

1 **Omnidirectional and omnifunctional connectivity**

2 **analyses with a diverse species pool**

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22 **Abstract**

23 Connectivity among habitat patches in both natural and disturbed landscapes needs to be
24 accounted for in conservation planning for biodiversity maintenance. Yet methods to assess
25 connectivity are often limited, because simulating the dispersal of many species is
26 computationally prohibitive, and current simulations make simplifying assumptions about
27 movement that are potentially erroneous. Here we show how these limits can be circumvented
28 and propose a novel framework for the assessment of omnifunctional and omnidirectional
29 connectivity in a 28000 km² area in the Laurentian region of Québec, Canada. Our approach
30 relies on (i) the use of *Omniscape*, an improved version of *Circuitscape* which allows
31 omnidirectional simulations that better emulate animal movement and (ii) the synthesis of large
32 volume of species-level dispersal simulations through *a posteriori* clustering of the current
33 intensity. Our analysis reveals that the movement of 93 species evaluated can be clustered into
34 three functional dispersal guilds, corresponding to mostly aquatic species, terrestrial species able
35 to use aquatic environments, and strictly terrestrial species. These functional guilds do not share
36 connectivity hotspots, suggesting that corridor planning would need to account for the
37 multiplicity of dispersal strategies. Although this approach requires a large volume of computing
38 resources, it provides richer information on which landscape features are critical to maintain or
39 need to be regenerated for broader biodiversity maintenance goals.

40 Keywords : Circuitscape, Functional Dispersal Guilds, Landscape connectivity, Omniscape,

41 **Introduction**

42 Natural ecosystems are facing unprecedented threats as a function of both direct and indirect
43 anthropogenic disturbances, leading to a global and accelerating decline in biodiversity (Hooper
44 et al., 2012; Merino et al., 2019). Some of the main threats to biodiversity maintenance are the
45 joint effect of reduced area of natural habitat and connectivity loss among different habitat
46 patches across the landscape (Thompson et al., 2017). It reduces population size, gene flow, and
47 diversity, which in turn can lead to inbreeding and local extinction (Jackson and Fahrig, 2011). It
48 can also prevent species from reaching new suitable habitats, and therefore limits their chance of
49 both survival (Smith et al., 2013) and adaptation to climate change (Nuñez et al., 2013). A
50 possible solution is to establish ecological corridors between protected areas (Rayfield et al.,
51 2011), or more broadly to facilitate movements across the landscape at large spatial scales
52 (McRae Brad H. et al., 2008). As ecosystems are home to multiple species with different needs
53 and behaviours, it is essential that these corridors be multifunctional, *i.e.* that they account for the
54 fact that the ability to move across a landscape is perceived differently by different species
55 (Albert et al., 2017). Corridors that are well planned and implemented have the potential to
56 promote survival, migration, and preserve small populations, for a large number of species
57 (Smith et al., 2013). Indeed, they are essential for successful biodiversity maintenance in the
58 long-term.

59
60 In order to establish new ecological corridors, several methods to assess connectivity have been
61 developed in recent years. Belote et al. (2016) selected corridors with a least-cost path analysis
62 across the continental US, using Linkage-mapper (McRae et al., 2011). Cote et al. (2009) used

63 graph theory to assess structural connectivity of the Big Brook river drainage network (Terra
64 Nova National Park, Newfoundland, Canada): lakes were nodes linked by river reaches. Finally,
65 McRae et al. (2008), created Circuitscape, which used circuit theory to quantify the possibility of
66 crossing each territorial patch and tested this for Caspers Wilderness Park in California. Despite
67 a large variety of accessible techniques, most studies focused on the needs of terrestrial species
68 only (Appendix 1). Indeed, according to Correa Ayram et al. (2016), only 7% of connectivity
69 studies were conducted on fluvial habitats, while terrestrial ecosystems represent 88% of
70 research efforts on this topic between 2000 and 2013. However, without proper consideration of
71 connectivity to freshwater habitats (lakes and rivers), downstream health of river reaches could
72 degrade and critical riparian wetlands could dry up, resulting in both terrestrial and freshwater
73 biodiversity loss (Herbert et al., 2010; Smith et al., 2013). These ecosystems are naturally
74 integrated through their watersheds (Ballinger and Lake, 2006), therefore we argue that this is
75 the most ecologically relevant unit in which connectivity should be assessed.

76 To evaluate landscape connectivity for entire communities, it has been suggested to analyse a
77 territory's features according to the needs of a diverse number of terrestrial and aquatic species
78 (Albert et al., 2017; Sahraoui et al., 2017). It should lead to a more robust and realistic output, as
79 a small number of focal species seldom encompass the whole range of dispersal behaviours (Liu
80 et al., 2018; Marrotte et al., 2017; Meurant et al., 2018). However, because multi-species
81 analyses are complex (Moilanen et al., 2005), most efforts have often relied on the movement of
82 a limited number of species (see Appendix 1). Moreover, according to Correa Ayram et al.
83 (2016), there is a great redundancy of the species selected for the connectivity analyzes.

