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ORIGINAL ARTICLE

Land conversion and lack of protection significantly reduce suitable wolf habitat amount and functional connectivity in the Adirondack-to-Laurentians (A2L) transboundary wildlife linkage

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Abstract

The Adirondack-to-Laurentians (A2L) transboundary wildlife linkage connects wilderness areas in the northeastern United States with southeastern Canada. However, land conversion is putting wolf habitat amount and functional connectivity at risk. With the exception of protected areas, hunting and trapping of wolves and coyotes are permitted within the Québec and Ontario portions, while hunting and trapping coyotes are permitted within the New York portion where wolves have been extirpated. Thus, the fear of humans strongly influences wolf habitat selection in this region. We assessed the impact of land conversion on wolf habitat amount, habitat fragmentation, and functional connectivity in the A2L between 2000 and 2015 and identified potential suitable habitat patches and corridors for protection. Suitable habitat patch area decreased by 18,245 km^2 (27%), with losses of 28% in the Québec portion, 95% in the Ontario portion, but only 0.3% in the New York portion. Habitat fragmentation, as measured by the effective mesh size, substantially increased in the Québec and Ontario portions, but only slightly in the New York portion. Functional connectivity significantly decreased, with mean distances and the cost of traveling these distances more than doubling. We propose nine recommendations centered on extensive habitat restoration and protected area expansion in the Québec and Ontario portions of the study area. Wolf recovery within the A2L will require collaborative and coordinated transboundary conservation and the protection of suitable habitat patches and corridors, or the legal protection of both wolves and coyotes within the suitable habitat patches and corridors, to ensure that wolves are not harvested as they disperse and colonize new locations.

Keywords Eastern wolf · Gray wolf · Habitat loss · Effective mesh size · Linkage mapper · Circuitscape

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Introduction

The majority of large terrestrial carnivores have experienced substantial population declines and geographic range contractions over the past two centuries (Wolf and Ripple 2017). Large carnivores face a wide variety of anthropogenic threats including persecution, hunting and trapping, habitat loss and degradation, and depletion of prey base (Crooks et al. 2011; Ripple et al. 2014; Wolf and Ripple 2016). Consequently, large carnivore populations are small, restricted to isolated habitat fragments, and predominantly occur only within protected areas (Woodroffe and Ginsberg 1998).

The wolf, once ranging across most of North America, Europe, and Asia, exhibited the largest geographical range of any terrestrial mammal other than humans (Mech and Boitani 2003). However, persecution, hunting and trapping, and habitat loss reduced their range considerably (Young and Goldman 1944, Mech 1995). In North America, the wolf was extirpated from most of southern Canada, Mexico, and the 48 contiguous United States, except for northern Minnesota, by 1970 (Mech and Boitani 2003). Today, large wolf populations (i.e., greater than 5000 individuals) are only found in Canada and Alaska (Musiani and Paquets 2004). However, in Europe and the United States, wolves are re-colonizing their former range in regions where they and their habitat have been granted legal protection (Chapron et al. 2014; Smith et al. 2016). This re-colonization of parts of their historical range could potentially restore the important regulatory role wolves and other large carnivores play within food webs and ecosystems (Estes et al. 2011; Ripple et al. 2014).

Wolves regulate ecosystem structure and function through both density-mediated and behaviorally mediated effects on prey and meso-predator populations and their associated trophic cascades (Estes et al. 2011; Ripple et al. 2014). Wolves typically occupy areas with high prey density, i.e., moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), and beaver (*Castor canadensis*), and low human-caused mortality (Fuller et al. 2003; Benson et al. 2024). In addition, wolves typically select forest and wetland areas for denning and rendezvous site locations (Benson et al. 2015; Sazatornil et al. 2016). In general, wolves spatially avoid humans (Carricondo-Sanchez et al. 2020). However, this behavior is modulated by the history of coexistence and persecution (i.e., stronger avoidance behavior in areas where they are harvested, such as North America, weaker avoidance behavior where they are protected, such as Europe) (Sazatornil et al. 2016). Even in low human-modified landscapes in North America, wolves typically avoid areas of human activity (Bubnicki et al. 2019). For example, Malcolm et al. (2020) showed that wolves avoided human-modified areas (i.e., housing structures, campsites, and park facilities), suggesting that wolves perceived them as a risk. This fear of humans resembles the "landscape of fear" (Laundré et al. 2001; 2010) that wolves impose on their prey species (Gaynor et al. 2019). Humans as "super-predators" (Darimont et al. 2015) directly influence food-chain dynamics (i.e., predators, meso-predators, and prey populations) by affecting their densities (i.e., hunting and trapping), their behavior (by creating a landscape of fear), and landscape structure (loss of habitat and connectivity) (Kuijper et al. 2016). These influences limit wolf population sizes and reduce their ecological effectiveness in unprotected landscapes compared to protected or remote wilderness areas (Suraci et al. 2019; Kuijper et al. 2019; 2024).

The Adirondack-to-Laurentians (A2L) transboundary wildlife linkage connects wilderness areas in the northeastern United States with southeastern Canada and includes portions of Québec, Ontario, and New York (Fig. 1). This region contains habitats of high ecological integrity and biodiversity; however, anthropogenic land transformation is putting habitat amount and transboundary connectivity at risk (Cole et al. 2023a, 2023b). While the coyote (*Canis latrans*) is ubiquitous throughout the A2L region, gray wolves (*Canis lupus*), and eastern wolves (*Canis lupus lycaon*) only occur within the Québec portion of the study area (Mainguy et al. 2017).

In 2015, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) recommended that the eastern wolf be recognized as a unique species (*Canus lycaon*) and its federal conservation status be re-classified to "Threatened," due to its low abundance and restricted geographic distribution (COSEWIC 2015; Benson et al. 2017). However, as of January 2024, the official scientific name of the eastern wolf remains a subspecies of the gray wolf "*Canis lupus lycaon*" and its legal conservation status remains "Species of Special Concern" under Canada's Species at Risk Act 2002 (ECCC 2021). In 2016, the eastern wolf was renamed the "Algonquin Wolf" (*Canis sp.*) by the Committee on the Status of Species at Risk in Ontario (COSSARO) and their provincial conservation status was re-classified to "Threatened" under Ontario's Endangered Species Act 2007 (BELW 2000 Consulting, 2018). In 2018, the Ontario government released a recovery strategy for the Algonquin Wolf in Ontario (BELW 2000 Consulting, 2018). However, its recovery is restricted to an area in and around Algonquin Provincial Park and does not include the entire province, nor the portion within the A2L. In 2021, the Canadian government released a management plan for the eastern wolf in Canada (ECCC 2021). The plan includes two primary conservation objectives: (1) achieve and maintain viable eastern wolf populations within the species' current range in Canada, and (2) achieve and maintain connectivity between occupied sites as well as potential suitable habitat sites to facilitate dispersal and maintain genetic

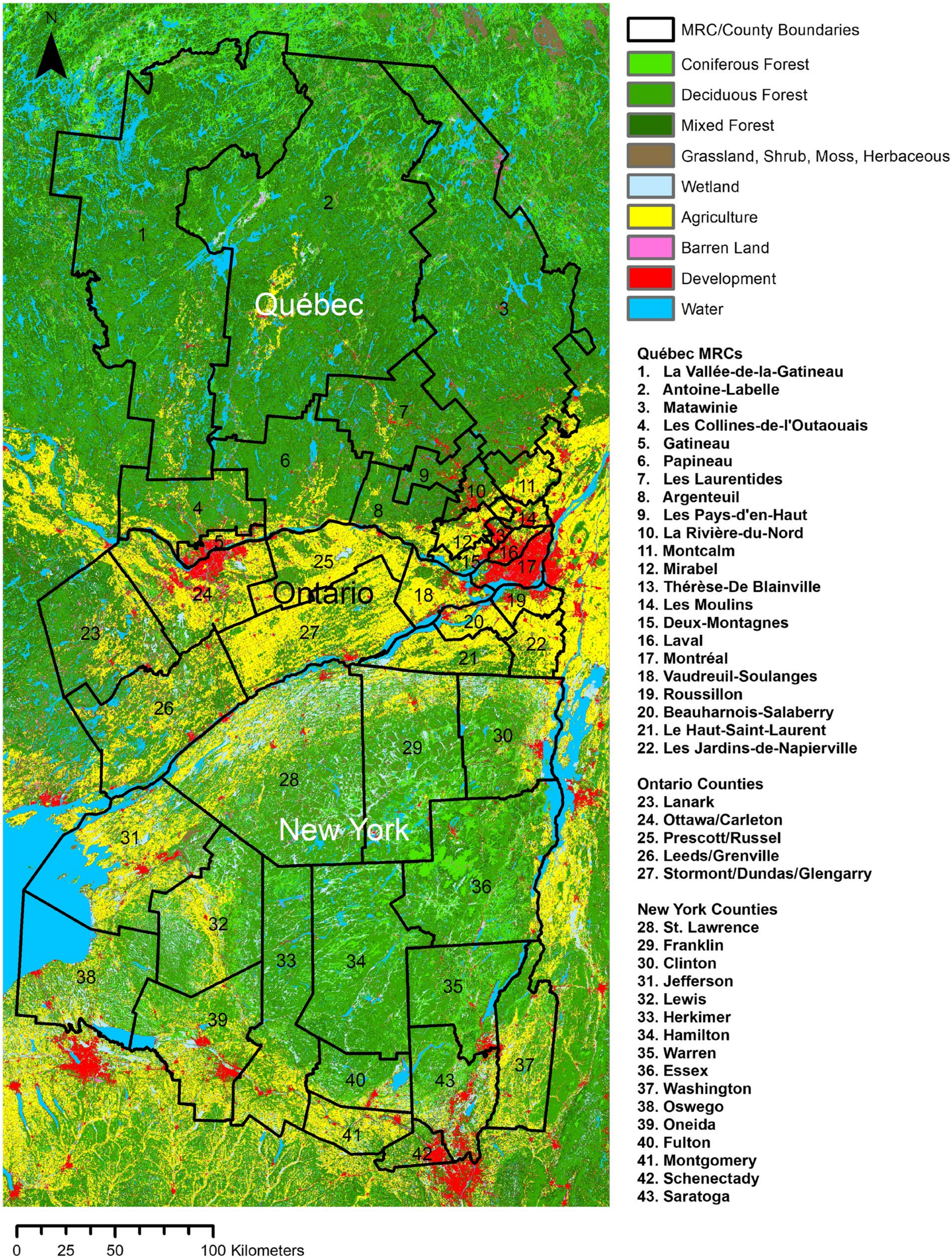

Fig. 1 Land cover map of the Adirondack-to-Laurentians (A2L) study area overlaid with municipalité régionale de comté (MRC)/county boundaries. MRC/county names are numbered and correspond to the numbers on the map

diversity (ECCC 2021). Potential suitable habitat and dispersal routes for the eastern wolf have not been re-examined since *circa* 2000 (Harrison and Chapin 1998; Mladenoff and Sickley 1998; Paquet et al. 1999; Carroll 2003). Thus, there is an urgent need for updated information to achieve these objectives.

