Connectivity among wetlands matters for vulnerable amphibian populations in wetlandscapes

Patrizia Zamberletti, Marta Zaffaroni, Francesco Accatino, Irena Creed, Carlo de Michele

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Authors:

Patrizia Zamberletti. Department of Civil and Environmental Engineering, Politecnico di

Milano, P.zza Leonardo da Vinci 32, 20133 Milano, Italy.

patrizia.zamberletti@gmail.com

Marta Zaffaroni. Department of Civil and Environmental Engineering, Politecnico di

Milano, P.zza Leonardo da Vinci 32, 20133 Milano, Italy. zaffaronimarta@gmail.com

Francesco Accatino. INRA UMR 1048 SAD-APT,16 Rue Claude Bernard 75501, Paris,

France. francesco.accatino@inra.fr

Irena F. Creed. Department of Biology, Western University, London, ON, Canada N6A

5B7. icreed@uwo.ca

Carlo De Michele. Department of Civil and Environmental Engineering, Politecnico di

Milano, P.zza Leonardo da Vinci 32, 20133 Milano, Italy. carlo.demichele@polimi.it

Corresponding author: Patrizia Zamberletti. patrizia.zamberletti@gmail.com.

Abstract

Wetlands have been degraded and destroyed, resulting in the decline of many

wetland-dependent species populations. Many conservation efforts are based on

protection of individual wetlands; however, fluxes of energy, materials and organisms

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21   between wetlands create important structural and functional connections upon which

22   several species depend. We investigated the role of individual wetlands within a

23   wetlandscape in sustaining an amphibian population. Wetlandscapes were represented as

24   networks, where nodes were wetlands and links were flows of organisms described by an

25   amphibian population model. Relationships between a wetland's connectivity to the other

26   wetlands and the abundance of amphibians under different wetland management

27   strategies were examined. The first finding was that wetlands within a network can be

28   classified into *sinks* (where local mortality exceeds birth rate), *sources* (where local birth

29   rate exceeds mortality), and *pseudo-sinks* (where excessive immigration maintains the

30   population above the carrying capacity). These three wetland classes have low, medium,

31   and high *indegree* (a parameter reflecting a wetland's connectivity), respectively. The

32   second finding was that management interventions in wetlands have different

33   consequences according to the wetland's *indegree*: wetland removal has the worst impact

34   on amphibian populations if the wetland is a source, and wetland restoration has the best

35   impact if the wetland is a pseudo-sink. These findings provide support for policies that

36   managing wetlands not as independent objects but as integral parts of the wetlandscape.

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1. Introduction

Wetlands are important ecosystems as they provide several functions and services (Calhoun et al. 2016, Yao et al. 2016, Creed et al. 2017) and constitute an important source of biodiversity (Costanza et al. 1997, Gibbs 2000). In recent decades, many wetlands have been drained because of urban or agricultural expansion (Davidson 2014, Dixon et al. 2016, Golden et al. 2017). Wetland loss impacts on biodiversity both directly, by removing habitat (Gibbs 2000), and indirectly, by increasing the distance among remaining wetlands and resulting in functional isolation and increasing mortality of organisms migrating from one wetland to another (Baguette et al. 2013). Wetlands are not isolated features; on the contrary, they are dynamic, complex ecosystem with biotic and abiotic connections to other wetlands on the wetlandscape (Cohen et al. 2016, Thorslund et al. 2017). Understanding the ecological dynamics of wetlandscapes is important to sustaining biodiversity (Semlitsch and Bodie 1998, Gibbs 2000).

In particular, amphibians' survival is influenced by both wetland habitat and wetland connections to other wetlands (Dudgeon et al., 2006). In fact, these wetland qualities determine the success of amphibians' breeding (Mushet et al., 2012): wetland habitat is used by adults for mating and by offspring to complete their metamorphosis from egg. Factors such as availability of resources and dispersal capabilities influence the amphibian population in wetlands (Pechmann et al. 1989, Semlitsch et al. 1996). Availability of resources depends on wetland habitat properties (e.g., area, vegetation) and on the number of amphibians competing for available resources. Amphibian dispersal relies on wetland distribution within the surrounding terrestrial habitat. Every year at the end of the summer, amphibians start their migration through the terrestrial

habitat and the following spring they reach a new aquatic breeding habitat (Pittman et al.

2014). Alteration of wetland habitat and distribution within the landscape, such as

wetland loss, negatively influences both breeding and dispersal success by decreasing

wetland density and increasing travel distances for amphibians (Gibbs, 1993)."

Management strategies have been implemented to protect biodiversity promoted

by wetlands. Many of these management strategies focus on wetlands of special

importance (Amezaga et al. 2002). Policy goals vary from "no net loss" to "net gain"

(Accatino et al., 2018) to general statements about the need to address adverse impacts to

these wetlands (e.g., Calhoun et al. 2016). Few of these management strategies focus on

the physical, chemical, or biological connections among wetlands (e.g., Cohen et al.

2016). Although it is widely recognized that wetland connectivity is important for

biodiversity (Semlitsch 1996, Semlitsch and Bodie 1998, Skelly et al. 1999, Marsh and

Trenham 2001, Cushman 2006), concrete strategies in policies are still not well

formulated. The lack in wetland policies of clear operational strategic schemes based on

wetland connectivity is at least in part due to the lack or rarity of quantitative assessments

of the role of wetland connectivity in sustaining wetland biodiversity. Important steps

forward would be to determine if and how wetland connectivity plays a role in sustaining

biodiversity in a wetlandscape (Fortuna et al. 2006, Albanese and Haukos 2017), and to

explore if management interventions on the wetland itself (i.e., wetland removal or

restoration) are influenced by wetland connectivity.

The "sink-source" framework describes the distribution of species in the variety

of interconnected habitat patches within a region (Pulliam 1988, Watkinson and

Sutherland 1995). According to this framework, a productive patch serves as a source of

89 individuals, which are dispersed to less productive patches called sinks (Pulliam 1988,

90 Dunning et al. 1992). Pulliam (1988) argued that in sink habitat patches reproduction is

91 insufficient to balance local mortality, whereas in source habitat patches reproduction

92 balances local mortality; the population in sinks is thus maintained by immigration from

93 sources. Most studies classify sinks and sources only by demographic measures (i.e.,

94 birth and death rate) (Watkinson and Sutherland 1995). The role of connectivity in the

95 classification of sinks and sources has not been explored.

