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RESEARCH ARTICLE

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

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Abstract

Context The Adirondack-to-Laurentians (A2L) transboundary wildlife linkage is one of three north–south movement linkages that connect natural areas in northeastern USA and southeastern Canada. This region still retains habitats of high ecological integrity and biodiversity; however, anthropogenic land transformation may be putting transboundary connectivity at risk.

Objectives We measured the impacts of anthropogenic land transformation on species-specific habitat amount, fragmentation, and connectivity in the A2L between 2000 and 2015.

Methods We developed suitable habitat and resistance models for the American black bear (*Ursus americanus*), fisher (*Pekania pennanti*), moose (*Alces alces*), and white-tailed deer (*Odocoileus virginianus*) to identify suitable and optimal habitat patches for each species. We quantified habitat amount, fragmentation, and connectivity, and used Linkage Mapper and Circuitscape to map corridors and pinch-points important for connectivity.

Results In the A2L between 2000 and 2015, suitable and optimal habitat patch area declined considerably, fragmentation increased, and inter-patch connectivity decreased for each species. Moose and black bear habitat patches experienced the greatest habitat loss, fragmentation, and decline in inter-patch connectivity. The majority of habitat patch area loss and fragmentation occurred in the southern Québec and Ontario portions.

Conclusions To achieve long-term functionality of the A2L, collaborative and coordinated measures will be necessary to preserve the integrity of the Québec mega-patch, restore extensive habitat in eastern Ontario, and reestablish or maintain connectivity throughout the linkage. Left unaddressed, continued

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anthropogenic land transformation is likely to have detrimental effects on the ability of the A2L to function as a transboundary wildlife linkage.

Keywords Habitat loss · Effective mesh size · Linkage mapper · Least-cost corridors · Circuitscape · Black bear · Fisher · Moose · White-tailed deer

Introduction

Habitat loss and fragmentation due to anthropogenic land transformation is one of the leading causes of biodiversity declines worldwide (Haddad et al. 2015; Maxwell et al. 2016; Diaz et al. 2019). Habitat loss and fragmentation contribute to long-term changes in ecosystem structure and function (Lindenmayer and Fischer 2013) and can lead to an overall reduction in species abundance and movement ability between fragments (Haddad et al. 2015; Crooks et al. 2017). In North America, monitored vertebrate population sizes have declined by an average of 20% since 1970, with habitat loss and fragmentation being the main driver of these declines (WWF 2020, 2022).

Landscape connectivity can facilitate animal movement among resource patches (Taylor et al. 1993). Indeed, long-term viability of wildlife populations is linked to landscape connectivity which consists of intra-patch connectivity (i.e., movements such as daily foraging; Tischendorf and Fahrig 2000; Spanowicz and Jaeger 2019) and inter-patch connectivity (movements such as dispersal, migration, and range shifts in response to climate change; Tischendorf and Fahrig 2000; Ament et al. 2014; Spanowicz and Jaeger 2019).

Successful dispersal events help to maintain long-term viability of populations by colonizing new areas, rescuing sink populations, and maintaining genetic variation and gene flow within meta-populations (Kokko and López-Sepulcre 2006). Ecological corridors facilitate movement between habitat patches, whereas wildlife linkages promote the movement of multiple species and ecological processes within a network of habitat patches (Beier et al. 2008; Meiklejohn et al. 2009).

Globally, 56% of all terrestrial mammals have transboundary geographic ranges (Mason et al. 2020). On the contrary, conservation programs generally do not span political borders, making positive conservation outcomes contingent on the alignment of similar conservation values across multiple jurisdictions (Kark et al. 2015). Transboundary conservation presents an opportunity to improve protection of species with transboundary ranges through coordinated and collaborative international conservation efforts (Vasilijević et al. 2015; Mason et al. 2020).

The Adirondack-to-Laurentians (A2L) transboundary wildlife linkage is one of three north–south movement linkages that connect natural areas in northeastern USA and southeastern Canada. This region features habitats of high ecological integrity and biodiversity; however, continued anthropogenic land transformation is putting transboundary connectivity at risk (Cole et al. 2023). As a result, there is an urgent need for strategic conservation and restoration intervention, as well as the development of coordinated transboundary management plans between Canada and the USA, to limit further deterioration of the linkage.

Our aim was to assess the impact of land-cover change on species-specific habitat amount, fragmentation, and connectivity in the A2L transboundary wildlife linkage between 2000 and 2015. We created suitable habitat and resistance models for four species: American black bear (*Ursus americanus*), fisher (*Pekania pennanti*), moose (*Alces alces*), and white-tailed deer (*Odocoileus virginianus*). We modelled suitable habitat patches (SHPs), optimal habitat patches (OHPs), and stepping-stone patches (SSPs) for each species, and used Linkage Mapper and Circuitscape to map least-cost corridors (LCCs) and pinch-points important for connectivity. We then identified priority habitat patches and corridors for conservation and restoration. Specifically, we asked: (1) to what degree has habitat loss and fragmentation occurred within the study area for each species? (2) to what degree has connectivity changed for each species? (3) what percentage of habitat patches and corridors are under protection for each species?

Methods

Study area

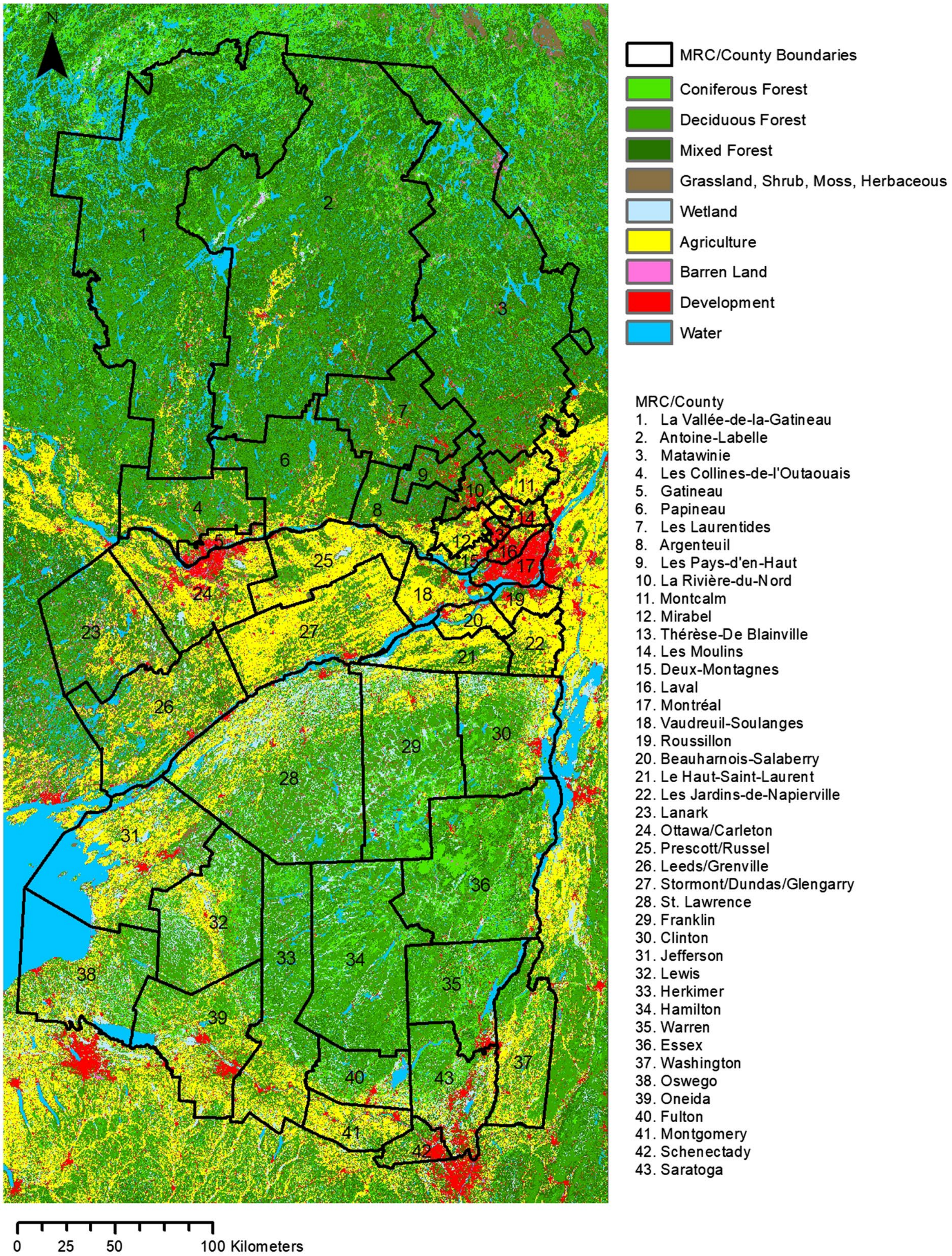
Our ~127,000 km^2 A2L study area spans portions of Québec and Ontario in Canada, and New York in the USA; and includes 43 municipalités régionales de comté (MRCs) and counties. The A2L is bounded by the Laurentian Mountains in Québec to the north, the Adirondack Mountains in New York to the south, and the cities of Ottawa, Ontario and Montréal, Québec to the west and east, respectively (Fig. 1). The A2L is situated 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). Dominant tree species in the Québec and Ontario portions include sugar maple, American basswood, white ash, American hop-hornbeam, butternut, yellow birch, American beech, northern red oak, and eastern hemlock (Tardif et al. 2005); dominant tree species in the New York portion include spruce-fir, evergreen-northern hardwood, and mesic upland hardwoods including sugar maple, American beech, yellow birch, and oak (Graves and Wang 2012). The geology of the A2L is comprised of Canadian Shield to the north, Saint Lawrence Platform in the centre, and Precambrian to the south (Tardif et al. 2005). The highest peak is Mount-Marcy in the Adirondacks at 1629 m. As of 2016, the area was home to over 6.8 million people (54 per km^2) (Statistics Canada 2023; US Census Bureau 2023).

Data sources

We identified four focal species to represent the broad range of habitat and movement requirements of native terrestrial, non-volant mammals in the study region (Beier and Loe 1992): American black bear (*Ursus americanus*), fisher (*Pekania pennanti*), moose (*Alces alces*), and white-tailed deer (*Odocoileus virginianus*). These species differ in home range size, habitat preferences, and intra- and inter-patch movement capabilities. Identifying potential habitat and connectivity routes for these "umbrella species" will undoubtedly identify potential habitat and connectivity routes for a variety of other species that reside within the same ecological community (Frankel and Soulé, 1981).

We obtained land-cover, road-network, MRC/county boundaries, and protected area maps for Québec, Ontario, New York, Vermont, and Massachusetts for the years 2000 and 2015 (Table S1). We created 30 m resolution maps of the study area for each time-period by converting each source map from polygon/polyline to raster using the "Polygon to Raster" and "Polyline to Raster" tools in ArcGIS10.7 (Environmental Systems Research Institute, Redlands, CA). We then reclassified the land-cover and road-network maps into 10 common land-cover classes and 3 common road classes unifying the classification scheme across all input maps (Table S2; S3). We then used the re-classified land-cover and road-network maps to create four additional environmental variable layers to represent human disturbance levels: (1) distance from development; (2) distance from primary roads; (3) distance from secondary roads; and (4) distance from tertiary roads. We created each of these layers by generating three buffers of 0–500, 500–1000, and 1000 + meters around the land-cover element of interest (i.e., roads, development) using the "Euclidean Distance" function in ArcGIS10.7. Buffers that overlapped did not impact the individual buffers because overlapping buffer areas remain part of all the individual buffers. These distances represent the medium and maximum distances disturbance-avoidance behaviour (i.e., from human activity, development, and roads) is displayed by black bear and moose; whereas fisher and white-tailed deer exhibit negligible disturbance-avoidance behaviour (Arthur et al. 1989; Laurian et al. 2008; Munro et al. 2012).

Analyses were performed at three spatial scales: "the study area" which included the surface area of all 43 MRCs/counties together; "the provincial/state portions" which included the surface area of each individual provincial/state portion only; and "the MRCs/counties", which included the surface area of each individual MRC/county only. The land area surrounding the outside of the study area (which included small areas of Vermont and Massachusetts) were not used in any of the analyses. This area was included as a buffer-zone to eliminate the overestimation of resistance values at artificial map boundaries during the least-cost path and Circuitscape analyses (Koen et al. 2010). We utilized these distinct hierarchical scales to: (1) allow for the direct comparison and ranking between provincial/state portions and MRCs/counties; and (2) provide stakeholders with the information necessary to develop coordinated and collaborative local, regional, and transboundary conservation plans.


