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## Cross-scale effects of structural and functional connectivity in pond networks on amphibian distribution in agricultural landscapes

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► **To cite this version:**

Alienor Jeliaskov, Romain Lorrillière, Aurélien Besnard, Josette Garnier, Marie Silvestre, et al.. Cross-scale effects of structural and functional connectivity in pond networks on amphibian distribution in agricultural landscapes. *Freshwater Biology*, 2019, 64 (5), pp.997-1014. 10.1111/fwb.13281 . hal-04413876

**HAL Id: hal-04413876**

**<https://hal.science/hal-04413876v1>**

Submitted on 24 Jan 2024

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1 TITLE

2 **Cross-scale effects of structural and functional connectivity: new insights for**  
3 **amphibian distribution in agricultural landscape**

4

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29 **Number of words in the abstract:** 326 (MAX 350)

30 **Number of words** (from abstract to fig leg): 9861 (MAX 7000) – **remove 2800 words**

31

32 **ABSTRACT**

- 33 1. Connectivity in pond ecosystems is essential for amphibian population persistence.  
34 However, to understand the role of connectivity, one needs to encompass a diversity  
35 of scales accounting for the different processes underlying species distribution.  
36 Moreover, there are several approaches for measuring connectivity, mainly structural  
37 vs. functional approaches. Our aim was to assess the relative performance of  
38 connectivity measures in predicting amphibian distribution when accounting for  
39 cross-scale effects, from pond to network scales, and to identify networks features  
40 relevant to amphibian conservation in agricultural landscapes of Seine-et-Marne  
41 (East of Paris, France).
- 42 2. We here proposed an original analytical framework that allows a scale-explicit  
43 investigation of connectivity. We analysed the distribution of three amphibian  
44 species (*Bufo bufo*, *Rana dalmatina* and *Triturus vulgaris*) in response to pond  
45 conditions (fish presence, water quality and nearby woodland habitat) and  
46 connectivity according to three connectivity approaches: (i) structural, (ii) area-  
47 functional, based on potential migration areas, and (iii) path-functional, based on  
48 least accumulated-cost paths. Values of landscape resistance were assigned  
49 according to a biological risk-based approach that is proposed as an enhanced,  
50 transparent expert-based approach. We further investigated cross-scale effects in  
51 amphibian responses to environment by determining the relative influence of pond  
52 and network characteristics, and of their interactions.
- 53 3. Despite some species-specific characteristics, the unconstrained functional measure  
54 of connectivity was generally the most efficient in explaining species distribution,  
55 emphasizing the relevance of potential migration areas as conservation units.  
56 Although pond conditions had usually a higher influence than network connectivity,  
57 we highlighted important cross-scale and threshold effects in species response to  
58 habitat connectivity.

59 **Policy implications:** From a general, ecological perspective, our cross-scale approach allows  
60 accounting for scale-dependent processes potentially underlying amphibian distribution,  
61 such as environmental filtering and metapopulation dynamics. Furthermore, both structural  
62 and functional connectivity have to be considered as complementary features of pond  
63 connectivity when dispersal traits are likely to be less limiting. From a management  
64 perspective, our results encourage conservation plans to combine functional network-  
65 centred strategies with preservation of local conditions.

66

67 **KEYWORDS**

68 Agricultural areas, amphibian conservation, connectivity, cross-scale effects, landscape  
69 resistance, pond networks, scales

70

71 **INTRODUCTION**

72 One of the major drivers of landscape fragmentation and homogenisation is agriculture  
73 intensification (Fahrig *et al.* 2011). It results in loss of habitats that are essential for many  
74 species (Saunders, Hobbs & Margules 1991; Benton, Vickery & Wilson 2003; Stuart 2004). In

75 such agricultural landscapes, maintaining or improving the connectivity between remaining  
76 habitats through ecological corridors is crucial for maintaining biodiversity (Bennett 2003;  
77 Hilty *et al.* 2006). For instance, hedgerows can play a major role in habitat connectivity by  
78 allowing animal and plant dispersal, and hence population persistence (e.g. Burel & Baudry  
79 2003; Vos *et al.* 2007).

80

81 Understanding the role of connectivity in species distribution is crucial to improve ecological  
82 corridor management but remains a challenging task because of the diversity of scales (Noss  
83 1991; Levin 1992) and processes underlying species distribution. Environmental control,  
84 metapopulation processes, migration are all key processes with different, and sometimes  
85 interacting, operating scales (Cottenie 2005; Chase 2014). Moreover, connectivity can be  
86 measured according to various paradigms (Calabrese & Fagan 2004; Fischer & Lindenmayer  
87 2007). Landscape connectivity *lato sensu* was defined as “the degree to which the landscape  
88 facilitates or impedes individual movement between resource patches” (Taylor *et al.* 1993),  
89 with some differences between structural and functional connectivity (Tischendorf & Fahrig  
90 2000; Uezu, Metzger & Vielliard 2005). The structural connectivity refers to the physical  
91 structure of the landscape (i.e. shape, number or distances of resource patches), and can be  
92 independent of any trait of the organism(s) of interest. On the contrary, the functional  
93 connectivity accounts for the ecological traits of organism(s) (Tischendorf & Fahrig 2000),  
94 e.g. maximum distance of dispersal, energetic cost of displacement across different types of  
95 land covers, mortality risks associated to the crossing through hostile habitats, etc. Based on  
96 species-specific characteristics, the functional connectivity often appears as a better proxy of  
97 the actual ecological connectivity between habitats resulting from biological processes  
98 (Fischer & Lindenmayer 2007).

99

100 Ponds are important shelters for a diversity of plants and animals (Williams *et al.* 2004).  
101 Several studies demonstrated the importance of pond connectivity on species and  
102 population persistence, notably for amphibians (e.g. (Fortuna, Gomez-Rodriguez &  
103 Bascompte 2006; Ribeiro *et al.* 2011)). As ground-dwelling animals, with inter-seasonal  
104 mobility due to the biphasic life cycle of some species – aquatic and terrestrial, amphibians  
105 are particularly dependent on habitat connectivity. In addition, many amphibian populations  
106 are likely to function according to metapopulation dynamics (e.g. (Smith & Green 2005)).  
107 This also implies that amphibian populations are sensitive to both local and regional  
108 environmental conditions (Werner *et al.* 2007; Skelly 2013) due to different processes (e.g.  
109 habitat fragmentation, introduction of predators, patch dynamics) operating at different  
110 spatial scales (Cushman 2006).

111

112 Pond connectivity is often tackled through buffer approaches by studying amphibian  
113 occurrence in a focal pond in response to landscape variables calculated in circular zones  
114 centred on ponds (Pellet, Hoehn & Perrin 2004; Zanini *et al.* 2008; Simon *et al.* 2008). Among  
115 buffer approaches, Prugh (2009) showed that the number of surrounding occupied habitats,  
116 as potential sources of propagules, are a more efficient measure of inter-pond connectivity,  
117 better predicting amphibian occupancy and colonization than the simple number of suitable  
118 habitats. Some studies also assessed the species distribution according to network-centred  
119 approaches, i.e. according to an explicit description of pond network connectivity, either

120 structural (Fortuna, Gomez-Rodriguez & Bascompte 2006; Ribeiro *et al.* 2011) or functional  
121 (Ray, Lehmann & Joly 2002; Joly, Morand & Cohas 2003). Comparing network-centred and  
122 buffer approaches, (Ray, Lehmann & Joly 2002) showed that functional network approach  
123 better performed than buffer approach in predicting amphibian occurrence. The former  
124 takes into account the energy costs associated with movement through particular types of  
125 habitats and thus, the area and shape of potential migration zone whereas the latter  
126 assumes a circular and homogeneously permeable migration zone. However, these  
127 comparative analyses do not take into account the local conditions effects although some  
128 studies showed the additive effects of pond characteristics and network variables (Ribeiro *et*  
129 *al.* 2011; Decout *et al.* 2012).

130

131 Moreover, no study investigated the interaction between pond- and network-level effects  
132 (multiplicative effects) while the alteration of local conditions could, for instance, limit the  
133 positive effect of connectivity by impeding settlement of colonizers (Joly, Morand & Cohas  
134 2003). Interaction between local habitat selection and metapopulation processes in  
135 amphibians have notably been shown to produce important signatures on the integrative  
136 distribution-abundance relationships (Werner *et al.* 2014). However, no framework was so  
137 far available, that allows investigating the complex interactions between functional habitat  
138 connectivity, and local conditions on species occurrence.

139

140 We propose a hierarchical analytical framework based on a nested structure with three  
141 “spatial scale-levels” (Schaldach *et al.* 2011): ponds, ponds in networks, and networks. This  
142 original approach allowed us to describe habitat and connectivity features which could be  
143 involved in different processes across scales while taking into account signatures of possible  
144 interactions between these processes.

145

146 Our general hypotheses are: (i) The functional measures of connectivity better explain  
147 amphibian species distribution than the structural ones because the former take into  
148 account potential species perception of the landscape, and the biological risks involved in  
149 migration/dispersal processes (Janin *et al.* 2012). We expect a positive effect of pond  
150 connectivity to any network on the species’ probability of occurrence as the population can  
151 benefit from the nearby presence of potential sources of propagules. Consequently, we  
152 expect a negative effect of network expansion, making the potential source further apart,  
153 and resistance, altering the connectivity to potential sources. (ii) As amphibians respond to  
154 several spatial levels of environmental influences (Jeliazkov *et al.* 2014), we expected that  
155 both pond and network-level effects would play a role in their distribution, as well as their  
156 cross-scale interactions. Because of species-specific dispersal abilities though, we expect  
157 contrasting responses depending on the species, with the best dispersers being less limited  
158 by connectivity compared to poor dispersers. (iii) We expect thresholds in the species  
159 responses to network variables because in fragmented landscapes where suitable habitats  
160 are initially scarce, the positive effects of the connectivity metrics may be detected only for  
161 highest values of habitat availability or accessibility (Metzger & Décamps 1997).

162

163 We estimated the occurrence probability of three amphibian species (*Bufo bufo*, *Rana*  
164 *dalmatina* and *Triturus vulgaris*) having different habitat requirements, distributional  
165 patterns, and dispersal abilities at the three spatial scale levels.

166 We (i) tested the effects of structural and functional connectivity on amphibian distribution  
167 in order to assess their relative influence in a context of agricultural landscape, (ii) assessed  
168 the scale-dependence and cross-scale effects of agricultural environment on amphibian  
169 distribution through an original analytical framework, and (iii) identified networks that could  
170 be considered as relevant management units and ranked by importance connectivity  
171 features that could constitute action targets in regard with amphibian conservation.

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**METHODS**

**Study area and pond survey**

The study area is located in the French Seine-et-Marne department (Eastern Ile-de-France Region; 48.6°N/3.2°E). This site is representative of an intensive agricultural landscape, with 80% of its area covered by cereal crops.

In this study area, we located ponds, based on the French national BD TOPO®v2 (IGN 2008), and two complementary pond regional censuses (2009-2012) (Département de Seine-et-Marne & SNPN 2012) (spatial precision 5m).

We selected 160 ponds out of some 300 ponds in the study area on the basis of two criteria. First, we selected permanent ponds to avoid major discrepancies in ecological functioning linked to the hydrological regime. Second, in order to get a gradient of network structures while remaining in the range of known migration distances of the species (e.g. ACEMAV coll. 2003; Semlitsch & Bodie 2003; Smith & Green 2005), we chose the ponds within clusters of different pond densities in which inter-pond distances did not exceed 2000m (Jeliazkov *et al.* 2014). Any interstitial ponds missed or unsampled in our area were few. We omitted particularly isolated, temporary ponds or destroyed during the survey, and with no hydrological connexion with other studied ponds ( Département de Seine-et-Marne & SNPN 2012; Jeliazkov 2013; Jeliazkov *et al.* 2014).

We assessed the occurrence of three amphibian species – *Bufo bufo*, *Rana dalmatina*, *Triturus vulgaris* –for the 160 sites in 2011 and 2012, using a standardised protocol (52 ponds in 2011, 65 in 2012, 35 in both years). Since there was no substantial year effect in occurrence data (Jeliazkov *et al.* 2014), we merged the data of the two annual campaigns into one single-visit dataset for the analyses (Chase & Ryberg 2004).

We conducted two two-week nocturnal sessions per year during the main reproductive seasons (March and June). We combined three complementary methods to detect, identify and count individuals of the target taxa at different stages, while minimising habitat destruction: records of the calling males, observations using lamps along the banks of the ponds, and dip-netting. We also recorded the presence/absence of potentially predatory fish on the basis of visual observations, by dip-netting and/or according to the information provided by pond owners.

Furthermore, four sessions (two per year) of physical-chemical measurements of the water allowed us to calculate an average Water Quality Index (WQI) ranging from 0% (very bad quality) to 100% (very good quality). WQI was adapted from (Pesce & Wunderlin 2000; Sánchez *et al.* 2007) and proven a good indicator of water quality with regard to amphibian response. The nearby availability of terrestrial habitat around ponds was represented by the proportion of wood cover within a 200m-radius buffer zone surrounding ponds (for more information on methods, see (Jeliazkov *et al.* 2014)).

215 **Definition of structural and functional networks**

216 To accurately characterize the habitat connectivity between the sampled ponds and delimit  
217 networks, we combined three GIS regional databases: MOS (IAU IDF 2008) providing  
218 detailed information about urban infrastructures and arable land, Ecomos (IAU IDF 2005)  
219 focused on semi-natural areas such as forest and grassland, and Ecoline (IAU IDF 2012) that  
220 censuses all semi-natural features of the landscape at a very fine spatial resolution (1:2500)  
221 and precision (20cm), such as single trees, hedgerows, groves, field margins, etc. (**Appendix**  
222 **S1**)

223

224 To create networks maps, we first converted all the vector layers to raster format at a 3\*3m  
225 pixel resolution (**Appendix S2a**) and then merged them to a single raster layer referred as to  
226 "landscape" (**Appendix S3**). All GIS treatments and network generation were performed with  
227 ArcView9.3/9.4®, Spatial Analyst and ETGeoWizard10®.