84 Mammals alone would represent 41% of the analyzes, mammal carnivores more than 20%. One
85 of the issues with assessing connectivity across multiple types of habitats is that it requires to
86 merge the results of several species-level connectivity analyses, to account for the variety of
87 ways in which different species react to different types of landscape elements (Albert et al.,
88 2017). When done with a large number of organisms, this imposes a double burden. One is to
89 reconcile the connectivity of possibly dozens of indicator species, not all of which may have
90 unbiased habitat use models (Olden et al., 2002). The other is having the computational capacity
91 to actually carry out this analysis. As the later is becoming less of a problem with increased
92 computational power and more diversified software offering to carry out connectivity
93 simulations, developing a general framework to include connectivity across ecosystem types,
94 with a diverse set of species, is an achievable and timely task.

95 A few studies have recently developed methods to aggregate multiple species-specific analyses
96 in a single result. For example, Albert et al. (2017) and Sahraoui et al. (2017) selected 14 and 16
97 eco-profiles respectively, each composed of one or more species, in order to represent a broader
98 range of dispersal behaviours and habitat requirements. These eco-profiles were designed
99 through dimensionality reduction based on species connectivity and habitat needs, either using
100 clustering or multivariate analysis. In another effort, Santini et al. (2016) selected all the 20 non-
101 volant mammal species of Italy that had a dispersal ability of a median of 3 km to identifying
102 defragmentation priorities. The three studies have created composite maps by summing the
103 single-species results or by calculating the mean score for each patch of habitat. Santini et al
104 (2016) went even further by testing seven other ways to merge the species-specific maps, using

105 weighted means of different landscape features to assess link probabilities, and two different
106 summation types for nodes in the network. These studies have demonstrated that it is possible to
107 create connectivity analyses for a large number of species, which may be ecologically more
108 relevant. Indeed the results could be meaningful for decision-makers, helping them to target new
109 protection areas, restore others, and inform more sustainable strategies in city development
110 projects (Ersoy et al., 2019). Despite these successes, they remain limited by three key aspects.
111 First, even a pool of 20 species cannot represent the entire functional diversity of realistic
112 communities. Second, selected species pools continue to under value the contribution of semi-
113 aquatic species and their habitats to landscape connectivity. Furthermore, freshwater biodiversity
114 is considered the most imperiled globally (Hendriks, 2016), suggesting that the need to include
115 aquatic and semi-aquatic species is urgent. Finally, because species clustering is done before the
116 simulations, this assumes that species connectivity depends on habitat requirements alone and
117 neglects differences that could emerge due to landscape configuration.

118 In this study we present a general framework for multi-species connectivity analysis, built
119 around the needs to (i) integrate terrestrial and aquatic ecosystems (Herbert et al., 2010), (ii) use
120 an ecologically relevant number of species to capture the diversity of ways in which species
121 interact with their landscape (Meurant et al., 2018), and (iii) provide measures of uncertainty
122 after different analyses have been merged. By contrast to previous studies relying on *a priori*
123 clustering of dispersal guilds (Lechner et al., 2017; Sahraoui et al., 2017) we propose an *a*
124 *posteriori* method for the creation of composite indicator species-guild. Our approach accounts
125 for the way species are predicted to move across the landscape by looking for similarities in their

126 dispersal simulations, rather than in the cost matrix of these species. We argue that this new way
127 of interpreting and post-processing connectivity simulations will result in a more integrative
128 view of landscape connectivity to favour biodiversity maintenance in the long-term.

129

130 **Methods**

131 **Study area**

132 We assessed our new connectivity approach using a 27 994 km² area located on the north shore
133 of the St. Lawrence River, near the city of Montréal, Québec, Canada (Fig. 1). Seven major
134 rivers are included in this region, and the area sits on two strikingly different geological
135 provinces, the Saint Lawrence lowlands, dominated by agriculture and urban areas, and the
136 Canadian Shield, covered largely by pristine temperate forests with a very high density of lakes
137 and rivers (19.8%). This high aquatic surface supports the need to account for more semi-
138 aquatic species in our simulations. This region was chosen because it shows a strong gradient of
139 anthropogenic disturbance, with heavy urbanization and agricultural development to the south,
140 major highways on the north-south axis, many roads, large forested areas particularly on the
141 Shield where there is an active forestry industry, some major National Parks (Mont Tremblant,
142 Oka, la Mauricie), and several small cities that service a large cottage industry. Moreover,
143 biological surveys conducted by conservation agencies and different government bodies resulted
144 in the creation of a curated list of species, which we integrated in this analysis.

145 **Selection of species**

146 In order to select the species for this study, two lists of recorded species from the main National
147 Parks were used (SEPAQa, 2019; SEPAQb, 2019). We kept 45 mammals, all amphibians (16)
148 and 9 reptile species, plus 15 avian species with a conservation status. We added five more avian

149 species, two amphibians and one reptile, which have been recorded in GBIF and Ebird database
150 since 2000, for a final list containing 93 species (see Appendix 2).