N
MRC/County Boundaries
Coniferous Forest
Deciduous Forest
Mixed Forest
Grassland, Shrub, Moss, Herbaceous
Wetland
Agriculture
Barren Land
Development
Water
MRC/County
1. La Vallée-de-la-Gatineau
2. Antoine-Labelle
3. Matawinie
4. Les Collines-de-l'Outaouais
5. Gatineau
6. Papineau
7. Les Laurentides
8. Argenteuil
9. Les Pays-d'en-Haut
10. La Rivière-du-Nord
11. Montcalm
12. Mirabel
13. Thérèse-De Blainville
14. Les Moulins
15. Deux-Montagnes
16. Laval
17. Montréal
18. Vaudreuil-Soulanges
19. Roussillon
20. Beauharnois-Salaberry
21. Le Haut-Saint-Laurent
22. Les Jardins-de-Napierville
23. Lanark
24. Ottawa/Carleton
25. Prescott/Russel
26. Leeds/Grenville
27. Stormont/Dundas/Glengarry
28. St. Lawrence
29. Franklin
30. Clinton
31. Jefferson
32. Lewis
33. Herkimer
34. Hamilton
35. Warren
36. Essex
37. Washington
38. Oswego
39. Oneida
40. Fulton
41. Montgomery
42. Schenectady
43. Saratoga
0 25 50 100 Kilometers

◂**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

Suitable habitat and resistance models

Suitable habitat

We estimated suitable habitat for each species by assigning relative values to our land-cover maps using a combination of previously published values, literature review, and expert opinion (Table S4). We then re-scaled the suitable habitat values for each species so that the values ranged between 0 and 1 using the following equation:

$$\mathrm{F}(x) = (x - \mathrm{min})/(\mathrm{max} - \mathrm{min})$$

where x is the assigned relative suitability value for a 30 m grid cell, and min and max are the minimum and maximum suitable habitat values of the habitat suitability surface, respectively (Keeley et al. 2016; Table S5). Values near one represent the most suitable habitat conditions and values near zero represent the least suitable habitat (Keeley et al. 2016). For each species, we created one aggregated 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 cell across all input layers.

Resistance layers

We created resistance layers for each species that represent the relative probability that the species will avoid a particular land-cover. Thus, we derived resistance values for each of the six raster layers for each species (24 raster layers total; Table S5) by calculating the inverse of our suitable habitat values (Koen et al. 2012; Keeley et al. 2016). We then used Gnarly Landscape Utilities: Resistance and Habitat Calculator toolset (McRae et al. 2013) in ArcGIS10.7 to overlay all six resistance layers; we created a single aggregated resistance layer for each species by retaining the maximum resistance value for each 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.

Species-specific habitat patches

To identify species-specific habitat patches, we used our 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 (SHPs) were identified as patches with an average suitable habitat value ≥ 0.6 within a circular moving window with a radius based on home range size (Online Appendix 1). Patches that fell below the species' minimum habitat patch cut-off size (Online Appendix 1) were removed. Because animals move among multiple habitat patches to obtain the resources they need within their home ranges, we expanded habitat patches outwards up to a total cost-weighted distance equal to each species' mean minimum home range radius (Tables S6 and S7) to potentially link proximate patches into larger aggregates, simulating intra-patch connectivity (Spanowicz and Jaeger 2019). Habitat patches still separated at this point require movements that exceed twice the species' cost-weighted mean minimum home range radius and were considered dispersal distances (i.e., inter-patch connectivity).

We identified optimal habitat patches (OHPs) by performing the same steps as above, however, we did not expand the patches, and we removed all raster cells with suitable habitat values ≤ 0.4 (black bear, fisher, and moose), and ≤ 0.2 (white-tailed deer) (Table S7) to exclude non-habitat types (i.e., roads, development, agriculture, etc.), leaving patches that represented the most suitable habitat. This removal of non-habitat fragmented the original patches further, creating significantly more patches. However, many of these patches fell below the species' minimum habitat patch cut-off size (Online Appendix 1) and were removed.

We identified stepping-stone patches (SSPs) by performing the same steps as above, however, this time we identified patches that were smaller than the species' minimum habitat patch cut-off size (Online Appendix 1) but still large enough to serve as a refuge area during dispersal (≥ 10 km^2 for black bear and moose, ≥ 5 km^2 for fisher, and ≥ 1 km^2 for white-tailed deer; Table S7).

Evaluation of the suitable habitat and habitat patch models

We used two empirical datasets collected in the Québec and Ontario portions of the study area to evaluate our suitable habitat layers: (1) unpublished trapping/harvest data for black bear, moose, and white-tailed deer provided by the Québec Ministère des Forêts, de la Faune et des Parcs, consisting of $n = 131{,}039$ trapping/harvest GPS locations collected in 1998–2002 and 2014–2019; and (2) previously published radiotelemetry data for fishers (Koen et al. 2007, 2014), consisting of $n = 1083$ locations obtained by triangulation for 26 adult fishers (10 M, 16 F) between 2003 and 2004. Hereafter, we refer to these two datasets together as "evaluation points". We evaluated the fisher suitable habitat layers for the year 2000 only, because we did not have evaluation points for this area for 2015. We were also unable to obtain similar evaluation points for the New York portion, as the New York State—Department of Conservation does not collect harvest data with high-resolution GPS locations. We did not use data points obtained from citizen science programs (e.g., iNaturalist) in our validation process because of the potential for spatial biases that may be present in the GPS locations (see Dickinson et al. 2010). The consequence of not using citizen science data was that we were only able to validate our suitable habitat maps for a portion of the study area.

Typically, species move across the landscape differently during winter months when snow is on the ground (i.e., some can cross frozen lakes in winter that they cannot cross in summer), or not at all (hibernating black bear). Thus, we used only evaluation points obtained between April 1st and November 30th of each year to characterize movement ability during spring, summer, and fall. Since the evaluation points only covered subsections of the study area, we delineated these subsections by creating a 100% minimum convex polygon (MCP) around all the data points for each species (Koen et al. 2007; Broduer et al., 2008) using the "Convex Hull" function in ArcGIS10.7 (Figures S1-S4).

We used three metrics to assess the performance of each map of suitable habitat (SH) (i.e., how well each map predicted suitable habitat for each species within the local landscape). First, we used the absolute validation index (*AVI*; Hirzel and Arlettaz 2003), calculated as the proportion of evaluation points that were located on raster cells with an SH value > 0.5 (Hirzel et al. 2006; Guisan et al. 2017):

$$\begin{aligned} AVI = {} & \text{Number of evaluation points found on raster} \\ & \text{cells with a SH value} \\ & > 0.5 \text{ within the MCP}/\text{Number of} \\ & \text{evaluation points within the MCP} \end{aligned}$$

Values for the *AVI* ranged between 0 (weak performance) and 1 (strong performance). Second, we used the contrast validation index (Hirzel et al. 2004, 2006), calculated as the *AVI* minus the *AVI* of a random chance model predicting presence within the MCP (Hirzel et al. 2006; Guisan et al. 2017):

$$\begin{aligned} CVI = {} & AVI - \text{Number of raster cells within the} \\ & \text{MCP with a SH value} \\ & > 0.5/\text{Number of raster cells within the MCP} \end{aligned}$$

Values for the *CVI* range between -0.5 (weak performance) and 0.5 (strong performance). Finally, we used the *Boyce Index* (Boyce et al. 2002; Hirzel et al. 2006; Guisan et al. 2017), whereby we calculated two frequencies for each of the 6 suitable habitat classes (i.e., 1, 0.8, 0.6, 0.4, 0.2, 0): (1) the proportion of observed evaluation points found in each SH class within the MCP (*P*); and (2) the expected proportion of evaluation points found in each SH class within the MCP (*E*) (Boyce et al. 2002; Hirzel et al. 2006). We then used these values to calculate the *P/E* ratio for each class. If the SH model predicted suitable habitat well, then a low SH class should contain fewer evaluation points than expected by chance (i.e., a *P/E* ratio < 1). Alternatively, a high SH class should contain more evaluation points than expected by chance (i.e., a *P/E* ratio > 1; Hirzel et al. 2006; Guisan et al. 2017). The *Boyce Index* can then be calculated using the Spearman rank correlation coefficient between the SH value and the *P/E* ratio (Boyce et al. 2002; Hirzel et al. 2006). A SH model that performs well is expected to show a monotonically increasing relationship between the SH value and the *P/E* ratio (Hirzel et al. 2006; Guisan et al. 2017). *Boyce Index* values ranged between − 1 (an incorrect model) and 1 (a model whose predictions are consistent with the evaluation dataset); values close to zero indicate the model is no different from a chance model (Hirzel et al. 2006; Guisan et al. 2017).

To measure the performance of the habitat patch (HP) models, we applied variations of the *AVI* and *CVI* metrics. We used the AVI_{patch} to calculate the proportion of evaluation points that were located within SHPs and OHPs as follows,

$$AVI_{patch} = \text{Number of evaluation points in HPs within the MCP/Number of evaluation points within the MCP}$$

Values for the AVI_{patch} ranged between 0 (weak performance) and 1 (strong performance). We used the CVI_{patch} as follows:

$$CVI_{patch} = AVI_{patch} - \text{Area of HPs within the MCP}\left(\text{km}^2\right)/\text{Area of MCP}\left(\text{km}^2\right)$$

Values for the CVI_{patch} ranged between -0.5 (weak performance) and 0.5 (strong performance).

Land-cover change

To quantify land-cover change, we measured and compared the area of three groups of land-cover classes between 2000 and 2015: (1) Natural land-cover, which included coniferous forest, deciduous forest, mixed forest, grassland, shrub, moss, and herbaceous vegetation, and wetlands (2) Agriculture, which included all agriculture classes, and (3) Development, which included all development classes. Land-cover area was calculated by multiplying the cell count of each land-cover class within the boundaries of the reporting unit (i.e., study area, provincial/state portion, MRC/county) by the area of a single cell (900 m^2), and then dividing by 1,000,000 m^2 / km^2 to convert to km^2.

Species-specific habitat amount and fragmentation

To quantify changes in species-specific habitat amount, we measured and compared the area of SHPs and OHPs between 2000 and 2015 within each reporting unit in ArcGIS10.7. We calculated habitat proportion by dividing the habitat area by the total area of the reporting unit.

The effective mesh size is based on the average probability that any two randomly chosen points in the study area are connected (i.e., not separated by a fragmentation barrier; Jaeger 2000; Moser et al. 2007). The effective mesh size also serves as a measure of structural connectivity, or the degree to which movement between different parts of the landscape is possible (Spanowicz and Jaeger 2019). Because the value of the effective mesh size can be profoundly influenced by the boundary of a reporting unit, we used two variations of the effective mesh size. First, we used the "cutting out" procedure ($m_{\text{eff\_CUT}}$) to measure fragmentation strictly within the boundaries of the reporting units. Second, we used the "cross-boundary connections" procedure ($m_{\text{eff\_CBC}}$) to include patches that crossed borders into adjacent reporting units. We performed all measurements using the effective mesh size tool from the ZonalMetrics ArcGIS toolbox (Wetzel 2019).

Species-specific connectivity

Least-cost paths and least-cost corridors

When modeling inter-patch connectivity, we assumed that each species would take the lowest-resistance path between two patches (i.e., the least cost path (LCP)). This gives one best-case measure of connectivity between patches across the resistance surface (Adriaensen et al. 2003). LCPs assume that animals can determine the single optimal path (Fletcher and Fortin 2018) and the method can be sensitive to the specific choice of resistance values used (Rayfield et al. 2010). As such, we also calculated least-cost corridors (LCCs) between patches. The LCC method relaxes the assumption of single best paths by calculating corridors representing similarly low-cost movement (Pinto and Kiett, 2009; Fletcher and Fortin 2018). We used the Linkage Pathways tool of the Linkage Mapper ArcGIS Toolbox (McRae and Kavanagh 2011) to create species-specific LCPs and LCCs. For the calculation of LCCs with this software, we calculated adjacency using both cost-weighted and Euclidean distances, dropped corridors that intersected other habitat patches, put no limit on the number of linkages originating from each habitat patch, and truncated the width of LCCs to 200 cost-weighted km. As a rule of thumb, ecological corridors should be at least 2 km wide, except at unavoidable bottlenecks such as wildlife crossing structures (Beier 2018). We used a least-cost corridor cut-off width of 200 cost-weighted km to ensure that even when corridors traversed regions with the highest resistance values (101), corridors would still maintain a width of at least 2 km wide.

Prior to running the Linkage Pathways software, we increased the cell size of the suitable habitat and resistance layers to 90 m × 90 m using the "Raster cell size coarsener" tool in Gnarly Landscape Utilities: Resistance and Habitat Calculator (Shirk and McRae 2013), to reduce computing time and memory use. The tool increased habitat and resistance raster cell sizes by smoothing grid cell values (i.e., taking the average in the *N*x*N* window) and then coarsening the result to a larger cell size (i.e., taking the average value of smoothed values in the *N*x*N* window; Shirk and McRae 2013).

