales. The strategies we recommend in this review can be successfully implemented for any species in the *Martes* Complex because they address common threats to their persistence. However, we need to learn much more about these species before we can develop comprehensive management programs, particularly for the subtropical martens (*Martes* spp.) and tayra (*Eira barbara*). Species in the *Martes* Complex play essential ecological roles that should be recognized in multi-species management and conservation efforts, and promoted in public education programs.

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## INTRODUCTION

Extant species in the *Martes* Complex occupy temperate boreal forests (American, Pacific, and European pine martens [*Martes americana*, *M. caurina*, and *M. martes*, respectively]; sable [*M. zibellina*]; fisher [*Pekania pennanti*]; wolverine [*Gulo gulo*]), coniferous-deciduous forests or hedges (fisher; European pine and stone martens [*M. foina*]), and subtropical and tropical forests (yellow-throated, Japanese, and Nilgiri martens [*M. flavigula*, *M. melampus*, and *M. gwatkinsii*, respectively]; tayra [*Eira barbara*) (Proulx and Aubry 2017). All species in the *Martes* Complex are associated with trees and forests to some degree, with the exception of some wolverine populations that inhabit the treeless tundra (Larivière and Jennings 2009). In addition, all exhibit a preference for interconnected landscapes comprising a variety of forest types and seral stages that offer protection from predators and adverse environmental conditions (Proulx and Aubry 2017). Furthermore, all members of the *Martes* Complex are threatened by habitat loss or degradation, which could impact their daily activity patterns, food habits, movements, reproductive activities, and dispersal processes (Proulx *et al.* 2004; Ruggiero *et al.* 2007; de Oliveira 2009).

Species in the *Martes* Complex have relatively low reproductive rates (Proulx and Aubry 2017) and some have relatively large home ranges (Hornocker and Hash 1981; Weir and Corbould 2006). In addition, they have low resilience when habitat loss or alteration is coupled with high mortality rates from trapping, hunting, or poisoning (Banci and Proulx 1999; Gabriel *et al.* 2012). Given increasing threats to boreal species from global climate change (McKelvey *et al.* 2011; Wasserman *et al.* 2012), and to tropical species from agricultural encroachment and industrial development (Rhim and Lee 2007; Lau *et al.* 2010), it will be challenging to maintain or improve the integrity of their populations and habitats in the coming decades. Accordingly, we argue that the best approach for effectively conserving species in the *Martes* Complex is to develop multi-species management and conservation strategies, especially for sympatric species with similar ecological requirements. In this paper, we present several strategies for population management and habitat conservation that can be combined or adapted to provide benefits to all species in the *Martes* Complex.

## CONSERVATION & MANAGEMENT ALTERNATIVES

Issues and concerns regarding the management and conservation of habitats and populations of *Martes* species are as diversified as the environmental conditions and socio-economic contexts where these species are found. Nonetheless, habitat loss, food limitation, and human activities appear to be the primary reasons for the decline of populations in the *Martes* Complex (Lin 2000; Proulx *et al.* 2004; Saeki 2006; Proulx and Aubry 2017; Zhu *et al.* 2017). In this review, we present strategies for population management and habitat conservation that previous researchers have identified as critical for the persistence of species in the *Martes* Complex.

Habitat management must be conducted at both the stand and landscape scales (Figure 1). Maintaining structural complexity at the stand scale and mosaics of interconnected forest stands of varying ages and structures at the landscape scale, are essential for the perpetuation of populations among the *Martes* Complex (Figure 1). Disturbances that degrade the integrity of stands and landscapes must also be managed to accommodate the ecology of *Martes* species. Although such disturbances may reduce the productivity and survival of individuals, human activities may result in mortalities that are additive to those occurring naturally, which can compromise the future of populations (Fortin and Cantin 1994; Banci and Proulx 1999). When populations have declined to a point where they can no longer sustain their numbers or their genetic diversity, actions must be taken to rebuild their populations in landscapes that meet their habitat requirements (Figure 1). In the following sections, we expand on strategies for population, habitat, and timber-harvest management that can help ensure the persistence of species in the *Martes* Complex.

## POPULATION MANAGEMENT & CONSERVATION STRATEGIES

The geographic distribution of species in the *Martes* Complex contracted substantially during the last century due to habitat loss and degradation, over-trapping, and poisoning (Proulx *et al.* 2004; Powell *et al.* 2012). Although the conservation of martens, fishers, wolverines, and tayras will require the protection and restoration of key habitats, many populations are at risk from either low numbers or restricted gene flow from other populations. American martens and fishers have life histories that are strongly

influenced by adult survival (Buskirk *et al.* 2012), a life history trait that likely applies to all species in the *Martes* Complex with delayed implantation. In addition, dispersing juveniles settle relatively close to their natal territories (Johnson *et al.* 2009; Thompson *et al.* 2012; Matthews *et al.* 2013; Aronsson *et al.* 2017). Thus, in temporarily favorable environments, it is unlikely that populations can grow quickly or effectively colonize habitats that are unoccupied by conspecifics (Buskirk *et al.* 2012; Matthews *et al.* 2013). However, the recovery of populations of *Martes* species that are at risk or have been extirpated can be addressed in various ways, including the management of reproductive denning habitat, the control of mortality factors, the establishment of refuges, and the implementation of translocation programs.

