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Applying network theory to prioritize multispecies habitat networks that are robust to climate and land-use change

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Running head: Prioritizing a network for biodiversity

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ABSTRACT

Designing connected landscapes is among the most widespread strategies for achieving biodiversity conservation targets. The challenge lies in simultaneously satisfying the connectivity needs of multiple species at multiple spatial scales under uncertain climate and land-use change. To evaluate the contribution of remnant habitat fragments to the connectivity of regional habitat networks, we developed a method to integrate uncertainty in climate and land-use change projections with the latest developments in network-connectivity research and spatial, multipurpose conservation prioritization. We used land-use change simulations to explore robustness of species' habitat networks to alternative development scenarios. We applied our method to 14 vertebrate focal species of periurban Montreal, Canada. Accounting for connectivity in spatial prioritization strongly modified conservation priorities and the modified priorities were robust to uncertain climate change. Setting conservation priorities based on habitat quality and connectivity maintained a large proportion of the region's connectivity, despite anticipated habitat loss due to climate and land-use change. The application of connectivity criteria alongside habitat quality criteria for protected-area design was efficient with respect to the amount of area that needs to be protected and did not necessarily amplify trade-offs among conservation criteria. Our approach and results are being applied in and around Montreal and are well suited to the design of ecological networks and green infrastructure for the conservation of biodiversity and ecosystem services in other regions, in particular regions around large cities, where connectivity is critically low.

INTRODUCTION

Conserving connectivity (Crooks & Sanjayan 2006) - the capacity of species to move across landscapes - is a preferred strategy for mitigating biodiversity loss due to land-use change and habitat fragmentation and for fostering the migration, natural adaptation, and increased persistence of species under climate change (Heller & Zavaleta 2009). In regions that have already been substantially transformed by human activities, such as metropolitan areas (Irwin & Bockstael 2007), conserving biodiversity given uncertain scenarios of climate and land-use change requires adopting a network approach that manages remnant habitat for connectivity (Schmitz et al. 2015).

Incorporating connectivity objectives and climate and land-use change uncertainties into the design of protected-area networks is a major challenge (Mumby et al. 2011) that requires new methods to prioritize areas that simultaneously satisfy multiple conservation criteria (Zetterberg et al. 2010). Habitat networks should account for the needs of multiple species with contrasting life histories and movement ecologies, rather than the needs of a single or few umbrella or flagship species (Nicholson et al. 2006). The network's structure should allow movement to occur at multiple spatial scales because the contributions of habitat patches to connectivity vary across species and movement types (Minor & Lookingbill 2010; Rayfield et al. 2016). Habitat networks should also account for uncertainties in climate-driven range shifts because the contribution of habitat patches to connectivity may change as species shift their ranges (Beier et al. 2011; Kujala et al. 2013). Finally, the network's connectivity must be robust to ongoing land-use change that can alter both habitat patches and the surrounding matrix (Coulter Riordan & Rundel 2014).

The integration of multiple objectives can be achieved by combining new approaches to connectivity - measurement and mapping of contributions of habitat patches to multiple connectivity criteria (Carroll et al. 2011) - with systematic conservation planning tools

designed for multipurpose spatial prioritization (Moilanen et al. 2005). These prioritization tools can balance (sometimes conflicting) needs in terms of habitat quality and connectivity for different species under distinct climate and land-use projections (e.g., Magris et al. 2015; Rayfield et al. 2016). Graph (or network) theory, in which landscapes are conceptualized as networks of weighted nodes (habitat patches with different qualities) connected by weighted links (potential movement based on properties of the intervening matrix) is a powerful tool to model habitat connectivity with available data (Calabrese & Fagan 2004).

Worldwide, governments are requesting research to help plan regional-scale habitat connectivity that is robust to both land-use and climate change (Beier et al. 2011; Brodie et al. 2016). There is thus a need for a general framework to support the design of multispecies global-change-proof habitat networks. To address this challenge, we developed an integrative framework that prioritizes areas for conservation based on maintaining regional habitat quality and connectivity for a broad set of species under climate and land-use change (Fig. 1). We focused on 2 dimensions of connectivity: short-range connectivity that alongside habitat quality facilitates the long-term persistence of multiple species within the habitat network and long-range connectivity that promotes the maintenance of seasonal and climate-driven migrations across the habitat network (Rayfield et al. 2016). This spatial prioritization can guide the implementation of protected-area networks for conservation of biodiversity and ecosystem services. Although our approach is general and could be applied to most highly fragmented regions, we used a specific study system to demonstrate its application.

We received a direct request from Quebec government to apply our framework to guide the selection of protected areas for the southwestern region of the St Lawrence lowlands around Greater Montreal, Canada (~27,500 km²) (Supporting Information). This highly fragmented periurban territory is undergoing rapid sprawl of low density urban areas, but there is strong political will and commitment from diverse stakeholders to conserve

habitat connectivity within and across the region to facilitate northward climate-driven range shifts expected between the Appalachian to the Laurentian Mountains (Mitchell et al. 2015; Dupras et al. 2016). This makes it a particularly suitable test situation for our framework.

We applied our framework to a broad set of species to provide a spatial conservation prioritization of the region's natural forest habitat. We compared prioritizations based on four sets of conservation criteria to show how balancing species-specific requirements for habitat quality, short- and long-range connectivity, and climate suitability modified conservation priorities. We derived different conservation scenarios from these prioritization schemes and investigated their effectiveness, relative to a business-as-usual scenario of land-use change, at maintaining habitat connectivity into the future with spatially explicit dynamic land-use simulations.

