



Rapid evaluation of habitat connectivity change to safeguard multispecies persistence in human-transformed landscapes

Jacqueline Oehri^{1,2} · Sylvia L. R. Wood² · Eluna Touratier¹ · Brian Leung¹ · Andrew Gonzalez^{1,2,3}

Received: 27 January 2024 / Revised: 6 September 2024 / Accepted: 10 September 2024 /
Published online: 24 September 2024
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Abstract

Following the adoption of the Post-2020 Kunming-Montreal Global Biodiversity Framework (KM-GBF) of the Convention on Biological Diversity (CBD) there is a clear science-policy need to protect habitat connectivity and track its change over time to safeguard biodiversity and inform conservation planning. In response to this need we describe an analytical, multi-indicator and multispecies approach for the rapid assessment of habitat connectivity at fine spatial grain and at the extent of an entire ecoregion. Out of 68 connectivity indicators we found through a literature review, we identified a key-set of six indicators that align with the Essential Biodiversity Variables framework and are suitable to guide rapid action for connectivity and conservation targets in the KM-GBF. Using these selected indicators, we mapped and evaluated connectivity change from 2011 to 2021 across the ecoregion of the St-Lawrence Lowlands in Quebec (~30,000 km²) for seven eco-profile species representing regional forest habitat needs. For most of these species, trends over the last decade indicate a decline in effective connected area and metapopulation carrying capacity, via a division of large contiguous habitat into smaller fragments, whereas on average, habitat area slightly increased. These results highlight that temporal changes in habitat area and connectivity are not necessarily correlated and the urgent need to conserve and restore connectivity to meet targets under the KM-GBF. We provide an R-tool to support our general approach, which enables a comprehensive evaluation of connectivity for regional spatial planning for biodiversity in regions with moderate to high human disturbance.

Keywords Connectivity conservation · Metapopulation carrying capacity · Essential Biodiversity Variables · Habitat fragmentation · Kunming-Montreal Global Biodiversity Framework · Rapid assessment of multispecies connectivity

Communicated by Michael Joy.

Extended author information available on the last page of the article

Introduction

Habitat fragmentation due to human land-use change is among the most important causes of global biodiversity loss (Crooks et al. 2017; Haddad et al. 2015; Sala et al. 2000). Habitat fragmentation, i.e., the division of habitat into smaller and more isolated fragments (Haddad et al. 2015), impairs ecological connectivity, the ‘unimpeded movement of species and the flow of natural processes that sustain life on Earth’ (CMS 2019). Ecological connectivity (hereafter ‘connectivity’) encompasses both the capacity of a landscape to maintain viable routes for potential species movement through physically linked habitat patches (structural connectivity, Calabrese and Fagan 2004) and the realized ability of species to move through the landscape (functional connectivity, Salgueiro et al. 2021; Tischendorf and Fahrig 2000). Both aspects of connectivity are expected to mediate the persistence of species in a landscape and the functional effects species have via their movements. Hence, safeguarding connectivity is essential for the maintenance of biodiversity, as well as the integrity and functioning of ecosystems (Crooks and Sanjayan 2006; Crooks et al. 2017; Correa Ayram et al. 2016; Hou et al. 2024; Morelli et al. 2017) and has been incorporated as a central element of the targets of the Post-2020 Kunming-Montreal Global Biodiversity Framework (KM-GBF) of the Convention on Biological Diversity (CBD 2021).

However, despite its importance, assessments of connectivity are not systematically considered in conservation planning and management (Baguette and Van Dyck 2007; Saura et al. 2018; Ward et al. 2020). This is reflected by the fact that only about 10% of the world’s protected area network are also connected (Ward et al. 2020). At this time, the Kunming-Montreal Global Biodiversity Framework of the UN Convention of Biological Diversity (GBF, hereafter) lacks an agreed headline indicator for monitoring connectivity, although some component indicators have been proposed (COP decision 15/5). Under the Monitoring Framework of the GBF countries have a key need to employ the measures and methods to rapidly assess connectivity and monitor connectivity change for a wide range of species, guiding conservation action to mitigate impacts and use indicators to assess progress toward national and global targets set for 2030 (UN CBD 2021; Gonzalez et al. 2023; Jetz et al. 2019; Tittensor et al. 2014).

There exists a multitude of indicators for monitoring the structural and functional facets of connectivity (Keeley et al. 2021) but how they compare and what they imply for conservation management is often not easy to interpret (Hanson et al. 2022; Lalechère and Bergès 2021; Wood et al. 2022). To date, common definitions, goals and standards to measure and evaluate connectivity change have not been well-established and consequently, criteria for critical connectivity thresholds are often not operationalized in spatial conservation planning (Beger et al. 2022; Ward et al. 2020; Wood et al. 2022). Additionally, most connectivity indicators are difficult to interpret biologically in terms of the long-term outcomes for the persistence (e.g., extinction risk) of multiple species over a range of scales (Wood et al. 2022). The situation exists in part because rapid assessments of the connectivity needs of a wide range of taxa across spatial scales remains both a theoretical and computational challenge (Wood et al. 2022).

A recent review by Wood et al., (2022) highlights the potential of modelling multispecies connectivity either using carefully constructed “ecoprofiles” (Opdam et al. 2008), where a single species is selected or a generic species with composite trait values is created to represent the movement and habitat needs of a particular set or group of species (Brodie et al. 2015). Alternatively, a “multiple focal species” approach (Albert et al. 2017; Correa Ayram et al. 2018; Meurant et al. 2018) can be used, where landscape connectivity is

modeled separately across a set of species with diverse ecological traits and their complementary connectivity priorities are identified and prioritized post hoc.

We conducted a literature review to identify commonly applied connectivity indicators that are suited for multispecies assessments, and that align with the criteria for Essential Biodiversity Variables (EBV) defined by the Group on Earth Observations Biodiversity Observation Network (GEO BON), such that they are feasible, (i.e. allow the monitoring of connectivity for multiple species with sufficient data inputs) are scalable, are sensitive to temporal change, and are relevant for biodiversity conservation targets (Jetz et al. 2019; Pereira et al. 2013). We searched for metrics that can be computed from relatively simple habitat distribution maps (Beger et al. 2022; Ward et al. 2020) to ensure wide scale applicability. The selected indicators include proxies of connectedness at patch-level, as well as estimates of habitat-network connectivity at the landscape-level. We also included metapopulation capacity as an indicator of potential long-term species persistence (Hanski and Ovaskainen 2000; Hanski 1994; Huang et al. 2020; Schnell et al. 2013; Stott et al. 2010; Strimas-Mackey and Brodie 2018). To facilitate the interpretation and use of these indicators, we compare and contrast their characteristics and assess their correlation and sensitivity to changing habitat amount and fragmentation using a set of simulated landscapes (Saura and Martínez-Millán 2000; Sciaini et al. 2018).

Using this set of selected multispecies connectivity indicators we developed a tool coded in R, “Rapid Evaluation for Connectivity Indicators and Planning” (Reconnect, Fig. 1, available at <https://github.com/oehrij/Reconnect>), and we used it to assess habitat connectivity and its temporal change from 2011 to 2021, for seven ecoprofile species

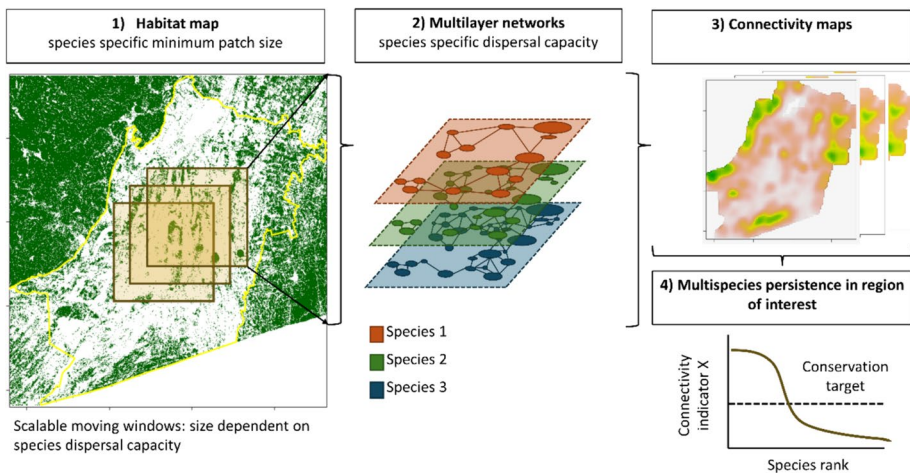


Fig. 1 Steps for conducting a rapid evaluation of multispecies connectivity using the Reconnect approach and R-tool. (1) Input data for the Reconnect tool is a species (or ecoprofile) specific, binary habitat map that can be determined a priori (e.g. from described habitat needs) or a posteriori (e.g., from species distribution models). (2) Multiple habitat maps can be “stacked”, and multilayer habitat networks can be extracted, in which links between habitat patches depend on species-specific dispersal capacities. Multilayer habitat networks can be computed in moving windows of relevant size and variable spatial overlap. (3) Multiple connectivity indicators can be computed simultaneously for multiple species in the moving windows. Moving window results can be aggregated into mosaics, i.e. coherent maps of connectivity at pixel-level, patch-level or landscape-level for the species of interest. (4) The resulting maps can be used to evaluate multiple connectivity indicators for the multiple species regarding a defined target- or minimum threshold

representative of regional forest habitat and connectivity needs (Albert et al. 2017; Meurant et al. 2018; Rayfield et al. 2016) in the ecoregion of the St-Lawrence Lowlands in Quebec, Canada (Fig. 2). We were particularly focused on assessing the correlation between changes in habitat area and habitat connectivity. Depending on the remaining cover and configuration of habitat one may expect positive, negative, or no correlation between the change in habitat area and habitat connectivity. To date, no analysis of this question has been conducted for this ecoregion.