Calculation of dispersal distance

To determine if any of the LCCs were too long to be considered dispersal corridors, we needed to define species-specific median and maximum dispersal distances; these data were not available for our focal species in our study area. Instead, we estimated median and maximum dispersal distances for each species based on the relationship between home range size (derived from the literature; Table S6) and dispersal distance (Table S8; Bowman et al. 2002),

Median dispersal distance = 7 · (linear dimension of home range)

Maximum dispersal distance = 40 · (linear dimension of home range)

Identifying pinch-points

Pinch-points are narrow sections within a corridor where movement is restricted due to natural or anthropogenic landscape features (McRae and Shah 2011; Pelletier et al. 2014). Pinch-points can be conservation and restoration priorities as their loss can disproportionately disrupt connectivity (McRea et al. 2008; Dickson et al. 2013). To identify pinch-points within the connectivity 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 the path of electric current through the LCCs, based on local resistances along the LCCs. This method assumes that individuals follow random walks through the LCCs, with a probability of moving into a location from a neighbouring one, dependent on the resistance of the location (McRea et al. 2008). We used the "pairwise" mode within the Linkage Mapper Toolbox to identify pinch-points between SHPs. We used the "all to one" mode within the Linkage Mapper Toolbox, where current flows from all source nodes (i.e., SHPs) iteratively to each ground node, to produce cumulative current density maps where areas of high current flow were identified as pinch-points critical for maintaining connectivity for the entire network of SHPs (McRea et al. 2008; Dutta et al. 2016).

Measuring connectivity

To quantify changes in species-specific connectivity between 2000 and 2015, we compared the values for Euclidean distance, cost-weighted distance, least-cost path length, and effective resistance (output from the Circuitscape runs) between SHPs for each species. We assumed that if connectivity had diminished for a specific species, then these distances would have increased significantly. We compared the distances between time points using a Welch two-sample *t*-test to account for unequal variances. A paired *t*-test was not appropriate because some of the SHPs disappeared in 2015 due to habitat loss. We used Cohen's effect size to further assess the change in connectivity between 2000 and 2015 ($d = 0.2$ represents a small effect size, $d = 0.5$ represents a medium effect size, and $d = 0.8$ represents a large effect size; Cohen 1988) using the rstatix package (Kassambara 2023) in R Studio.

Habitat patches and corridors under protection

To determine the percentage of species-specific SHPs, OHPs, and LCCs under legal protection, we obtained maps of government protected areas (e.g., state parks in the USA and provincial parks in Canada) and private protected areas secured by Nature Conservancy of Canada/The Nature Conservancy (Table S1). We measured the proportion of each SHP, OHP, or LCC currently under protection in ArcGIS10.7.

To determine which habitat patches and corridors were used by all species, we overlaid the species-specific SHP, OHP, and LCC layers in ArcGIS10.7 to create an intersect map. Our assumption was that conservation in these portions would be beneficial to all species.

Results

Evaluation of the suitable habitat and habitat patch models

Our maps of suitable habitat performed well at predicting suitable habitat for each species within the local landscape. AVI values ranged from 0.8 to 0.9 in 2000 and 2015 (Table 1), CVI values were 0.2 in 2000, and ranged from 0.1 to 0.3 in 2015 (Table 1), and *Boyce Index* values ranged from 0.8 to 0.9 in 2000 and 2015 (Table 1).

The suitable habitat patch (SHP) models performed well at predicting SHPs for each species within the local landscape. AVI_{patch} values ranged from 0.8 to 0.9 in 2000, and from 0.7 to 0.9 in 2015 (Table 1), and CVI_{patch} values ranged from 0.08 to 0.1 in 2000, and from 0.06 to 0.3 in 2015 (Table 1). The optimal habitat patch (OHP) models also performed well for black bear, moose, and white-tailed deer: AVI_{patch} values were 0.7 in 2000, and ranged from 0.5 to 0.7 in 2015, and CVI_{patch} values ranged from 0.03 to 0.2 in 2000, and 0.05 to 0.3 in 2015 (Table 1). However, the OHP model for fisher showed weak performance; the AVI_{patch} value was 0.1 and the CVI_{patch} value was $-$ 0.03. Because the CVI_{patch} value was negative, we did not use the fisher OHPs in any calculations. For R code and calculations see Online Appendix 1 and Supplemental Material.

Land-cover change

Between 2000 and 2015, natural land-cover (i.e., coniferous forest, deciduous forest, mixed forest, grassland, shrub, moss, and herbaceous vegetation, and wetlands) decreased by 1457 km^2 across the study area; with losses of 587 km^2 in the Québec portion, 966 km^2 in Ontario portion, and a gain of 96 km^2 in the New York portion (Table 2). Agriculture also decreased across the study area; with losses of 201 km^2 in the Québec portion, 148 km^2 in the New

Table 1 Results of suitable habitat model and habitat patch model validation for each species in 2000 and 2015. AVI = Absolute validation index, AVI_{patch} = Absolute validation index for patches, CVI = Contrast validation index, CVI_{patch} = Contrast validation index for patches, SHP = Suitable habitat patch, OHP = Optimal habitat patch

Species	2000				2015			
	AVI	*CVI*	*Boyce Index*	*p*-value	*AVI*	*CVI*	*Boyce Index*	*p*-value
Black Bear	0.9	0.2	0.9	0.03	0.9	0.2	0.8	0.1
Fisher	0.9	0.2	0.9	0.02	–	–	–	–
Moose	0.9	0.2	0.8	0.06	0.9	0.3	0.9	0.03
White-tailed deer	0.8	0.2	0.9	0.02	0.8	0.1	0.9	0.02

Species	Model	2000		2015	
		AVI_{patch}	CVI_{patch}	AVI_{patch}	CVI_{patch}
Black Bear	SHP	0.9	0.09	0.8	0.1
	OHP	0.7	0.08	0.5	0.08
Fisher	SHP	0.8	0.1	–	–
	OHP	0.1	–0.03	–	–
Moose	SHP	0.9	0.1	0.9	0.3
	OHP	0.7	0.2	0.7	0.3
White-tailed deer	SHP	0.9	0.08	0.7	0.06
	OHP	0.7	0.03	0.6	0.05

Table 2 Changes in land-cover area (km^2) and (%) for each set of grouped land-cover categories between 2000 and 2015, at the scale of the study area and each provincial/state portion

Location	2000 (km^2)	2015 (km^2)	2015-2000 (km^2)	Percent change (%)
Study area				
Natural land cover	93,210	91,752	− 1457	− 2
Agriculture	17,726	17,570	− 155	− 1
Development	4332	5743	1410	33
Québec portion				
Natural land cover	46,290	45,702	− 587	− 1
Agriculture	4749	4549	− 201	− 4
Development	1361	2194	833	61
Ontario portion				
Natural land cover	8202	7236	− 966	− 12
Agriculture	5629	5823	194	3
Development	564	1010	445	79
New York portion				
Natural land cover	38,718	38,814	96	0.2
Agriculture	7347	7199	− 148	− 2
Development	2407	2539	132	5

York portion, and a gain of 194 km^2 in the Ontario portion (Table 2). Development increased by 1410 km^2 across the study area; with increases of 833 km^2 in the Québec portion, 445 km^2 in the Ontario portion, and 132 km^2 in the New York portion (Table 2).

As of 2015, there were 17 MRCs/counties (13 in the Québec portion, 3 in the Ontario portion, and 1 in the New York portion) that had > 50% of their surface areas dedicated to agriculture and development (Table S9). The proportion of natural land-cover within these MRCs/counties ranged from 11% (Montréal) to 44% (MRC Montcalm; Table S9). In the three Ontario counties, natural land-cover decreased by 289 km^2 (Stormont/Dundas/Glengarry), 232 km^2 (Ottawa/Carleton), and 96 km^2 (Prescott/Russel; Table S9); whereas natural land-cover increased in all the Québec MRCs, except MRC Gatineau (-34 km^2), and Montgomery County (-1 km^2) in New York (Table S9). Agriculture increased in Stormont/Dundas/Glengarry (154 km^2), Ottawa/Carleton (52 km^2), Prescott/Russel (4km^2) and Gatineau (17 km^2; Table S9); and, development increased in all MRCs/counties, except Montréal and MRC Gatineau in Québec (Table S9).

Species-specific habitat amount

We detected net losses of both suitable and optimal habitat patch area for all four species between 2000 and 2015. The greatest SHP area loss within the study area occurred for moose, with a reduction of 16,842 km^2 (26%), followed by black bear with a reduction of 8894 km^2 (11%) (Table 3, Figs. 2 and 3). Most of these losses took place in the Québec portion of the study area, where SHP area for moose was reduced by 13,382 km^2 (28%) and SHP area for black bear was reduced by 6891 km^2 (14%) (Table 3, Figs. 2 and 3). The greatest OHP area loss also occurred for moose with a reduction of 6832 km^2 (17%), followed by black bear with a reduction of 4369 km^2 (9%) (Table 3, Figs. 2 and 3). The vast majority of these losses also took place in the Québec portion of the study area, where OHP area for moose was reduced by 6148 km^2 (21%) and OHP area for black bear was reduced by 4487 km^2 (14%) (Table 3, Figs. 2 and 3). The Ontario portion of the study area had the lowest proportion of suitable and optimal habitat area for each species in 2000, and the greatest relative reductions of habitat area between 2000 and 2015. In Ontario, SHP area was reduced by 95% for moose, 62% for black bear, 38% for fisher, and 30% for white-tailed deer. OHP area in Ontario was

Table 3 Changes in suitable habitat patch (SHP) and optimal habitat patch (OHP) area (km^2) and proportion (%) for each species between 2000 and 2015, at the scale of the study area and each provincial/state portion. Bold numbers = Greater than 25% reduction between 2000 and 2015

Location/Species	SHP area in 2000 (km^2)	SHP area in 2015 (km^2)	SHP area 2015-2000 (km^2)	Proportion of SHP area 2000 (%)	Proportion of SHP area 2015 (%)	Percent change 2000 to 2015 (%)
Study Area						
Black Bear	77,690	68,795	– 8895	61	54	– 11
Fisher	86,348	84,555	– 1793	68	66	– 2
Moose	64,266	47,424	– 16,842	50	37	**– 26**
White-Tailed Deer	89,303	86,147	– 3156	70	68	– 4
Québec Portion						
Black Bear	48,615	41,724	– 6891	83	71	– 14
Fisher	48,978	48,858	– 119	83	83	– 0.2
Moose	47,283	33,902	– 13,382	80	58	**– 28**
White-Tailed Deer	49,564	48,488	– 1076	84	82	– 2
Ontario Portion						
Black Bear	3286	1256	– 2030	21	8	**– 62**
Fisher	3971	2447	– 1524	26	16	**– 38**
Moose	3575	174	– 3401	23	1	**– 95**
White-Tailed Deer	7127	4964	– 2163	46	32	**– 30**
New York Portion						
Black Bear	25,789	25,816	26	49	49	0.1
Fisher	33,400	33,250	– 150	63	63	– 0.4
Moose	13,408	13,348	– 59	25	25	– 0.4
White-Tailed Deer	32,613	32,696	83	61	62	0.3

Location/Species	OHP area in 2000 (km^2)	OHP area in 2015 (km^2)	OHP area 2015–2000 (km^2)	Proportion of OHP area 2000 (%)	Proportion of OHP area 2015 (%)	Percent change 2000 to 2015 (%)
Study Area						
Black Bear	46,344	41,975	– 4369	36	33	– 9
Fisher	–	–	–	–	–	–
Moose	40,717	33,884	– 6832	32	27	– 17
White-Tailed Deer	77,361	73,979	– 3383	61	58	– 4
Québec Portion						
Black Bear	31,124	26,637	– 4487	53	45	– 14
Fisher	–	–	–	–	–	–
Moose	29,796	23,648	– 6148	51	40	**– 21**
White-Tailed Deer	42,682	41,461	– 1222	73	70	– 3
Ontario Portion						
Black Bear	416	144	– 271	3	1	**– 65**
Fisher	–	–	–	–	–	–
Moose	340	39	– 301	2	0.3	**– 89**
White-Tailed Deer	5729	3991	– 1738	37	26	**– 30**
New York Portion						
Black Bear	14,804	15,194	390	28	29	3
Fisher	–	–	–	–	–	–
Moose	10,581	10,197	– 383	20	19	– 4

Table 3 (continued)

Location/Species	OHP area in 2000 (km^2)	OHP area in 2015 (km^2)	OHP area 2015–2000 (km^2)	Proportion of OHP area 2000 (%)	Proportion of OHP area 2015 (%)	Percent change 2000 to 2015 (%)
White-Tailed Deer	28,950	28,527	− 423	55	54	− 1

reduced by 89% for moose, 65% for black bear, and 30% for white-tailed deer (Table 3 and Figs. 2 and 3). Whereas in New York, SHP area increased by 26 km^2 for black bear, 83 km^2 for white-tailed deer, and OHP area increased by 390 km^2 for black bear (Table 3 and Figs. 2 and 3).