#### **Management of natal and maternal dens, and resting sites**

Populations of species in the *Martes* Complex may be limited by a scarcity of natal (parturition site) and maternal (post-parturition sites used after the kits have been moved by their mother) dens, and resting sites (refuges where animals rest or sleep when they are inactive) that provide adequate protection from predators and help them conserve energy (Zalewski 1997; Ruggiero *et al.* 1998; Aubry *et al.* 2018). A lack of suitable dens and resting sites may compel animals to use suboptimal structures or habitats (Birks *et al.* 2005). In managed forests, retaining snags with relatively large cavities, or declining trees with cavities or heartrot (Bull *et al.* 1997; Weir and Almuedo 2010; Raley *et al.* 2012), is the most ecologically sound and economical approach to providing den trees (Figure 1). In forest stands where such structures are lacking or scarce, artificial den boxes can be installed to provide denning habitat (Messenger *et al.* 2006; Davis 2016). Importantly, logs and other fallen deadwood provide species in the *Martes* Complex with maternal dens, escape cover, and foraging opportunities (Gilbert *et al.* 1997), and should be added to forest stands and movement corridors that contain little or no structure at ground level (Figure 1).

#### **Mortality factors**

##### *Harvest protection*

Human activities, such as trapping or hunting, can have a large impact on populations of species in the *Martes* Complex (Ruelle *et al.* 2014), especially if they are small and isolated (Linnell *et al.* 2018) or experiencing habitat losses (Lacy and Clark 1993; Banci and Proulx 1999; Mowat *et al.* 2019) that may be unsustainable for species such as the wolverine (Lofroth and Ott 2007). In Scandinavia, the control of wolverines to minimize conflicts with reindeer

(*Rangifer tarandus*) and sheep industries has resulted in the extirpation of some wolverine populations (Helldin 2000; Landa *et al.* 2000).

When managing *Martes* populations that are trapped or hunted for their fur, or culled to resolve conflicts with human activities, sex and age ratios, reproductive performance, and fluctuations in population abundance should be closely monitored to avoid excessive harvests (Fortin and Cantin 1994) and unwarranted control programs (Proulx 2018a). Long-term data on pelt registration, trade-transaction reports, export permits, fur-taker reports, population sample surveys, catch-per-unit-effort indices, and quotas can all be used to identify geographical and temporal shifts in species' abundances and distributions (Erickson 1982; Proulx 2000; Fortin and Cantin 2004). The information gathered from analyzing carcasses and harvest data can also be supplemented with field data using noninvasive research methods (Long *et al.* 2008; Proulx and Do Linh San 2016; O'Mahony *et al.* 2017; Kinoshita *et al.* 2019). Harvest data collected over decades may reveal trends in relative abundance and distribution, and may be useful for assessing the effects of trapping on populations within the *Martes* Complex (Obbard *et al.* 1987; Golden 1999). Although changes in annual harvests may result from changes in abundance, they are also a function of pelt price, weather, trapping regulations, prey cycles, economic conditions, trapper's experience or interest, and other factors (Erickson 1982; Hamilton and Fox 1987). Trapping mortality may be additive to natural mortality (Fortin and Cantin 1994; Banci and Proulx 1999), particularly when food is scarce, reproduction is low, and animals are forced to disperse in search of prey (Thompson and Colgan 1994). An array of strategies can be used to reduce the impact of trapping on populations (Figure 1) and, under some circumstances, it may be necessary to stop all fur-harvest activities to allow populations to increase in number (Figure 1), as was done successfully for fishers in a portion of Québec (Garant and Crête 1997) and for sables in Russia (Monakhov 2011).

Species in the *Martes* Complex may also be vulnerable to unintentional captures in traps set for other species. For example, in North America, fishers are readily captured in traps set for red foxes (*Vulpes vulpes*), coyotes (*Canis latrans*), or Canada lynx (*Lynx canadensis*) (Coulter 1960; Cole and Proulx 1994; Suffice *et al.* 2017); in the United Kingdom, pine martens are killed in traps set for the so-called "small ground vermin" species, such as stoats (*Mustela erminea*), European mink (*Mustela lutreola*), brown rats (*Rattus norvegicus*) and grey squirrels (*Sciurus carolinensis*) (Birks 2017). Although the trapping season for the threatened Newfoundland marten had been closed, animals were still being killed in traps set for other furbearers and in