228

229 To assess the resistance of the landscape features, we attributed resistance coefficients to  
230 the main cover types based on previous studies that dealt with the same three amphibian  
231 species. Based on an extensive literature search, we found 10 studies that could provide  
232 either direct, indirect, or expert estimates. Because urodeles were usually proved to be  
233 worse migrators than anurans (e.g. Semlitsch & Bodie 1998; Smith & Green 2005), we  
234 amplified the resistance values of unfavourable habitats for the newt species in line with  
235 (Ray, Lehmann & Joly 2002). Although we found resistance values for most areal elements,  
236 there was no information for the fine elements censused in Ecoline, except for hedgerows  
237 (Lenhardt *et al.* 2013). Thus, based on a thorough reasoning of the potential biological risks  
238 for the species crossing various habitats, we classified these elements according to the cover  
239 structure (strata height and density), hierarchized the associated biological risks (i.e.  
240 predation, desiccation, poisoning, physical barrier or direct mortality) and attributed a value  
241 of resistance accordingly (**Table 1**).

242

243 The "landscape" raster was then reclassified into a "cost raster" using resistance values. The  
244 higher the probability for a species to migrate through a cell, the lower the cost.

245 Using the Cost Distance algorithm from ArcGIS Spatial Analyst, we built a map of the least  
246 accumulated costs (weighted distances) from any pixel of our study area to the nearest  
247 pond. This allowed defining some potential migration areas (PMA) around ponds which  
248 formed functional networks when merged together according to a set of species-specific  
249 maximal migration distances (MMD) (see next section). Then, to compute the least cost  
250 paths between prospected ponds, we used the Cost Path algorithm and recorded their  
251 length and mean accumulated cost (**Appendix S3**).

252

253 **Analytical framework for comparing effects of structural and functional connectivity and**  
254 **assessing cross-scale effects**

255 The structural and functional approaches were all constrained by the same set of species  
256 specific maximal migration distances (MMD, (Joly, Morand & Cohas 2003)) (ACEMAV coll.  
257 2003; Semlitsch & Bodie 2003; Smith & Green 2005):



- 258 - 1000, 1500 and 2000m for *Bufo bufo*  
259 - 300, 500 and 1000m for *Rana dalmatina*  
260 - 100, 200 and 800m for *Triturus vulgaris*.

261

262 We used three different approaches to build networks and to measure pond connectivity:

263 1) The *structural* approach (S) refers to pond “potential” connectivity (Calabrese &  
264 Fagan 2004) and was based on inter-pond Euclidean distances in the limit of the  
265 MMD (**Fig. 1a**).

266 2) The *area-functional* approach (AF) was based on the merging of the potential  
267 migration areas (PMA) around ponds resulting from the mapping of the landscape  
268 resistance (**Fig. 1b**). PMAs are proxies of habitat connectivity for migration between  
269 ponds by adult individuals (Ray, Lehmann & Joly 2002), and/or for dispersal and also  
270 reflect habitat quality around ponds including potential sources of resources (e.g.  
271 Janin, Léna & Joly 2011).

272 3) The *path-functional* approach (PF) consisted in considering the physiological  
273 constraint of cost accumulating along the least-cost paths which linked the ponds to  
274 each other among all the possible distances in the limit of MMD (**Fig. 1c**). In this case,  
275 a dispersing animal accumulates costs along its displacement in relation to potential  
276 biological risks encountered over the distance travelled in the limit of the MMD (e.g.  
277 Bartelt, Klaver & Porter 2010). The path-functional networks can in some cases  
278 appear less limited than the area-functional ones in terms of the number of  
279 connected ponds but implies linear directional inter-pond movement (**Fig 1**). Because  
280 the accumulated cost measures are shown to be more realistic than the least-cost  
281 path measures for assessing habitat connectivity (Etherington & Holland 2013), the  
282 path-functional measure of network connectivity was expected to better explain the  
283 species distribution than the structural measure and to be complementary with the  
284 area-functional one.

285

286 We also described pond-level environmental conditions. We thus represented influences  
287 emerging from three levels: pond, pond-in-network, and network levels (**Table 2**; for  
288 detailed hypotheses, see **Appendix S4**).

289

## 290 **Statistical analyses**

291 The objective of the analyses was to assess the relative effect of the different connectivity  
292 measures (hypothesis (i)), and of the interactions between conditions from different levels  
293 (hypothesis (ii)) as well as the potential thresholds (hypothesis (iii)) on species distribution.  
294 To do so, we modelled the occurrence probability of the three species in response to all  
295 variables of different level of influence under the three different MMD (thus one model per  
296 species per MMD=nine models).

297

298 For all models, we first checked for multi-collinearity within our set of explanatory variables.  
299 The 3 variables of Degree Centrality (*PondCentral\_S/AF/PF*) were collinear. For the sake of

300 models comparability while solving the problem of collinearity, we kept the Degree  
301 Centrality calculated based on the area-functional approach and excluded the two others in  
302 all models (**Appendix S2b**).

303

304 To analyse the relative and interactive effects of pond, pond-in-network, and network level  
305 variables on the species distribution, we used the Boosted Regression Trees (BRT) method  
306 (De'ath 2007) (package {dismo} in R (Hijmans *et al.* 2016)) (**Appendix S2c**). We modelled  
307 residual distribution using logit link function for binary response. In order to get a reasonable  
308 number of trees (> 1000) (see Elith, Leathwick & Hastie 2008), we used a bag fraction of 0.5,  
309 and a learning rate of 0.001 for all models.

310

311 We assessed explanatory power of the final models using the pseudo-R2 calculated as  
312  $(TotalDeviance - ResidualDeviance)/TotalDeviance$ .

313

314 To ensure model parsimony, we performed model simplification (Elith, Leathwick & Hastie  
315 2008) and estimated percentage of deviance explained by each variable from the total  
316 deviance of the model. This allowed us to rank variables according to their relative influence  
317 on species occurrence probability (hypothesis (i)). Also, we tested and selected all the  
318 pairwise interactions on their relative importance (according to the residual variance  
319 generated by linear model) (hypothesis (ii)). As BRT supports non-linear relationships (Elith,  
320 Leathwick & Hastie 2008), a graphical visualisation of the estimated species' response across  
321 levels allowed us to identify potential thresholds (hypothesis (iii)).

322

323 All statistical analyses were performed with the statistical program R 3.3.1 (R Core Team  
324 2016).

325

## 326 RESULTS

327

### 328 Species distribution and network description

329 We illustrated species occurrence and potential migration areas (PMA) in **Figure 2**. In  
330 general, the network number varied from 8 to 39, depending on the species, migration  
331 distance, and network type, i.e. structural, area-functional, and path-functional. A  
332 substantial number of ponds turned out to be isolated, especially in the case of area-  
333 functional network, this being generally amplified as the MMD decreases (**Appendix S5**).

334

### 335 Effects of functional vs. structural network connectivity measures on species occurrence

336 Overall, all 3 connectivity measures had an influence on species occurrence. However, the  
337 functional measures of network connectivity better explained species occurrence than the  
338 structural one (network expansion, *NetExpan\_S*). The mean resistance within area-functional  
339 network (*NetResist\_AF*) better explained *Rana dalmatina*'s and *Triturus vulgaris*'  
340 occurrences whereas the mean accumulated cost within path-functional network better  
341 explained *Bufo bufo*'s occurrence (*NetCost\_PF*) (**Fig. 3a**).

342

343 *B. bufo*'s and *R. dalmatina*'s responded negatively to network-level variables, especially to  
344 the mean network expansion from 700m, and 100m respectively, and to the mean network  
345 resistance from 35%, and 30% respectively (**Fig. 4a-b**). In contrast, *T. vulgaris*' responded  
346 positively to the mean network resistance from a threshold value of 50% (**Fig. 4c; Appendix**  
347 **S6**).

348

### 349 Scale-dependence and cross-scale effects of pond and network variables

350 In average, the pond variables explained a slightly higher deviance than network variables in  
351 the cases of *R. dalmatina* and *T. vulgaris*, whereas pond and network variables were quite  
352 equally ranked in the case of *B. bufo* (**Fig. 3**). However, this pattern highly depended on the  
353 maximum migration distance; the pond-level relative influence decreased with the increase  
354 of MMD in the case of *R. dalmatina*, and *T. vulgaris*; the opposite relationship was observed  
355 in the case of *B. bufo* (**Table 3**).

356

357 The Water Quality Index (*WQI*) had a positive effect on species occurrence, generally from  
358 70%, the average level of good water quality (**Fig. 4**). The distance to the nearest pond  
359 occupied by the focal species (*DistOccPond*) showed a negative effect for all species (**Fig. 3,**  
360 **Fig. 4**). Its effect was particularly strong for *T. vulgaris* (**Fig. 3c**) and expressed as a U-shaped  
361 response in the case of *B. bufo* (**Fig. 4a**).

362

363 The BRT analysis highlights interaction effects among pond-, pond-in-network- and network-  
364 level variables – although most of the interaction effects were relatively weak compared to  
365 the additive ones (**Appendix S7**). Most of the interactions involved pond- along with higher

366 level-variables, i.e. network-level variables (40% of the cases), and pond-in-network-level  
367 variables (25%), while pond-level variables also interacted with each other (20%).

368

369 In particular, we observed a sharper decrease of *T. vulgaris*' occurrence in response to fish  
370 when the water quality was better (**Fig. 5a**). Pond variables like fish presence, and WQI can  
371 also interact with pond-in-network level variables like *DistOccPond* (**Fig. 5b-c**); e.g. the more  
372 connected the focal pond is, the stronger is the response of *T. vulgaris* to water quality (**Fig.**  
373 **5b**). The same observation can be made for *R. dalmatina* in the case of fish presence (**Fig.**  
374 **5c**). Interactions among pond- and network-level variables showed how the positive  
375 response to connectivity can be moderately reduced by the negative effects of local  
376 conditions (**Fig. 5d-f**).

377

378 **DISCUSSION**

379 **Structural vs. functional characteristics of connectivity in relation to amphibian**  
380 **distribution**

381 We showed the overall efficiency of functional connectivity variables in explaining  
382 amphibian species distribution, in line with previous studies (Ray, Lehmann & Joly 2002; Joly,  
383 Morand & Cohas 2003). However, network expansion also proved to be important. This  
384 suggests that for investigating the distribution of amphibians, functional measures of habitat  
385 connectivity are relevant and should be considered in complement to structural measures.

386 Area-functional connectivity better explained *R. dalmatina's* and *T. vulgaris'* distribution  
387 than path-functional and structural connectivity. Most likely, connectivity measure includes  
388 both effects of habitat availability/quality (sources of resources), and of habitat connectivity  
389 (potential migration and dispersal routes). For several species, movement directions for  
390 migration and dispersal are not randomly distributed (Sinsch 1990, 2014; Miaud, Sanuy &  
391 Avriillier 2000; Marty *et al.* 2005). The path-functional measure of connectivity, based on the  
392 hypothesis of directional movement, performed worse likely because directional movement  
393 is highly disrupted in areas disturbed by human activities, such as intensive agriculture areas  
394 (Mazerolle & Desrochers 2005).

395 In the case of *B. bufo* and lower migration distances, the structural connectivity explained  
396 almost as much of species occurrence variation as the functional one. This suggests that at  
397 this scale, both network resistance, and network expansion are relevant predictors of toad  
398 distribution. Common toad was shown to have better dispersal abilities than smooth newt  
399 and agile frog (e.g. ACEMAV coll. 2003; Smith & Green 2005). Thus, functional and structural  
400 features of the connectivity shouldn't be treated exclusively, but rather in complementarity  
401 to get a more complete view of the connectivity at the light of species' ecology.

402 Although less influential than the network connectivity, distance to the nearest occupied  
403 pond remained a good predictor of species occurrence, in particular for *T. vulgaris*. Moilanen  
404 & Nieminen (2002) showed that while the nearest neighbour-type connectivity metrics are  
405 generally less reliable than buffer-type metrics (*contra* (Prugh 2009)), the distance to  
406 potential source populations was an efficient predictor of habitat use (Marsh, Fegraus &  
407 Harrison 1999), of colonization, extinction (Skelly *et al.* 2007) and of population genetic  
408 differentiation (Rowe, Beebee & Burke 2000; Ficetola & De Bernardi 2004) in the particular  
409 case of amphibians in highly fragmented habitats. Sensitivity of amphibians to the distance  
410 to the nearest occupied pond is often attributed to metapopulation processes and  
411 individuals movements between close ponds (e.g. Ficetola & De Bernardi 2004) but it can  
412 also be due to habitat availability for adults (Van Buskirk 2005). In our case, the  
413 metapopulation hypothesis cannot be rejected because our distance-based metrics,  
414 considering ponds as potential *sources of propagules*, showed more effect than the  
415 centrality degree assimilated to the number of ponds – occupied or not by the species -  
416 within a limited neighbourhood around the focal pond, i.e. *potential habitats*.