151 Collecting species habitat preference data

152 From the list of focal species, we got information on habitat preference and the way they move
153 across the landscape. Since these data are very heterogeneous, we gathered them from several
154 sources. We used data from the IUCN Red list (IUCN, 2019.), identification guides of Quebec
155 fauna (Desroches and Rodrigue, 2018 ; Prescott and Richard, 2014) and expert-curated websites
156 for the herpetofauna (“aarq | EcoMuseum,” 201.) and the avian fauna (Écopains d'abord, 2019.)
157 The complete cost matrix for all species is given in **APPENDIX 2**.

158 Creating the resistance maps

159 **Resistance maps** are a mix between energetic landscape and habitat quality modelling. They
160 represent the energetic and ecological cost to cross a certain plot as a function of its
161 configuration (topography, human structures) and composition (land cover) (Table I) (McRae
162 Brad H. et al., 2008). Matching preference data with the information on the land cover and
163 human structures present in the area allowed us to create a landscape resistance canvas for every
164 species, where 0 represents the absence of resistance and 100 the most important obstacle to
165 dispersal. Resistance maps are the sums of every spatial feature that could influence a species
166 dispersal.

167 According to the resistance canvas, we created the different layers composing the final resistance
168 map, using Qgis 3.4 (Qgis Development Team, 2019). We began with the land cover layer,
169 formed by thousands of polygons of 18 habitat types (agglomeration, crops, coniferous forest,
170 herbaceous wetland, etc.). To transform it into a resistance layer, we integrated the resistance
171 score of each species, to each type of land cover in the layer's data (Appendix 2). This is the
172 basic landscape features which influence species dispersal. In order to assess landscape
173 complexity to its fullest extent, we added the effect of slope, buildings presence, waterbodies,
174 roads, trails, and railways (Appendix 2) on species dispersal. For the roads, we have accounted
175 for their effect on a broader scale (150 m), with the resistance score decreasing according to the
176 distance from the road (Forman and Alexander, 1998). For the "slope" layer, we have considered
177 the degree of the slope as the degree of resistance (a slope of 50 degree equals a resistance of
178 50). Indeed, slope is known to have an impact on species displacement movement (Gaudry et al.,
179 2015; Leblond et al., 2010).

180 In order to create a resistance map by summing the layers for each species, we converted vector
181 resistance layers to raster layers. We first chose to use square cells at a resolution of 2 meters²,
182 which represents the smallest disturbance width considered in this study, hiking trails. Then, for
183 each individual species, we summed the resistance layers corresponding to their canvas, which
184 produced the 93 species-specific resistance maps. The resistance score of each cell represents the
185 sum of all landscape features, according to the species dispersal behaviour canvas.

186

187 Table 1 – Compilation of the data use, their type, resolution, the possible scores attributed to and their source

Variable	Vector or Raster	Scale / Resolution	Possible scores	Source
Hydrological network	Vector	1:50 000	0, 25, 50, 75 or 100	NTDB + National Hydro Network
Dames	Vector	1:50 000	100	NTDB
Slope	Raster	1:50 000	0 to 59	NTDB
Road Network	Vector	1:50 000	0, 25, 50, 75 or 100	NTDB
Railway network	Vector	1:50 000	0, 25, 50, 75 or 100	NTDB
Land cover	Vector	1 : 50 000	0, 25, 50, 75 or 100	Land Cover, circa 2000-Vector

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189 Analyzing landscape connectivity using Omniscape

190 We analysed species-specific resistance maps in *Omniscape* 0.1.2 (McRae et al., 2016),
191 implemented with julia 1.2.0 (Bezanson et al., 2015). *Omniscape* uses a round sliding windows
192 approach to connectivity simulations, which amounts to assuming that the species is aware of its
193 immediate surroundings, but not of the entire landscape. Indeed, species use the landscape
194 without knowing it entirely, which is assumed by the least-cost analysis (McRae Brad H. et al.,
195 2008). We used three different radiuses (30, 60 or 120 blocks, each block being a square parcel
196 of 180m²), and averaged the quantiles of the cumulative current map for all. This resulted in
197 connectivity scores ranging from close to 0 (specifically the inverse of the number of simulated
198 pixels) to 1. The choice to examine quantiles as opposed to raw cumulative current values was

199 driven by the fact that although different species will disperse at different rates (and therefore
200 will have different total cumulative currents), quantiles provide information as to their relative
201 use of the landscape. This would therefore facilitate the search for functional dispersal guilds.
202 Note that for some applications, analyzing the normalized current (*i.e.* the cumulative current
203 divided by the potential flow, as in *e.g.* McRae (2008), which is to say measuring how *surprising*
204 the observed current is compared to a null expectation) is preferable, notably for corridor
205 mapping or the identification of dispersal bottlenecks. In this analysis, we focus on how
206 organisms could disperse in the landscape, and therefore use the cumulative maps.

207 All simulations were performed on the beluga supercomputer, operated by Calcul Québec; the
208 project required an estimated total of 3 core-years to complete, being roughly equivalent to 3
209 years of time on a single-core machine.

