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TITLE

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

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ABSTRACT

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

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

KEYWORDS

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

INTRODUCTION

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

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

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

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

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

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

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

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

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

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.

172

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)).

Definition of structural and functional networks

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

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

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

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

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

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

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

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

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

- 1) The *structural* approach (S) refers to pond “potential” connectivity (Calabrese & Fagan 2004) and was based on inter-pond Euclidean distances in the limit of the MMD (**Fig. 1a**).
- 2) The *area-functional* approach (AF) was based on the merging of the potential migration areas (PMA) around ponds resulting from the mapping of the landscape resistance (**Fig. 1b**). PMAs are proxies of habitat connectivity for migration between ponds by adult individuals (Ray, Lehmann & Joly 2002), and/or for dispersal and also reflect habitat quality around ponds including potential sources of resources (e.g. Janin, Léna & Joly 2011).
- 3) The *path-functional* approach (PF) consisted in considering the physiological constraint of cost accumulating along the least-cost paths which linked the ponds to each other among all the possible distances in the limit of MMD (**Fig. 1c**). In this case, a dispersing animal accumulates costs along its displacement in relation to potential biological risks encountered over the distance travelled in the limit of the MMD (e.g. Bartelt, Klaver & Porter 2010). The path-functional networks can in some cases appear less limited than the area-functional ones in terms of the number of connected ponds but implies linear directional inter-pond movement (**Fig 1**). Because the accumulated cost measures are shown to be more realistic than the least-cost path measures for assessing habitat connectivity (Etherington & Holland 2013), the path-functional measure of network connectivity was expected to better explain the species distribution than the structural measure and to be complementary with the area-functional one.

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

Statistical analyses

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

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

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

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

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

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

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

RESULTS

Species distribution and network description

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

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

Overall, all 3 connectivity measures had an influence on species occurrence. However, the functional measures of network connectivity better explained species occurrence than the structural one (network expansion, *NetExpan_S*). The mean resistance within area-functional network (*NetResist_AF*) better explained *Rana dalmatina*'s and *Triturus vulgaris*' occurrences whereas the mean accumulated cost within path-functional network better explained *Bufo bufo*'s occurrence (*NetCost_PF*) (**Fig. 3a**).

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

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

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

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

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

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

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

DISCUSSION

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

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

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

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

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

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

Additive effects of pond and network variables across spatial scales

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

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

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

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

Interaction effects of pond and network variables across spatial scales

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

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

Methodological insights and challenges for a cross-scale expertise of ecological connectivity

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

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

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

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

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

CONCLUSION

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

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

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

AUTHOR'S CONTRIBUTIONS

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

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DATA ACCESSIBILITY

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

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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.