417 **Cross-scale effects of pond and network variables on species distribution**

418 *Additive effects of pond and network variables across spatial scales*

419 The pond-level effects on species occurrence usually dominated, or equated to the other  
420 levels' conditions. For instance, *B. bufo's* occurrence was more conditioned by water quality  
421 than by any other higher-level habitat or connectivity variables, while *R. dalmatina* was

422 particularly responsive to the proportion of woodland cover surrounding focal ponds.  
423 Habitat preference thus may be one major limiting process underlying toad and agile frog  
424 population persistence in this landscape (e.g. Van Buskirk 2005). In contrast, *T. vulgaris* was  
425 especially responsive to the pond isolation, with a sharp negative relationship, suggesting  
426 that its distribution is strongly spatially auto-correlated and may rely on source-sink  
427 processes (Pulliam 1988; Harrison 1991).

428 At the network level, connectivity alteration had expected negative effects on both anurans'  
429 distribution, but a positive effect on *T. vulgaris*, either in terms of network resistance, or in  
430 terms of accumulated cost for joining the focal pond. *T. vulgaris*' occurrence has already  
431 proved to be favoured by open landscapes, notably grasslands, and to positively respond to  
432 the distance of the nearest woodland (Denoël & Ficetola 2007). If woodlands constitute  
433 barriers for this species, then what we considered as a resistance decrease for other species  
434 might represent the strict opposite for *T. vulgaris*. In this case, our evaluation and  
435 assumptions according to which the tree-filled areas were favourable habitats for this  
436 species might be reconsidered (Garshelis 2000). Although relatively low resistance had been  
437 assigned to densely vegetated, low strata habitats - supposed to be favourable habitats to *T.*  
438 *vulgaris* (e.g. Marnell 1998) - these might not be in sufficient amount to allow detecting  
439 positive effects of connectivity. The results for *T. vulgaris*' are difficult to interpret also  
440 because they include many isolated ponds (see **Appendix S5**) for which the measure of  
441 network resistance actually corresponds to a measure of habitat quality, and not of  
442 connectivity.

443 The relative ranking of influences from pond, pond-in-network and network levels is  
444 sensitive to the species-specific, relative scale tested (Turner *et al.* 1989). This sensitivity  
445 gives some indications on the relevance of the range of maximum distances we used for  
446 each species. Interestingly, the models in which network level had the best ranking over the  
447 other levels were obtained for the minimal distance tested in the case of *B. bufo*, and for the  
448 maximal distance tested in the case of *R. dalmatina* (1000m for both). This suggests that the  
449 relative scale of ~1000m is relevant to capture both effects of dispersal limitations, and  
450 habitat suitability for these species, suggesting habitat complementation (Janin *et al.* 2009).  
451 This also suggests that we may have tested ranges on the edge and over- and under-  
452 estimated the potential migration distances for *B. bufo*, and *R. dalmatina*, respectively. The  
453 fact that both 300m, and 1000m worked well for *R. dalmatina* might indicate different  
454 movement patterns. For instance, natal dispersal has been shown to operate on longer  
455 distances than adult habitat use in other anuran species (e.g. Angelone, Kienast &  
456 Holderegger 2011). In contrast, the ranking of influence levels in the case of *T. vulgaris* was  
457 not sensitive to these relative scales; the pond connectivity towards its network was always  
458 ranked as the most influential effect. This can be explained by some potential source-sink  
459 effect ensured by surrounding occupied ponds, especially when potential sources are  
460 numerous in a radius of 250m (Ficetola & De Bernardi 2004), or up to 500m in our case  
461 (probably due to the relative homogeneity of the landscape (Turner, 1998)). It is possible  
462 that maximum migration distances were underestimated given the thresholds we observed  
463 in the species' response to the distance of nearest occupied pond.

#### 464 *Interaction effects of pond and network variables across spatial scales*

465 The interaction effects were relatively low compared to the main effects.. Nevertheless, our  
466 results support the existence of cross-scale effects in amphibian-environment relationships  
467 (Werner *et al.* 2014), especially between pond and network levels. As expected, the positive

468 effect of network connectivity, either structural or functional, was usually amplified in  
469 absence of fish and with a good water quality. These favourable local conditions are  
470 important for biological conservation in line with Van Buskirk (2005) but an overall well-  
471 connected network can further mitigate the negative effect of individual pond isolation. This  
472 result highlights that the different processes shaping species distribution are likely to  
473 operate and interact with each other across a gradient of scales (Chase 2014).

#### 474 **Methodological insights and challenges for a cross-scale expertise of ecological** 475 **connectivity**

476 Cross-scale effects detection of the environment on species occurrence proves that our  
477 analysis design gives a reasonable picture of the intrinsic scales (Wu & Li 2006) at which  
478 processes may operate in shaping species distribution. Our approach integrates multi-level  
479 processes (Peters, Bestelmeyer & Turner 2007) and should be considered for more efficient  
480 pond management (Semlitsch 2002), like designing management units which have  
481 ecologically meaningful contours and spatial coherence at the landscape level.

482 We used biological risk-based criteria related to vegetation stratum to classify landscape  
483 features and assign them resistance coefficients. This approach, even though deriving from  
484 expert knowledge, is more transparent, standardized and evaluable than a classical, fuzzy  
485 expert-based approach because it relies on a framework of explicit hypotheses along with  
486 the relevant literature. Other approaches estimated ecological connectivity directly based on  
487 biological data, either of species distribution (Janin *et al.* 2009), or of population genetic  
488 structure (Stevens *et al.* 2006). When applicable, these methods of course appear as more  
489 robust than any expert-based approach as they avoid choosing the resistance values based  
490 on subjective opinion. With the increasing availability of these methods, expert-based  
491 approaches have become the subject of strong and intuitive but sometimes poorly justified  
492 criticism.

493 Likely, both approaches should be considered as complementary for finding a congruent and  
494 stable analytical framework (Zeller, McGarigal & Whiteley 2012). There are reasons and  
495 situations for which our risk-based approach, and any expert-based approach, can still be  
496 valuable. First, expert-based methods have proven to give useful insights for amphibian  
497 conservation under human-modified landscapes (Ray, Lehmann & Joly 2002; Lenhardt *et al.*  
498 2013). While several studies well showed the indisputable power of field data-based  
499 approaches in assessing ecological connectivity (e.g. Janin *et al.* 2009; Van Buskirk 2012),  
500 both methods have not yet been compared and there is no clear evidence so far that  
501 justifies the strict abandonment of expert-based or literature-based approaches (Clevenger  
502 2002; Spear *et al.* 2010). Second, in the context of applied ecology, using the risk-based  
503 approach offers a good compromise between cost and time of implementation, notably  
504 when rapid decisions have to be made for protecting a whole group of species. In a time  
505 where ecology research expresses the need for bridging the gap between scientists and  
506 practitioners, it is especially counter-productive to simply sweep away the value of expert  
507 opinions. When genetic and field data of good quality and of reasonable spatial coverage are  
508 available, it seems highly recommendable to use them for connectivity analyses; otherwise,  
509 the risk-based approach is a good alternative for guiding cost-effective, applied  
510 conservation.

511

512 **Thresholds in local and connectivity effects: implications for amphibian conservation in**  
513 **agricultural landscapes**

514 The responses to local conditions as water quality differed quantitatively among *B. bufo*, *R.*  
515 *dalmatina*, and *T. vulgaris*, reflecting differential habitat selection by these species.  
516 Connectivity results also highlighted potential optimal pond networks for these species in  
517 agricultural contexts. For *B. bufo* the appropriated network would have a mean resistance  
518 below 40, corresponding to half woodlands and half crops areas, composed by at least six  
519 ponds with a water quality index above 70% and separated by less than 500m, or by least-  
520 cost paths measuring less than 1500m, crossing low resistance features (5, e.g. woodlands,  
521 continuous shrub hedges). Similarly, a potentially viable pond network for *R. dalmatina*  
522 could at least have a mean network resistance below 30, be composed of fish-less ponds  
523 separated by less than 200m, and immediately surrounded by more than 20% of woody  
524 areas. Finally, in the case of *T. vulgaris*, one should favour patchy networks in more open  
525 areas with inter-pond distances not exceeding 800m. These simple statements allow  
526 highlighting threshold values that could be used as a general guidance for orientating  
527 “pondscape” (Boothby 1997) management in agricultural areas according to a network  
528 strategy.

529 **CONCLUSION**

530 Our work provides an original analytical framework for investigating the multifactorial  
531 relationships between amphibian distribution and environment, and highlighting cross-scale  
532 effects and non-linearities in amphibian response to habitat quality and connectivity. This  
533 can help prioritizing conservation actions.

534 Thanks to a nested design, we successfully ranked the importance of factors influencing  
535 amphibian distribution at pond, pond-in-network and network levels and highlighted the  
536 possible interaction effects across scales, which are signatures from ecological processes  
537 operating along a gradient of scales (Peters, Bestelmeyer & Turner 2007; Werner *et al.*  
538 2014).

539 Our study verifies the relevance of network-approaches as a complement to pond-centred  
540 approaches for amphibian conservation (Boothby 1997; Roe & Georges 2007; Jeliakov *et al.*  
541 2014) and gives clear guidelines on the features of such networks to help maintaining  
542 amphibian populations in agricultural landscapes. In particular, we encourage conservation  
543 plans to adopt functional network-centred strategies, that is also consistent with landscape-  
544 centred conservation strategies recommended by (Mimet *et al.* 2013). In line with (Ray,  
545 Lehmann & Joly 2002), we defend that potential migration areas can represent relevant  
546 ecological units for amphibian conservation. We further highlight that structural and  
547 functional connectivity metrics have to be considered as complementary features of pond  
548 connectivity, especially when dispersal traits are likely to be less limiting. Our results and  
549 approach can help stakeholders to find possible compromises between the constraints  
550 which are inherent to agricultural activities and the conservation of the biodiversity in these  
551 areas.

552



553 **AUTHOR'S CONTRIBUTIONS**

554 AJ, FC, JG and AB conceived the ideas, AJ, AB, RL and MS designed methodology; AJ and MS  
555 analysed the data; AJ collected the data and led the writing of the manuscript. All authors  
556 contributed critically to the drafts and gave final approval for publication.

557

558 **ACKNOWLEDGEMENTS**

559 The Fédération d'Ile-de-France pour la Recherche en Environnement (FIRE FR-3020) is  
560 greatly acknowledged for the PhD grant awarded to Alienor Jeliaskov. We also thank  
561 Annabelle Boucher (NATUREPARIF), Vincent Vignon (OGE), Théo Flavenot (UMR 7204),  
562 Pierre Joly (UMR 5023), Dirk Schmeller (UFZ), Reinhard Klenke (UFZ), SNP and Département  
563 de Seine-et-Marne, for their help, advices and support. Thanks are due to Pierre Rivallin  
564 (Seine-et-Marne Environnement) for providing early training with species identification, and  
565 to Benjamin Mercier (UPMC) for water analyses; to the student interns, Fabien Michel, Flora  
566 Guillier, Victor Court, Pietro Viacava, Nicolas El Battari, Elodie Rey, and other companions,  
567 for their help on the field. We are grateful to the landowners, farmers and authorities from  
568 Seine-et-Marne.

569

570 **DATA ACCESSIBILITY**

571 Should the manuscript be considered for publication in Journal of Applied Ecology, the  
572 amphibian data will be made available on Dryad repository.

573

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- 844
- 845

846 **TABLES**

847 **Table 1** Risk-based classification of landscape features according to their resistance coefficients. Coefficients for main land covers like  
848 woodlands, crops, grasslands, urban areas, and roads were taken from (Ray, Lehmann & Joly 2002; Joly, Morand & Cohas 2003; Vos *et al.* 2007;  
849 Janin *et al.* 2009; Cushman, Compton & McGarigal 2010; Zetterberg, Mörtberg & Balfors 2010; Patrick *et al.* 2012; Decout *et al.* 2012; Van  
850 Buskirk 2012; Lenhardt *et al.* 2013). Note: Information from Van Buskirk (2012) was used only for relative indications of resistance across  
851 habitat types as it did not provide directly comparable measures of resistance.



Strata/ habitat types	Relative height of the feature in its stratum	Stratum continuity	Examples of landscape features	Biological cost/risk associated to the crossing of the feature	Attributed resistance value for <i>Bufo bufo</i> and <i>Rana dalmatina</i>	Attributed resistance value for <i>Triturus vulgaris</i>
Pond (water surface)	-	-	Ponds	No cost assumed*	1	1
Ligneous strata	High	Dense	Woodlots, continuous hedgerows	Minimal cost	5	5
	Low	Dense	Continuous shrub hedges, thicket/coppices	Minimal cost	5	5
	High	Sparse	Isolated trees, discontinuous hedgerows	Predation	10	20
	Low	Sparse	Spontaneous shrubs	Predation	10	20
Herbaceous strata	High	Dense	Natural grasslands, fallow lands	Predation	10	20
	Low	Dense	Field margins, grassy paths	Predation + desiccation	20	30
	High	Sparse	Spontaneous vegetation of road margins	Predation + desiccation	20	30
	Low	Sparse	Partially grassy paths	Predation + desiccation	20	30

Crops / Cities	-	-	Crops and highly urbanized areas	Predation + desiccation + pollution/toxicity	45	80
Infrastructures	-	-	Roads, transport infrastructures, construction sites	Predation + desiccation + pollution/toxicity + dominant human activities + quasi-impassable physical barrier or linked to direct mortality	100	100

\*The resistance value of pond has been fixed at 1 in order to ensure that they are the main attractors in the friction maps that is required to study the connectivity precisely between ponds.