210 A posteriori functional dispersal guilds

211 After all the simulations were complete, we aggregated the maps using fuzzy C-means (C.
212 Bezdek, 1981; Dunn, 1973). This approach allows to have species contribute to more than a
213 single cluster (for example, species that are terrestrial but have an affinity for water will have
214 landscape use that borrows from strictly aquatic and strictly terrestrial species), as captured by
215 the fuzziness parameter. Following community-established best practices, we set this parameter
216 to 2. Specifically, we applied fuzzy C-means by transforming all the connectivity scores into a s
217 by p matrix, with s the number of species and p the number of pixels with non-null connectivity
218 values, then by calculating the s by s Euclidean distance matrix between all pairs of species. We

219 extracted the centers of every cluster, and the species with the highest weight was the most
220 representative species for the dispersal guild. It may therefore be used as an indicator species in
221 the future. In addition, the weight of each species for each cluster can be used to measure species
222 specificity; we used PDI (Poisot et al., 2012) as a specificity estimator, which has the desirable
223 property of returning values that are lower than 0.5 for generalist species, and values above 0.5
224 for specialist species.

225 Fuzzy C-means lacks an established way to optimize the number of clusters[12] . As our goal is
226 to identify functional dispersal guilds that move across the landscape in different ways, we relied
227 on a simple heuristic to identify the optimal grouping. Fuzzy C-means results in a c by s matrix,
228 where c is the number of clusters; every column in this matrix is therefore the contribution of all
229 species to a cluster. Based on this information, we computed a c by c correlation matrix between
230 clusters, and retained the solution in which no pair of clusters had a positive significant
231 correlation.

232 Uncertainty analysis

233 To produce the final connectivity map, we averaged the scores for the centroids of the clusters
234 identified in the previous step, measured the standard deviation within each pixel, and finally
235 measured the coefficient of variation and Pielou's evenness within each pixel. The average
236 connectivity gives an idea of dispersal potential, and the coefficient of variation and evenness
237 informs about the areas in which the guilds differ markedly in their landscape use. In addition, in
238 keeping with the Aichi objectives (SCBD, 2011), we mapped the best 17% of pixels (*i.e.* with the

239 highest connectivity scores), using the average connectivity map as well as the map for every

240 dispersal guild.

241

242 Results

243 Guild clustering

244 From the 93 connectivity maps created, the fuzzy C-means identified an optimal fuzzy
245 partitioning into three functional dispersal guilds (FDG henceforth), whose most representative
246 species are the Horned grebe (*Podiceps auratus*, Linnaeus, 1758) (FDG1; fig. 3a), (FDG2; fig.
247 3b), the American black bear (*Ursus americanus*, Linnaeus, 1758) and Northern Two-lined
248 Salamander (*Eurycea bislineata*, Green, 1818) (FDG3; fig. 3c). All of these guilds share a very
249 poor connectivity score in the lowlands (although FDG3 can use some of the wooded areas for
250 east-west traversal), and differ in how they use the rest of the study area. In particular, FDG3
251 tends to have almost unrestricted movement outside of the lowlands, while FDG2 is predicted to
252 be more canalized in some places. Interestingly, while the two guilds for the more terrestrial
253 species were not correlated ($\rho = 0.054$), they were both correlated negatively to the cluster with
254 more aquatic species (ρ approx. -0.7 in both cases). This reveals not only that the needs of
255 aquatic and semi-aquatic species are different, but that favoring terrestrial species only in
256 connectivity planning will impede the movement of semi-aquatic species. The complete
257 clustering result, including specificity analysis, is given in **Appendix 3**. Applying PDI on the
258 clustering weight identified 15 generalist species, including notably the Canada Lynx (*Lynx*
259 *canadensis*, Kerr, 1792) (PDI = 0.45), moose (*Alces Alces*, Linnaeus, 1758), (PDI = 0.44), Red-
260 headed woodpecker (*Melanerpes erythrocephalus*, Linnaeus, 1758) (PDI = 0.27), and Hoary bat
261 (*Aeorestes cinereus*, Beauvois, 1796) (PDI = 0.42). Whereas specialist species, or species with

262 high affinity for a specific FDG can be good indicator species, generalist species can provide an
263 overall view of landscape connectivity.

264 Average connectivity and variation

265 As expected, the St-Lawrence lowlands performed uniformly worse in terms of connectivity,
266 with nevertheless some areas running parallel to the shore that can work as dispersal avenues (fig
267 3a), though these are mostly used by FDG3. Even in the more forested areas it is strikingly easy
268 to identify more developed regions or axes, corresponding to highways connecting the island of
269 Montréal to smaller clusters of anthropogenic activity. With the exception of these areas, the
270 region is remarkably well connected overall. The coefficient of variation and Pielou's evenness
271 for connectivity reveals areas in which the needs of species that favour either aquatic or
272 terrestrial habitats are more difficult to reconcile (fig 4b, 4c). This includes, trivially, the St
273 Lawrence river itself, but also areas surrounding large water bodies such as the *Lac Taureau* to
274 the North. It should be noted that although both the coefficient of variation and Pielou's evenness
275 provide a similar information (namely, the homogeneity in the use of every pixel by the three
276 FDGs), the later is a more appropriate measure. Although widely used, the coefficient of
277 variation performs better on ratio scales, whereas the quantiles of dispersal, being bounded, are
278 expressed on an interval scale.

279 Best-connected pixels

280 In fig. 5a, we represent the 17% of pixels with the highest *average* connectivity, which can be
281 thought of as forming the basis for a dispersal network across the region, independent of guilds.