96   Models are useful to test the "sink-source" framework for exploring organism

97 dispersal through wetlandscapes, especially when empirical data are lacking or extremely

98 difficult and costly to collect (Pittman et al. 2014). Patch-based models (e.g., Skelly and

99 Meir 1997, Trenham 1998) focus on population dynamics within patches, which are

100 important to describe fundamental ecological processes such as breeding (Marsh and

101 Trenham 2001), interspecific competition, and predation (Wilbur 1997, Beebee et al.

102 1996). Patch-based models were successfully applied to wetlandscape (Marsh and

103 Trenham 2001, Wilbur 1997). However, an exclusively patch-based approach does not

104 consider the role of wetland isolation and the mobility of individuals to other wetlands

105 (Cushman 2006). In contrast, network-based models focus on connectivity within

106 network's node and they can be applied to wetlandscape, too (e.g., Albanese and Haukos

107 2017). They allow to quantify changes to the connectivity of wetlands and identify

108 wetlands critical to the maintenance of system connectivity. Network-based models are

109 useful tools for combining both the within-wetland population dynamics and the dispersal

110 of individuals among wetlands (Estrada and Bodin 2008). Network-based models can be

111 used to identify keystone patches that are integral to the persistence of populations

112 (Urban & Keitt 2001, Keitt 2003) and to quantify the robustness of populations to

113 wetland loss (Bunn et al. 2000, Hanski 2001, Jordán et al. 2003).

114   In this paper, we addressed the role of wetland connectivity in determining the

115 role of different wetlands to sustain amphibian populations. We focused on amphibian

116 species characterized by a bi-phasic life-cycle, migrating into different wetlands during

117 the course of their life. We built a model of amphibian population dynamics in a wetland

118 network and we formulated scenarios to address two research questions: how does the

119 connectivity of a wetland influence the abundance of the local population in the wetland

120 itself? And, how does a management intervention on a single wetland (e.g., wetland

121 removal or wetland restoration) influence the total landscape population by changing

122 connectivity within the wetlandscape?

123

124   **2. Methods**

125   We focused on amphibian species with life history traits characterized by a

126 terrestrial and an aquatic phase, but the approach could be adapted to amphibian species

127 with other life history traits. In summer, amphibians congregate in wetland for mating. At

128 the end of the summer, amphibians leave wetlands and migrate through the terrestrial

129 habitat searching food and refuges for overwintering until the next spring, when they

130 disperse again, looking for aquatic breeding habitat (Pittman et al. 2014). Examples of

131 species having such as life cycle are the northern leopard frog (Rana pipiens) having a

132 dispersal distance ranging between 2 km and 10 km (Kendell 2002), and the great plains

133   toad (Anaxyrus cognatus) having a dispersal distance ranging between 300 m and 1300 m

134   (COSEWIC 2010).

135   *2.1 Model description*

136   We built a theoretical model for simulating the dynamics of a biphasic life-cycle

137   amphibian population within a wetlandscape. The population dynamics of amphibians

138   consist of a continuous repetition of reproduction phase and migration phase. In the

139   reproduction phase, new offspring are produced in each wetland as a function of the

140   abundance of the local population. In the migration phase, amphibians migrate from a

141   wetland to another, according to how wetlands are connected and their mortality. Our

142   model was conceived in the Medawar zone (Loehle 1990, Grimm et al. 2005) (i.e., we

143   included only the necessary elements for addressing our research questions and to avoid

144   unnecessary details, such as predation phenomena or climate variables like air and

145   surface water temperature of wetlands).

146   *2.2 Wetlandscape*

147   A network consists of a set of nodes that are defined as spatial elements, and links

148   that represent linkages between nodes (Urban and Keitt 2001). We represented a

149   wetlandscape as a network, where the nodes are wetlands, whereas the links are flows of

150   amphibians between wetlands. We connected two wetlands by a link if the distance

151   between a given pair of wetlands was less than or equal to the maximum distance

152   walkable by the amphibians. Links were assigned a weight equal to the potential

153   connectivity, $\tilde{c}_{ij}$, which is defined as the probability of an amphibian leaving wetland *i* to

154   choose wetland *j* as breeding site the following year. The potential connectivity was

155 determined by the Euclidean distance and the adjacency between two wetlands. To

156 determine the connectivity between two wetlands either a boundary approach or a

157 distance approach could be used. The boundary approach consists of methods that

158 determine the weight based on the presence or the length of a shared boundary (Ermagun

159 and Levinson 2018). The distance approach consists of a spectrum of methods that

160 determine the weight using the geographic distance (Ermagun and Levinson 2018). Both

161 the boundary approach and the distance approach or a combination of them have been

162 used to construct a theory-driven spatial weighting matrix (Dray 2006), as well as

163 biological considerations such as propagation process (Sokal and Oden 1978), patch size

164 (Hanski 1994) and dispersion capability (Knapp et al. 2003). In our work, the potential

165 connectivity represented only the spatial interactions among wetlands and combined the

166 boundary approach and distance approach using a weighted average, with the parameter β

167 as the weight to balance the relative importance of adjacency over the inverse distance

168 (Figure 1). The underlying assumption is that amphibians will move from wetland i to

169 wetland j if the two wetlands are adjacent (see below for definition) or if two wetlands

170 are close each other. The potential connectivity has this expression:

171 $\tilde{c}_{ij} = \beta \cdot a_{ij} + (1 - \beta) \cdot \frac{1}{x_{ij}}$ Eqn 1

172 The term a_{ij} was the adjacency term and was computed with the Voronoi tessellation

173 (Galpern et al. 2012). This method consisted of a subdivision of the landscape into

174 polygons, each polygon associated with a wetland. The polygon was formed by all the

175 points of the landscape nearer to that wetland than to any other (Kenkel et al. 1989).

176 Since each wetland was the centroid of a polygonal region, for each one we assigned an

177   adjacency value of $a_{ij} = 1$ if the polygons of the two wetlands were adjacent, and $a_{ij} = 0$

178   otherwise. The adjacent polygons in the tessellation described hypothesized regions of

179   proximity for the organism within which there is high connectivity (Galpern et al. 2012).

180   The term x_{ij} was the Euclidean distance between wetlands i and j. This term took into

181   account that an amphibian was more likely to go to a wetland at a shorter distance. We

182   set $\beta = 0.5$ as a constant value assuming an equal effect played by adjacency and

183   distance.