852

853 **Table 2** Description of the pond, pond-in-network and network level variables of which the main and interaction effects were tested on species  
 854 occurrence. S, AF, and PF refer to “Structural”, “Area-Functional”, and “Path-Functional” approaches of connectivity, respectively

Analysis level	Variable	Description
Pond	Fish	Fish presence
	WQI	Water Quality Index
	WoodProp	Woodland proportion in a buffer zone of 200-m radii
Pond in network	DistOccPond	Distance from the focal pond to the nearest sampled pond occupied by the focal species
	PondCentral_S	Degree centrality in structural networks i.e. the number of edges linking the focal pond to the others ponds of the structural network
	PondCentral_AF	Degree centrality in unconstrained functional networks i.e. the number of edges linking the focal pond to the others ponds of the unconstrained functional network
	PondCentral_PF	Degree centrality in constrained functional networks i.e. the number of edges linking the focal pond to the others ponds of the constrained functional network
Network	NetExpan_S	The mean inter-pond Euclidean distances within the structural network which the focal pond belongs to
	NetResist_AF	The mean resistance calculated within the unconstrained functional network which the focal pond belongs to
	NetCost_PF	The mean accumulated cost along the least paths connecting ponds within the constrained functional network which the focal pond belongs to



856 **Table 3** Ranking of the three levels of influence (Pond, Pond-in-Network, Network) on  
 857 species occurrence according to the total amount of deviance explained by the variables  
 858 from each level, each species, and each maximum migration distance tested; in grey, the  
 859 best models in terms of deviance explained

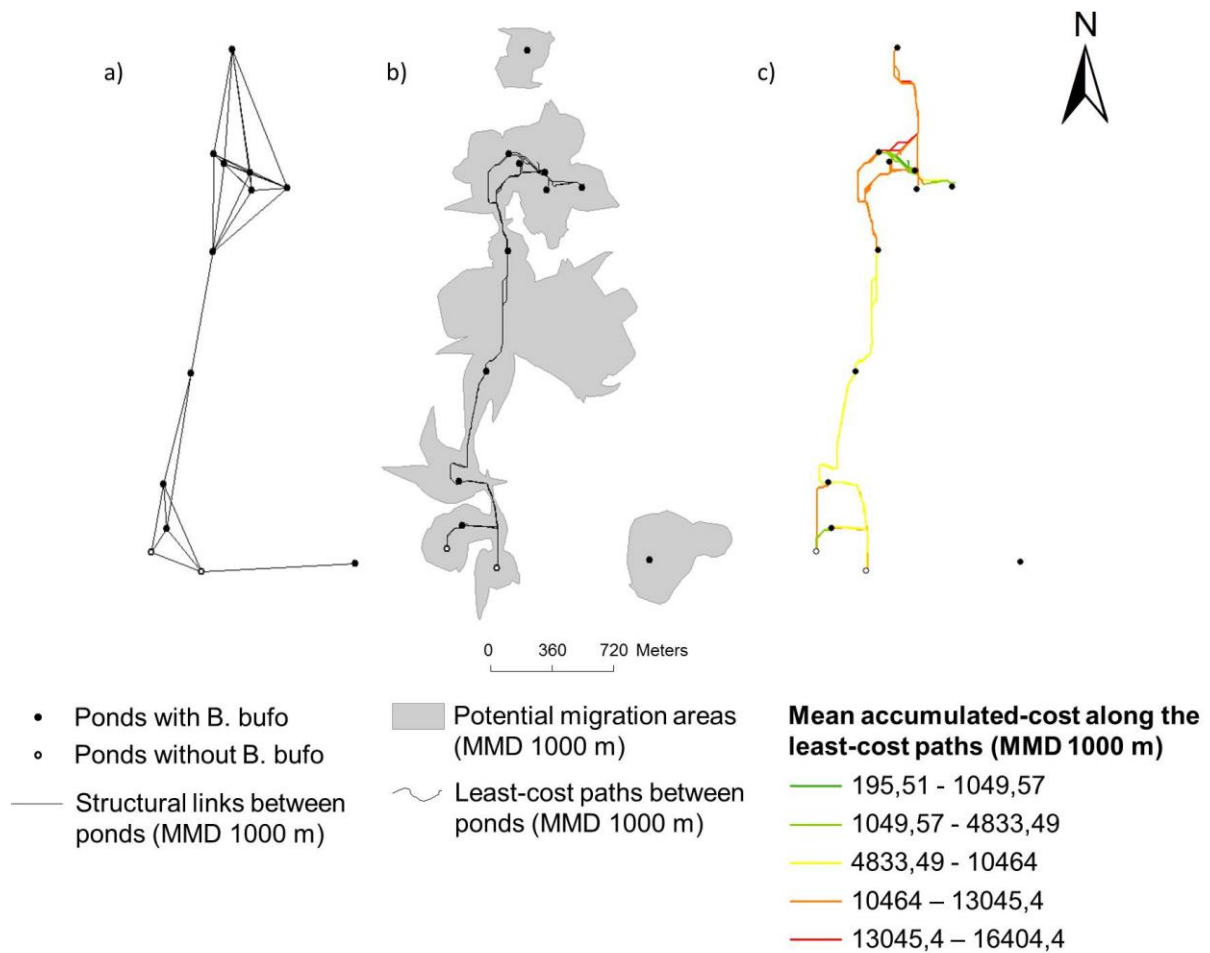
Species	MMDmin	MMDmed	MMDmax
<i>Bufo bufo</i>	N >> P >> PN	P > N > PN	P >> N > PN
<i>Rana dalmatina</i>	P >> PN >> N	P >> N > PN	N > P > PN
<i>Triturus vulgaris</i>	PN > P > N	PN > P > N	PN > P > N

860

861

862 **FIGURES**

863 **Figure 1**



864

865 **Fig. 1** Example of a pond network under the three different connectivity approaches: a) 866 structural (Euclidean distance), b) area-functional (PMA and least-cost paths within PMA), c) 867 path-functional (mean-accumulated-cost along least-cost paths) here for *Bufo bufo*, and a 868 MMD of 1000m. Mean accumulated-cost values are weighted distances that are based on 869 the resistance values of the different types of habitats crossed by the least-cost path, and on 870 the pixel resolution (3\*3m). The cost unit is meter-equivalent, e.g. to reach one pixel of 871 woodland (of resistance value=5) through a straight line (=3m length), the cost equals 872 5\*3m=15 meters-equivalent

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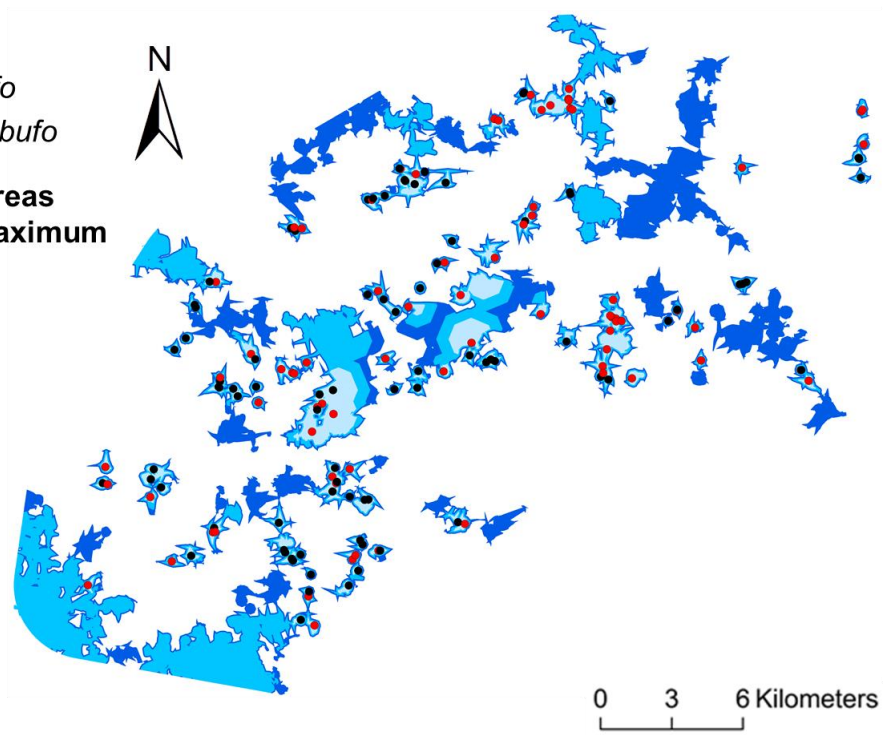
875 **Figure 2**

a)

- Ponds with *B. bufo*
- Ponds without *B. bufo*

**Potential migration areas according to three maximum migration distances:**

- MMD 1000 m
- MMD 1500 m
- MMD 2000 m



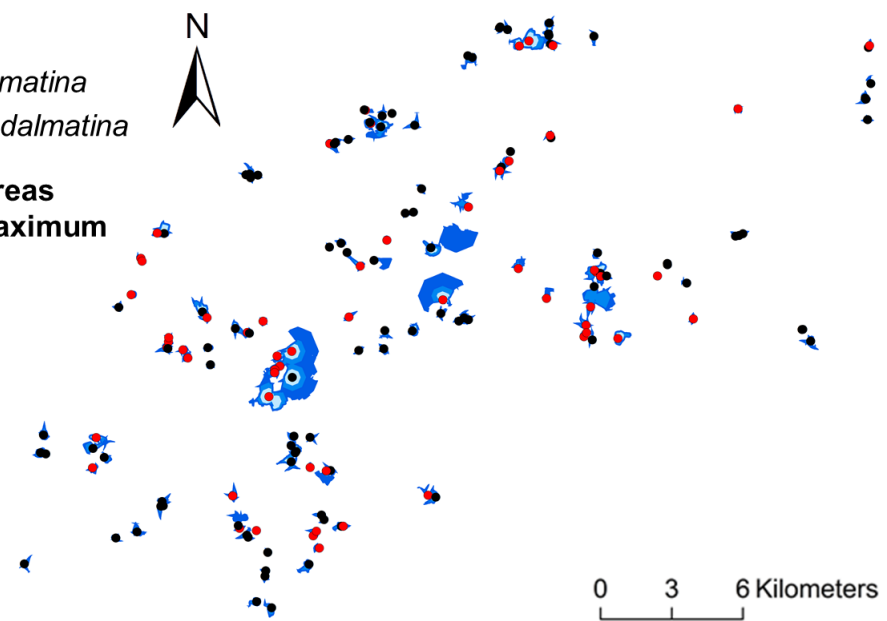
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b)

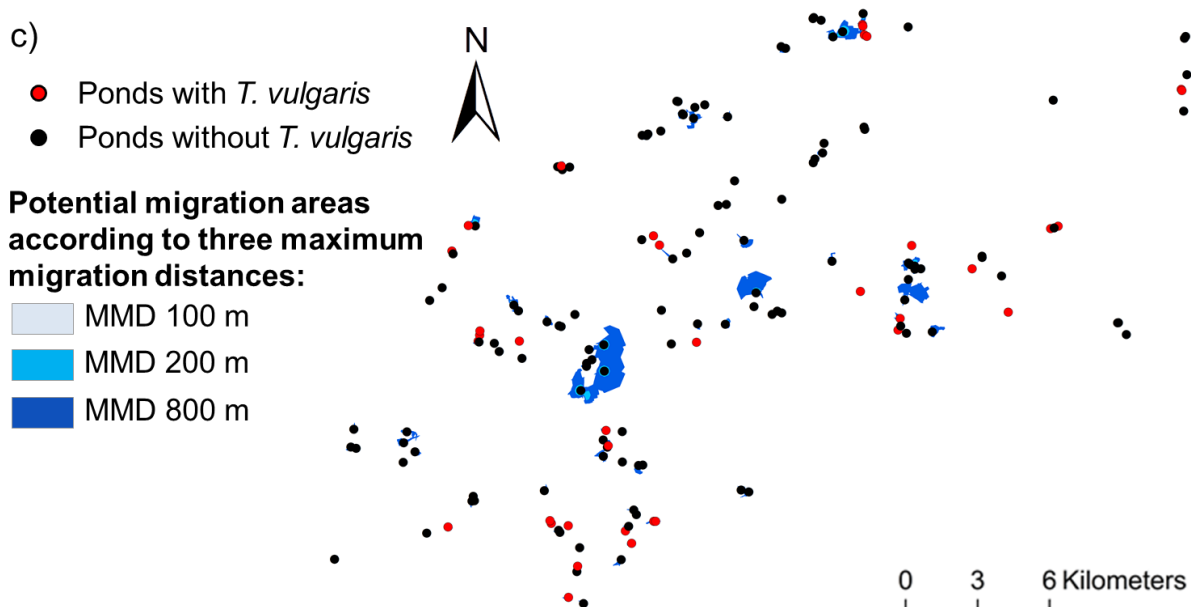
- Ponds with *R. dalmatina*
- Ponds without *R. dalmatina*