The St-Lawrence Lowlands study region has unique biogeographic characteristics, significant biodiversity and is affected by urbanization, agricultural expansion and habitat fragmentation, especially of forests and wetlands (Albert et al. 2017; Dupras et al. 2016; Lucet and Gonzalez 2022; Mitchell et al. 2015; Rayfield et al. 2021). This ecoregion is one of eleven priority places within the “Pan-Canadian Approach to Transforming Species at Risk Conservation in Canada” (ECCC 2018; Jobin et al. 2020).

Based on the results of our study, we identify areas with high priority for connectivity conservation. By assessing connectivity for multiple species with diverse habitat and movement needs, our work is contributing to the systematic evaluation of long-term species persistence. This work is designed to support conservation planning and management of connectivity currently undertaken by the conservation NGOs and municipal and provincial governments in the ecoregion that are active partners in this research and tool development.

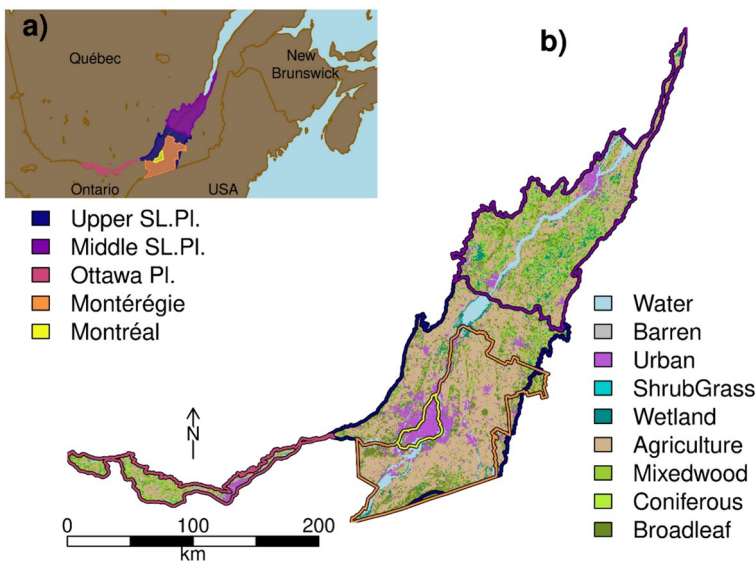


Fig. 2 St-Lawrence Lowlands study region. **a** The St-Lawrence Lowlands ecoregion in Eastern Canada spans ~30,000 km² and is a priority landscape within the “Pan-Canadian Approach to Transforming Species at Risk Conservation in Canada” (ECCC 2018; Jobin et al. 2020). **b** The St-Lawrence Lowlands consists of five subregions: The Upper St-Lawrence Plain (including the regions of interest Montreal and Montérégie), the Middle St-Lawrence Plain, the Ottawa Plain, as well as the Montérégie and Montréal subregions, and is composed predominantly of agricultural, urban and mixedwood land-cover classes

Methods

Multispecies connectivity indicators literature review

We conducted a literature review according to the PRISMA approach to identify indicators suitable for the rapid assessment of multispecies connectivity across scales and regions of interest (Liberati et al. 2009).

Specifically, on January 24th, 2022, we searched all journal articles published since January 1, 2000, on the Scopus and Web of Science databases using the following search string: habitat OR ecosystem OR “protected area” AND connectivity AND indicator OR metric OR indice OR index AND (multi OR several OR group) NEAR/3 species OR community AND conservation OR management OR monitoring OR planning AND biodiversity. This search led to a total of 1028 unique articles across queried databases. In a first screening step, we excluded all articles that did not mention either connectivity or monitoring in their title, leading to a total of 431 articles. In a second screening step, we excluded articles that (1) were not concerned with habitat connectivity, (2) were not primary research articles, (3) did not use any indicator of connectivity, or (4) were focused on a single species only, however articles that used a single species as umbrella species were kept. We reviewed the resulting 208 articles, identified the connectivity indicators they used, as well as the ecosystem types and taxa they were concerned with. Articles that did not align with our earlier criteria were removed, leaving a final set of 171 articles (SI Fig. 1, SI Table 1).

These 171 articles featured 68 indicators applied to quantify connectivity for multiple species. To distill a comprehensive subset of these indicators suitable for multispecies connectivity monitoring, we evaluated their correspondence with criteria established for the Essential Biodiversity Variable’s framework of GEO BON (Jetz et al. 2019; Pereira et al. 2013; geobon.org/ebvs/). In more detail, we scored each indicator according to (i) its feasibility (it can be computed from readily available data), (ii) its relevance (it allows for a coherent interpretation and alignment with biodiversity targets), (iii) its scalability, (it is computable across spatial scales and generalizable across a range of species and ecosystems), (iv) its sensitivity to connectivity change over time and space (SI Table 2). The selected set of key-indicators should further consist of (v) indicators which are complementary regarding scale and interpretation (Fletcher et al. 2023).

Based on our literature review and the EBV-criteria scores (SI Table 2), we summarise a set of six complementary connectivity indicators that are well suited for the multispecies connectivity monitoring, offer a coherent interpretation, are relevant for conservation targets and can be efficiently computed based on simple habitat distribution maps across many species and environmental contexts (Table 1). Our EBV-criteria scores revealed three functional connectivity metrics with high relevance regarding interpretability and alignment with biodiversity conservation targets: the betweenness centrality at patch-level (BC; Albert et al. 2017; Brandes 2001; Freeman 1978), approximating the stepping-stone functionality of habitat patches for long-range movements, the node degree at patch-level (ND; Minor and Urban 2008), approximating the stepping-stone functionality of habitat patches for short-range movements and the effectively connected habitat area at landscape-level (ECA; Saura et al. 2011), approximating the area of effectively connected habitat relevant for area-based conservation targets. Additionally, to compare ECA among administrative regions of different sizes, it is useful to use a relative measure, e.g., ECA as a fraction of the total habitat- or landscape area. Several recent studies assess relative ECA as a fraction

Table 1 Selected set of connectivity indicators

Nr	Indicator name	Abbr	Scale, interpretation and relevance for conservation target	Formula	Unit [value range]	Ref
1	Metapopulation capacity	MPC	Scale <i>landscape-level</i> Interpretation Metapopulation carrying capacity, based on area and connectance of habitat Relevance Approximates potential long-term species persistence in a given habitat network	$m_{ij} = \begin{cases} MPC = \lambda_m & i \neq j \\ f(d_{ij})a_jd_i^x & i = j \\ a_jd_i^x & i = j \end{cases}$ <p>where λ_m is the leading eigenvalue of a square 'landscape matrix' m, in which elements m_{ij} reflect rates of change for the occupancy of patches i (π_i) as a function of patch attributes (often patch area in m^2, a_i and a_j), a dispersal probability function of interpatch distance $f(d_{ij})$ and an extinction probability constant x (commonly set to 0.5)</p>	No unit [0, λ_{max}] where λ_{max} corresponds to the leading eigenvalue of the maximum landscape matrix, i.e. where the rates of change of patch occupancy is 1 for all patches	Hanski and Ovaskainen (2000), Hanski (1994), Schnell et al. (2013)

Table 1 (continued)

Nr	Indicator name	Abbr	Scale, interpretation and relevance for conservation target	Formula	Unit [value range]	Ref
2	MPC patch importance	MPC _i	Scale <i>patch-level</i> Interpretation The degree to which a patch contributes to the MPC of the habitat network Relevance Approximates the contribution of a site to potential long-term species persistence in a given habitat network	$m_{ij} = \begin{cases} MPC_i = \lambda_{mi} & i \neq j \\ \frac{f(d_{ij})a_j d_i^x}{a_j a_i^x} & i = j \end{cases}$ <p>where λ_{mi} is the leading eigenvector at position i, for patch i of a square ‘landscape matrix’ m, in which elements m_{ij} reflect rates of change for the occupancy of patches i (p_i). a_i and a_j are patch attributes (often patch area in m^2), $f(d_{ij})$ is a dispersal probability function of interpatch distance x denotes an extinction probability constant (commonly set to 0.5)</p>	No unit [0, λ_{max}], where λ_{max} corresponds to the leading eigenvalue of the maximum landscape matrix, i.e. where the rates of change of patch occupancy is 1 for all patches	Hanski and Ovaskainen (2000)
3	Equivalent Connected Area index	ECA	Scale <i>landscape-level</i> Interpretation Size of a single habitat patch that would provide the same probability of connectivity than the actual habitat patch in the landscape Relevance Approximates the area of effectively connected habitat (area-based conservation)	$ECA = \sqrt{\sum_{i=1}^n \sum_{j=1}^n a_i a_j p_{ij}^*}$ <p>where n is the total number of habitat patches in the landscape, a_i and a_j are attributes of habitat patches i and j (commonly area in m^2) and p_{ij}^* is the maximum product probability of dispersal between patches i and j</p>	Unit of a (e.g. area) [0, AI], where AI is the attribute (e.g. area) of the entire landscape	Saura et al. (2011), Saura and Pascual-Hortal (2007)