Species-specific fragmentation

We detected a net increase in suitable and optimal habitat patch fragmentation for all species within the study area between 2000 and 2015. The highest level of SHP fragmentation was for moose, with an 8674 km^2 (46%) reduction in m_{eff_CUT} size, and an 11,918 km^2 (42%) reduction in m_{eff_CBC} size (Table 4). In the Québec portion, moose also had the highest level of SHP fragmentation with an 18,672 km^2 (49%) reduction in m_{eff_CUT} size and a 25,606 km^2 (44%) reduction in m_{eff_CBC} size (Table 4). This was followed by black bear with a 10,578 km^2 (26%) reduction in m_{eff_CUT} size and a 13,949 km^2 (23%) reduction in m_{eff_CBC} size. In the Ontario portion, moose had a 298 km^2 (99%) reduction in m_{eff_CUT} size and a 622 km^2 (99%) reduction in m_{eff_CBC} size (Table 5). For black bear, we detected a 236 km^2 (81%) reduction in m_{eff_CUT} size and a 432 km^2 (73%) reduction in m_{eff_CBC} size. For white-tailed deer, we found a 1051 km^2 (52%) reduction in m_{eff_CUT} size and a 28,170 km^2 (94%) reduction in m_{eff_CBC} size (Table 4). The lowest level of SHP fragmentation for each species was in New York, with m_{eff_CUT} and m_{eff_CBC} size reductions of less than 3%, with the exception being white-tailed deer, which had a 3619 km^2 (17%) reduction in m_{eff_CBC} size (Table 4). At the level of the MRC/county, mean values for m_{eff_CUT}, m_{eff_CBC}, and the difference between the m_{eff_CUT} and m_{eff_CBC} (a measure of patch sharing between adjacent reporting units) decreased for each species between 2000 and 2015, except for fisher, for which we detected an increase in both the mean m_{eff_CBC} and the difference between the m_{eff_CUT} and m_{eff_CBC} values (Tables S10-S16).

The highest level of OHP fragmentation that we detected was for moose, with a 1592 km^2 (71%) reduction in m_{eff_CUT} size and an 1865 km^2 (71%) reduction in m_{eff_CBC} size (Table 4). This was followed by black bear with a 1623 km^2 (70%) reduction in m_{eff_CUT} size and a 1908 km^2 (70%) reduction in m_{eff_CBC} size (Table 4). This same pattern was also observed in the Québec and Ontario portions of the study area. In the New York portion, we found that white-tailed deer had the highest level of OHP fragmentation with a 283 km^2 (59%) reduction in m_{eff_CUT} size, and a 284 km^2 (59%) reduction in m_{eff_CBC} size. (Table 4). At the level of the MRC/county, mean values for m_{eff_CUT}, m_{eff_CBC}, and the difference between the m_{eff_CUT} and m_{eff_CBC} decreased for each species between 2000 and 2015 (Tables S10-S16).

Species-specific connectivity

Least-cost paths and least-cost corridors

For black bear, 8 of the 14 LCPs between SHPs in 2000 were longer than the median female dispersal distance of 40.1 km and 3 of the 14 LCPs were longer than the median male dispersal distance of 91.7 km (Table S8). However, all the LCPs were less than both the maximum female and male dispersal distances of 229.1 km and 523.8 km, respectively (Table S8). In 2015, 6 of the 12 LCPs were longer than the median female black bear dispersal distance, and 3 LCPs were longer than the median male black bear dispersal distance; however, all the LCPs were less than the female and male maximum dispersal distances (Table S8). For fisher, 13 of the 31 LCPs in 2000 were longer than the median female dispersal distance of 26.6 km (Table S8), and 10 of the 31 were longer than the median male dispersal distance of 33.9 km. However, all the LCPs were less than both the maximum female and male dispersal distances of

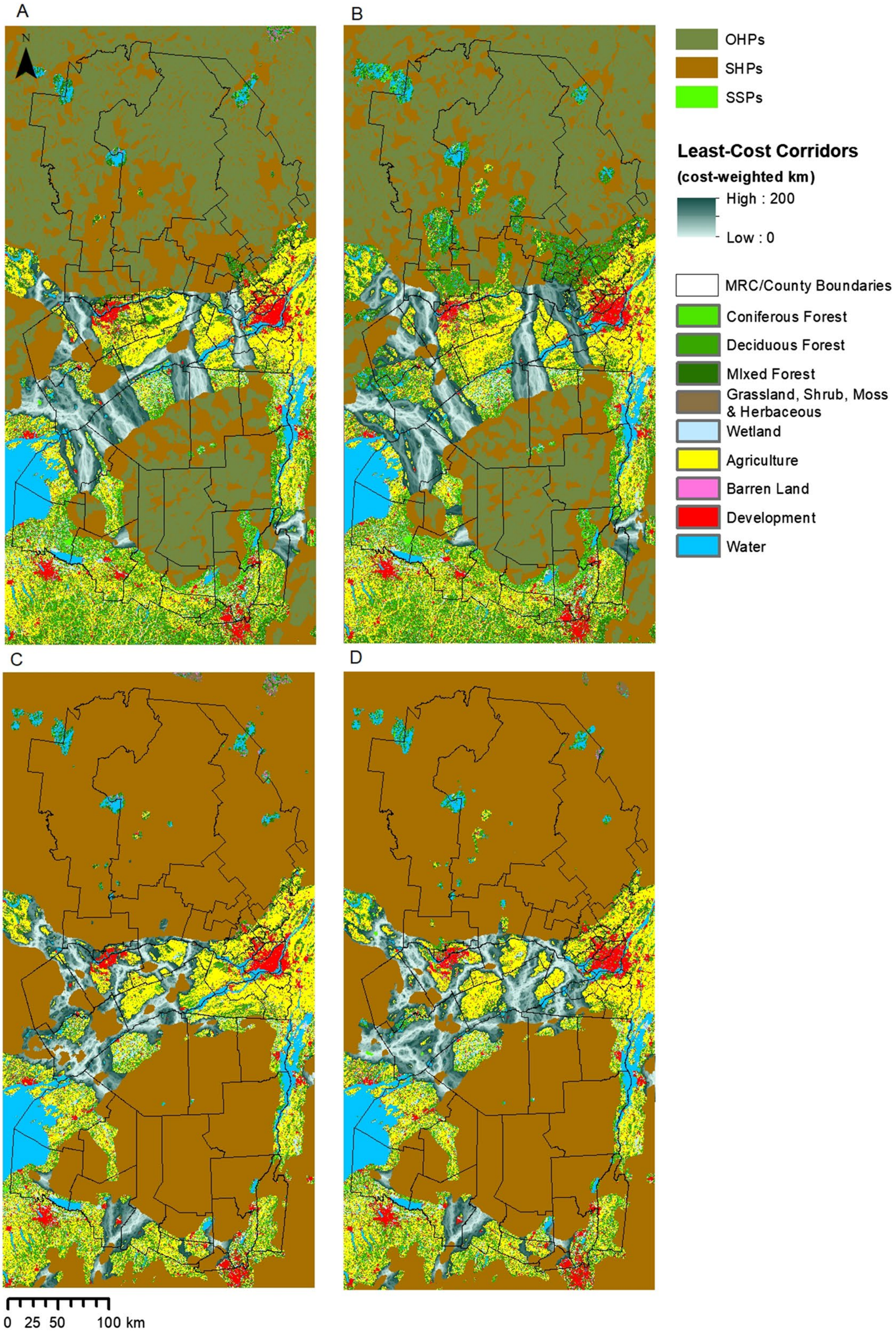
151.8 km and 193.5 km, respectively (Table S8). In 2015, 13 of the 27 LCPs were longer than the median female and male fisher dispersal distances; however, all the LCPs were less than the female and male maximum dispersal distances (Table S8). For moose, 8 of the 16 LCPs in 2000 and 9 of the 12 LCPs in 2015 were longer than the median moose dispersal distance of 44.6 km; however, all the LCPs in 2000 and 2015 were less than the maximum moose dispersal distance of 260.5 km (Table S8). In contrast, for white-tailed deer, 37 of the 72 LCPs in 2000, and 77 of the 114 LCPs in 2015, were longer than the median white-tailed deer dispersal distance of 10.1 km; and 1 of the 72 LCPs in 2000, and 4 of the 114 LCPs in 2015, were longer than the maximum dispersal distance of 58 km (Table S8). The number of LCCs decreased for each species between 2000 and 2015, except for white-tailed deer, which had an increase of 42 LCCs (Table 5, Figs. 2 and 3).

Changes in connectivity

Euclidean distances between SHPs increased for each species between 2000 and 2015, with fisher, moose, and white-tailed deer distances being statistically significant (*p*-values = 0.03, 0.03, 0.06 respectively; Table 5). The greatest change in Euclidean distances was for moose, with a mean increase of 41 km (*df* = 16, *95% CI* = -77 - -5, *Cohen's d* = 0.9; Table 5). Cost-weighed distances between SHPs increased for each species between 2000 and 2015: increases in fisher, moose, and white-tailed deer cost-weighted distances were significant (*p*-values = 0.02, 0.03, 0.08 respectively; Table 5). The greatest change in cost-weighted distance was for moose, with a mean increase of 1954 cost-weighed km (*df* = 16, *95% CI* -3634 - -275, *Cohen's d* = 0.9; Table 5). LCP distances also increased for each species, with significant increases for fisher, moose, and white-tailed deer (*p*-values = 0.05, 0.03, 0.04 respectively; Table 5). The largest increase in LCP distance was for moose with a mean increase of 58 km (*df* = 16, *95% CI* -107 - -8, *Cohen's d* = 0.9; Table 5). Effective resistance values also increased for each species, with significant increases for fisher, moose, and white-tailed deer (*p*-values = 0.05, 0.05, 0.02 respectively; Table 5). The largest increase in effective resistance was for moose, with a mean increase of 4371 Ohms (*df* = 17, *95% CI* -8776 - 33, *Cohen's d* = 0.8; Table 5).

Pinch-points

Most pinch-points changed locations or disappeared between 2000 and 2015 for all species. Pairwise current flow between black bear SHPs in 2015 identified a very narrow bottleneck of high current flow density between the patch shared by the counties of Lanark and Ottawa/Carleton in Ontario and the patch located in the county of Leeds/Grenville in Ontario (Fig. 4). This pinch-point became even more pronounced when current was run in the "all to one" mode in Circuitscape (i.e., a measure of current flow centrality) highlighting its importance in maintaining connectivity across the entire network of suitable habitat patches in the study area (Figure S5). Pairwise current flow for the fisher in 2015 identified a long pinch-point in the LCC traversing the county of Ottawa/Carleton (Fig. 4). However, when current was run "all to one" this pinch-point disappeared, indicating its lower relevance in maintaining connectivity across the entire network (Figure S5). Instead, pinch-points in Leeds/Grenville in Ontario, and St. Lawrence and Saratoga counties in New York are more important in maintaining overall network connectivity for the fisher. Pairwise current flow in 2015 for moose identified two main pinch-points in the LCCs traversing Lanark County in Ontario, MRC Les Collines-de-l'Outaouais in Québec, and Warren and Washington counties in New York with less pronounced pinch-points throughout many of the remaining LCCs (Fig. 5). These less pronounced pinch-points disappeared when current was run "all to one", indicating that only the pinch-points in Lanark County in Ontario, MRC Les Collines-de-l'Outaouais in Québec, and Warren and Washington counties in New York are important for overall network connectivity (Figure S6). Pairwise current flow between white-tailed deer SHPs in 2015 revealed a high concentration of pinch-points in the county of Ottawa/Carleton in Ontario (Fig. 5). This concentration disappeared when current was run "all to one" and was replaced by a concentration of pinch-points between the SHPs traversing the counties of Leeds/Grenville in Ontario and St. Lawrence in New York (Figure S6).


A
B
C
D
N
OHPs
SHPs
SSPs
Least-Cost Corridors
(cost-weighted km)
High : 200
Low : 0
MRC/County Boundaries
Coniferous Forest
Deciduous Forest
MIxed Forest
Grassland, Shrub, Moss & Herbaceous
Wetland
Agriculture
Barren Land
Development
Water
0 25 50 100 km

◂**Fig. 2** Changes in suitable habitat patches (SHPs), optimal habitat patches (OHPs), stepping-stone patches (SSPs), and least-cost corridors between 2000 and 2015. (**A**) Black bear habitat 2000, (**B**) Black bear habitat 2015, (**C**) Fisher habitat 2000, (**D**) Fisher habitat 2015

Stepping stones patches

In 2000, there was one stepping-stone patch (SSP) for black bear within the LCC just west of Leeds/Grenville County in Ontario. However, this patch disappeared in 2015 (Fig. 2). There were no SSPs for fisher in 2000, however, in 2015 there were four; two in the LCC west of MCR Les Collines-de-l'Outaouais in Québec, one in the LCC west of Leeds/Grenville County in Ontario, and one in a LCC inside Leeds/Grenville County, Ontario (Fig. 2). There were four SSPs for moose in 2000, one within Stormont/Dundas/Glengarry County in Ontario, one within St. Lawrence County in New York, one within Washington County in New York, and one other just east of Washington County in New York. In 2015, number of SSPs for moose increased to 6: one in MRC Papineau, Québec, one shared by the MRCs Les Laurentides and Papineau, Québec, one in Lanark County, Ontario, one west of Leeds/Grenville County, Ontario, one within Washington County, New York, and one just east of Washington County, New York (Fig. 3). There were five SSPs for white-tailed deer in 2000: one in Prescott/Russel County, Ontario, three in St. Lawrence County, New York, and one in Herkimer County, New York. In 2015, there was one SSP for white-tailed deer in Ottawa/Carleton County, Ontario, one east of Montréal in Québec, one in Prescott/Russel County, Ontario, one in St. Lawrence County, New York, and one in Herkimer County, New York (Fig. 3).