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

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

FIGURES

Figure 1

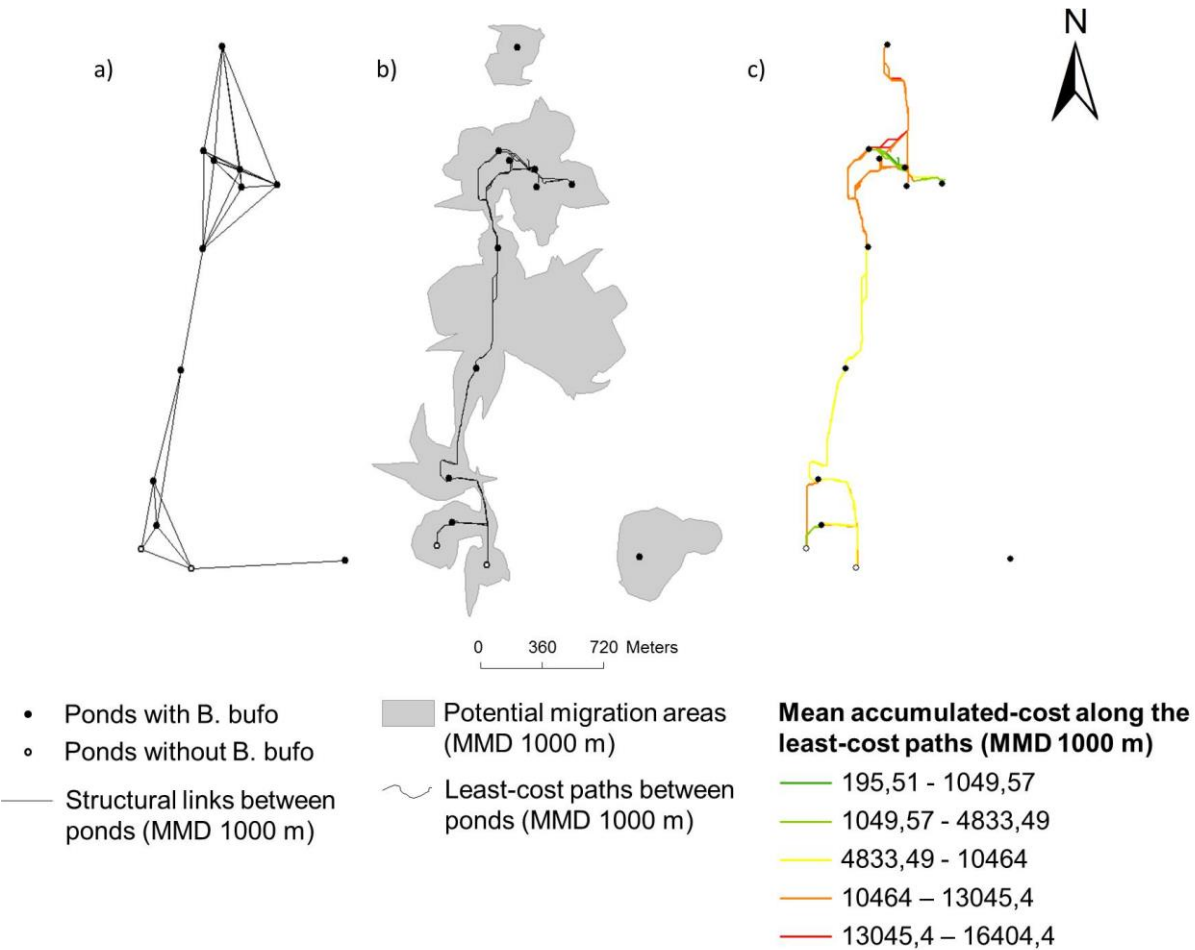
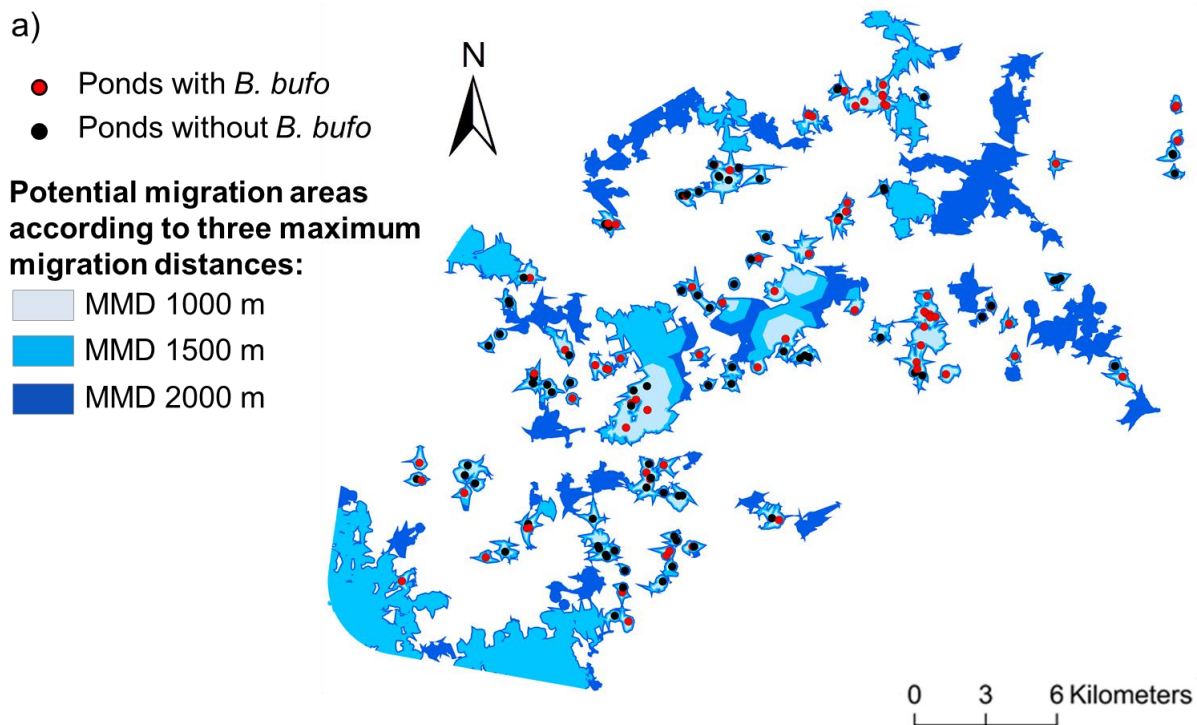
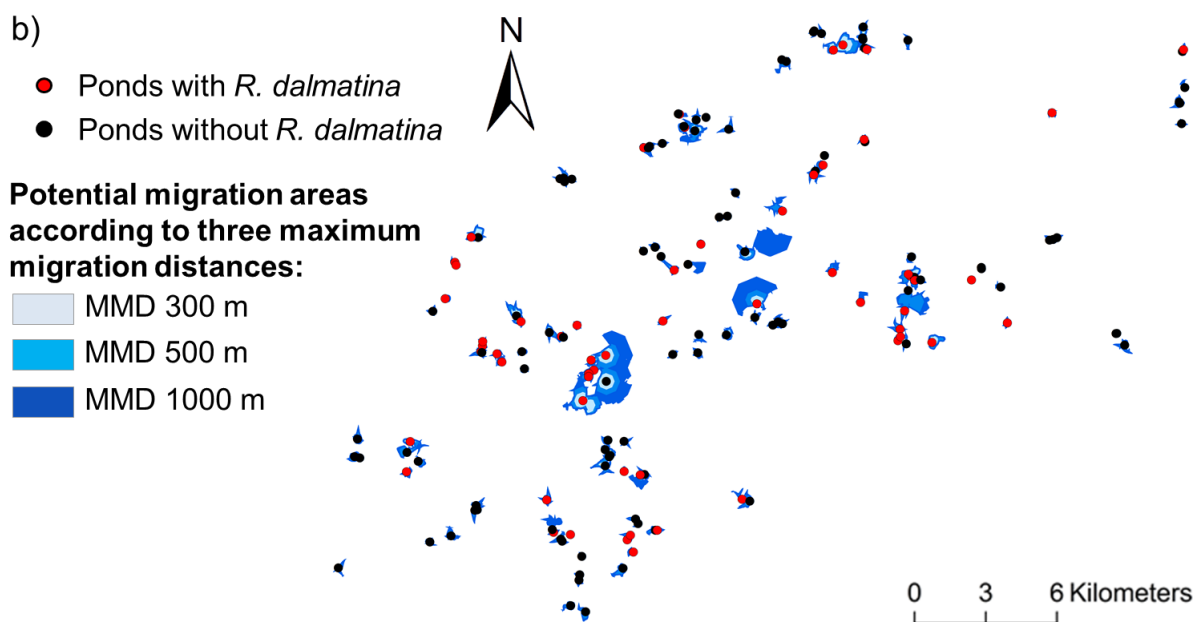


