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RESEARCH ARTICLE

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

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Abstract
Context Although many species have transboundary geographic ranges, most conservation initiatives do not cross political boundaries. The landscape between the Adirondack Mountains in New York and the Laurentian Mountains in Québec includes one of three potential north–south transboundary wildlife movement linkages that connect wilderness areas in northeastern USA and southeastern Canada. Although this region still maintains habitats of high ecological integrity and biodiversity, increasing land-cover changes and fragmentation are putting landscape connectivity at risk.
Objectives We measured changes in landscape composition and configuration within the Adirondack-to-Laurentians transboundary wildlife linkage (A2L) between 1992 and 2018 to identify priority areas for conservation and restoration.
Methods Land-cover change was calculated by measuring area and proportion of land-cover classes, and landscape fragmentation was determined by measuring patch number, mean patch size, the effective mesh size, and road density, at three spatial scales and four fragmentation geometries (i.e., combinations of fragmenting elements).
Results Extensive changes in land-cover and landscape fragmentation occurred within the A2L between 1992 and 2018. Forest areas declined by 1363 km^2 and wetlands declined by 1365 km^2 (69%). This was most pronounced in the Québec portion of the A2L where wetland areas declined by 872 km^2 (88.5%). Forest areas in the Québec portion experienced the greatest amount of fragmentation with a $m_{\mathrm{eff\_CUT}}$ decline of 3262.5 km^2 (58.5%) since 2000.
Conclusions Coordinated and collaborative transboundary conservation efforts help improve protection of species with transboundary ranges. Monitoring of land-cover changes and landscape fragmentation is an effective way to identify priority areas for conservation and support transboundary coordination. Strengthening conservation strategies that enhance landscape connectivity and protect ecosystems at the local level will help achieve post-2020 biodiversity commitments at the national and transboundary levels.

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Keywords Land-cover change · Landscape fragmentation · Patch number · Mean patch size · Effective mesh size · Road density · Transborder · Post-2020 Biodiversity Framework

Introduction

Land conversion from natural areas to human modified uses is the leading cause of biodiversity loss worldwide (Hooke et al. 2012). Humans have altered greater than 50% of the Earth's terrestrial surface (77% excluding Antarctica) (Hooke et al. 2012; Allen et al. 2017; Watson et al. 2018). Land conversion results in habitat loss and fragmentation (i.e., "where a large expanse of habitat is transformed into a number of smaller patches of smaller total area, isolated from each other by a matrix of habitats unlike the original"; Wilcove et al. 1986), which contributes to long-term changes in landscape structure and function (Lindenmayer and Fischer 2013; Haddad et al. 2015). Landscape structure consists of landscape composition (the amount of each land-cover type present in the landscape) and landscape configuration (the spatial arrangement of land-cover elements) (Turner et al. 2001). Habitat loss and fragmentation then relate to both changes in landscape composition and configuration (Fletcher et al. 2016). Roads are a major contributor to habitat loss and fragmentation (van der Ree et al. 2011). The global road network spans over 40 million km (Dulac 2013). Since 2000 this network has grown by approximately 12 million km, and it is expected to continue to grow by more than 35% by 2050 (Dulac 2013).

Movement is crucial for long-term viability of wildlife populations including daily foraging, dispersal, migration, and range shifts in response to climate change (Ament et al. 2014). 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 (Ewers and Didham 2006; Traill et al. 2010; McGuire et al. 2016; Blazquez-Cabrera et al. 2016). Animal movements and many other ecological processes require connectivity ("the degree to which the landscape facilitates or impedes movement among resource patches"; Taylor et al. 1993). Connectivity is subdivided into two main branches in terms of its measurement: "Structural connectivity" refers to the arrangement, permeability, and contiguity of land-cover elements (Lindenmayer and Fischer 2013; Hilty et al. 2020), whereas "functional connectivity" is species-specific and is described as the product of both landscape structure and the responses of a species to that structure (i.e., the ability of a species to move between resource patches within a landscape) (Meiklejohn et al. 2009; Lindenmayer and Fischer 2013). In heterogeneous landscapes, connectivity is attained through wildlife corridors and linkages. Wildlife corridors facilitate the movement of species between habitat patches, whereas wildlife linkages promote the movement of multiple species and ecological processes within a network of habitat patches across a large region (Beier et al. 2008; Meiklejohn et al. 2009).

Globally, 56% of all terrestrial mammals, 27% of all amphibians, and 69% of all birds, as well as 21% of all threatened species within these taxa, have transboundary geographic ranges (Mason et al. 2020). Although geographic ranges span political borders, conservation usually does not, making conservation outcomes contingent on similar decisions being made across multiple provincial/state or national boundaries (Kark et al. 2015; Mason et al. 2020). 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 Convention on Biological Diversity (CBD) and the Convention on the Conservation of Migratory Species of Wild Animals (CMS) now promote the requirement for ecological connectivity across species ranges and national borders (Trouwborst 2012; CMS 2019), and transboundary conservation is currently recognized as a key component in the post-2020 global biodiversity framework discussions (SCBD 2018; Díaz et al. 2020; Mason et al. 2020). The International Union for the Conservation of Nature (IUCN) - World Commission on Protected Areas (WCPA) recognizes three types of transboundary conservation (Vasilijević et al. 2015): type 1. Transboundary Protected Area (i.e., protected areas ecologically connected across one or more international boundaries; type 2. Transboundary Conservation Landscape and/or Seascape (i.e., ecologically connected areas that include both protected areas and multiple resource use areas across one or more international boundaries); and type 3. Transboundary

Migration Conservation Area (i.e., wildlife habitats in two or more countries that are necessary to sustain populations of migratory species). Subsequently, a special designation of Park for Peace (i.e., protected areas established for the conservation of biodiversity, cultural resources, and regional peace and stability; Sandwith et al 2001) can be applied to each of the three types (Vasilijević et al. 2015).

The landscape between the Adirondack Mountains in New York State, USA, and the Laurentian Mountains in Québec, Canada, (hereafter, referred to as the A2L) is one of three potential north–south transboundary wildlife movement linkages that connect natural areas in Northeastern USA with Southeastern Canada. This region boasts a wide variety of habitats that still maintain a high degree of ecological integrity and are rich in biodiversity (Tardif et al. 2005). However, land conversion due to urban and industrial development, agriculture, roads, and other infrastructure, have led to the current mosaic that includes a central band of intensive agricultural and urban areas running parallel to the St Lawrence and Ottawa rivers, while forest fragments dominate the northern and southern domains (Pan et al. 1999; Bélanger and Grenier 2002; Brisson and Bouchard 2003).

In this study we measure changes in landscape structure within the A2L transboundary wildlife linkage to identify priority areas for conservation and ecological restoration at three spatial scales (the complete study area; the three provincial/state portions; and the 43 municipalités régionales de comté (MRCs)/counties that reside within the transboundary wildlife linkage). To evaluate changes in landscape composition, we calculated and compared the area and proportion of five grouped land-cover themes between 1992 and 2018. To assess changes in landscape configuration (i.e., landscape fragmentation and structural connectivity), we measured and compared patch number, mean patch size, the effective mesh size, and road density, between 2000 and 2018. Calculating landscape fragmentation and structural connectivity requires the specification of the natural and anthropogenic landscape elements that cause fragmentation (i.e., roads, development, agriculture, waterbodies, etc.). The specific choices of these fragmenting elements define what is called the "fragmentation geometry" (Girvetz et al. 2008). In this study we analyze and compare four different fragmentation geometries, each representing different land-cover scenarios.

We asked the following research questions: (1) To what degree have land-cover change and landscape fragmentation occurred within the A2L transboundary wildlife linkage? (2) Are there spatiotemporal differences in land-cover change between grouped land-cover themes, and between scales? (3) Are there spatiotemporal differences in landscape fragmentation between the four fragmentation geometries, and between scales?

Methods

Study area

The A2L spans an area of over 127,000 km^2 from the Adirondack Mountains in New York, USA to the Laurentian Mountains in Québec, Canada (Fig. 1). This region is within the northern temperate ecozone which is home to 440 vertebrate species and 1600 vascular plant species (Tardif et al. 2005). Its geology is comprised of Canadian Shield to the north and St. Laurence Platform to the south (Tardif et al. 2005). The highest peak is Mount-Marcy in the Adirondacks at 1629 m above sea level. The three bioclimatic domains within the A2L region include the maple/bitternut hickory which has the mildest climate and is made up of diverse forests containing butternut and shagbark hickories, hackberries, black maple, swamp white oak, rock elm, and pitch pine (Tardif et al. 2005). The maple/basswood domain further to the north and east contains forests of sugar maple, American basswood, white ash, American hophornbeam, and butternut (Tardif et al. 2005). The most northern is the maple/yellow birch domain. It is the least diverse and includes yellow birch, sugar maple, American basswood, American hophornbeam, American beech, northern red oak, and eastern hemlock (Tardif et al. 2005). As of 2016, the area was home to over 6.8 million people (54 per km^2), an increase of 1.1 million people since 1990 (45 per km^2) (Statistics Canada 1991; 2016; US Census bureau 1990; 2016).

