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Marta Zaffaroni, Patrizia Zamberletti, Irena F. Creed, Francesco Accatino, Carlo de Michele, Ben Devries

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1 **Safeguarding wetlands and their connections within wetlandscapes to improve conservation outcomes**
2 **for threatened amphibian species**

3 Marta Zaffaroni, Patrizia Zamberletti, Irena F. Creed, Francesco Accatino, Carlo De Michele, Ben
4 DeVries

5 Department of Civil and Environmental Engineering (Zaffaroni, Zamberletti, De Michele),
6 Politecnico di Milano, Milan, IT; School of Environment and Sustainability (Creed), University
7 of Saskatchewan, Saskatoon, Saskatchewan, CA; INRA (Institute National de la Recherche
8 Agronomique) UMR (Unité Mixte de Recherche) 1048 SAD (Sciences pour l'Action et le
9 Développement)-APT (AgroParisTech) (Accatino), Paris, FR; Department of Geographical
10 Sciences (DeVries), University of Maryland, College Park, Maryland, 20742, US.

11 (Correspondence to Creed: irena.creed@usask.ca)

12

13 **Research Impact Statement:** Both wetland habitat quality and connectivity act jointly but
14 differently on amphibian population dynamics and should both be considered when managing
15 wetlandscapes.

16

17 **Abstract**

18 Wetlands should not be considered as independent objects but as dynamically connected objects,
19 collectively known as wetlandscapes. We developed a framework that analyzes the influences of
20 wetland suitability and connectivity on amphibian distributions. We defined two indices: a
21 Wetland Suitability Index describing wetland quality and a Movement Permeability Index
22 characterizing wetland connectivity for amphibian population dynamics. These indices were
23 calculated from raster datasets and time-varying inundation estimates. The indices were used to

24 define a wetlandscape and an amphibian model was used to simulate population dynamics within
25 the wetlandscape. The framework was applied to the Nose Creek watershed, a highly modified
26 wetlandscape in Alberta, Canada. Two amphibian species were selected with different habitat
27 preferences: the Northern Leopard Frog that prefers wet habitats and has high mobility over land,
28 and the Great Plains Toad that prefers terrestrial habitats and has low mobility over land. We
29 found that each amphibian species had a “preferred” wetlandscape, reflecting their life cycle
30 traits and migration strategies which in turn were dependent on the hydrological and ecological
31 connections within the wetlandscape. This study highlights the importance of investigating both
32 individual wetlands and the wetlandscape and considering both wetland habitat quality and
33 connectivity as non-substitutable properties that act jointly, but differently, on population
34 dynamics.

35 **Key terms:** wetland; geospatial analysis; remote sensing; wetland networks; amphibian
36 population dynamics

37

38 INTRODUCTION

39 Wetlands are strongholds of biodiversity and support a disproportionately large number of species
40 by offering protection and breeding sites (Cohen *et al.*, 2016). Amphibians are particularly
41 vulnerable to the effects of wetland degradation and destruction, because their survival often
42 depends on both wetlands themselves and surrounding terrestrial matrix among wetlands
43 (Dudgeon *et al.*, 2006). This vulnerability is a consequence of their biphasic life cycle: they rely
44 on wetland habitats for breeding (Semlitsch, 2000; Mushet *et al.*, 2012), and use the terrestrial
45 matrix (Joly, 2001) for foraging and moving to other wetlands (Harper *et al.*, 2008). Breeding
46 success is determined by the quality of the wetland itself (Mushet *et al.*, 2012), and migration

47 success is determined by the distribution of wetlands and by the permeability of the terrestrial
48 matrix, both providing resting and foraging habitat for migrating species (Calhoun et al., 2017).
49 Wetland loss decreases wetland density and increases travel distances for amphibians,
50 simultaneously impacting breeding and migration success (Gibbs, 1993).

51 Habitat Suitability Models (HSMs) are frequently used by conservation planners to
52 estimate the likelihood of occurrence and the abundance of threatened species in a geographic
53 area (Carvalho and Gomes, 2003), with the purpose of evaluating the capacity of a given habitat
54 to support a selected wildlife species (U.S. Fish and Wildlife Service, 1981). HSMs are typically
55 developed by assessing statistical relationships between existing occurrences of a species and
56 habitat features (Store and Kangas, 2001). These statistical models require empirical data, which
57 are expensive and time-consuming to obtain (Store and Kangas, 2001). Large spatial and
58 temporal scales are recognized to be fundamental for amphibian research because changes to
59 landscape conditions across scales may have important impacts on habitat connectivity and
60 migration (Hazell, 2003; Bishop-Taylor et al., 2015). Earth observation satellite data (Bishop-
61 Taylor et al., 2017), expert knowledge (Store and Kangas, 2001) and Geographical Information
62 Systems (GIS) (Store and Jokimäki, 2003) have been successfully combined for developing
63 HSMs. When such data are not available, HSMs can be developed by aggregating habitat features
64 using expert knowledge (Store and Kangas, 2001).

65 Despite the increasing interest in HSMs, wetland conservation policies and management
66 strategies often focus on wetlands as stand-alone features on the landscape (Amezaga *et al.*,
67 2002). In other words, the focus is often on wetland habitats and the capacity of a given wetland
68 habitat to support a selected wildlife species (USDA Fish and Wildlife Service, 1981). The
69 species life history traits, which are especially important for species requiring migration to
70 different wetlands in their life cycle, and the suitability of the corridors that connect wetlands and

71 allow for organism migration are often not considered. Such a “wetland-by-wetland” approach
72 focuses on compensating for wetland loss through various mechanisms, such as wetland
73 protection, restoration, and construction (National Research Council, 2001), and has led to
74 fundamental changes in the types and distribution of wetlands in the landscape (Thomas and
75 Lamb, 2005; Accatino et al., 2018). There is an emerging recognition that wetland conservation
76 strategies must consider not only the wetland itself, but also the connections among wetlands,
77 which act as conduits of energy and mass among wetlands (Cohen et al., 2016). For example, in
78 their review on amphibians metapopulation dynamics, Marsh and Trenham (2001) highlight the
79 importance of considering not only breeding wetlands, but also the terrestrial matrix, in research
80 and management applications. Moreover, they suggest using modeling approaches to explore the
81 consequences of amphibian dispersal behavior.

82 The aim of our study is to develop an integrated framework to improve habitat suitability
83 evaluation for amphibian populations in a wetlandscape. Wetlandscapes are defined as multiple
84 wetlands that present biotic and abiotic connections within an associated hydrological catchment
85 larger area than that of individual wetlands (Thorslund *et al.*, 2017). We demonstrate the
86 framework in the wetlandscape of the Nose Creek watershed in Alberta, Canada, selecting two
87 amphibian species: the northern leopard frog (*Rana pipiens*) and the great plains toad (*Anaxyrus*
88 *cognatus*). The framework focuses on two assumptions: (1) both wetlands and their connections
89 within the wetlandscape must be characterized by indices considered in defining HSMs
90 (Cushman, 2006; Mushet et al., 2014; Kininmonth et al., 2015); and (2) wetlands and their
91 connections are integral parts of a network-based HSM and amphibian population model
92 (Fortuna et al. 2006). To operationalize assumption (1), we develop two indices: the Wetland
93 Suitability Index (WSI), which assesses the goodness-of-fit of each wetland according to the
94 requirements of the amphibian species; and the Movement Permeability Index (MPI), which

95 assesses the permeability of the surrounding terrestrial matrix for amphibian migration. To
96 operationalize assumption (2), we describe the wetlandscape as a wetland network where we
97 simulate an amphibian population dynamics model (Zamberletti et. al., 2018). The use of a
98 dynamic ecological model makes it possible to take into account the phenomena linked to
99 metapopulations and migration dynamics, especially defining sink and source habitats (Iles et al.,
100 2018; Zamberletti et al., 2018). Model results and indices were compared to determine the
101 interactive/integrated importance of the two assumptions on amphibian survival. The aim of this
102 study is not to give specific management prescriptions, but to pave the way for a holistic
103 approach to the management of wetlandscapes for amphibians, highlighting the general principles
104 and proposing methodological directions to be improved with future refinements.