Fig. 1 Example of a pond network under the three different connectivity approaches: a) structural (Euclidean distance), b) area-functional (PMA and least-cost paths within PMA), c) path-functional (mean-accumulated-cost along least-cost paths) here for *Bufo bufo*, and a MMD of 1000m. Mean accumulated-cost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

875 **Figure 2**



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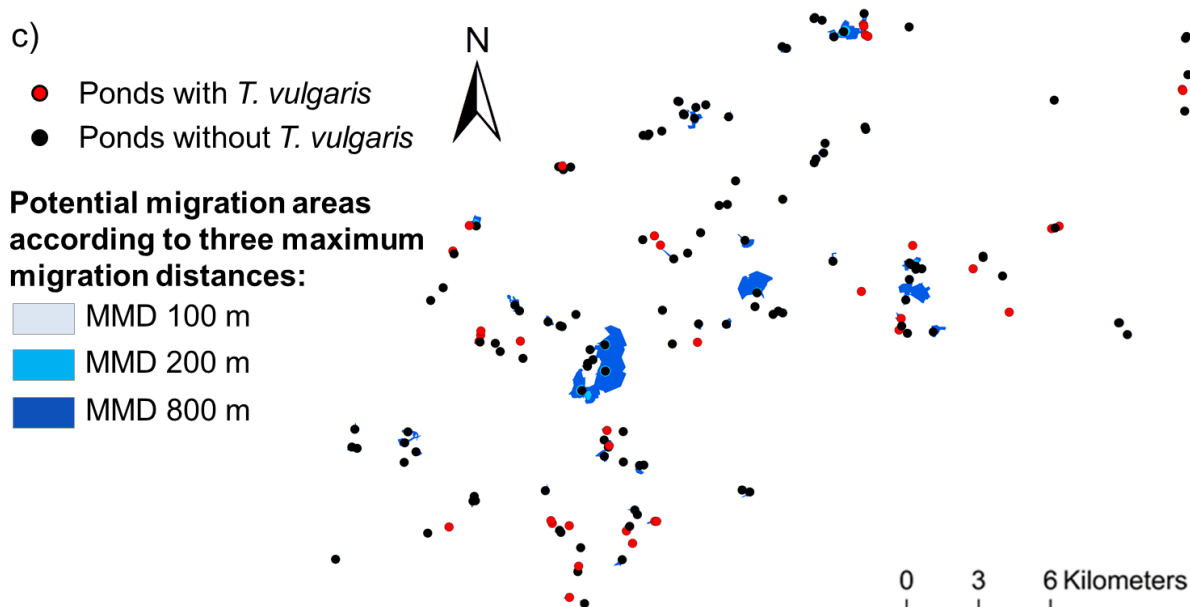
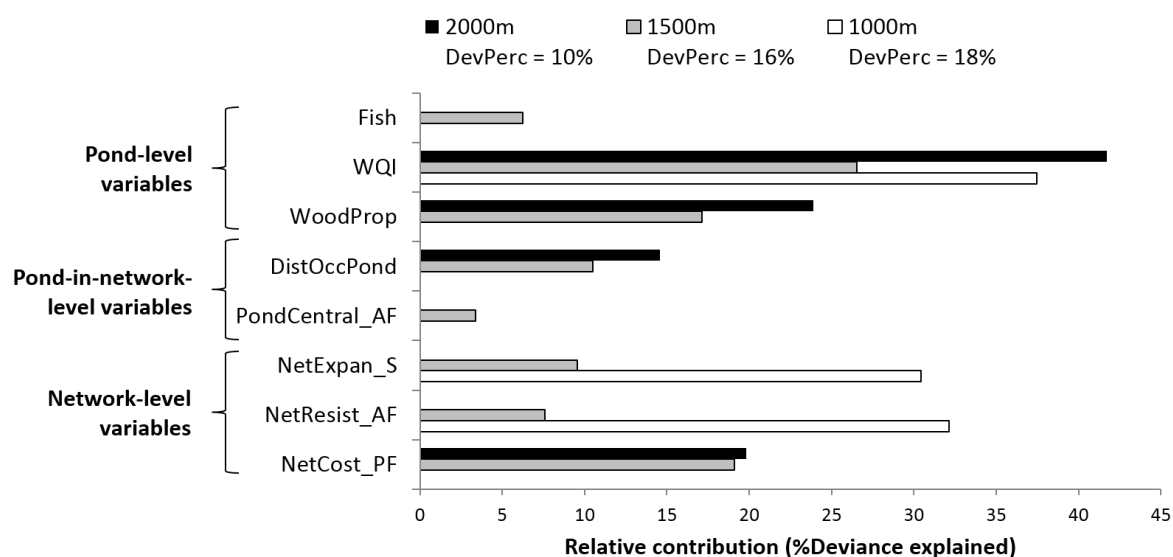