Table 1 (continued)

Nr	Indicator name	Abbr	Scale, interpretation and relevance for conservation target	Formula	Unit [value range]	Ref
4	ECA fraction of habitat area	ECA_{Ap}	Scale <i>landscape-level</i> Interpretation Size of equivalent connected area (ECA) relative to maximum possible with a given habitat area (Ap) Relevance Approximates the degree of connectedness of existing habitat	$ECA_{Ap} = \frac{ECA}{Ap}$, where Ap is the total area of habitat in a given landscape	No unit [0, 1]	Saura et al. (2017), Saura et al. (2018)
5	Betweenness centrality	BC	Scale <i>patch-level</i> Interpretation Number of shortest paths between each pair of habitat patches passing through a focal patch Relevance Approximates the stepping-stone functionality of patches for long-range movements	$BC_v = \sum_{i \neq j, i \neq v, j \neq v} \frac{g_{ij}}{g_{vj}}$, where g_{ij} is the total number of shortest paths between each pair of habitat patches ij going through a focal patch v in the habitat network. g_{ij} is the total number of all the shortest paths between each pair of habitat patches ij in the habitat network	No unit $[0, \frac{(n-1)(n-2)}{2}]$, where n corresponds to the number of patches in the landscape	Albert et al. (2017), Brandes (2001), Freeman (1978)

Table 1 (continued)

Nr	Indicator name	Abbr	Scale, interpretation and relevance for conservation target	Formula	Unit [value range]	Ref
6	Node Degree	ND	Scale <i>patch-level</i> Interpretation Number of other habitat patches connected to a focal patch Relevance Approximates the stepping-stone functionality of patches for short-range movements	$ND_v = \sum_{j \neq v} e_{vj}$ $e_{vj} = \begin{cases} 1 & p_{vj}^* > c \\ 0 & p_{vj}^* \leq c \end{cases}$ where e_{vj} denotes a habitat patch j connected to the focal patch v . A habitat patch can be considered connected ($e_{vj} = 1$) if p_{vj}^* , the maximum product probability of dispersal between patches j and v is greater than a threshold probability c	No unit [0, n – 1], where n corresponds to the number of patches in the landscape	Minor and Urban (2008)

This set of connectivity indicators has been identified through a literature review and selection criteria aligned with the Essential Biodiversity Variables (Jetz et al. 2019; Pereira et al. 2013) framework (SI Fig. 1, SI Tables 1 and 2). These indicators can be calculated based on simple habitat or protected area distribution maps, species-specific habitat needs and dispersal capacities. Note that the distance between patches (relevant for dispersal probability functions) can be Euclidean or scaled by a resistance surface (Albert et al. 2017; Chubaty et al. 2020; Shahnasari et al. 2019). Nr: index number; Indicator name: name of indicator; Abbr.: abbreviation of indicator name; Scale: the scale at which indicator is typically calculated (patch-, or landscape-level). Landscape-level indicators can also be calculated at patch level using the ‘patch importance for landscape-level connectivity indicators’ computation I_v (Eq. 3), or in the case of metapopulation capacity, the dominant eigenvector value for patch i (MPC_{*i*}). Note that patch-level indicators can usually be aggregated at the landscape-level, using any aggregation function of interest (e.g. mean, range, variation). Interpretation: interpretation of the indicator; relevance: relevance of indicator for biodiversity conservation targets. Formula: formal definition of indicator, Unit: unit and value range of indicator, Ref.: reference with background information on indicators. Note that our Reconnect approach is not limited to these indicators but can be implemented with any indicator that is computable based on habitat, protected area or resistance surface maps

of total landscape area (Castillo et al. 2020; Saura et al. 2017, 2018; Shi et al. 2023; Ward et al. 2020). We chose to include relative ECA as a fraction of total habitat area in a landscape (ECA_{Ap} , Table 1), because it offers a more nuanced interpretation of the degree of connectedness of existing habitat, relevant for the identification of underused connectivity potential and allowing the distinction of landscapes with high amounts of habitat that are not well connected from landscapes with low amounts of habitat that are well connected (Saura et al. 2017, 2018). The indicators “buffer habitat” (Keeley et al. 2021) and “Probability of Connectivity” (PC, Saura and Pascual-Hortal 2007) with high EBV-criteria scores are structurally and conceptually very similar to ECA; therefore, we did not include these in our key-set of indicators (SI Table 2; note that ECA is based on PC, Saura et al. 2011). To add an indicator with a more coherent ecological interpretation, we included the meta-population capacity indicator, relevant for long-term species persistence at landscape-level (MPC; Hanski 1994; Hanski and Ovaskainen 2000; Schnell et al. 2013). We included MPC instead of the Incidence Function Measure (IFM; Hanski 1994; Moilanen and Nieminen 2002), a conceptually and structurally similar indicator with high EBV-criteria scores (SI Table 2) for two reasons: first, MPC can simultaneously be assessed at landscape-level and at patch-level (cf. MPC_i, Table 1) whereas aggregating the IFM measure at landscape-level has been shown to be challenging (Saura and Pascual-Hortal 2007). Second, MPC approximates long-term dispersal outcomes and therefore adds an important temporal perspective relevant for long-term species persistence targets (Hanski and Ovaskainen 2000; Hanski 1994; Huang et al. 2020; Schnell et al. 2013; Stott et al. 2010; Strimas-Mackey and Brodie 2018).








The remainder of this paper demonstrates the application of these indicators to evaluate change in connectivity in a real-world case study in southern Quebec. In addition to the calculation of the six key-indicators of connectivity, we also calculate habitat area and patch area indicators at the landscape and patch-level, respectively, to assess the relationship between the change in habitat area and connectivity in the landscape.

Case study region, species and habitat selection

We focused on the St-Lawrence Lowlands ecoregion of Quebec, Canada as defined by the Quebec Ecological Reference Framework (Direction de l'expertise en biodiversité 2018, Fig. 2), consisting of five subregions: the upper St-Lawrence Plain (including the areas of Montréal and parts of the Montérégie, 17,315 km²), the middle St-Lawrence Plain (11,156 km²), the Ottawa Plain (2223 km²), as well as the Montérégie (9514 km²) and Montréal subregions of interest (627 km²). The St-Lawrence Lowlands harbors a relatively large fraction of Quebec's biodiversity and is home to more than 55 species at risk (Tardif et al. 2005). At the same time, more than 4 million people (more than half of Quebec's human population) live in this ecoregion, and anthropogenic activities that compromise the integrity of ecosystems are extensive, driven by urbanization, intensive agriculture and forestry, as well as the presence of invasive species (Jobin et al. 2020).

To model multispecies connectivity, we focused on seven species that depend on forest habitat and connectivity, and which were used by previous research (Albert et al. 2017; Meurant et al. 2018; Rayfield et al. 2016): American marten (*Martes americana*), black bear (*Ursus americanus*), northern short-tailed shrew (*Blarina brevicauda*), red-back salamander (*Plethodon cinereus*), wood frog (*Rana sylvatica*), ovenbird (*Seiurus aurocapilla*) and barred owl (*Strix varia*, Table 2). These species are a representative subset (Meurant et al. 2018) of an initial set of 14 surrogate species identified in Albert et al. (2017) that

Table 2 Selection of focal species for multispecies forest connectivity assessment

Legend	Common name	Scientific name	Habitat needs		Dispersal capacity	
			Habitat type	Minimum patch size (ha)	Gap-crossing distance (m)	
	American marten	<i>Martes americana</i>	Forest (mixed and coniferous)	150	220	
	Barred owl	<i>Strix varia</i>	Forest (broadleaf and mixed)	1	209	
	Black bear	<i>Ursus americanus</i>	Forest (broadleaf and mixed)	1200	236	
	Northern short-tailed shrew	<i>Blarina brevicauda</i>	Forest (broadleaf and mixed)	1	39	
	Red-back salamander	<i>Plethodon cinereus</i>	Forest (broadleaf and mixed)	0.27	10	
	Ovenbird	<i>Seiurus aurocapilla</i>	Forest (broadleaf and mixed)	5	54	
	Wood frog	<i>Rana sylvatica</i>	Forest (broadleaf, mixed and coniferous)	0.5	39	