Data collection

We used four, 300 m resolution, global land-cover maps from the European Space Agency Climate

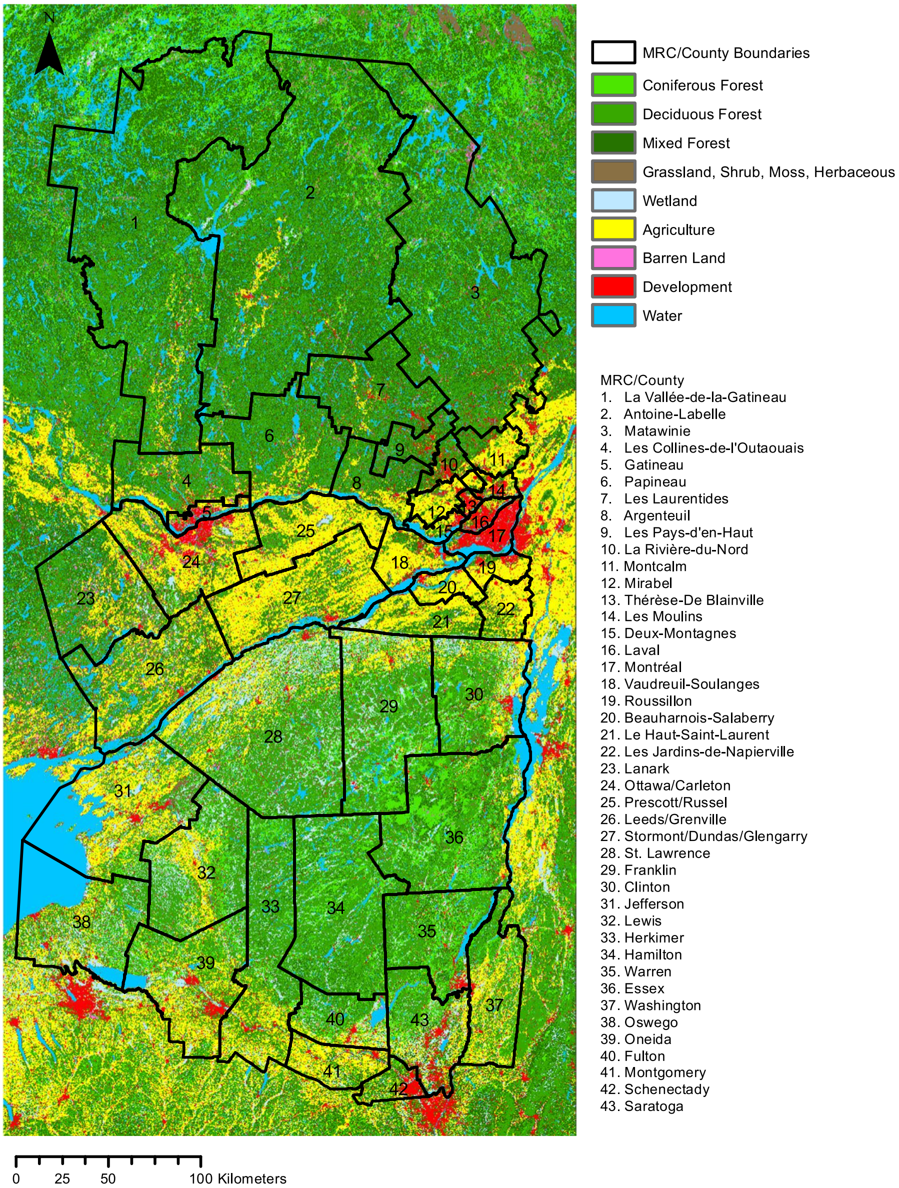

Fig. 1 Land-cover map of the Adirondack-to-Laurentians (A2L) study area overlaid with municipalité régionale de comté (MRC)/county boundaries. MRC/county names are numbered and correspond to the numbers on the map

Change Initiative Land-Cover Project (ESA-CCI-LC). Each map contained 24 consistent land-cover classes based on the United Nations (UN) Land-Cover Classification System (LCCS) (Table 1 and S9). The ESA-CCI-LC dataset had higher classification accuracy (~73.9–74.2%) and stability across timepoints than any other existing dataset (i.e., MODIS annual series from 2001 to 2020—500 m resolution, and GLASS Products annual series from 1982 to 2018—5 km resolution; Sun et al. 2022). The primary limitation of the dataset was some inaccuracy in land-cover classification which varied according to global region. Most classification errors were between classes within the same theme (i.e., broad-leaved forest vs. needle-leaved forest) (Santoro et al. 2017). However, North America was in a high-quality region, and we also grouped classes into themes (i.e., Forests, Non-Forest Vegetation, Wetlands, etc.) which would have considerably reduced any prevailing classification errors. All land-cover classes were subject to the resolution of the ESA-CCL-LC dataset. For example, a cell (300 m × 300 m) was classified as water if the cell contained greater than 50% water (Lamarche et al. 2017). Nevertheless, there are patches smaller than

Table 1 Map categories included in each of the (**A**) "Land-Cover Themes" and (**B**) "Fragmentation Geometries"

(A)

Land-Cover Class/Element	Natural and Anthropogenic Fragmentation Elements	Forests	Non-Forest Vegetation	Wetlands	Combined Habitats
Development	✓				
Bare areas	✓				
Waterbodies	✓				
Agricultural land	✓				
Forests		✓			✓
Grassland			✓		✓
Wetlands				✓	✓

(B)

Land-Cover Class/Element	FG-Forests	FG-Non-Forest Vegetation	FG-Wetlands	FG-Combined Habitats
Development	✓	✓	✓	✓
Bare areas	✓	✓	✓	✓
Waterbodies	✓	✓	✓	✓
Agricultural land	✓	✓	✓	✓
Forests			✓	
Grassland	✓	✓	✓	
Wetlands	✓	✓		
Primary roads (10 m buffer)	✓	✓	✓	✓
Secondary roads (5 m buffer)	✓	✓	✓	✓
Tertiary roads (3 m buffer)	✓	✓	✓	✓

Agricultural land included the land-cover classes: cropland, rainfed; cropland, rainfed, herbaceous cover; mosaic cropland (>50%) / natural vegetation (tree, shrub, herbaceous cover) (<50%); mosaic natural vegetation (tree, shrub, herbaceous cover) (>50%) / cropland (<50%). Forests included the land-cover classes: broad-leaved evergreen closed to open tree / broad-leaved semi-deciduous closed to open trees; tree cover, broad-leaved, deciduous, closed to open (>15%); tree cover, broad-leaved, deciduous, closed (>40%); tree cover, broadleaved, deciduous, open (15-40%); tree cover, needle-leaved, evergreen, closed to open (>15%); tree cover, needle-leaved, evergreen, closed (>40%; tree cover, needle-leaved, evergreen, open (15-40%); tree cover, needle-leaved, deciduous, closed to open (>15%); tree cover, mixed-leaf type (broad-leaved and needle leaved); mosaic tree and shrub (>50%) / herbaceous cover (<50%). Grassland, shrub, moss, herbaceous cover included the land-cover classes: mosaic herbaceous cover; shrubland; grassland; lichens and mosses; sparse vegetation (tree, shrub, herbaceous cover) (<15%). Wetlands included the land-cover classes: tree cover, flooded, fresh or brackish water; shrub or herbaceous cover, flooded, fresh/saline/brackish water

(✓) = included

90,000 m^2 in the fragmentation analysis because the surface area of the roads and their buffers were erased from the vectorized land-cover maps prior to the fragmentation calculations (see *Creating fragmentation geometry patches*).

The ESA-CCI-LC maps did not contain a separate road category. To complete the landscape fragmentation analysis, a set of compatible road-network maps were required for Québec, Ontario, and New York. Road maps for Québec and Ontario were obtained from DMTI Spatial Inc., for the years 2000, 2010, and 2018. Road maps for New York State were obtained from New York State Information Technology Services for 2010 and 2018. Due to a lack of digital road maps for 1992 and inconsistencies in the maps for 2000, the landscape fragmentation analysis was performed for 2000, 2010, and 2018 in the Québec and Ontario portions, and for 2010 and 2018 in the New York portion. Road categories were reclassified into: (1) Primary Roads; (2) Secondary Roads; and (3) Tertiary Roads (Table S1).

The railway network was not considered in the landscape fragmentation analysis because compatible data for all provincial/state portions and timepoints were unavailable. However, railway density, traffic, and speed within the study area are considerably low, especially compared to European and Asian equivalents. Many railway tracks run parallel to other natural and anthropogenic fragmentation elements such as roads, development, waterbodies, barren areas, and agriculture, which would capture their fragmentation by proximity.

We analyzed land-cover change and landscape fragmentation at three spatial scales (study area, provincial/state portion, MRC/county). We utilized these distinct hierarchical scales to: (1) visualize how land-cover change and landscape fragmentation were spatiotemporally distributed; (2) allow for the direct comparison and ranking between provincial/state portions and MRCs/counties; (3) determine priority areas for conservation and/or ecological restoration; and (4) provide multiple levels of governance with the information necessary to develop coordinated and collaborative local, regional, and transboundary conservation plans.

Land-cover change

Land-cover classes were grouped into five themes: (1) "Natural and Anthropogenic Fragmentation Elements", which included development, barren areas, waterbodies and agricultural land; (2) "Forests", which contained all forest types; (3) "Non-Forest Vegetation", which included all grassland, shrub, moss, and herbaceous land-cover types; (4) "Wetlands", which included all wetland types; and (5) "Combined Habitats", which included the combined themes of "Forests", "Non-Forest Vegetation", and "Wetlands" (Table 1and S9).

To quantify land-cover change over time, we calculated and compared the area and proportion of the five grouped land-cover themes between 1992, 2000, 2010, and 2018. Land-cover area was calculated by multiplying the cell count of each land-cover class (within the boundaries of the reporting unit; see below) by the area of a single cell (90,000 m^2), and then dividing by 1,000,000 m^2/km^2 to convert to km^2. Land-cover proportion was calculated by dividing the land-cover area by the total area of the reporting unit, and then multiplying by 100%, to convert to percent.

Landscape fragmentation

Fragmentation geometries and reporting units

A fragmentation geometry specifies all the land-cover classes and elements that will be considered barriers in the fragmentation analysis. Including more barriers in a fragmentation geometry will increase the degree of fragmentation (Roch and Jaeger 2014). The justification for including, or not including, a specific barrier depends on the type of fragmentation being analyzed. For instance, if the goal is to quantify the overall degree of "forest" fragmentation, then every land-cover type that is not "forest" will be included as a barrier (Roch and Jaeger 2014).

The spatial boundaries in which land-cover change and the degree of landscape fragmentation are calculated are referred to as "reporting units" (Girvetz et al. 2008). Reporting units (i.e., political boundaries or ecological regions) can occur at a range of spatial scales and are often hierarchically organized (Girvetz et al. 2008). The reporting units in this study represent three scales of analysis: the entire study area, the Québec, Ontario, and New York portions, and 22

MRCs in Québec, 5 counties in Ontario, and 16 counties in New York (Fig. 1).