184   *2.3 Amphibian population dynamics*

185   The amphibian population dynamics was described using a time-discrete model

186   with a time step t of one year, divided in two sub-steps, the first for breeding in wetlands

187   and the second for migration from one wetland to another (Fig. 1c). In the notation of our

188   model, N_t^i represented the number of amphibians in wetland *i* at the beginning of year *t*,

189     $N_{t+\frac{1}{2}}^i$ represented the number of amphibians in wetland *i* after the breeding phase, and

190   N_{t+1}^i represented the number of amphibians in wetland *i* after the dispersal phase of year *t*.

191   In the breeding phase, the adults in each wetland produced offspring that went

192   through the metamorphic cycle and became juveniles ready to move to reproduce in

193   another wetland the following year. The population $N_{t+\frac{1}{2}}^i$ consisted of the population N_t^i

194   increased by the number of new individuals generated that successfully completed the

195   metamorphic cycle (here after called *newborns*) in wetland *i*.

196     $$N_{t+\frac{1}{2}}^i = N_t^i + max\left(0, rN_t^i\left(1 - \frac{N_t^i}{K}\right)\right) \quad \text{Eqn 2}$$

197   The survival of the new individuals generated was density-dependent: at low

198   density, individuals did not interfere with each other, whereas at higher densities,

199   resources became less available for each individual. We characterized each wetland by its

200   carrying capacity, K, which is the maximum size of the population that each wetland can

201   sustain. Parameter r represented the intrinsic growth rate. The *max* operator assured that

202   the number of new individuals generated was not negative.

203   In the migration phase, each amphibian in wetland i moved to wetland j with a

204   certain probability. Such a probability corresponded to the *effective connectivity w_{ij}*,

205   which consisted of the *potential connectivity $\tilde{c}_{ij}$* modified for taking into account the

206   dispersal distance of amphibians p_{ij}, and the probability of mortality due to distance

207   travelled d_{ij}, and the natural mortality μ:

208     $w_{ij} = \tilde{c}_{ij} \cdot p_{ij} \cdot (1 - d_{ij}) \cdot (1 - \mu)$ Eqn 3

209   The dispersal distance was computed with a negative exponential function of the distance

210   travelled x_{ij}: $p_{ij} = e^{-\delta x_{ij}}$, where δ is the dispersal capacity evaluated as a function of the

211   amphibian maximum walkable distance x_{max}: $\delta = \frac{1}{x_{max}}$. The same functional shape was

212   used in other similar models (e.g., Bunn et al. 2000, Hanski and Ovaskainen 2000, Saura

213   and Pascual-Hortal 2007).

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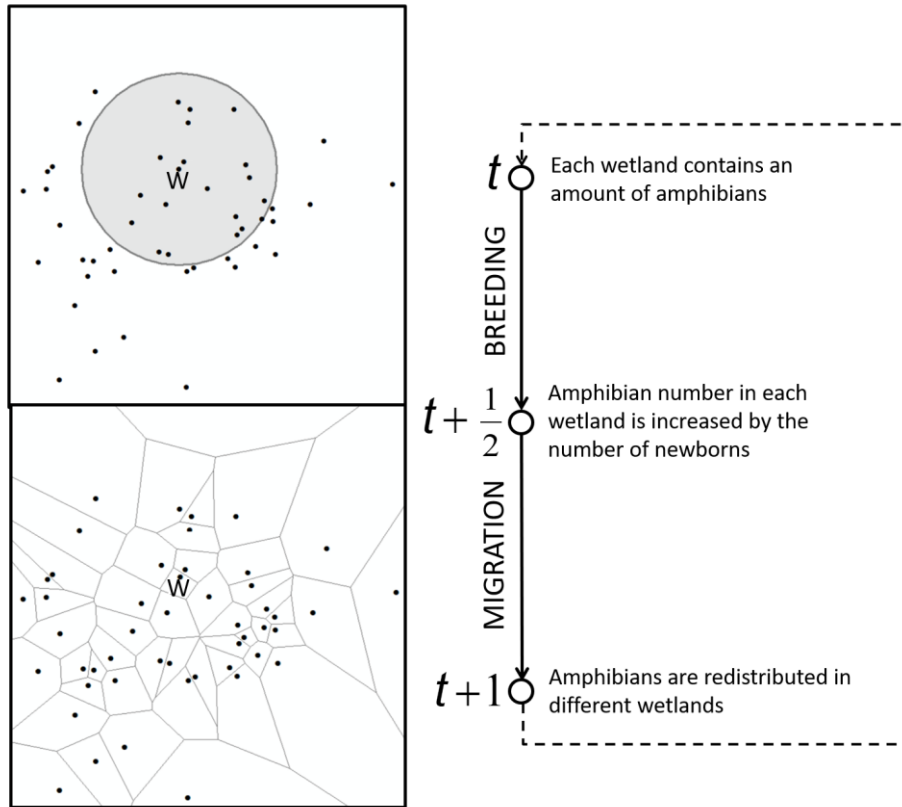
Figure 1. Spatial (panels (a) and (b)) and temporal (panel (c)) schematization of the model. Wetlands are represented by points on a plane. Panel (a): The gray circle around the wetland marked with "W" represents all wetlands within the maximum walking distance that can be reached by the adults in wetland W, but the connectivity probability decreases with the Euclidean distance. Panel (b): Thiessen polygons are represented around each wetland. In case the two polygons have a common boundary, the relative wetlands are considered as adjacent. Panel (c): The cyclic succession of the fundamental events in the model is represented along with notation about time.

The term d_{ij} described the mortality during the winter for migration and it is proportional to the distance x_{ij} between the two wetlands $d_{ij} = \gamma \cdot x_{ij}$. The term γ was a coefficient representing the probability of mortality per distance unit, implicitly including the probability of dying in the search of a wintering place. The natural mortality μ was considered a constant parameter of the amphibian species.

228   The effective connectivity w_{ij} is the fraction of amphibians in pond j, which

229   choose wetland i as destination and arrive there safely in the following time step. The

230   number of amphibians at the time $t+1$ that reached wetland i was calculated as:

231     $N_{t+1}^i = \sum_{i=1}^{N} w_{ij} N_{t+\frac{1}{2}}^j$ Eqn 4

232   The sum $\sum_{i=1}^{N} w_{ij}$ (i.e., the sum of weights of the ingoing links of wetland i) represented

233   the fraction of the amphibians $N_{t+\frac{1}{2}}^i$ incoming from the other wetlands of the network at

234   time $t+1$. N_{t+1}^i are defined as *Immigrants*. The sum $\sum_{i=1}^{N} w_{ij}$ gave a measure of how

235   much the wetland i was reachable from other wetlands in the network and was called

236   *indegree* (Jordán et al. 2003, Estrada and Bodin 2008): we used indegree for quantifying

237   wetland connectivity.