105

106

METHODS

107 A flowchart outlining the integration among the amphibian population model and two indices
108 (i.e., WSI and MPI) is presented in Figure 1. Satellite and ancillary data were used to derive the
109 information required for index development (Figure 1 a.1). MPI assigned the amphibian
110 migration permeability to each cell of the terrestrial matrix (Figure 1 a.2). WSI assigned the
111 amphibian goodness-of-fit to each wetland (Figure 1 a.3). MPI was used to define the
112 connections of wetland network (Figure 1 a.4), and WSI was used to compute the carrying
113 capacity for each wetland (Figure 1 a.5). Wetland network and wetland carrying capacity were
114 coupled within amphibian population model to simulate the amphibian dynamics on the
115 wetlandscape (Figure 1 a.6). The influence of indices on model output were analyzed to assess
116 amphibian survival within the wetlandscape (Figure 1 a.7). The methods are organized focusing
117 on the two indices, MPI, WSI, and the amphibian population model. Then, the combination of the

118 model and indices is described. Finally, a case study of a highly modified wetlandscape (i.e.,
119 Nose Creek watershed) is presented as an example of application.

120 (Fig1)

121 *Index definitions*

122 The typical life cycle of amphibians, which involves spring breeding in wetland habitat, foraging
123 in wetland surrounding terrestrial habitat, and late summer migration through the terrestrial
124 landscape, was modeled using two indices: the Movement Permeability Index (MPI) and the
125 Wetland Suitability Index (WSI). The first aimed to determine the permeability of the terrestrial
126 matrix resulting in the aquatic and terrestrial corridor suitability among wetlands to support
127 amphibian migration, and the second aimed to quantify the suitability of a wetland to sustain an
128 amphibian population. The list of variables considered for index evaluation is presented in Table
129 1 which explains the reasoning, the index in which the variable is used and for which species.

130 (Table1)

131 **Movement Permeability Index (MPI).** The MPI describes the permeability of the
132 terrestrial landscape used by amphibians during their migration (i.e., month of September)
133 evaluating the role of a wetland as “stepping stone”. The MPI was computed for each grid cell of
134 the wetlandscape. The MPI ranged from 0 to 1, where 0 meant that the cell was not suitable for
135 the amphibian’s movement (i.e., it contained obstacles that would make amphibian movement
136 difficult, such as road barriers (COSEWIC, 2009)), and 1 meant that the cell was very suitable for
137 the amphibian’s movement. The MPI was a function of both terrestrial and aquatic features of the
138 landscape, since amphibians could migrate both through terrestrial corridors (e.g., roads,
139 agricultural fields) and aquatic corridors (e.g., streams and riparian areas). The suitability of
140 migration through the wetland area was a function of calculated scores reflecting the amphibian’s

141 ability to migrate through terrestrial corridors on the wetlandscape (Terrestrial Corridor
142 subfunction) and aquatic corridors on the wetlandscape (Aquatic Corridor subfunction). The
143 terrestrial and aquatic corridor subfunctions were scored between 0 and 1, and the minimum of
144 the two scores was used to represent the MPI:

$$145 \quad \quad \quad MPI = \min(TC, AC) \quad \quad \quad (1)$$

146 where TC is the Terrestrial Corridor score and AC is the Aquatic Corridor score. Figure 1b shows
147 the aggregation schemes for MPI and a detailed description is given in Appendix S1.

148 **Wetland Suitability Index (WSI).** The WSI describes the ability of a wetland to meet the
149 needs of an amphibian for reproduction and the survival of offspring through their metamorphic
150 cycle. The WSI was evaluated for each wetland of the wetlandscape. The index ranged from 0 to
151 1, where 0 indicated that the wetland was not suitable for the amphibian's needs and 1 indicated
152 that the wetland was very suitable for the amphibian's needs. The wetland "area" was defined as
153 the wetland itself plus a buffer of surrounding terrestrial habitat whose size was defined by the
154 maximum walking distance that an amphibian species could travel during the breeding and
155 foraging phase (i.e., NLF buffers: 200 m for breeding and 2000 m for foraging (Kendell and
156 Prescott, 2007); GPT buffers: 1300 m for breeding and foraging (COSEWIC, 2010)). The
157 suitability of the wetland was expressed as a function of calculated scores reflecting the wetland's
158 ability to meet the amphibian's requirements:

$$159 \quad \quad \quad WSI = \min(WSI_{breeding}, WSI_{foraging}) \quad \quad \quad (2)$$

160 Where $WSI_{breeding}$ is the suitability during the breeding phase (i.e., from April to May) and
161 $WSI_{foraging}$ is the suitability during the foraging phase (i.e., from June to August). $WSI_{breeding}$ and
162 $WSI_{foraging}$ resulted from the aggregation of functions representing features that were fundamental
163 for amphibian breeding and foraging (i.e., if one of these characteristics was missing, amphibians

164 perceived the habitat as completely unsuitable), and were not fundamental (i.e., they contributed
165 to make a habitat more suitable, but if they were missing the habitat remained suitable for an
166 amphibian to breed or to forage). Fundamental and non-fundamental functions were evaluated
167 separately by aggregating wetland sub-functions, with sub-functions resulting from variables
168 derived from satellite imagery and land use/land cover maps. Figure 1c shows the aggregation
169 scheme with all variables, sub-functions, functions and final scores (see further Appendix S2).
170 The lack of amphibian data for our study area presented a major limitation to the MPI and WSI
171 model formulation. Therefore, we developed the models to be adherent to amphibian scientific
172 literature. Additionally, we performed a global sensitivity analysis using the SAFE Matlab
173 Toolbox (Pianosi et al., 2015) to assess the parameters that had the most influence on the MPI
174 and WSI. The results of the sensitivity analysis are fully described in the Appendix S3.

175

176 *Amphibian population dynamics model*

177 Amphibian population dynamics within the wetlandscape were simulated using a model
178 described in Zamberletti *et al.* (2018) and summarized here. There were two key periods during
179 the year (t): amphibian breeding in the wetland and amphibian migration among wetlands. N_t^i is
180 the number of amphibians at the beginning of year t in wetland i , $N_{t+\frac{1}{2}}^i$ is the number of
181 amphibians in the wetland after the breeding phase, and N_{t+1}^i is the number of amphibians in
182 wetland i after the migration phase of year t .

183 **Breeding.** During the breeding stage of the life cycle, the adults in each wetland produced
184 offspring that complete the metamorphic cycle, subsequently migrating and reproducing in other
185 wetlands the following year. The population $N_{t+\frac{1}{2}}^i$ is composed of the population N_t^i and the

186 offspring that successfully completed the metamorphic cycle. The survival of offspring in a
 187 wetland was negatively affected by the “density effect”, where a deficiency of resources occurred
 188 as a result of increased population density. The carrying capacity (K) of the amphibian species
 189 represented the maximum population size of the species that the environment could sustain,
 190 considering existing resources:

$$191 \quad N_{t+\frac{1}{2}}^i = N_t^i + \max(0, rN_t^i(1 - \frac{N_t^i}{K})) \quad (3)$$

192 where r is the intrinsic growth rate.

