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## Connectivity among wetlands matters for vulnerable amphibian populations in wetlandscapes

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1 **Connectivity among wetlands matters for vulnerable amphibian**  
2 **populations in wetlandscapes**

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16

17 **Abstract**

18 Wetlands have been degraded and destroyed, resulting in the decline of many  
19 wetland-dependent species populations. Many conservation efforts are based on  
20 protection of individual wetlands; however, fluxes of energy, materials and organisms

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.

### 37 **Key Words**

38 Connectivity, Ecological network, Wetland configuration, Amphibian model, Graph  
39 theory, Population dynamics.

40

41

42

43 **1. Introduction**

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

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

66 habitat and the following spring they reach a new aquatic breeding habitat (Pittman et al.  
67 2014). Alteration of wetland habitat and distribution within the landscape, such as  
68 wetland loss, negatively influences both breeding and dispersal success by decreasing  
69 wetland density and increasing travel distances for amphibians (Gibbs, 1993).”

70 Management strategies have been implemented to protect biodiversity promoted  
71 by wetlands. Many of these management strategies focus on wetlands of special  
72 importance (Amezaga et al. 2002). Policy goals vary from “no net loss” to “net gain”  
73 (Accatino et al., 2018) to general statements about the need to address adverse impacts to  
74 these wetlands (e.g., Calhoun et al. 2016). Few of these management strategies focus on  
75 the physical, chemical, or biological connections among wetlands (e.g., Cohen et al.  
76 2016). Although it is widely recognized that wetland connectivity is important for  
77 biodiversity (Semlitsch 1996, Semlitsch and Bodie 1998, Skelly et al. 1999, Marsh and  
78 Trenham 2001, Cushman 2006), concrete strategies in policies are still not well  
79 formulated. The lack in wetland policies of clear operational strategic schemes based on  
80 wetland connectivity is at least in part due to the lack or rarity of quantitative assessments  
81 of the role of wetland connectivity in sustaining wetland biodiversity. Important steps  
82 forward would be to determine if and how wetland connectivity plays a role in sustaining  
83 biodiversity in a wetlandscape (Fortuna et al. 2006, Albanese and Haukos 2017), and to  
84 explore if management interventions on the wetland itself (i.e., wetland removal or  
85 restoration) are influenced by wetland connectivity.

86 The “sink-source” framework describes the distribution of species in the variety  
87 of interconnected habitat patches within a region (Pulliam 1988, Watkinson and  
88 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  $\beta$   
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 
$$\tilde{c}_{ij} = \beta \cdot a_{ij} + (1 - \beta) \cdot \frac{1}{x_{ij}} \quad \text{Eqn 1}$$

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  $i$ .

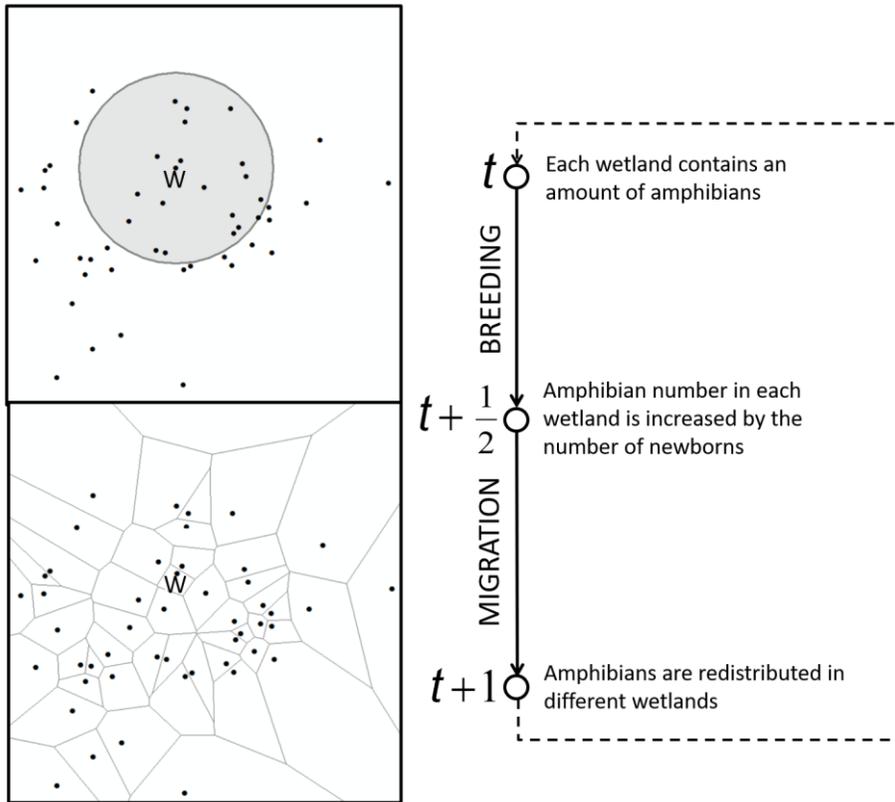
$$196 \quad N_{t+\frac{1}{2}}^i = N_t^i + \max\left(0, rN_t^i\left(1 - \frac{N_t^i}{K}\right)\right) \text{ Eqn 2}$$