238   *2.4 Scenarios for different wetlandscapes*

239   We used the population model to run simulations over different randomly

240   generated wetland networks. To investigate the role of wetland indegree on the local

241   amphibian populations we first analyzed the behavior of the system on a single randomly

242   generated wetland network (S*ingle-network scenario*) and then analyzed the relationship

243   between wetlands indegree and population on a set of randomly generated wetland

244   networks using a Monte Carlo simulation approach (M*ulti-networks scenario*). To

245   investigate the impact of wetland removal and restoration on the population, we

246   conducted wetland removal and restoration scenarios also using a Monte Carlo

247   simulation approach (*Wetland removal and restoration scenarios*).

248   The *single-network scenario* was used to explore the overall population dynamics

249   and the local population dynamics in single wetlands of the network, with each wetland

250   characterized by a different value of *indegree*. We randomly generated a network of 50

251   wetlands and ran the population dynamics model on it. For generating the random

252   network we used the algorithm developed by Fachada et al. (2014). This algorithm

253   generates a random network configuration starting from deterministic topological

254   parameters (e.g., Slope, Number of clusters, Total points) and stochastic parameters (e.g.,

255   Average separation of line centers along the X axis, Average separation of line centers

256   along the Y axis, "Cluster fatness"). Stochastic parameters varied for each network and

257   were randomly extracted from a uniform distribution of values. Stochastic parameters

258   made it possible to define a network configuration that was not deterministically assigned

259   but had some random variations. The model was initialized to 20 amphibians per wetland

260   and parameterized as in Table 1 with a fixed simulation time horizon. All the wetlands in

261   the network were characterized by the same carrying capacity, K; this allowed us to

262   explore the relationship between wetlands indegree and population, since wetlands only

263   differed for their indegree value, without other confounding factors due to habitat

264   difference. We classified the wetlands of the network into three classes of indegree (low,

265   medium or high) using the Jenks natural breaks classification, a data clustering method

266   that minimizes each class's average deviation from the class mean while maximizing

267   each class's deviation from the means of the other cluster (Jenks 1967). We then explored

268   the local population dynamics in three wetlands, each one belonging to a different class

269   of indegree. Specifically, we investigated 1) the number of newborns produced in the

270   wetlands, and 2) the number of immigrants.

Parameter	Range of values	Description	Source*
Breeding			
r (/)	6 - 8	Growth rate without density effect	Dray et. al., 2006
K (individuals)	400 - 600	Carrying Capacity	-
Mortality			
μ (/)	0.4 – 0.6	Natural probability of dead	Vonesh and De la Cruz, 2002
Dispersal			
MWD (Km)	3	Maximum Walkable Distance	Ray et al., 2002
β (/)	0.5	Connectivity matrix weight	-

271   * The reference in which the parameter has a similar range.

272   *The multi-network scenario* consisted of running simulations for several randomly

273   generated networks (all having the same topologic characteristic). This scenario served to

274   assess if the observations made from the single-network scenario could be considered

275   general and to explore with more detail the relationship between *indegree* of the wetland

276   and its local population. We generated 100 networks of 50 wetlands each and ran the

277   population dynamics model for each one of the networks. For each network

278   configuration, the values of *r*, *K* and *μ* were extracted from a uniform distribution within

279   a fixed range. Within each experiment, the parameters were kept constant and *K* was

280   equal for all the wetlands. The model was initialized to 20 amphibians per wetland with

281   the range of values of parameters provided in Table 1, i.e., the same demographic

282   parameters of the single-network scenario. As in the single network scenario, wetlands

283   carrying capacity was set equal for all the wetlands for all the networks. We ran the

284   simulations over a period of 60 years, checking that this time horizon was long enough to

285   reach a steady state. We compared the population size in each wetland with its *indegree*

286   value, pulling together all the wetlands in all the simulations. We then explored how the

287   population dynamics evolved within the wetland network analyzing the different

288   contribution played by Immigrants, Newborns and Survivals at each time step. The

289   wetlands within the random networks were divided into three classes (low, medium,

290   high) according to their *indegree*, using the Jenks method. We made pairwise comparison

291   between the distribution of amphibian population abundance within classes with the

292   Kolmogorov-Smirnov and Student's t-test (significance level = 0.05). Kolmogorov-

293   Smirnov test was used to detect the significance of the difference between the

294   distributions of the amphibian population abundance at the steady states in the different

295   classes of *indegree.* Student's t-test was used to detect the difference between the means

296   of the amphibian population abundance at the steady states in the different classes of

297   *indegree.*

298   *Wetland-removal-and-restoration-scenarios* were used to estimate the role of

299   wetland indegree on amphibian population when a wetland was removed or restored. The

300   wetland removal scenario consisted of removing a wetland from the network, simulating

301   the amphibian population dynamics in the altered network, and comparing the result with

302   the non-altered network. For a given network, the experiment was repeated by iteratively

303   removing one wetland at a time. For all the other wetlands, we set an equal value for

304   carrying capacity, *K*. We repeated the procedure with 100 randomly generated wetlands

305   and then examined the relationship between the *indegree* of the wetland removed and the

306   impact on the total population. This relationship was independent from the carrying

307   capacity of the removed wetland, since all the wetlands have the same K. The wetland

308   restoration scenario consisted of increasing the carrying capacity of a wetland in the

309   network by duplicating its original value while keeping constant the carrying capacity of

310   the other wetlands in the network. The population dynamics of the altered network was

311   simulated and the results compared to the non-altered network. For a given network, the

312 experiment was repeated by iteratively enhancing one wetland at a time. We repeated the

313 procedure with 100 randomly generated wetlands and examined the relationship between

314 the *indegree* of the wetland improved and the impact on the total population. We

315 generated 100 wetland networks and repeated the wetland restoration scenario for each

316 network. We then compared the population of the altered and non-altered networks to

317 analyze the impact of management strategies. As in t*he multi-network scenario*, the

318 wetlands within the random networks were divided into three classes (low, medium,

319 high) according to their *indegree*, using the Jenks method. We made pairwise comparison

320 between the distribution of amphibian population abundance within classes with the

321 Kolmogorov-Smirnov and Student's t-test (significance level = 0.05) to detect

322 statistically significant differences in the distribution and in the mean value respectively.

323 The methodology and all the simulations are implemented with Matlab R2016a.

324

325 **3. Results**

326 *3.1 Single-network scenario*

327 The simulation on the single-network scenario showed that the total population

328 abundance, after a transient phase, reached a steady state. The local population in each

329 wetland behaved in the same way. This shows that the length of the time horizon (60

330 years) was sufficient to represent the population dynamics of the wetland network.