**Potential migration areas according to three maximum migration distances:**

- MMD 300 m
- MMD 500 m
- MMD 1000 m



877



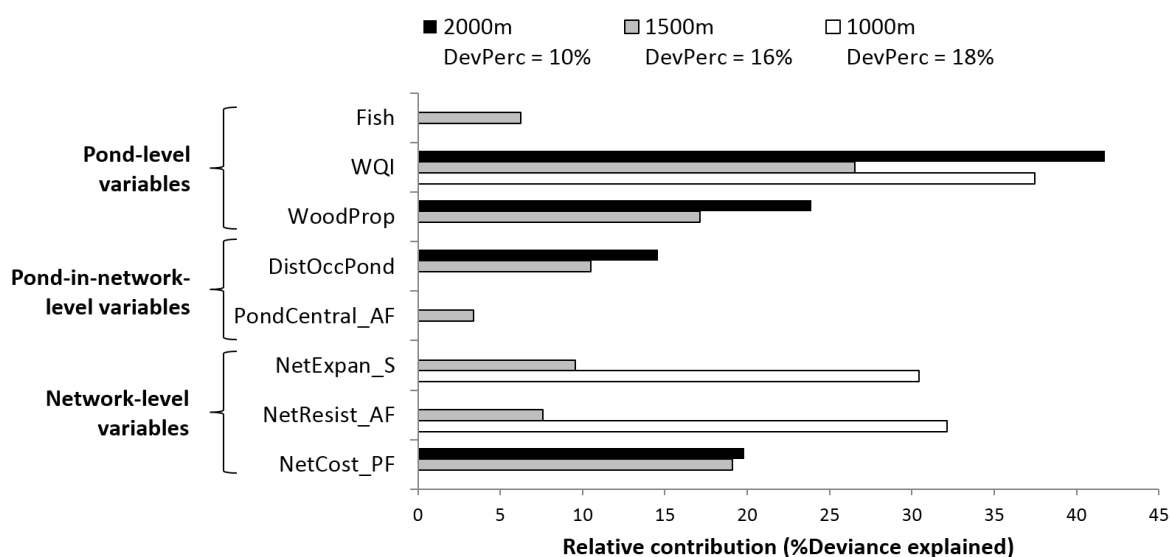
878

879 **Fig. 2** Potential migration areas (PMA) obtained from the resistance map analyses for the  
 880 three species according to their respective maximum migration distances (MMD): a) *Bufo*  
 881 *bufo*, b) *Rana dalmatina*, and c) *Triturus vulgaris*. Species distribution is represented by red  
 882 (presence) and black (absence) circles

883

884 **Figure 3**

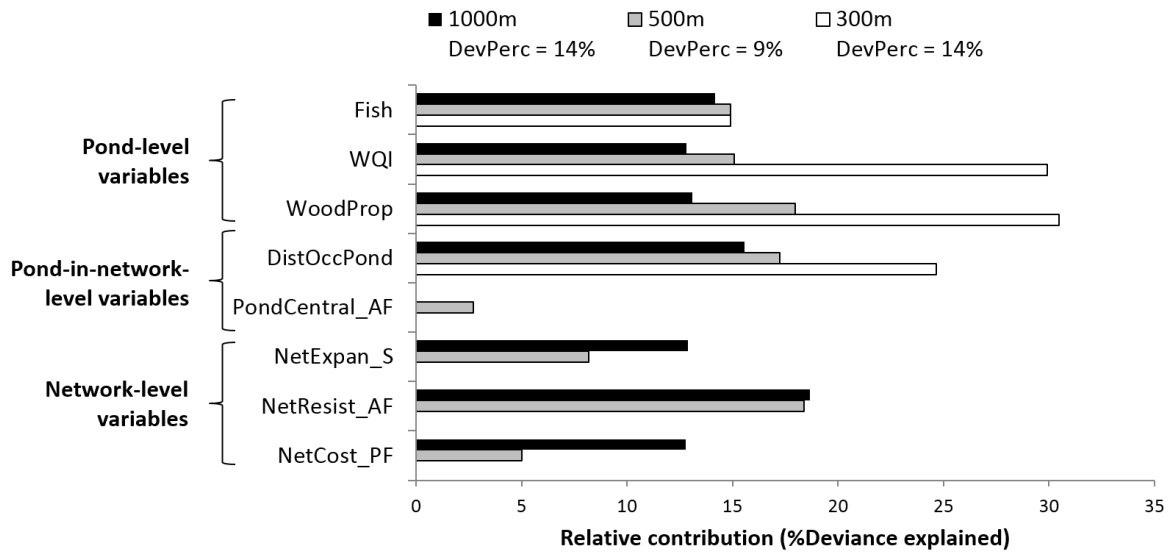
a) Relative influence of pond and network variables on *Bufo bufo*'s occurrence



885

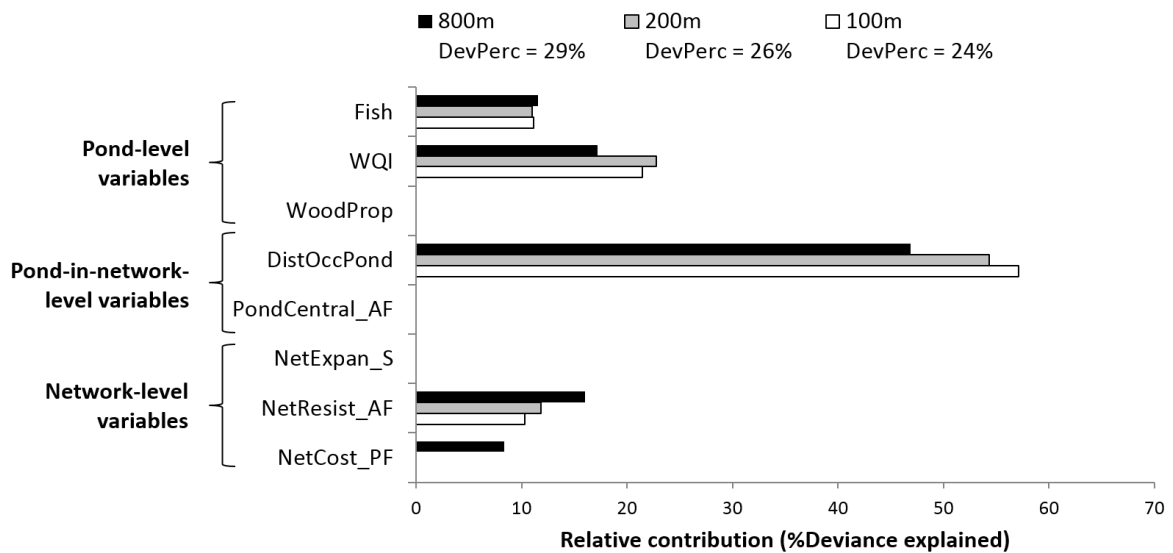


b) Relative influence of pond and network variables on *Rana dalmatina's* occurrence



886

c) Relative influence of pond and network variables on *Triturus vulgaris's* occurrence



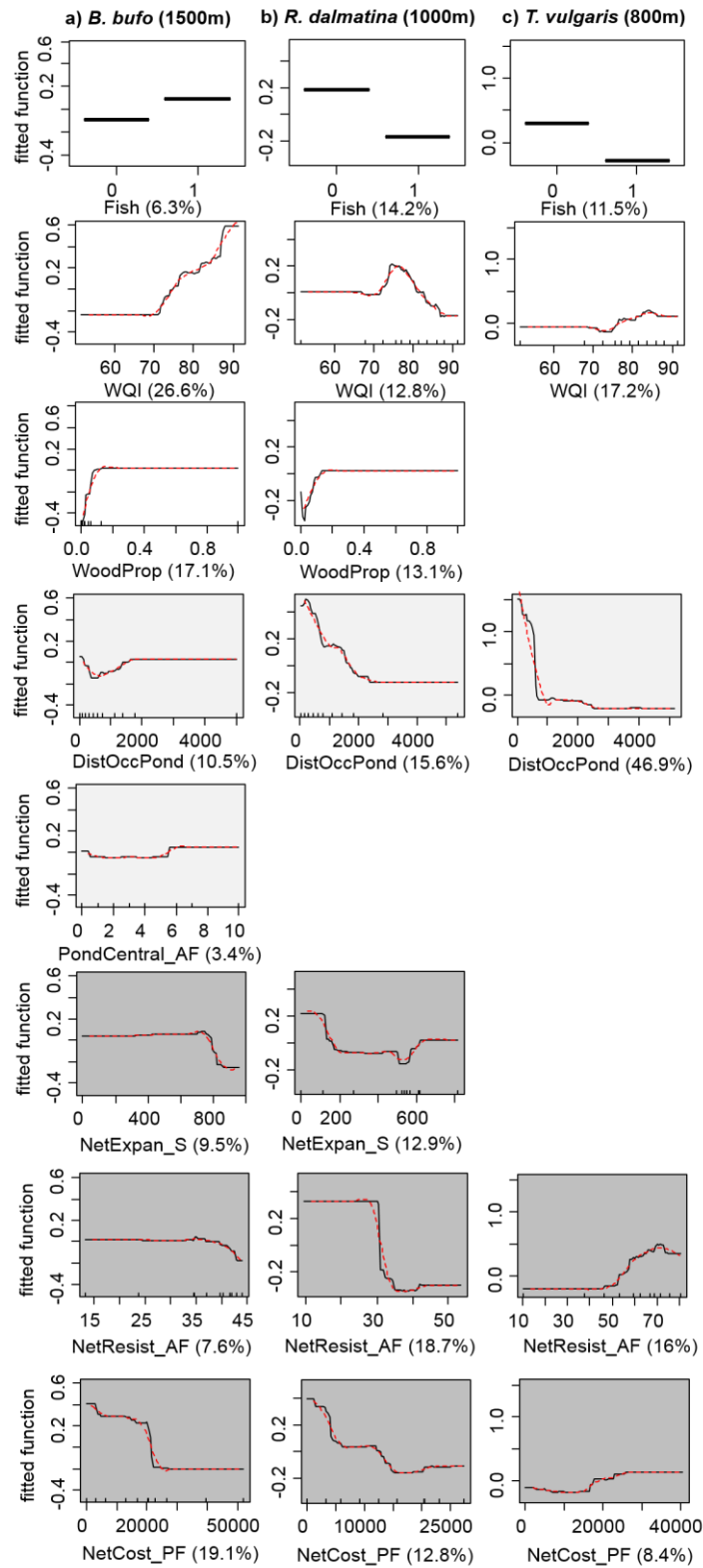
887

888 **Fig. 3** Ranking of local and network variables obtained from BRT analyses for the three  
 889 species and for each migration distance considered after model simplification. The variables  
 890 are coded according to the **Table 2**. DevPerc = the percentage of deviance explained by the  
 891 final BRT model

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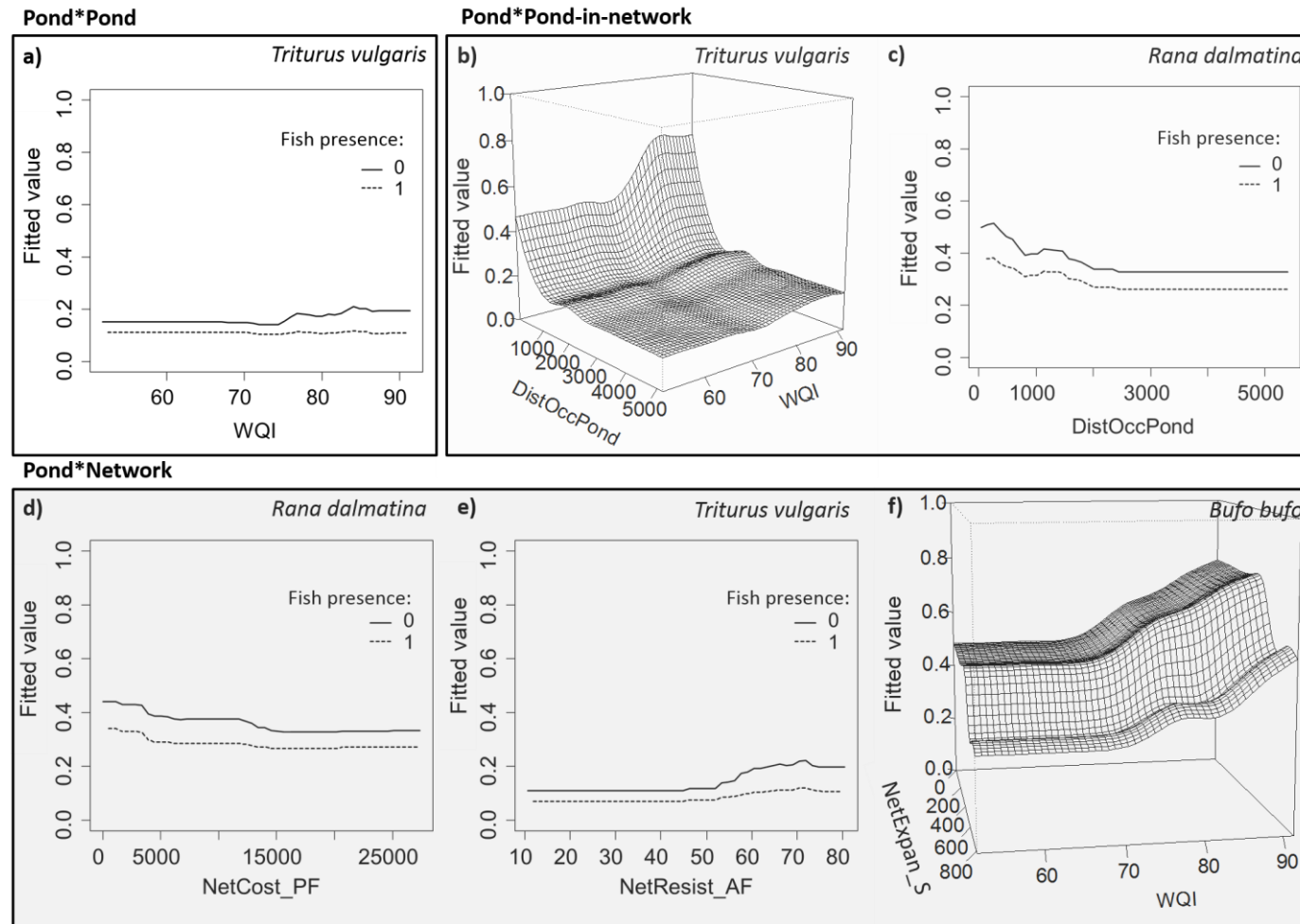
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897 **Fig. 4** Plots of the BRT-fitted relationships of species occurrence in response to pond-  
 898 (white), pond-in-network- (light grey), and network-level (dark grey) variables (described in  
 899 **Table 2**) for a) *Bufo bufo* in the 1500m-model, b) *Rana dalmatina* in the 1000m-model and c)  
 900 *Triturus vulgaris* in the 800m-model. Only the variables selected by the final BRT models are  
 901 shown. In parenthesis are the relative percentages of explained deviance



903

904 **Fig. 5** 3D-plots to illustrate the major interaction effects selected and estimated by BRT models of species occurrence, involving a) only pond  
 905 (P)-, b, c) pond and pond-in-network (PN)-, and d, e, f) pond and network-level (N) variables for *Triturus vulgaris* under MMDs of 100m (b),  
 906 200m (a), and 800m (e), *Rana dalmatina* under MMDs of 300m (c), and 1000m (d), and *Bufo bufo* under MMD of 1000m (f)

907 **SUPPORTING INFORMATION**

908 Jeliaskov A., Lorrillièr R., Besnard A., Garnier J., Silvestre M. and Chiron F. 2017. Cross-scale  
909 approach of structural and functional connectivity: new insights for amphibian conservation  
910 in agricultural landscape. *Journal of Applied Ecology* 000: 000-000.