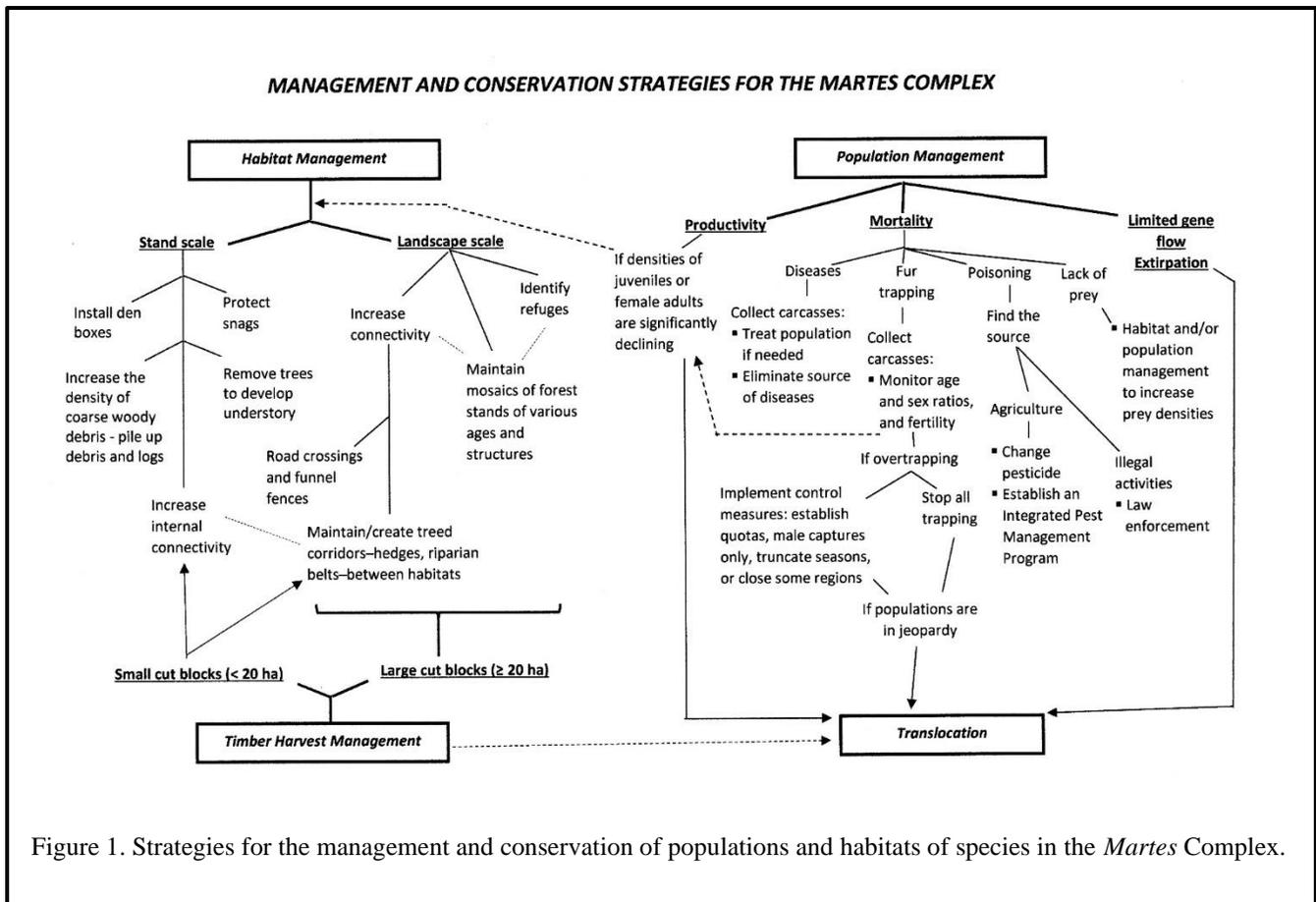


Figure 1. Strategies for the management and conservation of populations and habitats of species in the *Martes* Complex.

snowshoe hare (*Lepus americanus*) snares (Canadian-Newfoundland Marten Recovery Team 1995). If trapping cannot be prohibited in areas containing populations of *Martes* Complex species that are in jeopardy, the use of selective trapping devices (Proulx *et al.* 1994a) or live-traps (see examples in Proulx *et al.* [2012]) should be required to protect such species from trapping mortality. In circumstances where the trapping of species in the *Martes* Complex remains legal, live-trapping can be used to selectively harvest males, and protect females from trapping mortality (Proulx 2000).

**Other factors**

Other factors will also adversely affect the persistence of populations within the *Martes* Complex. For example, the use of anticoagulants to control rodents (Gabriel 2012) or strychnine to kill predators (Proulx 2016) should be scrutinized by those involved in the conservation of species in the *Martes* Complex. Poaching, and the use of unselective kill-trapping devices, such as snares, could have significant impacts on their populations (Birks 2017; Proulx 2018b). In addition, the expansion of some populations may be affected by human influences, including vehicle collisions and diseases carried by domestic cats (*Felis catus*) and dogs

(*Canis lupus familiaris*) (Oliveira 2006; Chow 2009; Spencer *et al.* 2011).

**Refuges**

Nearly 70 years ago, de Vos (1951) recommended establishing refuges where fur trapping is prohibited to protect marten and fisher populations. He showed that, in such refuges, fishers and American martens increased in numbers significantly over the course of 2 decades, and produced excess individuals that dispersed into areas adjacent to the refuge. Proulx and Aubry (2017) argued that refuges may be particularly important for species such as the wolverine, which can be sensitive to human disturbance and infrastructures (May *et al.* 2006), and generally needs large, undisturbed areas for population persistence (Copeland and Whitman 2003). Wolverines require deep snow (Magoun and Copeland 1998) and/or persistent spring snow cover (Copeland *et al.* 2010) for successful reproduction, because such conditions enable wolverines to create snow caves for denning that provide kits with protection from both predators and adverse environmental conditions. Although it has been speculated that wolverines may be able to persist in lowland boreal forest without deep snowpack (Webb *et al.* 2016; Jokinen *et al.* 2019), there is no evidence that wolverines can

successfully reproduce and maintain stable populations in areas with little or no snow cover.