193 **Migration.** The migration stage simulated the movement of amphibians from wetland i to
 194 wetland j . The number of amphibians at the time $t+1$ that reached the wetland i was given by:

$$195 \quad N_{t+1}^i = \phi(1 - \mu)N_{t+\frac{1}{2}}^i + \sum_{j=1}^{M_i} w_{ij}(1 - \phi) N_{t+\frac{1}{2}}^j \quad (4)$$

196 where M_i is the number of wetlands connected to wetland i , ϕ is the fraction of amphibians
 197 returning to the same wetland the year after (philopatric behavior, see Appendix S4 for further
 198 explanation), μ is the natural mortality, w_{ij} is the fraction of the amphibian population that left
 199 wetland j and reached wetland i alive, which was computed considering the suitability of the
 200 connections between wetlands i and j , the mortality that occurred during migration between
 201 wetlands i and j and during overwintering, and natural amphibian mortality. We performed a
 202 global sensitivity analysis on the parameters of the amphibian model using the SAFE Matlab
 203 Toolbox (Pianosi et al., 2015), described in Appendix S4.

204

205 *Coupling MPI and WSI with the amphibian dynamic model.*

206 The WSI estimated the carrying capacity K of wetlands and the MPI evaluated the connectivity,
 207 w_{ij} , among wetlands. The carrying capacity K of each wetland was therefore defined as:

208
$$K = WSI \cdot A \cdot N \quad (5)$$

209 where A is wetland area (m^2) and N represents the number of amphibians supported by a unit of
210 wetland area (amphibians/ m^2). If $WSI = 1$, the carrying capacity corresponded to the nominal
211 carrying capacity, whereas if $WSI < 1$ the carrying capacity was reduced. The connectivity w_{ij}
212 between wetland i and wetland j was defined as a function of the connection costs and suitability
213 for migration. First, the cost (c_u) of moving through a wetlandscape cell (u) was calculated as:

214
$$c_u = 1 - MPI_u \quad (6)$$

215 The least-cost connectivity network between wetlands was computed using the Cost
216 Connectivity tool implemented in ArcGIS (ArcGIS 10.5, Spatial Analyst toolbox, Distance
217 toolset). The Cost Connectivity tool identified the connections from each wetland to each of its
218 least-cost neighbors. The corridors were weighted by the corridor's cost, which could vary from 0
219 to 200 and represented the sum of the costs c_u of the cells along the corridors. Connections that
220 were greater than the amphibian maximum walking distance during dispersal (10 km for NLF
221 and 1.3 km for GPT, for the entire migration period) were discarded. The remaining connections'
222 costs (c_{ij}) were normalized so that the sum of all connections exiting a wetland had a cost equal
223 to one. We computed the corridors' suitability as follows:

224
$$s_{ij} = 1 - c_{ij} \quad (7)$$

225 where i and j were the wetlands that were connected to each other, and c_{ij} was the normalized
226 connection's cost.

227 The corridor's suitability was used to define the mortality due to migration d_{ij} . We
228 assumed that the higher the suitability of the connection, the lower the mortality due to migration
229 through the connection itself. The mortality due to migration was therefore equal to the
230 normalized cost of the connection:

231
$$d_{ij} = 1 - s_{ij} = c_{ij} \quad (8)$$

232 The suitability s_{ij} was normalized so that the sum of all connections exiting a wetland had
233 a suitability equal to one. The normalized suitability term \widetilde{s}_{ij} represented the probability that an
234 amphibian in wetland i chose to move to wetland j .

235 The fraction of the amphibians that left wetland i and reached wetland j alive (w_{ij}) was
236 given by a combination of the connection's normalized suitability \widetilde{s}_{ij} , the mortality occurring
237 during migration and during winter d_{ij} , and the natural mortality μ :

238
$$w_{ij} = \widetilde{s}_{ij} \cdot (1 - d_{ij}) \cdot (1 - \mu) \quad (9)$$

239 Wetland connectivity was then defined as the sum of the w_{ij} terms for all wetlands i entering
240 wetland j .

241

242 *Case Study*

243 The Prairie Pothole Region (PPR) of North America is a glacial landscape characterized by
244 depressional wetlands known as prairie potholes. The PPR extends from Alberta, Canada in the
245 north to the north-central United States in the south. Prairie potholes tend to be small (<1 ha)
246 (Watmough & Schmoll, 2007), shallow (< 1 m in depth) (Huang *et al.*, 2011), and generally dry
247 out through summer and fall (Winter 1989). The Nose Creek watershed (51°16'57"N,
248 114°7'14"W) is located in the eastern portion of the PPR along the northern edge of Calgary,
249 Alberta, and is 886 km² in size. The climate is continental and dry. The landscape consists of
250 plains, with the altitude ranging from 1048 m to 1336 m above sea level. The western half of the
251 watershed is covered by aspen forests and willow scrublands mixed with grasslands, and the
252 eastern half of the watershed is covered by grasses (Natural Regions Committee, 2006). The
253 Nose Creek watershed has been modified extensively by humans, with only small amounts of

254 native vegetation remaining. Development covers approximately 12% of the watershed and
255 agricultural activities (i.e., crop and pasture) cover approximately 70% of the watershed
256 (Agriculture and Agri-Food Canada, 2013) (Figure 2b,c). All data acquired and used as part of
257 this study may be found in Appendix S5.

258 (Fig2)

259 *Amphibian species*

260 Two amphibian species were selected to evaluate the sensitivity of their populations to
261 wetland suitability and connectivity. The selected species were the Northern Leopard Frog (*Rana*
262 *pipiens*) and the Great Plains Toad (*Anaxyrus cognatus*), which have contrasting preferred
263 habitats (i.e., the Northern Leopard Frog spends most of its time in aquatic habitat, whereas the
264 Great Plains Toad spends most of its time in terrestrial habitat) and migration abilities (i.e.,
265 Northern Leopard Frog migrates over longer distances than the Great Plains Toad).

266 **Northern Leopard Frog.** The Northern Leopard Frog (NLF) requires two different
267 habitat types to complete its life cycle: (1) an aquatic habitat, where it breeds in the spring and
268 hibernates in the winter, and (2) a terrestrial habitat where it forages in summer. Breeding starts in
269 spring and lasts until the middle of summer. Eggs are laid near the surface in shallow water,
270 where aquatic vegetation is abundant enough to provide protective cover and a substrate on
271 which to attach egg masses (Kendell, 2002; COSEWIC, 2009). After breeding, adults leave the
272 water and migrate towards the foraging areas, where their preferred habitat is open areas with
273 low-growing vegetation (COSEWIC, 2009). Adults return to the water to hibernate in winter,
274 seeking permanent waterbodies deep enough that they do not freeze to the bottom and are well
275 oxygenated. The NLF can migrate up to 10 km in any direction into suitable habitat using mesic
276 corridors and waterbodies (Kendell & Prescott, 2007). The NLF used to be widely distributed in
277 the eastern half of Alberta (Figure 2a), but in the late 1970s their population declined

278 dramatically, and they are now found only in the mixed grasslands in the south of the province.
279 They are presently classified as “at-risk” and are designated as a threatened species under the
280 Wildlife Act (Alberta Sustainable Resource Development, 2003).

281 **Great Plains Toad.** The Great Plains Toad (GPT) requires two different habitats during
282 its life cycle: (1) an aquatic habitat where it breeds in the spring, and (2) a terrestrial habitat
283 where it forages during summer and hibernates in winter. Breeding starts after the first spring
284 rain, when the toads congregate in the wetlands. Eggs are laid over vegetation, preferably in
285 temporary and shallow wetlands with standing and clear water (COSEWIC, 2010). After
286 breeding, the adults leave the water and migrate towards the foraging area, where the preferred
287 habitat is moderately coarse, sandy soil that allows them to burrow to avoid dry condition during
288 summer. In winter, adults hibernate by burrowing in coarse sandy soil below the frost line. The
289 GPT can migrate up to 1.3 km in any direction into suitable habitat such as moist coarse soil
290 environments but not through waters and streams (COSEWIC 2010). The GPT is distributed from
291 the South Saskatchewan River to its tributaries and is also found in the extreme southwest corner
292 of Saskatchewan. It is presently classified as “may be at-risk” (Alberta Sustainable Resource
293 Development and Alberta Conservation Association, 2009) and as a “species of special concern”
294 (COSEWIC, 2010).