With the exception of protected areas, hunting and trapping of gray wolves and coyotes are permitted within the Québec portion of the study area between October and March each year (Québec 2023), all-year-round in the Ontario portion (Ontario 2023a), and although gray wolves have been extirpated from New York State since 1893, they are still protected under both the federal Endangered Species Act 1973 and New York's Endangered and Threatened Species Regulations (NYS-DEC 2023a), while hunting and trapping of coyotes are permitted between October and March (NYS-DEC 2023b). In Ontario, eastern wolves are protected from hunting and trapping under Ontario's Endangered Species Act 2007, while in Québec and New York they are simply recognized as gray wolves. However, despite this "protected" status, their similar size and appearance to gray wolves and coyotes, as well as the indiscriminate nature of trapping, leave them extremely vulnerable to death by mistaken identity when they venture outside of protected areas (Benson et al. 2014).

The Adirondack region has been identified as a location with suitable habitat for wolf re-colonization or re-introduction (Harrison and Chapin 1998; Paquet et al. 1999; Carroll 2003; van den Bosch et al. 2022). However, both natural re-colonization and re-introduction would require numerous long-distance dispersal events from existing populations in Ontario and Québec to establish new territories and facilitate gene flow (Harrison and Chapin 1998). Where wolves are protected, they are highly capable of long-distance dispersal through human-modified landscapes (Chapron et al. 2014; Kuijper et al. 2016). However, where wolves are unprotected, leaving safe protected areas significantly increases their mortality risk (i.e., hunting, trapping, collisions with vehicles, and conflicts with humans), especially in highly fragmented landscapes (Crooks et al. 2011). Thus, the potential for wolves to successfully disperse into the Adirondack region or expand their range into unprotected suitable habitats within the A2L is unlikely without the implementation of legislation to protect wolves outside of protected areas (Rutledge et al. 2017; Benson et al. 2024). Identifying and protecting large areas of suitable habitat with sufficient prey density, and ecological corridors that interconnect them, may provide the greatest potential to maximize the ecological role that wolves play in ecosystem structure and function, while expanding the range and number of wolves in the region.

In this study, we created wolf habitat and resistance models to identify potential suitable habitat patches (HPs), optimal HPs, and stepping stone patches. Hunting and trapping are permitted outside protected areas; thus, fear of humans strongly influences habitat selection. We then applied Linkage Mapper and Circuitscape to the habitat network to map least-cost corridors and pinch points important for functional connectivity. The aim was to assess the impact of land conversion on wolf habitat amount, habitat fragmentation, and functional connectivity in the A2L transboundary wildlife linkage between 2000 and 2015, and identify potential suitable habitat patches and corridors for protection.

Methods

Study area

The A2L study area is approximately 127,408 km^2 in size and is made up of 22 municipalités régionales de comté (MRCs) in Québec (58,867 km^2; 46%), five counties in Ontario (15,445 km^2; 12%), and sixteen counties in New York (53,096 km^2; 42%) (Fig. 1). The A2L is located in the northern forest and eastern temperate forest eco-regions and is home to 440 vertebrate species and 1600 vascular plant species (Tardif et al. 2005; CEC 2023). The geology of the A2L is comprised of Canadian Shield to the north, St. Lawrence Platform in the centre, and Precambrian to the south (Tardif et al. 2005), with the highest peak being Mount-Marcy in New York (1629 m). In 2016, the region was home to over 6.8 million people (54 per km^2) (Statistics Canada 2023; US Census Bureau 2023).

Suitable habitat and resistance models

Land cover and road network maps were re-classified into ten common land cover classes and three common road network classes unifying the classification scheme across all input maps (Table S1; S2). In unprotected landscapes where mortality risk is high due to hunting and trapping, wolves can exhibit significant avoidance behavior of up to 1 km from human activity (including human presence, development, agriculture, and roads; Singleton 1995; Paquet et al. 1996). To incorporate this landscape of fear, we generated buffers of 0–500 and 500–1000 m around roads and development using the "Euclidean Distance" function in ArcGIS10.7 to represent the median and maximum distances from roads and development at which avoidance behaviors are displayed. This created four additional environmental variable layers that incorporated wolf avoidance behavior: (1) distance from development; (2) distance from primary roads; (3) distance from secondary roads; and (4) distance from tertiary roads (Figure S3). Because prey density is adequate throughout the forest and wetland regions of the A2L, this model assumes that suitable wolf habitat is concentrated in large forest and wetland areas with sufficient prey density to accommodate at least one wolf pack.

We computed a habitat suitability index by assigning relative values to the land cover maps using a combination of previously published values, literature review, and expert opinion (Table S3). Previously published values were re-scaled so that the values ranged between 0 and 1 using the following equation:

$$F(x) = (x - \min)/(\max - \min),$$

where x is the assigned relative suitability value for a 30 m grid cell, and min and max are the minimum and maximum suitability values of the habitat suitability surface, respectively (Keeley et al. 2016). Values near 1 represent the relative highest habitat suitability in the area, and values near 0 represent the relative lowest habitat suitability (Keeley et al. 2016). We created one aggregate suitable habitat map by overlaying all six layers in ArcGIS10.7, using Gnarly Landscape Utilities: Resistance and Habitat Calculator toolset (McRae et al. 2013), and retaining the minimum suitability value for each 30 m × 30 m cell across all input layers. Thus, each spatial layer received equal weighting (i.e., effect size), and the same relative importance to wolf habitat selection. This was because (1) all layers were derivative of the land cover layer, (2) all values, across all layers, where relative to ideal wolf habitat on the land cover layer, and (3) all values were obtained from previous studies, literature review, and expert option, where equal weighing was implied (Singleton 2002; Carroll et al. 2012; WWHCWG 2010; 2012).

We derived resistance values for each of the six raster layers by calculating the inverse of our suitable habitat values (Table S3; Koen et al. 2012, Keeley et al. 2016). A single aggregate resistance surface was created by overlaying all six layers in ArcGIS10.7, using Gnarly Landscape Utilities: Resistance and Habitat Calculator toolset (McRae et al. 2013), and retaining the maximum resistance value for each 30 m × 30 m cell across all six input layers (McRae et al. 2013). We added a value of one to each cell, such that habitats with a relatively low movement cost had a value of 1, and habitats with a high cost had values up to a maximum of 101. Bowman et al. (2020) found that landscape connectivity models tend to be insensitive to absolute cost values, provided that the rank order is correct.

Identifying suitable and optimal habitat patches

To identify potential habitat patches, we used the aggregated suitable habitat and resistance layers and the software Gnarly Landscape Utilities: Core Mapper toolset (Shirk and McRae 2013) in ArcGIS10.7. Suitable habitat patches were identified as patches with an average habitat value ≥ 0.6 (WWHCWG (2010; 2012), within a circular moving window with a radius of 9788.3 m (i.e., the radius of the average maximum home range size of 301 km^2; Tables S4 & S5). This ensured that habitat patches contained no more than 50% unsuitable habitat types, i.e., agriculture, development, water, and forest and wetland areas less than 500 m from development and primary roads. This step generated a surface layer representing where the largest concentrations of suitable habitat occurred (WWHCWG 2010; 2012). To correct for the variability in minimum home range sizes within the literature we multiplied the average minimum home range size of 93.5 km^2 (Table S4; S5) by 0.75 to compensate for the fact that wolves can occur within smaller home range sizes when resource patches are of high quality (Loveless 2010). This reduced value of 70.1 km^2 was used as the minimum habitat patch cutoff size to ensure smaller potentially suitable habitat patches were not overlooked. Patches that fell below the minimum habitat patch cutoff size were removed (WWHCWG 2010; 2012). This is in agreement with Fuller et al. (2003), that state that even at the highest prey densities (i.e., 15 deer or 3 moose/km^2), an individual pack of four wolves would still require a territory of at least 75 km^2 to meet its nutritional requirements. We then expanded habitat patches outwards up to a total cost-weighted distance of 5455.5 m (i.e., the radius of the average minimum home range size of 93.5 km^2; Tables S4 & S5) to potentially link proximate patches into larger aggregates, simulating intra-patch connectivity (WWHCWG 2010; Spanowicz and Jaeger 2019). Habitat patches still separated at this point require movements that exceed twice the cost-weighted distance of the mean minimum home range radius and were considered dispersal distances (i.e., inter-patch connectivity). We identified optimal habitat patches by performing the same steps as above; however, we did not expand the patches, and we removed all raster cells within the habitat patches with values ≤ 0.4 (consistent with Cole et al. (2023b); Table S3) to exclude unsuitable habitat types, i.e., agriculture, development, water, and forest and wetland areas less than 500 m from development and primary roads, leaving habitat patches devoid of anthropogenic transformations. Stepping stone patches were identified as suitable HPs that were smaller than the 70.1 km^2 minimum habitat patch cutoff size, but still large enough to serve as a refuge area during dispersal (≥ 10 km^2; Table S5).

We chose not to use a traditional species distribution model such as MaxEnt for three reasons: (1) there were no occurrence data available for the majority of the study area due to the extirpation of wolves from the Ontario and New York portions of the A2L. However, populations still inhabit the Québec portion of the study area and we used GPS location data from one of these populations to validate our suitable habitat patch models; (2) one of our main goals was to quantify the degree of habitat fragmentation within the study area; thus, we needed a model that could delineate potential suitable habitat patches (i.e., allowing for the incorporation of minimum home range size, minimum habitat patch size, and intra- and inter-patch connectivity into the model), and not just identify habitat suitability; and (3) we wanted to integrate avoidance behavior distances into the model. Therefore, by applying the Core Mapper toolset (Shirk and McRae 2013), we were able to incorporate all of these elements into the model and identify suitable and optimal habitat patches (also called habitat concentration areas (HCAs); WWHCWG 2010; 2012).

Validation of the suitable habitat and habitat patch models

To validate our suitable habitat and habitat patch models, we used previously published telemetry data collected between 2015 and 2017 (Malcolm et al. 2020) from a canid population in the Québec portion of the study area (i.e., Parc National du Mont-Tremblant and adjacent areas) that contained gray wolves, eastern wolves, and coyotes. The dataset consisted of 24,550 GPS locations, hereafter referred to as "validation points," obtained from five adult males and five adult females fitted with telemetry collars that were programmed to acquire location coordinates every 3 h for a period of 12 months (Malcolm et al. 2020). Because of changes in movement ability and behavior in the winter months (i.e., ability to cross frozen lakes; nomadic period), only GPS locations acquired between April 1st and November 30th were used for validation. We were unable to obtain wolf validation points for *circa* 2000; therefore, suitable habitat and habitat patches were only validated for 2015. Since the validation points only covered a subsection of the study area, we delineated this subsection by creating a 100% minimum convex polygon (MCP) around all the validation points (Koen et al. 2007; Brodeur et al. 2008) using the "Convex Hull" function in ArcGIS10.7 (Figure S1).