Squires *et al.* (2007) found that refuges, such as Glacier National Park in Montana, were important for wolverines because they reduced trap mortality and provided immigrants to the surrounding population. However, if animals travelling outside the refuges are being legally trapped, as was the case for American martens dispersing from a reserve into a managed forest in Maine (Hodgman *et al.* 1997), an increase in population numbers in areas adjacent to refuges may not occur. Thus, the creation of refuges would necessitate reviewing nearby fur-trapping practices, and should include the establishment of buffer zones where trapping is not allowed to give dispersers a better chance of colonizing other areas (Hodgman *et al.* 1997). There has been no study on the minimum width of a buffer zone that is needed to protect *Martes* Complex species from trapping activities; however, it is likely that wider is better. Considering that most *Martes* species have home ranges exceeding 1 km<sup>2</sup>, we believe that buffer zones should be >2-km wide. Also, to our knowledge, no refuge has been established solely to conserve any of the species in the *Martes* Complex, so it is difficult to propose a minimum size. The size of refuge needed would likely vary with the quality and quantity of habitats that provide *Martes* species with adequate cover and prey. National parks and large natural reserves that are protected from trapping and poaching can function as refuges (Squires *et al.* 2007) if they encompass habitats that are favorable for martens, fishers, wolverines, and tayras, and if they are protected through adequate law enforcement (e.g., Rauset *et al.* 2006). We recommend that refuges be considered in any management plan being developed for species in the *Martes* Complex (Figure 1).

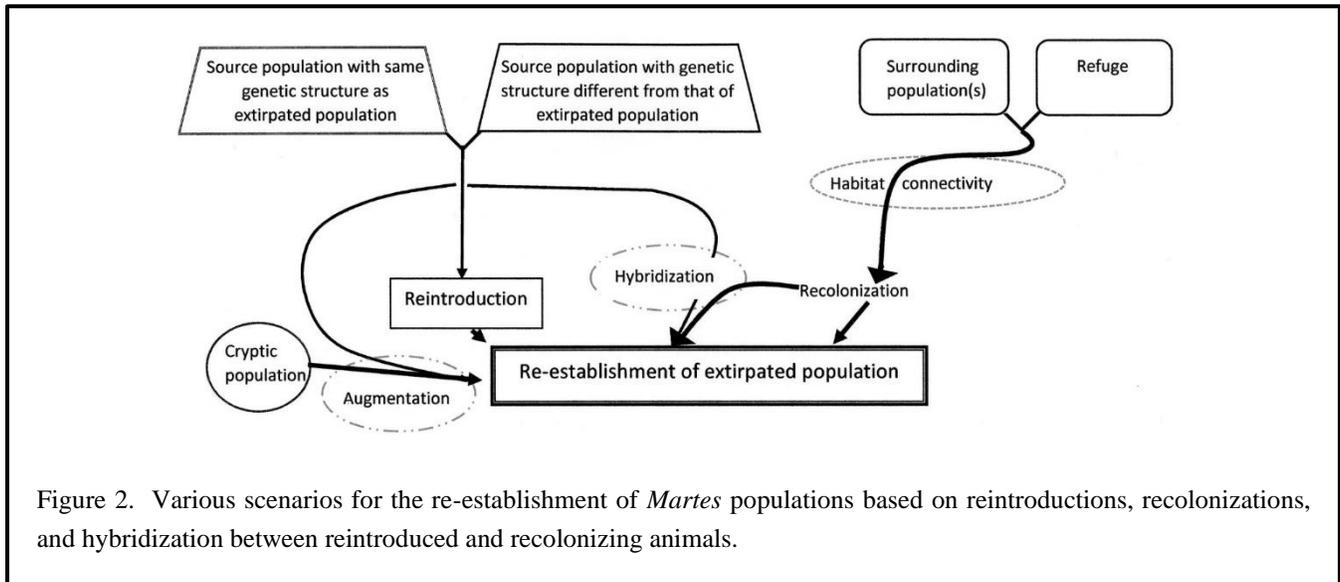
### Translocations

Dispersal distances among species in the *Martes* Complex are usually <30 km from the natal home range (Arthur *et al.* 1993; York 1996; Aubry and Raley 2006; Broquet *et al.* 2006a; Johnson *et al.* 2009; Matthews *et al.* 2013), although wolverines may disperse further (Vangen *et al.* 2001; Aronsson *et al.* 2017). Thus, dispersers may not move far enough to recolonize the areas where extirpations have occurred. Furthermore, some landscape features (e.g., mountains, large water bodies, agricultural fields without tree cover) may impede animal movements and limit gene flow (Hapeman *et al.* 2011). Matthews *et al.* (2013) indicated that habitat restoration can facilitate recolonization of extirpated areas by fishers; however, if long distances or landscape barriers preclude natural recolonization, translocations can expedite the establishment or expansion of populations. Also, the presence of reintroduced animals in target areas may encourage animals from surrounding

populations to settle in that area (Doty 1986; Stamps 1988; Smith and Peacock 1990). A preference for dispersing to areas that contain conspecifics has been suggested for both fishers (Proulx *et al.* 2018) and pine martens (McNicol *et al.* 2020). Moreover, this dispersal pattern may result in hybridization between reintroduced and recolonizing animals, which can increase population numbers and genetic diversity and enhance population persistence (Proulx *et al.* 2018).