METHODS

We used 6 steps structured within a loop to identify spatial conservation priorities (Fig. 1). First, we identified a set of vertebrate species that represented the range of responses to habitat fragmentation and climate change present in the region based on their life-history and movement traits. Second, we mapped habitat quality and parameterized a resistance surface for each species. Third, we derived habitat networks from habitat quality maps and estimated species dispersal abilities to quantify the contribution of habitat pixels to short- and long-range connectivity for each species. Fourth, we assessed changes in species-specific climate suitability under different regional climate projections with species distribution models. Fifth, we obtained spatial conservation priorities based on species-specific criteria for habitat quality, connectivity, and climate suitability with a multi-objective prioritization tool. Sixth, we established the effectiveness of different prioritization schemes into the future with spatially-explicit dynamic land-use simulations. Each step is described in detail in Supporting Information.

Selecting focal species

We selected 14 ecoprofiles in our study area; each was represented by a mammal, bird, or amphibian species (Beier et al. 2011) (Table 1). We selected species that encompassed the regional diversity - regarding their connectivity and habitat needs - from a multivariate analysis based on traits known to characterize how vulnerable species are to habitat fragmentation: habitat requirements, population dynamics, and dispersal abilities (Supporting Information) (Henle et al. 2004). The species also reflected the diversity of potential changes in climate suitability in temperate North America (i.e., increase, decrease or no change in area of suitable climate) (Fig. 1 & Supporting Information), as expected with a northward range expansion for most taxa (e.g. Kerr & Packer 1998).

Assessing species-specific habitat quality and resistance maps

Due to the heterogeneity of available data on species occurrences and habitat in the study area, we developed habitat-quality models through a literature review (Table 1) and used raw data from multiple sources (Supporting Information). For each species, we derived a baseline habitat-quality map from a customized 8-class land-cover map at a resolution of 30 x 30 m. These baseline quality maps were then modified by a set of spatial multipliers (range 0-1) to further account for landscape composition (e.g. forest attributes) and configuration (e.g. forest edge, distance to wetlands).

Maps of habitat patches were derived from habitat-quality maps by forming groups of habitat pixels that were large enough ($\text{area} > \text{minimum patch area}$) and close enough ($\text{distance} < \text{gap size}$) to be used by a particular species (Table 1). This organism-centered definition of *habitat patch* reduces discrepancies between the resolution of the habitat maps (30 x 30 m) and species-specific grain perception (Baguette & Van Dyck 2007) while keeping the number of habitat patches manageable (<10,000).

Species-specific 5-class maps of dispersal resistance were developed in the non-habitat pixels to quantify the degree to which pixels in the matrix limit inter-patch movement relative to habitat (Adriaensen et al. 2003). Resistance values were assigned based on land-cover type (e.g. intermediate in cropland, high on highways) and on the presence of linear elements (e.g. hedges). Following a scale that doubles between classes (from 1 to 32), resistance values were tailored to each species based on a literature review of their dispersal success through the different class types (Supporting Information).

Analyzing connectivity

Habitat networks were assembled by connecting habitat patches (nodes of the network) from edge to edge via least-cost paths (links of the network) through species-specific resistance surfaces (Adriaensen et al. 2003). Due to the large number of nodes, we identified links between nodes with a minimum planar graph model (Fall & Fall 2001). Nodes and links had associated weights. Node weights included area, mean habitat quality, and mean climate suitability. Link weights included length (i.e., distance along the least-cost path), cumulative resistance, and dispersal flux. Dispersal flux between nodes i and j separated by a distance d_{ij} (i.e., the probability that an individual in node i will disperse to node j) was calculated as a negative exponential kernel, $P_{ij} = \exp(-d_{ij} \times \log(0.5)/D_{50})$, where D_{50} is the species-specific median dispersal distance. We considered 2 estimates of D_{50} per species based on upper (natal dispersal distance) and lower (gap-crossing distance) limits of dispersal (Table 1). Species-specific dispersal distances were parameterized by combining a literature review and dispersal distances estimated from species body size and life-history traits.

We used 4 connectivity metrics as input for the prioritization schemes (Table 2 & Supporting Information) (Rayfield et al. 2016). The contribution of nodes to short-range connectivity was quantified in terms of a node's importance to the total amount and quality of reachable

habitat (dEC) (Saura et al. 2011) and its ability to serve as a stepping stone within the network (node betweenness centrality) (Freeman 1978). The contribution of nodes to long-range connectivity was assessed based on the frequency with which they were included in the shortest path between randomly selected pairs of nodes within the Appalachian and Laurentian Mountains (modified betweenness). The contribution of each pixel to long-range connectivity was also determined based on the amount of flow through each pixel associated with moving across the landscape in multiple directions (current density) (Pelletier et al. 2014).

We used 2 network-level connectivity metrics to evaluate the effectiveness of alternative land-use planning scenarios through time (Table 2). Short-range connectivity was quantified as the total amount and quality of reachable habitat within the network, which is related to the carrying capacity of a metapopulation (EC) (Saura et al. 2011). Long-range connectivity was quantified by the conductance (easiness) associated with traversing the network and calculated as the inverse of the mean cumulative resistance of shortest paths between randomly selected pairs of nodes within the Appalachian and Laurentian Mountains ($1/CR$).