For this study, we used four different fragmentation geometries (Table 1 and S9) that complimented the range of grouped land-cover themes that were assessed for land-cover change: (1) “FG-Forests” included all land-cover classes and elements (i.e., all three road classes) that were not forest types. FG-Forests represented the patches of remaining unfragmented forest cover within the study area; (2) “FG-Non-Forest Vegetation” included all land-cover classes and elements that were not grassland, shrub, moss, or herbaceous land-cover types. FG-Non-Forest Vegetation represented the remaining patches of unfragmented grassland, shrub, moss, and herbaceous cover; (3) “FG-Wetlands” included all land-cover classes and elements that were not wetlands. FG-Wetlands represented the patches of remaining unfragmented wetland areas; and (4) “FG-Combined Habitats” included all land-cover classes and elements that were not forest types, grassland, shrub, moss, herbaceous, or wetland cover types. FG-Combined Habitats represented the patches of remaining contiguous natural land-cover within the transboundary wildlife linkage. These four fragmentation geometries were created to represent land-cover themes that are potential habitats for species living within the transboundary linkage. Consequently, the results of the fragmentation analysis can be applied to a range of species, for example, habitat specialists, which can only live in a specific habitat type (i.e., “FG-Forests”, “FG-Non-Forest Habitats”, or “FG-Wetlands”) and/or habitat generalists, which can live in a range of habitats (i.e., “FG-Combined Habitats”).

Creating fragmentation geometry patches

Each of the ESA-CCI-LC raster maps were reclassified in ArcGIS10 (Environmental Systems Research Institute, Redlands, CA) to represent each of the fragmentation geometry classifications (i.e., fragmenting elements/barriers = 1; non-fragmenting elements/non-barriers = 2), and then converted to vector using the ‘‘Raster to Polygon’’ function, with the parameter ‘‘no simplify’’, to ensure the resulting polygons matched their raster counterparts. The fragmenting elements were then removed from each map using “Select by Attributes” and selecting for the non-fragmenting elements. Next, each of the road classes were buffered to represent real-world widths. Primary roads were buffered by 10 m (on either side), secondary roads by 5 m, and tertiary roads by 3 m (Girvetz et al. 2008). The surface of the buffered road networks (for each timepoint) were erased from each fragmentation geometry map using the “Erase” function, resulting in vector maps of patches of the non-fragmenting elements, for each fragmentation geometry scenario.

Patch number and mean patch size

We calculated “patch number” (i.e., the number of patches within a reporting unit for a specific fragmentation geometry) and “mean patch size” (i.e., the sum of each patch area within a reporting unit of a specific fragmentation geometry divided by the number of patches) for each scale of the analysis using the “Feature Area” function in ArcGIS10. The combined use of these two metrics presents a simple approach for quantifying landscape fragmentation. In general terms, as landscape fragmentation increases within a reporting unit, patch number increases and mean patch size decreases (Santiago-Ramos and Feria-Toribio 2021).

Effective mesh size

The effective mesh size fragmentation metric is a more advanced approach for quantifying landscape fragmentation (Jaeger 2000; Moser et al. 2007). The effective mesh size is based on the average probability that any two randomly chosen points in the study area are connected with one another (i.e., not separated by a fragmentation barrier) (Jaeger 2000). The effective mesh size therefore also serves as a measure of structural connectivity (i.e., the degree to which movement between different parts of the landscape is possible) (Jaeger et al. 2011). By multiplying this probability by the total area of the reporting unit, it is converted into a surface area: the effective mesh size. The more barriers fragmenting the landscape, the lower the probability that the two points are connected, and the lower the effective mesh size (Girvetz et al. 2008; Jaeger et al. 2011). Because the boundary of a reporting unit can profoundly influence the effective mesh size, two variations of the effective mesh size were used to quantify the degree of landscape fragmentation and structural connectivity. The “cutting out” procedure

($m_{\text{eff\_CUT}}$) was used to measure fragmentation strictly within the boundaries of the reporting units, with

$$m_{\text{eff\_CUT}} = \frac{1}{A_{\text{total}}} \sum_{i=1}^{n} A_i^2,$$

where n = the number of patches inside the reporting unit; A_i = the sizes of the n patches ($i = 1, \ldots, n$); and

A_{total} = total terrestrial area of the reporting unit (excluding waterbodies). Patches that extend outside the boundary are "cut" along the border leaving only the portion that resides within the reporting unit to be measured. This procedure enables multiple reporting units to be compared on the basis of the fragmentation of the terrestrial area strictly within their borders (e.g., MRCs/counties). The value of $m_{\text{eff\_CUT}}$ varies between zero, when the reporting unit is completely fragmented (i.e., contains no habitat of interest), and the total area of the reporting unit, when there is no fragmentation (i.e., the reporting unit contains only habitat of interest).

The "cross-boundary connections" procedure ($m_{\text{eff\_CBC}}$) was used to include the area of patches that cross the boundaries of the reporting units. This metric allocates the area of the boundary-crossing patches to both reporting units (Moser et al. 2007), with

$$m_{\text{eff\_CBC}} = \frac{1}{A_{\text{total}}} \sum_{i=1}^{n} A_i \cdot A_i^{\text{cmpl}}$$

where A_i = the size of patch i inside the boundary of the reporting unit ($i = 1, 2, 3, \ldots, n$) and A_i^{cmpl} = the area of the complete patch that A_i is a part of (i.e., including the area on the other side of the boundary) and n and A_{total} as above. This procedure considers the overall fragmentation pattern in the landscape rather than just within each reporting unit (Moser et al. 2007).

Although the effective mesh size is typically calculated using the entire area of the reporting unit, the proportion of waterbodies within the reporting units in this study varied between 1% and 30%. Therefore, we followed the approach of Jaeger et al. (2007a; 2008) by comparing landscape fragmentation only between the terrestrial areas of the reporting units. Accordingly, for both $m_{\text{eff\_CUT}}$ and $m_{\text{eff\_CBC}}$, A_{total} = total terrestrial area of the reporting unit (i.e., excluding waterbodies).

Road density

Road length and density were measured for each timepoint (2000, 2010, and 2018) to determine by how much the road network had increased as well as its spatiotemporal pattern of increase. Road length was measured by summing the polyline lengths (in metres) of each road category within each reporting unit, and then dividing by 1000 m/km, to convert to km. Road density was calculated by dividing the road length by the area of the reporting unit and then dividing by 1,000,000 m^2/km^2 to convert to kilometres of road per km^2.

Priority areas for conservation and ecological restoration

We applied the following criteria to prioritize reporting units for conservation and/or restoration intervention. For all land-cover change and landscape fragmentation measurements, changes of less than 10% were considered low priority (i.e., of least concern), changes between 10% and 30% were considered medium priority, changes between 30% and 50% were considered medium–high priority, and changes > 50% were considered high priority. Also, for reasons discussed in the "*Recommendations*" sub-section, we considered all reporting units with less than 30% combined habitats remaining, all habitat patches greater than 100 km^2, and all habitat patches shared by two or more reporting units as high priority for conservation and/or ecological restoration actions.

Results

Land-cover change

Proportions

Proportions of the grouped land-cover themes stayed fairly consistent between 1992 and 2018, with the exception of wetlands, which decreased from 1.2% of the study area down to 0.4% by 2018 (Table 2). This decline was seen in the Québec portion (from 1.2% down to 0.1%) and in the New York portion (from 1.4% down to 0.7%). In 2018, the average proportion of wetlands within each MRC/county was 0.4% (Table S2). Proportions of the grouped land-cover themes were not equivalent between the provincial/state portions. While the composition of the study area was roughly 75% combined habitats and 25% natural and anthropogenic fragmentation elements, within the Québec and New York portions this ratio was roughly 80% combined habitats and 20% natural and anthropogenic fragmentation elements, while in the Ontario portion this ratio was lower: 57% combined habitats and 43% natural and anthropogenic fragmentation elements (Table 2).

Area

At the level of the study area, natural and anthropogenic fragmentation elements (i.e., development, barren areas, waterbodies, and agricultural lands) increased by 2284 km^2 between 1992 and 2018, (Table 2) with increases of 695 km^2 in the Québec portion, 659 km^2 in the Ontario portion, and 932 km^2 in the New York portion (Table 2); and in 42 of the 43 MRCs/counties (Table S2; Fig. 2 and S1). Agricultural lands increased by 964 km^2, with a net loss of 57 km^2 in the Québec portion, and net gains of 434 km^2 and 588 km^2 in the Ontario and New York portions, respectively) (Table S3). Forests decreased by 1363 km^2, with losses of 637 km^2 in the Ontario portion and 819 km^2 in the New York portion (Table 2), and declines in 34 of the 43 MRCs/counties (Table S2; Fig. 2 and S1). Non-forest vegetation (i.e., grassland, shrub, moss, and herbaceous land-cover types) increased by 444 km^2, with increases of 86 km^2 in the Ontario portion, and 359 km^2 in the New York portion (Table 2), and increases in 27 of the 43 MRCs/counties (Table S2; Fig. 2 and S1). Wetlands experienced a loss of 1365 km^2 (68.9%), with losses of 871.9 km^2 (88.5%) in the Québec portion, 20.4 km^2 (30.5%) in the Ontario portion, and 472.4 km^2 (50.8%) in the New York portion (Table 2), with 19 MRCs/counties losing more than 50%, 13 losing more than 75%, and 8 losing more than 90% of their wetlands since 1992 (Table S2; Fig. 2 and S1). Natural and anthropogenic fragmentation elements and non-forest vegetation experienced the greatest increases across the study area, while forests and wetlands suffered the greatest declines. While forest loss was gradual between 1992 and 2018, wetland loss occurred rapidly between 2000 and 2010, with the vast majority occurring in 5 MRCs/counties: La Vallée-de-la-Gatineau (− 269.5 km^2); Antoine-Labelle (− 268.8 km^2); Hamilton (− 249.3 km^2); Matawinie (− 187.8 km^2); and Herkimer (− 111.1 km^2) (Figs. 2 and S1).