Proulx *et al.* (2004) showed how valuable previous translocation programs have been for conserving *Martes* populations. Multiple translocations over time have enabled both the fisher (Proulx *et al.* 1994b; Lewis *et al.* 2012) and sable (Bakeyev and Sinitsyn 1994) to reoccupy large portions of their historical ranges. In their extensive evaluation of *Martes* translocations based on Vortex population modeling, Powell *et al.* (2012) reported that the 2 variables most strongly linked to reintroduction success for fishers, American martens, and sables were the total number of animals released (both females and males) and the number of release sites. General guidelines (IUCN 1987, 2013) and specific protocols (Lewis 2013) have been developed for translocations, and it is clear that the likelihood of reintroduction success is greatly enhanced by careful planning. Interspecific competition, predation, genetic diversity, harvest restrictions, phenological periods, and habitat protection must all be taken into consideration when developing a translocation program (Hobson *et al.* 1999; Proulx *et al.* 1994; Williams *et al.* 2006; LaPoint *et al.* 2015; Manlick *et al.* 2017). Translocations may be considered for various conservation objectives (Figure 2), including:

- *The reestablishment of a population within its historical range* – Successful translocations of fishers and/or American martens in central Alberta (Proulx *et al.* 1994b), Michigan and Wisconsin (Williams *et al.* 2006), and Washington (Lewis *et al.* 2016), and pine marten in Wales (McNicol *et al.* 2020) are examples of such conservation efforts.
- *The augmentation of a population (i.e., movement of individuals into an extant population of conspecifics) to improve reproductive success or increase genetic variation* – Augmentation can be used in threatened species conservation programs to increase population size and avoid the stochastic loss of a small population, inbreeding depression, and reduced genetic diversity (Weeks *et al.* 2011). For example, multiple translocations into a small fisher population in Montana likely improved its resilience and probability of persistence by increasing its genetic diversity (Vinkey *et al.* 2006).



- *The maintenance of evolutionary potential under environmental change* – Translocations may be used to mitigate the effects of adverse environmental changes on populations in the *Martes* Complex (Weeks *et al.* 2011). This may involve moving individuals outside their current range to future suitable climates, or to rescue a species at immediate risk of extinction (Weeks *et al.* 2011). Whenever possible, a reintroduction program should involve local animals that are familiar with environmental conditions in the target area. However, although “local is best” sourcing practice prevails, there are situations where doing so may facilitate inbreeding and low levels of genetic diversity, which can result in the establishment of populations that contain insufficient genetic variation and evolutionary potential to survive future environmental challenges (Broadhurst *et al.* 2008). In such cases, animals translocated from more distant (geographically and ecologically) populations may contain genetic characteristics that are better suited to the environment of the focal restoration site, both today and into the future. Carr *et al.* (2007) speculated that multiple source populations may have played an important role in the reestablishment of fishers in southern Ontario. They suggested that managers planning to restore populations through translocations should consider using animals from multiple sources, and releasing them at multiple sites.

## HABITAT MANAGEMENT & CONSERVATION STRATEGIES

Species in the *Martes* Complex inhabit a diverse array of forest seral stages, and some species occupy woodlots or hedges (Proulx and Aubry 2017), but none are known to depend on any particular forest type for population

persistence. Furthermore, juveniles may occupy a wider range of habitat types than adults (Burnett 1981; Buskirk *et al.* 1989), and some wolverine populations inhabit the treeless tundra (Larivière and Jennings 2009). Nevertheless, most populations in the *Martes* Complex prefer forest stands containing relatively high basal areas and large-diameter trees ( $\geq 20$ -cm dbh) that provide complex vertical and horizontal structure and  $\geq 20\%$  canopy closure, and contain snags and decadent trees, high volumes of fallen deadwood (e.g.,  $>30$  m<sup>3</sup>/ha of coarse woody debris), and a well-developed understorey (Caza 1993; Buskirk *et al.* 1996; Badry *et al.* 1997; Miyoshi and Higashi 2005; Proulx and Aubry 2017). Greater structural complexity near the ground provides animals with a diversity of microhabitats that are resilient to variation in environmental conditions and provide access to a diverse and abundant food base. In such habitats, when one type of food becomes scarce, martens, fishers, wolverines, and tayras can switch to using other food items. A shift in the use or availability of a given food item would be much more challenging in simple environments, such as regenerating forests, plantations, and forests with little structure near the ground (Proulx and Aubry 2017). Hisano *et al.* (2018) found that the Japanese marten was a flexible and opportunistic feeder with the potential to maintain its key macronutrient requirements by adapting its feeding strategy to changes in resource availability and environmental conditions. They suggested that this trophic plasticity may help the Japanese marten cope with rapid, human-induced environmental changes, as it does for other marten species (Genovesi *et al.* 1996; Zhou *et al.* 2011).

Martens, fishers, wolverines, and tayras require habitat areas that are large enough to sustain viable populations, i.e., that encompass many home ranges, or contain enough