Modelling changes in climate suitability

We modeled changes in climate suitability for the focal species with species distribution models. After preliminary tests, we selected the five types of models with the highest predictive power and synthesized their results with a committee-averaging procedure (Araújo & New 2007). Models were calibrated from 1971 to 2000 with continental distribution data (Supporting Information) and three uncorrelated variables (mean annual temperature, mean annual precipitations, and the ratio summer:annual precipitations) at a resolution of 10 x 10 km for all eastern North America. Models were projected for two future horizons (2025, 2050) and four extreme climate-change projections selected to characterize the full range of

change in precipitation and temperature for the study region in 2050 and to represent extremes of the 136 available projections derived from different climate models and emission scenarios (Supporting Information). The most likely future is thus expected to fall within them (Beier et al. 2011). Climate-suitability and habitat-quality modeling were decoupled because climate-specific measures of habitat quality were not available, which precluded the investigation of interactions between these components of habitat.

Identifying spatial conservation priorities

We identified spatial conservation priorities with the conservation decision-support software Zonation version 4 (Moilanen et al. 2005). Zonation identifies near-optimal trade-offs among multispecies conservation criterion and provides a ranking of all pixels in the landscape from lowest to highest conservation priority. We tested four prioritization schemes with different combinations of input criteria that expanded on existing protected areas (currently 1.2% of the St. Lawrence Lowlands): habitat quality (quality based); habitat quality and connectivity (quality and connectivity based); habitat quality and climate suitability; habitat quality, connectivity, and climate suitability. Directly accounting for current and future climate-suitability layers for different climate projections in the prioritization process meant nodes that remained suitable under all climate projections were considered as relatively more important (Kujala et al. 2013) (Supporting Information). For all prioritizations, we used a core-area and edge-based cell removal rule to protect core habitat for all species, increase the importance of rare features, and save computing time. All species were given equal weights. Criteria were weighted to balance importance among habitat quality, connectivity, and climate and between short- and long-range connectivity (Table 2).

Simulating land-use change and defining land-use scenarios

To test how changes in landscape configuration affect connectivity of species habitat networks and how efficient our prioritization schemes were at maintaining short- and long-range connectivity, we simulated land-use change from 2000 to 2050. We used a model with top-down demand for new urban and agricultural areas, bottom-up constraints (e.g. soil quality), and spatial processes (e.g. diffusion) (Verburg & Overmars 2009).

We compared five contrasting land-use scenarios that differed only in the way changes were allocated spatially (Supporting Information). In the business-as-usual (BAU) scenario, protected areas covered the 1.2% of terrestrial St. Lawrence Lowlands actually protected in 2000. Four conservation scenarios were developed within a factorial design to test the quantity of protected areas (expansion of current protected areas based on the top-ranked spatial conservation priorities to reach 10% or 17% of the area) and criteria used to define them (prioritizations based on either quality [Fig. 2a] or quality and connectivity criteria [Fig. 2b]). Climate criteria were not included in the conservation scenarios because their inclusion did not have a strong enough effect on the configuration of priority areas. We chose 17% of protected land to follow target 11 of the Aichi biodiversity targets (Convention on Biological Diversity 2010) and 10% of protected land arbitrarily as an intermediate level of protection. The five scenarios differed only in terms of landscape configuration. All 5 were based on the same fixed rate of development: increase of 30% for urban and 4% for agriculture areas (derived from historical changes in the study region from 1990 to 2012). In our simulations, most croplands were protected from urbanization by agricultural zoning, and protected areas were fully protected from any land transformation. Habitat quality and network analyses were repeated for each species and each scenario to assess the variation in outcome through time.

Analyses were performed in R version 3.2.3 (R Development Core Team 2012); SELES version 3.4 (Fall & Fall 2001) within the R package grainscape; ArcMap version 10.2.0.3348

(ESRI 2011); and Python version 2.7.6 (Python Software Foundation 2001-2013). The R codes are available on GitHub (https://github.com/CecileHALbert/CB_connectivity).

RESULTS

Ongoing erosion of poorly connected habitat networks

Depending on the species, habitat of focal species covered 4-25% of the St. Lawrence Lowlands area. The habitat networks had 113-16,590 patches (mean area 35-5,989 ha), and 8 (Pileated woodpecker) to 124 (Wood frog) km of links were required for individuals to traverse the 150 km separating the Laurentian and Appalachian Mountains (Supporting Information).

The BAU baseline scenario showed a loss of 12% forest cover, which translates into species-specific habitat loss of 10-14% by 2050. Relative to the year 2000, under BAU habitat networks were more fragmented, and there were on average 6% fewer habitat patches (range: 16% fewer - 6% more) of smaller size (17% smaller - 3% larger; average 5% smaller) and with more irregular edges (edge:area ratio: 3% less - 15% more; average 5% more) (Supporting Information). Short-range connectivity, measured by the amount of reachable habitat (EC: 5-18% less; average 11% less), and long-range connectivity, measured by the ease of traversing the network (1/CR: 1-22% more difficult; average 12% more difficult), were reduced (Fig. 3). Habitat fragmentation in 2000 was already acute for poor dispersers (e.g. wood frog), so future land-use change caused the largest loss of connectivity for species that currently disperse well through the landscape (e.g. Pileated Woodpecker) (Fig. 3).

Differences among quality-based and quality and connectivity-based prioritizations

From the prioritization maps, we derived a hierarchy of conservation solutions with an increasing fraction of the area to be protected (Fig. 2). For a given amount of area protected, the quality and connectivity-based prioritization encompassed fewer and more compact blocks of land than the quality-based prioritization, including a series of large stepping-stone patches to the north that delineated the easiest paths to traverse the lowlands between the Appalachian and Laurentian Mountains (Fig. 2b). Quality-based and quality and connectivity-based prioritizations strongly differed in their highest priority areas, but the differences were weaker for lower priorities (Fig. 2a,b, Supporting Information). In both cases the protection of the top 17% of the area encompassed around 55% of the lowland forests. Little of the remaining forest could be lost without some loss of conservation value (Fig. 4, Supporting Information).