This set of species was selected based on previous research (Albert et al. 2017; Rayfield et al. 2016) that identified suitable ecoprofile species (Opdam et al. 2008; Wood et al. 2022) for assessing forest connectivity across the St-Lawrence Lowlands spanning the ecologically relevant range of forest habitat needs and dispersal capacities. Habitat type: type of forest species depends upon; Minimum patch size (ha): minimum habitat patch size in hectares that sustains a reproductive pair of a species population; Gap-crossing distance (m): average distance in meters a species can cross from one habitat patch to another, across a swath of inhospitable landscape area (Albert et al. 2017; Grubb and Doherty 1999)

cover the connectivity needs of forest-dependent terrestrial vertebrates across the St-Lawrence Lowlands. We selected the same subset of five species identified by Meurant et al. (2018) but also included the ovenbird and barred owl in order to represent birds with distinct forest needs. These species can simultaneously be interpreted as surrogate as well as ecoprofile species (Wood et al. 2022), which represent a regionally relevant range of forest habitat needs and dispersal capacities (Albert et al. 2017). Habitat needs were identified by Albert et al. (2017) and reflect the type of forest each species depends upon (coniferous, broadleaf and mixed) as well as the minimum habitat patch area that sustains a reproductive pair of a species population. Similarly, we adopted species-specific dispersal capacities as the corresponding mean gap-crossing distances identified by Albert et al. (2017; Table 2). Gap-crossing distance can be defined as the distance a species is able to cross from one habitat patch to another, across a swath of inhospitable landscape area (Albert et al. 2017; Grubb and Doherty 1999).

Decadal change of multispecies connectivity across the St-Lawrence Lowlands

We assessed the state of habitat connectivity as captured by all our indicators (Table 1), for the seven species (Table 2) across the St-Lawrence Lowlands ecoregion for the years 2011 and 2021, using the Reconnect tool (Fig. 1).

The Reconnect R-tool is based on recently developed R-packages (Csardi and Nepusz 2006; van Etten 2017; Godínez-Gómez and Correa Ayram 2020; Hesselbarth et al. 2019) and R-functions found in Huang et al. (2020) and Strimas-Mackey and Brodie (2018). It allows for the assessment of multiple connectivity indicators simultaneously for multiple species (cf. multilayer habitat networks in Hartfelder et al. 2020), using simple habitat distribution maps and a parallel implementation of moving windows that are adjustable in form, size and spatial overlap (Drielsma and Ferrier 2009; Hughes et al. 2023).

Specifically, we derived species-specific, binary habitat maps (i.e. gridded spatial data with location of habitat vs. non-habitat areas) from land-cover information provided by the Annual Crop Inventory data layer (30 m resolution, Agriculture and Agri-Food Canada 2023) for the years of 2011 and 2021. To classify discrete, species-specific habitat patches from the Annual Crop Inventory data, we extracted the land-cover classes “Coniferous”, “Broadleaf”, “Mixedwood” and combined these with minimum habitat patch size criteria for each species in Table 2 (habitat maps for the seven species and years 2011 and 2021 are provided in SI Figs. 2 and 3). In these species-specific habitat networks, we determined the species-specific dispersal probabilities among habitat patches by a negative exponential kernel (Hartfelder et al. 2020; Moilanen and Nieminen 2002; Strimas-Mackey and Brodie 2018):

$$p_{ij} = \exp(-\alpha d_{ij}) \quad (1)$$

, where α is the inverse mean gap-crossing distance (Table 2, cf. Hanski and Ovaskainen 2000; Hartfelder et al. 2020; Moilanen and Nieminen 2002) and d_{ij} is the Euclidean edge-to-edge distance between patch i and patch j in the habitat network.

Using our Reconnect tool, we computed connectivity indicators in square moving windows with a side length of 8700 m and an area of $\sim 75 \text{ km}^2$, similar to previous research (Huang et al. 2020; Strimas-Mackey and Brodie 2018). To build seamless landscape results across our moving window analysis we chose a window overlap of 1500 m. Using these settings, we generated species-specific maps of landscape-level connectivity indicators, by averaging the connectivity values in $\sim 75 \text{ km}^2$ overlapping

moving window landscapes for each pixel at a 1.5 km effective resolution. Similarly, we generated species-specific maps of patch-level connectivity indicators, by computing the weighted mean values for each patch covered by overlapping moving window landscapes (weighted by the respective area patches covered in the overlapping moving-window landscapes).

To quantify the decadal change in the spatial distribution of species-specific connectivity, we subtracted Reconnect results for 2011 from those calculated for 2021, for each species and connectivity indicator separately. Next, we averaged the species-specific results to generate a map of the spatial distribution of multispecies connectivity gains and losses across the St-Lawrence Lowlands for each of the selected connectivity indicators separately (Fig. 3).

In a supplementary analysis, we provide ensemble connectivity maps for the year 2021 (SI Fig. 4), which resulted from averaging species-specific connectivity maps in 2021 that were previously normalized using the feature scaling approach:

$$x' = 100 \times \frac{x - \min(x)}{\max(x) - \min(x)}, \quad (2)$$

where x is the vector of all values contained in the respective connectivity maps.

This normalization was done to focus on the relative magnitude of connectivity values and to give each species equal weight when aggregating post hoc.

Evaluating multispecies connectivity change for species persistence

To shift the focus from a spatial assessment to an actionable evaluation of connectivity across species, we used a species-rank approach (Chowdhury et al. 2023; Hartfelder et al. 2020; Silvestro et al. 2022) to rank the summed, species-specific connectivity change magnitudes across five subregions of interest in the St-Lawrence Lowlands (Direction de l'expertise en biodiversité 2018; Fig. 4).

In particular, in the cases of landscape-level metapopulation capacity (MPC), equivalent connected area (ECA) and habitat area, we scaled the species-specific, Reconnect-derived connectivity change values by dividing by the area of the moving window size ($8700 \text{ m} \times 8700 \text{ m} = 75.69 \text{ km}^2$). Then, we multiplied these landscape-level connectivity change values by the area they cover, and consequently summed these values to assess the total amount of connectivity change for each species and subregion of interest.

In the case of the patch-level connectivity indicators of metapopulation capacity patch importance (MPC_{imp}), node degree (ND) and betweenness centrality (BC), as well as patch size (patch area), we extracted the distribution of values for each species and subregion of interest for the years 2011 and 2021. We then assessed the decadal change of patch-connectivity magnitudes by comparing connectivity magnitudes of all habitat patches in 2021 to those in 2011 using two-sided Welch's unequal variances t-tests. We used Welch's t-tests because they are more robust than Student's t-tests when the two samples have unequal variances and/or unequal sample sizes, as was the case for our habitat patch values in 2021 and 2011, respectively (Ruxton 2006).

In a supplementary analysis, we summarized and ranked connectivity results for each ecoprofile species within five subregions of interest for the year 2021 (SI Fig. 5).