interconnected habitat to facilitate gene flow among breeding units (Hornocker and Hash 1981; Broquet *et al.* 2006b; Copeland *et al.* 2007; Krebs *et al.* 2007; Garroway *et al.* 2011; Hughes 2012; Koen *et al.* 2012). Large habitat patches exceeding 75 km<sup>2</sup> will likely meet the needs of several breeding pairs of martens and tayras (Lacy and Clark 1993; Ruggiero *et al.* 1994; Potvin *et al.* 2000; Linnell *et al.* 2018) but for the fisher and wolverine, a suitable landscape may need to be several hundred square kilometers in size (Whitman *et al.* 1986; Weir and Corbould 2008). Habitat fragmentation in as little as 30-40% of a home range, can adversely affect the persistence of American martens (Thompson and Harestad 1994; Chapin 1995; Hargis and Bissonette 1997; Potvin *et al.* 2000; Cheveau *et al.* 2013), European pine martens (Grakov 1972; Mergely 2007), Japanese martens (Tatara 1994), and fishers (Weir and Corbould 2008). Roads can adversely affect the integrity of ecosystems by acting as barriers to animal movements and fragmenting landscapes (Shepard *et al.* 2008). Sawaya *et al.* (2019) reported sex-biased dispersal across a major highway in western Canada in a protected wolverine population, and speculated that it could lead to genetic isolation and demographic fragmentation. Grilo *et al.* (2009) found higher road casualties among stone martens that were provisioning young, and Caceres (2011) suggested that tayras avoided roads, which could result in populations becoming isolated from one another. The arrangements of small habitat patches and linkages among them are important for martens, which generally avoid crossing openings and rarely venture far from overhead cover (Lyon *et al.* 1994; Brainerd and Rolstad 2002; Pereboom *et al.* 2008; Proulx 2009). Accordingly, maintaining riparian buffer zones (Potvin *et al.* 2000; Balestrieri *et al.* 2014) and upland connectivity corridors (Gyug 1998; Proulx 2009) may help sustain species in the *Martes* Complex within fragmented landscapes (Figure 3).

The structural characteristics of forest stands preferred by *Martes* Complex species should be taken into consideration when managing disturbances. The creation or retention of stands with horizontal and vertical structural complexity should be a priority in landscapes managed for timber production. In addition, connectivity corridors within cut blocks to allow animals to reach residual stands or cross openings, and between cut blocks to allow animals to travel through the landscapes, will be essential for meeting their ecological requirements (Figure 1). Conservation strategies in boreal and temperate ecozones should involve the maintenance of mosaics of forest stands in various sizes and successional stages interconnected by riparian and upland corridors (Proulx 2009; Weir and Almuedo 2010) (Figure 3a). In agricultural and suburban regions, landscapes with woodlots interconnected by hedges and riparian shelterbelts,

and rock piles and shrub patches near tree cover will be used by both pine and stone martens (Figure 3b). Also, as we described previously, species in the *Martes* Complex will benefit from the retention of live trees and snags that contain cavities or decadent trees with heartrot decay, the creation of artificial den boxes (Messenger *et al.* 2006), and the addition of coarse woody debris to forest stands and hedges in areas with a scarcity of natural dens.

In suburban landscapes, dispersal may be enhanced by constructing crossings under or over highways (Bekker 2002; Broekhuizen 2006; Grilo *et al.* 2012); (Figure 4) or by installing partial fences, which can reduce road mortalities nearly as well as full fencing and help maintain population connectivity in roaded areas (Grilo *et al.* 2009; Ascensão *et al.* 2013). Sawaya *et al.* (2019) suggested that crossings can play an important role in keeping wolverine populations connected, and reducing road mortalities. However, the success of these habitat-conservation practices depends on the presence of continuous forest cover provided by trees of various sizes and ages, shrubs, snags, and downed woody debris, and the maintenance of vertical and horizontal structure for protection from predators and harsh weather, and cover for foraging and denning.

## TIMBER-HARVEST MANAGEMENT

Timber harvest is an anthropogenic disturbance that can dramatically affect habitat suitability for *Martes* Complex species, and biodiversity in general. Because organisms have adapted to the natural disturbance regimes of forest ecosystems, such as wildfires and windstorms, it has been suggested that timber-harvest systems be designed to imitate natural disturbance regimes (Hunter 1993), e.g., large clearcuts that mimic the spatial characteristics of wildfires (DeLong and Tanner 1996; Bergeron *et al.* 2002). In the past, clearcutting was used to maximize wood fiber production and establish homogeneous plantations of genetically superior trees (Lieffers and Woodard 1997). However, a large body of scientific literature has demonstrated that many of the ecological impacts of forest harvesting (especially clearcutting) and wildfire differ in important ways, and that it is inappropriate to assume that timber harvest plays the same ecological role as wildfire (McRae *et al.* 2001). Clearcutting was once the dominant harvesting method in North America (Gingras 1993); in recent decades, however, forest managers have recommended using alternative silvicultural systems and harvest methods, including various types of partial cutting (Lieffers *et al.* 1996; Renzie and Han-Sup 2008), which are likely to improve resulting ecological conditions for species in the *Martes* Complex.