Robustness of connectivity-based prioritization to climate change

Niche modeling identified three types of potential effects on our focal species relative to climate suitability: decrease in regional climate suitability for four species, increase in suitability for one species, and relative no change in suitability for the other nine species (Fig. 1, Supporting Information).

Including present and potential future climate suitability in the quality and connectivity-based prioritization did not greatly modify the spatial conservation priorities (Fig. 2b,d, Supporting Information). Relatively few components of the top priority areas differed from when climate suitability was included (Supporting Information). Changes in top priority areas were slightly larger under quality-based prioritization and in lower priority areas (Fig. 2, Supporting Information). In both cases, a few large blocks in the northern part of the region, that offered more stable climatic conditions for coniferous-dependent species (e.g. American marten,

Red-breasted Nuthatch) from 2000 to 2050 were among the top priorities when climate suitability was included in the prioritization.

Prioritizing conservation based on connectivity in a changing landscape

With the 17% quality and connectivity-based scenario, the negative effects of land-use change on connectivity were notably reduced relative to BAU (Fig. 3). Long-range connectivity, decreased slightly for all species (1/CR: 0.7 - 8% less; average 3% less), whereas under BAU this decrease reached up to 22% less (Fig. 3d). Less short-range connectivity was lost in the lowlands compared with BAU (EC: 3 -15% less; average 8% less) (Fig. 3b) because the greater amount of protected-area in the lowlands caused more habitat to be lost in upland areas. This 17% quality and connectivity-based scenario led to a greater retention of the different conservation criteria: habitat quality, connectivity criteria, and even climate criteria that were not targeted in the corresponding prioritization; this was close to what would be achieved with 30% of land being protected (approximately all the forest protected) (Fig. 4).

When the top 10% of the area was protected, results differed between quality-based and quality and connectivity-based scenarios. These 2 scenarios did not significantly reduce the loss of short-range connectivity (EC: 3 - 16% less and 4 - 17% less respectively) and led to an intermediate loss when compared with BAU and the 17% connectivity-based scenarios (Fig. 3b). However, the quality-based scenario led to a decrease in long-range connectivity similar to BAU (1/CR: 5 - 24% less), whereas the quality and connectivity-based scenario led to a significantly smaller decrease (1/CR: 0 - 8% less), almost similar to the 17% quality and connectivity-based scenario (Fig. 3d). Although both 10% scenarios lead to lower overall conservation values than the 17% connectivity-based scenario, they both largely increased the retention of the different conservation criteria in comparison with BAU (Fig. 4). The 10% quality and connectivity-based scenario was better than, or at least almost as good as, the

10% quality-based scenario for all the criteria, which implies that trade-offs in the data were not too large. The 10% quality and connectivity-based scenario was also more efficient than the 17% quality-based scenario at retaining long-range connectivity (Fig. 3) but not the other conservation criteria (Fig. 4).

DISCUSSION

We used graph-based connectivity analyses to design habitat networks for biodiversity conservation that account for uncertainties in both future land-use and climate change. To do so, we solved several computational challenges of regional-scale analyses (e.g., analyzing landscapes with several thousand of nodes [Pelletier et al. 2014; Rayfield et al. 2016]) and combined recent advances in habitat-network modeling and reserve design into a single workflow. Our framework goes one step further than the previous attempts to include connectivity into spatial prioritization that were conceptual (Lehtomäki & Moilanen 2013), static (Magris et al. 2015) or single-species oriented (Rayfield et al. 2016). Moreover, by combining fine-scaled land-use simulations with a set of regional climate projections (Coulter Riordan & Rundel 2014), we evaluated the performance and robustness of our case study habitat networks to future threats. Thus, we join the few researchers who have tackled the consequences of both land-use and climate change on biodiversity (but see, e.g., Jetz et al. 2007; Mazaris et al. 2013). We kept our framework as general as possible and applied it to a landscape that has features typical of highly fragmented urbanizing landscapes around the world. Our framework and methods can thus be applied to any other highly fragmented landscape; include other connectivity measures; include other types of conservation criteria (e.g. ecosystem services, Jantz et al. 2014); or be derived with other parameterizations (e.g. prioritization weighting schemes).

Some of our results inform land planning and biodiversity conservation under climate change. First, we showed that managing landscapes specifically for connectivity and habitat quality remains a potential lever for conservation action because it slows the breakdown of sparse habitat networks subjected to ongoing land-use change. Accounting for diverse connectivity facets in spatial prioritization strongly modified conservation priorities (Crouzeilles et al. 2013) and connectivity conservation scenarios were especially effective at protecting long-range connectivity. Protecting the top 10% of quality and connectivity-based priorities was more efficient than protecting the top 10% of quality-based priorities for the retention of all conservation criteria and almost as efficient as protecting the top 17% of quality and connectivity-based priorities for the maintenance of long-range connectivity. Nonetheless, little of the remaining forest can be lost without some loss of conservation value, and short-range connectivity (here related to the metapopulation carrying capacity) was highly sensitive to further habitat loss especially for long-distance dispersers (Mazaris et al. 2013) due to the loss of large stepping-stone habitat patches (Saura et al. 2014). This will be true of regions, like ours, that are already heavily modified by human activities, where natural habitat area is well below thresholds at which negative impacts of fragmentation become critical (Andren 1994; Saura et al. 2011). Although prioritizing a network for connectivity and habitat quality can lead to efficient outcomes for biodiversity conservation it cannot compensate for further habitat loss (Minor & Lookingbill 2010), which would require a reduction of land-conversion rates and the restoration of habitat optimally contributing to short- and long-range connectivity (Zetterberg et al. 2010). To identify areas where connectivity can be improved, such as the implementation of corridors to reduce dispersal bottlenecks, our framework could be tailored with criteria related to the importance of links for both short- and long-range connectivity.