We validated the performance of the suitable habitat model (i.e., how well the model predicted wolf suitable habitat) using three validation metrics. First, we used the absolute validation index (*AVI*), calculated as the proportion of validation points that were located on raster cells with a habitat value ≥ 0.6 within the MCP (Hirzel and Arlettaz 2003; Hirzel et al. 2006; Guisan et al. 2017). Values for the *AVI* range between 0 and 1. Second, we used the contrast validation index (*CVI*), calculated as the *AVI* minus the proportion of raster cells with a habitat value of ≥ 0.6 within the MCP (Hirzel et al. 2004; Hirzel et al. 2006; Guisan et al. 2017). Values for the *CVI* range between − 0.5 and 0.5. Finally, we used the *Boyce Index* (Boyce et al. 2002; Hirzel et al. 2006; Guisan et al. 2017), using two calculated frequencies for each of the 6 habitat classes (i.e., 1, 0.8, 0.6, 0.4, 0.2, 0): (1) the proportion of observed validation points found in each habitat class within the MCP (*P*) and (2) the expected proportion of validation points found in each habitat class within the MCP (*E*) (Boyce et al. 2002; Hirzel et al. 2006). We then calculated the *P/E* ratio for each class. If the model predicted suitable habitat well, then a low habitat class should contain fewer validation points than expected by chance (i.e., a *P/E* ratio < 1), whereas a high habitat class should contain more validation points than expected by chance (i.e., a *P/E* ratio > 1; Hirzel et al. 2006; Guisan et al. 2017). The *Boyce Index* was then calculated using Spearman's rank correlation coefficient between the habitat value and the *P/E* ratio (Boyce et al. 2002; Hirzel et al. 2006). *Boyce Index* values range between −1 (incorrect model) and 1 (a highly consistent model); values close to zero indicate no difference from chance (Hirzel et al. 2006; Guisan et al. 2017).

To measure the performance of the habitat patch model, we applied variations of the *AVI* and *CVI* metrics. We used the AVI_{patch} to calculate the proportion of validation points that were located within suitable HPs and optimal HPs, calculated as the number of validation points in HPs within the MCP divided by the number of validation points within the MCP. Values for the AVI_{patch} ranged between 0 (weak performance) and 1 (strong performance). Next, we used the CVI_{patch}, calculated as the AVI_{patch} – the area of HPs within the MCP (km^2) divided by the area of the MCP (km^2). Values for the CVI_{patch} ranged between − 0.5 (weak performance) and 0.5 (strong performance).

Habitat amount and fragmentation

We measured the area of suitable HPs and optimal HPs in 2000 and 2015 using ArcGIS10.7. We calculated proportion by dividing the HP area by the total area of the reporting unit (i.e., study area, provincial/state portion). To quantify fragmentation, we used the effective mesh size, which is based on the average probability that any two randomly chosen points in the study area are connected, i.e., not separated by some barrier (Jaeger 2000). Because the boundary of a reporting unit can influence the value of the effective mesh size, two variations of the effective mesh size were used. The "cutting out" procedure (m_{eff_CUT}) was used to measure fragmentation strictly within the boundaries of the reporting units, while the "cross-boundary connections" procedure (m_{eff_CBC}) was used to include patches that cross boundaries into adjacent reporting units (Moser et al. 2007). All measurements were performed using the effective mesh size tool from the ZonalMetrics ArcGIS toolbox (Wetzel 2019). We measured the road density of each suitable HP by dividing the total length of roads within a patch by the area of the patch.

Functional connectivity

We mapped functional connectivity between the suitable HPs using the Linkage Pathways tool of the Linkage Mapper ArcGIS Toolbox (McRae and Kavanagh 2011). We calculated adjacency using both cost-weighted and Euclidean distances, omitted corridors that intersected other HPs, put no limit on the number of linkages originating from each HP, and truncated the width of least-cost corridors to 200 cost-weighted km. It is recommended that least-cost corridors should be at least 2 km wide (i.e., accommodate a wide variety of species, reduce edge effects, allow for recreational use; Beier 2018). Thus, we used a cutoff width of 200 cost-weighted km to ensure that even when corridors navigated regions with the highest resistance values (101), corridors would still maintain a width of at least 2 km. Prior to running Linkage Pathways, the resistance layers were coarsened by three times to reduce computing time and memory use, which resulted in a final resistance layer resolution of 90 m.

To identify pinch points within the least-cost corridors, we used the Pinch-Point Mapper tool of the Linkage Mapper ArcGIS Toolbox (McRae 2012). Pinch-Point Mapper uses Circuitscape (McRae and Shah 2011) to simulate a path of electric current through the least-cost corridors. We ran Circuitscape in both "pairwise" and "all to one" modes to identify pinch points important for connectivity between pairs of suitable HPs and for maintaining connectivity for the entire network of suitable HPs (Dutta et al. 2016).

To quantify changes in connectivity, we compared Euclidean distance, cost-weighted distance, least-cost path length, and effective resistance values between suitable HPs in 2000 and 2015. We assumed that if there was a decline in functional connectivity then these distances would have increased. We compared the distances between time points with a two-sided Welch's t-test to account for unequal variances. We measured the effect size of the differences in distances with Cohen's effect size ($d = 0.2$ represents a small effect size, $d = 0.5$ represents a medium effect size, and $d = 0.8$ represents a large effect size; Cohen 1988).

Proportion of habitat patches and least-cost corridors under protection

To determine the percentage of suitable HPs, optimal HPs, and least-cost corridors under protection, we obtained maps of government-protected areas and private protected areas secured by Nature Conservancy of Canada/The Nature Conservancy (Table S6). We measured the proportion of suitable HP area, optimal HP area, and least-cost corridor area currently under protection.

Results

Validation of the suitable habitat and habitat patch models

The suitable habitat model performed well at predicting suitable wolf habitat within the local landscape as measured by the absolute validation index (*AVI*) with a value of 0.8 (Hirzel et al. 2006), whereas the contrast validation index (*CVI*) gave a value of 0.07 indicating that although 80% of the validation points were located on suitable habitat, the amount of available suitable habitat was only slightly less (73%). The *Boyce index* value of 0.89, however, suggests a stronger performance as it signifies that low habitat classes contained fewer validation points than expected by chance and that high habitat classes contained more validation points than expected by chance (Hirzel et al. 2006; Guisan et al. 2017). The habitat patch models also performed well at predicting suitable and optimal HPs within the local landscape with AVI_{patch} values of 0.93 and 0.71, respectively (Hirzel et al. 2006), whereas CVI_{patch} values were 0.09 for suitable HPs and 0.07 for optimal HPs. Consequently, although 93% and 71% of the validation points were located on suitable and optimal HPs respectively, overall HP area was only slightly less (suitable HP area 84% and optimal HP area 64%).

Habitat amount and fragmentation

Suitable HP area decreased by 18,245 km^2 (27%), and optimal HP area decreased by 7082 km^2 (17%) between 2000 and 2015 (Table 1, Fig. 2). The majority of these losses took place in the Québec portion of the study area where suitable HP area was reduced by 13,369 km^2 (28%) and optimal HP area was reduced by 6314 km^2 (20%) (Table 1, Fig. 2). The Ontario portion showed the lowest amount of both suitable and optimal HP area in 2000, and the greatest relative losses in 2015, with a suitable HP area reduction of 4830 km^2 (95%) and an optimal HP area reduction of 399 km^2 (91%) (Table 1, Fig. 2). In contrast, the New York portion had a suitable HP area loss of 46 km^2 (0.3%), while optimal HP area loss was 369 km^2 (3.3%), due to 323 km^2 of optimal HP area being degraded to suitable HP area (Table 1, Fig. 2).

Substantial habitat fragmentation occurred across the study area (Table 2). For suitable HPs, m_{eff_CUT} size decreased by 45%, and m_{eff_CBC} size decreased by 41%; for optimal HPs, both m_{eff_CUT} size and m_{eff_CBC} size decreased by 71% (Table 2). Fragmentation was most pronounced in the Ontario portion of the study area, whereas the New York portion experienced the least amount of fragmentation. At the MRC/county level, the mean suitable HP m_{eff_CUT} size decreased by 479 km^2, and the mean suitable HP m_{eff_CBC} size decreased by 8460 km^2 (Table S7). This same pattern was seen with optimal HPs at the MRC/county level (Table S8).

In 2000, 27 of the 43 MRCs/counties shared suitable HPs with at least one other MRC/county, as identified by m_{eff_CUT} - m_{eff_CBC} values > 0 (Table S7). However, in 2015,

Table 1 Changes in wolf suitable habitat patch (SHP) and optimal habitat patch (OHP) area (km^2) and proportion (%) between 2000 and 2015, at the scale of the study area and each provincial/state portion. Values in bold represent changes greater than 20%

Location	SHP area in 2000 (km^2)	Percent of land area in 2000 (%)	SHP area in 2015 (km^2)	Percent of land area in 2015 (%)	SHP area 2015–2000 (km^2)	Percent change 2015–2000 (%)
Study Area	67878	53	49633	39	–18245	**–27**
Québec Portion	48047	82	34679	59	–13369	**–28**
Ontario Portion	5098	33	269	2	–4830	**–95**
New York Portion	14732	28	14686	28	–46	–0.3
Location	OHP area in 2000 (km^2)	Percent of land area in 2000 (%)	SHP area in 2015 (km^2)	Percent of land area in 2015 (%)	SHP area 2015–2000 (km^2)	Percent change 2015–2000 (%)
Study Area	42516	33	35435	28	–7082	–17
Québec Portion	30996	53	24682	42	–6314	–20
Ontario Portion	439	3	40	0.3	–399	**–91**
New York Portion	11081	21	10712	20	–369	–3

only 22 MRCs/counties shared suitable HPs with at least one other MRC/county. This was also the case with optimal HPs, where in 2000, 20 MRCs/counties shared optimal HPs with at least one other MRC/county, and in 2015, only 18 MRC/counties shared optimal HPs (Table S8). Not only are fewer patches being shared, the average amount of patch sharing between MRCs/counties also declined: The mean difference in suitable HP $m_{\mathrm{eff\_CBC}}$ - $m_{\mathrm{eff\_CBC}}$, a measure of habitat sharing between MRCs/counties, decreased by 7981 km^2 (Table S7), and the mean difference in optimal HP $m_{\mathrm{eff\_CBC}}$ - $m_{\mathrm{eff\_CBC}}$ decreased by 350 km^2 (Table S8).

In 2015, road density was highest in the Papineau patch in Québec and the patch east of Washington County, New York, with road densities of 0.67 km/km^2 and 0.66 km/km^2, respectively (Table S9). The suitable HP west of Lanark County in Ontario had the lowest road density at 0.30 km/km^2 (Table S9). Suitable HPs with the highest primary and secondary road densities were the Warren-Washington patch in New York (0.06 km/km^2), the Adirondack mega-patch in New York (0.07 km/km^2), and the patch east of Washington County in New York (0.11 km/km^2) (Table S9).