295

296 *Model scenarios*

297 The amphibian model was applied to the Nose Creek watershed, which has been largely modified
298 by urban expansion and agricultural development (see Appendix S5 for information on data
299 sources). Starting population sizes were equal to 20 individuals in each wetland and
300 parameterized as in Table S7 in Appendix S4, and after a simulation period of 100 years, the total
301 population abundance reached a steady state that was sufficient to capture the population

302 dynamics of the wetland network. We plotted the carrying capacity of a wetland (x-axis
303 dependent on WSI), the connectivity of the wetland within the wetlandscape (y-axis dependent
304 on MPI), and the simulated mean population of the wetland for each amphibian species (Figure
305 5). The plots allowed for the exploration of the dependence of the population on carrying
306 capacity and connectivity, and to determine if the selected species-at-risk could survive in the
307 wetlandscape. The plots were then classified using a Jenks natural break classification method
308 (Jenks, 1967), and based on this classification, wetlands were prioritized for the specific
309 conservation management strategy needed to support the amphibian population.

310

311 RESULTS

312 The WSI values computed for each wetland within the wetlandscape are presented in Figure 3.

313 The WSI values were generally higher for the NLF. This is due to the fact that almost all wetlands
314 are marshes (Fig 2c), thus characterized by muddy water, which limits GPT breeding (Alberta
315 Sustainable Resource Development and Alberta Conservation Association, 2009). The MPI
316 values computed for each grid cell within the wetlandscape are shown in Figure 4. The
317 wetlandscape was permeable for the NLF and individuals could easily move in the landscape
318 resulting in highly connected wetlands (Fig 4c). Consequently, the NLF migrated more easily
319 throughout the wetlandscape than the GPT.

320 (Fig3)

321 (Fig4)

322 In Figure 5a, we plotted wetland carrying capacity (x-axis, dependent on WSI) vs. wetland
323 connectivity (y-axis, dependent on MPI) and classified wetlands into three classes according to
324 their mean amphibian population abundance. Wetlands in class 1 were characterized by both high

325 carrying capacity and high connectivity and had the largest mean populations. These wetlands
326 were classified as prioritized for protection; 2% of wetlands for NLF and no wetlands for GPT
327 were in class 1. Wetlands in class 2 were characterized by low carrying capacity and high
328 connectivity, resulting in low mean populations; 44% of wetlands for NLF and 3% wetlands for
329 GPT were in class 2. The amphibian populations in these wetlands would benefit by improving
330 the wetland's carrying capacity (i.e., improve the WSI score). Wetlands in class 3 were
331 characterized by high carrying capacity and low connectivity, resulting in low mean populations;
332 54% of wetlands for NLF and 97% wetlands for GPT were in class 3. The amphibian population
333 would benefit by improving the wetland's connectivity (i.e., improve the MPI score).
334 (Fig5)

335 Three wetlands that belonged to the three different regions were selected randomly to
336 present the results of the population dynamics model (Figure 5b). Wetlands in class 1 had many
337 incoming amphibians and many newborns resulting in a large total population. Wetlands in class
338 2 had many incoming amphibians but a small number of newborns as the wetland did not have
339 the properties to support breeding, leading to an intermediately sized population. Wetlands in
340 class 3 had a small number of incoming amphibians and consequently also a small number of
341 newborns.

342 The global sensitivity analysis on amphibian model parameters revealed that amphibian
343 growth rate and mortality and wetland carrying capacity were the key variables explaining the
344 total population within each wetland of the wetlandscape (See Appendix S4 for a detailed
345 description of the global sensitivity analyses). In the case of the WSI, key variables that emerged
346 from the global sensitivity analysis for the NLF included land cover in the buffer, wetland
347 vegetated area, average surface inundation probability and wetland elevation. For the GPT the
348 key variables were land cover in the buffer, wetland vegetated area, average surface inundation

349 probability, percentage of cover cropland, marsh, stream intersection, soil texture and land cover
350 and wetland elevation. In the case of MPI, key variables that emerged from the global sensitivity
351 analysis for both amphibian species included land cover, soil texture, and road (i.e., the variables
352 used to define the terrestrial corridor sub-function). See Appendix S3 for detailed results on the
353 global sensitivity analysis.

354

355 DISCUSSION

356 Wetlands have been recognized as important refuges of biodiversity (Semlitsch & Bodie, 1998;
357 Millennium Ecosystem Assessment, 2005) and their destruction and degradation have contributed
358 to the decline and extinction of many freshwater organisms (Dudgeon *et al.*, 2006; Clarkson *et*
359 *al.*, 2013), especially amphibians (Mushet *et al.*, 2012; Whittaker *et al.*, 2013). Amphibians rely
360 on both aquatic and terrestrial habitats within wetlandscapes (Semlitsch, 2000; Mushet *et al.*,
361 2012). This study aimed to demonstrate the importance of both the wetland itself (i.e., aquatic
362 habitat) and its connectivity (i.e., terrestrial and aquatic connections among wetlands) for
363 amphibian populations, describing the wetlandscape as a wetland network (Marton *et al.*, 2015;
364 Calhoun *et al.*, 2017). General principles that have emerged from this study that could inform
365 management of wetlandscapes for amphibians are summarized in Table 2.

366 (Table2)

367

368 *Principle 1. Adopt a holistic approach to the management of wetlandscapes.*

369 Population dynamics operate at both local and landscape scales. At local scales,
370 occupancy is influenced by processes such as habitat quality and intra-specific competition. At
371 landscape scales, occupancy is influenced by processes such as migration (Dunning *et al.* 1992;

372 Browne et al., 2009). Coupling two indices at different spatial scales (i.e., the WSI at wetland
373 scale and the MPI at landscape scale) within a wetlandscape made it possible to deal with multi-
374 scale levels describing amphibian dynamics within the wetlandscape. Following the principles of
375 landscape ecology (Cushman, 2006; U.S. Environmental Protection Agency, 2015), we applied a
376 holistic approach by considering the wetlandscape not as sum of its elements, but as the
377 integration of the elements (Naveh, 2000; Turner, 2005): wetland removal or terrestrial habitat
378 modification affects amphibian dynamics in the whole wetlandscape.

379

380 *Principle 2. Wetland habitat quality and connectivity are non-substitutable properties.*

381 The joint effects of WSI and MPI reveal that the quality of wetland habitat and its
382 surrounding terrestrial habitat and wetland connectivity are non-substitutable properties. Habitat
383 suitability affects the occupancy of wetlands influencing all terrestrial and aquatic activities (Piha
384 et al., 2007; Mushet et al., 2012). Habitat connectivity affects the individuals immigrating into
385 each wetland and is fundamental to sustain a viable population (Browne et al., 2009). These
386 properties act jointly but differently on population dynamics. It is therefore important to consider
387 the two indices separately without building aggregated indices. Principles 3, 4, and 5 are a direct
388 consequence of this principle.

389

390 *Principle 3. Some wetlands are suitable both for their habitat quality and their connectivity.*

391 Wetlands with high suitability (i.e., high carrying capacity) that are surrounded by
392 landscapes with high permeability for movement (i.e., high connectivity) have the highest
393 populations. High carrying capacity leads to high newborn production and survival creating
394 amphibian hotspots (Semlitsch, 2000). High connectivity leads to wetlands serving as “stepping
395 stones” that results in a high number of immigrants as well as emigrants to other wetlands

396 (Kramer-Schadt *et al.*, 2011; Saura *et al.*, 2014). A balance between carrying capacity and
397 connectivity leads to wetlands with the highest populations – the immigrants are able to find a
398 wetland that can sustain them without producing the negative effect of density dependence
399 (Vonesh & De la Cruz, 2002; Harper & Semlitsch, 2007), and wetland connections allow for
400 successful emigration. These wetlands play a key role in the wetlandscape and should be
401 prioritized for conservation.