Second, in our case study, spatial conservation prioritizations made without climate as a criterion were robust to future climate change out to 2050, especially the quality and connectivity-based prioritization. This indicates the uncertainties related to climate change (socioeconomic scenarios, circulation models, species distribution models) did not greatly affect the prioritization of habitat patches for conservation within this habitat network (but see Mumby et al. 2011; Kujala et al. 2013). This event is likely in ecotone regions between temperate and boreal ecosystems, where species richness is expected to be driven by landscape heterogeneity more than by climate (Kerr & Packer 1998) and where climate is expected to change rather homogeneously (Berteaux et al. 2010). In low-contrast temperate regions, conservation priorities are expected to be little modified by the interactions between land-use and climate change (Jetz et al. 2007; Mantyka-Pringle et al. 2015). It would be valuable to apply our framework to other more climatically heterogeneous or extreme regions over longer periods to examine how climate change would alter connectivity-based prioritization. Also, methods to combine current connectivity with changing connectivity through time are emerging and should make it possible to optimize the prioritization and loss process (Hodgson et al. 2016).

Third, we included multiscale and species-specific parameters for dispersal ability and habitat requirements, thus rooting our approach in metapopulation theory (Saura et al. 2011). We believe this is necessary to move from structural to functional connectivity assessments, which cannot be properly done with coarsely defined habitat maps and dispersal distances. Future research on functional connectivity and connectivity dynamics needs to better connect network theory with field data and individual-based stochastic movement simulators to update resistance surfaces and dispersal kernels, validate dispersal pathways, and quantify the spatiotemporal connectivity among patches through time (Bocedi et al. 2014). For example, movement data associated with genetic analyses have helped improve connectivity estimates

and so validated the ongoing northward range expansion of the white-footed mouse in our region (e.g. Marrotte et al. 2014).

We identified 3 key recommendations to guide regional land planning. First, it is crucial to combine multiple criteria for both connectivity and habitat quality into a prioritization analysis for multiple species at a species-specific level (but see, Magris et al. 2015). The relative contribution of individual patches to the regional connectivity depends on multiple factors, and only by accounting for these divergent conservation criteria can a good balance between the current and future habitat and connectivity requirements of all species within the network be ensured (Meller et al. 2014). We found that conserving connectivity and habitat quality for multiple species requires substantial increases in total habitat area protected and efficient prioritization of the habitat to be protected based on multiple criteria.

Second, we recommend the use of realistic scenario-based projections of climate and land-use change so as to future-proof the structure of the habitat network being prioritized. Given the investment required to acquire, restore, and protect habitat within a network, it is important for the network to be robust to as many likely scenarios of change as possible (Titeux et al. 2016). Although experiments at the landscape scale are impractical (Haddad et al. 2015), scenario simulations can be used to capture the range of impacts of future fragmentation on biodiversity and explore how regional network planning will interact with regional development to modify connectivity. Landscape simulations go beyond basic graph-based simulations because land-use change does not lead to random patch deletion but rather to spatially structured changes that affect the habitat network including the matrix surrounding the protected areas.

Third, there is value in working with stakeholders from the start (Beier et al. 2011; Brodie et al. 2016). In the case of Montreal, stakeholders have been engaged at many levels (e.g.

governments, environmental nongovernmental organizations, agricultural unions, and private landowners) (Mitchell et al. 2015) during and after the modeling process. This engagement helped bridge a disparate array of conservation initiatives (i.e. corridor projects with plans for the city greenbelt) into a regional plan for connectivity conservation. The ongoing implementation of the network has been fostered by an open process allowing for the co-development of the vision and goals of the ecological network. Additional criteria have since been added (e.g. ecosystem services) to broaden the value and appeal of the network to functional dimensions of biodiversity, which are vital to human well-being in the region.

We showed that accounting for connectivity in spatial prioritization strongly modifies conservation priorities. Through our framework, we applied multiple connectivity criteria to meet the habitat and dispersal needs of many species facing uncertain future land-use and climate change. The quality and connectivity-based conservation priorities we identified for periurban Montreal were area efficient and provided favorable trade-offs among multiple conservation criteria. Our framework is general and well suited to the design of ecological networks and green infrastructure for biodiversity and ecosystem services in other regions, in particular regions where habitat connectivity is critically low.

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Supporting Information

Supplementary figures and methods (Appendix S1) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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Table1. Characteristics of the 14 focal species used to identify spatial conservation priorities that are robust to climate and land-use change.