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  $\mu$ :

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

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  $\delta$  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).



214

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

223 The term  $d_{ij}$  described the mortality during the winter for migration and it is  
 224 proportional to the distance  $x_{ij}$  between the two wetlands  $d_{ij} = \gamma \cdot x_{ij}$ . The term  $\gamma$  was a  
 225 coefficient representing the probability of mortality per distance unit, implicitly including  
 226 the probability of dying in the search of a wintering place. The natural mortality  $\mu$  was  
 227 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:

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

232 The sum  $\sum_{j=1}^N w_{ij}$  (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  $\sum_{j=1}^N w_{ij}$  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 (*Single-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 (*Multi-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*
<b>Breeding</b>			
$r$ (/)	6 - 8	Growth rate without density effect	Dray et. al., 2006
$K$ (individuals)	400 - 600	Carrying Capacity	-
<b>Mortality</b>			
$\mu$ (/)	0.4 – 0.6	Natural probability of dead	Vonesh and De la Cruz, 2002
<b>Dispersal</b>			
$MWD$ (Km)	3	Maximum Walkable Distance	Ray et al., 2002
$\beta$ (/)	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  $\mu$  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 *the 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.

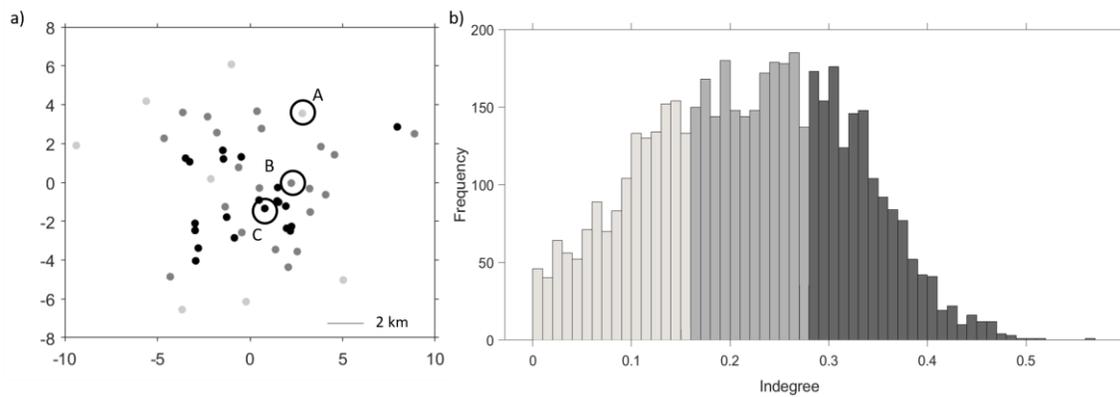
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### 325 **3. Results**