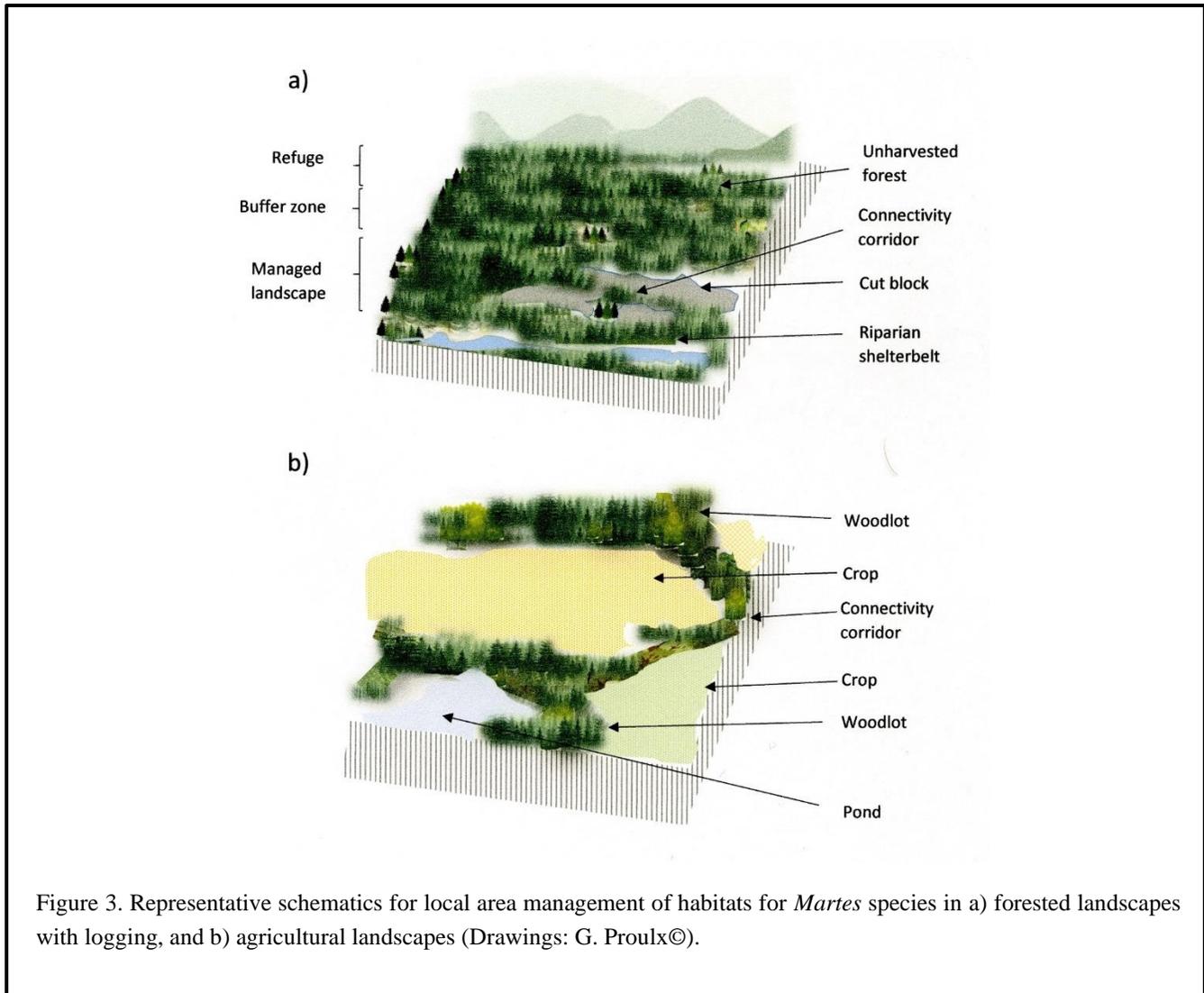


Figure 3. Representative schematics for local area management of habitats for *Martes* species in a) forested landscapes with logging, and b) agricultural landscapes (Drawings: G. Proulx©).

The impacts of logging on *Martes* species include the removal of overhead cover, the loss of large coarse woody debris and, in the case of clearcutting, the conversion of mesic sites to xeric sites, with associated changes in prey communities (Campbell 1979). To enhance the persistence of *Martes* populations in anthropogenically altered landscapes, cut blocks should retain some of the characteristics of the habitat conditions selected by *Martes* species (Figure 1). For example, the size of openings crossed by American martens is usually <250 m (Koehler and Hornocker 1977; Soutiere 1979; Simon 1980; Spencer *et al.* 1983). Also, Gyug (1998) found that marten use of recent clearcuts without slash piles was very low. Cut blocks <20 ha in size are used by American martens if they retain  $\geq 2$ -ha residual stands (representing  $\geq 20\%$  of biodiversity retention within cut blocks, i.e., in a 20-ha cut block, 4 ha should be protected as residual patches) with a minimum of 6  $\geq 20$ -cm-diameter snags (Proulx 2001). However, shrubs,

unmerchantable trees (Potvin and Breton 1997), and coarse woody debris corridors and piles (Lofroth and Steventon 1990; Seip *et al.* 2018) should be maintained between residual stands and forest edges to enable martens and their prey to access residual stands. Post-harvest sites should be messy and variable, not clean and uniform (Proulx 2001; Weir and Almuedo 2010).

At the landscape scale, large ( $\geq 20$  ha) cut blocks should be interspersed with smaller ones and uncut forests that meet the habitat requirements of *Martes* species to create mosaics of forest stands with varying ages and structures (e.g., Brainerd 1990; Lofroth *et al.* 2010) (Figure 1). Logging must be implemented at appropriate spatial and temporal scales. In landscapes containing >80-year-old forests that meet the habitat requirements of *Martes* Complex species, we recommend that  $\geq 50\%$  of the landscape be protected from timber harvest (Thompson and Harestad 1994; Potvin *et al.* 2000; Proulx 2009). Large openings should be connected to



Figure 4. A wildlife crossing structure over the Trans-Canada Highway, Banff National Park, Alberta, Canada (Photo: G. Proulx©).

uncut forests with  $\geq 100$ -m-wide treed corridors that include riparian habitats (Watt *et al.* 1996; Huggard 1999; Potvin *et al.* 2000; Proulx and Verbisky 2001).