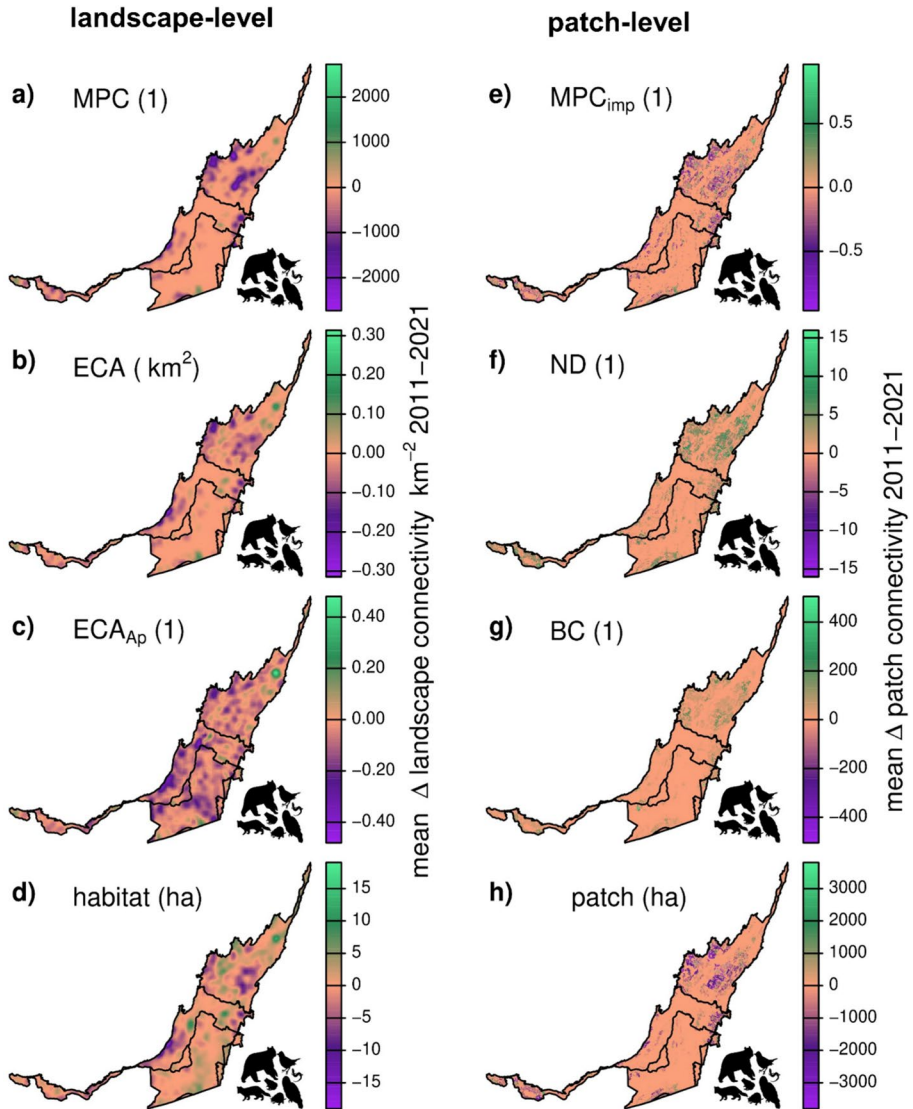


Fig. 3 Decadal change (2011–2021) in multispecies connectivity indicators at the landscape-level (**a–d**) and patch-level (**e–h**) across the St-Lawrence Lowlands as calculated by Reconnect. **a** MPC: metapopulation capacity, **b** ECA: equivalent connected area index (km²), **c** ECA_{Ap}: fraction of habitat that is connected, **d** habitat (ha): habitat area in hectares, **e** MPC_{imp}: metapopulation capacity patch importance, **f** ND: node degree of focal patches, **g** BC: betweenness centrality of focal patches, **h** patch (ha): area of focal patches in hectares. We scaled connectivity values by the area of the Reconnect moving window size (8700 m × 8700 m = 75.69 km²) if necessary, i.e. in the cases of MPC, ECA and habitat area. See Table 1 for more detailed explanations of connectivity indicators

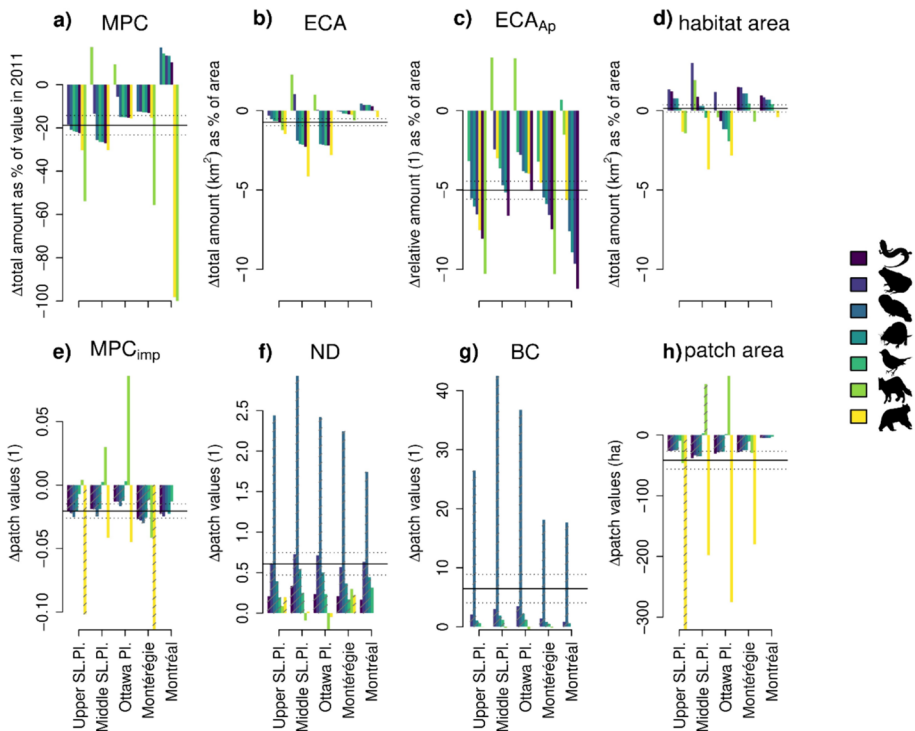


Fig. 4 Decadal change (2011–2021) of multispecies connectivity indicators at landscape-level (**a–d**) and patch-level (**e–h**) for 5 different regions in the St-Lawrence Lowlands by species. **a** MPC: metapopulation capacity, **b** ECA: equivalent connected area index, **c** ECA_{Ap} : fraction of habitat that is connected, **d** habitat area: species-specific area of habitat, **e** MPC_{imp} : metapopulation capacity patch importance, **f** ND: node degree of focal patches, **g** BC: betweenness centrality of focal patches, **h** patch area: area of focal patches in hectares. Horizontal bars indicate the mean and s.e. of change across all regions and species. Hashed bars in **e–h** indicate significant changes ($P < 0.05$) in patch-connectivity magnitudes as indicated by two-sided Welch's t-tests comparing patch values in 2021 and 2011. See Table 1 for more detailed explanations of connectivity indicators. See SI Tables 3 and 4 for more details

Comparing multispecies connectivity in simulated and real-world landscapes

To facilitate interpretation and use of the selected key-set of connectivity indicators, we generated a reference set of simulated landscapes orthogonal in their gradients of habitat amount and fragmentation using the “random-cluster” algorithm (Saura and Martínez-Millán 2000) and implemented in the NLMR R-package (Sciaini et al. 2018, SI Fig. 6). In particular, we generated five landscape replicates (250×250 cells) along a gradient of habitat amount (0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8 and 0.9 fractional cover in the landscape, parameter A_i in Saura and Martínez-Millán 2000), and habitat fragmentation (clumping factor 0.1, 0.2, 0.3, 0.4, 0.5 and 0.6, parameter p in Saura and Martínez-Millán 2000). In the resulting set of $5 \times 9 \times 6 = 270$ simulated reference landscapes, we computed patch- and landscape-level connectivity indicators using our Reconnect tool for five dispersal capacities— α for a negative exponential distribution [Eq. 1 above]. α values ranged from the inverse of 1 cell unit to 355 cell units, whereby 355 is slightly larger than the diagonal of the simulated landscapes (250×250 cells). We assessed the sensitivity of connectivity

indicators to changes in habitat area (SI Fig. 6a–d), and habitat fragmentation as approximated by the number of habitat patches (SI Fig. 6e–h) across all gap-crossing distances from 1 to 355 cell units by estimated and predicted relationships among connectivity indicators and habitat area (fragmentation) using a smooth spline function (npreg R-package, Helwig 2021). This analysis allowed us to capture non-linearities in relationships among connectivity indicators and habitat area (or fragmentation), as well as assessing the effect of different gap-crossing dispersal capacities.

Compared with landscape size, a gap-crossing distance of 6.8 cells is comparable with the maximum gap-crossing distance among our selected species (236 m, Table 2) in the moving window landscapes of $\sim 75 \text{ km}^2$ (i.e. both gap-crossing distances correspond to $\sim 1/36$ of the landscape side length). Using these 270 reference landscapes, we assessed Spearman's correlations suitable for non-normally distributed data, as well as their strength (strong: Spearman's $\rho \geq 0.7$, weak-moderate: Spearman's $\rho < 0.7$; Schober et al. 2018) among connectivity indicators for a gap-crossing distance of 6.8 units (Fig. 5a).

Finally, for each connectivity indicator, we sampled 10,000 cells (i.e., pixels with 1.5 km resolution) from the multispecies connectivity maps we generated for the year 2021 (SI Fig. 4). We used a simple random sampling (SRS) approach without sampling intervals ensuring representativeness of the conditions in the St-Lawrence Lowlands (Pawley and McArdle 2021). With these 10,000 cells, i.e., “real-world landscapes” of 2.25 km^2 area, we repeated the correlation analysis described above and compared the results to the results obtained with the simulated landscapes. The simulated landscapes served as a benchmark and comparing real-world patterns to simulated patterns of connectivity allowed us to assess if the real-world patterns can be generalized across a large range of habitat area and -fragmentation configurations (patterns in simulated and real-world landscapes are the

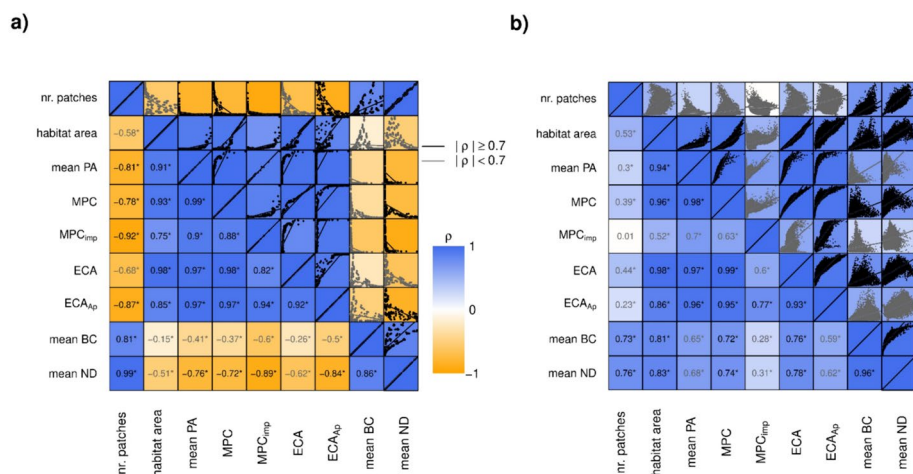


Fig. 5 Spearman correlations among multiple connectivity indicators in simulated landscapes (a) and real-world landscapes in the St-Lawrence Lowlands (b). Upper triangle: data points with fitted linear regression line. Lower triangle: Spearman's correlation coefficient (ρ); strong correlation ($\rho \geq 0.7$, black), weak-moderate correlation ($\rho < 0.7$, grey), significant correlations ($P < 0.1$) are marked by an asterisk (*). Nr. patches: number of habitat patches in the landscape; habitat area: total amount of habitat area in landscape in hectares; mean PA: average patch size in hectares; MPC: metapopulation capacity, MPC_{imp}: average metapopulation capacity patch importance, ECA: Equivalent Connected Area index, ECA_{Ap}: fraction of habitat that is connected, mean BC: average Betweenness Centrality index; mean ND: average Node Degree index. See Table 1 for more detailed explanations of connectivity indicators

same) or do only hold in a specific context (patterns in simulated and real-world landscapes differ; Fig. 5).