282 This information should be contrasted to fig. 4b, in which we show the spatial distribution of the
283 best 17% of pixels for each of the different FDGs and superimposed them. Because the guilds
284 are optimized to maximize the differences between them, their most connected areas rarely
285 overlap. As a result, protecting the top 17% of pixels for all guilds combined would cover up to
286 three times more surface than the best 17% pixels on average. Furthermore, note that very few
287 aquatic habitats would be protected using the average classification as a target.

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291 **Discussion**

292 We have simulated the dispersal of 93 species across a 220 by 230 km area in the Laurentian
293 region of Québec. We then classified the multi-model average of connectivity maps using Fuzzy
294 C-means, to provide a regional average (Fig. 4a). Based on this result, we identified areas of
295 higher uncertainty (Fig. 4b, 4c) as well as candidate indicator species for each of the three
296 Functional Dispersal Guilds (FDGs). We found that connectivity is lower in the St Lawrence
297 Lowlands, which is more impacted by anthropogenic activities, and generally better in the
298 forested areas of the Canadian Shield. Although this result was expected, our approach was the
299 first to assess connectivity across such a large heterogeneous landscape, by accounting for the
300 full taxonomic diversity of both terrestrial and semi-aquatic species. Furthermore, these species
301 belong to different guilds representing three emergent dispersal landscapes that coexist within
302 the study region. Conservation actions that may neglect the protection of a specific guild due to
303 poor representativity of indicator species could have overall negative consequences on the
304 biodiversity maintenance of the entire region. Indeed, semi-aquatic, which form a guild on their
305 own, are often neglected.

306 We have used fuzzy C-means to cluster the species into FDGs, as it represents a more objective
307 approach in which species are able to contribute relatively among dispersal guilds. Indeed, we
308 identified about 16% of species classified as generalists that contribute in similar proportions to
309 all FDGs. Under a non-fuzzy scheme, this information would be lost as species would be forced
310 into one guild only. This being said, as we show in fig 6, the results of the fuzzy C-means

311 algorithm are directly comparable with a hierarchical clustering using Ward's agglomeration on
312 the pre-squared distance matrix. Although simple hierarchical clustering would have led to the
313 same dispersal guilds, the rich information of the movement of generalists species among guilds
314 could only be achieved using the fuzzy C-means approach.

315 Clustering returns groups of species based on predicted dispersal, and therefore represents a
316 process to select indicator species within each guild. By contrast, the *a priori* selection of
317 indicator species risks either underrepresenting or over representing different dispersal modes.
318 This is a particularly concerning issue, since as we illustrate in fig 4, the identification of the
319 most connected pixels varies greatly depending on whether the FDGs, or the average
320 connectivity, are used. Knowing the importance of the choice of representative species, the more
321 ecologically relevant *a posteriori* clustering should be favored, especially given that this amount
322 of simulations is computationally feasible. Indeed, among the 93 species used in this study,
323 several that would be considered "terrestrial" only, were found to benefit from freshwater
324 habitats for travel and therefore clustered differently. For example, this was notably the case for
325 the clustering of moose (*Alces alces*, Linnaeus 1758) with the common garter snake
326 (*Thamnophis sirtalis*, Linnaeus 1758) and many avian species, among others. This
327 counterintuitive association demonstrates that with regards to landscape connectivity, our
328 preconceived ideas of species groupings do not apply.

329 Despite the large diversity of species and their habitat preferences, fuzzy C-means identified an
330 optimal grouping of three functional dispersal guilds only. Surprisingly this is a lower number of
331 classes than most multi-species simulations have been using, and so it calls into question whether

332 using more species would have led to pseudo-replication, or to over-representing the needs of
333 some groups of organisms. Previous methods to suggest surrogate species for connectivity
334 modeling also resulted in a larger number of species (*e.g.* between 5 to 7 for Meurant et al.
335 2018). We argue that the number of species guilds should not be determined *a priori*, since these
336 classifications would rely only on between-species differences in habitat preferences, and would
337 not be able to account for how these differences interact with the spatial configuration and
338 habitat diversity in the landscape. Therefore we suggest our approach be used with the largest
339 number of species available, particularly in biophysically complex and species rich landscapes.

340 Once initial clustering is made, the entire species list may no longer be required for subsequent
341 simulations carried out for the same region. In a context such as a predicting the effect of land-
342 use or climate change on connectivity, which would involve many thousands of simulations, one
343 strategy would be to identify the most representative species for the optimal number of FDGs,
344 and then use these indicator species in the simulations. While this results in the loss of some
345 information, this offers a reasonable compromise between the effort to identify relevant species
346 in initial computationally intensive analysis, and the effort to perform projections of future
347 connectivity maps. Additional schemes to pick a subset of species to work on should be
348 evaluated on a case by case basis and can involve picking a mix of specialist and generalist
349 species.