911

912 Additional Supporting Information may be found in the online version of this article:

913

914 **Appendix S1** Typology of landscape databases used and resistance values assigned to  
915 features

916 **Table S1** Typology of Ecoline, Ecomos and MOS land-cover databases and resistance values  
917 assigned to each feature class

918

919 **Appendix S2** Additional information on landscape and statistical analyses

920

921 **Appendix S3** Protocol of GIS processing for building resistance maps

922 **Figure S3** Protocol of GIS treatments performed on landscape databases to build resistance  
923 maps

924

925 **Appendix S4** Supplementary Information on the hypotheses tested under structural and  
926 functional variables

927

928 **Appendix S5** Summary of the characteristics of the structural and functional networks built

929 **Table S5** Summary of the characteristics of the networks built under structural,  
930 unconstrained functional and constrained functional approaches of connectivity

931

932 **Appendix S6** Species response to pond- and network-level effects

933 **Figure S6** Supplementary plots of species response to pond- and network-level effects at  
934 different MMDs

935

936 **Appendix S7** Interactions effects of pond and network level variables on amphibian response

937 **Table S7** List of the most important interactions detected by BRT involved in the species  
938 response to pond-, pond-in-network-, and network-level variables

939

940 **APPENDIX S1**

941 **Table S1** Typology of the three databases Ecoline (IAU IDF 2012), Ecomos (IAU IDF 2005) and  
 942 MOS (IAU IDF 2008) used and the resistance values assigned to each feature class for the  
 943 three species *Bufo bufo*, *Rana dalmatina*, and *Triturus vulgaris* based on biological  
 944 hypothesis approach

Original feature code	Database	Feature class	Resistance values for:		
			<i>B. bufo</i>	<i>R. dalmatina</i>	<i>T. vulgaris</i>
171	Ecoline	Pond	1	1	1
172	Ecoline	Seasonal pond	1	1	1
173	Ecoline	Retention pond	1	1	1
512	Ecomos	Flowing permanent pool	1	1	1
3	MOS	Water	1	1	1
13	Ecoline	Group of trees (<500m <sup>2</sup> )	5	5	5
14	Ecoline	Group of shrubs (<500m <sup>2</sup> )	5	5	5
21	Ecoline	Small wood (500-650m <sup>2</sup> )	5	5	5
22	Ecoline	Wood (500-650m <sup>2</sup> )	5	5	5
31	Ecoline	Wood (5000-40000m <sup>2</sup> )	5	5	5
41	Ecoline	Continuous (>85%) arboreal riparian forest	5	5	5
44	Ecoline	Continuous (>85%) lignified and low riparian forest	5	5	5
51	Ecoline	Continuous (>85%) line of trees	5	5	5
54	Ecoline	Continuous (>85%) line of lignified and low trees	5	5	5
61	Ecoline	Road associated with a continuous (>85%) line of trees	5	5	5
62	Ecoline	Road significantly associated with old trees	5	5	5
71	Ecoline	Arboreal continuous (>85%) hedgerow	5	5	5
81	Ecoline	Continuous (>85%) hedgerow of lignified and low trees	5	5	5
101	Ecoline	Hedgerow designed for the small game of plains	5	5	5
102	Ecoline	Dense ornamental hedgerow	5	5	5
202	Ecoline	Abandoned area	5	5	5
221	Ecoline	Embankment continuously (>85%) planted with trees	5	5	5
231	Ecoline	Embankment continuously (>85%) planted with lignified and low trees	5	5	5
241	Ecoline	Embankment continuously (>85%) covered with spontaneous shrubs	5	5	5
311	Ecomos	Xero- to meso-phile deciduous trees	5	5	5
312	Ecomos	Conifers	5	5	5
313	Ecomos	Mixed mesophile forest	5	5	5
324	Ecomos	Multistrata vegetation associated with infrastructures	5	5	5
1	MOS	Wood or forest	5	5	5

11	Ecoline	Isolated tree	10	10	20
12	Ecoline	Isolated shrub	10	10	20
42	Ecoline	Discontinuous (33-85%) arboreal riparian forest	10	10	20
43	Ecoline	Sparse (<33%) arboreal riparian forest	10	10	20
45	Ecoline	Discontinuous (33-85%) line of lignified and low trees	10	10	20
46	Ecoline	Sparse (<33%) line of lignified and low trees	10	10	20
52	Ecoline	Discontinuous (33-85%) line of trees	10	10	20
53	Ecoline	Sparse (<33%) line of trees	10	10	20
55	Ecoline	Discontinuous (33-85%) line of lignified and low trees	10	10	20
56	Ecoline	Sparse (<33%) line of lignified and low trees	10	10	20
63	Ecoline	Road associated with a discontinuous (33-85%) line of trees	10	10	20
72	Ecoline	Arboreal discontinuous (33-85%) hedgerow	10	10	20
73	Ecoline	Arboreal sparse (<33%) hedgerow	10	10	20
82	Ecoline	Discontinuous (33-85%) hedgerow of lignified and low trees	10	10	20
83	Ecoline	Sparse (<33%) hedgerow of lignified and low trees	10	10	20
121	Ecoline	Type 1 herbaceous riparian strip (2.5-5m width)	10	10	20
122	Ecoline	Type 2 herbaceous riparian strip (>5m width)	10	10	20
132	Ecoline	Herbaceous path	10	10	20
134	Ecoline	Hidden path	10	10	20
181	Ecoline	Orchards	10	10	20
191	Ecoline	Natural meadow	10	10	20
201	Ecoline	Fallow land designed for wild fauna	10	10	20
211	Ecoline	Meadowy embankment	10	10	20
222	Ecoline	Embankment discontinuously (33-85%) planted with trees	10	10	20
223	Ecoline	Embankment sparsely (<33%) planted with trees	10	10	20
232	Ecoline	Embankment discontinuously (33-85%) planted with lignified and low trees	10	10	20
233	Ecoline	Embankment sparsely (<33%) planted with lignified and low trees	10	10	20
242	Ecoline	Embankment discontinuously (33-85%) covered with spontaneous shrubs	10	10	20
251	Ecoline	Park planted with isolated trees	10	10	20
231	Ecomos	Mesophile meadow	10	10	20
321	Ecomos	Calcareous grassland	10	10	20
411	Ecomos	Pond shore	10	10	20
111	Ecoline	Type 1 herbaceous strip (2.5-5m width)	20	20	30
112	Ecoline	Type 2 herbaceous strip (>5m width)	20	20	30

131	Ecoline	Path of bare soil	20	20	30
133	Ecoline	Path partially covered with grasses	20	20	30
243	Ecoline	Embankment sparsely (<33%) covered with spontaneous shrubs	20	20	30
332	Ecomos	Rocky or sandy outcrop	20	20	30
333	Ecomos	Sparse vegetation	20	20	30
151	Ecoline	Road (<25m width) or railroad	45	45	80
161	Ecoline	Ditch	45	45	80
2	MOS	Agricultural fields	45	45	80
4	MOS	Other agricultural areas	45	45	80
5	MOS	Urban open spaces	45	45	80
6	MOS	Single-family detached home	45	45	80
7	MOS	Multi-family residential	45	45	80
8	MOS	Activities	45	45	80
9	MOS	Infrastructure	100	100	100
10	MOS	Transports	100	100	100
11	MOS	Construction site	100	100	100

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945

946

947

948 **APPENDIX S2**

949 **Additional information regarding choice of grain size and statistical analyses**

950

951 **a) Choice of grain size**

952 The grain size used for connectivity analyses is known to have important effect on the results  
953 when inappropriately chosen (Baguette & Van Dyck 2007; Galpern & Manseau 2013). In our  
954 case, the grain of 3\*3m was a good compromise between the species potential perception  
955 abilities (Rothermel 2004) and the high precision level (both in spatial and thematic  
956 resolutions) provided by the landscape database Ecoline, allowing the conservation of a  
957 maximum of valuable information.

958

959 **b) Statistical analyses - Check of multi-collinearity**

960 We checked for multi-collinearity within our set of explanatory variables by a Variance  
961 Inflation Factor analysis (VIF, package {AED} in R (Zuur, Ieno & Elphick 2010)). According to  
962 Zuur et al. (2009), multi-collinearity is considered as acceptable if the VIFs remained below  
963 the threshold value of 5. Variables which generated collinearity exceeding this threshold  
964 were removed from the analyses.

965 The structural and the functional variables of Degree Centrality (i.e. *CD\_S*, *CD\_UF*, and  
966 *CD\_CF*) measuring the connectivity of focal ponds in respect with the surrounding ponds in  
967 the networks, were highly redundant for all the models with high Variance Inflation Factor  
968 and correlation coefficient ( $>> 5$ ;  $> 0.50$ , respectively). In order to keep models comparable  
969 to each other across all species and migration distances and scales while solving the problem  
970 of collinearity, we kept the constrained functional Degree Centrality variable (i.e. *CD\_UF*) in  
971 the model and excluded the two others. The reasons for choosing *CD\_UF* are that: i) in  
972 contrast to structural and constrained functional approaches, unconstrained functional  
973 approach did not imply any directional assumption in amphibian movement (i.e. assumes  
974 isotropy), thus it was less spatially restrictive and implied that the organisms could move in  
975 any direction around the pond, and ii) the information of pond-in-network and network  
976 connectivity were less redundant with each other when based on the unconstrained  
977 functional approach than when based on the two others (as also expected after (Etherington  
978 & Holland 2013)).

979 In addition, interestingly, the structural and the constrained functional measures of network  
980 connectivity, i.e. *DistMoyNet* and *MeanNetCost*, revealed to be strongly correlated (from  
981 0.40 up to 0.70, depending on the species and the MMD). However these measures were  
982 not collinear according to the VIF analysis which allowed us to include both of them in the  
983 model.

984 The correlation between the structural and the least cost path-based measures of  
985 connectivity may be due to the fact that the surrounding landscape may be so homogeneous  
986 with intermediary resistance that the shortest route is in most cases the least cost one.  
987 While these both connectivity measures might constitute strict dispersal routes, the  
988 unconstrained functional measure (*MeanResistMoy*) might include the effect of migration  
989 and habitat and resource availability and favourability.

990



991 **c) Statistical analyses - Boosted Regression Tree analysis**

992 To analyse relative effects of pond, pond-in-network, and network level variables, as well as  
993 their interactions on the species distribution, we used the Boosted Regression Trees (BRT)  
994 method (De'ath 2007; Elith, Leathwick & Hastie 2008) (package {dismo} in R (Hijmans *et al.*  
995 2016)). This method is an advanced form of regression (Friedman, Hastie & Tibshirani 2000),  
996 and consists in optimizing prediction of a pattern by iteratively fitting and combining many  
997 regression trees instead of a single one. BRT method has particular interests in the case of  
998 complex datasets, non-parametrical (supported by machine learning method) and multiple  
999 interaction tests, and in handling outliers and non-linear relationships (Elith, Leathwick &  
1000 Hastie 2008). We modelled residual distribution using logit link function (binary response  
1001 variable presence/absence). In order to get a reasonable number of trees (> 1000) (see Elith,  
1002 Leathwick & Hastie 2008), we used a bag fraction of 0.5, and a learning rate of 0.001 for all  
1003 models.