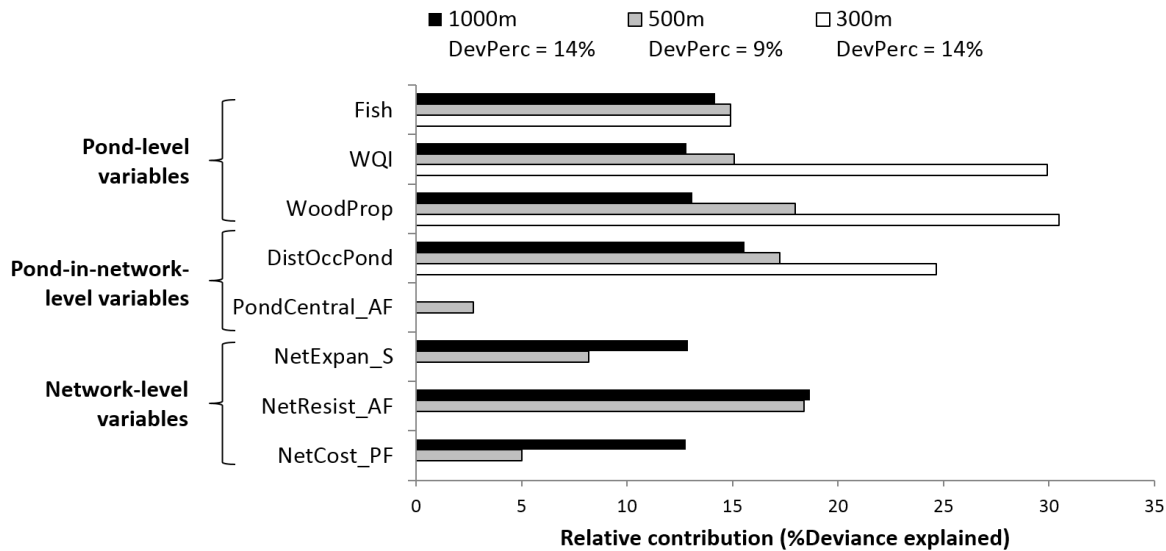
Fig. 2 Potential migration areas (PMA) obtained from the resistance map analyses for the three species according to their respective maximum migration distances (MMD): a) *Bufo bufo*, b) *Rana dalmatina*, and c) *Triturus vulgaris*. Species distribution is represented by red (presence) and black (absence)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