Habitat patches and corridors under protection

In 2015, the proportion of SHP area under protection ranged from 21% (white-tailed deer) to 29% (moose); the proportion of OHP area under protection ranged from 23% (white-tailed deer) to 33% (moose); and the proportion of LCC area under protection ranged from 3% (fisher) to 14% (moose) (Table 6; Fig. 6). Protection was not equally distributed across the study area. The average SHP area under protection was 9.5% in the Québec portion, 0.2% in the Ontario portion, and 54% in the New York portion; the average OHP area under protection was 10% in the Québec portion, 0.1% in the Ontario portion, and 67% in the New York portion; and the average LCC area under protection was 12% in the Québec portion, 2% in the Ontario portion, and 10% in the New York portion (Table 6; Fig. 6).

When SHP, OHP, and LCC layers were overlaid to create an intersect map to identify which habitat patches and corridors could be used by all species in 2015, we identified that three of the north–south LCCs could potentially be utilized by all four species (Fig. 7).

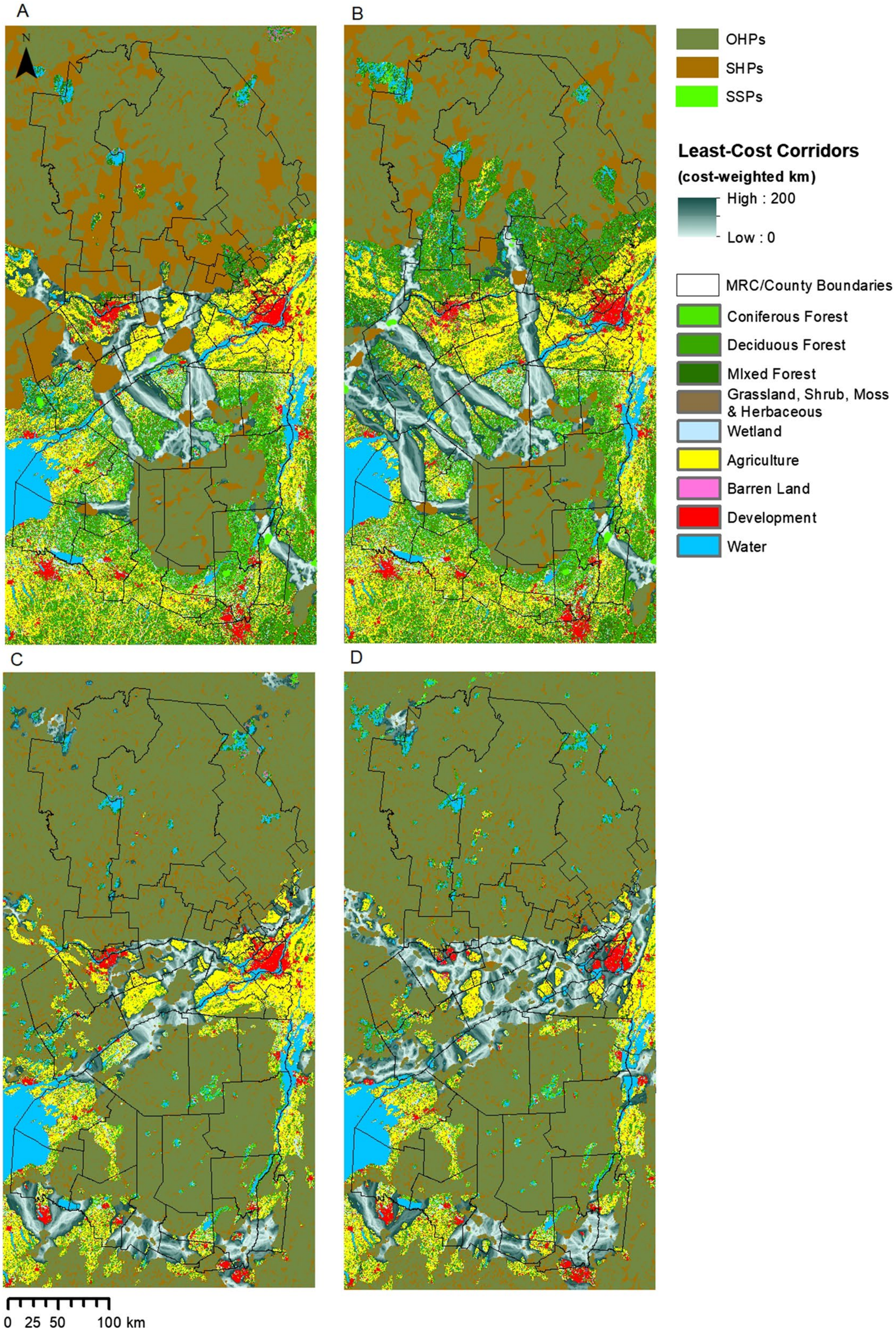
Discussion

Evaluation of the suitable habitat and habitat patch models

Our results showed that AVI_{patch} values were higher for suitable habitat patches (SHPs) than optimal-habitat patches (OHPs); whereas CVI_{patch} values were similar for SHPs and OHPs (Table 1). This can be explained by the fact that the AVI_{patch} value for SHPs is the percentage of evaluation points that fall within SHPs divided by the number of evaluation points within the MCP (Hirzel and Arlettaz 2003); whereas the AVI_{patch} value for OHPs is the percentage of evaluation points that fall within OHPs divided by the number of evaluation points within the MCP (Hirzel and Arlettaz 2003). SHPs have an average suitable habitat value of >0.5 and have been expanded to include adjacent patches, whereas OHPs have only suitable habitat values >0.5 and have not been expanded; therefore, SHPs are much bigger than OHPs and usually contain multiple OHPs within them.

The fact that AVI_{patch} values are less for OHPs compared to SHPs demonstrates that the majority of evaluation points fall within OHPs; however, when we evaluate the larger and expanded SHPs, we get slightly more evaluation points (i.e., OHP AVI_{patch} value $=0.7$, SHP AVI_{patch} value $=0.9$ for black bear and white-tailed deer in 2000; Table 1).

The CVI_{patch} formula, which is the AVI_{patch} value minus the area of habitat patches within the MCP divided by the area of the MCP, takes into consideration the difference in SHP and OHP proportions


A
B
C
D
N
OHPs
SHPs
SSPs
Least-Cost Corridors
(cost-weighted km)
High : 200
Low : 0
MRC/County Boundaries
Coniferous Forest
Deciduous Forest
MIxed Forest
Grassland, Shrub, Moss & Herbaceous
Wetland
Agriculture
Barren Land
Development
Water
0 25 50 100 km

◂**Fig. 3** Changes in suitable habitat patches (SHPs), optimal habitat patches (OHPs), stepping-stone patches (SSPs), and least-cost corridors between 2000 and 2015. (**A**) Moose habitat 2000, (**B**) Moose habitat 2015, (**C**) White-tailed deer habitat 2000, (**D**) White-tailed deer habitat 2015

within the MCP (Hirzel et al. 2004, 2006). Consequently, SHP and OHP CVI_{patch} values are very similar, or the same, for each species and time-point, which effectively validates how well the models fit the evaluation points (Table 1). Only the fisher and the white-tailed deer in 2000 had discrepancies between their SHP and OHP CVI_{patch} values. For the fisher we rejected this model because the discrepancy was very large, whereas the white-tailed deer was much less and there was no discrepancy in 2015.

Land-cover change

As of 2015, there were 17 MRCs/counties that had > 50% of their surface area dedicated to agriculture and development (13 in the Québec portion, 3 in the Ontario portion, and 1 in the New York portion; Table S9). These MRCs/counties could be considered "working lands" (Kremen and Merenlender 2018) or "C1- cities and farms regions" according to the "3Cs" framework (i.e., three global conditions for biodiversity conservation and sustainable use; Locke et al. 2019). These MRCs/counties are distinct from the wilderness areas of the Québec and Adirondack mega-patches in that they have been, and continue to be, highly modified by humans (i.e., development, agriculture, roads, etc.) and thus require specialized management and conservation strategies. Most working lands still contain natural land-cover areas (i.e., hedgerows, wooded areas, wetlands, natural pastures, etc.) for which Garibaldi et al. (2021) use the term "native habitats within working landscapes". If these working lands are appropriately managed with area-based conservation and restoration approaches they could provide essential habitat for patches and corridors between the Québec and Adirondack mega-patches. Such an approach would require government and non-government agencies and organizations providing monetary incentives to farmers and ranchers to create, improve upon, and/or maintain natural land-cover habitats on their agricultural lands (i.e., nature-based solutions; ALUS Canada 2023). Nature-based solutions such as wetland restoration, riparian buffers, shelterbelts, afforestation, and grassland restoration would provide habitat, cleaner air and water, carbon sequestration, climate resiliency and many other ecosystem services to the region (ALUS Canada 2023).

Lancaster et al. (2008) found that forest area increased from 29 to 40% within Stormont/Dundas/Glengarry and Leeds/Grenville counties in Ontario between 1934 and 1995, which they proposed significantly contributed to the recovery of fisher populations in the region. We found that between 2000 and 2015 this trend continued in the county of Leeds/Grenville with a 94 km^2 net gain in forest area; however, the county of Stormont/Dundas/Glengarry had a 243 km^2 net loss in forest area, and the adjacent counties of Ottawa/Carleton and Prescott/Russell in Ontario also had forest area net losses of 243 km^2 and 11 km^2, respectively. However, natural land-cover area (which includes all forest types) decreased, and agriculture and development increased, in all of these Ontario counties (Table S9). This may be the reason for the underperformance of our fisher OHP models. With such significant losses in natural habitat areas and equivalent increases in agriculture and development, fishers in these locations may presently be (1) settling for sub-optimal habitat to survive, (2) more habitat generalist than previously understood, or (3) a sink population. This trend was not the case for the 12 working lands in the Québec portion, which all experienced increases in natural land-cover area and decreases in agricultural area between 2000 and 2015 (Table S9).

Species-specific habitat amount

Our results demonstrate that anthropogenic land transformation between 2000 and 2015 yielded drastic changes in habitat amount for the four focal species. The greatest suitable and optimal habitat patch area losses occurred for moose, with a reduction of 16,842 km^2 (26%) SHP area, and 6832 km^2 (17%) OHP area, followed by black bear with a reduction of 8894 km^2 (11%) SHP area, and 4369 km^2 (9%) OHP area (Table 3, Figs. 2 and 3). However, these significant losses do not translate into actual land-cover loss. We found that natural land-cover area decreased by 1457 km^2, agriculture area decreased by 155 km^2, and development increased by 1410 km^2 within the A2L between 2000 and 2015 (Table 2). What these results reveal is that the majority of moose and black

Table 4 Changes in Effective Mesh Size for suitable habitat patches (SHPs) and optimal habitat patches (OHPs) for each species between 2000 and 2015, at the scale of the study area and each provincial/state portion

Species/Location	$m_{\text{eff\_CUT}}$ 2000 (km^2)	$m_{\text{eff\_CUT}}$ 2015 (km^2)	Change in $m_{\text{eff\_CUT}}$ 2015-2000 (km^2)	$m_{\text{eff\_CBC}}$ 2000 (km^2)	$m_{\text{eff\_CBC}}$ 2015 (km^2)	Change in $m_{\text{eff\_CBC}}$ 2015-2000 (km^2)	$m_{\text{eff\_CBC}}$– $m_{\text{eff\_CUT}}$ 2015 (km^2)
Study Area							
Black Bear	23,181	18,275	– 4907	33,000	26,510	– 6491	8235
Fisher	27,243	27,026	– 217	38,417	38,312	– 105	11,287
Moose	18,799	10,125	– 8674	28,326	16,408	– 11,918	6283
White-Tailed Deer	31,180	25,655	– 5524	45,018	35,213	– 9805	9557
Québec Portion							
Black Bear	40,017	29,439	– 10,578	61,212	47,263	– 13,949	17,824
Fisher	40,677	40,151	– 526	61,580	61,533	– 47	21,382
Moose	37,979	19,308	– 18,672	58,509	32,903	– 25,606	13,595
White-Tailed Deer	40,912	38,752	– 2159	69,924	59,361	– 10,563	20,609
Ontario Portion							
Black Bear	293	57	– 236	595	162	– 432	105
Fisher	345	196	– 150	742	493	– 249	297
Moose	300	2	– 298	627	5	– 622	3
White-Tailed Deer	2025	974	– 1051	29,965	1794	– 28,170	820
New York Portion							
Black Bear	11,091	11,102	11	11,134	11,152	19	50
Fisher	20,106	19,969	– 137	23,678	23,552	– 126	3583
Moose	2907	2884	– 23	2907	2884	– 23	0
White-Tailed Deer	18,121	17,618	– 503	21,763	18,144	– 3619	526