Functional connectivity

Although the number of least-cost corridors remained at fourteen, distances between suitable HPs increased (Fig. 2). The mean Euclidean distance between suitable HPs increased by 46 km (df = 16, p-value = 0.02, 95% CI = − 82.9 to − 9.9 km, Cohen's d = 1.0); the mean cost-weighted distance increased by 2189 cost-weighted km (df = 16, p-value = 0.01, 95% CI = − 3836.5 to − 541.8 km, Cohen's d = 1.1); the mean least-cost path length increased by 63 km (df = 16, p-value = 0.01, 95% CI = − 110.6 to − 14.4 km, Cohen's d = 1.0); and the mean effective resistance value increased by 4997 Ohms (df = 17, p-value = 0.03, 95% CI = − 9331.0 to − 663.7 Ohms, Cohen's d = 0.9).

Pinch points were evident in most corridors; however, due to considerable suitable HP loss, the locations changed considerably between 2000 and 2015 (Fig. 3). When Circuitscape was run in the "pairwise" mode, we identified areas of high current flow as pinch points critical for movement between pairs of suitable HPs. Of particular importance were pinch points located in the MRC Les Collines-de-l'Outaouais in Québec; Leeds/Grenville, and Stormont/Dundas/Glengarry counties in Ontario; and Jefferson, St. Lawrence, and Franklin counties in New York (Fig. 3b). When Circuitscape was run in the "all to one" mode, we identified areas of high current flow as pinch points critical for maintaining connectivity for the entire network of suitable HPs. Although there were considerably fewer pinch points produced by this method, the pinch point in MRC Les Collines-de-l'Outaouais, Québec, was still prominent, as was the pinch point in Stormont/Dundas/Glengarry, Ontario (Fig. 3d).

In 2000, six stepping stone patches were identified within the least-cost corridors connecting suitable HPs. In 2015, 5 stepping stone patches were identified (Fig. 2). Of particular importance was the patch shared by MRC Papineau and MRC Les Laurentides, Québec, as well as the patches in St. Lawrence County and Franklin County, New York (Fig. 2).

Proportion of habitat patches and least-cost corridors under protection

In the A2L, 19% of suitable HP area, 22% of optimal HP area, and 9% of least-cost corridor area were protected by Canadian/United States government agencies and Nature Conservancy of Canada/The Nature Conservancy in 2015 (Figure S2; Table S10). However, this protection was not evenly distributed across the study area. In the Québec portion, 10% of suitable HP area, 11% of optimal HP area,

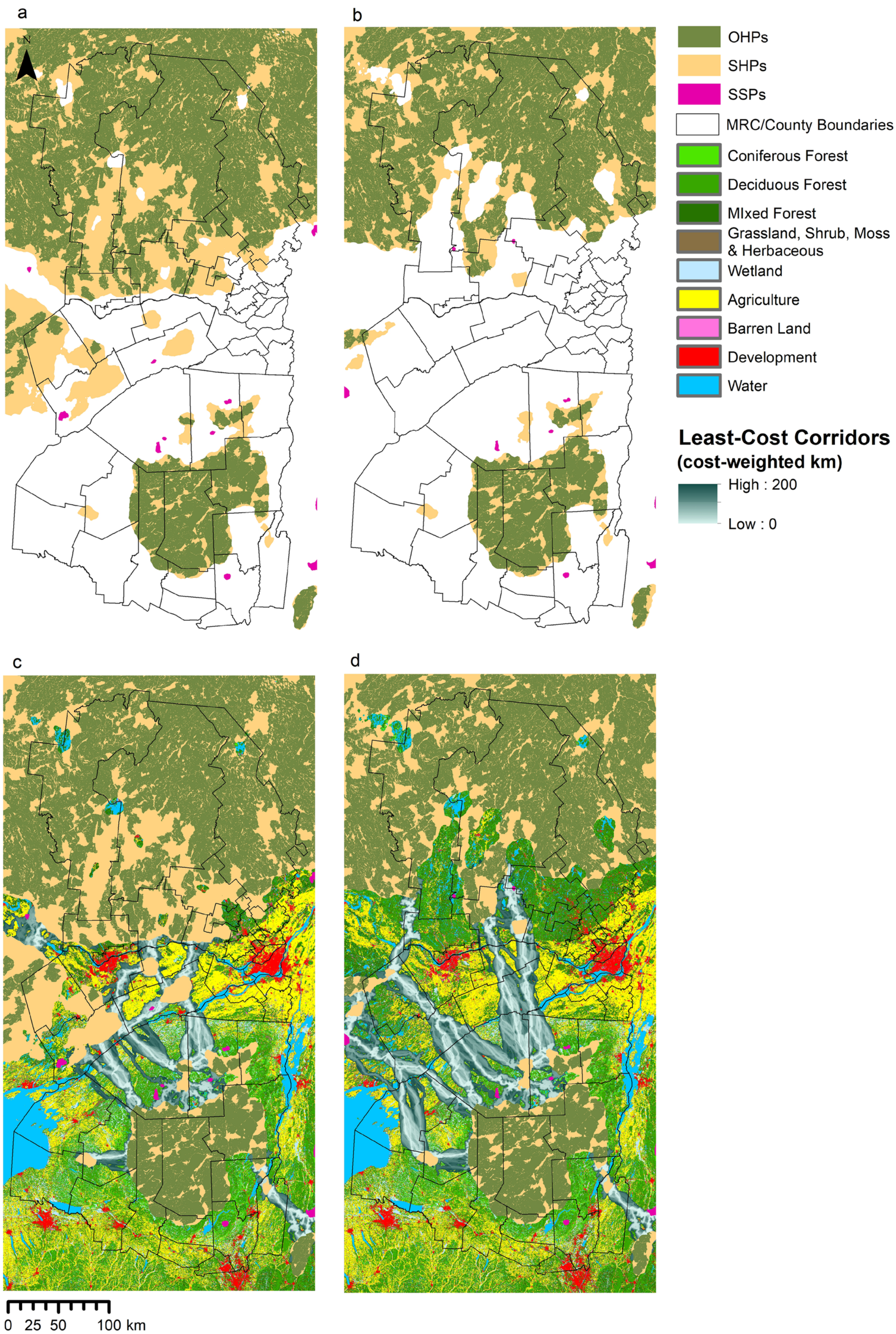

Fig. 2 Habitat patches and least-cost corridors (LCCs). **a** Habitat patches in 2000, **b** habitat patches in 2015, **c** habitat patches and least-cost corridors in 2000, and **d** habitat patches and least-cost corridors in 2015. SHPs, suitable habitat patches; OHPs, optimal habitat patches; SSPs, stepping stone patches

Table 2 Changes in the effective mesh size between 2000 and 2015 for suitable habitat patches (SHPs) and optimal habitat patches (OHPs), at the scale of the study area and in each provincial/state portion. Values in bold represent changes greater than 20%

Location	SHPs 2000 m_{eff_CUT} (km^2)	SHPs 2015 m_{eff_CUT} (km^2)	SHPs 2015–2000 m_{eff_CUT} (km^2)	SHPs 2015–2000 m_{eff_CUT} (%)
Study area	19,822	10,886	– 8937	**– 45**
Québec	39,216	20,205	– 19,012	**– 48**
Ontario	1200	5	– 1195	**– 99.6**
New York	3729	3714	– 15	– 0.4
Location	SHPs 2000 m_{eff_CBC} (km^2)	SHPs 2015 m_{eff_CBC} (km^2)	SHPs 2015–2000 m_{eff_CBC} (km^2)	SHPs 2015–2000 m_{eff_CBC} (%)
Study area	29,842	17,485	– 12,357	**– 41**
Québec	60,638	34,484	– 26,154	**– 43**
Ontario	2189	11	– 2178	**– 99.5**
New York	3729	3714	– 15	– 0.4
Location	OHPs 2000 m_{eff_CUT} (km^2)	OHPs 2015 m_{eff_CUT} (km^2)	OHPs 2015–2000 m_{eff_CUT} (km^2)	OHPs 2015–2000 m_{eff_CUT} (%)
Study area	2342	681	– 1661	**– 71**
Québec	4889	1323	– 3567	**– 73**
Ontario	3	0.1	– 3	**– 96**
New York	198	167	– 31	– 15
Location	OHPs 2000 m_{eff_CBC} (km^2)	OHPs 2015 m_{eff_CBC} (km^2)	OHPs 2015–2000 m_{eff_CBC} (km^2)	OHPs 2015–2000 m_{eff_CBC} (%)
Study area	2755	789	– 1967	**– 71**
Québec	5783	1555	– 4227	**– 73**
Ontario	3	0.3	– 3	**– 92**
New York	198	167	– 31	– 15

and 14% of least-cost corridor area were protected; in the Ontario portion, no suitable nor optimal HP area were protected, and only 2% of least-cost corridor area was protected; whereas in the New York portion, 76% of suitable HP area, 85% of optimal HP area, and 14% of least-cost corridor area were protected in 2015 (Figure S2; Table S10).

Discussion

Habitat amount

Wolf suitable HP area decreased by 27% and optimal HP area decreased by 17%. However, these declines in HP area were not equivalent to land cover loss. Natural land cover area (i.e., coniferous forest, deciduous forest, mixed forest, grassland, shrub, moss, herbaceous vegetation, and wetlands) only decreased by 1457 km^2 (2%) within the A2L between 2000 and 2015 (Cole et al. 2023b). Thus, the majority of HP area decline was due to suitable habitat becoming less desirable to wolves. In unprotected landscapes where mortality risk is high due to hunting and trapping, wolves can exhibit significant avoidance behavior of up to 1 km from human activity (including human presence, development, agriculture, and roads; Singleton 1995, Paquet et al. 1996). Thus, each new kilometer of anthropogenic land conversion between 2000 and 2015 created a 2 km^2 area of degraded habitat, reducing the size as well as eliminating many suitable and optimal HPs. The greatest amount of suitable and optimal HP area loss took place in the Québec and Ontario portions of the study area in response to increases in development and road network length. In the Québec portion, development increased by 833 km^2 and the length of the road network increased by 7684 km; in the Ontario portion, development increased by 445 km^2 and the length of the road network increased by 2380 km (Cole et al. 2023a, 2023b).