402

403 *Principle 4. Some wetlands are suitable habitats but are not adequately connected to other*
404 *wetlands.*

405 Low connectivity leads to low immigration, as wetlands are difficult to reach because they
406 are physically isolated or surrounded by an unsuitable terrestrial matrix, preventing migration
407 (Baum *et al.*, 2004). For wetlands with low connectivity, it is important to improve the
408 permeability of the surrounding terrestrial matrix to enhance migration to suitable aquatic habitat.

409

410 *Principle 5. Some wetlands are adequately connected to other wetlands but are not suitable*
411 *habitats.*

412 Low carrying capacity leads to low newborn production and low amphibian survival as
413 the wetland environment does not meet the criteria for all life cycle requirements. Low carrying
414 capacity also leads to low immigration, as immigrants face the negative effect of density
415 dependence because resources are limited (Vonesh & De la Cruz, 2002). For wetlands with low
416 carrying capacity, it is important to improve habitat quality to allow incoming amphibians to
417 perform their life cycle functions and generate new individuals successfully.

418

419 *Principle 6. Wetlandscapes are perceived in different ways by different species.*

420 Different species vary in their life cycle requirements resulting in a different
421 “relationship” with the wetlandscape (Taylor, 1993; D’Eon *et al.*, 2002; Piha *et al.*, 2007). The
422 studied wetlandscape was more suitable for the NLF which prefers shallow standing water and
423 has a higher migration ability (COSEWIC, 2009) than the GPT which requires clear waters to
424 breed (COSEWIC, 2010). In particular, our outcomes highlight that the studied wetlandscape is
425 not suitable at all for GPT dispersal: this is linked to both limited dispersal ability and the scarcity
426 of coarse sandy soil which is preferred by the toad for dispersing. This result is consistent with
427 the scattered distribution of the GPT in Alberta (Fig. 2) and also reported on the Government of
428 Alberta website (Government of Alberta, 2019). Decision makers face trade-offs when protecting
429 multiple species. Optimization techniques that explore these trade-offs can inform conservation
430 priorities and restoration targets (Mushet *et al.*, 2012). A future challenge will be developing
431 optimization techniques that allow for the improvement of wetlandscapes for some species
432 without harming other species.

433 *Limitations of our approach*

434 Limitations of our approach were related to the formulation of the two indices, the MPI
435 and WSI. Based on the lack of available and existing data in our study area, our model could not
436 be validated with empirical data of amphibian occupancy. This is a limitation faced by many
437 studies of habitat assessments at wetlandscape scales (Store and Kangas, 2001; Zulian *et al.*,
438 2013; Bishop-Taylor *et al.*, 2015). In some of these studies, maps of amphibian movement were
439 generated based on models (Zulian *et al.*, 2013) or expert opinion (Bishop-Taylor *et al.*, 2015).
440 We attempted to overcome these limitations by performing a global sensitivity analysis on WSI
441 and MPI to understand the most important parameters influencing each index and to compare
442 them with other experimental studies. For the WSI, we found that land-cover and wetland
443 vegetation were the most sensitive indices, a finding corroborated by Mushet *et al.* (2012). For

444 the MPI, we found that indices related to terrestrial corridors were the most sensitive indices, a
445 finding corroborated by Browne et al. (2009). Another clear limit to our indices is the turbidity
446 evaluation. Since measured values are not available, we used wetland classification and stream
447 intersection as a proxy for turbidity (see also table S3 in the supporting information). We
448 recognise that this poor surrogate greatly influences the GPT indices and population dynamic
449 results since clear water is critical for GPT breeding.

450 Additionally, the model that we used to reproduce amphibian dynamics (Zamberletti et
451 al., 2018) and, consequently, the MPI that we designed, did not explicitly consider the
452 overwintering phase. This could be a critical point for amphibian species like NLF, which
453 requires a specific habitat (e.g. deep permanent wetlands (Kendell, 2002)) to overwinter.
454 However, we attempted to implicitly consider overwintering habitats in the MPI, through
455 including the index hydrological features, such as the presence of wetlands in the terrestrial
456 corridors. This assumption could lead to an overestimation or underestimation of amphibian
457 survival during this phase. Future amphibian meta-population models should explicitly consider
458 the overwintering phase, in order to better reproduce the dynamics of amphibians which requires
459 unique habitats to overwinter.

460 Our model represents a novel, multi-scale framework to studying the effects of wetland
461 habitat quality and connectivity on amphibian populations. Model simulations highlight the
462 importance of jointly considering wetland habitat quality and connectivity as complementary
463 information for understanding amphibian population dynamics. General principles that emerged
464 from the modelling exercise could be easily extended to other species and other wetlandscapes.
465 However, before applying the presented framework to species conservation, validation with field
466 data is needed.

467

468

SUPPORTING INFORMATION

469 Additional supporting information may be found online under the Supporting Information tab for
470 this article. Supporting Information is organized in Appendices: Appendix S1 - Calculating the
471 Movement Permeability Index (MPI), Appendix S2 - Calculating the Wetland Suitability Index
472 (WSI), Appendix S3 - Sensitivity Analysis on MPI and WSI, Appendix S4 - Sensitivity Analysis
473 on Amphibian Model Parameters, Appendix S5 - Description of Data. The authors are solely
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475

476

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488

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687 **Tables**

688 **Table1:** List of variables used to define the indices (in alphabetical order). Species (NLF or GPT)
 689 and index (MPI and WSI) used for each indicator are listed. For WSI, the phase (B: breeding, F:
 690 = foraging) is also indicated. An extended version of this table can be found in the Supporting
 691 Information. The citations list is reported in the footnote.

Indicator	Description	Activity	
		NLF	GPT
Average surface inundation probability	The NLF and GPT breed in wetlands (5, 7) and forage in moist habitats (9, 5). NLF uses mesic corridors and water bodies to migrate (4, 8); GPT uses mesic corridors to migrate, but there is no evidence that it migrates through water bodies (5).	WSI=B, F MSI	WSI=B, F MSI
Ditches	NLF breeding is impaired by ditches because they affect the hydrology of a wetland through drainage (6). The GPT may breed in flooded shallow ditches of clear water (5). Both amphibian species can use ditches as foraging habitats (9). NLF can migrate through ditches (4, 8).	WSI=B, F MSI	WSI=B, F
Ephemeral stream intersection	Ephemeral streams intersecting wetlands are useful for breeding and tadpole development as they deliver food and nutrients (11), and do not excessively disturb wetland water.	WSI=B	WSI=Not applicable (n/a)
Flowing stream intersection	Flowing stream intersections are permanent streams that disturb wetland water, making the wetland not suitable for NLF reproduction (6).	WSI=B	WSI=n/a
Lacustrine	Lacustrine water bodies are not suitable for reproduction because they are too deep (2, 9).	WSI=B	WSI=B
Land cover	Amphibians have preferred habitats (e.g., grassland or shrubs), while other habitats are avoided (e.g., developed). Scores are determined for each cell of the landscape according to the documented NLF and GPT behaviors in literature (1, 3, 6, 8, 9). Land cover scores can be found in the Supporting Information (Table S1, S2, S4).	WSI=B, F MPI	WSI=B, F MPI
Marsh	GPT prefers clear water over muddy water for breeding (2).	WSI=n/a	WSI=B
Percentage of cropland within a buffer	Wetlands which have a large amount of pesticides tend to be unfavorable to amphibians because pesticides delay metamorphosis and contribute to immunosuppression, hermaphroditism, sex reversal, and outright mortality (10).	WSI=B, F	WSI=B, F
Permanent stream	NLF can migrate through waterbodies, such as channels, ditches, creeks, rivers, streams, ponds, spillways below dams, springs (4, 8).	MSI	n/a
Riparian areas	Riparian areas are preferred for migration, especially in drier environments, because riparian areas are characterized by moist soils (4, 5, 8, 12).	MSI	MSI
Roads	Amphibians have been observed moving through roadways during their migration because of the flat and open surface (1, 10). However, walking through roads may involve a high probability of road mortality (1, 10). In order to consider both roads as a conductor and the mortality risk related to roads, we set a low score for roads that have a high level of traffic (e.g., paved road with many lanes) and a high score for roads	MSI	MSI