331 Hereafter, we present the results referred to the steady state. For the wetland network

332 generated (Fig. 2A), we calculated the frequency distribution of the *indegree* and divided

333 the wetlands into three classes (low, medium, and high) (Fig. 2B). We investigated the

16

334   abundance of the population in three wetlands (marked in Fig. 2A), each one belonging to

335   a different class: Wetland A (low indegree) showed the smallest population, wetland B

336   (medium indegree) showed the largest population, and wetland C (high indegree) showed

337   an intermediate population. Wetland A had a relatively small proportion of newborns,

338   wetland B had a larger proportion of newborns compared to wetland A and C, and

339   wetland C had no newborns (Fig. 3).
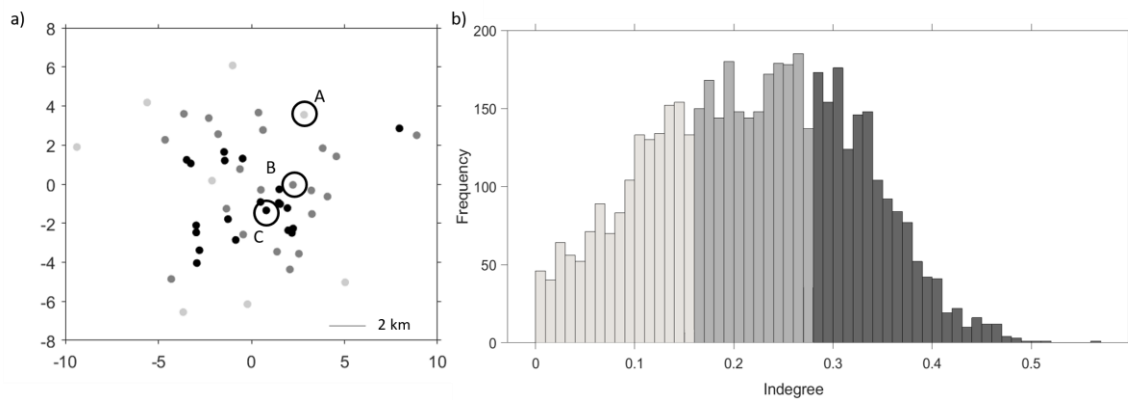
340

341   Figure 2. a) Spatial configuration of the 50 wetlands that form a single network; the total
342   population of three wetlands (A, B and C) are given in Figure 3. b) Frequency distribution of
343   indegree in the 100 simulated wetland networks. Indegree was computed for each wetland, and
344   the wetland was then classified into one of three classes (i.e., low (light grey), medium (grey) or
345   high (black) indegree), with the classes defined using the Jenks natural breaks classification
346   method.

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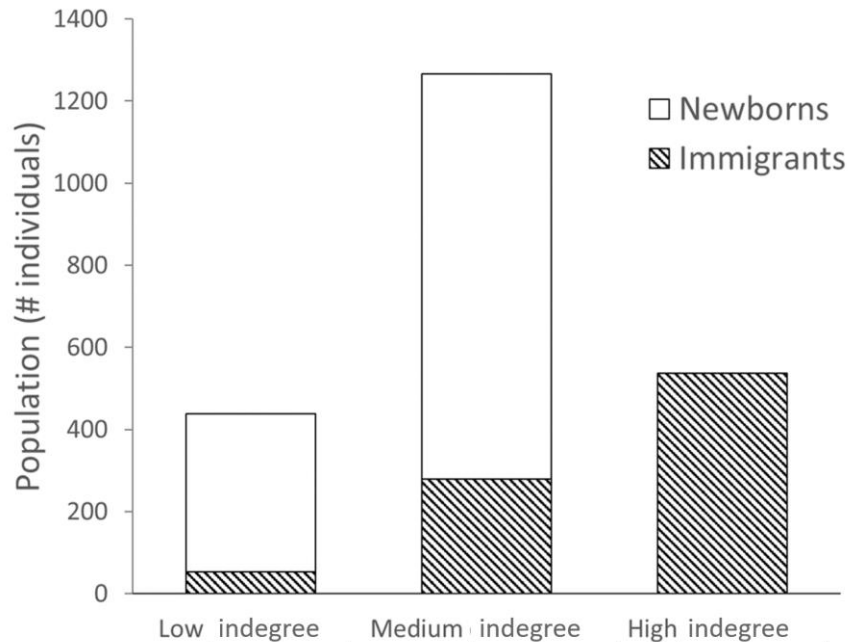
Figure 3. The wetland population, with relative contribution of *Immigrants* and *Newborns*, for

three wetlands (A, B, C, see Figure 2a) for the wetland network depicted in Figure 2.

3.2 Multi-network scenario

The behavior of the single-network scenario (Fig. 3) was generalizable (Fig. 4).

The low indegree class had the smallest population, the medium indegree class had the

largest population, and the high indegree class had an intermediate population (Fig. 4A).

The Kolmogorov-Smirnov test revealed that the data belonging to different indegree

classes had significantly different distribution (p-value < 0.001). The Student's t-test

revealed that data belonging to different indegree classes had significantly different mean

values (p-value < 0.02). The contribution of immigrants and newborns to the population

for the different classes is shown in the pie charts in Figure 4B. Wetlands in all indegree

classes showed that the majority of the population was composed of newborns, but that

the proportion of newborns in the population of the high indegree class was not as high as

in the low or medium indegree classes. This was because the pie chart could not capture

362 the natural oscillation given by the model of the population dynamics, but only displayed