## DISCUSSION

The strategies we recommend for improving the conservation of populations can be implemented for any species in the *Martes* Complex. These strategies aim to increase population numbers and minimize mortalities, particularly those caused by human activities. Translocations have been effective at augmenting *Martes* populations and re-establishing extirpated populations within their historical range. Although conservation scientists and managers consider translocation to be an important management tool, there is no clear consensus on the strategies needed to achieve translocation success (Weeks *et al.* 2011). Conservation goals will vary among projects, and such uncertainties should not impede wildlife managers from taking the initiative when translocations are deemed necessary. There is no general agreement on what constitutes a successful translocation. Several definitions have been proposed (Seddon 1999), but we caution against focusing too narrowly on what constitutes success (Proulx *et al.* 2018). Whether a translocation program leads to population persistence because the animals that were released reproduced with resident animals, survived and reproduced on their own, facilitated natural recolonization of the area by animals from surrounding areas, or moved and selected a different area than the original release site, such

translocations have been successful. Moreover, if a translocation encourages wildlife agencies and the public to restore landscapes and improve and reconnect key habitats, then it can also be considered successful. Translocating animals involves more than just moving animals from one location to another and hoping they become established; it also enables wildlife managers to increase biodiversity and the complexity of wildlife communities.

The habitat conservation strategies presented here are applicable to all species in the *Martes* Complex because they address common threats to their persistence. Accordingly, these habitat strategies can be used to improve any landscape, boreal or tropical, because they focus on the basic needs of all species in the *Martes* Complex—forests that provide denning opportunities and protection from predators and inclement weather, stand structural complexity that provides a diversity of prey and further protection, and connectivity among suitable habitats to foster movements and dispersal. Implementing these strategies will help to ensure that species in the *Martes* Complex persist in both time and space. However, Proulx and Aubry (2017) argued that, to provide for the integrity of populations and habitats over time, landscape management plans should focus on an array of species with similar ecological requirements. Proulx (2005) and Marcot and Raphael (2012) provided examples of such planning, which may be particularly important when establishing refuges or modifying landscapes to accommodate both wildlife conservation and human activities. Conservation programs for species in the *Martes*

Complex can be scaled-up from local or jurisdictional management to broader landscapes, e.g., region, state, or province (Proulx and Santos-Reis 2012). Marcot and Raphael (2012) pointed out that an often overlooked benefit of multi-species management programs is that economic and social costs that result from the conservation and restoration of key habitats are shared among multiple species. This helps to counter the perception that a particular species is responsible for such costs, as was the case with conserving mature and old-growth forests for the northern spotted owl (*Strix occidentalis caurina*) (e.g., Beuter 1990; Montgomery *et al.* 1994).

The effects of climate change on snowfall, vegetation communities, and fire dynamics will undoubtedly alter the distribution of species in the *Martes* Complex. With increases in temperatures, and reductions in the size and connectivity of contiguous areas of spring snow cover, it is likely that wolverine populations will become smaller and more isolated in the coming decades (McKelvey *et al.* 2011; Peacock 2011). Such concerns are warranted, as there is compelling historical evidence that the effects of warming climatic conditions during the last 300 years altered the geographic distributions of both American martens and fishers in eastern North America (Krohn 2012; Suffice *et al.* 2020), and the Kenai Peninsula in Alaska (Baltensperger *et al.* 2017). Lawler *et al.*'s (2012) bioclimatic models indicate that climate change, which can alter vegetation communities, human land use, and both predator-prey and competitive relationships, will likely result in large changes in the distribution of both North American and European *Martes* species. Ultimately, the future distribution of species in the *Martes* Complex will be determined by their ability to adapt to changing environmental conditions and new landscape configurations.

There is probably no limit to the amount of biological information that is needed to maximize the effectiveness of management and conservation strategies for the *Martes* Complex. In particular, when management actions are aimed at increasingly finer spatial and temporal scales, the quality and quantity of information required also increases (Lyon 1978). Extensive research has been conducted in recent decades to better understand the evolution, taxonomy, morphophysiology, genetics, population dynamics, habitat and predator-prey relationships, nutrition and energetics, parasites, and diseases of species in the *Martes* Complex (Proulx and Santos-Reis 2012; Proulx and Aubry 2017). However, we need to learn much more about these species before we can develop comprehensive and effective conservation programs (Proulx and Aubry 2017). For example, data on resting microsites used by the wolverine, tayra, and subtropical martens (yellow-throated and Nilgiri

martens) are lacking (Joyce *et al.* 2017). Additionally, as this review suggests, there is a need to investigate the key characteristics of refuges, buffer zones, and connectivity corridors in different regions, species, and phenological periods. The maintenance of large interconnected refuges may be critical for the persistence of some populations at a time when climatic changes and increased human activities can result in the loss or deterioration of important habitat conditions. We recognize that habitat requirements can vary within (Virgós *et al.* 2012; Proulx 2017) and among (Vergara *et al.* 2017) species; nonetheless, we believe that the management and conservation strategies we have identified in this review can provide benefits to all species in the *Martes* Complex.

Mesocarnivores play important ecological roles in wildlife communities (Roemer *et al.* 2009), yet their conservation often suffers from a lack of public knowledge about their role in the ecosystems they occupy and their current conservation status. Thus, we strongly encourage wildlife biologists and managers to conduct public outreach whenever possible—the public can't be expected to support the protection of animals they are unfamiliar with or know little about. Accordingly, population management, habitat protection and restoration, and public education programs are all important tools for conserving the species in the *Martes* Complex.

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