Indicator	Description	Activity	
		NLF	GPT
	that have less traffic (e.g., unpaved roads or paved roads with only one or two lanes). See Supporting Information (Table S5).		
Soil texture and land cover	GPT prefers coarse sandy soil to burrow and avoid desiccation in summer and cold temperatures in winter (3, 6, 8, 9). The score of each cell is computed by multiplying (i) the land cover type score, and (ii) the soil texture score that could be found in the Supporting Information (Table S2).	WSI=n/a	WSI=B, F MPI
Stream and waterbodies density	Since NLF migrates through mesic corridors and waterbodies (4, 8) we evaluated stream and waterbody density for each cell considering the average surface inundation probability value for each 3 x 3 neighborhood of cells.	MSI	n/a
Stream intersection	The presence of inflowing water suspends sediments in the water which impairs GPT breed (2).	WSI=n/a	WSI=B
Wetland elevation	Since amphibians prefer warmer environments, we assumed wetland elevation as a proxy of temperature (6, 9). Higher elevations tend to be cooler.	WSI=B, F	WSI=B, F
Wetland vegetated area	Aquatic vegetation is an important characteristic of breeding sites. NLF need abundant aquatic and emergent vegetation that provide cover and a substrate on which egg masses can attach (6, 7). GPT needs a considerable vegetation presence because they lay eggs in long loose strings over vegetation (7).	WSI=B	WSI=B

692 1. Alberta Sustainable Resource Development. 2003; 2. Alberta Sustainable Resource Development and Alberta Conservation
693 Association. 2009; 3. Alberta Environment and Sustainable Resource Development 2012; 4. Cenovus Energy Inc. 2011; 5.
694 COSEWIC 2002; 6. COSEWIC 2009; 7. COSEWIC 2010; 8. Environment and Climate Change Canada 2016; 9. Kendell 2002;
695 10. Kendell and Prescott 2007; 11. Nussbaum et al. 1983; 12. Seburn et al. 1997.

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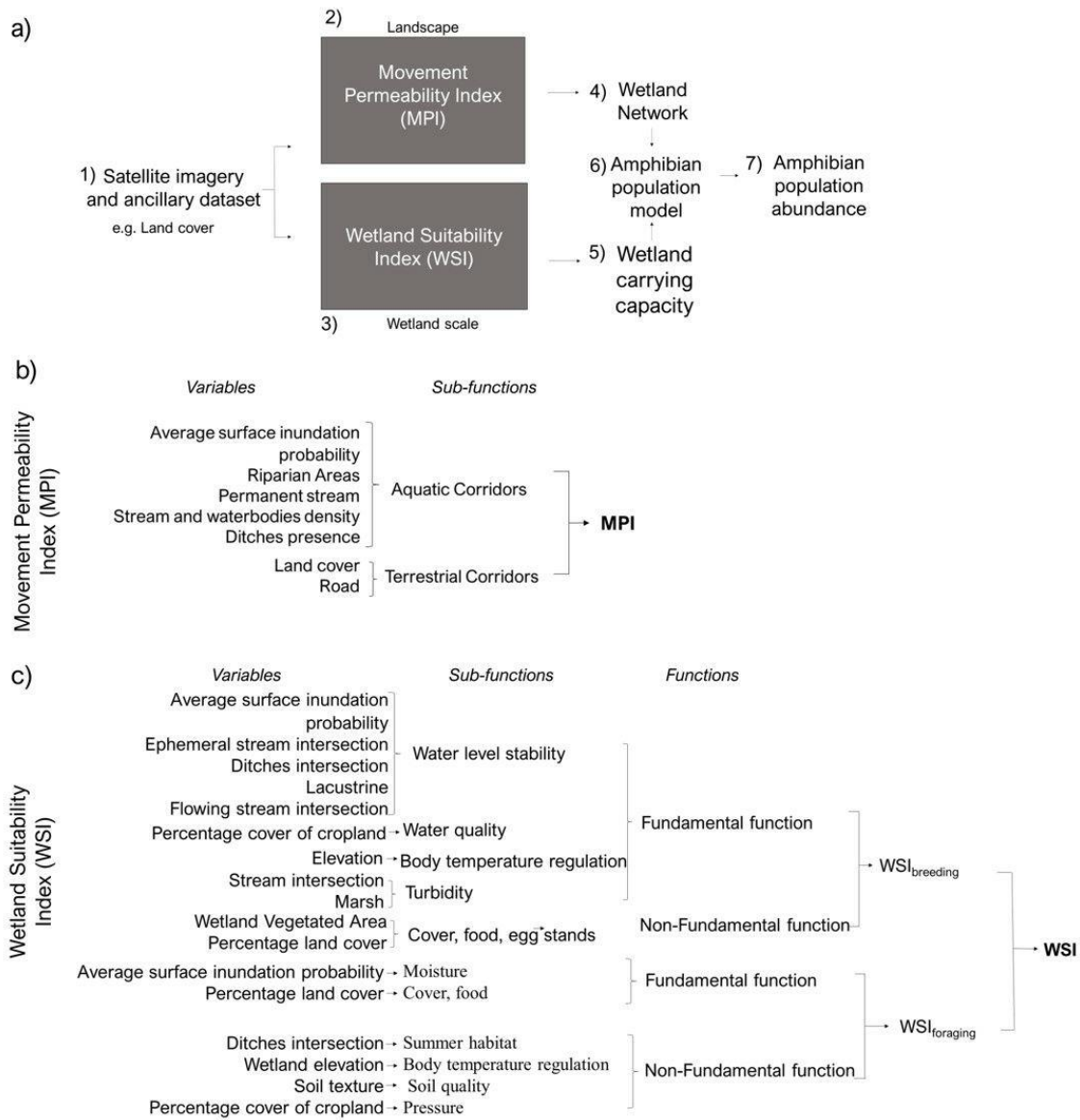
697 Table 2: General principles that could inform management of wetlandscapes for amphibians

n.	Principle	Potential consequence for management	Operationalization of the principle	Future research efforts needed
1	Adopt a holistic approach to the management of wetlandscapes.	Management intervention in one part of the wetlandscape can have important consequences on the entire wetlandscape.	Use a dynamic modelling approach based on complex network theory.	Improve the understanding and the modelling of animal ecology and movements.
2	Wetland habitat quality and connectivity are non-substitutable properties.	Conservation policies should explicitly target habitat quality and connectivity as separate but complementary objectives.	Develop separate indices for habitat quality and connectivity and analyse them independently (rather than building an aggregated index).	Further develop and validate indices with field-based observations.
3	Some wetlands are suitable both for their habitat quality and their connectivity.	Conservation priorities of wetlands should reflect a wetland's suitability for both habitat quality and connectivity.	Define indices for describing habitat quality and connectivity.	

4	Some wetlands are suitable habitats but are not adequately connected to other wetlands.	Identify parts of the wetlandscapes where habitat connectivity should be improved.		
5	Some wetlands are adequately connected to other wetlands but are not suitable habitats.	Identify parts of the wetlandscapes where habitat should be enhanced or restored.		
6	Wetlandscapes are perceived in different ways by different species.	Management interventions that improve the wetlandscape for a single species should do so without harming other species.	Indices of habitat quality and connectivity should be species-specific. But multiple benefits for different species should be sought.	Develop optimization techniques that can define conservation priorities and restoration targets taking multiple species into account.