363 a median value.
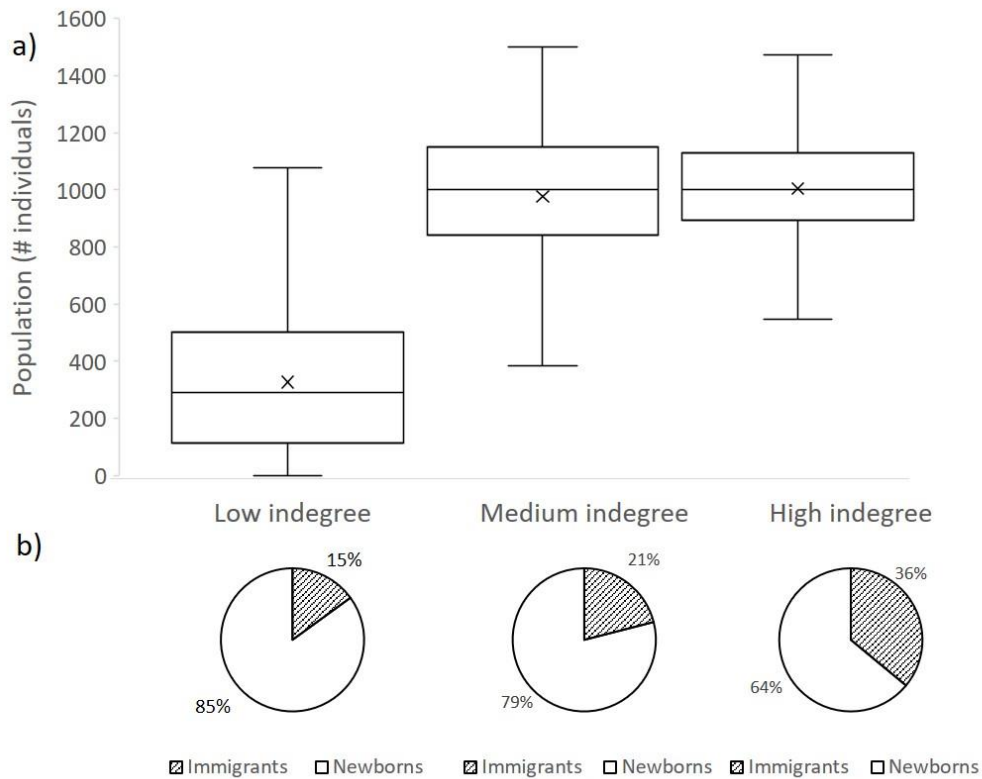
364

365 Figure 4. (a) The wetland population in the three classes of indegree, resulting from the Monte

366 Carlo experiment, and (b) the contribution of *Immigrants* and *Newborns* to the total population.

367 The number of spatial configurations of wetlands' network is equal to 100 and each network is

368 made up of 50 wetlands. For each spatial configuration, the population dynamics were simulated,

369 and for each wetland the total population, the number of *Newborns* and the number of *Immigrants*

370 were computed and related to the indegree of each wetland. The three classes of indegree were

371 defined by the Natural Jenks algorithm.

372 The multi-network scenario showed a non-linear relationship (Figure 5A)

373 between wetland indegree and wetland population; as indegree increased from low to

374 medium the population increased, at medium indegree the population reached a peak, and

375   as indegree increased from median to high the population decreased. The number of

376   immigrants showed a linear increase as indegree increased (Fig. 5B), and the number of

377   newborns showed a non-linear relationship, similar to the total population (Fig. 5C).
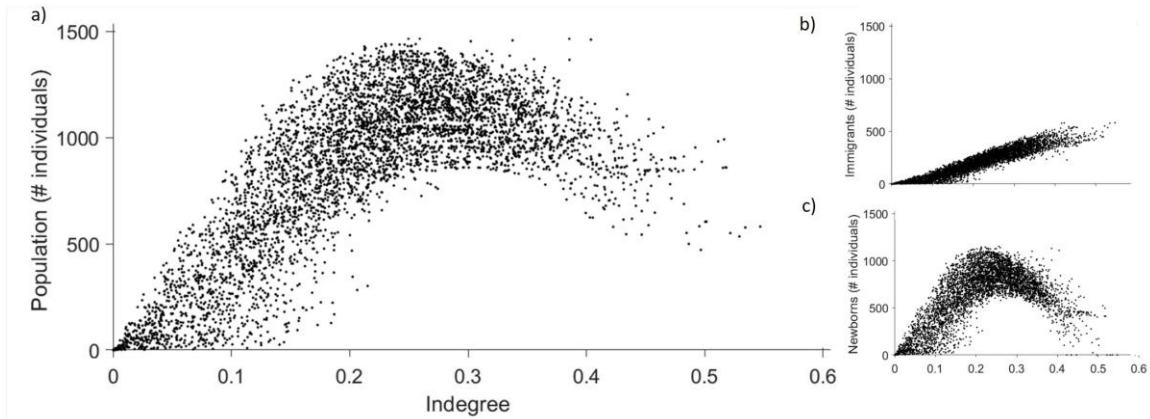
378

379   Figure 5. *Indegree* vs. (a) Population in each wetland for each network, which is the sum of (b)
380   the number of *Immigrants* and (c) the number of *Newborns*.

381   *3.3 Wetland removal and restoration scenarios*

382   The wetland removal scenario showed greater negative effects on the amphibian

383   population when the removed wetland belonged to a medium indegree class (Fig. 6B). In

384   contrast, the wetland restoration scenario showed greater positive effects on the

385   amphibian population when the restored wetland belonged to the high indegree class

386   (Fig. 6A). Fig. 7 directly compares the wetland removal and restoration scenarios by

387   showing the deviation in the population abundance of the entire wetland network between

388   altered and non-altered networks, based on the class of indegree of the altered wetland

389   within the network. As before, the Kolmogorov-Smirnov test revealed that the data

390   belonging to different indegree classes had significantly different distribution (p-value <

391   0.001). The Student's t-test revealed that the data belonging to different indegree classes

392   had significantly different mean values (p-value < 0.001).