Results

Decadal change of multispecies connectivity across the St-Lawrence Lowlands

We assessed the spatial distribution of decadal patch- and landscape-level connectivity change for each species and indicator separately, by calculating the difference between 2021 and 2011. We then averaged results over all species to create a map of multispecies connectivity change for each indicator (Fig. 3).

At the landscape-level, decreases in average multispecies metapopulation capacity (MPC) and equivalent connected area (ECA) are more abundant than gains across the St-Lawrence Lowlands (MPC: losses in 21,342 km², gains in 9663 km², range: −2727 to 1101 km²; ECA: losses in 18,876 km², gains in 12,130 km², range: −0.31 to 0.20 km² km^{−2}), especially in the Middle St-Lawrence Plain (Fig. 3a, b). Similarly, decreases in the fraction of effectively connected habitat (ECA_{Ap}, Fig. 3c) prevail and can reach up to 48% (losses in 24,675 km², gains in 6331 km², range: −0.44 to 0.48 km²), whereas habitat area changes are more variable (losses in 12,510 km², gains in 18,495 km², range: −19 to 14 ha km^{−2}) across the St-Lawrence Lowlands ecoregion (Fig. 3d).

Despite the declines described above, in 2021, the Middle St-Lawrence and Ottawa Plain subregions harbor the highest values of MPC, ECA, ECA_{Ap} and habitat area, and low connectivity indicator values are predominantly found in the Upper St-Lawrence Plain subregion (SI Fig. 4).

Patch-level multispecies connectivity in 2021 (SI Fig. 4) and connectivity changes from 2011 to 2021 (Fig. 3e–h) show a similar spatial distribution as those at the landscape-level. In particular, patch importance for metapopulation capacity (MPC_{imp}) tended to decrease, especially in the Middle St-Lawrence Plain (losses in 6091 km², gains in 4139 km², range: −0.96 to 0.95 per patch; Fig. 3e). In contrast, betweenness centrality (BC) and node degree (ND) show large increases, in the case of BC up to 505 shortest paths between each pair of habitat patches passing through a focal patch (BC: losses in 1650 km², gains in 8160 km², range: −122 to 505 per patch; ND: losses in 2048 km², gains in 8151 km², range: −7 to 16 per patch; Fig. 3f, g). Also, habitat patch size tended to decrease across the entire ecoregion of St-Lawrence Lowlands, sometimes up to 3806 hectares per patch (losses in 6273 km², gains in 4004 km², range: −3767 to 3806 ha per patch; Fig. 3h).

Evaluating multispecies connectivity change for species persistence

We summed and ranked connectivity change for each indicator and ecoprofile species within five subregions of interest in the St-Lawrence Lowlands ecoregion (Fig. 4).

Analyses of decadal changes in landscape-level connectivity indicators (MPC, ECA, ECA_{Ap}), reveal declines for the majority of species and subregions of interest. For example, metapopulation capacity declined by $18.8 \pm 4.5\%$ (mean and s.e.) of its average value in 2011 (4,991,781 units) across species and subregions (black horizontal line, Fig. 4a). Relative metapopulation capacity declines were most pronounced for the Upper St-Lawrence Plain (on average by −27.0% of its 2011 value) and for the black bear and American marten (on average by −38.0 and −36.6 of their respective 2011 values). However, relative

metapopulation capacity increased in the case of the American marten in the Middle St-Lawrence and Ottawa Plains by 17.3 and 9.3% of its 2011 value, respectively. Metapopulation capacity increased in the Montreal area for all species except the black bear and the American marten.

A similar pattern is shown for the equivalent connected area index (ECA, Fig. 4b), which declined on average by $0.7 \pm 0.2\%$ (mean and s.e.) of the total area across subregions and species. Relative declines were most pronounced in the Middle St-Lawrence and Ottawa Plains (average loss of 1.3% and 1.5% of area) and for the black bear (average loss of 1.8% of area). The fraction of connected habitat (ECA_{Ap} , Fig. 4c) showed declines across subregions and species, with an average decline equivalent to a complete loss of habitat connectivity in $5 \pm 0.6\%$ (mean and s.e.) of the total area. Similar to the case of metapopulation capacity and that of equivalent connected area index, ECA_{Ap} increased in the case of American marten in the Middle St-Lawrence and Ottawa Plains, as well as for the ovenbird in Montreal. Contrasting the connectivity indicator changes, changes in habitat area (Fig. 4d) varied across subregions and species and increased on average by $0.1 \pm 0.2\%$ (mean and s.e.). Hence, patterns of habitat area and connectivity change do not overlap and are not correlated across the species of interest. This result is supported by our finding that correlations among changes in habitat area and changes in connectivity metrics tend to be weak to moderate (except in the case of ECA, SI Fig. 7).

In the case of the current status (2021) of landscape-level multispecies connectivity (SI Fig. 5), metapopulation capacity (MPC) values are highest in the Middle St-Lawrence Plain, and are generally high for ecoprofile species with small patch size requirements, such as the wood frog, or species with larger gap-crossing capabilities, such as the barred owl. In the case of the effectively connected area index (ECA), on average, 14.6% of the St-Lawrence Lowlands total area consists of species habitat that is effectively connected. An ECA of 30% is only achieved in the Ottawa Plain (SI Fig. 5). Also, the percentage of habitat area is on average higher across subregions and species (average: 20.8%), than the percentage of effectively connected habitat area (ECA, average: 14.6%).

Using two-sided Welch's t-tests, we compared patch-connectivity values in 2021 and 2011 and found significant declines in average metapopulation capacity patch importance (MPC_{imp}), and average habitat patch sizes, as well as significant increases in average node degree and betweenness centrality of habitat patches across most subregions and species of interest (Fig. 4e–h).

Patch-level connectivity distributions in 2021 tend to be skewed, with predominantly low median values across all subregions and all species except the American marten and the black bear, which had higher median values due to larger minimum patch size requirements (Table 2, SI Fig. 5e–h).

Comparing multispecies connectivity in simulated and real-world landscapes

We summarise a set of six multispecies connectivity indicators, their characteristics and interpretation in Table 1. An analysis of indicator correlations across our 270 simulated landscapes revealed that metapopulation capacity (MPC)-based and equivalent connected area (ECA)-based indicators form a cluster that is positively correlated with habitat area and negatively correlated with fragmentation (nr. patches, Fig. 5a). Hence, MPC and ECA show a very similar relationship with habitat area and fragmentation, although MPC is focused on long-term dispersal outcomes and is therefore less sensitive to differences in dispersal capacity compared to ECA (SI Fig. 6).

In contrast to MPC and ECA, average betweenness centrality (BC) and node degree (ND) tend to be negatively correlated with habitat area and positively correlated with the number of patches in the simulated landscapes. Interestingly, this correlation pattern was less pronounced in the 10,000 randomly sampled cells across the St-Lawrence Lowlands (Reconnect $\sim 75 \text{ km}^2$ -moving window results for the year 2021), where all connectivity indicators tend to be positively correlated with habitat area and number of patches (Fig. 5b). Further analyses of the simulated landscapes revealed important non-linearities in the relationships between habitat area, number of patches and connectivity indices (SI Fig. 6). For example, average landscape-level node degree shows a hump-shaped relationship with habitat area (SI Fig. 6d), with a peak around a habitat area of $\sim 1.5 \text{ ha}$, i.e. when habitat covers $\sim 24\%$ of the total landscape area. Since in the simulated landscapes, the amount of habitat area varied between 10 and 90% of the total landscape area (cf. Methods), the negative relationship between habitat area and node degree dominated in the correlation analysis (Fig. 5a). However, in the moving window landscapes of the St-Lawrence Lowlands ecoregion, median habitat cover ranged from 3% (American marten) to 27% (wood frog), depending on the species, and therefore, the positive relationship between habitat area and node degree prevailed in the correlation analysis (Fig. 5b).