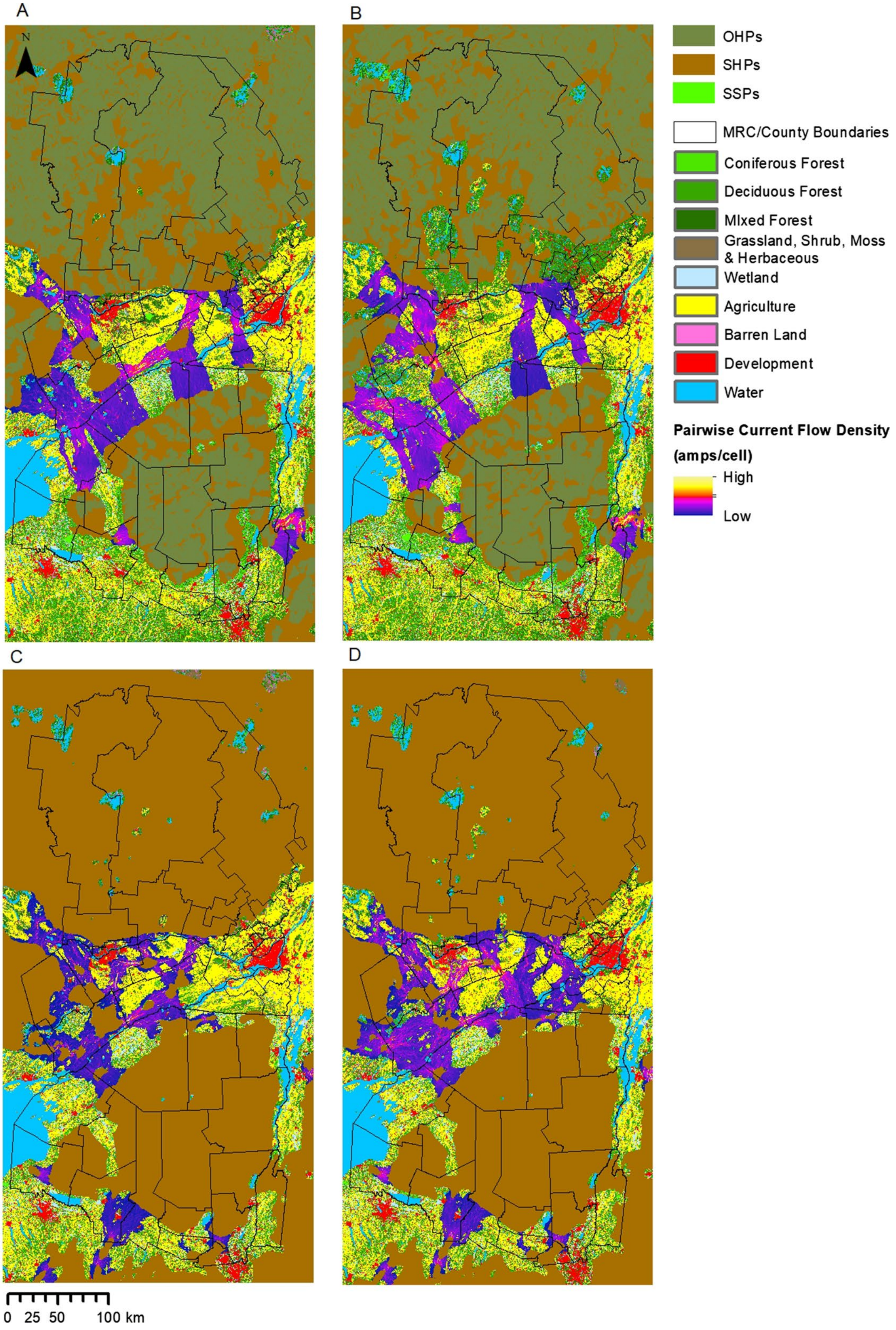
Species/Location	$m_{\text{eff\_CUT}}$ 2000 (km^2)	$m_{\text{eff\_CUT}}$ 2015 (km^2)	Change in $m_{\text{eff\_CUT}}$ 2015-2000 (km^2)	$m_{\text{eff\_CBC}}$ 2000 (km^2)	$m_{\text{eff\_CBC}}$ 2015 (km^2)	Change in $m_{\text{eff\_CBC}}$ 2015-2000 (km^2)	$m_{\text{eff\_CBC}}$– $m_{\text{eff\_CUT}}$ 2015 (km^2)
Study Area							
Black Bear	2334	711	– 1623	2729	821	– 1908	110
Fisher	–	–	–	–	–	–	–
Moose	2237	645	– 1592	2615	750	– 1865	104
White-Tailed Deer	2406	981	– 1425	2724	1145	– 1578	165
Québec Portion							
Black Bear	4848	1366	– 3482	5702	1603	– 4099	237
Fisher	–	–	–	–	–	–	–
Moose	4669	1252	– 3417	5487	1478	– 4009	226
White-Tailed Deer	4773	1945	– 2829	5459	2301	– 3158	357
Ontario Portion							
Black Bear	2.4	0.8	– 2	3.2	1.0	– 2	0.2
Fisher	–	–	–	–	–	–	–
Moose	2.0	0.1	– 2	2.7	0.2	– 2	0.2
White-Tailed Deer	7.8	5.8	– 2	8.7	6.2	– 3	0.4
New York Portion							
Black Bear	225	191	– 33	225	191	– 33	0.04
Fisher	–	–	–	–	–	–	–
Moose	189	160	– 29	189	160	– 29	0
White-Tailed Deer	478	195	– 283	479	195	– 284	0.1

Table 5 Changes in number of least-cost paths (LCPs), mean Euclidean distance (EucD, km), mean cost-weighted distance (CWD, weighted km), mean least-cost path length (LCP, km), and effective resistance (Ohms), for each species between 2000 and 2015

Species/Year	Number of LCPs	Mean EucD (km)	Mean CWD (weighted km)	Mean LCP (km)	Effective Resistance (Ohms)
Black Bear					
2000	14	42.5	1420.9	58.9	3525.0
2015	12	44.4	1683.6	60.8	3580.1
2015-2000	– 2	2	263	2	55
t-value		– 0.1	– 0.5	– 0.1	– 0.96
df		21	20	21	21
p-value		0.9	0.6	0.9	0.5
95% CI		- 29 - 25	- 1411 - 885	-43 - 39	-2138 - 2028
Cohen's d		0.06	0.2	0.04	0.02
Fisher					
2000	31	16.0	353.8	25.3	1620.3
2015	27	26.7	702.5	41.1	3022.4
2015-2000	– 4	11	349	16	1402
t-value		– 2.3	– 2.4	– 2.0	– 2.0
df		39	34	39	36
p-value		0.03	0.02	0.05	0.05
95% CI		-20 - -1	-645 - -52	-32 - 0.2	-2790 - -14
Cohen's d		0.6	0.7	0.5	0.6
Moose					
2000	16	38.0	1271.8	52.6	4378.0
2015	14	78.9	3226.3	110.5	8749.4
2015-2000	– 2	41	1954	58	4371
t-value		– 2.4	– 2.5	– 2.5	– 2
df		16	16	16	17
p-value		0.03	0.03	0.03	0.05
95% CI		-77 - -5	-3634 - -275	-107- -8	-8776 - 33
Cohen's d		0.9	0.9	0.9	0.8
White-Tailed Deer					
2000	69	11.4	352.3	15.5	1431.3
2015	111	14.7	460.9	20.9	1950.5
2015-2000	42	3	109	5	519
t-value		– 1.9	– 1.7	– 2.1	– 2.3
df		177	178	178	177
p-value		0.06	0.08	0.04	0.02
95% CI		-7 - 0.1	-232 - 15	-11 - -0.3	-961 - -77
Cohen's d		0.3	0.3	0.3	0.3

bear habitat patch decline was the result of indirect habitat loss due to limiting habitat constraints.

Moose and black bear require considerably large territories, ranging from 25 km^2 to 63 km^2 (Moose; Table S6), and 18 km^2 to 290 km^2 (Black bear; Table S6). In this study, we used an area of 75 km^2 (Moose) and 68 km^2 (Black bear) as the minimum habitat patch cut-off size for each species, where patches smaller than these cut-off sizes were not considered suitable moose and black bear habitat patches, respectively. As a result, small amounts of land transformation, between 2000 and 2015, caused habitat


A
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OHPs
SHPs
SSPs
MRC/County Boundaries
Coniferous Forest
Deciduous Forest
MIxed Forest
Grassland, Shrub, Moss & Herbaceous
Wetland
Agriculture
Barren Land
Development
Water
Pairwise Current Flow Density (amps/cell)
High
Low
0 25 50 100 km

◂**Fig. 4** Changes in pairwise current flow density within least-cost corridors between 2000 and 2015. A) Black bear habitat 2000, B) Black bear habitat 2015, C) Fisher habitat 2000, D) Fisher habitat 2015

patches with areas close to the minimum cut-off size, to fall below, and be eliminated as suitable or optimal moose and black bear habitat. We recognized the ecological importance of these smaller-sized patches, however, by identifying stepping-stone patches ≥ 10 km^2 (Table S7).

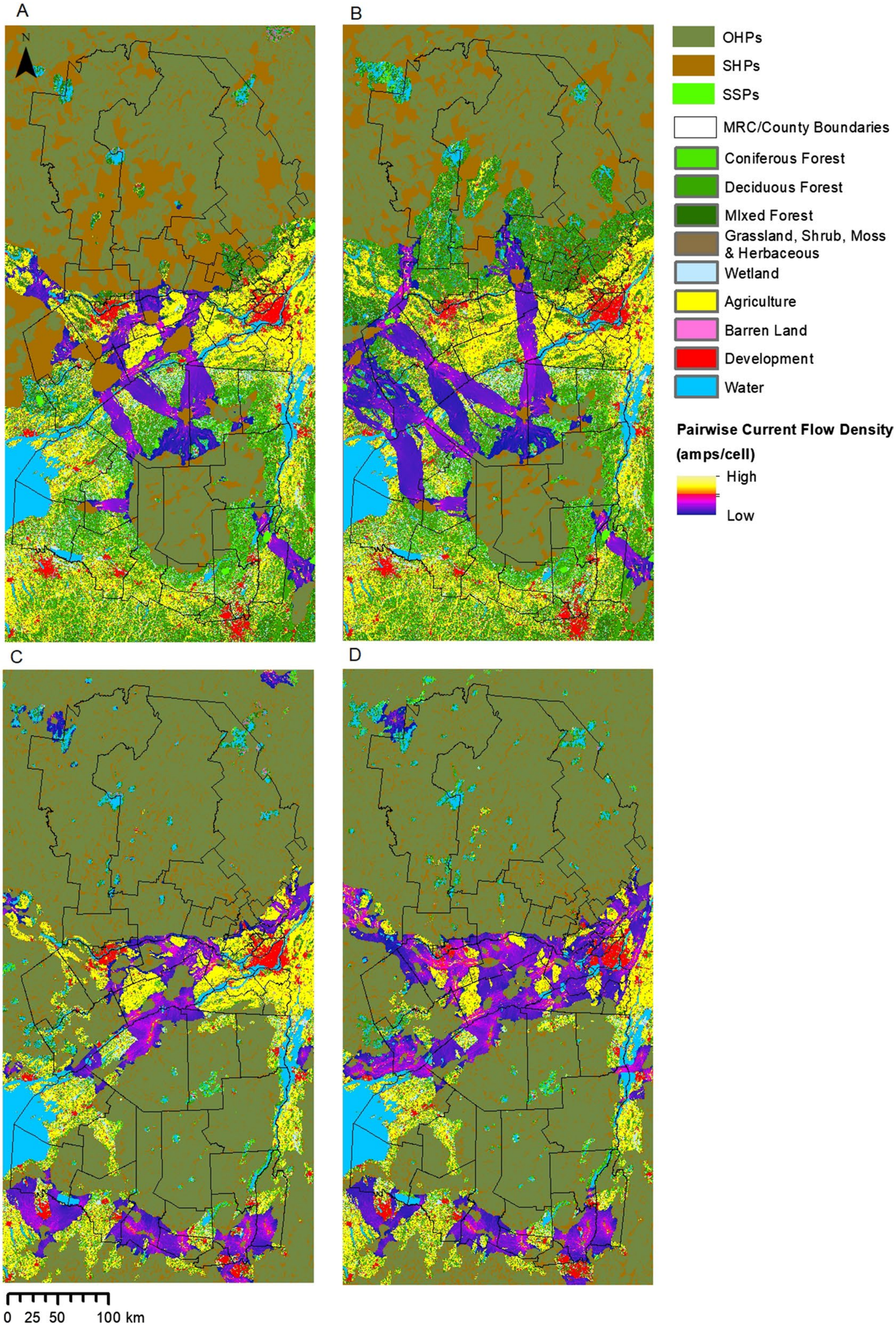
Moose and black bear also exhibit significant avoidance behavior of up to 1 km from human activity, including human presence, urban and industrial development, agriculture, and roads (Jalkotzy et al. 1997; Laurian et al. 2008). This disturbance distance, also referred to as the "zone of influence" and the "road effect zone", cause avoidance of, or displacement from, preferred habitats due to disturbances such as noise, light, pollutants, habitat degradation and other anthropogenic alterations (Forman and Alexander 1998; Benítez-López et al. 2010; Polfus et al., 2011). Between 2000 and 2018, the length of the road network within the Québec portion of the study area increased by 7684 km (16%), with primary road length increasing by 29%; and in the Ontario portion, the length of the road network increased by 2380 km (12%), with primary road length increasing by 13% (Cole et al. 2023). With a road effect zone of up-to 1 km, each new kilometer of road added to the landscape has the potential to create a 2 km^2 area of degraded moose and/or black bear habitat.