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715 **List of figures**



716
 717 Figure 1. Flowchart of methods and details on the index's aggregation. Panel a) The general
 718 flowchart of methods: 1. Selection of maps of variables related to amphibian life cycle from
 719 satellite imagery and ancillary datasets (more details in Table 1); 2. Movement Permeability
 720 Index evaluated the permeability of the whole landscape to amphibian migration; 3. Wetland
 721 Suitability Index; 4. Wetland network connections were derived from MPI. 5. Wetland carrying
 722 capacity was derived from WPI. 6. The amphibian population model within the wetland network

723 was based on wetland connections and carrying capacity; 7. Amphibian population model
724 returned amphibian abundance used to assess how connectivity and carrying capacity influence
725 amphibian survival within the wetlandscape. Panel b) shows the aggregation of the MPI index.
726 Panel c) shows the aggregation of the WSI index.

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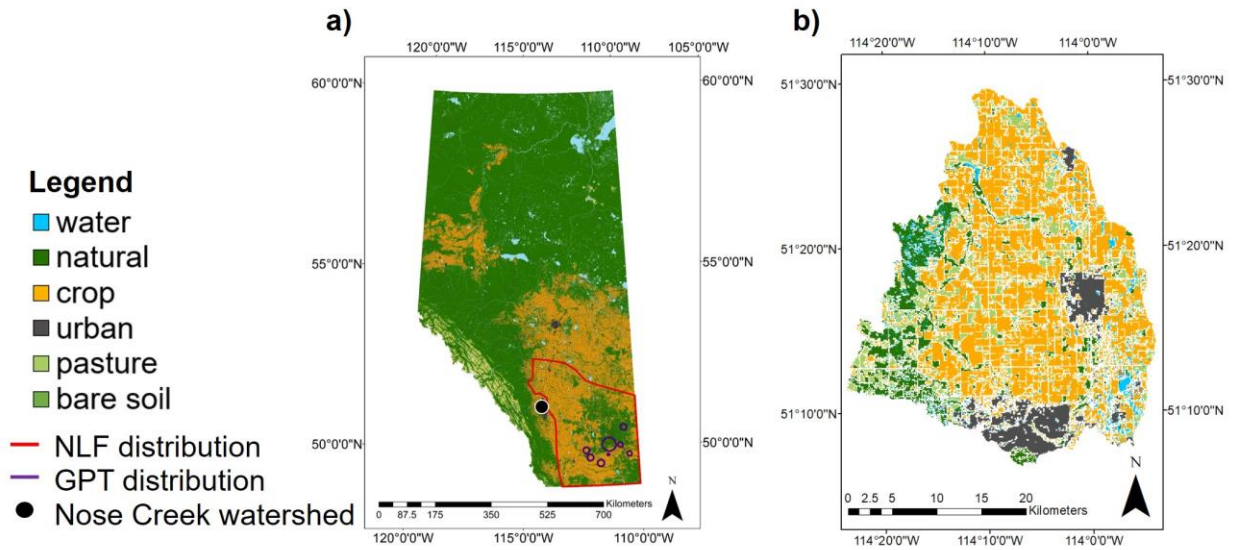
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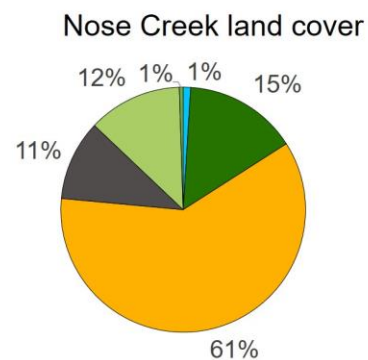
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c) Nose Creek information

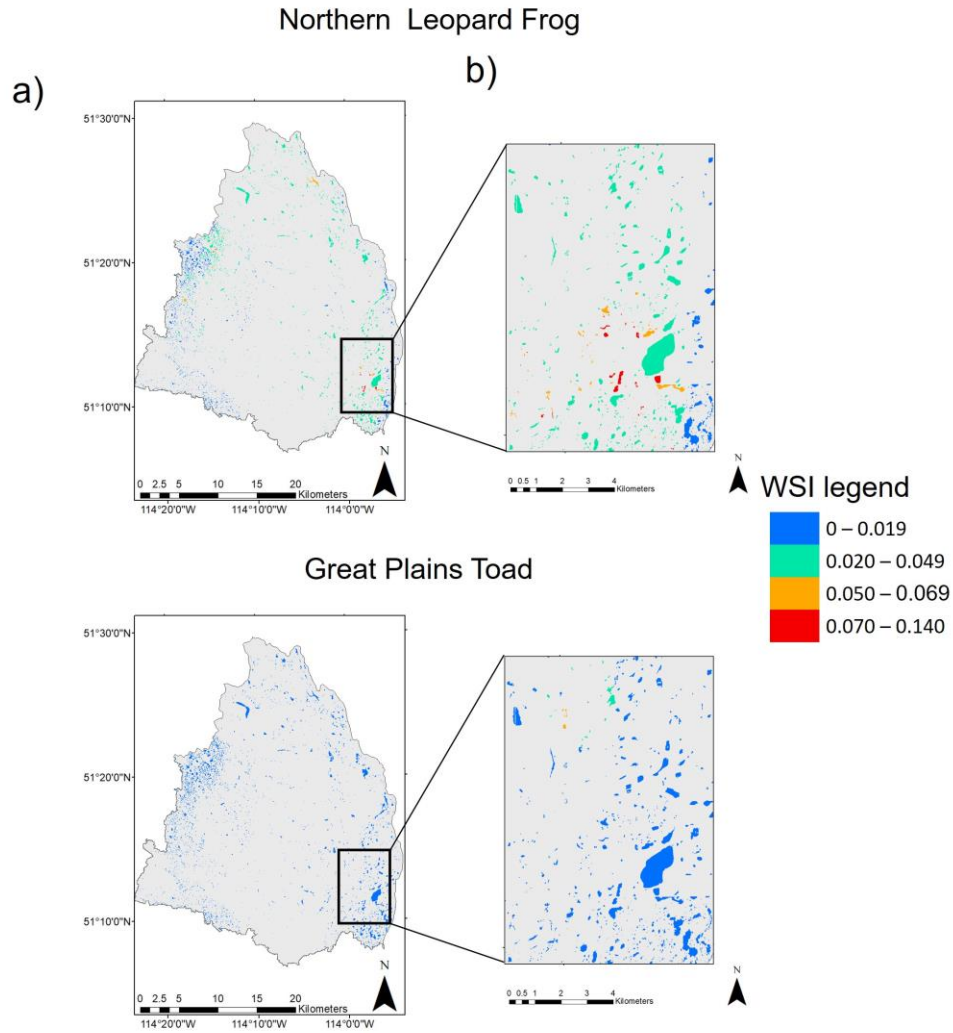
Nose Creek area: 886.1 km²
 # of wetlands: 6617

Wetland data:	Mean	Standard deviation
Area [m ²]	4145.9	20792.1
Closest wetland [m]	81	99.3
Vegetated area [%]	96	0.2
Marsh [%]	100	0



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 739 Figure 2. The Nose Creek watershed was selected to demonstrate our framework. (a) Land cover
 740 map of the Province of Alberta (Canada) highlighting the geographical distribution of Northern
 741 Leopard Frog and Great Plain Toad (Government of Alberta, 2019). (b) Close-up of Nose Creek
 742 watershed land cover map. (c) Proportions of land cover type and wetland type, area, distribution
 743 and habitat within the Nose Creek watershed.

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750 Figure 3. Wetland Suitability Index for the Northern Leopard Frog (top panel) and the Great
 751 Plains Toad (bottom panel). Map of entire region (a), and an example close-up showing the
 752 results (b).