Although wolves have only been documented within the Québec mega-patch (Rogic et al. 2014; Mainguy et al. 2017; Hénault 2019; ECCC 2021), we identified 8 additional (potentially unoccupied) suitable HPs, with the largest being the Adirondak mega-patch in New York. Our results substantiate earlier studies that identified suitable wolf habitat in the Adirondack region. We identified 14,732 km^2 of suitable HP area within the New York portion in 2000. This agrees with estimates by Mladenoff and Sickley (1998) who reported 16,020 km^2, and Harrison and Chapin (1998) who reported 14,618 km^2 of suitable wolf habitat in the New York region. For 2015, we identified 14,686 km^2 of suitable HP area in the New York portion, which was considerably smaller than the 22,847 km^2 estimated by van den Bosch (2022). This discrepancy could be due to the differences in map resolution used (i.e., 30 m vs 1 km), and/or how the two

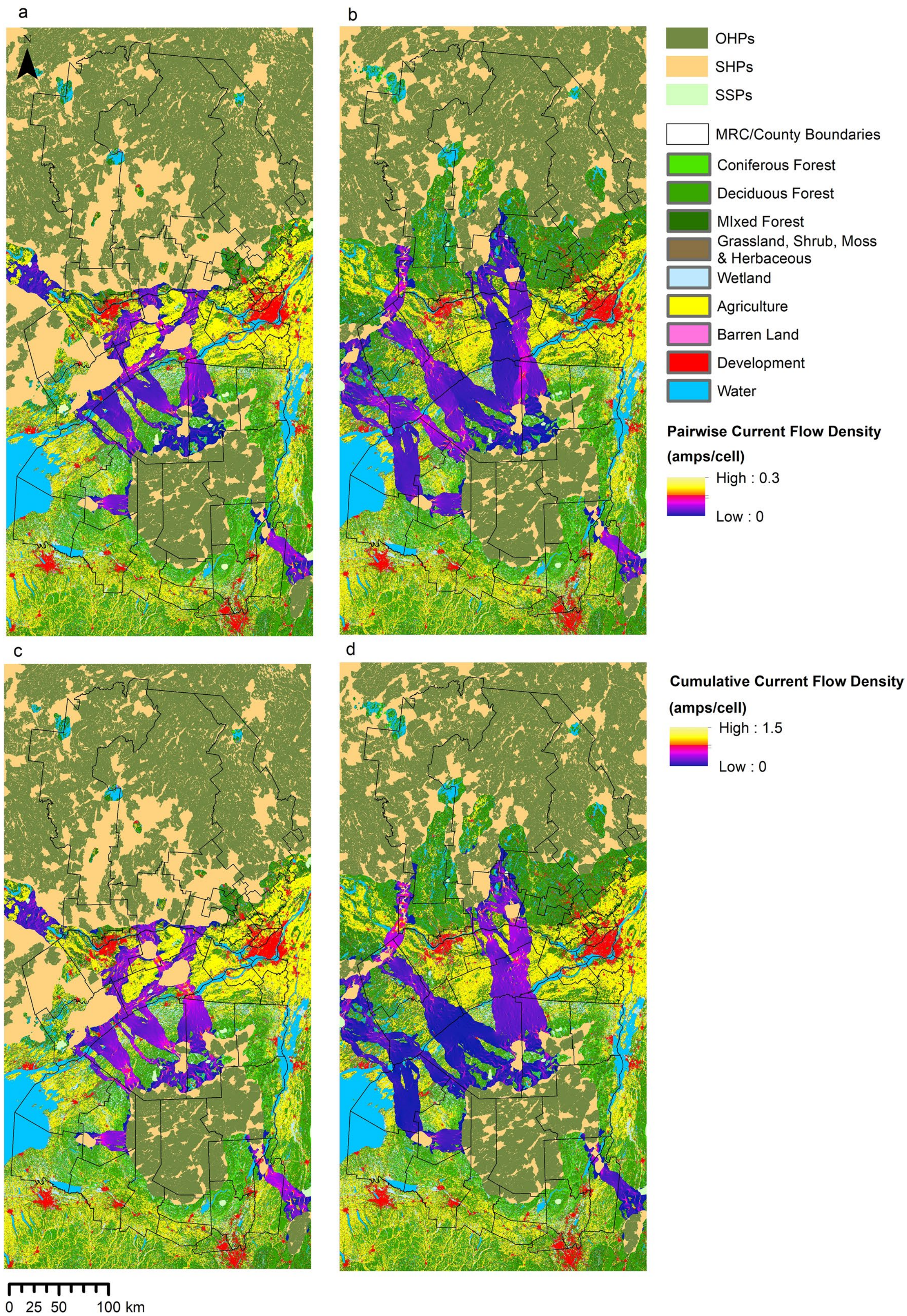

Fig. 3 Pinch points in the least-cost corridors (LCCs). **a** Pairwise current flow density in 2000, **b** pairwise current flow density in 2015, **c** cumulative current flow density in 2000, and **d** cumulative current flow density in 2015. SHPs, suitable habitat patches; OHPs, optimal habitat patches; SSPs, stepping stone patches

regions were delineated (habitat patch area vs habitat area). The nine suitable HPs identified within the A2L ranged in size from 137 km^2 to over 58,000 km^2. It has been estimated that gray wolf populations require an area of at least 12,800 km^2 for the persistence of an immigration-dependent population, and over 25,000 km^2 for a viable long-term independent population (USFWS 1992). Using these criteria, of the nine suitable HPs, only the Québec mega-patch is large enough to contain a viable long-term independent population, whereas the Adirondack mega-patch would be large enough to maintain an immigration-dependent population; the remaining seven suitable HPs would be considered sink populations. However, Fritts and Carbyn (1995) suggest that a protected area of at least 3000 km^2 with a sufficient prey base would be adequate to maintain a viable population in complete isolation; whereas Woodroffe and Ginsberg (1998) proposed that a critical reserve size of 766 km^2 would be necessary for a gray wolf population to have a long-term viability of 50%. Under these criteria, both the Québec mega-patch and the Adirondack mega-patch would be large enough to contain viable long-term independent wolf populations.

Fragmentation

Habitat fragmentation increases the probability of encounters and conflicts with humans. This increased pervasiveness of human presence in more fragmented landscapes reduces the potential for wolves to be ecologically effective (Kuijper et al. 2016). Habitat fragmentation significantly increased throughout the study area. Similar to the declines in HP area, the majority of habitat fragmentation occurred in the Québec and Ontario portions of the A2L. This result correlates with the increases in development and road network length in both regions (Cole et al. 2023a; 2023b). Although wolves can travel up to three times faster along tertiary roads and typically select these to increase prey encounter rates (Dickie et al. 2017; Muhly et al. 2019), primary and secondary roads contribute to habitat loss (due to avoidance behavior), increase mortality (due to collisions with vehicles), and can act as complete barriers to movement (due to fencing and traffic) leading to resource inaccessibility (Forman and Alexander 1998; Benson et al. 2015, 2024). Thus, wolves generally select habitats with low road density (i.e., < 0.3–0.7 km of roads per km^2, with the density of primary and secondary roads being < 0.02 km of roads per km^2; Fuller et al. 1992; Wydeven et al. 1998; Rateaud et al. 2001). In 2015, all suitable HPs had road densities higher than 0.3 km/km^2, but less than 0.7 km/km^2. However, the Lanark, Adirondack mega-patch, the Warren-Washington, and the East of Washington patches all had combined primary and secondary road densities ≥ 0.02 km/km^2 which could deter wolf re-colonization of these habitat patches.

On the contrary, optimal HPs do not contain roads. In 2015, there were 101 optimal HPs (total area of 35,435 km^2; 68 in Québec, 1 in Ontario, and 32 in New York). They constitute the remaining large roadless areas > 70 km^2. Large roadless areas generally represent relatively undisturbed ecosystems with high ecological value, making their safeguarding important for the preservation of biodiversity and ecosystem services (Ibisch et al. 2016). Other than the "2001 Roadless Area Conservation Rule" which tentatively protects 236,700 km^2 of roadless areas on U.S. National Forest System lands, there is no legally binding legislation in place to protect large roadless areas in Canada and the U.S. (Coffin et al. 2021). Consequently, large roadless areas are scarcely considered in regional land development and transportation infrastructure planning (Selva et al. 2015).

Functional connectivity

Functional connectivity (i.e., the ability to move between resource patches within a landscape; Lindenmayer and Fischer 2013) is crucial for facilitating dispersal events between fragmented habitat patches. Dispersing individuals maintain long-term viability of populations by colonizing new areas, re-colonizing sink populations, and maintaining genetic variation and gene flow within meta-populations (Gonzalez et al. 1998; Kokko and López-Sepulcre 2006; Crooks et al. 2017). Re-colonization of suitable habitat patches within the A2L will require functional connectivity. However, functional connectivity is reduced when mortality risk outside of protected areas is high and habitat fragmentation increases the probability of encounters with humans. Between 2000 and 2015, functional connectivity among suitable HPs significantly decreased as measured by increases in mean Euclidean distance, mean least-cost path, mean cost-weighted distance, and mean effective resistance. Mean Euclidean distance increased directly, due to anthropogenic land conversion, and indirectly, due to the addition of avoidance buffers around these new land cover elements, which degraded adjacent habitat (i.e., habitat patches were reduced in size or completely lost) and resulted in greater distances between suitable HPs in 2015. Increases in mean least-cost path, mean cost-weighted distance, and mean effective resistance were due to anthropogenic land conversion, and the addition of avoidance buffers, which degraded adjacent habitat (i.e., increasing resistance values) and resulted in an overall increase in the cost of traveling between suitable HPs. Consequently, wolves in occupied sites in the Québec mega-patch will need to travel farther through less suitable habitat to re-colonize unoccupied suitable HPs in the A2L, and the cost of traveling these distances will be higher. This reduced landscape-level connectivity may translate into longer time spent and farther distances traveled in both human-modified and unprotected landscapes (i.e., increased mortality and interactions with humans) during the transience stage and an overall reduction in the probability of dispersal success (Morales-González et al. 2022). This result suggests that protecting suitable HPs and the corridors that interconnect them may be critical for successful dispersal (Chapron et al. 2014) and expansion of wolf populations in the A2L. These declines in functional connectivity are consistent with other large mammal species within the A2L (fisher, moose, and white-tailed deer; Cole et al. 2023b).

We identified fourteen least-cost corridors that interconnected the suitable HPs in both 2000 and 2015. In 2000, these corridors did not exceed 100 km in length. However, by 2015, three corridors were longer than 100 km, and four corridors were longer than 200 km. Although wolves have been recorded dispersing distances of up to 800 km (Linnell et al. 2005), typical dispersal events in the Great Lakes region range from 20 to 100 km (Treves et al. 2009). Thus, distance alone may reduce the probability of successful long-distance dispersal events within the A2L.

Long-distance dispersal events between occupied sites in the Québec mega-patch and unoccupied sites in the Ontario and New York portions will require wolves to cross multiple primary and secondary roads. Road mortality is the second highest source of wolf fatality after hunting and trapping (Hebblewhite and Whittington 2020; ECCC 2021). Locations where least-cost corridors and pinch points intersect primary and secondary roads could be further evaluated as potential locations for wildlife passages and fencing to reduce mortality and increase landscape connectivity (Nussey and Noseworthy 2018; Spanowicz et al. 2020).

Wolves may also need to traverse at least one of two large rivers (i.e., the Ottawa and St. Lawrence Rivers). While both rivers are major deterrents to long-distance dispersal, they are not complete barriers for wolves. Sections of the rivers freeze in the winter months permitting crossing, with some locations less than 1 km wide (Koen et al. 2015; ECCC 2023). Over the past 20 years, multiple wolves have been reported south of the St. Lawrence River, demonstrating that they are capable of crossing the rivers (Villemure and Jolicoeur 2004; McAlpine et al. 2015; Maine Wolf Coalition 2024).