Landscape fragmentation

Patch number and mean patch size

For the fragmentation geometries FG-forests, FG-wetlands, and FG-combined habitats, patch numbers increased and mean patch size decreased between 2010 and 2018 indicating that landscape fragmentation had occurred (Table 3). For FG-non-forest vegetation, patch number decreased and mean patch size increased, signifying growth in the fragmentation geometry similar to the growth seen in the non-forest vegetation land-cover theme (Tables 2 and 3).

In 2018, FG-forests were made up of 56,760 patches (Table 4). Of these patches, 49,910 were less than 1 km^2 (covering an area of 4455 km^2); 985 were greater than 10 km^2 (66,447 km^2); 99 were greater than 100 km^2 (42,998 km^2), with 55 located in Québec, 43 in New York, and 1 in Ontario; 13 were greater than 500 km^2 (28,347 km^2), with 5 in Québec, and 8 in New York; 7 were greater than 1000 km^2 (24,511 km^2), with 4 in Québec, and 3 in New York; 2 were greater than 5000 km^2 (16,445 km^2, both in Québec) (Table 4; Fig. 3). FG-non-forest vegetation were made up of 32,145 patches (an area of 5986 km^2). Of these, 4 were greater than 10 km^2 (46 km^2), with 1 in Québec and 3 in New York (Table 4; Fig. 3). FG-wetlands were made up of 3716 patches (an area of 468 km^2). Of these, 61 were greater than 1 km^2 (127 km^2), with 11 in Québec, 2 in Ontario, and 47 in New York (Table 4; Fig. 3). Consequently, the land area of FG-combined habitats comprised 75.5% of the landscape (96,161 km^2) and was made up of 67,790 patches (Table 4; Fig. 3).

Effective mesh size

The effective mesh size ($m_{\text{eff\_CUT}}$), used to measure fragmentation strictly within the boundaries of the reporting units, decreased between 2010 and 2018 for each of the fragmentation geometries, indicating that landscape fragmentation had occurred (Table 5). Within the A2L, $m_{\text{eff\_CUT}}$ values ranged from 0.0036 km^2 (FG-wetlands) to 1468.8 km^2 (FG-combined habitats) in 2010; and from 0.0035 km^2 (FG-wetlands) to 1235.9 km^2 (FG-combined habitats) in 2018 (Table 5). Between 2000 and 2018, $m_{\mathrm{eff\_CUT}}$ for FG-combined habitats decreased by 3726.1 km^2 (60.4%) within the Québec portion (Table 5). For FG-forests, FG-wetlands, and FG-combined habitats, the majority of fragmentation took place in the Québec portion of the study area, whereas for FG-non-forest vegetation, the majority of fragmentation occurred in the New York portion (Table 5). This pattern was also observed at the level of the MRC/county where the mean $m_{\mathrm{eff\_CUT}}$ decreased for each of the fragmentation geometries (Table S4–7). The mean $m_{\mathrm{eff\_CBC}}$, used to measure fragmentation that considered patches that "crossed" reporting unit boundaries, also decreased for each of the fragmentation geometries in the MRCs/counties (Table S4–7); and the mean $m_{\mathrm{eff\_CBC}}$ - $m_{\mathrm{eff\_CUT}}$, decreased for all of the fragmentation geometries indicating that the area of patches shared by multiple MRCs/counties also decreased between 2010 and 2018 (Table S4–7). In 2018, the lowest effective mesh values (highest fragmentation) for FG-forests were located in the MRCs/counties of the central region of the study area and along the west edge of the New York portion (Figure S2). The lowest effective mesh values for FG-non-forest vegetation were located in the MRCs/counties just north of the central region with the highest values (lowest fragmentation) occurring in the west edge of the New York portion (Figure S2). FG-wetlands had a very similar pattern to FG–non-forest vegetation, whereas FG-combined habitats had a near identical pattern to FG-forests (Figure S2).

Road density

Between 2010 and 2018, the length of the road network increased by 2588 km within the study area (Table 6). Primary roads increased by 439 km (10.6%), secondary roads increased by 551 km, and tertiary roads increased by 1598 km. These increases were spread out between the provincial/state portions. Since 2000, roads in the Québec portion expanded by 7684 km (15.7%), with primary roads increasing by 473 km (28.5%). Ontario roads expanded by 2380 km (11.6%), and New York roads increased by 369 km between 2010 and 2018. Accordingly, road density also increased throughout the study area between 2010 and 2018 (Table 6). As of 2018, the Ontario portion had the highest road density with 1.12 km/km^2, followed by the New York portion with 0.78 km/km^2, and the Québec portion with 0.70 km/km^2. These increases were distributed across 39 of the 43 MRCs/counties with a mean road length increase of 60 km, and a mean road density increase of 0.04 km/km^2 (Table S8).

Priority areas for conservation and ecological restoration

For forest losses between 1992 and 2018, there were 6 MRCs/counties at medium priority (10%–30% change) and 2 at medium–high priority (30%–50%) for conservation and ecological restoration intervention (Table S2); for non-forest vegetation losses, there were 4 MRCs/counties at medium priority, 1 at medium–high priority, and 2 at high priority (> 50% change) (Table S2); for wetland losses there were 7 at medium, 2 at medium–high, and 19 at high priority (Table S2); and for combined habitat losses, 5 MRCs/counties were at medium, and 2 were at medium–high priority (Table S2). There were also 11 MRCs/counties that had less than 30% combined habitats remaining, these were also given high priority for conservation and ecological restoration actions (Table S2).

For FG-forest fragmentation between 2000/2010 and 2018, there were 4 MRCs/counties at medium priority and 3 at medium–high priority for conservation and ecological restoration intervention when measured by $m_{\mathrm{eff\_CUT}}$ (Table S4); and 8 at medium priority and 2 at medium–high priority when measured by $m_{\mathrm{eff\_CBC}}$ (Table S4). For FG-non-forest vegetation fragmentation, there were 12 MRCs/counties at medium priority, 10 at medium–high priority, and 11 at high priority, as measured by both $m_{\mathrm{eff\_CUT}}$ and $m_{\mathrm{eff\_CBC}}$ (Table S5).For FG-wetlands fragmentation, there were 6 MRCs/counties at medium priority and 1 at medium–high priority when measured by $m_{\mathrm{eff\_CUT}}$ (Table S6); and 7 at medium priority and 1 at medium–high priority when measured by $m_{\mathrm{eff\_CBC}}$ (Table S6). For FG-combined habitats fragmentation, there were 5 MRCs/counties at medium priority and 3 at medium–high priority when measured by $m_{\mathrm{eff\_CUT}}$ (Table S7);and 7 at medium priority and 2 at medium–high priority, when measured by $m_{\mathrm{eff\_CBC}}$ (Table S7).

These MRCs/counties represent areas of medium priority, medium–high priority, and high priority within the A2L where continued monitoring, planning, and conservation and restoration actions are

Table 2 Changes in land-cover area (km^2) and proportion (%) for each grouped land-cover theme between 1992 and 2018, at the scale of the study area and each provincial/state portion

Land-cover theme	Area (Km^2)				Proportion (%)				Land-Cover Change		
									Area (Km^2)	Area (%)	Proportion (%)
Study area	1992	2000	2010	2018	1992	2000	2010	2018			
Natural and anthropogenic fragmentation elements	38,683	39,611	40,416	40,967	22.8	23.3	23.8	24.1	2284	5.9	1.4
Forests	121,703	120,512	121,001	120,340	71.7	71.0	71.3	70.9	−1363	−1.1	−0.8
Non-forest vegetation	7413	7643	7742	7857	4.4	4.5	4.6	4.6	444	6.0	0.3
Wetlands	1982	2015	622	617	1.2	1.2	0.4	0.4	-1365	***-68.9***	-0.8
Combined habitats	131,098	130,170	129,365	128,813	77.2	76.7	76.2	75.9	−2284	−1.7	−1.3
Québec portion											
Natural and anthropogenic fragmentation elements	15,400	15,691	16,015	16,095	19.1	19.5	19.9	20.0	695	4.5	0.9
Forests	63,858	63,559	64,103	63,948	79.2	78.8	79.5	79.3	91	0.1	0.1
Non− forest vegetation	415	422	427	501	0.5	0.5	0.5	0.6	86	20.7	0.1
Wetlands	985	987	113	113	1.2	1.2	0.1	0.1	−872	***−88.5***	−1.1
Combined habitats	65,258	64,967	64,643	64,563	80.9	80.5	80.1	80.0	−695	−1.1	−0.9
Ontario portion											
Natural and anthropogenic fragmentation elements	10,958	11,286	11,456	11,616	53.4	55.0	55.9	56.6	659	6.0	3.2
Forests	9350	9005	8878	8714	45.6	43.9	43.3	42.5	−637	−6.8	−3.1
Non-forest vegetation	132	132	129	130	0.6	0.6	0.6	0.6	−2	−1.0	0.0
Wetlands	67	83	43	47	0.3	0.4	0.2	0.2	−20	−30.5	−0.1
Combined habitats	9549	9221	9050	8890	46.6	45.0	44.1	43.4	−659	−6.9	−3.2
New York portion											
Natural and anthropogenic fragmentation elements	12,355	12,666	12,976	13,287	18.0	18.4	18.9	19.4	932	7.5	1.4
Forests	48,497	47,949	48,020	47,678	70.6	69.8	69.9	69.5	−819	−1.7	−1.2
Non-forest vegetation	6866	7088	7187	7225	10.0	10.3	10.5	10.5	359	5.2	0.5
Wetlands	931	946	466	458	1.4	1.4	0.7	0.7	−472	***−50.8***	−0.7
Combined habitats	56,294	55,983	55,672	55,362	82.0	81.6	81.1	80.6	−932	−1.7	−1.4

Bold italic text (> 50% change), areas of high priority for conservation and ecological restoration