Figure 3

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



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



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

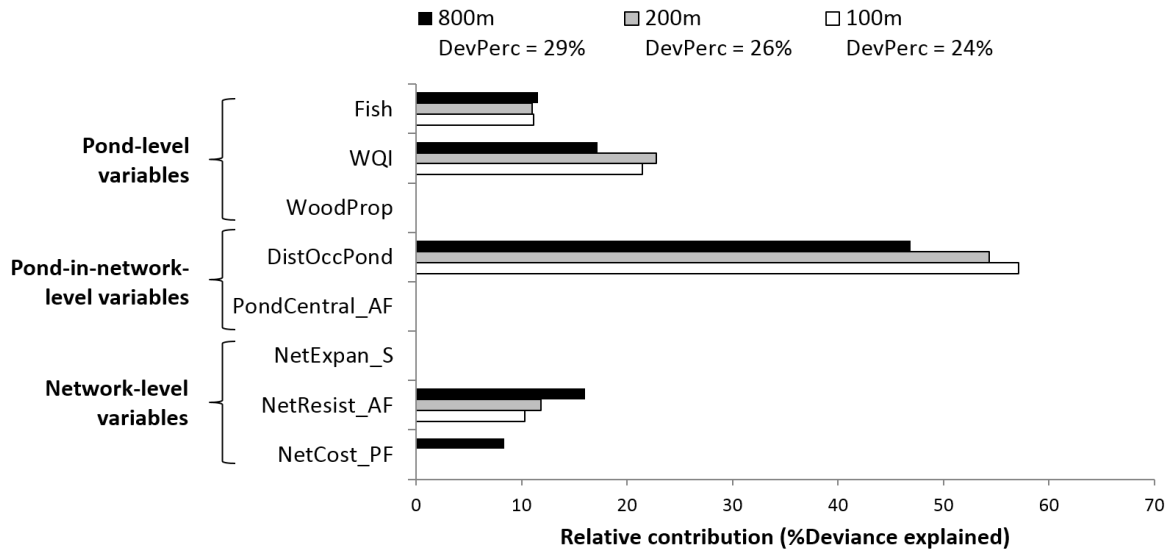
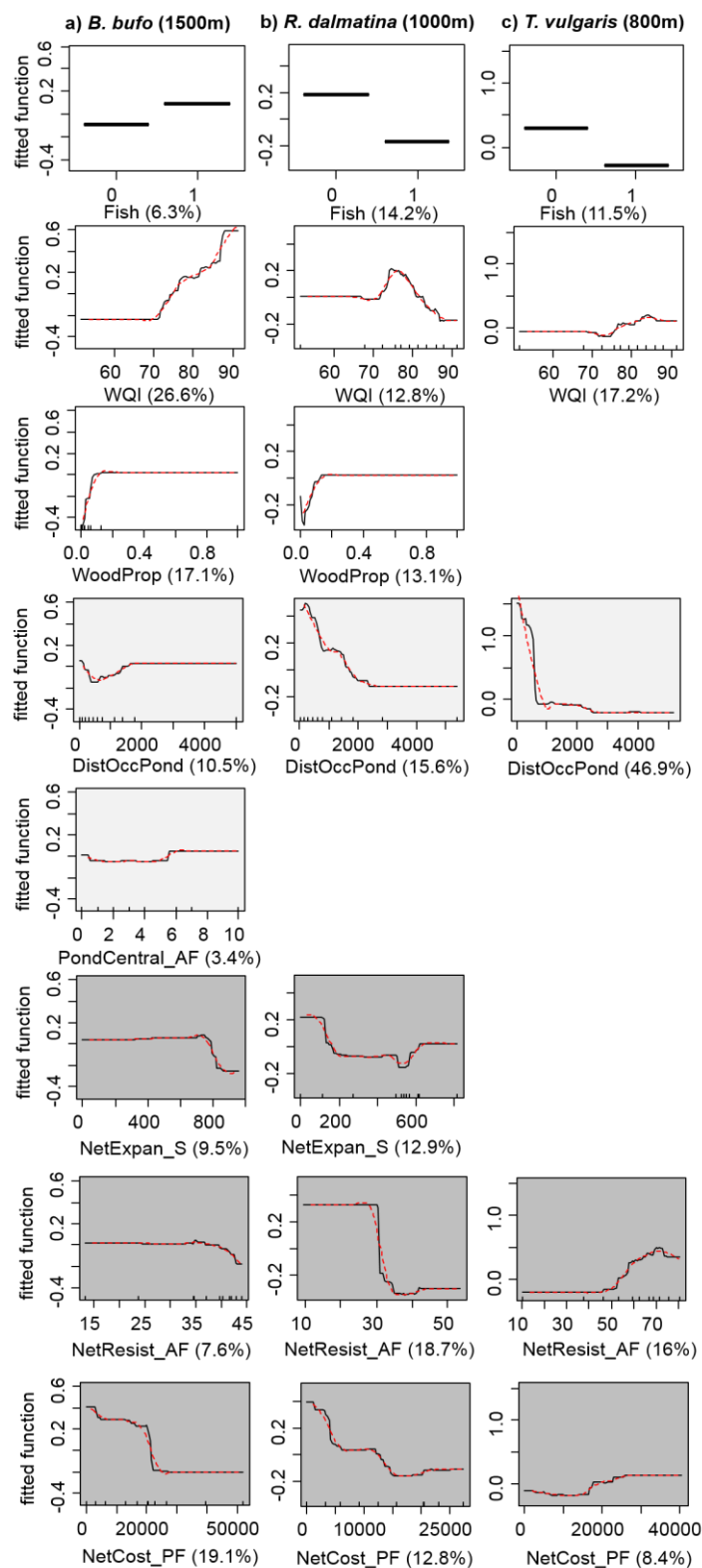
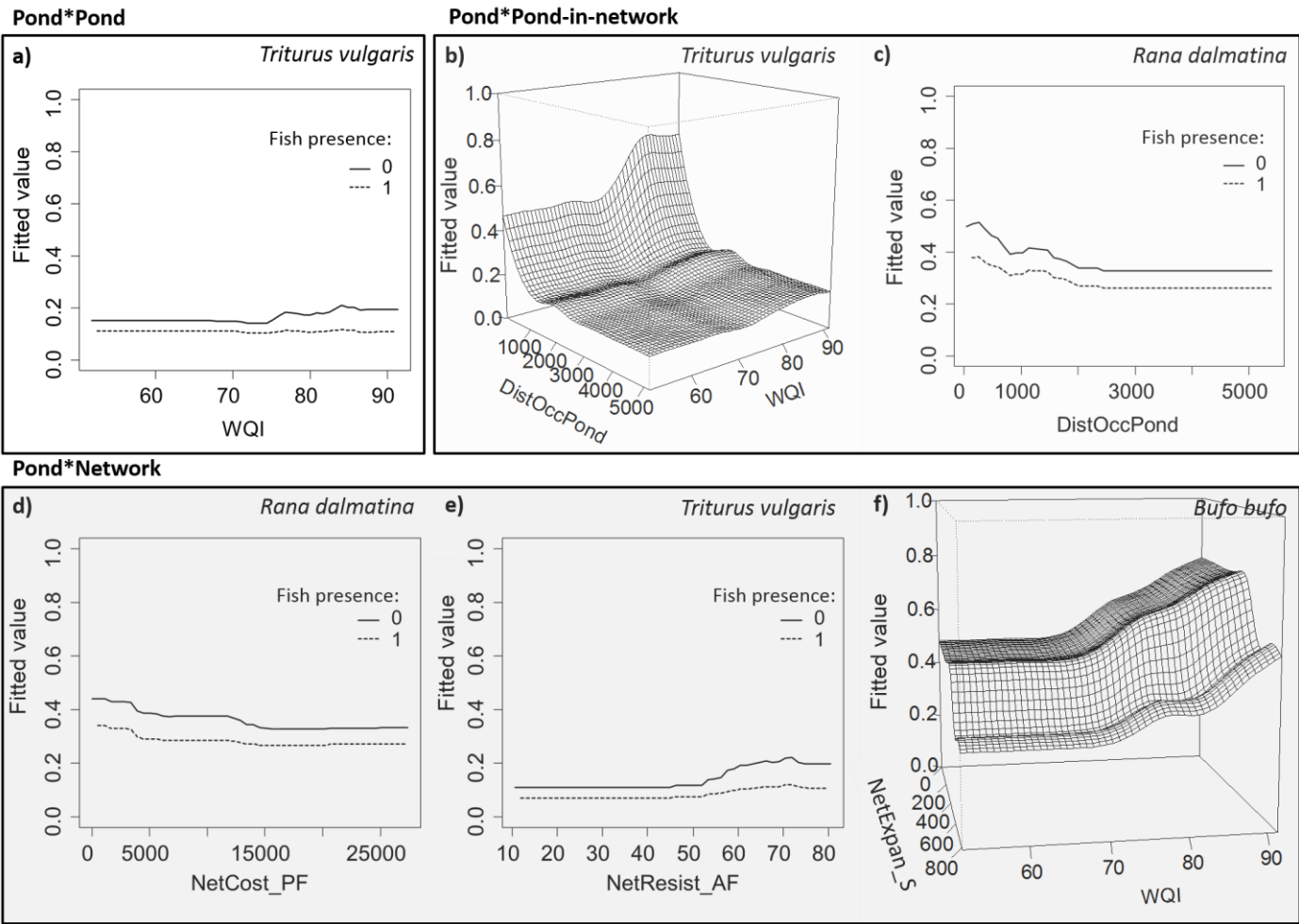