350 Here we provide, to our knowledge, the most robust and fully integrated terrestrial and aquatic
351 multi-dispersal connectivity assessment at a regional scale. We used a broad suite of diverse taxa
352 in a heterogeneous landscape structured by a number of different anthropogenic disturbances

353 across two major geological provinces. The integration of the multiple dispersal pathways
354 provides a robust connectivity conservation plan and our approach offers a road map for future
355 connectivity assessments. Given the ongoing biodiversity crisis, identifying and implementing
356 corridors to maintain habitat connectivity for conservation for as many species as possible is
357 increasingly urgent. Yet, current conservation strategies often neglect the diversity of ways in
358 which species actually use the landscape, since they focus largely on terrestrial species. For
359 example, as a worst case scenario, habitat patches crucial to the dispersal of a specific functional
360 group would not be adequately protected; this connectivity loss for an entire subgroup of species
361 could have a cascading effect with the potential to destabilize the entire ecosystem.

362 **Data availability:** Data will be deposited on DataDryad upon acceptance.

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375 **Figure legends**

376 Figure 1 - Study area, on the North Shore of the Saint Lawrence river, province of Québec,
377 Canada. A. Oka National Park B. Mont-Tremblant National Park C. La Mauricie National Park
378 D. Lac Taureau. The study area is astride two geological provinces, the Saint Lawrence
379 Lowlands (yellow) and the Canadian Shield (green).

380 Figure 2. - Representation of the overall method flow. For each species (93), landscape layers
381 features got scored between 0 and 100 for their resistance (1). Then, the layers were converted in
382 a raster format to be summed, which created one resistance map by species (2). Following this
383 step, the maps were analysed using Omniscape, which created connectivity maps (3). We
384 assigned to each pixel its quantile in the observed map of the cumulative current for the species
385 (4) and conducted a clustering fuzzy C-means analysis on the unfolded 93 connectivity map to
386 get the *a posteriori* dispersal guilds (5). After the clustering, we extracted the weighted centroids
387 of each cluster (6) and measured the additional indices (evenness, variation, location of the most
388 connected pixels) (7).

389 Figure 3 – Connectivity scores for the three different guilds. Higher values indicate more
390 potential for movement. St. Lawrence Lowlands have areas with medium connectivity potential
391 for FDG1 and FDG2 but are globally lowly connected and do not have real potential to facilitate
392 the movement of species from FDG3. The Canadian shield, however, show high connectivity
393 potential for the three guilds, especially FDG2. A. FDG1 – Species of open and undisturbed
394 habitats B. FDG2 – Species of forested habitats C. FDG3 – Species of freshwater habitats

395 Figure 4 – Representation of the Average connectivity score (A), Coefficient of variation (B) and
396 Pielou’s evenness (C) A. Average connectivity across the three functional guilds. The St.
397 Lawrence Lowlands have a lower connectivity overall, though some more intact habitats running
398 parallel to the shore allow for traversal. B. Coefficient of Variation across the three FDGs (n=3),
399 corrected for small sample size by a coefficient of $(1+1/4n)$. Values on the map have been
400 capped at 1, as values larger than unity are generally regarded as noise. C. Pielou’s evenness
401 across FDGs. Note that the color scale has been inverted, to reflect the fact that high values
402 correspond to more similar connectivity across FDGS.

403 Figure 5 – Spatial distribution of the best 17% of pixels with the highest average connectivity
404 (A) and the best 17% of pixel for all guilds combined (B). The pixels in panel B cover
405 approximately 40% of the entire territory, suggesting that the three functional guilds have very
406 high complementarity.

407 Figure 6 – Comparison between Ward’s clustering (A) and the Fuzzy C-Means (B) results. Both
408 methods identify three distinctives groups of dispersal behaviour (guilds), but only Fuzzy C-
409 means allows to uncover the fact that some species are actually generalists.

410

411 **References**

- 412 Albert, C.H., Rayfield, B., Dumitru, M., Gonzalez, A., 2017. Applying network theory to
413 prioritize multispecies habitat networks that are robust to climate and land-use change. *Conserv.*
414 *Biol.* 31, 1383–1396. <https://doi.org/10.1111/cobi.12943>
- 415 Ballinger, A., Lake, P.S., 2006. Energy and nutrient fluxes from rivers and streams into
416 terrestrial food webs. *Mar. Freshw. Res.* 57, 15–28. <https://doi.org/10.1071/MF05154>
- 417 Belote, R.T., Dietz, M.S., McRae, B.H., Theobald, D.M., McClure, M.L., Irwin, G.H.,
418 McKinley, P.S., Gage, J.A., Aplet, G.H., 2016. Identifying Corridors among Large Protected
419 Areas in the United States. *PLOS ONE* 11, e0154223.
420 <https://doi.org/10.1371/journal.pone.0154223>
- 421 Bezanson, J., Edelman, A., Karpinski, S., Shah, V.B., 2015. Julia: A Fresh Approach to
422 Numerical Computing. ArXiv14111607 Cs.
- 423 C. Bezdek, J. (1981). *Pattern Recognition with Fuzzy Objective Function Algorithms*. Boston,
424 MA: Springer
- 425 Desroches, J.-F., Rodrigue, D. (2018) *Amphibiens et reptiles Édition revue et augmentée du*
426 *Québec et des Maritimes*. Montréal, Québec: Éditions Michel Quintin
- 427 Dunn, J.C., 1973. A Fuzzy Relative of the ISODATA Process and Its Use in Detecting Compact
428 Well-Separated Clusters. *J. Cybern.* 3, 32–57. <https://doi.org/10.1080/01969727308546046>