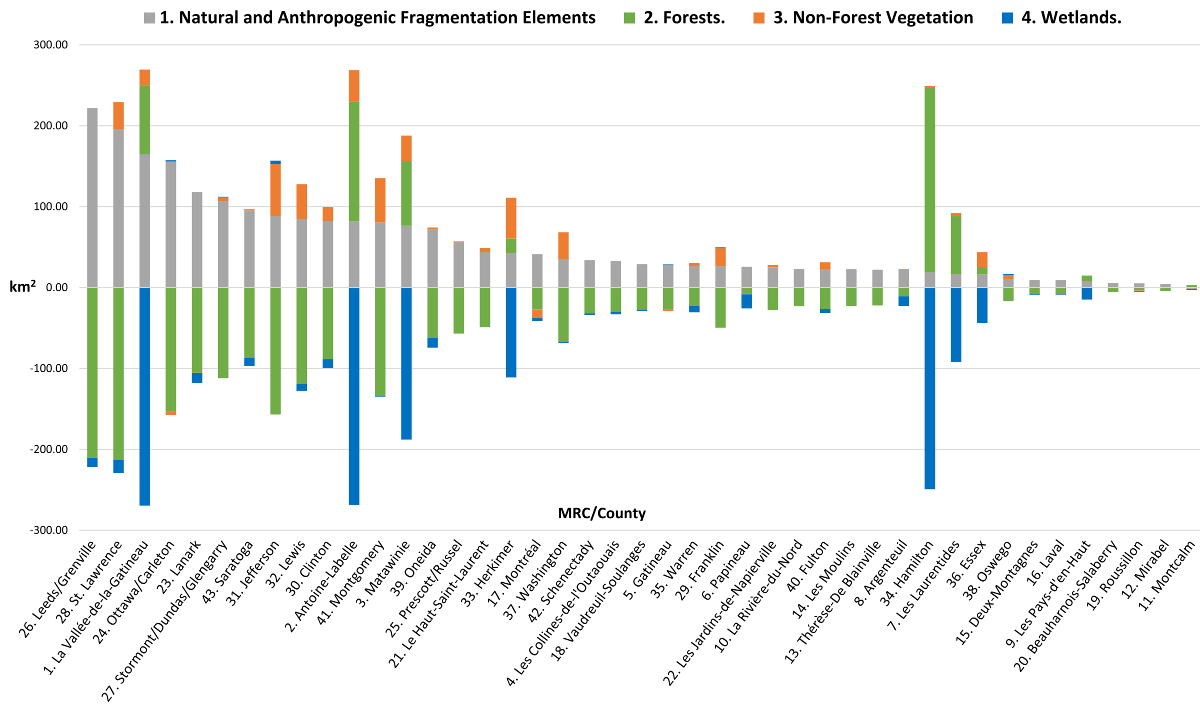

Fig. 2 Changes in area (km^2) of the grouped land-cover themes in each MRC/county between 1992 and 2018. From left to right, MRC/counties are ranked from greatest to least amount of areal change in natural and anthropogenic fragmentation elements. MRC/county names are numbered and correspond to the numbers on the map in Fig. 1

required to ensure habitats are restored and no further land-cover change and landscape fragmentation continues.

Discussion

Land-cover change and landscape fragmentation

Although there have been several "static" studies of the extent of landscape connectivity within the larger region, such as the Algonquin-to-Adirondacks (A2A) region (Quinby et al. 1999), Southeastern Canada/Northeastern USA (Carroll 2003), and Montréal and the Saint Lawrence Lowlands (Mitchell et al. 2015; Albert et al. 2017; Rayfield et al. 2019; Gonzalez et al. 2019), this is the first "dynamic" study of changes in landscape structure within one of the three potential north–south transboundary wildlife movement linkages that connect wilderness areas in northeastern USA and southeastern Canada.

Our results clearly show that extensive land-cover change and landscape fragmentation have occurred within the A2L between 1992 and 2018. These findings are in agreement with a proximal study of the Montréal Metropolitan Region (MMR) by Dupras et al. (2016), who reported that "*land-use changes which occurred in the MMR between 1966 and 2010 have in turn caused profound changes on both the structural (landscape patterns such as fragmentation) and functional (landscape processes such as barrier effects and ecological connectivity) properties of the landscape*" (p. 69).

Changes in land-cover varied between the grouped land-cover themes. Natural and anthropogenic fragmentation elements and non-forest vegetation experienced net increases in land-cover area, whereas forests and wetlands suffered net declines in land-cover area between 1992 and 2018 (Table 2). This pattern is striking at the MRC/county level where one can visualize how gains in natural and anthropogenic fragmentation elements, forests, and non-forest vegetation were the direct result of losses in forests, wetlands, or both (Fig. 2). These losses could be the result of wetland drainage. Wetland drainage for development and agriculture is the leading cause of wetland loss

Table 3 Changes in patch number and mean patch size (km^2) for each fragmentation geometry between 2000 and 2018, at the scale of the study area and each provincial/state portion

Reporting unit	Year	FG—Forests		FG—Non-Forest Vegetation		FG—Wetlands		FG—Combined Habitats	
		Patch number	Mean patch size (km^2)	Patch number	Mean patch size (km^2)	Patch number	Mean patch size (km^2)	Patch number	Mean patch size (km^2)
Study Area	2010	53,981	1.67	40,933	0.172	3598	0.131	64,114	1.51
	2018	56,760	1.58	32,145	0.186	3716	0.126	67,790	1.42
Change		2779	−0.09	−8788	0.014	118	−0.005	3676	−0.09
Change (%)		5.1	−5.4	*−21.5*	8.3	3.3	−4.0	5.7	−5.8
Québec	2000	17,564	2.62	3571	0.085	2054	0.348	18,420	2.57
	2010	19,654	2.36	6573	0.088	752	0.110	20,715	2.27
	2018	20,802	2.23	3731	0.096	751	0.110	21,779	2.16
Change		3238	−0.40	160	0.012	−1303	−0.238	3359	−0.41
Change (%)		18.4	*−15.1*	4.5	13.6	***−63.4***	***−68.4***	18.2	*−16.0*
Ontario	2000	8440	0.80	1259	0.078	466	0.134	9112	0.76
	2010	9199	0.72	2147	0.060	329	0.099	9910	0.69
	2018	9548	0.68	1396	0.069	377	0.093	10,261	0.65
Change		1108	−0.12	137	−0.009	−89	−0.042	1149	−0.11
Change (%)		13.1	*−14.5*	10.9	*−11.4*	*−19.1*	*−<u>30.9</u>*	12.6	*−14.4*
New York	2010	25,166	1.47	32,230	0.196	2530	0.141	33,537	1.28
	2018	26,452	1.39	27,032	0.205	2604	0.135	35,805	1.19
Change		1286	−0.08	−5198	0.008	74	−0.006	2268	−0.09
Change (%)		5.1	−5.5	*−16.1*	4.2	2.9	−4.6	6.8	−6.9

Italic text (10%–30% change), areas of medium priority for conservation and ecological restoration; Underline italic text (30%–50% change), areas of medium/high priority; and Bold italic text (> 50% change), areas of high priority for conservation and ecological restoration

in Canada (Council of Canadian Academies 2013). Gains in forests and non-forest vegetation could indicate areas of "dried" wetlands (i.e., seasonally flooded forests, wooded swamps, and marshes), after the draining process. Gains in non-forest vegetation could also be the result of forest harvest. After forest harvesting, these areas would be in various stages of succession and constitute non-forest vegetation types (i.e., grassland, shrub, moss, and herbaceous cover types).

Landscape fragmentation, however, occurred within all fragmentation geometries (with FG–forests undergoing the greatest amount of fragmentation), as measured by the effective mesh size and road density. Patch number and mean patch size indicated fragmentation took place in FG-forests, FG-wetlands, and FG-combined habitats, but not in FG-non-forest vegetation, which was due to the loss of 8788 patches (Table 3) causing an overall increase in the mean patch size. Mean patch size can increase when small patches are lost due to habitat loss, even when landscape fragmentation has occurred (Jaeger et al. 2011). Consequently, mean patch size is not a suitable metric for landscape fragmentation on its own and is only valuable when used in combination with more appropriate metrics such as the effective mesh size (Jaeger 2000).

Priority areas for conservation and ecological restoration

We directly compared reporting units as well as ranked them in terms of land-cover change and landscape fragmentation. MRCs/counties with the lowest proprotion of potential habitat (for each grouped land-cover theme) and/or the lowest effective mesh size for each fragmentation geometry (highest fragmentation) were identified (Tables S2, and S4–7).