Species		Taxonomy		Traits			Preferred habitat							Patch				
		Class	Order	Longevity (Yr)	Upper D ₅₀ (m)	Lower D ₅₀ (m)	Open / Closed	Forest				SD	EE	DW	MA (ha)	GS (m)		
								D	M	C	T							
	<i>Blarina brevicauda</i>	Northern short-tailed shrew	Mammal	Insectivora	1.5	549	39	Both	X	X		dense & old	X				1	0
	<i>Bufo americanus</i>	American toad	Amphibian	Anura	10	2 795	73	Both	X	X		any			X		0.5	0
	<i>Dryocopus pileatus</i>	Pileated woodpecker	Bird	Piciformes	12	8 187	112	Closed	X	X		dense & old					1	120
	<i>Lepus americanus</i>	Snowshoe hare	Mammal	Lagomorpha	5	6 038	99	Closed		X	X	low height					2	60
	<i>Martes americana</i>	American marten	Mammal	Carnivora	7	46 659	220	Closed		X	X	old					150	120
	<i>Odocoileus virginianus</i>	White-tailed deer	Mammal	Artiodactyla	7	20 521	160	Closed		X	X	medium dense					5	120
	<i>Peromyscus leucopus</i>	White-footed mouse	Mammal	Rodentia	0.38	2 533	71	Closed	X	X		dense	X				2.4	0
	<i>Plethodon cinereus</i>	Red-back salamander	Amphibian	Caudata	20	16	10	Closed	X	X		dense	X	X			0.27	0
	<i>Rana sylvatica</i>	Wood frog	Amphibian	Anura	3.5	564	39	Closed	X	X	X	dense			X		0.5	0
	<i>Scolopax minor</i>	American woodcock	Bird	Charadriiformes	8	34 317	195	Both	X	X		low height	X				2	60
	<i>Seiurus aurocapilla</i>	Ovenbird	Bird	Passeriformes	11	1 286	54	Closed	X	X		dense & old			X		5	0
	<i>Sitta canadensis</i>	Red-breasted nuthatch	Bird	Passeriformes	7	1 827	44	Closed		X	X	dense & old			X		3	0
	<i>Strix varia</i>	Barn owl	Bird	Strigiformes	18	40 889	209	Closed	X	X		old					1	120
	<i>Ursus americanus</i>	American black bear	Mammal	Carnivora	12.5	55 088	236	Both	X	X		dense					1 200	60

Table2. Summary of habitat quality and connectivity metrics used as input criteria in the prioritization schemes.

Metric	Definition	Method of calculation	Level of measurement	Scale of connectivity	We use it for:	
					input for the conservation prioritizations (weights)	evaluate the effectiveness of alternative land-use scenarios
habitat quality	Measure of the habitat quality within each pixel regarding the potential availability of food and shelter during the limiting season.	Based on land-cover types and modified by a set of spatial multipliers to further account for landscape composition (e.g. forest attributes) and configuration (e.g. forest edge, distance to wetlands).	pixel-level		1	
EC (Equivalent connectivity)	Measure of the quality-weighted area of a single habitat patch that would provide the same probability of connectivity, i.e. probability that two points randomly placed within the landscape fall into habitat areas that are reachable from each other (Saura et al. 2011).	$EC = \sqrt{\sum_{i=1}^n \sum_{j=1}^n \exp(-d_{ij} / D_{50}) A_i Q_i A_j Q_j}$ where A_i and Q_i are the area and quality for patch i and d_{ij} the length of the shortest path connecting patches i and j ; n is the number of patches in the network.	network-level	short-range		Yes
dEC (derived from EC)	Patch importance based on equivalent connectivity (Saura et al. 2011). Measures how much EC the patch provides to the entire network. It can be high for large patches of good quality and for patches that serve as connectors between subareas of the network.	$dEC_i = \frac{EC - EC_i}{EC}$ where EC is the equivalent connectivity of the entire network and EC_i the EC of the network when patch i has been removed.	node-level	short-range	1*	
betweenness (betweenness centrality)	Quantifies the degree to which the node serves as a stepping stone to promote movement between other non-adjacent nodes in the network.	$b(i) = \sum_{j \neq k} \frac{g_{jk}(i)}{g_{jk}}$ where g_{jk} is the total number of shortest paths (cost-based) between j and k and $g_{jk}(i)$ the number that pass through node i . For any j and k in the network.	node-level	short-range	1	
modified betweenness (derived from betweenness)	Quantifies the degree to which the node serves as a stepping stone to promote movement between the Appalachian and Laurentian mountain ranges, the general direction of expected climate-driven range shifts.	Same as above but j are nodes in the Appalachian mountains and k are nodes in the Laurentians.	node-level	long-range	1	
1 / CR (Inverse of mean cumulative resistance)	Provides a measure of how easily the network can be traversed to move between the Appalachian and Laurentian mountain ranges, the general direction of expected climate-driven range shifts.	$1/CR = \frac{p}{\sum_{k=1}^p CR_k}$ CR _k being the cumulative resistance of the shortest-path between a randomly-selected pair of nodes k , one from the Appalachians and one from the Laurentians. Pairs were drawn p times.	network-level	long-range		Yes
current density	Assess omnidirectional traversability of the habitat network based on the conductance of the intervening landscape (inverse of the resistance map).	Calculated with circuitscape (McRae 2008) using the method in Pelletier et al. (2014).	pixel-level	long-range	1	

FIGURES

Figure 1. The 6 sequential and parallel steps (structured in a loop) of the general framework to identify spatial conservation priorities: 1, select focal species; 2, assess species-specific habitat quality and resistance maps; 3, analyze connectivity of habitat networks and quantify contribution of habitat pixels to short- and long-range connectivity; 4, model changes in regional climate suitability (type 1, decrease; 2, no change; 3, increase; green, climatically suitable areas); 5, identify spatial conservation priorities; and 6, establish effectiveness of different prioritization schemes. Details of the process are in Supporting Information.