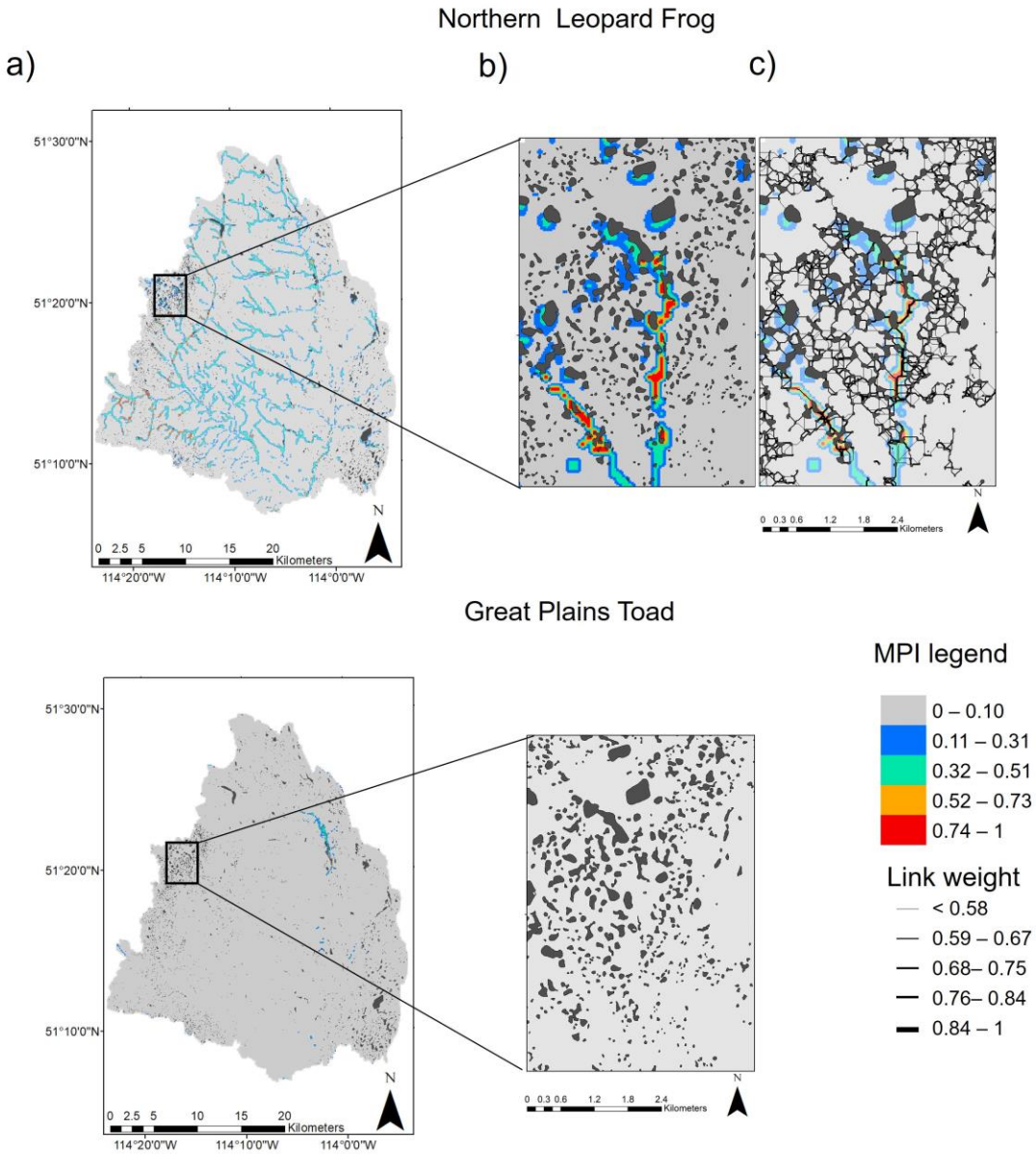
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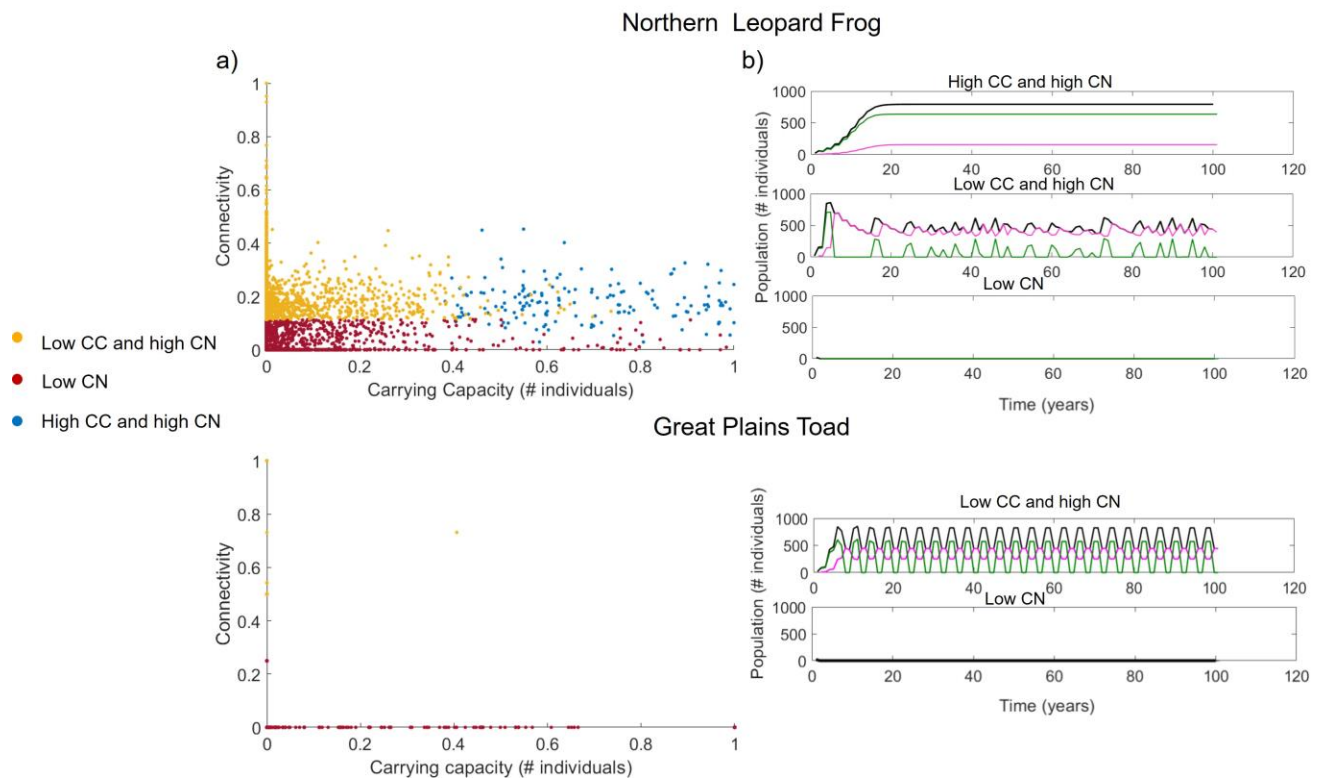
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 759 Figure 4. Movement Permeability index for the Northern Leopard Frog (top panel) and the Great
 760 Plains Toad (bottom panel). (a) Map of entire region, (b) a close-up showing the MPI results, and
 761 (c) the resulting network derived from MPI values for Northern Leopard Frog as the Great Plains
 762 Toad had no network.

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766 Figure 5. (a) a plot of the carrying capacity (i.e. CC) vs. connectivity (i.e. CN) of wetlands for the
 767 Northern Leopard Frog (top) and Great Plains Toad (bottom). Wetlands are classified according a
 768 cluster analysis on population and then on connectivity. The clusters show (1) wetlands that
 769 should be protected; (2) wetlands where there should be an improvement in wetland carrying
 770 capacity; and (3) wetlands where there should be an improvement in wetland connectivity, (b)
 771 time series of population dynamics showing the total population (thick black line), immigrant
 772 population (purple dashed line) and newborn population (fine green line) for representative
 773 wetlands from each wetland class. For the Great Plains Toad, there were no wetlands that
 774 belonged to class 1, and wetlands belonging to class 2 were characterized by an oscillatory trend
 775 due to the high connectivity and the low carrying capacity.