These direct and indirect habitat losses can be seen in the southern portion of the Québec megapatch and the entire Ontario portion in 2015 as compared to 2000 (Fig. 2; Table 3) and have the potential to severely influence long-term transboundary connectivity within the A2L. Consequently, moose populations are declining in the southern portions of Québec and Ontario (Environmental Commissioner of Ontario 2016; Québec 2022), and the situation is being exacerbated by climate change. As temperatures rise, white-tailed deer populations are expanding poleward and sharing more landscapes with moose (Kennedy-Slaney et al. 2018). White-tailed deer are a host to many parasite species including winter ticks (*Dermacentor albipictus*), liver fluke (*Fascioloides magna*), and meningeal worm (*Parelaphostrongylus tenuis*), that can be transmitted to moose with detrimental and sometimes lethal effects (Murray et al. 2006).

Species-specific fragmentation

Anthropogenic land transformation between 2000 and 2015 also caused substantial habitat fragmentation for the four focal species within the A2L. The greatest suitable and optimal habitat patch fragmentation occurred for moose, with a SHP $m_{\mathrm{eff\_CUT}}$ size reduction of 46%, and a SHP $m_{\mathrm{eff\_CBC}}$ size reduction of 42%, and an OHP $m_{\mathrm{eff\_CUT}}$ size, and a OHP $m_{\mathrm{eff\_CBC}}$ size reduction of 71% (Table 4). This was followed by black bear with a SHP $m_{\mathrm{eff\_CUT}}$ size reduction of 21%, and a SHP $m_{\mathrm{eff\_CBC}}$ size reduction of 20%, and an OHP $m_{\mathrm{eff\_CUT}}$ size, and an OHP $m_{\mathrm{eff\_CBC}}$ size reduction of 70% (Table 4). Mammals with large area requirements are especially vulnerable to the effects of fragmentation (Woodroffe and Ginsberg 1998). As new roads, infrastructure, agriculture, and development are added to the landscape, suitable and optimal habitat patches are increasingly fragmented, producing smaller and more isolated patches; with some being reduced below the species-specific minimum habitat patch size, and others being lost altogether. Future road development plans should be evaluated for their exacerbating effects on habitat amount and fragmentation in this already degraded and sensitive landscape. One solution would be to decrease the overall density of the road network. Road density can be reduced through several measures, including (1) closing low-traffic roads, (2) upgrading and widening existing roads over construction of new ones, and (3) bundling roads and other transportation infrastructure close together (i.e., constructing roads and railways in parallel) (Jaeger et al. 2006, 2011). To reduce the barrier effect of these strategies, wildlife crossing structures and fencing can be placed strategically along the widened/bundled infrastructures allowing animals access to both sides and maintaining connectivity (Rytwinski et al. 2016).

Many suitable and optimal habitat patches cross political borders and their land area is thus shared by multiple MRCs/counties (Figs. 2 and 3). However, the number of patches and the amount of patch area shared between MRCs/counties considerably decreased between 2000 and 2015 (Tables S10-S16).


A
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OHPs
SHPs
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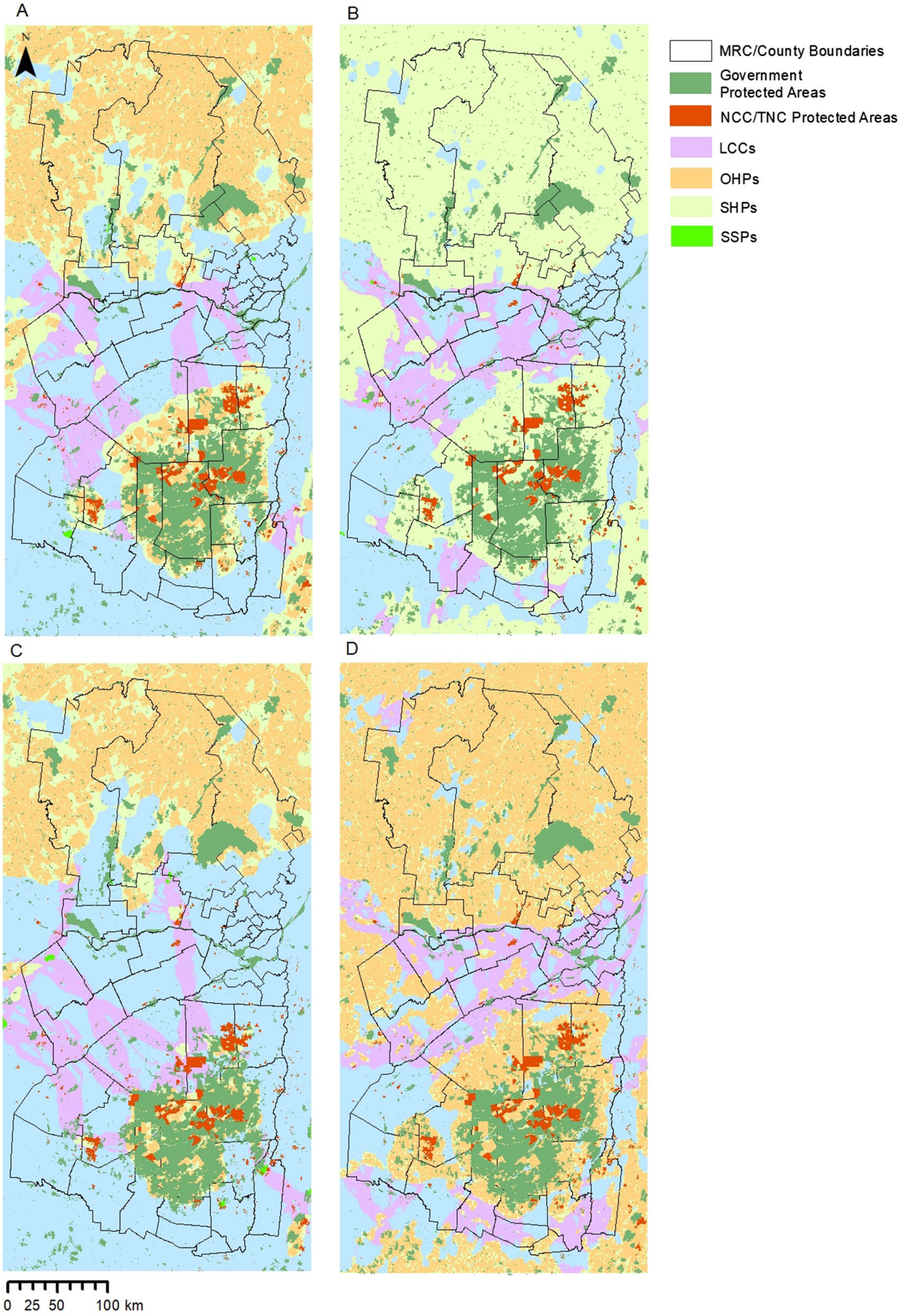
MRC/County Boundaries
Coniferous Forest
Deciduous Forest
Mixed Forest
Grassland, Shrub, Moss & Herbaceous
Wetland
Agriculture
Barren Land
Development
Water
Pairwise Current Flow Density (amps/cell)
High
Low
0 25 50 100 km

◂**Fig. 5** Changes in pairwise current flow density within least-cost corridors between 2000 and 2015. A) Moose habitat 2000, B) Moose habitat 2015, C) White-tailed deer habitat 2000, D) White-tailed deer habitat 2015

Because of the importance of these transboundary patches for species-specific habitat amount and connectivity, and their disproportionate risk of being reduced or fragmented, we recommend collaborative conservation strategies between MRCs/counties to ensure that these patches continue to serve as vital habitats for a wide range of species within the A2L.

Table 6 Amount of suitable habitat patch (SHP) area, optimal habitat patch (OHP) area, and least-cost corridor (LCC) area protected in 2015, at the scale of the study area and each provincial/state portion. Area = total area of patches; Protected = total area of patches protected; Number of PAs = number of Protected Areas; Mean PA Size = Mean Protected Area size; and Proportion = Proportion of total area of patches protected

Location/Species	SHP area (km^2)	SHP area protected (km^2)	Proportion of SHP area Protected (%)	OHP area (km^2)	OHP area protected (km^2)	Proportion of OHP area Protected (%)	LCC area (km^2)	LCC area protected (km^2)	Proportion of LCC area Protected (%)
Study Area									
Black bear	68,796	17,817	26	41,975	13,620	32	15,630	1488	10
Fisher	84,555	18,820	22	–	–	–	14,598	438	3
Moose	47,424	13,786	29	33,884	11,190	33	16,249	2346	14
White-tailed deer	86,148	18,176	21	73,979	17,048	23	28,666	1246	4
Québec Portion									
Black bear	41,724	3972	10	26,637	2801	11	3055	559	18
Fisher	48,858	4410	9	–	–	–	2462	203	8
Moose	33,902	3368	10	23,648	2539	11	1719	246	14
White-tailed deer	48,488	4285	9	41,461	3819	9	9012	589	7
Ontario Portion									
Black bear	1256	3	0.2	144	0	0	5713	140	2
Fisher	2447	4.6	0.2	–	–	–	7777	158	2
Moose	174	0	0	39	0	0	5433	94	2
White-tailed deer	4964	17	0.3	3991	13	0.3	9778	305	3
New York Portion									
Black bear	25,816	13,842	54	15,194	10,819	71	6861	790	12
Fisher	33,250	14,405	43	–	–	–	4360	77	2
Moose	13,348	10,418	78	10,197	8651	85	9097	2007	22
White-tailed deer	32,696	13,874	42	28,527	13,216	46	9876	352	4


A
N
B
C
D
MRC/County Boundaries
Government Protected Areas
NCC/TNC Protected Areas
LCCs
OHPs
SHPs
SSPs
0 25 50 100 km

◂**Fig. 6** Suitable habitat patches (SHPs), optimal habitat patches (OHPs), stepping-stone patches (SSPs), and least-cost corridors (LCCs) in 2015, with Protected Areas superimposed. (**A**) Black bear habitat, (**B**) Fisher habitat, (**C**) Moose habitat, (**D**) White-tailed deer habitat. NCC/TNC = Nature Conservancy of Canada/The Nature Conservancy