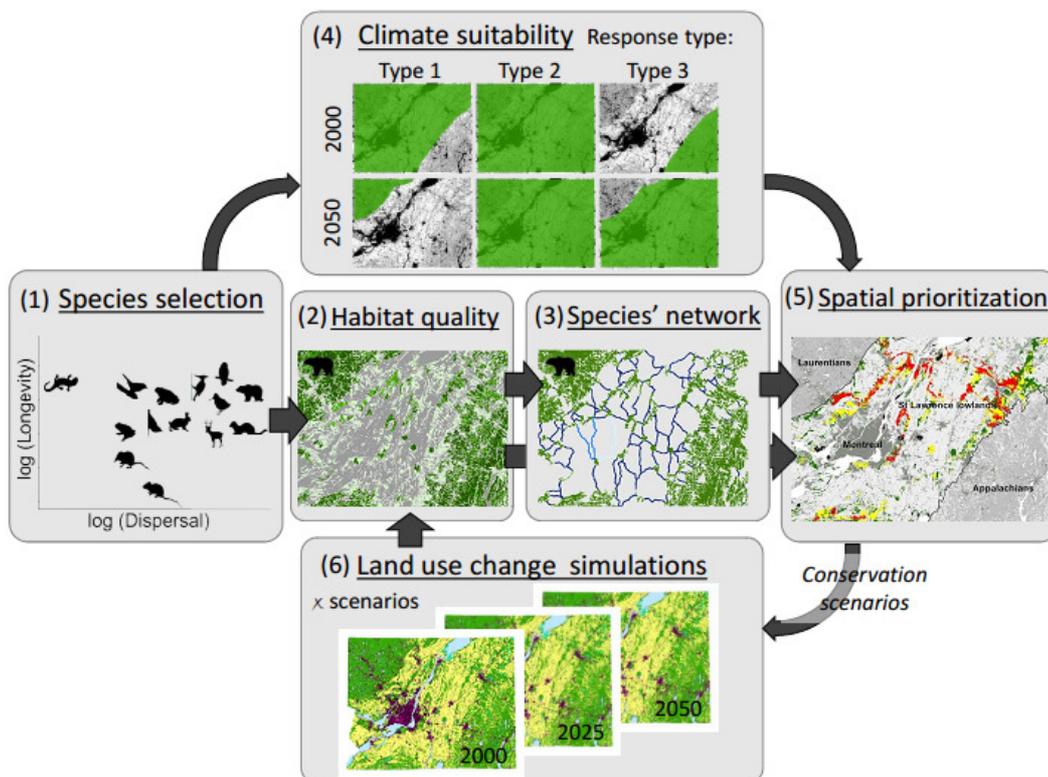


Figure 2. Comparison of spatial conservation prioritizations based on (a) habitat quality, (b) habitat quality and connectivity, (c) habitat quality and climate suitability, and (d) habitat quality, connectivity and climate suitability for 14 focal species (5, 10 and 17% areas with highest priorities).

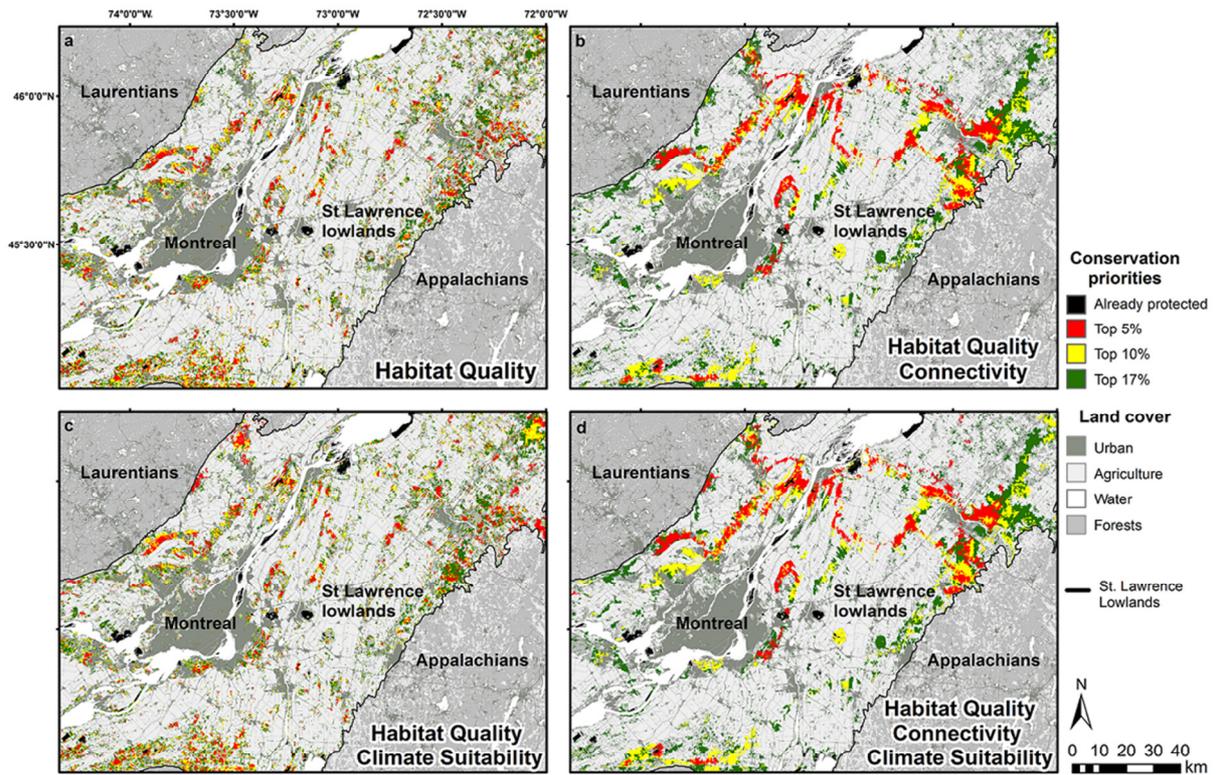


Figure 3. Changes in (a, b) short-range (equivalent connectivity in St. Lawrence Lowlands) and (c, d) long-range (mean cumulative resistance of shortest paths between mountain ranges) connectivity for the (a, c) business-as-usual (BAU) scenario over time and for (b, d) all conservation scenarios in 2050 (open symbols, mammals; closed symbols, birds; line symbols [e.g., +], amphibians; blue, low dispersal ability; green, yellow, orange; moderate dispersal ability; red, high dispersal ability; black dots, average effect across species).