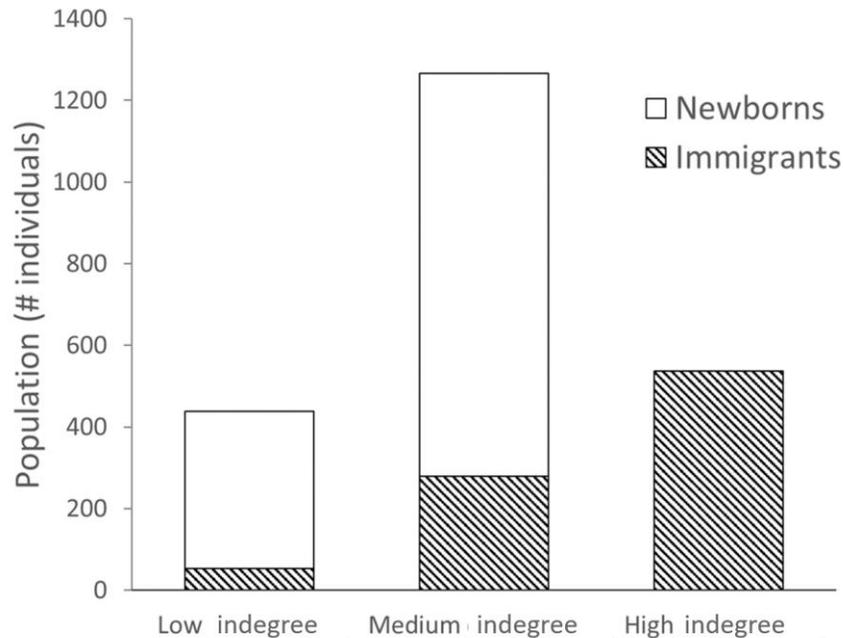
#### 326 *3.1 Single-network scenario*

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

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.



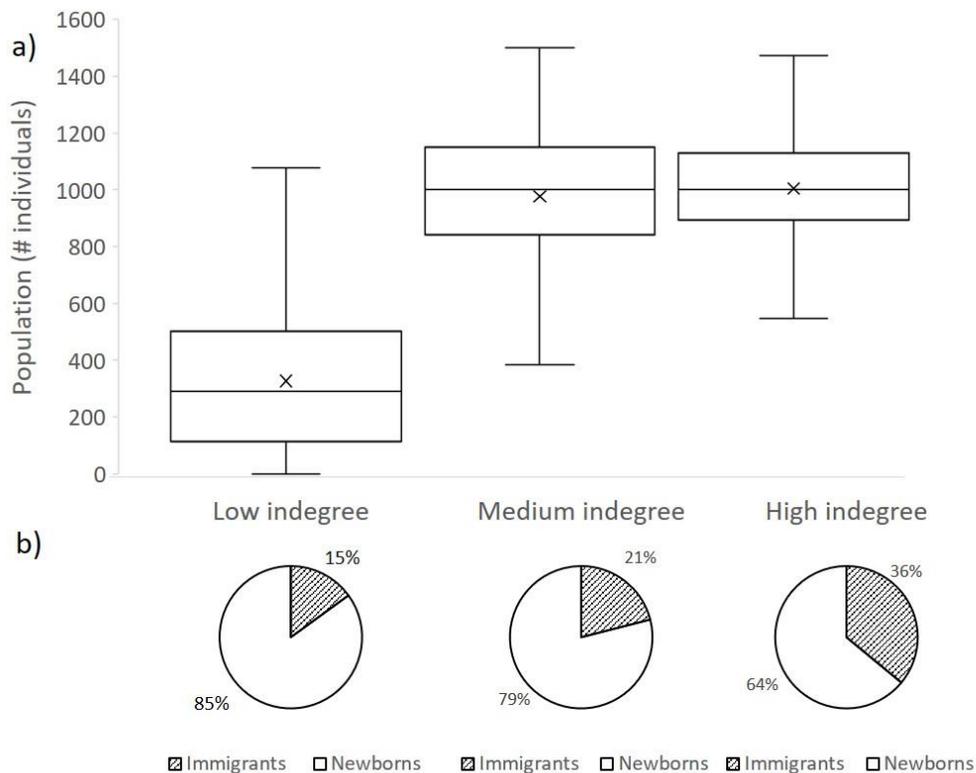
347

348 Figure 3. The wetland population, with relative contribution of *Immigrants* and *Newborns*, for  
 349 three wetlands (A, B, C, see Figure 2a) for the wetland network depicted in Figure 2.

350 *3.2 Multi-network scenario*

351 The behavior of the single-network scenario (Fig. 3) was generalizable (Fig. 4).  
 352 The low indegree class had the smallest population, the medium indegree class had the  
 353 largest population, and the high indegree class had an intermediate population (Fig. 4A).  
 354 The Kolmogorov-Smirnov test revealed that the data belonging to different indegree  
 355 classes had significantly different distribution (p-value < 0.001). The Student's t-test  
 356 revealed that data belonging to different indegree classes had significantly different mean  
 357 values (p-value < 0.02). The contribution of immigrants and newborns to the population  
 358 for the different classes is shown in the pie charts in Figure 4B. Wetlands in all indegree  
 359 classes showed that the majority of the population was composed of newborns, but that  
 360 the proportion of newborns in the population of the high indegree class was not as high as  
 361 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.