393
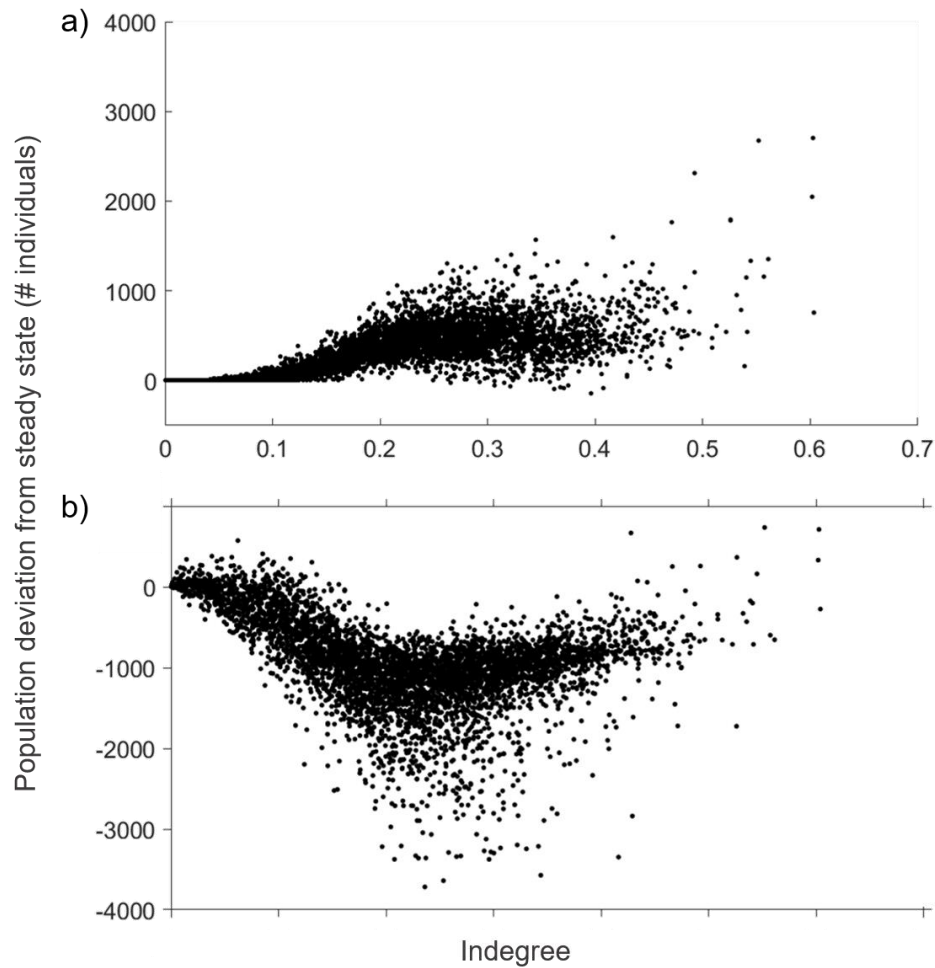
Figure 6. Changes in the population (expressed as deviation from steady state of the altered with respect to the non-altered networks) for different spatial configurations of wetlands' network under the (a) wetland restoration and (b) wetland removal scenario. The deviation from steady state of the altered with respect to the non-altered networks is plotted against the indegree of the altered wetland.
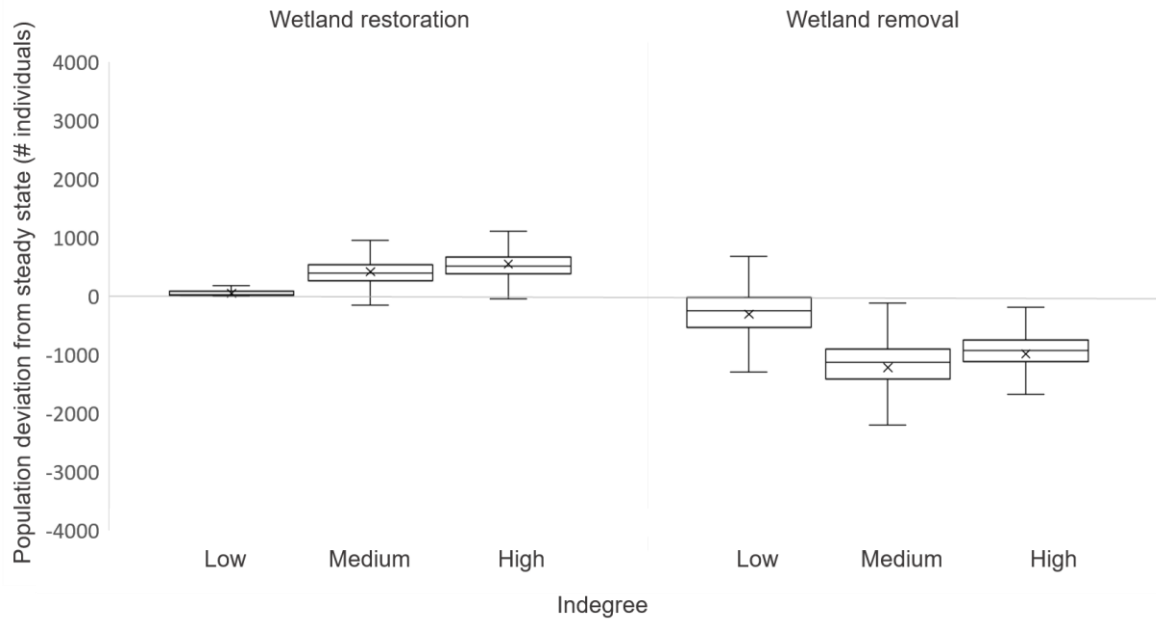
Figure 7. Changes in the total population (expressed as deviation from steady state) within the wetlands' network for different spatial configurations of wetlands classified as low, medium or high indegree and under scenarios of wetland restoration and removal.

4. Discussion

Wetlandscapes sustain sink-source population dynamics with individual wetlands playing different roles (sources or sinks) according to their indegree. We identified source wetlands (where local birth rate is greater than mortality) and sink wetlands (where local mortality is greater than the birth rate, and the population is maintained by continued immigration from source wetlands nearby). Among sink wetlands, we identified two types: those in which the population goes extinct in the absence of immigration, and those in which immigration maintains the population above the carrying capacity. Such a distinction corresponds to true sinks and pseudo-sinks, respectively, according to Watkinson and Sutherland's (1995) terminology. Mortality in pseudo-sinks

414   is caused by excessive immigration, which provokes excessive mortality due to "density

415   effect", the decline in population growth caused by crowding, predators and competition

416   (Hixon and Johnson 2009). If immigration stops in a pseudo-sink, the population would

417   decline, but only to the carrying capacity. Both true sinks and pseudo-sinks have been

418   observed in nature (Watkinson et al. 1989, Engelhard et al. 2017, Erickson et al. 2017).

419   *Indegree* is a useful proxy for classifying wetlands into *sources*, *sinks*, and

420   *pseudo-sinks*. Wetlands with a low indegree – representing relatively isolated wetlands –

421   could be classified as *sinks* because few amphibians migrated to these wetlands and

422   consequently they produced few newborns. Wetlands with medium indegree could be

423   classified as *sources* because they had the highest population. In fact, the number of

424   immigrants arriving in the wetlands and the generated offspring were fully sustained by

425   wetlands resources (expressed by the carrying capacity, *K*). Specifically, the population

426   within each wetland did not exceed carrying capacity and a large number of amphibians

427   was able to successfully emigrate from these wetlands. These wetlands were highly

428   productive, in fact the number of *Newborns* exceeded the number of *Immigrants* and

429   contributed positively to the total wetland population growth. Wetlands with a high

430   indegree – representing relatively connected wetlands – could be classified as *pseudo-*

431   *sinks* because the largest number of *Immigrants* arrived at these wetlands, but the

432   available resources in these wetlands were insufficient to sustain both the immigrant

433   population and the generated offspring. The number of *Newborns* declined until all

434   newborns died due to a "density effect", that is the population of these wetlands exceeded

435   carrying capacity. Most of the amphibians in these wetlands were *Immigrants*, since the

436   breeding success within the wetland was low due to the competition for resources during

437   the breeding phase (Fortuna et al. 2006). It should be noted that all the wetlands had the

438   same carrying capacity value, K, within each simulation; therefore, the difference

439   between non-competition for resources in source wetlands and competition for resources

440   in *pseudo-sink* was due to differences in the wetland's indegree.