Table 4 Proportion of each fragmentation geometry and size distribution of remaining patches in 2018, at the scale of the study area and each provincial/state portion

Fragmentation Geometry	Proportion of Study Area (%)	Number of Remaining Patches							
		Total	< 1 km^2	> 1 km^2	> 10 km^2	> 100 km^2	> 500 km^2	> 1000 km^2	> 5000 km^2
Study Area									
FG-Forests	70.3	56,760	49,910	6850	985	99	13	7	2
FG-Non-Forest Vegetation	4.7	32,145	30,840	1305	4	0	0	0	0
FG-Wetlands	0.4	3716	3655	61	0	0	0	0	0
FG-Combined Habitats	75.5	67,790	59,589	8201	1047	100	13	7	2
Québec Portion									
FG-Forests	78.3	20,802	17,614	1929	474	55	5	4	2
FG-Non-Forest Vegetation	0.6	3721	3694	77	1	0	0	0	0
FG-Wetlands	0.1	751	740	11	0	0	0	0	0
FG-Combined Habitats	80.3	21,779	19,832	1947	475	55	5	4	2
Ontario Portion									
FG-Forests	42.3	9549	8373	1175	111	1	0	0	0
FG-Non-Forest Vegetation	0.6	1396	1386	10	0	0	0	0	0
FG-Wetlands	0.2	377	375	2	0	0	0	0	0
FG-Combined Habitats	43.2	10,261	9072	1189	114	1	0	0	0
New York Portion									
FG-Forests	69.0	26,452	22,697	3755	397	43	8	3	0
FG-Non-Forest Vegetation	10.4	27,032	25,774	1258	3	0	0	0	0
FG-Wetlands	0.7	2604	2557	47	0	0	0	0	0
FG-Combined Habitats	80.1	35,805	30,729	5076	454	44	8	3	0

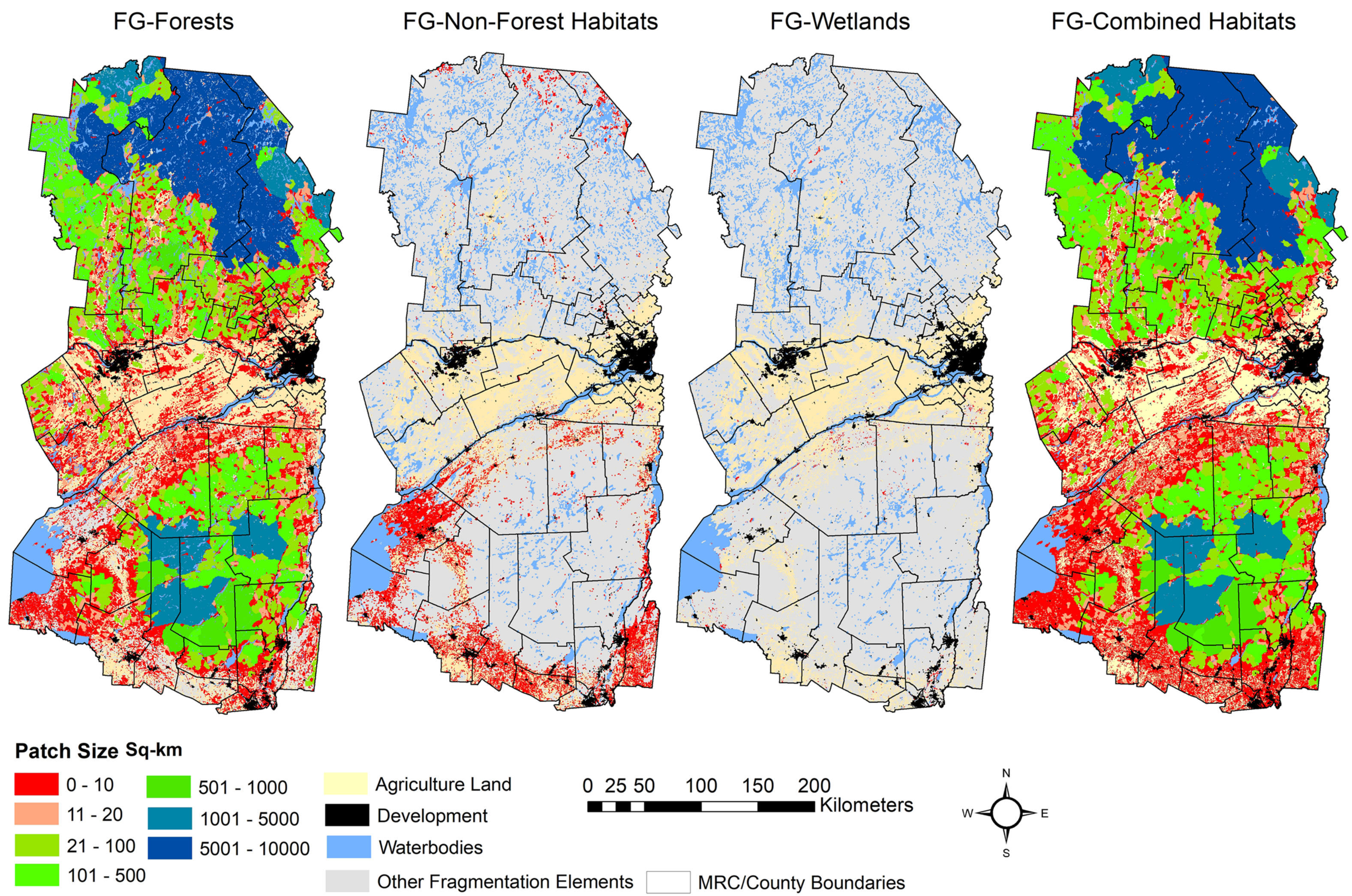

Fig. 3 Size distribution of remaining patches for each fragmentation geometry in 2018. Municipalité régionale de comté (MRC)/county boundaries overlaid on each map

Table 5 Changes in the Effective Mesh Size (m_{eff_CUT}) for each fragmentation geometry between 2000 and 2018, at the scale of the study area and each provincial/state portion

Reporting Unit	Year	m_{eff_CUT} (km^2)			
		FG—Forests	FG—Non-Forest Vegetation	FG—Wetlands	FG—Combined Habitats
Study Area	2010	1428.7	0.092	0.0036	1468.8
	2018	1173.9	0.080	0.0035	1235.9
Change		−254.8	−0.012	−0.0001	−232.9
Change (%)		*−17.8*	*−12.9*	−2.1	*−15.9*
Québec Portion	2000	5572.5	0.003	0.0172	6167.9
	2010	2851.5	0.009	0.0015	2936.5
	2018	2310.0	0.007	0.0015	2441.8
Change		−3262.5	0.005	−0.0156	−3726.1
Change (%)		***−58.5***	185.7	***−91.0***	***−60.4***
Ontario Portion	2000	7.1	0.002	0.0031	7.3
	2010	6.4	0.003	0.0021	6.6
	2018	6.2	0.002	0.0021	6.4
Change		−0.9	0.000	−0.0010	−0.9
Change (%)		*−12.7*	−3.9	−*<u>31.2</u>*	*−12.3*
New York Portion	2010	264.8	0.210	0.0063	266.8
	2018	254.0	0.184	0.0061	256.4
Change		−10.8	−0.027	−0.0002	−10.4
Change (%)		−4.1	*−12.6*	−3.2	−3.9

Ilatic text (10%–30% change), areas of medium priority for conservation and ecological restoration; Underline italic text (30%–50% change), areas of medium/high priority; Bold italic text (>50% change), areas of high priority for conservation and ecological restoration

Reporting units were also prioritized for conservation and/or restoration intervention. Many MRCs/counties have reached or exceeded thresholds of habitat loss and fragmentation (see below) and to endure further changes in landscape structure would significantly jeopardize the overall integrity and connectivity of the transboundary wildlife linkage. These MRCs/counties should be given the highest priority for conservation and restoration actions within the A2L to ensure the functionality of the transboundary wildlife linkage.

The implications for land-use planning are clear. Development in these locations should be implemented strategically to avoid further habitat loss and fragmentation. Such tactics include: (1) limiting the area of urban and agricultural development, while promoting "up instead of out" development practices, salvaging brownfield sites, and adopting agro-ecological diversification techniques (Jaeger et al. 2011; Kremen and Merenlender 2018); (2) addition of "greenbelts" surrounding urban areas which have been shown to significantly reduce urban sprawl as well as provide habitat and maintain landscape connectivity (Pourtaherian and Jaeger 2022); (3) addition of wildlife crossing structures (WCS) to restore landscape connectivity; (4) preference to upgrading and widening of existing highways over construction of new highways at additional locations (Jaeger et al. 2011); and (5) bundling of transportation infrastructure (i.e., constructing roads and railways in parallel). Although these last two strategies will increase the barrier effect of each individual transportation route, they are still considered better options than the fragmentation of a much larger area; especially if WCSs can be placed strategically along the widened/bundled infrastructures so that they can be traversed all at once (Jaeger et al. 2011).

Recommendations

2020 conservation targets

In 2015, federal, provincial, and territorial governments established the "2020 Biodiversity Goals and Targets for Canada" to achieve its commitments to the United Nations Convention on Biological Diversity (CBD) "Strategic Plan for Biodiversity 2011–2020" and its global "Aichi Biodiversity

Table 6 Changes in road length (km) and road density (km/km^2) for each road category between 2000 and 2018, at the scale of the study area and each provincial/state portion

Road Network	Road Length (km^2)				Road Density (km/km^2)				Change (%)
Study Area	2000	2010	2018	Change	2000	2010	2018	Change	
Primary roads (10 m buffer)		4127	4566	439		0.02	0.03	0.003	*10.6*
Secondary roads (5 m buffer)		20,222	20,772	551		0.12	0.12	0.003	2.7
Tertiary roads (3 m buffer)		106,112	107,710	1598		0.63	0.64	0.009	1.5
Total		130,460	133,048	2588		0.77	0.79	0.015	2.0
Québec									
Primary roads (10 m buffer)	1661	1783	2134	473	0.02	0.02	0.03	0.006	*28.5*
Secondary roads (5 m buffer)	5859	6275	6442	583	0.07	0.08	0.08	0.007	10.0
Tertiary roads (3 m buffer)	41,546	46,917	48,174	6628	0.52	0.58	0.60	0.082	*16.0*
Total	49,066	54,975	56,750	7684	0.61	0.68	0.70	0.095	*15.7*
Ontario									
Primary roads (10 m buffer)	1077	1147	1218	141	0.05	0.06	0.06	0.007	*13.1*
Secondary roads (5 m buffer)	4731	4829	4862	131	0.23	0.24	0.24	0.006	2.8
Tertiary roads (3 m buffer)	14,682	16,450	16,791	2109	0.72	0.80	0.82	0.103	*14.3*
Total	20,491	22,426	22,871	2380	1.00	1.09	1.12	0.116	*11.6*
New York									
Primary roads (10 m buffer)		1197	1213	16		0.02	0.02	0.000	1.4
Secondary roads (5 m buffer)		9118	9468	350		0.13	0.14	0.005	3.8
Tertiary roads (3 m buffer)		42,745	42,747	2		0.62	0.62	0.000	0.0
Total		53,059	53,428	369		0.77	0.78	0.005	0.7

Italic text (10%—30% change), areas of medium priority for conservation and ecological restoration

Targets" (Environment and Climate Change Canada 2019). Target 1 declared that by 2020, at least 17% of terrestrial areas and inland water, and 10% of coastal and marine areas would be conserved through a network of protected areas and other conservation measures (Environment and Climate Change Canada 2019). The USA also signed the strategic plan for biodiversity; however, it was never ratified (CBD 2021). In 2016 the New England Governors and Eastern Canadian Premiers adopted "Resolution 40–3—Resolution on ecological connectivity, adaptation to climate change, and biodiversity conservation" (CICS 2016; Arkilanian et al. 2020). The objectives highlighted the necessity for its partners to work across landscapes and borders to restore and maintain ecological connectivity and for all levels of governance, especially municipalities, to incorporate habitat connectivity objectives into their regional land-use plans and policies (CICS 2016).