Fig. 3 Ranking of local and network variables obtained from BRT analyses for the three species and for each migration distance considered after model simplification. The variables are coded according to the **Table 2**. DevPerc = the percentage of deviance explained by the final BRT model



896
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

902 **Figure 5**



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 *Rana dalmatina* under MMDs of 300m (c), and 1000m (d), and *Bufo bufo* under MMD of 1000m (f)

SUPPORTING INFORMATION

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

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

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

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

Appendix S2 Additional information on landscape and statistical analyses

Appendix S3 Protocol of GIS processing for building resistance maps

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

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

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

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

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

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

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

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

APPENDIX S1

Table S1 Typology of the three databases Ecoline (IAU IDF 2012), Ecomos (IAU IDF 2005) and MOS (IAU IDF 2008) used and the resistance values assigned to each feature class for the three species *Bufo bufo*, *Rana dalmatina*, and *Triturus vulgaris* based on biological 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 ²)	5	5	5
14	Ecoline	Group of shrubs (<500m ²)	5	5	5
21	Ecoline	Small wood (500-650m ²)	5	5	5
22	Ecoline	Wood (500-650m ²)	5	5	5
31	Ecoline	Wood (5000-40000m ²)	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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APPENDIX S2

Additional information regarding choice of grain size and statistical analyses

a) Choice of grain size

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

b) Statistical analyses - Check of multi-collinearity

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

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

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

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

c) Statistical analyses - Boosted Regression Tree analysis

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

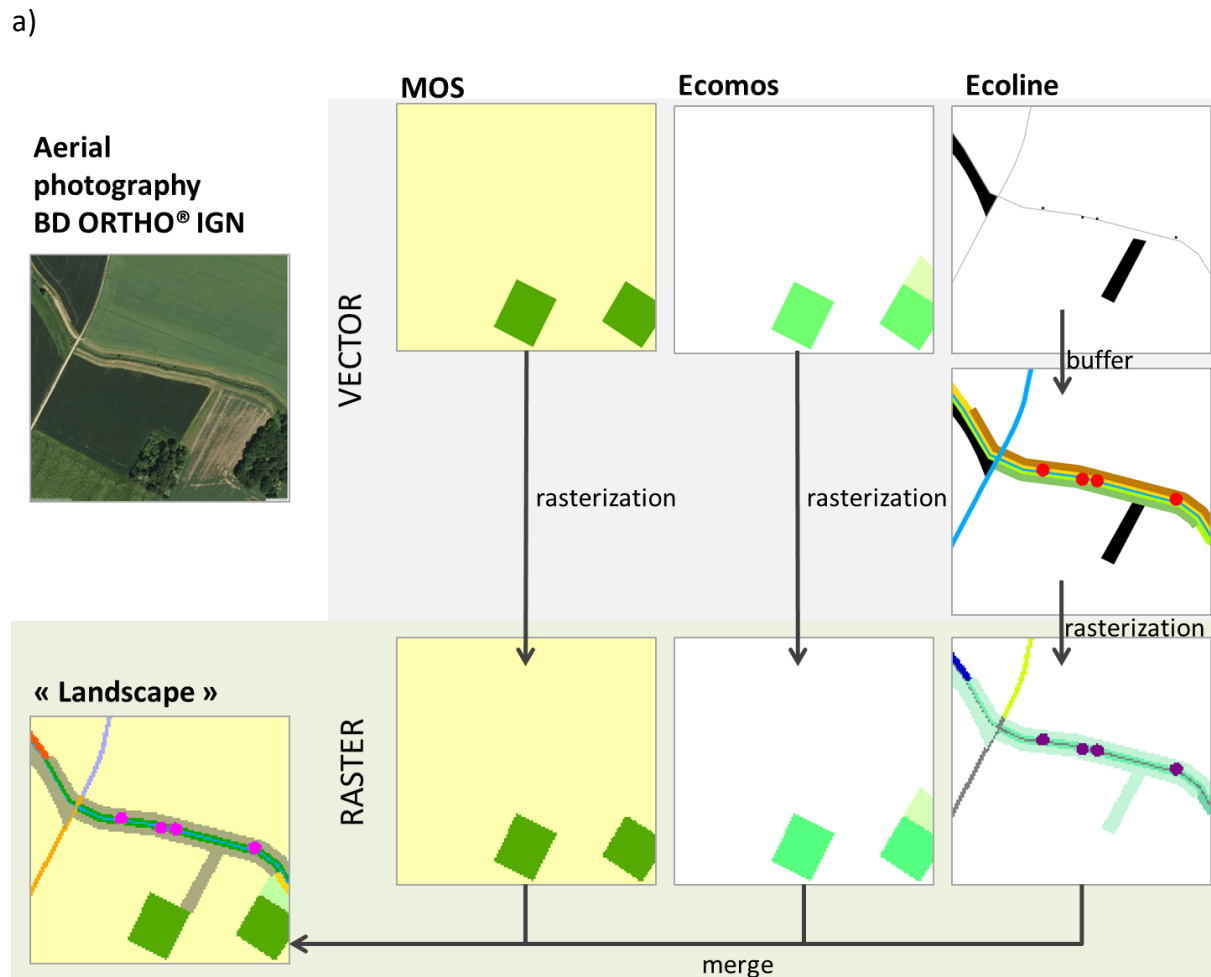
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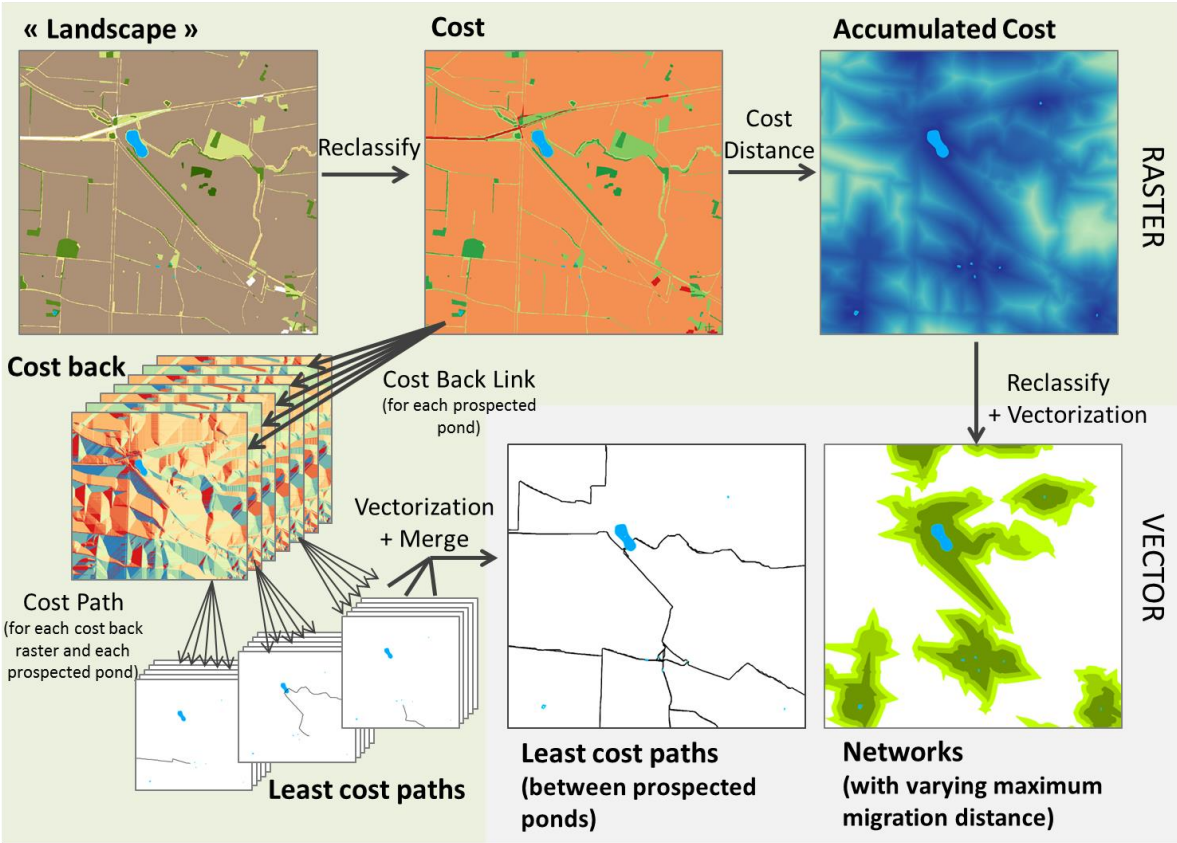
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APPENDIX S3

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



1044 b)