441   Management strategies have different impacts on amphibian populations

442   depending on the *indegree* of the wetland. For example, the largest negative impact to

443   the amphibian population was produced when the removed wetland belonged to the

444   medium *indegree* class since a *source* wetland was removed (Fig. 6B). Removing

445   wetlands with high amphibian productivity results in a large loss to the amphibian

446   population of the wetlandscape. Furthermore, the largest positive impact to the amphibian

447   population was produced when the enhance wetland bellowed to the high *indegree* class

448   since the enhanced wetland was originally limited by its carrying capacity (i.e., *pseudo-*

449   *sink* wetlands) (Fig. 6A). In fact, restoring wetlands with high indegree means that a high

450   number of immigrants can now come to the wetland and reproduce successfully,

451   potentially shifting the wetland from a *pseudo-sink* to a *source*. In contrast, restoring

452   wetlands with low or medium indegree (i.e., *source* or *sinks*) did not lead to an increase

453   in the amphibian population because they were limited by low indegree and not by low

454   carrying capacity.

455   Wetland removal and restoration strategies produced impacts on amphibian

456   population dynamics that varied with wetland indegree (Fig. 6). The impacts were not

457   "symmetrical" (Fig. 7). A loss in the amphibian population caused by wetland removal

458   could not be compensated equally by wetland restoration. In fact, wetland removal had

459   "cascading" consequences to the remaining wetlands because of: (1) reducing the number

460   or density of individuals dispersing; and (2) increasing the dispersal distance among the

461   remaining wetlands and thus reducing effective indegree in the network (Semlitsch and

462   Bodie 1998). In contrast, wetland restoration had "cascading" consequences to the

463   remaining wetlands because of reducing "density effect" of individuals breeding.

464   The modelled amphibian population dynamics are supported by empirical studies

465   (Eggert et al. 2015, Arntzen et al. 2017, Lannoo et al. 2017). Amphibians occur on a

466   continuum of *source-pesudo-sink* wetlands and contribute differentially to the population

467   of the wetlandscape (Eggert et al. 2015). Knowledge of the *sink-source-pseudo-sink*

468   behavior can improve wetland management strategies designed for conservation of

469   species-at-risk (Pulliam 1988, Lawton 1993, Eggert et al. 2015). For example,

470   reintroducing a species into presently unoccupied parts of a species' range is more likely

471   to succeed if the reintroduction occurs into a *source* wetland rather than a *sink* wetland

472   (Pulliam 1988). Furthermore, wetland removal could focus on wetlands with low

473   indegree, and wetland restoration could focus on wetlands with high indegree to increase

474   species population. With these insights, the conservation strategies can include design of

475   wetland networks to optimize *sink-source* dynamics.

476   In the future, our model can be improved by adding a two-step migration system, which

477   would enable us to simulate the migration from breeding habitat to winter habitat at the

478   end of summer and the dispersal from winter habitat to breeding habitat at the beginning

479   of spring. In addition, simulation scenarios where wetlands are added to the network

480   could be analyzed to assess the wetland positions leading to the highest positive impact

481   on the population.

482

483   **5. Conclusion**

484   It is important to recognize the role of individual wetlands as defined by their

485   connectivity within wetlandscapes. The adoption of a single-object perspective for

486   wetland management is incomplete given the flux of energy, materials, and organisms

487   that occur among wetlands and in light of our results. Wetlands can have different roles

488   (*sink*, *source*, *pseudo-sinks*) in sustaining an amphibian population within wetlandscapes.

489   Wetland indegree is a key property for 1) quantifying wetland connectivity and 2)

490   classifying wetlands into *sources*, *sinks* and *pseudo-sinks*. Wetland removal and

491   restoration are not compensatory. Rather, these management strategies have different

492   impacts on species population dynamics depending on the indegree among wetlands; for

493   example, wetland removal can result in population loss that is not compensated for by

494   wetland restoration. Understanding the role of indegree of wetlands within

495   wetlandscapes, and the differential impacts of wetland management strategies on these

496   connections, is important for sustainable management of wetland dependent species-at-

497   risk.

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Supporting information

669   **Appendix S1**

670   Networks of wetlands were generated with the algorithm by Fachada et al. (2014)

671   using the software MATLAB (The MathWorks 2016). The algorithm generates a network

672   on a two-dimensional plane through the coordinates of nodes; the coordinates are the

673   centroids of wetlands, and a spatial unit corresponds to 1 km. The algorithm's parameters

674   are listed in Table S1, with their values and their ranges, and a brief description of their

675   meaning. Deterministic parameters were fixed for all the networks (i.e. *Slope, Slope*

676   *standard deviation, Number of clusters, Length average, Length standard deviation,*

677   *Total points*). Stochastic parameters (i.e., *Cluster separation on X axis, Cluster*

678   *separation on Y axis* and*"Cluster fatness"*) varied for each network and were randomly

679   extracted from uniform distributions according to the range of variation of each

680   parameter. When the coordinates of nodes were generated, the distances between each

681   node were used to compute the *indegree* index.

682   The parameter values were selected in order to simulate a wetlandscape where

683   amphibians could move according to their dispersal capabilities. We focused on anuran

684   species that were reported to be able to move up to 10 km during their dispersal stage

685   (Kendell 2002). Thus, we created wetlandscapes where distances are generated in order

686   to have different degree of connectivity.

687

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689

690   Table S1. Parameters of the network algorithm used in the simulations.

Parameter	Value*	Description
Slope (/)	1	Growth rate without density effect
Slope Standard deviation (/)	1	Standard deviation of the slope; used to obtain a random slope variation from the normal distribution, which is added to the base slope in order to obtain the final slope of each cluster.
Number of clusters (/)	1	Number of clusters to generate
Cluster separation on X axis (km)	2.5 – 20	Average separation of line centers along the X axis.
Cluster separation on Y axis (km)	2.5 – 20	Average separation of line centers along the Y axis.
Length Average (km)	1	The base length of lines on which clusters are based.
Length standard deviation (km)	1	Standard deviation of line length; used to obtain a random length variation from the normal distribution, which is added to the base length in order to obtain the final length of each line.
"Cluster fatness" (km)	0.5 – 6	The standard deviation of the distance from each point to the respective line, in both x and y directions; this distance is obtained from the normal distribution.
Total points	50	Total points in generated data (will be randomly divided among clusters).

719   * Where a range is given, the parameter is randomly selected from a uniform distribution
720   within the range (bounds included).