- 429 Écopains d'abord. 2019. Les oiseaux. <http://www.oiseaux.net/> (accessed 6.21.19).
- 430 Ersoy, E., Jorgensen, A., Warren, P.H., 2019. Identifying multispecies connectivity corridors and
431 the spatial pattern of the landscape. *Urban For. Urban Green.* 40, 308–322.
432 <https://doi.org/10.1016/j.ufug.2018.08.001>
- 433 Forman, R.T.T., Alexander, L.E., 1998. Roads and Their Major Ecological Effects. *Annu. Rev.*
434 *Ecol. Syst.* 2, 207-C2.
- 435 Gaudry, W., Saïd, S., Gaillard, J.-M., Chevrier, T., Loison, A., Maillard, D., Bonenfant, C.,
436 2015. Partial migration or just habitat selection? Seasonal movements of roe deer in an Alpine
437 population. *J. Mammal.* 96, 502–510. <https://doi.org/10.1093/jmammal/gyv055>
- 438 Hendriks, E. 2016. Les écosystèmes d'eau douce font face à des menaces imminentes.
439 [https://blog.wwf.ca/fr/2016/10/26/les-ecosystemes-deau-douce-font-face-a-des-menaces-](https://blog.wwf.ca/fr/2016/10/26/les-ecosystemes-deau-douce-font-face-a-des-menaces-imminentes/)
440 [imminentes/](https://blog.wwf.ca/fr/2016/10/26/les-ecosystemes-deau-douce-font-face-a-des-menaces-imminentes/) (accessed 5.15.18).
- 441 Herbert, M., B McIntyre, P., J Doran, P., David Allan, J., Abell, R., 2010. Terrestrial Reserve
442 Networks Do Not Adequately Represent Aquatic Ecosystems. *Conserv. Biol. J. Soc. Conserv.*
443 *Biol.* 24, 1002–11. <https://doi.org/10.1111/j.1523-1739.2010.01460.x>
- 444 Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L.,
445 Gonzalez, A., Duffy, J.E., Gamfeldt, L., O'Connor, M.I., 2012. A global synthesis reveals
446 biodiversity loss as a major driver of ecosystem change. *Nature* 486, 105–108.
447 <https://doi.org/10.1038/nature11118>

448 IUCN. (2019). “The IUCN Red List of Threatened Species. <https://www.iucnredlist.org/en>
449 (accessed 6.21.19).

450 Jackson, N.D., Fahrig, L., 2011. Relative effects of road mortality and decreased connectivity on
451 population genetic diversity. *Biol. Conserv.* 144, 3143–3148.
452 <https://doi.org/10.1016/j.biocon.2011.09.010>

453 Leblond, M., Dussault, C., Ouellet, J.-P., 2010. What drives fine-scale movements of large
454 herbivores? A case study using moose. *Ecography* 33, 1102–1112.
455 <https://doi.org/10.1111/j.1600-0587.2009.06104.x>

456 Lechner, A.M., Sprod, D., Carter, O., Lefroy, E.C., 2017. Characterising landscape connectivity
457 for conservation planning using a dispersal guild approach. *Landsc. Ecol.* 32, 99–113.
458 <https://doi.org/10.1007/s10980-016-0431-5>

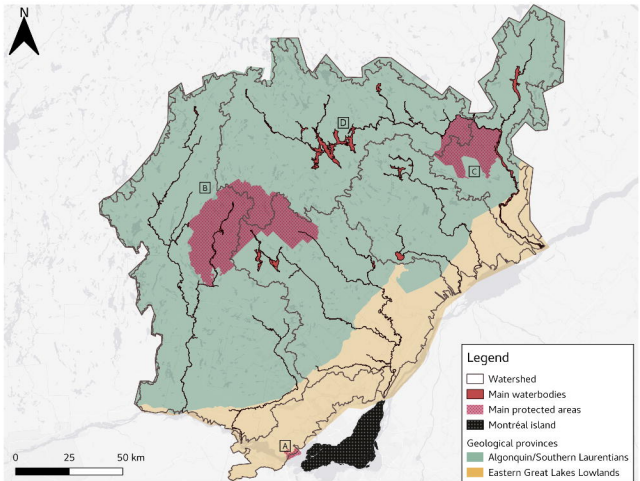
459 Liu, C., Newell, G., White, M., Bennett, A.F., 2018. Identifying wildlife corridors for the
460 restoration of regional habitat connectivity: A multispecies approach and comparison of
461 resistance surfaces. *Plos One* 13, e0206071. <https://doi.org/10.1371/journal.pone.0206071>

462 Marrotte, R.R., Bowman, J., Brown, M.G.C., Cordes, C., Morris, K.Y., Prentice, M.B., Wilson,
463 P.J., 2017. Multi-species genetic connectivity in a terrestrial habitat network. *Mov. Ecol.* 5.
464 <https://doi.org/10.1186/s40462-017-0112-2>