By the end of 2020, only 10.2% of Canadian terrestrial areas and 11.8% of USA terrestrial areas were under some level of protection (UNEP-WCMC, 2021a/b). Nevertheless, the province of Québec reached 17% (~257,000 km^2) of its terrestrial area protected (Environment and Climate Change Canada 2020), as did New York State, with approximately 20% (~24,000 km^2) of its terrestrial area protected (New York Protected Areas Database 2020), whereas Ontario achieved only 10.7% (115,593 km^2) of its terrestrial areas protected by the end 2020 (Ontario 2022). At the global level, none of the 20 Aichi Biodiversity Targets agreed by Parties to the CBD in 2010 have been fully achieved (IUCN 2022).

Post-2020 conservation targets

In 2019, the Trudeau government pledged to protect 25% of Canada's land and oceans by 2025 and 30% by 2030 (One Planet Summit 2021). In 2021, the Biden administration also committed to conserving at least 30% of USA lands and waters by 2030 (The White House 2021). In December 2022, members of the CBD will meet in Montréal, Canada for the 15th meeting of the Conference of the Parties

(COP 15) to adopt a "Post-2020 Global Biodiversity Framework" which will act as a stepping-stone towards the 2050 vision of "living in harmony with nature" (IUCN 2022). Parties to the CBD aim to halt the loss of biodiversity by 2030 and achieve recovery and restoration by 2050 (IUCN 2022). The post-2020 strategy includes the expansion of protected areas and other effective area-based conservation measures (OECMs) to cover at least 30% of the planet by 2030 ("30 × 30"), while recognizing the rights and roles of Indigenous peoples and local communities (IUCN 2022). With conservation outcomes often conditional to decisions made across multiple boundaries, a key component in the post-2020 framework is a commitment to coordinated and collaborative international conservation at the transboundary level (SCBD 2018; Díaz et al. 2020; Mason et al. 2020).

Based on our findings, the following sub-sections propose recommendations for conservation at the local level (MRC/county) that will complement post-2020 commitments at the provincial/state, national, and transboundary levels (i.e., "Think globally, act locally").

Minimum 30% combined habitats

Although the proportion of remaining combined habitats (forests, grassland, shrub, moss, herbaceous cover, and wetlands) in the A2L was 75.9% in 2018 (Table 2), at the MRC/county level, this proportion ranged from 7.1% (MRC Beauharnois-Salaberry) to 99.7% (Hamilton County), with 11 of the 43 MRCs/counties having less than 30% combined habitats remaining within their borders (Table S2). Studies suggest that to conserve biodiversity and meet the area requirements for large-ranging species, up to 75% combined habitats within a landscape should be protected (Noss et al. 2012; Lovejoy and Nobre 2018; Mogg et al. 2019). While this value is dependent on a variety of landscape and species-specific characteristics (i.e., size of landscape, rate of habitat loss, degree of fragmentation, landscape connectivity, and matrix quality), simulation and empirical studies have suggested that with less than 30% habitat remaining, the ecological effects of habitat loss and fragmentation (including species richness and abundance) begin to increase exponentially and population extinctions become increasingly inevitable (Andrén 1994; Swift and Hannon 2010).

Increasing the number and total amount of protected areas has, thus far, been the most important tool for the conservation of biodiversity (at the provincial/state and national levels). 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). Because the remaining natural and semi-natural areas between protected areas are vulnerable to continued habitat loss and fragmentation, it is only a matter of time before protected areas become islands in a sea of human modified landscape (Wilson and MacArthur 1967).

According to the principle of subsidiarity, management issues should be dealt with at the most proximal level that is competent of resolution (Jefferies and Sawyer 2019). One such solution is to establish area-based conservation targets at the level of the MRC/county to help achieve federal and provincial biodiversity conservation objectives and ensure connectivity between protected areas. MRCs/counties are the primary planners of regional land-use. They are well positioned to assess local ecosystems and develop area-based conservation and restoration plans to protect biodiversity and maintain connectivity with surrounding MRCs/counties (Jefferies and Sawyer 2019). Goal A of the "2020 Biodiversity Goals and Targets for Canada" states that by 2020 Canada's lands and waters will be managed using an ecosystem approach to support biodiversity conservation outcomes at *local*, *regional*, and national scales; and Target 4 states that by 2020 biodiversity considerations will be integrated into *municipal planning* (Environment and Climate Change Canada 2019); however, neither goal nor target established area-based objectives for conservation at the MRC/county level. Similarly, there are no such area-based targets for conservation at the county level in the USA either. Therefore, in most cases, it is up to the discretion of the MRCs/counties themselves to implement any area-based conservation and restoration targets.

Accordingly, we recommend maintaining the A2L at, or above, 75% combined habitats, and ecologically restoring combined habitats to a "minimum" of 30% land area in MRCs/counties where they are already below this threshold. These restoration actions will offer additional habitats and resources, improve landscape connectivity by providing corridors and stepping-stones, and increase the overall integrity of the transboundary wildlife linkage (Kremen and Merenlender 2018; Locke et al. 2019; Garibaldi et al. 2020).

Wetland conservation and restoration

North America is home to 30% of the world's wetlands with 25% (~ 1.3 million km^2) solely in Canada (Government of Canada 2016a). In the last 200 years, Canada has lost 15% (~ 200,000 km^2) of its wetland ecosystems, while the USA have lost 53% (~ 473,000 km^2) (Dahl 1990). In 1981, Canada signed the "Ramsar Convention on Wetlands of International Importance", which was followed by the USA in 1986 (RCS 2016). Through international cooperation, policy creation, and technology transfer, the Ramsar Convention's aim is to halt the worldwide loss of wetlands and to conserve those that remain (RCS 2016). In 1986, the Canadian and American governments established the "North American Waterfowl Management Plan" to conserve declining waterfowl and migratory bird habitats in North America (Government of Canada 2016b); and in 1989, the U.S. Congress passed the "North American Wetlands Conservation Act", which authorizes grants to public–private partnerships in Canada, Mexico, and the United States, to protect, enhance, and/or restore, wetland ecosystems, consistent with the North American Waterfowl Management Plan (USFW 2022). Despite these global and international obligations, wetlands have still declined by 68.9% within the A2L since 1992 (Table 2).

In 1975, the New York State Legislature passed "The Freshwater Wetlands Act" with the intent to protect freshwater wetlands and their ecosystem benefits (DEC 2022). Regardless, wetlands within the New York portion have declined by 472 km^2 (50.8%) since 1992 (Table 2). In the same timeframe, the Québec portion experienced a critical loss of 872 km^2 (88.5%), and the Ontario portion lost 20 km^2 (30.5%) of wetland habitats (Table 2).

At the regional level, 19 of the 43 MRCs/counties lost more than 50%, 12 lost more than 80%, and 8 lost more than 90% of their wetlands since 1992 (Table S2). Consequently, in 2017, the National Assembly of Québec passed "An act respecting the conservation of wetlands and bodies of water" (Bill 132). This set of legislation, which includes a no-net-loss principle for both wetlands and bodies of water, affords the MRCs the responsibility of developing and implementing a "plan régional des milieux humides et hydriques (PRMHH)", a regional conservation and restoration plan for wetlands and waterbodies in their territories (Assemblée nationale du Québec 2017); and in 2021, the Ontario government invested $30 million in the "Wetlands Conservation Partner Program" to assist conservation organizations in conserving and restoring wetlands in priority areas across the province (Ontario 2022).

With such extensive wetland losses across the A2L, a no-net-loss policy is simply not enough. To ensure an abundance of wetland habitat for both local and migratory species, to safeguard the ecosystem services they provide (i.e., water purification, flood and erosion control, groundwater recharge, etc.), to generate connectivity between wetland habitats, and to preserve ecosystem integrity and productivity, wetland losses need to be recovered. As a result, we recommend that all provincial/state wetland policies be based on a net gain of area (extent and quality of wetland habitats), and function (ecosystem services).

Species-appropriate effective mesh sizes

The more barriers fragmenting the landscape, the lower the effective mesh size (Jaeger et al. 2007b). In 2018, the effective mesh size $m_{\text{eff\_CUT}}$ for FG-combined habitats was 1235.9 km^2 within the A2L (Table 5). At the level of the MRC/county, this value ranged from 0.1 km^2 (Montréal and MRC Beauharnois-Salaberry) to 2863.6 km^2 (MRC Antoine-Labelle), with 14 out of 43 MRCs/counties with a $m_{\text{eff\_CUT}}$ less than 2 km^2, and 13 with a $m_{\text{eff\_CBC}}$ less than 2 km^2 (Table S7).

When the effective mesh size is smaller than the size of a species' home range then the likelihood decreases drastically that individuals of the species will be able to move freely in the landscape without encountering barriers (Jaeger et al. 2011). For example, if we assume that the fragmentation elements within "FG-combined habitats" (i.e., development, barren areas, waterbodies, agricultural land, and roads) can act as complete barriers for a specific group of species, then it would be essential for those species to have effective mesh sizes larger than their home range size (Jaeger et al. 2011). We therefore recommend restoring landscape connectivity (i.e., reducing fragmentation) to accommodate effective mesh sizes that are appropriate for the species that inhabit the region or may move into (or through) the region following the transboundary wildlife linkage.