1004

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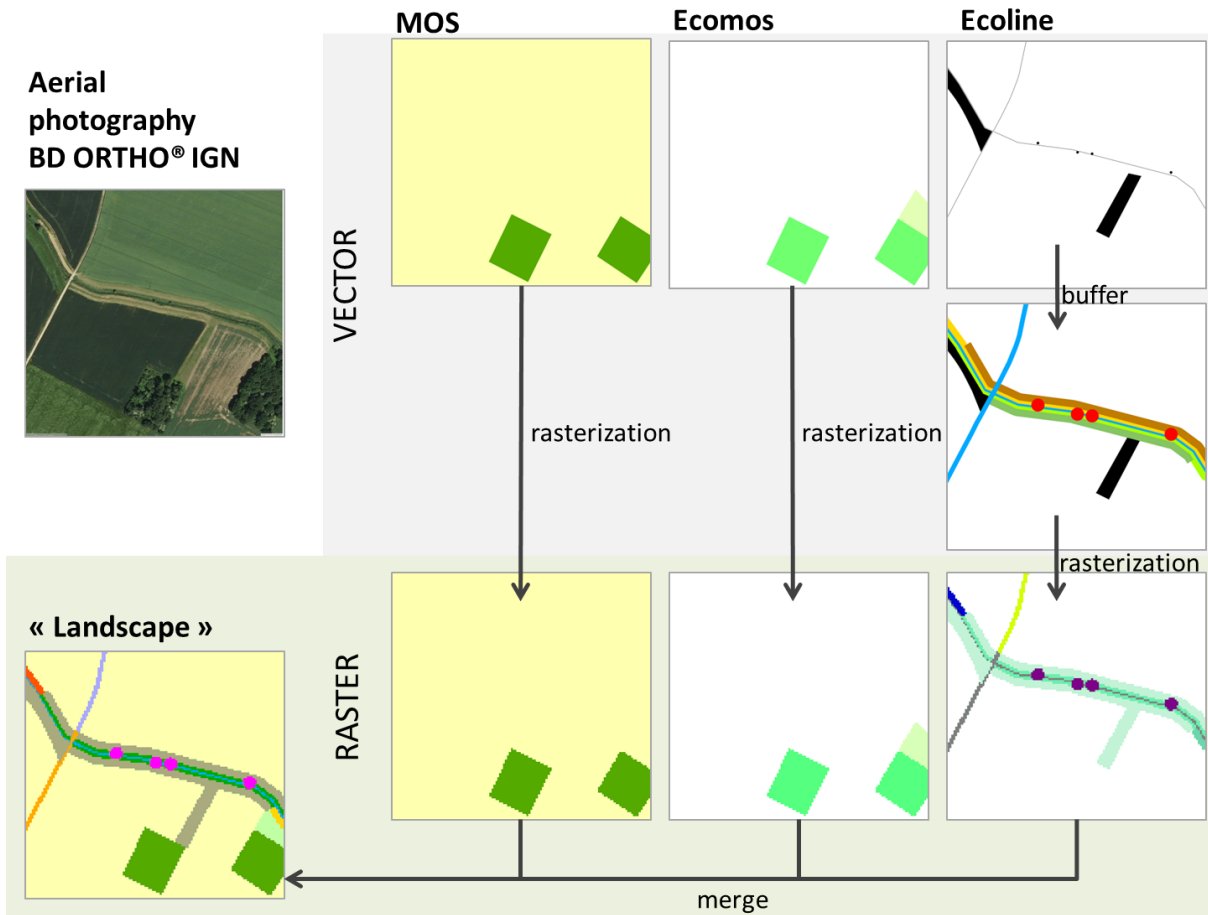
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1035 *extensions in ecology with R*. Springer, New York, New York, USA.

1036 **APPENDIX S3**

1037 **Figure S3** Protocol of GIS treatments achieved on landscape databases MOS, Ecomos and  
 1038 Ecoline a) to generate a complete and high resolution landscape map and b) to build friction  
 1039 maps. A cost back raster defines in which direction (i.e. to which neighbour pixel)  
 1040 from each pixel to follow the least cost path back to the pond

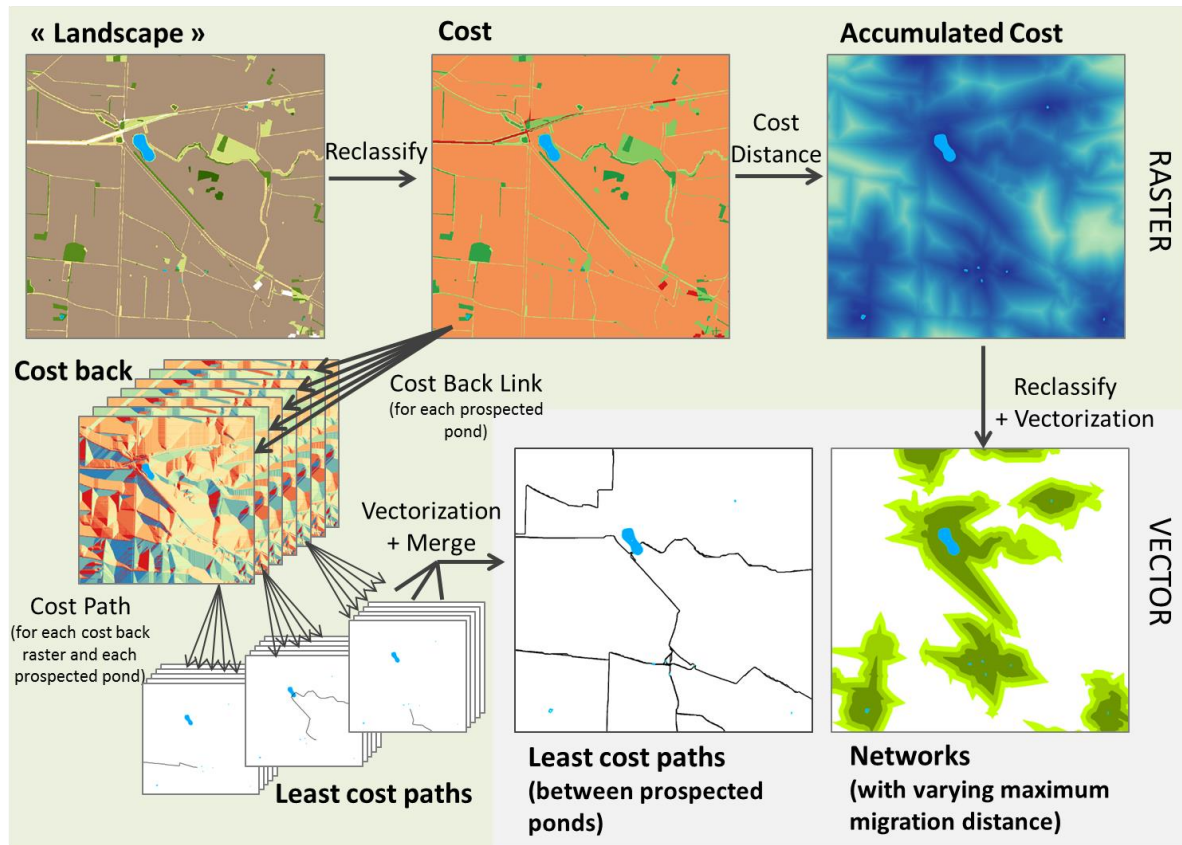
1041

1042 a)



1043

1044 b)



1045

1046

1047 **APPENDIX S4**

1048 **Supplementary Information on the hypotheses tested through the choice of structural and**  
1049 **functional variables**

1050

1051 **Hypothesis 1: The functional measures of connectivity are more efficient than the**  
1052 **structural one in explaining species distribution**

1053 We expected functional approaches to be substantially more efficient than the structural  
1054 approach in explaining species distribution because the formers take into account species  
1055 ecological traits, and their potential perception of the landscape. Moreover, the  
1056 accumulated cost measures are supposed to be more realistic and efficient for measuring  
1057 habitat connectivity because they take into account both the distance and the cost  
1058 associated to animal movement whereas the least-cost path length is often highly correlated  
1059 with Euclidean distances (Etherington & Holland 2013). Therefore the constrained functional  
1060 approach based on accumulated costs was expected to be more relevant than the  
1061 unconstrained one. Note however that constrained networks can in some cases appear  
1062 spatially less limited than unconstrained functional ones in terms of *potential migration*  
1063 *space*.

1064

1065 *Positive effect of the pond connectivity within the networks*

1066 In particular, we expected a positive effect on species occurrence of the pond connection to  
1067 any network, especially in the case of functional networks. As a corollary, species occurrence  
1068 probability would decrease with the increase of the distance to the nearest pond occupied  
1069 by the focal species (*Distance to the nearest occupied pond*) acting as a potential source of  
1070 individuals. The more there are ponds connected to the focal pond (*Degree Centrality*), the  
1071 more likely this pond would be occupied by species, such central pond being essential for  
1072 the whole network connectivity and the species persistence (Urban & Keitt 2001). Note that  
1073 degree centrality considers all potential breeding sites instead of only occupied ones, thus it  
1074 simply aims at predicting species occupancy, whereas the distance to the nearest occupied  
1075 pond considers only occupied patches, which can relate to potential colonization events  
1076 (Moilanen & Nieminen 2002).

1077

1078 *Negative effect of the network spatial expansion and resistance*

1079 For an equivalent number of ponds, we expected a negative influence of the network spatial  
1080 expansion (*Mean within-network inter-pond Euclidean distances*) on amphibian occurrence  
1081 probability due to the increase of dispersal limitations with the increase of inter-pond  
1082 distances. However, based on a presumed better efficiency of the functional approach, we  
1083 hypothesized that the effect of the network resistance (*Mean network resistance*) would  
1084 dominate, though in a lesser extent if the displacement cost had accumulated through the  
1085 network (*Mean within-network accumulated cost along inter-pond least cost paths*).

1086

1087 **Hypothesis 2: Amphibian responses to connectivity are scale-dependent and subject to**  
1088 **cross-scale interactions**

1089 *Scale-dependency and effect ranking*

1090 Influences originating from three levels would be considered: the pond, the pond within and  
1091 towards its network, and the network. We suspected that species responses were scale-  
1092 dependent, and in particular, that network-level effects combined to pond-level effects  
1093 could play a major role in species distribution. We thus ranked pond-level, pond-in-network-  
1094 level and network-level effects. We also expected our results to be sensitive to the relative  
1095 scales chosen (i.e. migration distance) (Turner *et al.* 1989; Wu & Li 2006).

1096

1097 *Cross-scale interactions*

1098 The idea of cross-scale interactions comes as a corollary of the hierarchy theory (Allen &  
1099 Starr 1982) according to which a relationship at one given level can be constrained by the  
1100 characteristics of the upper level and can get new properties emerging from the  
1101 combination of characteristics from the lower level (O'Neill, Johnson & King 1989). Processes  
1102 operating at different scales can interact with each other and generate some particular  
1103 biological pattern at a given scale (Lawler & Edwards Jr 2006).

1104

1105 Therefore we expected the influences from pond-, pond-in-network- and network-level  
1106 could either match, or amplify, or suppress each other. We thus tested potential interactions  
1107 between variables from these different levels in order to detect antagonistic or facilitative  
1108 effects across levels. Because we already showed the importance of the local conditions on  
1109 species occurrence (i.e. fish presence, water quality and neighbouring proportion of  
1110 woodland cover, Jeliaskov *et al.*, 2013), we here focused on the relative effects of network  
1111 characteristics in addition to, and in interaction with, local conditions.

1112

1113 The importance of local conditions could indeed limit the positive effect of connectivity: a  
1114 pond with bad local conditions, even if well connected, will not allow the species to settle  
1115 (Joly, Morand & Cohas 2003). Thus, the effect of connectivity would be most often  
1116 dominated by local variables, and a high interaction between local and network variables.

1117 In addition, we assumed that i) the pond connectivity (i.e. *Degree Centrality*) would directly  
1118 interact with the other network variables, and ii) the structural and functional connectivity  
1119 variables would interact with each other. Indeed, for instance the spatial expansion of the  
1120 network could have a positive effect in the case of low network resistance because this  
1121 would offer a higher number of available AND reachable ponds, but this effect could turn up  
1122 negative if the resistance was too high. Thus, all the possible interactions were integrated  
1123 and tested in the analyses.

1124

1125 **Hypothesis 3: Non-linearities and threshold effects occur in amphibian response to local**  
1126 **conditions and connectivity**

1127 Interaction effects can introduce non-linearities (Rastetter *et al.* 1992; Peters *et al.* 2004) in  
1128 the species response to environment. In particular, we expect thresholds in the species  
1129 responses to some network variables, notably because in a fragmented landscape where  
1130 suitable habitats are initially scarce, the positive effects of the connectivity metrics may be

1131 detected only for high values of habitat availability or accessibility (Metzger & Décamps  
1132 1997). The existence of such threshold values for the habitat connectivity is consistent with  
1133 the principle of percolation theory (Stauffer & Aharony 1992) according to which critical  
1134 connectivity thresholds depend on the abundance and arrangement of favourable patches  
1135 and on the displacement abilities of the species.

1136

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1166

1167

1168 **APPENDIX S5**

1169 **Table S5** Summary of the main characteristics of the networks obtained from the structural, unconstrained functional and constrained  
1170 functional approaches of connectivity, for the three species *Bufo bufo* (bufbuf), *Rana dalmatina* (randal) and *Triturus vulgaris* (trivul), and  
1171 according to the set of maximum migration distances (MMD) used for networks construction. Prevalence is the ratio of occupied elements on  
1172 the total number of elements



Network type	Species	MaxDist	Nb of networks (> 1 pond)	Nb of occupied networks	Nb of isolated ponds	Nb of occupied isolated ponds	Average network size (average nb of ponds) [max]	Species prevalence in isolated ponds	Species prevalence in networks	Species prevalence in networks averaged over MMD
<b>STRUCTURAL NETWORKS (S)</b>										
bufbuf	1000	32	27	11	8	6 [13]	0.73	0.84	0.89	
	1500	21	19	6	4	10 [21]	0.67	0.9		
	2000	13	12	2	2	26 [50]	1	0.92		
randal	300	35	20	74	28	2 [5]	0.38	0.57	0.62	
	500	37	22	49	20	3 [7]	0.41	0.59		
	1000	32	22	11	7	6 [13]	0.64	0.69		
trivul	100	17	5	125	28	1 [3]	0.22	0.29	0.4	
	200	31	13	91	16	2 [4]	0.18	0.42		
	800	33	16	20	3	5 [12]	0.15	0.48		
<b>AREA-FUNCTIONAL NETWORKS (UF)</b>										
bufbuf	1000	37	24	50	25	3 [11]	0.5	0.65	0.76	
	1500	34	24	33	16	5 [12]	0.48	0.71		
	2000	24	22	18	9	9 [21]	0.5	0.92		
randal	300	26	14	101	38	2 [4]	0.38	0.54	0.57	
	500	37	22	70	25	2 [6]	0.36	0.59		
	1000	37	22	50	17	3 [11]	0.34	0.59		
trivul	100	8	4	143	31	1 [3]	0.22	0.5	0.43	
	200	10	4	138	31	1 [3]	0.22	0.4		
	800	37	14	70	16	2 [7]	0.23	0.38		
<b>PATH-FUNCTIONAL NETWORKS (CF)</b>										
bufbuf	1000	34	27	22	13	5 [12]	0.59	0.79	0.86	
	1500	29	24	11	9	7 [12]	0.82	0.83		
	2000	19	18	6	5	11 [19]	0.83	0.95		
randal	300	36	21	77	29	2 [5]	0.38	0.58	0.6	
	500	39	22	58	23	2 [5]	0.4	0.56		
	1000	34	22	22	11	5 [12]	0.5	0.65		
trivul	100	18	6	122	27	1 [3]	0.22	0.33	0.39	
	200	29	12	94	17	2 [5]	0.18	0.41		
	800	34	15	40	6	3 [7]	0.15	0.44		