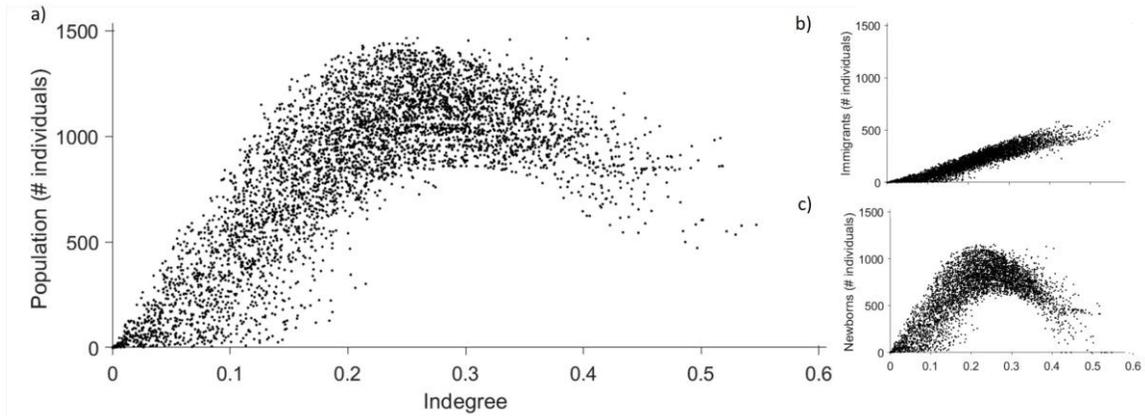


364

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).

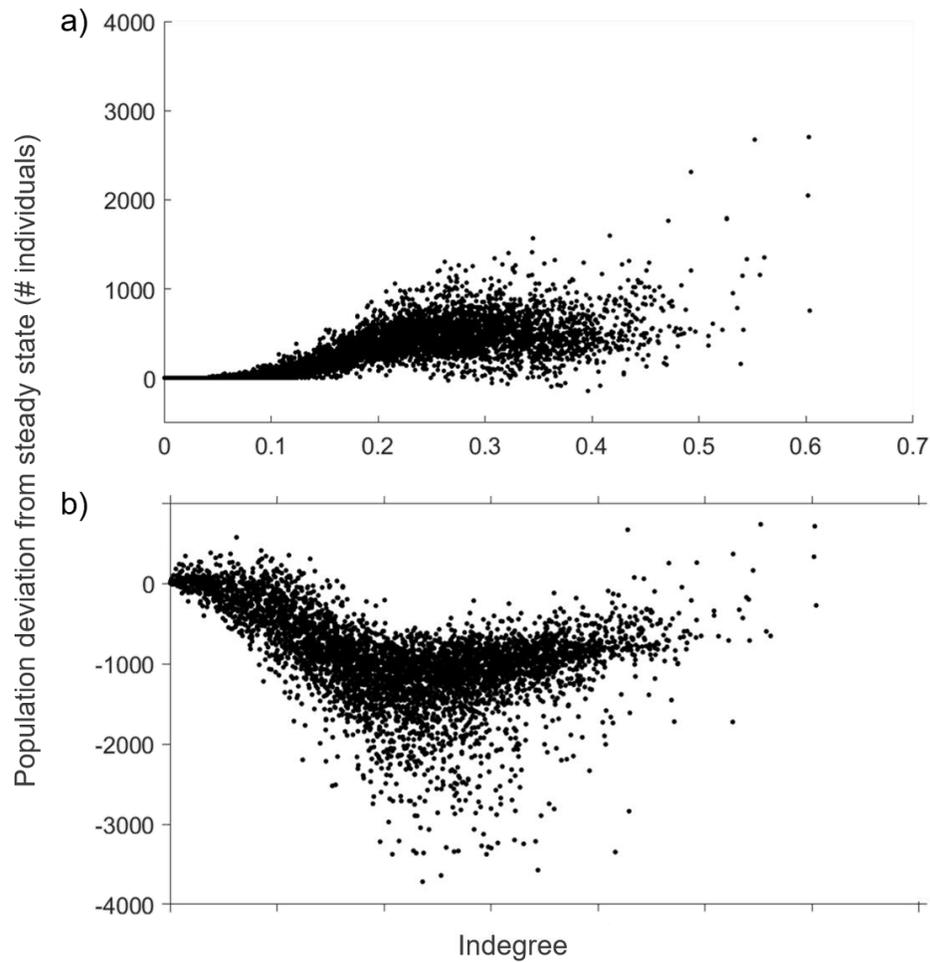


378

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*.