Proportion of habitat patches and least-cost corridors under protection

Where wolves have been granted legal protection, they have been highly successful at re-colonizing their former range, even in human-dominated landscapes (Linnell et al. 2001; Chapron et al. 2014; Smith et al. 2016). However, wolf recovery in unprotected landscapes is extremely challenging due to high rates of human-caused mortality (i.e., hunting, trapping, and conflicts with humans) when they venture outside of protected areas (Rutledge et al. 2017; Benson et al. 2024). For example, hunting and trapping outside park boundaries accounted for ~ 62% of annual mortality of wolf populations in Algonquin Park, Ontario (Theberge et al. 1996), and Benson et al. (2014) found that wolf survival declined outside of Algonquin Park as hunting and trapping access increased. In Parc National de la Mauricie, Québec, Villemure and Festa-Bianchet (2002) found that 88% of radio-collared wolf mortality occurred outside park boundaries. In Banff National Park, Alberta, wolves experienced up to 12.7 times higher daily risk of mortality when they ventured outside the park in winter during the hunting and trapping season (Hebblewhite and Whittington 2020). Therefore, wolf expansion into the Adirondack region or other suitable habitats within the A2L is unlikely without the enactment of legislation to protect wolves outside of protected areas (Rutledge et al. 2017; Benson et al. 2024). However, despite legal protection in New York under the Endangered Species Act 1973 (NYS-DEC 2023a), all wolves that have been reported within the region were killed by hunters or trappers mistaking them for coyotes (Villemure and Jolicoeur 2004; McAlpine et al. 2015; Maine Wolf Coalition 2024). Consequently, since wolves and coyotes are almost indistinguishable without genetic assessment (Vilaça et al. 2023), wolf expansion in the A2L would necessitate protection of both wolves and coyotes within the region. A similar ruling was passed in North Carolina to protect the critically endangered red wolf (*Canis rufus*) from mistaken identification by coyote hunters and trappers (Murray et al. 2015). Thus, identifying and protecting large areas of suitable habitat with sufficient prey density and ecological corridors that interconnect them would provide the greatest potential to maximize the ecological role that wolves play in ecosystem structure and function, while expanding the range and number of wolves in the region.

Only large protected areas reduce mortality risk for wolves when human-caused mortality is high within adjacent landscapes (Larivière et al. 2000; Benson et al. 2024). However, most protected areas are simply too small to support viable populations of large-ranging species (Pimm et al. 2014; Williams et al. 2022). For example, in 2015, 14,605 km^2 (19%) of suitable HP area was protected, comprising 1056 Canadian/United States government sites and 381 Nature Conservancy of Canada/The Nature Conservancy sites. However, the average Canadian/United States government-protected area size was 13.3 km^2, and the average Nature Conservancy of Canada/The Nature Conservancy-protected area size was 5.6 km^2. With the average regional wolf home range size being ~ 182 km^2 (Potvin 1988;

Loveless 2010; Benson and Patterson 2015), and the area required to accommodate a viable long-term independent population being 25,600 km^2 (USFWS 1992), protected area sizes within the A2L are thus orders of magnitude too small, requiring wolves to inhabit large areas of unprotected land where hunting and trapping are permitted.

In 2015, the proportion of suitable and optimal HP area under protection was not evenly distributed across the A2L study area. While 10% of suitable HP area and 11% of optimal HP area were protected in Québec, zero suitable and optimal HP area were protected in the Ontario portion where the losses have been most pronounced. This was in stark contrast to the 76% of suitable and 85% of optimal HP area protected in the New York portion. This much more substantial amount of protection explains the stability in habitat amount and habitat fragmentation in the New York portion between 2000 and 2015. The amount of habitat patch area protected was considerably higher than the amount of corridor area protected. This result highlights the necessity to not only establish new and expand existing protected areas within the A2L, but also to restore and protect connectivity corridors between them (Hilty et al. 2020).

Conclusion

Although land conversion has diminished habitat amount, increased habitat fragmentation, and eroded functional connectivity between 2000 and 2015, we identified nine suitable HPs in the A2L, with the Québec and Adirondack megapatches having the potential to accommodate long-term viable wolf populations. We also identified 14 least-cost corridors that interconnect the suitable HPs that have the potential to facilitate long-distance dispersals. However, with the region under high development pressure from a diversity of economic sectors (including agriculture, forestry, and urban development), it is unlikely that habitat loss and habitat fragmentation will subside without considerable conservation intervention.

Based on our findings, we propose the following nine recommendations to recover wolf habitat and functional connectivity within the A2L: (1) Commence extensive habitat restoration and protected area expansion, predominantly within the Québec and Ontario portions; (2) within the suitable HPs, maintain primary and secondary road density below 0.02 km of roads/km^2 and total road density below 0.7 km of roads/km^2; (3) avoid transportation development within the 101 optimal habitat patches that were identified as the last remaining large roadless areas; (4) develop collaborative conservation strategies to ensure that cross-border habitat patches, shared by multiple MRCs/counties, remain intact; (5) enhance and protect connectivity corridors between suitable HPs; (6) expand and protect stepping stone patches and pinch points within corridors to facilitate movement between suitable HPs; (7) determine priority locations for wildlife crossing structures to reduce road mortality and increase landscape connectivity; (8) maintain riparian access to ensure connectivity across waterways; and (9) although prey densities within the nine suitable HPs are adequate to accommodate wolf populations presently (Boucher et al. 2004; Hinton et al. 2022; NYS-DEC 2023c; Ontario 2023b; Rosenblatt et al. 2023), monitor prey densities as wolves re-colonize these locations.

However, to facilitate wolf recovery within the A2L, either the protection of suitable habitat patches and corridors or the legal protection of both wolves and coyotes within the suitable habitat patches and corridors will be required to ensure that wolves are not harvested as they disperse and colonize new locations. This will necessitate collaborative and coordinated transboundary conservation between Québec, Ontario, and New York. However, beyond protecting habitats, corridors, and species, expansion and persistence within the A2L will ultimately depend on the willingness of humans to share the landscape with the wolf (van den Bosch et al. 2022).

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Declarations

Conflict of interest The authors declare no competing interests.

References

Beier P (2018) A rule of thumb for widths of conservation corridors. Conserv Biol 33(4):976–978. https://doi.org/10.1111/cobi.13256

BELW 2000 Consulting (2018) Beacon Environmental Limited and Wildlife 2000 Consulting. DRAFT Recovery Strategy for the Algonquin Wolf (*Canis sp.*) in Ontario. Ontario Recovery Strategy Series. Prepared for the Ontario Ministry of Natural Resources and Forestry, Peterborough

Benson JF, Patterson BR, Mahoney PJ (2014) A protected area influences genotype-specific survival and the structure of a Canis hybrid zone. Ecol 95(2):254–264. https://doi.org/10.1890/13-0698.1

Benson JF, Mills KJ, Patterson BR (2015) Resource selection by wolves at dens and rendezvous sites in Algonquin park, Canada. Biol Conserv 182:223–232. https://doi.org/10.1016/j.biocon.2014.12.010

Benson JF, Patterson BR (2015) Spatial overlap, proximity, and habitat use of individual wolves within the same packs. Wildlife Soc Bullet 39(1):31–40. https://doi.org/10.1002/wsb.506

Benson JF, Loveless KM, Rutledge LY, Patterson BR (2017) Ungulate predation and ecological roles of wolves and coyotes in eastern North America. Ecol Appl 27(3):718–733. https://doi.org/10.1002/eap.1499

Benson JF, Mahoney PJ, Wheeldon TJ, Thompson CA, Ward ME et al (2024) Humans drive spatial variation in mortality risk for a threatened wolf population in a *Canis* hybrid zone. J Appl Ecol 61(4):700–712. https://doi.org/10.1111/1365-2664.14589

Boucher S, Crête M, Ouellet JP, Daigle C, Lesage L (2004) Large-scale trophic interactions: white-tailed deer growth and forest understory. Ecoscience 11(3):286–295. https://doi.org/10.1080/11956860.2004.11682835

Bowman J, Adey E, Angoh SY, Baici JE, Brown MG et al (2020) Effects of cost surface uncertainty on current density estimates from circuit theory. PeerJ 8:e9617. https://doi.org/10.7717/peerj.9617

Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FK (2002) Evaluating resource selection functions. Ecol Model 157(2–3):281–300. https://doi.org/10.1016/S0304-3800(02)00200-4

Brodeur V, Ouellet JP, Courtois R, Fortin D (2008) Habitat selection by black bears in an intensively logged boreal forest. Can J Zool 86(11):1307–1316. https://doi.org/10.1139/Z08-118

Bubnicki JW, Churski M, Schmidt K, Diserens TA, Kuijper DP (2019) Linking spatial patterns of terrestrial herbivore community structure to trophic interactions. eLife 8:e44937. https://doi.org/10.7554/eLife.44937

Carricondo-Sanchez D, Zimmermann B, Wabakken P, Eriksen A, Milleret C et al (2020) Wolves at the door? Factors influencing the individual behavior of wolves in relation to anthropogenic features. Biol Conserv 244:108514. https://doi.org/10.1016/j.biocon.2020.108514

Carroll C, (2003) Impacts of landscape change on wolf viability in the Northeastern U.S. and Southeastern Canada: implications for wolf recovery. Wildlands Project Special Paper No. 5. Richmond

Carroll C, McRae BH, Brookes A (2012) Use of linkage mapping and centrality analysis across habitat gradients to conserve connectivity of gray wolf populations in western North America. Conserv Biol 26(1):78–87. https://doi.org/10.1111/j.1523-1739.2011.01753.x

Chapron G, Kaczensky P, Linnell JD, Von Arx M, Huber D et al (2014) Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346(6216):1517–1519. https://doi.org/10.1126/science.1257553

CEC (2023) Commission for Environmental Cooperation. Terrestrial Ecoregions: Level I. http://www.cec.org/north-american-environmental-atlas/terrestrial-ecoregions-level-i/ Accessed 21 February 2023

Coffin AW, Ouren DS, Bettez ND, Borda-de-Água L, Daniels AE, et al (2021) The ecology of rural roads: effects, management, and research. Issues in Ecology. Report No. 23. The Ecological Society of America, Washington

Cohen J (1988) Statistical power analysis for the behavioral sciences. Lawrence Erlbaum Associates Inc, New Jersey

Cole JR, Kross A, Jaeger JAG (2023a) Monitoring changes in landscape structure in the Adirondack-to-Laurentians (A2L) transboundary wildlife linkage between 1992 and 2018: Identifying priority areas for conservation and restoration. Landsc Ecol 38:383–408. https://doi.org/10.1007/s10980-022-01561-2

Cole JR, Koen EL, Pedersen EJ, Gallo JA, Kross A et al (2023b) Impacts of anthropogenic land transformation on species-specific habitat amount, fragmentation, and connectivity in the Adirondack-to-Laurentians (A2L) transboundary wildlife linkage between 2000 and 2015: Implications for conservation and ecological restoration. Landsc Ecol 38:2591–2621. https://doi.org/10.1007/s10980-023-01727-6