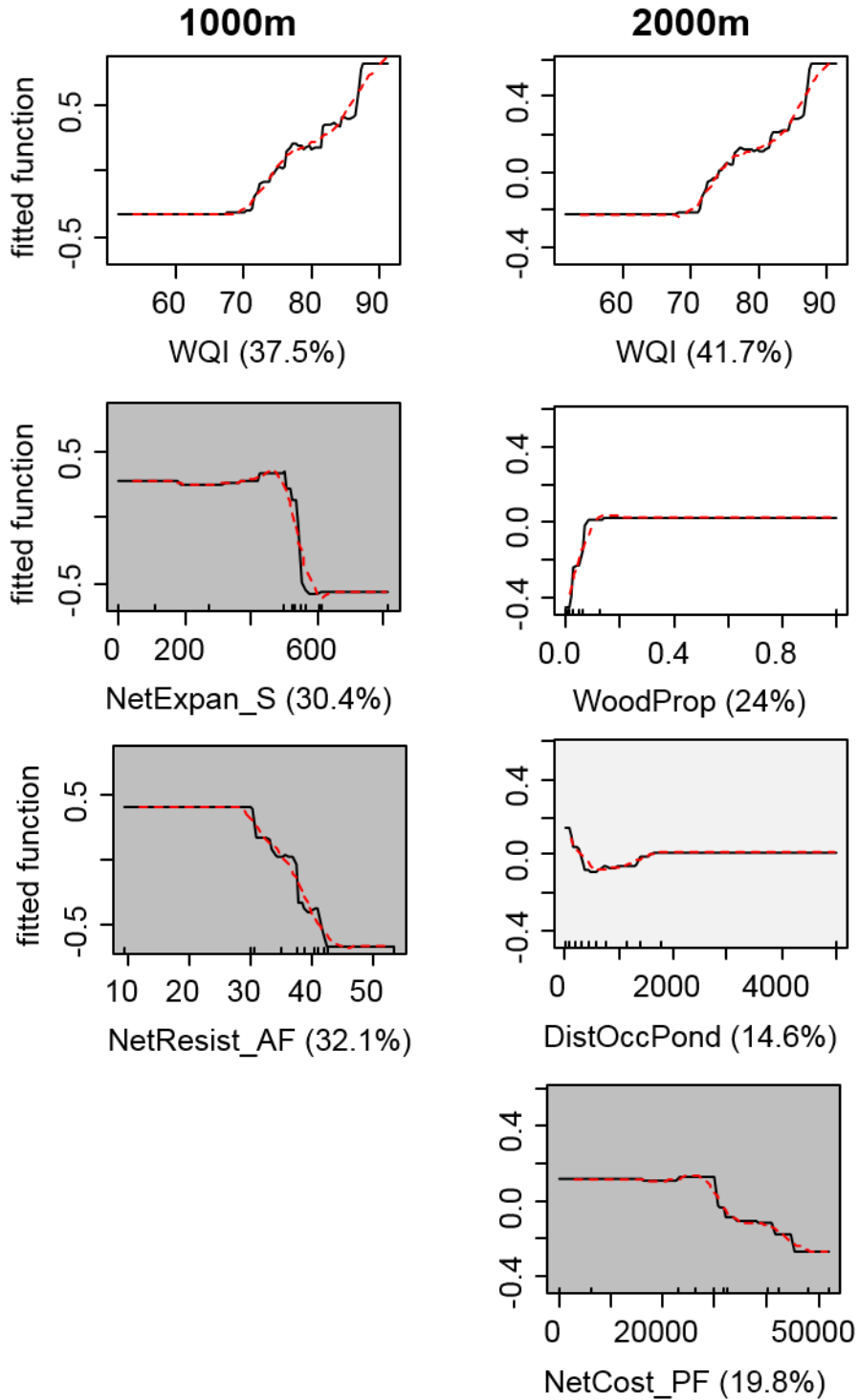
1173

1174 APPENDIX S6

1175 **Figure S6** Supplementary plots of the BRT-fitted function of species occurrence in response  
1176 to pond- (white), network- (light grey) and pond-in-network-level (dark grey) variables for  
1177 the three species *Bufo bufo*, *Rana dalmatina* and *Triturus vulgaris*, for the sets of distances  
1178 1000m/2000m, 300m/500m, and 100m/200m, respectively

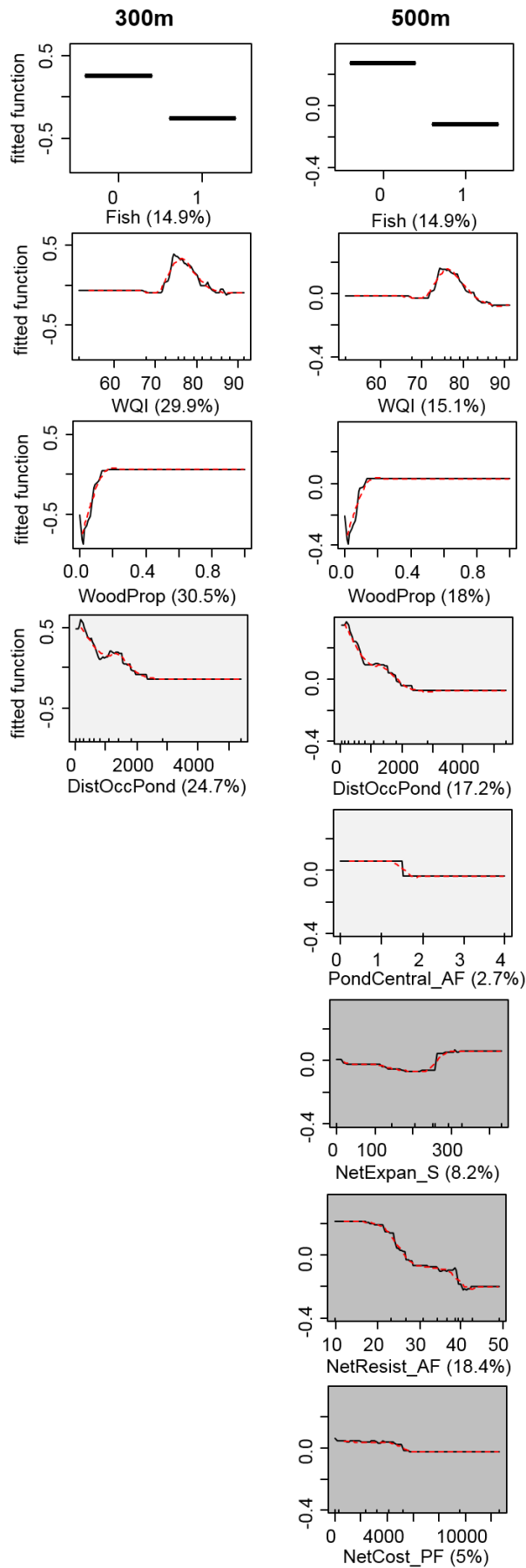
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a) *B. bufo*

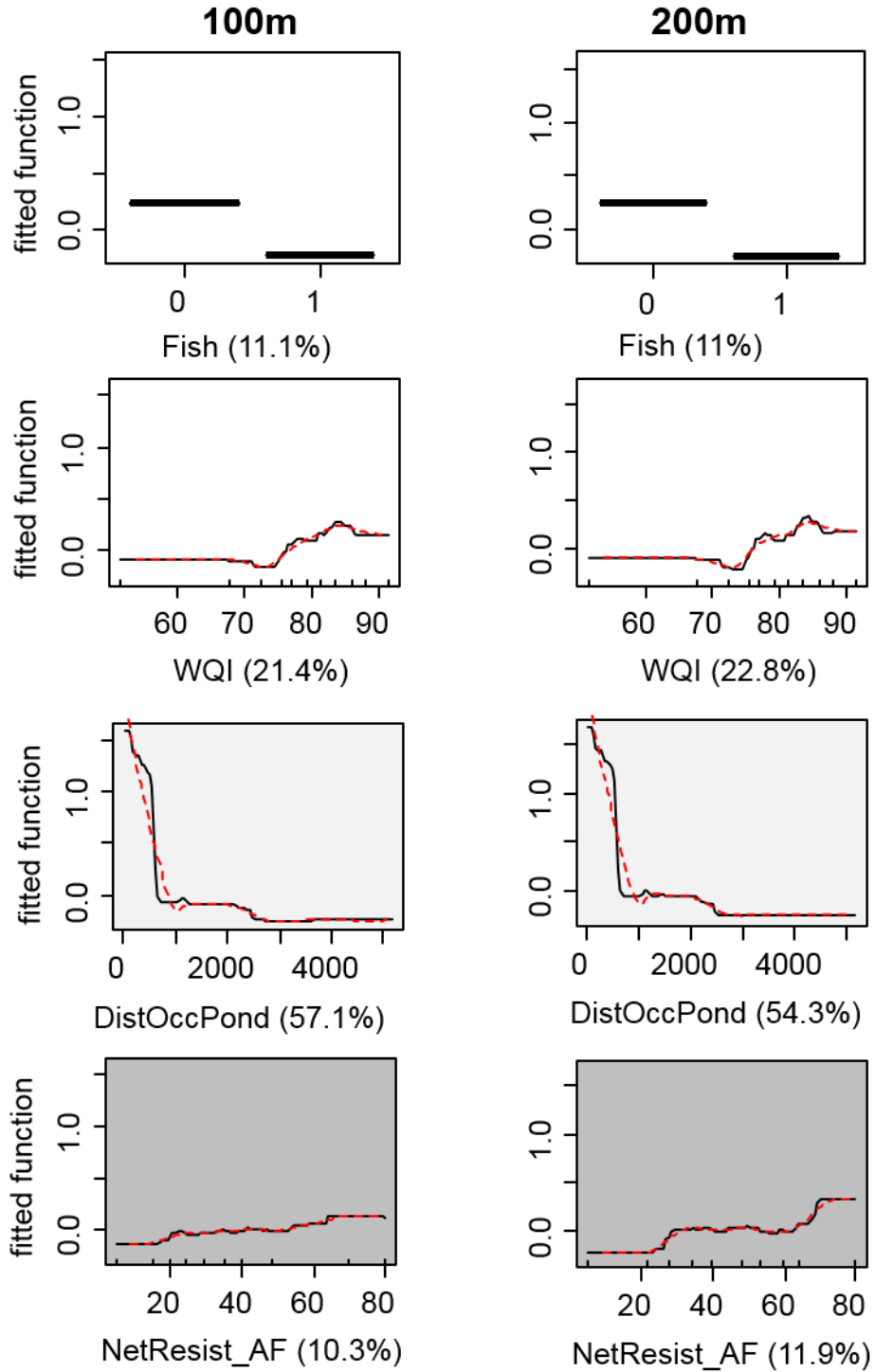


1180

b) *R. dalmatina*



c) *T. vulgaris*



1182

1183

1184

1185

1186 **APPENDIX S7**

1187 **Table S7** Full list (a) and summary (b) of the most important interactions detected by BRT  
 1188 procedure modelling species occurrence in response to pond- (P), pond-in-network- (PN) and  
 1189 network-level (N) variables; for *Bufo bufo* under MMDs of 1000, 1500, and 2000m, *Rana*  
 1190 *dalmatina* under MMDs of 300, 500, and 1000m, and *Triturus vulgaris* under MMDs of 100,  
 1191 200, and 800m

1192 a)

<b>Model</b>	<b>Predictor 1</b>	<b>Predictor 2</b>	<b>Interaction size</b>	<b>Type of cross-scale interaction</b>
Buf1000	NetExpan_S	WQI	1.9	P * N
	NetResist_AF	WQI	0.61	P * N
Buf1500	NetCost_PF	DistOccPond	0.38	PN * N
	NetCost_PF	WQI	0.36	P * N
	NetCost_PF	WoodProp	0.13	P * N
Buf2000	WoodProp	WQI	0.27	P * P
	NetCost_PF	WQI	0.24	P * N
Ran300	DistOccPond	Fish	1.13	P * PN
	WoodProp	WQI	0.91	P * P
Ran500	NetExpan_S	Fish	0.27	P * N
	DistOccPond	Fish	0.17	P * PN
	NetResist_AF	DistOccPond	0.12	PN * N
Ran1000	NetCost_PF	Fish	0.86	P * N
	NetResist_AF	NetExpan_S	0.32	N * N
Tri100	DistOccPond	WQI	5.41	P * PN
	WQI	Fish	4.92	P * P
Tri200	DistOccPond	WQI	6.8	P * PN
	WQI	Fish	5.35	P * P
Tri800	DistOccPond	WQI	5.31	P * PN
	WQI	Fish	3.72	P * N

1193

1194 b)

<b>Type of cross-scale interaction</b>	<b>Number</b>	<b>Proportion</b>
P * N	8	40
P * PN	5	25
P * P	4	20
PN * N	2	10

N * N	1	5
Tot	20	100

1195

1196

1197