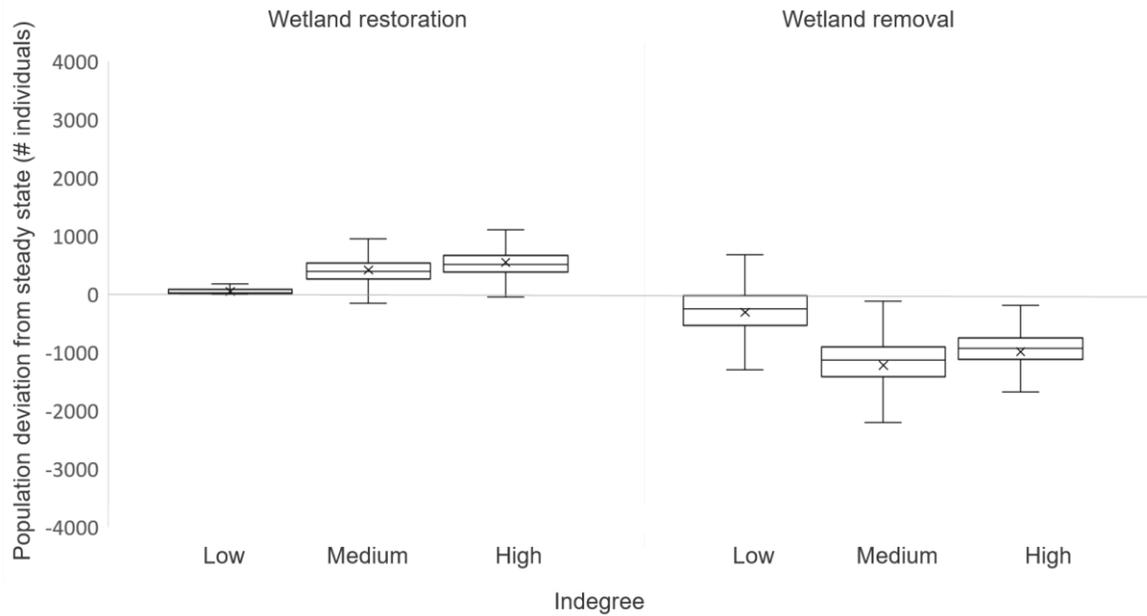
### 381 3.3 Wetland removal and restoration scenarios

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

394 Figure 6. Changes in the population (expressed as deviation from steady state of the altered with  
 395 respect to the non-altered networks) for different spatial configurations of wetlands' network  
 396 under the (a) wetland restoration and (b) wetland removal scenario. The deviation from steady  
 397 state of the altered with respect to the non-altered networks is plotted against the indegree of the  
 398 altered wetland.



399

400 Figure 7. Changes in the total population (expressed as deviation from steady state) within the  
 401 wetlands' network for different spatial configurations of wetlands classified as low, medium or  
 402 high indegree and under scenarios of wetland restoration and removal.

403

#### 404 **4. Discussion**

405 Wetlandscapes sustain sink-source population dynamics with individual wetlands  
 406 playing different roles (sources or sinks) according to their indegree. We identified  
 407 source wetlands (where local birth rate is greater than mortality) and sink wetlands  
 408 (where local mortality is greater than the birth rate, and the population is maintained by  
 409 continued immigration from source wetlands nearby). Among sink wetlands, we  
 410 identified two types: those in which the population goes extinct in the absence of  
 411 immigration, and those in which immigration maintains the population above the carrying  
 412 capacity. Such a distinction corresponds to true sinks and pseudo-sinks, respectively,  
 413 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 belonged 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-pseudo-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.

498

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502

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668 **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

688

689

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

691	<b>Parameter</b>	<b>Value*</b>	<b>Description</b>
692	<i>Slope (/)</i>	1	Growth rate without density effect
693	<i>Slope Standard deviation (/)</i>	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.
694			
695			
696			
697			
698	<i>Number of clusters (/)</i>	1	Number of clusters to generate
699	<i>Cluster separation on X axis (km)</i>	2.5 – 20	Average separation of line centers along the X axis.
700			
701	<i>Cluster separation on Y axis (km)</i>	2.5 – 20	Average separation of line centers along the Y axis.
702			
703	<i>Length Average (km)</i>	1	The base length of lines on which clusters are based.
704			
705	<i>Length standard deviation (km)</i>	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.
706			
707			
708			
709			
710			
711	<i>“Cluster fatness” (km)</i>	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.
712			
713			
714			
715			
716	<i>Total points</i>	50	Total points in generated data (will be randomly divided among clusters).
717			
718			

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