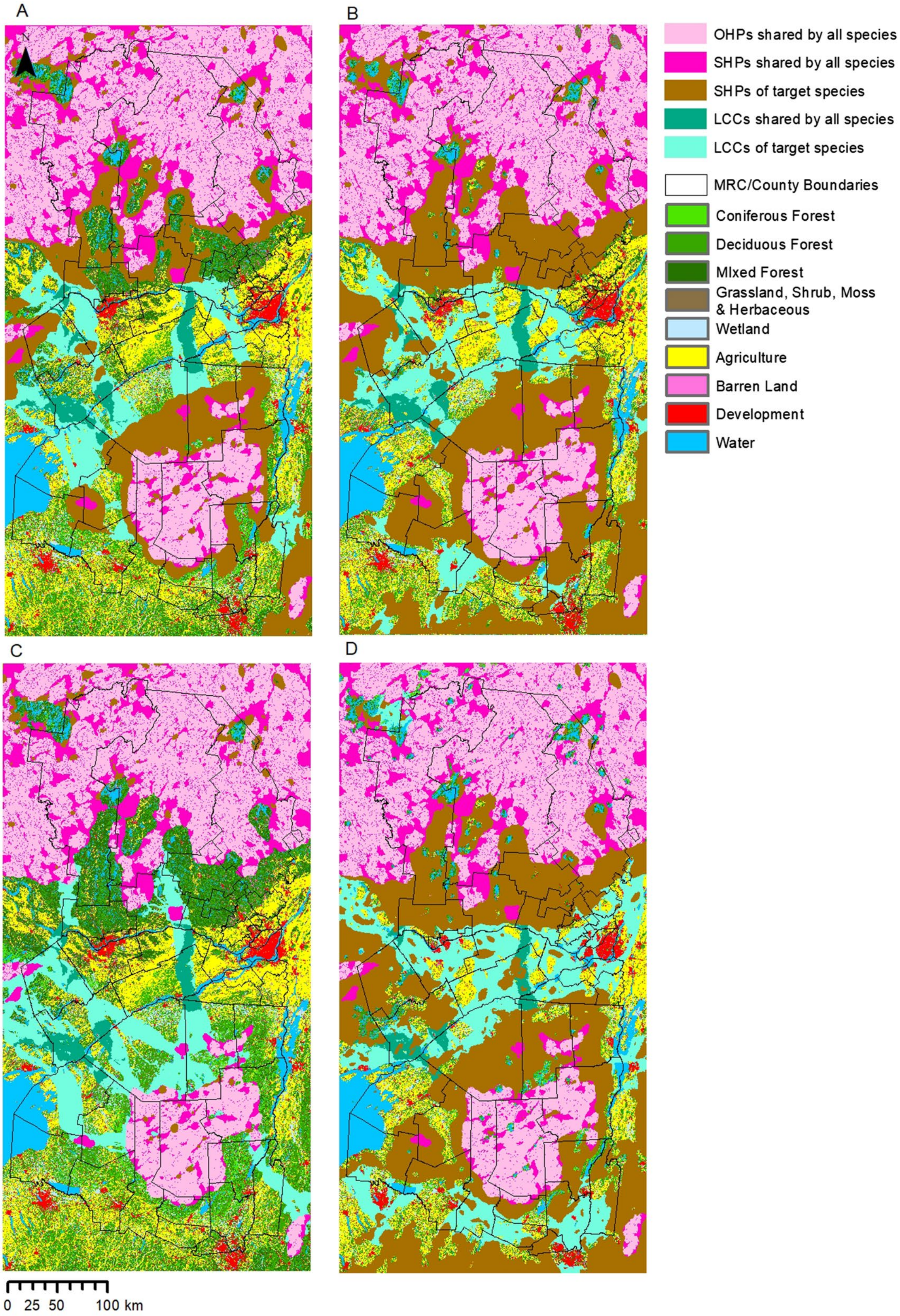
Species-specific connectivity

Within the study area, inter-patch connectivity decreased for each species, as measured by increases in mean Euclidean distance, mean least-cost path, mean cost-weighted distance, and effective resistance (Table 5). Euclidean distance increased because habitat patches were either reduced in size, fragmented into multiple smaller patches, or completely lost due to land conversion which resulted in greater distances between patches in 2015 (Table 5, Figs. 2 and 3). Whereas increases in least-cost path, cost-weighted distance, and effective resistance were due to a combination of land conversion reducing suitable habitat values (i.e., increasing resistance values) in the matrix and the increased distance between patches (Table 5, Figs. 2 and 3). Accordingly, each species must now travel farther between suitable habitat patches and the cost of travelling these distances is higher. This could potentially translate into a reduction in the probability of successful dispersals. Inter-patch and intra-patch connectivity are essential for ecosystem functioning, and a landscape-wide decrease in functional connectivity could have severe negative consequences on key ecosystem processes such as seed dispersal, food web interactions, metapopulation dynamics, and disease transmission (Gonzalez et al. 1998; Bauer and Hoye 2014; Tucker et al. 2018; Plowright et al. 2021).

Dispersal movements between the three provincial/state portions requires the crossing of at least one of two large rivers, the Ottawa River that separates the Québec portion from the Ontario portion, and the St. Lawrence River that separates the Ontario portion from the New York portion (Fig. 1). Although both rivers have swift-moving currents, sections of the Ottawa River between Montréal and Ottawa, and sections of the St. Lawrence River between Montréal and Lake Ontario freeze-over 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, there have been many sightings/reports of animal movement across the rivers. Alice the moose, the Algonquin-to-Adirondack Collaborative's animal inspiration was a female moose collared and released into the Adirondack Park, New York in 1998. Alice left the Adirondack Park in 2000, and after crossing both the St. Lawrence River and highway 401 in Ontario, ended up in Algonquin Provincial Park in Ontario (A2A 2023). Genetic analysis confirms that fishers have been crossing the St. Lawrence River from the Adirondack region to recolonize eastern Ontario since the 1950s (Carr et al. 2007); and black bear have been reported swimming across the rivers, whereas white-tailed deer have been spotted crossing the ice during winter (Ottawa Citizen 2020, 2022). Other large mammals such as lynx (Koen et al. 2015) and eastern wolves (McAlpine et al. 2015) have also been reported crossing the rivers. Nevertheless, while both rivers are almost certainly a major deterrent to long-distance dispersal, they are not complete barriers to animal movement. We recommend further detailed study to identify priority locations where these focal species are crossing the Ottawa and St. Lawrence rivers within the LCCs, and where applicable, the expansion and protection of these sites.

Pinch-points represent narrow sections within LCCs where movement is restricted due to natural or anthropogenic landscape features and alternative pathways are limited (McRae and Shah 2011; Pelletier et al. 2014). Pinch points can be critical for both facilitating movement between habitat patches as well as contributing to the long-term maintenance of functional connectivity throughout the linkage (McRae et al. 2008). We identified multiple pinch-points within LCCs where movement could become increasingly limited for each species (Figs. 4, 5, S5 and S6). These pinch-point locations should be prioritized for both conservation and restoration interventions: (1) to ensure that additional habitat loss does not further restrict the pinch-point, and (2) to decrease the constrictive severity of the pinch-point and increase its connectivity potential. In addition, pinch-points that intersect primary and secondary roads should be further evaluated for their potential as locations for wildlife crossing structures and fencing (Nussey and Noseworthy 2018; Spanowicz et al. 2020).

SSPs are small habitat patches that offer refuge to individuals as they travel through the matrix between SHPs (Baum et al. 2004). These small patches can disproportionately contribute to species-specific connectivity when distances between SHPs are greater


A
B
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OHPs shared by all species
SHPs shared by all species
SHPs of target species
LCCs shared by all species
LCCs of target species
MRC/County Boundaries
Coniferous Forest
Deciduous Forest
MIxed Forest
Grassland, Shrub, Moss & Herbaceous
Wetland
Agriculture
Barren Land
Development
Water
0 25 50 100 km

◂**Fig. 7** Suitable habitat patches (SHPs) and least-cost corridors (LCCs) in 2015, with SHPs, optimal habitat patches (OHPs) and LCCs shared by all species in 2015 superimposed. (**A**) Black bear habitat, (**B**) Fisher habitat, (**C**) Moose habitat, (**D**) White-tailed deer habitat

than the maximum dispersal distance of a species (Dutta et al. 2016). We located several SSPs within LCCs that could offer shelter and resources to individuals as they travel through the LCCs (Figs. 2 and 3). These patches should be considered a high priority for conservation and ecological restoration as they have the potential to facilitate movement between habitat patches and contribute to maintaining connectivity throughout the A2L.

Habitat patches and corridors under protection

In 2015, only 2.2% of the Ontario portion was protected, whereas 8.7% of the Québec portion, and 28% of the New York portion was protected. This sizable protection of 14,914 km^2 in the New York portion includes 54% SHP, 71% OHP, and 12% LCC area protected (black bear); 43% SHP and 2% LCC area protected (fisher); 78% SHP, 85% OHP, and 22% LCC area protected (moose); and 42% SHP, 46% OHP, and 4% LCC area protected (white-tailed deer), and is the primary reason for the observed stability of habitat amount and fragmentation in this region between 2000 and 2015 (Table 6, Fig. 6). Consequently, to ensure functional connectivity between the Québec and Adirondack mega-patches, increasing protection while synchronously increasing habitat restoration in the southern Québec and Ontario portions (Currie et al. 2023) will be crucial to reduce or eliminate further habitat loss and fragmentation.

Protected areas have been an important tool for the conservation of biodiversity in North America. However, many protected areas are simply not large enough to support viable populations of species with large home ranges nor do they include the range of species, processes, and habitats necessary to fully conserve ecosystem integrity and biodiversity (Boyd et al. 2008; Pimm et al. 2014). For example, in 2015, 20,389 km^2 (16%) of the study area was under protection. This was made up of 1314 sites protected by the Canadian/U.S. Government, and 1278 sites protected by Nature Conservancy of Canada/The Nature Conservancy (Fig. 6). However, the average Canadian/U.S. Government protected area size was 13 km^2, and the average Nature Conservancy of Canada/The Nature Conservancy protected area size was 2 km^2, which are considerably below the average home range size of black bear (101 km^2), moose (42 km^2), fisher (19 km^2), and many other large-ranging species.

The average proportion of SHP area (25%) was lower than the average OHP area protected (29%). This was due to the fact that SHP area contains non-habitat land-cover classes such as roads, development, and agriculture lands which would not be included in protected areas, whereas OHPs only contain natural habitat types such as forests, grasslands and wetlands. The average proportions of SHP and OHP area protected, however, were both higher than the average proportion of LCC area protected (8%) (Table 6). This result highlights that to achieve long-term transboundary connectivity for large ranging species, active measures should be taken to not only create new and expand existing protected areas within the A2L, but also restore, maintain, enhance, and protect connectivity corridors between them (Hilty et al. 2020).

While protected area conservation has been around since the founding of Yellowstone National Park in 1872, conservation of connectivity corridors is a relatively new idea (National Park Service 2022). In April 2022, Parks Canada launched the “National Program for Ecological Corridors”, the first of its kind in Canada. The program will invest $60.6 million over five years to help support other jurisdictions and organizations develop better ecological connections between protected areas (Government of Canada 2022). In the USA, nearly 50 corridor conservation policies have been released from different levels of government since 2007 (Breuer et al. 2022; Conservation Corridor 2022). One of the most significant is the Wildlife Corridors Conservation Act of 2019, which establishes a “National Wildlife Corridors System” to designate corridors on federal public lands as well as provide funding for states, tribes, and other entities to protect wildlife corridors on non-federal lands (116th Congress, 2019–2020). Protection of connectivity corridors will require cooperation at the MRC/county, provincial/state and transboundary levels to develop an ecological network-based conservation and restoration strategy. Such an approach should comprise of a system of protected areas interconnected by a network of protected ecological corridors that would enhance ecosystem integrity, biodiversity, and connectivity (Hilty et al. 2020). Such harmonized efforts will improve the protection of shared conservation features (i.e., species, ecosystems, and natural resources), as well as reduce the financial costs for each cooperating member (Kark et al. 2015); and managing transboundary conservation for these umbrella species will simultaneously conserve and restore connectivity for a variety of other species that utilize the A2L linkage.

Conclusion

Our results highlight the degree to which anthropogenic land transformation has impacted species-specific habitat amount, fragmentation, and connectivity in the A2L transboundary wildlife linkage between 2000 and 2015. Suitable and optimal habitat patch area decreased for each species with moose suitable and optimal habitat patch area declining by 26% and 17%, respectively. This was followed by black bear with SHP area losses of 11%, and OHP area losses of 9% (Table 3). Habitat fragmentation increased for each species with moose experiencing an OHP effective mesh size decrease of 71% ($m_{\mathrm{eff\_CUT}}$ and $m_{\mathrm{eff\_CBC}}$); and black bear experiencing an OHP effective mesh size decrease of 70% ($m_{\mathrm{eff\_CUT}}$ and $m_{\mathrm{eff\_CBC}}$). Inter-patch connectivity also decreased significantly for fisher, moose, and white-tailed deer (Table 5). Consequently, to achieve long-term functionality of the A2L, collaborative and coordinated measures will be necessary to preserve the integrity of the Québec mega-patch, restore extensive habitat in eastern Ontario, and reestablish or maintain connectivity throughout the linkage. Left unaddressed, continued anthropogenic land transformation is likely to have detrimental effects on the ability of the A2L to function as a transboundary wildlife linkage.

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Author contributions JRC and JAGJ contributed to the study conception and design. JRC, JAG, EJP, AK and JAGJ contributed to the methodology. Material preparation, data collection and analysis were performed by JRC. Fisher data collection was performed by ELK. The first draft of the manuscript was written by JRC, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Declarations

Conflict of interest All authors agree that there are no conflicts of interest.

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