Discussion

In this study, we summarised the characteristics of six key-indicators of ecological connectivity and developed a scalable, generalizable analytical approach and R-tool (Reconnect) to rapidly evaluate connectivity indicators for multiple species with different habitat needs in any region of interest. With this tool we analysed the change in forest connectivity for the period 2011–2021 in the St Lawrence Lowlands ecoregion. We found a decline in forest connectivity for multiple species, as measured by metapopulation capacity and equivalent connected area. By combining these results with results of increasing betweenness centrality and decreasing average patch area, we demonstrate a trend of increasing fragmentation of large contiguous habitat into smaller, more isolated patches, while the total habitat area remained largely unchanged. Additionally, we found that for the year 2021, the St-Lawrence Lowlands harbor on average 14.6% effectively connected forest habitat area, which is about half the target value of 30% (cf. Target 3 in the Post-2020 Global Biodiversity Framework of the Convention on Biological Diversity; CBD 2021). These findings offer guidance to Quebec's planning for connectivity in the south of the province where human impacts are great.

Multispecies connectivity indicators supporting the global biodiversity framework

Our connectivity indicators support connectivity assessments in regions with moderate to high human disturbance (Keeley et al. 2021), where biodiversity is under intense land-use pressure. They were selected to align with criteria for Essential Biodiversity Variables (EBV), such that they are feasible, (i.e. allow the monitoring of connectivity for multiple species with minimal data inputs) are scalable, are sensitive to spatial and temporal change, and are relevant for biodiversity conservation targets (Jetz et al. 2019; Pereira et al. 2013). While a wide range of EBVs have already been established, an EBV-based connectivity indicator has yet to be incorporated into the EBV framework (geobon.org/ebvs/). We believe that the indicators selected here have the potential to support the implementation

and continued monitoring of connectivity targets for multiple species at local, national and global scales, and as complementary indicators for the KM-GBF.

For example, at the landscape-level, metapopulation capacity (MPC) captures the potential long-term persistence of species across a landscape (Drielsma and Ferrier 2009; Hanski and Ovaskainen 2000; Hanski 1994; Hanski et al. 2017; Schnell et al. 2013). Meanwhile, the effectively connected area index (ECA; Saura et al. 2011; Saura and Pascual-Hortal 2007) is relevant for area-based connectivity targets (CBD 2021; Ward et al. 2020). The fraction of the effectively connected area index (ECA_{Ap} ; Saura et al. 2011; Saura et al. 2017, Saura et al. 2018) can be used to identify areas with underused connectivity potential (i.e. where habitat exists but is not connected). Further indices at the patch-level can highlight the degree to which a habitat patch is a stepping stone for movement over short distances (i.e. node degree, ND; Minor and Urban 2008) or short and long distances (betweenness centrality, BC Albert et al. 2017; Brandes 2001; Freeman 1978) in the habitat network. Hence, BC and ND enable the spatial prioritization for the establishment and protection of stepping-stones enabling movement between habitat areas, a fundamental connectivity conservation strategy in human-modified landscapes (Rocha et al. 2021).

These selected key-connectivity indicators scored high on EBV-criteria (SI Table 2) and cover connectivity dimensions at different scales (patch- and landscape-level, respectively; Fletcher et al. 2023). Additionally, the selected patch-level indices can be assessed at landscape-level and vice-versa: for example, BC and ND are typically assessed at the patch-level but can be aggregated at the landscape-level via any aggregation function of interest (e.g. mean, range, variation). ECA, typically assessed at the landscape-level, can also be assessed at the patch-level, using a generic patch-importance formula (I_v), applicable to any landscape-level connectivity indicator (Saura and Pascual-Hortal 2007).

$$I_v = \frac{I - I'}{I} \times 100, \quad (3)$$

where I is an index value when habitat patch v is present and I' is the same index value when patch v is not present in the landscape. However, an indicator reflecting site- (or pixel) level connectivity is still missing in the key-set of indicators evaluated in this manuscript (e.g. least-cost distance, SI Table 2). We highlight the omnidirectional inverse cumulative resistance (invCR) as a promising potential connectivity indicator reflecting landscape traversability at pixel-level (Albert et al. 2017; Chubaty et al. 2020; Shahnaseri et al. 2019). InvCR could be useful to quantify the degree to which barriers limit movement in a landscape, an important strategy complementary to identifying best movement routes (McRae et al. 2012). Hence, the list in Table 1 is not exclusive, but nevertheless covers connectivity indicators that together allow the quantitative and spatially explicit assessment of complementary connectivity facets at patch-and landscape-level, i.e. the long-term species dynamic outcomes in a given network of habitat (MPC), the relative (ECA_{Ap}) and absolute (ECA) amount of habitat that is effectively connected (i.e., reachable) from a species-specific perspective and the spatial distribution of stepping stones for long-range (BC) and short range movement (ND).

Our analyses highlight the existence of clusters of correlated indicators, such as MPC and ECA, that are positively correlated with habitat area, and negatively correlated with betweenness centrality (BC), node degree (ND) and number of patches in simulated landscapes (Fig. 5a). However, as our connectivity change assessment across the St-Lawrence Lowlands showed, despite being in a correlated cluster, the trends in MPC and ECA did not reflect the trend of habitat area from 2011 to 2021 (Fig. 4). This finding is supported by our

supplementary analysis showing decadal changes in habitat area and decadal changes in multiple connectivity indicators across the St-Lawrence Lowlands tend to be only weakly-moderately correlated (SI Fig. 7). Additionally, because of non-linear relationships among habitat area (or fragmentation) and measures of connectivity (SI Fig. 6), large changes in connectivity are possible even with quite modest changes in total amount of available habitat, and directionality of changes in connectivity indicators do not always reflect the same process: For example, in landscapes with up to ~24% habitat cover, increasing average node degree can be interpreted as an increase in connectivity, whereas in landscapes beyond 24% habitat cover, decreasing average node degree can be interpreted as a sign of increasing habitat-patch contiguity and therefore increasing connectivity (SI Fig. 6d).

Hence, a combination of multiple connectivity indicators at different levels (e.g., patch and landscape), selected according to specific conservation needs might be best to robustly assess and evaluate observed connectivity patterns. We found the use of simulated reference landscapes useful to identify environmental conditions with non-linear habitat area—connectivity relationships and to identify target thresholds for connectivity conservation.

Diverging trends in habitat area and connectivity in the St-Lawrence Lowlands

The St-Lawrence Lowlands ecoregion is characterized by decades of profound landscape changes via intensification of agriculture and forestry, as well as urbanization. Currently, around 40% of its territory is characterized by agriculture of annual crops, forests cover 24%, urban lands 12% and wetlands around 10%. A recent analysis of land-cover changes in the last 25 years (Drapeau et al. 2019; Jobin et al. 2020; Regos et al. 2018) shows that the forest cover slightly increased, which matches the pattern we observed for the last decade in our study. However, our results show that habitat area and connectivity trends do not necessarily strongly correlate (SI Fig. 7): despite the slight average increase in total forest habitat area, losses in connectivity dominate for most of our focal species (Fig. 4). Losses in MPC and ECA were most prevalent for the black bear, which was the species with the largest minimum patch size requirements in deciduous and mixed forest habitats. Combining these results of MPC and ECA with our finding of increasing average betweenness centrality (implying well-connected patches became more important for connecting all habitat areas in the network, and isolated patches became more isolated) and decreasing average patch size allowed us to uncover the typical phenomenology of habitat fragmentation: the division of habitat area into smaller and more isolated fragments (Haddad et al. 2015).

These patterns suggest that area-based habitat conservation alone might not be enough to safeguard biodiversity in the St-Lawrence Lowlands (Maxwell et al. 2020). Subregions with strong recent connectivity declines, such as the Middle St-Lawrence Plain, as well as subregions where connectivity values are generally low, such as the Upper St-Lawrence Plain should be the focus of connectivity conservation action in the future. These subregions were also ranked as highly important for maintaining species connectivity between large wilderness areas (provincial parks) and represent critical migration corridors for species moving north with climate change (Rayfield et al. 2021). Hence, reconnecting fragmented landscapes in these subregions could contribute to the long-term persistence of threatened species and contribute to the Pan-Canadian Approach to Transforming Species at Risk Conservation in Canada (ECCC 2018).

Our results are focused on the connectivity of forest habitats and a set of forest eco-profile species relevant in the ecoregion of the St-Lawrence Lowlands in Quebec, Canada (Albert et al. 2017; Meurant et al. 2018; Rayfield et al. 2016). However, there are other

species and habitat types relevant for biodiversity and connectivity conservation at local to global scales, such as wetlands, grasslands, and freshwater ecosystems (Bardgett et al. 2021; Fluet-Chouinard et al. 2023; Jobin et al. 2020). The selected key-indicators and Reconnect approach presented in our study are based on two, and optionally, three (ecoprofile-) species specific elements of input information: (i) a binary map of the spatial distribution of ecologically valuable areas (habitat or protected areas, for example), (ii) formal definition of movement probability with distance (a negative exponential dispersal kernel, for example; Moilanen and Nieminen 2002), and optionally, (iii) a landscape-resistance map, indicating cost to movement at every site (allowing for resistance-weighted distance; McRae et al. 2016; Rayfield et al. 2023). In many cases, such information is partially available (existing spatial data on land-cover, protected areas, human disturbance, etc. on open-data and government platforms; Bush et al. 2017; UNEP-WCMC and IUCN 2024; Venter et al. 2016) and needs partially to be assembled or estimated based on literature, experiments, models or expert opinion (movement probability with distance; Albert et al. 2017; Straus et al. 2024), prior to the connectivity analysis. Once the information above is assembled, our selected indicators and Reconnect approach can generalize the rapid evaluation of connectivity assessment to other habitat types, species-dispersal capacities and spatial scales of interest.