- 465 McRae Brad H., Dickson Brett G., Keitt Timothy H., Shah Viral B., 2008. Using circuit theory
466 to model connectivity in ecology, evolution, and conservation. *Ecology* 89, 2712–2724.
467 <https://doi.org/10.1890/07-1861.1>
- 468 McRae B., Shar V., Anantharaman R., Mohapatra T. Linkage Mapper Tools. 2011. Linkage
469 Mapper Tools | Circuitscape. <https://circuitscape.org/linkagemapper/linkage-mapper-tools/>
470 (accessed 6.20.19).
- 471 Merino, L., Minang, P.A., Sidorovich, A., Andrade, L., Aumeeruddy-Thomas, Y., Badola, R.,
472 Bai, X., Benessaiah, K., 2019. IPBES Global Assessment on biodiversity en Ecosystem Services
473 : Status and trends; indirect and direct drivers of change - Drivers of Change.
- 474 Meurant, M., Gonzalez, A., Doxa, A., Albert, C.H., 2018. Selecting surrogate species for
475 connectivity conservation. *Biol. Conserv.* 227, 326–334.
476 <https://doi.org/10.1016/j.biocon.2018.09.028>
- 477 Moilanen, A., Franco, A.M.A., Early, R.I., Fox, R., Wintle, B., Thomas, C.D., 2005. Prioritizing
478 multiple-use landscapes for conservation: methods for large multi-species planning problems.
479 *Proc. R. Soc. B Biol. Sci.* 272, 1885–1891. <https://doi.org/10.1098/rspb.2005.3164>
- 480 Nuñez, T.A., Lawler, J.J., Mcrae, B.H., Pierce, D.J., Krosby, M.B., Kavanagh, D.M., Singleton,
481 P.H., Tewksbury, J.J., 2013. Connectivity Planning to Address Climate Change. *Conserv. Biol.*
482 27, 407–416. <https://doi.org/10.1111/cobi.12014>

- 483 Olden, J.D., Jackson, D.A., Peres-Neto, P.R., 2002. Predictive models of fish species
484 distributions: A note on proper validation and chance predictions. *Trans. Am. Fish. Soc.* 131,
485 329–336. [https://doi.org/10.1577/1548-8659\(2002\)131<0329:PMOFSD>2.0.CO;2](https://doi.org/10.1577/1548-8659(2002)131<0329:PMOFSD>2.0.CO;2)
- 486 Poisot, T., Canard, E., Mouquet, N., Hochberg, M.E., 2012. A comparative study of ecological
487 specialization estimators. *Methods Ecol. Evol.* 3, 537–544. <https://doi.org/10.1111/j.2041->
488 210X.2011.00174.x
- 489 Prescott, J., Richard, P. (2014). *Mammifères du Québec et de l'Est du Canada*. Waterloo,
490 Québec : Éditions Michel Quintin
- 491 Qgis Development Team 2019. 2019. Geographic Information System. Open Source Geospatial
492 Foundation Project. <http://qgis.osgeo.org>. (accessed 11.27.19).
- 493 Rouleau, S. 2019. “Espèces | aarq”, Ecomuseum. <https://www.atlasamphibiensreptiles.qc.ca/wp/>
494 (accessed 7.3.19).
- 495 Rayfield, Fortin Marie-Josée, Fall Andrew, 2011. Connectivity for conservation: a framework to
496 classify network measures. *Ecology* 92, 847–858. <https://doi.org/10.1890/09-2190.1>
- 497 Sahraoui, Y., Foltête, J.-C., Clauzel, C., 2017. A multi-species approach for assessing the impact
498 of land-cover changes on landscape connectivity. *Landsc. Ecol.* 32, 1819–1835.
499 <https://doi.org/10.1007/s10980-017-0551-6>
- 500 SCBD. 2011. Quick guide to the Aichi Biodiversity Targets Protected areas increased and
501 improved. <https://www.cbd.int/nbsap/training/quick-guides/> (accessed 6.20.19)

- 502 SEPAQ. 2019. Portrait du parc - Parc national d'Oka.
503 https://www.sepaq.com/pq/oka/decouvrir/portrait.dot?language_id=2 (accessed 11.13.19).
- 504 SEPAQ. (2018) Portrait du parc - Parc national du Mont-Tremblant.
505 <https://www.sepaq.com/pq/mot/decouvrir/portrait.dot> (accessed 6.4.18).
- 506 Smith, T.M., Smith, R.L., Waters, I. (2014). Elements of Ecology (1st Canadian Edition).
507 Toronto, Ontario : Pearson Canada.
- 508 Thompson, P.L., Rayfield, B., Gonzalez, A., 2017. Loss of habitat and connectivity erodes
509 species diversity, ecosystem functioning, and stability in metacommunity networks. *Ecography*
510 40, 98–108. <https://doi.org/10.1111/ecog.02558>
- 511 WWF. 2016. Living Planet Report 2016. Risk and resilience in a new era. WWF International,
512 Gland, Switzerland



1)

Landscape
layers1 variable
by map

3)

Connectivity
matrixConnectivity
matrix1 species
by map

5)

Dispersal
pathsDispersal
pathsMultiple
species
by group

7)

Uncertainty
analysisUncertainty
analysis3 maps
by cluster