Protection of large roadless areas

Not only are roads a major contributor to habitat loss and fragmentation, their impacts on the surrounding landscape (described by the "road-effect zone"; Forman and Alexander 1998) can extend up to several kilometers from the road edge, reducing the quality of adjacent habitats (Benítez-López et al. 2010; Torres et al. 2016). For some species, roads can act as barriers to movement and lead to resource inaccessibility, for others, roads can cause increased mortality due to animal-vehicle collisions (Forman and Alexander 1998; Jaeger et al. 2005). Roads also facilitate "contagious development" by providing access to previously isolated areas (Laurance and Balmford 2013; Selva et al. 2015; Ibisch et al. 2016). Large roadless areas are characterized by high ecological value, integrity, and connectivity, making their safeguarding a significant contribution to the prevention of biodiversity loss (IENE 2015; Ibisch et al 2016). There is no legislation in place to protect the remaining large roadless areas in Canada. In the USA, the "2001 Roadless Area Conservation Rule" established prohibitions on road construction, road reconstruction, and timber harvesting on 236,700 km^2 of inventoried roadless areas on "National Forest System" lands (IENE 2015; Coffin et al. 2021). However, since its inception, the roadless rule has been under threat from multiple states seeking their own special roadless rule exemptions. The "Roadless Area Conservation Act of 2021" (H.R.279; 117th Congress, 2020–2021), which has been introduced consecutively since 2018, would codify the protections provided by the 2001 roadless area conservation rule ensuring the protection of these public lands for future generations. As of November 2022, this act has not been passed by the U.S. Congress.

In 2018, there were only 100 large roadless areas (patches) of combined habitats (> 43,000 km^2 in total area) remaining in the A2L (Fig. 3; Table 4), 13 of which were greater than 500 km^2 (5 in the Québec portion, 8 in the New York portion); 7 of which were greater than 1000 km^2 (4 in the Québec portion, 3 in the New York portion); and 2 larger than 5000 km^2, both in the Québec portion. These locations represent the last large roadless areas within the A2L transboundary wildlife linkage and are vital to wide-ranging mammals and species vulnerable to habitat fragmentation. These large roadless areas should be given high priority for conservation within the A2L to ensure their persistence in the wildlife linkage.

Protection of border-crossing patches

In 2018, 36 of the 43 MRCs/counties shared combined habitat patches with at least one other MRC/county (i.e., patches crossing MRC/county boundaries in Fig. 3) as calculated by the difference between the $m_{\text{eff\_CUT}}$ and $m_{\text{eff\_CBC}}$ values (Table S7). This was also the case with the other land-cover themes with 34 out of 43 MRCs/counties sharing forest patches, 32/43 sharing non-forest vegetation patches, and 22/43 sharing wetland patches (Tables S4–S6; Fig. 3). Because of the importance of these transboundary patches for landscape connectivity and their disproportionate risk of being reduced or fragmented, we recommend coordinated and collaborative conservation strategies between MRCs/counties to ensure that these patches continue to serve as vital habitats, connectivity corridors, and stepping-stones for a wide range of species within the A2L.

Inclusion of Ontario and New York in resolution 40-3

"Resolution 40-3—Resolution on ecological connectivity, adaptation to climate change, and biodiversity conservation" promotes regional collaborations in order to identify priority habitat corridors that connect and expand existing protected areas; as well as the design and/or modification of transportation infrastructure to improve habitat connectivity including reducing the risk of wildlife-vehicle collisions (CICS, 2016). The members of the New England Governors and Eastern Canadian Premiers (NEG/ECP) include Québec, New Brunswick, Prince Edward Island, Nova Scotia, Newfoundland and Labrador, Maine, Vermont, New Hampshire, Massachusetts, Rhode Island, and Connecticut (Arkilanian et al. 2020). Ontario and New York are not included in the NEG/ECP. However, not only do they share the A2L, but they also share another potential north–south transboundary linkage, the "Algonquin-to-Adirondack"

(A2A) linkage (Algonquin to Adirondacks Collaborative 2016) and a potential east–west linkage, the "Adirondack Mountains to the Green Mountains" linkage (Staying Connected Initiative 2022). Ontario and New York are also the last westward province and state to share a land border before the natural barrier of Lake Ontario (Fig. 1). Consequently, it would be advantageous for both Ontario and New York to join the NEG/ECP and adopt Resolution 40-3 to benefit from collaborations between transportation and natural resource agencies that aim to improve habitat connectivity (CICS, 2016).

Continued monitoring of land-cover change and landscape fragmentation

Monitoring is an important requirement for transboundary conservation (Vasilijević et al. 2015). Land-cover change and landscape fragmentation are essential indicators of threats to biodiversity, sustainable land-use, and landscape quality; and the distribution of conservation and restoration resources is dependent on the knowledge of ongoing trends in landscape structure (Jaeger et al. 2011). The data presented here provides valuable information for land-use, transportation, and conservation planning and can be used as a baseline to evaluate the impacts of future land-use development scenarios. By applying the same parameters, the effects of multiple projects can be compared and the least intrusive can be selected. This same logic can also be applied for the continuous monitoring of the region. Accordingly, we strongly recommend continued monitoring within the A2L utilizing the same grouped land-cover themes and fragmentation geometries. Doing so will not only enable the detection of long- and short-term changes in landscape structure but will also allow monitoring agencies to determine whether past conservation targets are being achieved (Roch and Jaeger 2014).

Limitations

Transboundary analysis involves the inherent challenge of gathering and working with GIS data from multiple jurisdictions (i.e., provinces/states, countries, etc.). This challenge is only exacerbated when the study involves multiple timepoints (i.e., time-series, dynamic analysis). Data not only need to be compatible between maps (i.e., format, resolution, attributes, etc.), but also consistent over time. Although there were a variety of recent (circa ~ 2015) Canadian, American, and continental North American land-cover maps available at resolutions down to 15 m, none of these GIS datasets had equivalent datasets for past years; and different datasets from earlier timepoints had both attribute and resolution disparities with the most recent maps. Thus, we opted for the ESA-CCI-LC global land-cover dataset that was updated yearly and had consistent map resolution (300 m) and attributes (24 land-cover categories) throughout the entire time period (1992–2018). The only drawback was that the ESA-CCI-LC dataset did not include a separate roads network category. To compensate, we initially applied the Census Road Network files from Statistics Canada and the U.S. Census Bureau, however, we found that not only were they incompatible between countries (i.e., road classifications), but were also incompatible between timepoints within each dataset (i.e., we found inconsistencies (increases and decreases) in the length and density of the road network over time, within both datasets). As a result, we opted for commercial datasets from DMTI Spatial Inc. (Québec and Ontario) and New York State Information Technology Services (New York State). Although both datasets were highly compatible and consistent over time, the data for Québec and Ontario only went back to 2000, and the data for New York only back to 2010. Thus, the tradeoff for accuracy was that we could only do the landscape fragmentation analysis (which required roads) between 2000/2010 and 2018. We ran into similar difficulties when we tried to add additional map layers used in traditional static land-cover analyses, such as population density, forest attributes (i.e., age, height, density, etc.), and agricultural attributes (i.e., hedgerows, wooded areas, wetlands, natural pastures, etc.). Nevertheless, by selecting accuracy and compatibility over complexity, we were able to measure changes in landscape composition and configuration within the A2L and identify priority areas for conservation and ecological restoration.

Since the completion of this work, a new global land-cover dataset "GlobeLand30" was introduced. It includes the years 2000, 2010, and 2020, has a resolution of 30 m, and a very high classification accuracy (~ 86.7%) (Sun et al. 2022). Its major drawbacks are that it only utilizes 10 land-cover classes, and it also does not contain a separate road network category.

However, it does give researchers a higher-resolution option for future multi-timepoint transboundary analysis.

Conclusions

Many MRCs/counties within the A2L have reached or exceeded thresholds of habitat loss and fragmentation and further changes in landscape structure will significantly jeopardize the integrity and connectivity of the transboundary wildlife linkage. These results highlight the necessity for coordinated and cooperative transboundary conservation efforts. Coordinated conservation across boundaries not only improves the protection of shared conservation features (i.e., ecosystems, species, and natural resources), but can also prove to be considerably cost-effective (Kark et al. 2015). Transboundary conservation is especially valuable when neighbours share common objectives and practices, socioeconomic networks, and information and technology (Bodin and Crona 2009; Kark et al. 2015). Canada and the USA are neighbours that possess these attributes, making an A2L transboundary conservation collaboration highly feasible (Mason et al. 2020). A prime example of the benefits of a transboundary collaboration between Canada and the USA is the Yellowstone-to-Yukon Conservation Initiative (Y2Y). The Y2Y is made up of a network of public, private, and Indigenous protected areas that are critical for the protection of large-ranging transboundary species (Graumlich and Francis 2010; Chester 2015). The strength of the Y2Y initiative comes from its diverse multiscale partnerships across the region. These partnerships have permitted the organization to develop policies for the construction of WCSs, to secure priority lands, and to prevent habitat loss and reduce fragmentation (Graumlich and Francis 2010; Chester 2015; Kark et al. 2015; Mason et al. 2020). Worldwide, there are now over 200 active cases of transboundary conservation (Vasilijević et al. 2015).

The post-2020 global biodiversity framework includes the expansion of protected areas and OECMs to cover at least 30% of the planet by 2030 (CBD 2021). Nevertheless, biodiversity will continue to decline if protected areas become isolated from one another by a landscape vulnerable to increasing habitat loss, fragmentation, and a rapidly changing climate (Kremen and Merenlender 2018). Measuring and monitoring of land-cover changes and landscape fragmentation is an effective way to identify priority locations for conservation and ecological restoration and should be included in regional conservation planning and monitoring programs. We have offered seven recommendations for conservation at the local level that will increase habitats and resources and enhance landscape connectivity between protected areas. Strengthening conservation strategies that safeguard and restore landscape connectivity and protect local ecosystems at the MRC/county level will ultimately help achieve post-2020 biodiversity commitments at the provincial, national, and transboundary levels.

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Declarations

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