Towards an actionable evaluation of multispecies connectivity

Ranking species according to the values within and across connectivity indicators is a simple, coherent and generalizable way to quantitatively evaluate the state and temporal trend of multispecies connectivity while also retaining species-specific information across any region of interest (Chowdhury et al. 2023; Hartfelder et al. 2020; Silvestro et al. 2022).

To meaningfully evaluate species-specific connectivity values, an explicit formulation of conservation targets is necessary (Drielsma and Ferrier 2009). Area-based conservation targets such as “30% by 2030” in the KM-GBF (CBD 2021; Gurney et al. 2023) should also account for connectivity. To this end the effective connected area index (ECA) can be used to assess the number of species and regions that meet a minimum habitat area threshold of 30% whilst also being effectively connected (SI Fig. 5b).

Importantly, if area-based conservation efforts are to address the global biodiversity crisis, they must not only consider connectivity, but also species persistence (Maxwell et al. 2020). Identifying explicit value ranges of indicators that represent a regionally relevant “safe operating space” (Gonzalez et al. 2017; Steffen et al. 2015) for species persistence has been a notorious challenge (Bulman et al. 2007; Flather et al. 2011; Hanski et al. 2017). The original model of the metapopulation capacity (MPC) indicator implies that a metapopulation persists in a habitat network if MPC is greater than the ratio of colonization and extinction rate parameters (cf. extinction threshold $\delta = e/c$ in Drielsma and Ferrier 2009; Hanski and Ovaskainen 2000; Hanski et al. 2017; Schnell et al. 2013). Because colonization and extinction rate parameters are hard to estimate in nature, minimum MPC and ECA values for species persistence could be based on a minimum viable number of reproductive pairs in a population (Albert et al. 2017) or the habitat requirements for a minimum viable metapopulation size (Bulman et al. 2007; Drielsma and Ferrier 2009; Taylor et al. 2016). Nevertheless, more research combining models with empirical data is needed to assess the uncertainty around adequate thresholds for long term species (or community) persistence or extinction risk (Bulman et al. 2007; Flather et al. 2011; Hanski et al. 2017). The metapopulation capacity indicator, calibrated with empirical data offers a sound basis for that

goal and its use can be expanded to capture different aspects of population, species and community dynamics, such as the extrapolated metapopulation persistence time (Schnell et al. 2013) and the potential food-chain length (Wang et al. 2021).

Overcoming common challenges of multispecies connectivity modelling and future directions with the Reconnect tool

We used a priori definitions of species dispersal capacity and a negative exponential kernel based on Euclidean distances to approximate dispersal probability among habitat patches. Hence, our approach lies between quantifying the capacity of a landscape to foster potential species movement (structural connectivity; Calabrese and Fagan 2004) and expected realized species movement (functional connectivity; Salgueiro et al. 2021; Tischendorf and Fahrig 2000). Realized species movement does not only depend on the structure of habitat networks, but also on other external factors such as population dynamics (Chu and Claramunt 2023), and the behavior of individuals (Nathan et al. 2008; Rayfield et al. 2023). To generate more realistic connectivity estimates, movement traits could be estimated from species traits (e.g. body mass or wing length; Chu and Claramunt 2023; Hartfelder et al. 2020; Straus et al. 2024) and included in more sophisticated dispersal probability kernels with resistance-weighted distance (McRae et al. 2016; Rayfield et al. 2023) or even in trait-based movement models (Hirt et al. 2018). Alternatively, dispersal could be derived empirically from *realized* movement trajectories (e.g. via GPS tracking or camera traps; Tucker et al. 2018), but such data can be difficult and costly to obtain (Wood et al. 2022).

Data scarcity is also among the reasons why connectivity assessments are rarely empirically validated (Daniel et al. 2023; Foltête et al. 2012, 2020; Lalechère and Bergès 2021; Laliberté and St-Laurent 2020; Wood et al. 2022). Combining multispecies connectivity assessments with species distribution models based on openly accessible data constitutes a promising avenue to empirically test the importance of connectivity for species movement and persistence (Curd et al. 2022; Daniel et al. 2023; Lalechère and Bergès 2021; Van Moorter et al. 2023; Vasudev et al. 2015). The ensemble connectivity maps generated with our Reconnect approach could be combined with such species distribution models.

Modeling connectivity across large spatial extents at fine resolution can rapidly become computationally demanding (Albert et al. 2017; Koen et al. 2019; Santini et al. 2016). One set of strategies to address this challenge is based on decreasing the spatial extent by splitting a large study area into smaller, distinct windows with overlap (Drielsma and Ferrier 2009; Hughes et al. 2023; Koen et al. 2019; Landau et al. 2021) or without overlap (Strimas-Mackey and Brodie 2018). Another set of strategies is related to decreasing the spatial resolution of the input data (Koen et al. 2019), and thereby effectively aggregating (and reducing the number of) habitat patches (Albert et al. 2017). A third set of strategies is focused on removing habitat patches with attribute values transgressing a threshold (e.g. minimum habitat patch size; Albert et al. 2017). Our Reconnect analytical tool can be adjusted to include all these strategies. Recent advances highlight the possibility of a generalizable subsampling of habitat networks to estimate whole network properties (Song et al. 2022), such as metapopulation persistence, with the limitation that estimates can only be assessed at the whole network scale.

In the current study, we assessed connectivity at a single spatial extent (moving windows of $\sim 75 \text{ km}^2$). However, connectivity at multiple scales of space and time affects the spatial distribution of ecological and evolutionary processes (Gilarranz et al. 2017; Rayfield et al. 2023). Thus, there is a pressing need to estimate connectivity change and facilitate the

movements of multiple species at multiple spatial scales (Gonzalez et al. 2011; Rayfield et al. 2016; Thompson and Gonzalez 2017; Wood et al. 2022). The Reconnect approach could be applied at several spatial scales to identify both short- and long-range connectivity priorities for distinct species (Albert et al. 2017; Fletcher et al. 2023).

Conclusions

In our study, we identified a key-set of indicators suitable for monitoring habitat connectivity change to assess progress toward national and international targets, such as formulated in the GBF. Using our multi-indicator, multispecies approach and R-tool “Reconnect”, we evaluated the status and decadal change of habitat connectivity for a set of forest species with a representative range in forest habitat needs and dispersal capacities. We found that despite a trend of increasing forest habitat area from 2011 to 2021, connectivity indicators, as well as average forest patch sizes decreased, revealing the effects of ongoing habitat fragmentation across the St-Lawrence Lowlands in Quebec. Efforts to meet the targets of the KM-GBF highlight the need for connectivity conservation from subnational to national and to global scales. This will require a rapid prioritization of areas and species for conservation actions and assessment of the efficacy of alternative conservation scenarios for the coming decades. The research presented here and the “Reconnect” approach and R-tool can help to support conservation management with quantitative indicators to monitor connectivity change at different scales for a wide range of species.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10531-024-02938-2>.

Acknowledgements We acknowledge the funding and the financial support by McGill University, Habitat (habitat-nature.com) and the Mitacs foundation (IT19834). We also thank Environment Climate Change Canada (ECCC) for their financial support (GCXE22S043) and Dr. Amanda Martin for stimulating discussions. A.G. acknowledges the support of the Liber Ero Chair in Biodiversity Conservation.

Author contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Jacqueline Oehri. The first draft of the manuscript was written by Jacqueline Oehri and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding This work was supported by McGill University, Habitat (habitat-nature.com) and the Mitacs foundation (IT19834), as well as Environment Climate Change Canada (ECCC, GCXE22S043).

Data availability The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

Code availability The Reconnect R-tool can be accessed at <https://github.com/oehrij/Reconnect>.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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Authors and Affiliations

Jacqueline Oehri^{1,2} · Sylvia L. R. Wood² · Eluna Touratier¹ · Brian Leung¹ · Andrew Gonzalez^{1,2,3}

✉ Jacqueline Oehri
jacqueline.oehri@gmail.com

¹ Department of Biology, McGill University, 1205 Avenue Docteur Penfield, Montreal, QC H3A 1B1, Canada

² Habitat, 5818 Saint-Laurent Boulevard, Montreal, QC H2T1T3, Canada

³ Group on Earth Observations Biodiversity Observations Network, Quebec Centre for Biodiversity Science, McGill University, 1205 Avenue Docteur Penfield, Montreal, QC H3A 1B1, Canada