COSEWIC (2015) Committee on the Status of Endangered Wildlife in Canada. COSEWIC assessment and status report on the Eastern Wolf Canis sp. cf. lycaon in Canada. COSEWIC, Ottawa

Crooks KR, Burdett CL, Theobald DM, Rondinini C, Boitani L (2011) Global patterns of fragmentation and connectivity of mammalian carnivore habitat. Philos Trans R Soc Lond B Biol Sci 366:2642–2651. https://doi.org/10.1098/rstb.2011.0120

Crooks KR, Burdett CL, Theobald DM, King SR, Di Marco M et al (2017) Quantification of habitat fragmentation reveals extinction risk in terrestrial mammals. PNAS 114(29):7635–7640. https://doi.org/10.1073/pnas.1705769114

Darimont CT, Fox CH, Bryan HM, Reimchen TE (2015) The unique ecology of human predators. Science 349(6250):858–860. https://doi.org/10.1126/science.aac4249

Dickie M, Serrouya R, McNay RS, Boutin S (2017) Faster and farther: wolf movement on linear features and implications for hunting behaviour. J Appl Ecol 54(1):253–263. https://doi.org/10.1111/1365-2664.12732

Dutta T, Sharma S, McRae BH, Roy PS, DeFries R (2016) Connecting the dots: mapping habitat connectivity for tigers in central India. Reg Environ Change 16:53–67. https://doi.org/10.1007/s10113-015-0877-z

ECCC (2021) Environment and Climate Change Canada Management Plan for the Eastern Wolf (*Canis lupus lycaon*) in Canada, *Species at Risk Act* Management Plan Series, Environment and Climate Change Canada, Ottawa

ECCC (2023) Environment and Climate Change Canada Ice thickness data. https://www.canada.ca/en/environment-climate-change/services/ice-forecasts-observations/latest-conditions/archive-overview/thickness-data.html Accessed 12 March 2023

Estes JA, Terborgh J, Brashares JS, Power ME, Berger J et al (2011) Trophic downgrading of planet Earth. Sci 333(6040):301–306. https://doi.org/10.1126/science.1205106

Forman RT, Alexander LE (1998) Roads and their major ecological effects. Annu Rev Ecol Evol Syst 29:207–231. https://doi.org/10.1146/annurev.ecolsys.29.1.207

Fritts SH, Carbyn LN (1995) Population viability, nature reserves, and the outlook for gray wolf conservation in North America. Restor Ecol 3(1):26–38. https://doi.org/10.1111/j.1526-100X.1995.tb00072.x

Fuller TK, Berg WE, Radde GL, Lenarz MS, Joselyn GB (1992) A history and current estimate of wolf distribution and numbers in Minnesota. Wildlife Soc Bullet 20:42–55. http://www.jstor.org/stable/3782759

Fuller TK, Mech LD, Cochrane JF (2003) Wolf population dynamics. In: Mech D, Boitani L (eds) Wolves: behavior, ecology, and conservation. The University of Chicago Press, Chicago, pp 161–191

Gaynor KM, Brown JS, Middleton AD, Power ME, Brashares JS (2019) Landscapes of fear: spatial patterns of risk perception and response. Trends Ecol Evol 34(4):355–368. https://doi.org/10.1016/j.tree.2019.01.004

Gonzalez A, Lawton JH, Gilbert FS, Blackburn TM, Evans-Freke I (1998) Metapopulation dynamics, abundance, and distribution in a microecosystem. Science 281(5385):2045–2047. https://doi.org/10.1126/science.281.5385.2045

Guisan A, Thuiller W, Zimmermann NE (2017) Habitat suitability and distribution models: with applications in R. Cambridge University Press, Cambridge. https://doi.org/10.1017/9781139028271

Harrison DJ, Chapin TG (1998) Extent and connectivity of habitat for wolves in eastern North America. Wildlife Soc Bullet 26:767–775

Hebblewhite M, Whittington J (2020) Wolves without borders: transboundary survival of wolves in Banff National Park over three decades. Glob Ecol Conserv 24:e01293. https://doi.org/10.1016/j.gecco.2020.e01293

Hénault M (2019) Évaluation de la présence du loup de l'Est dans la réserve faunique Papineau-Labelle et sa périphérie. Report for Environment and Climate Change Canada, Canadian Wildlife Service - Québec Region. Québec

Hilty J, Worboys GL, Keeley A, Woodley S, Lausche B, et al (2020) Guidelines for conserving connectivity through ecological networks and corridors. Best practice protected area Guidelines Series, IUCN, Gland

Hinton JW, Hurst JE, Kramer DW, Stickles JH, Frair JL (2022) A model-based estimate of winter distribution and abundance of white-tailed deer in the Adirondack Park. PLoS ONE 17(8):e0273707. https://doi.org/10.1371/journal.pone.0273707

Hirzel AH, Arlettaz R (2003) Modelling habitat suitability for complex species distributions by the environmental distance geometric mean. Environ Manage 32:614–623. https://doi.org/10.1007/s00267-003-0040-3

Hirzel AH, Posse B, Oggier PA, Crettenand Y, Glenz C et al (2004) Ecological requirements of reintroduced species and the implications for release policy: the case of the bearded vulture. J Appl Ecol 41(6):1103–1116. https://doi.org/10.1111/j.0021-8901.2004.00980.x

Hirzel AH, Le Lay G, Helfer V, Randin C, Guisan A (2006) Evaluating the ability of habitat suitability models to predict species presences. Ecol Model 199(2):142–152. https://doi.org/10.1016/j.ecolmodel.2006.05.017

Ibisch PL, Hoffmann MT, Kreft S, Pe'er G, Kati V et al (2016) A global map of roadless areas and their conservation status. Science 354(6318):1423–1427. https://doi.org/10.1126/science.aaf7166

Jaeger JAG (2000) Landscape division, splitting index, and effective mesh size: new measures of landscape fragmentation. Landsc Ecol 15:115–130. https://doi.org/10.1023/A:1008129329289

Keeley AT, Beier P, Gagnon JW (2016) Estimating landscape resistance from habitat suitability: effects of data source and nonlinearities. Landsc Ecol 31:2151–2162. https://doi.org/10.1007/s10980-016-0387-5

Koen EL, Bowman J, Findlay CS, Zheng L (2007) Home range and population density of fishers in eastern Ontario. J Wildl Manage 71(5):1484–1493. https://doi.org/10.2193/2006-133

Koen EL, Bowman J, Walpole AA (2012) The effect of cost surface parameterization on landscape resistance estimates. Mol Ecol Resour 12(4):686–696. https://doi.org/10.1111/j.1755-0998.2012.03123.x

Koen EL, Bowman J, Wilson PJ (2015) Isolation of peripheral populations of Canada lynx (*Lynx canadensis*). Can J Zool 93(7):521–530. https://doi.org/10.1139/cjz-2014-0227

Kokko H, López-Sepulcre A (2006) From individual dispersal to species ranges: perspectives for a changing world. Science 313(5788):789–791. https://doi.org/10.1126/science.1128566

Kuijper DPJ, Sahlén E, Elmhagen B, Chamaillé-Jammes S, Sand H, et al (2016) Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. Proc Royal Soc B 283:20161625. https://doi.org/10.1098/rspb.2016.1625

Kuijper DPJ, Churski M, Trouwborst A, Heurich M, Smit C et al (2019) Keep the wolf from the door: how to conserve wolves in Europe's human-dominated landscapes? Biol Conserv 235:102–111. https://doi.org/10.1016/j.biocon.2019.04.004

Kuijper DPJ, Diserens TA, Say-Sallaz E, Kasper K, Szafrańska PA et al (2024) Wolves recolonize novel ecosystems leading to novel interactions. J Appl Ecol 61(5):906–921. https://doi.org/10.1111/1365-2664.14602

Larivière S, Jolicoeur H, Crête M (2000) Status and conservation of the gray wolf (*Canis lupus*) in wildlife reserves of Québec. Biol Conserv 94(2):143–151. https://doi.org/10.1016/S0006-3207(99)00185-8

Laundré JW, Hernández L, Altendorf KB (2001) Wolves, elk, and bison: reestablishing the "landscape of fear" in Yellowstone National Park, USA. Can J Zool 79(8):1401–1409. https://doi.org/10.1139/z01-094

Laundré JW, Hernández L, Ripple WJ (2010) The landscape of fear: ecological implications of being afraid. Open Ecol J 3(3):1–7. https://doi.org/10.2174/1874213001003030001

Lindenmayer DB, Fischer J (2013) Habitat fragmentation and landscape change: an ecological and conservation synthesis. Island Press, London

Linnell JD, Swenson JE, Anderson R (2001) Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. Anim Conserv 4(4):345–349. https://doi.org/10.1017/S1367943001001408

Linnell JD, Brøseth H, Solberg EJ, Brainerd SM (2005) The origins of the southern Scandinavian wolf *Canis lupus* population: potential for natural immigration in relation to dispersal distances, geography, and Baltic ice. Wildlife Biol 11:383–391. https://doi.org/10.2981/0909-6396(2005)11[383:TOOTSS]2.0.CO;2

Loveless K (2010) Foraging strategies of eastern wolves in relation to migratory prey and hybridization. Dissertation, Trent University

Maine Wolf Coalition (2024) Wolves in the Northeast. https://mainewolfcoalition.org/wolves-in-the-northeast/ Accessed 14 December 2022

Mainguy J, Hénault M, Jolicoeur H, Dalpé-Charron E (2017) Identification génétique et répartition spatiale des grands canidés sauvages au Québec. Ministère des Forêts, de la Faune et des Parcs, Direction de l'expertise sur la faune terrestre, l'herpétofaune et l'avifaune et Direction de la gestion de la faune de Lanaudière et des Laurentides, Québec

Malcolm K, Cheveau M, St-Laurent MH (2020) Wolf habitat selection in relation to recreational structures in a national park. J Mammal 101(6):1638–1649. https://doi.org/10.1093/jmammal/gyaa115

McAlpine DF, Soto DX, Rutledge LY, Wheeldon TJ, White BN et al (2015) Recent occurrences of wild-origin wolves (*Canis* spp.) in Canada south of the St. Lawrence river revealed by stable isotope and genetic analysis. Can Field-Nat 129(4):386–394. https://doi.org/10.22621/cfn.v129i4.1761

McRae BH, Kavanagh DM (2011) Linkage mapper connectivity analysis software. The Nature Conservancy, Seattle

McRae BH, Shah VB (2011) Circuitscape User Guide. The University of California, Santa Barbara

McRae BH (2012) Pinchpoint mapper connectivity analysis software. The Nature Conservancy, Seattle

McRae BH, Shirk AJ, Platt JT (2013) Gnarly landscape utilities: resistance and habitat calculator user guide. Fort Collins, The Nature Conservancy

Mech LD (1995) The challenge and opportunity of recovering wolf populations. Conserv Biol 9(2):270–278. https://doi.org/10.1046/j.1523-1739.1995.9020270.x