Scenario comparisons in 2050 show the effects of protecting habitat in the context of ongoing land use: BAU (1.2% of area currently protected) versus 10% or 17% of area protected based on habitat quality (10Q and 17Q) or habitat quality and connectivity (10Q&C and 17Q&C).

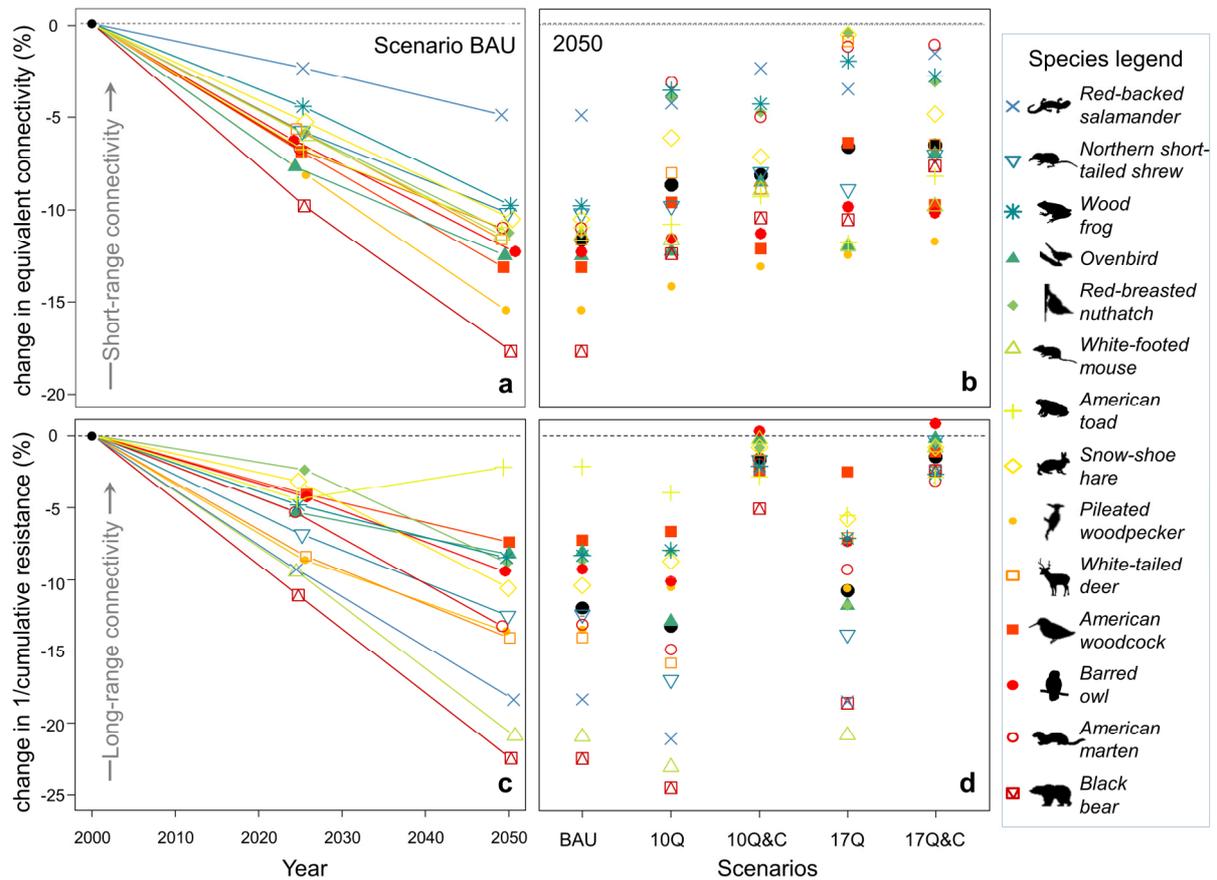


Figure 4. The mean percentage of conservation criteria (mean among the fourteen focal species) retained by Zonation in the quality and connectivity-based conservation prioritization scheme as a function of the percentage of the St. Lawrence Lowlands protected. These are potential criteria retention levels from Zonation without applying land-use change or recalculating network metrics. The retention of all criteria is displayed, even the climate criterion that is not targeted by this prioritization scheme. Stacked columns highlight the relative potential conservation value of criteria for our business-as-usual (BAU) (the 1.2% currently protected) and conservation scenarios (10% and 17% of area protected) and for all habitat protected (30%). The overall mean potential conservation value of each scenario is displayed in grey. The stacked column for *Quality (10%) and *Quality (17%) correspond to the quality-based prioritization scheme (Supporting Information) and are displayed here to emphasize differences between quality- and quality and connectivity-based prioritizations. Relative change in equivalent connectivity after systematic node removal (dEC) quantifies node importance in terms of the total amount and quality of habitat species can reach (Table 2). ‘Climate’ is an average of the climatic suitability layers across species, climate projections and horizons (2025, 2050).