Mech LD, Boitani L (eds) (2003) Wolves: behavior, ecology, and conservation. University of Chicago Press, Chicago

Mladenoff DJ, Sickley TA (1998) Assessing potential gray wolf restoration in the northeastern United States: a spatial prediction of favorable habitat and potential population levels. J Wildl Manage 62(1):1–10. https://doi.org/10.2307/3802259

Morales-González A, Fernández-Gil A, Quevedo M, Revilla E (2022) Patterns and determinants of dispersal in grey wolves *(Canis lupus*). Biol Rev 97(2):466–480. https://doi.org/10.1111/brv.12807

Moser B, Jaeger JAG, Tappeiner U, Tasser E, Eiselt B (2007) Modification of the effective mesh size for measuring landscape fragmentation to solve the boundary problem. Landsc Ecol 22:447–459. https://doi.org/10.1007/s10980-006-9023-0

Muhly TB, Johnson CA, Hebblewhite M, Neilson EW, Fortin D et al (2019) Functional response of wolves to human development across boreal North America. Ecol Evol 9(18):10801–10815. https://doi.org/10.1002/ece3.5600

Murray DL, Bastille-Rousseau G, Adams JR, Waits LP (2015) The challenges of red wolf conservation and the fate of an endangered species recovery program. Conserv Lett 8(5):338–344. https://doi.org/10.1111/conl.12157

Musiani M, Paquet PC (2004) The practices of wolf persecution, protection, and restoration in Canada and the United States. BioScience 54(1):50–60. https://doi.org/10.1641/0006-3568(2004)054[0050:TPOWPP]2.0.CO;2

Nussey P, Noseworthy J (2018) A wildlife connectivity analysis for the Chignecto Isthmus. Nature Conservancy of Canada, Toronto

NYS-DEC (2023a) New York State Department of Environmental Conservation. The Gray Wolf. https://dec.ny.gov/nature/animals-fish-plants/gray-wolf Accessed 15 March 2023

NYS-DEC (2023b) New York State Department of Environmental Conservation. Coyote Hunting Seasons. https://www.dec.ny.gov/outdoor/28945.html Accessed 10 April 2023

NYS-DEC (2023c) New York State Department of Environmental Conservation. Moose. https://www.dec.ny.gov/animals/6964.html Accessed 4 June 2023

Ontario (2023a) Ontario Hunting Regulations Summary. https://www.ontario.ca/document/ontario-hunting-regulations-summary Accessed 14 April 2023

Ontario (2023b) Cervid ecological framework. https://www.ontario.ca/page/cervid-ecological-framework Accessed 14 April 2023

Paquet PC, Wierzchowski J, Callaghan C (1996) Chapter 7. Summary report on the effects of human activity on gray wolves in the Bow River Valley, Banff National Park, Alberta. In: Green J, Pacas C, Bayley S, Cornwell L (eds) A cumulative effects assessment and futures outlook for the Banff Bow Valley. Prepared for the Banff Bow Valley Study, Department of Canadian Heritage, Ottawa

Paquet PC, Strittholt JR, Staus NL (1999) Wolf reintroduction feasibility in the Adirondack Park. Conservation Biology Institute, Corvallis

Pimm SL, Jenkins CN, Abell R, Brooks TM, Gittleman JL et al (2014) The biodiversity of species and their rates of extinction, distribution, and protection. Science 344(6187):1246752. https://doi.org/10.1126/science.1246752

Potvin F (1988) Wolf movements and population dynamics in Papineau-Labelle reserve, Québec. Can J Zool 66(6):1266–1273. https://doi.org/10.1139/z88-185

Québec (2023) 2022-2024 hunting seasons for small game. https://www.quebec.ca/en/tourism-and-recreation/sporting-and-outdoor-activities/sport-hunting/seasons-bag-limits/small-game#c116746 Accessed 22 October 2023

Rateaud W, Jolicoeur H, Etcheverry P (2001) Habitat du loup dans le sud-ouest du Québec: occupation actuelle et modèles prédictifs. Direction du développement de la faune, Société de la faune et des parcs du Québec, Québec

Ripple WJ, Estes JA, Beschta RL, Wilmers CC, Ritchie EG et al (2014) Status and ecological effects of the world's largest carnivores. Science 343(6187):1241484. https://doi.org/10.1126/science.1241484

Rogic A, Tessier N, Lapointe F-J (2014) Identification of canids found within Parc national du Mont-Tremblant and its surroundings using microsatellite markers. University of Montréal and Ministère des Forêts, de la Faune et des Parcs, Montréal

Rosenblatt E, Gieder K, Donovan T, Murdoch J, Smith TP et al (2023) Genetic diversity and connectivity of moose (*Alces americanus americanus*) in eastern North America. Conserv Genet 24:235–248. https://doi.org/10.1007/s10592-022-01496-w

Rutledge LY, Desy G, Fryxell JM, Middel K, White BN et al (2017) Patchy distribution and low effective population size raise concern for an at-risk top predator. Divers Distrib 23(1):79–89. https://doi.org/10.1111/ddi.12496

Sazatornil V, Rodríguez A, Klaczek M, Ahmadi M, Álvares F et al (2016) The role of human-related risk in breeding site selection by wolves. Biol Conserv 201:103–110. https://doi.org/10.1016/j.biocon.2016.06.022

Selva N, Switalski A, Kreft S, Ibisch PL (2015) Chapter 3. Why keep areas road-free? The importance of roadless areas. In: van der Ree R, Smith DJ, Grilo D (eds) Handbook of Road Ecology. John Wiley & Sons Ltd, Oxford. pp 16-26

Shirk AJ, McRae BH (2013) Gnarly landscape utilities: core mapper user guide. Fort Collins, The Nature Conservancy

Singleton PH (1995) Winter habitat selection by wolves in the North Fork of the Flathead River Basin Montana and British Columbia. Dissertation. University of Montana

Singleton PH (2002) Landscape permeability for large carnivores in Washington: a geographic information system weighted-distance and least-cost corridor assessment. US Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland

Smith JB, Nielsen CK, Hellgren EC (2016) Suitable habitat for recolonizing large carnivores in the midwestern USA. Oryx 50(3):555–564. https://doi.org/10.1017/S0030605314001227

Spanowicz AG, Jaeger JAG (2019) Measuring landscape connectivity: on the importance of within-patch connectivity. Landsc Ecol 34:2261–2278. https://doi.org/10.1007/s10980-019-00881-0

Spanowicz AG, Teixeira FZ, Jaeger JAG (2020) An adaptive plan for prioritizing road sections for fencing to reduce animal mortality. Conserv Biol 34(5):1210–1220. https://doi.org/10.1111/cobi.13502

Statistics Canada (2023) Census Profile, 2016 Census. https://www12.statcan.gc.ca/census-recensement/2016/dp-pd/prof/index.cfm?Lang=E Accessed 16 March 2023

Suraci JP, Clinchy M, Zanette LY, Wilmers CC (2019) Fear of humans as apex predators has landscape-scale impacts from mountain lions to mice. Ecol Lett 22(10):1578–1586. https://doi.org/10.1111/ele.13344

Tardif B, Lavoie G, Lachance Y (2005) Québec Biodiversity Atlas. Threatened or vulnerable species. Gouvernement du Québec, Ministère du Développement durable, de l'Environnement et des Parcs, Direction du développement durable, du patrimoine écologique et des parcs, Québec

Theberge JB, Theberge MT, Forbes G (1996) What Algonquin Park wolf research has to instruct about recovery in the northeastern United States. In: Proceedings: Defenders of Wildlife's Wolves of America Conference, pp 14-16

Treves A, Martin KA, Wiedenhoeft JE, Wydeven AP (2009) Dispersal of gray wolves in the Great Lakes region. Recovery of gray wolves in the Great Lakes region of the United States: an endangered species success story. Springer, New York, pp 191–204

US Census Bureau (2023) Census 2016. https://www.census.gov/acs/www/data/data-tables-andtools/data-profles/2016/ Accessed 22 March 2023

USFWS (1992) U.S. Fish & Wildlife Service. Recovery plan for the Eastern Timber Wolf. Minnesota

van den Bosch M, Beyer DE Jr, Erb JD, Gantchoff MG, Kellner KF et al (2022) Identifying potential gray wolf habitat and connectivity in

the eastern USA. Biol Conserv 273:109708. https://doi.org/10.1016/j.biocon.2022.109708
Vilaça ST, Donaldson ME, Benazzo A, Wheeldon TJ, Vizzari MT et al (2023) Tracing eastern wolf origins from whole-genome data in context of extensive hybridization. Mol Biol Evol 40(4):msad055. https://doi.org/10.1093/molbev/msad055
Villemure M, Festa-Bianchet M (2002) Écologie du loup au parc national du Canada de la Mauricie. Département de biologie, Université de Sherbrooke. Sherbrooke, Rapport préparé pour Parcs Canada
Villemure M, Jolicoeur H (2004) First confirmed occurrence of a wolf, *Canis lupus*, south of the St. Lawrence River in over 100 years. Can Field-Nat 118(4):608–610. https://doi.org/10.22621/cfn.v118i4.66
Wetzel S (2019) User Manual: Fragmentation/connectivity/urban sprawl metrics extensions for ArcGIS Python toolbox ZonalMetrics. https://gitlab.com/simeonwetzel/landscape-metrics-tools/tree/master Accessed 17 July 2022
Williams DR, Rondinini C, Tilman D (2022) Global protected areas seem insufficient to safeguard half of the world's mammals from human-induced extinction. PNAS 119(24):e2200118119. https://doi.org/10.1073/pnas.2200118119
Wolf C, Ripple WJ (2016) Prey depletion as a threat to the world's large carnivores. Royal Soc Open Sci 3(8):160252. https://doi.org/10.1098/rsos.160252
Wolf C, Ripple WJ (2017) Range contractions of the world's large carnivores. Royal Soc Open Sci 4(7):170052. https://doi.org/10.1098/rsos.170052
Woodroffe R, Ginsberg JR (1998) Edge effects and the extinction of populations inside protected areas. Science 280(5372):2126–2128. https://doi.org/10.1126/science.280.5372.2126
WWHCWG (2010) Washington Wildlife Habitat Connectivity Working Group. Washington connected landscapes project: statewide analysis. Washington Departments of Fish and Wildlife, and Transportation, Olympia
WWHCWG (2012) Washington Wildlife Habitat Connectivity Working Group. Washington connected landscapes project: analysis of the Columbia Plateau Ecoregion. Washington's Department of Fish and Wildlife, and Department of Transportation, Olympia
Wydeven AP, Fuller TK, Weber W, MacDonald K (1998) The potential for wolf recovery in the northeastern United States via dispersal from southeastern Canada. Wildlife Soc Bullet 26(4):776–784. https://www.jstor.org/stable/3783551
Young SP, Goldman EA (1944) The wolves of North America: Part I. Their history, life habits, economic status, and control. American Wildlife Institute. Dove Publications, New York