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APPENDIX S4

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

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

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

Positive effect of the pond connectivity within the networks

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

Negative effect of the network spatial expansion and resistance

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

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

Scale-dependency and effect ranking

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

Cross-scale interactions

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

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

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

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

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

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

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

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1168 **APPENDIX S5**

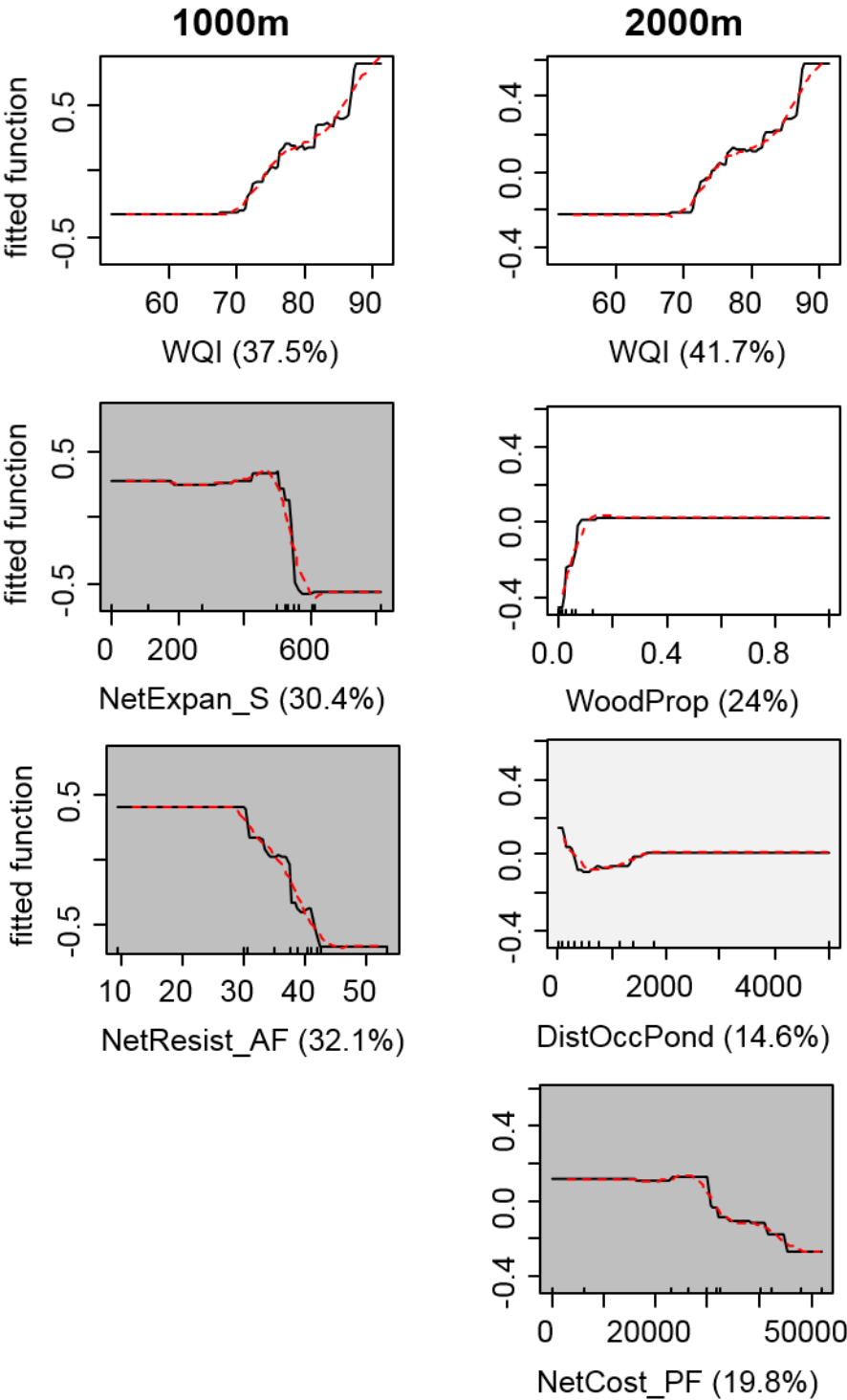
1169 **Table S5** Summary of the main characteristics of the networks obtained from the structural, unconstrained functional and constrained
1170 functional approaches of connectivity, for the three species *Bufo bufo* (bufbuf), *Rana dalmatina* (randal) and *Triturus vulgaris* (trivul), and
1171 according 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
STRUCTURAL NETWORKS (S)										
	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	
AREA-FUNCTIONAL NETWORKS (UF)										
	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	
PATH-FUNCTIONAL NETWORKS (CF)										
	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	

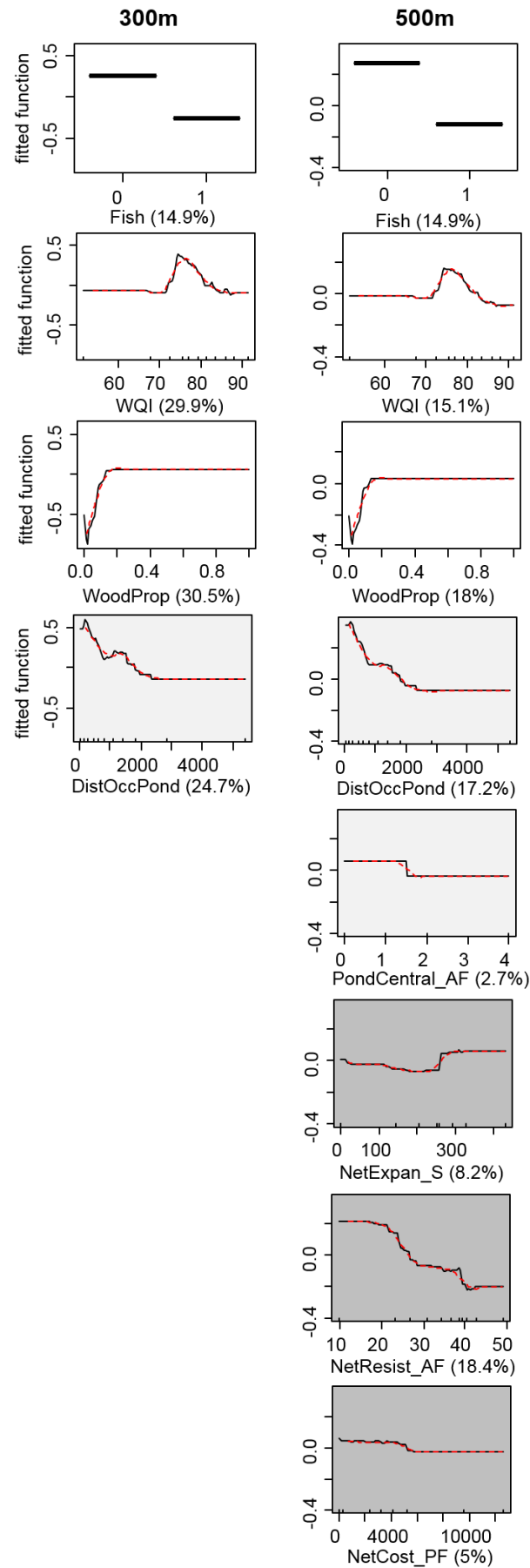
APPENDIX S6

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

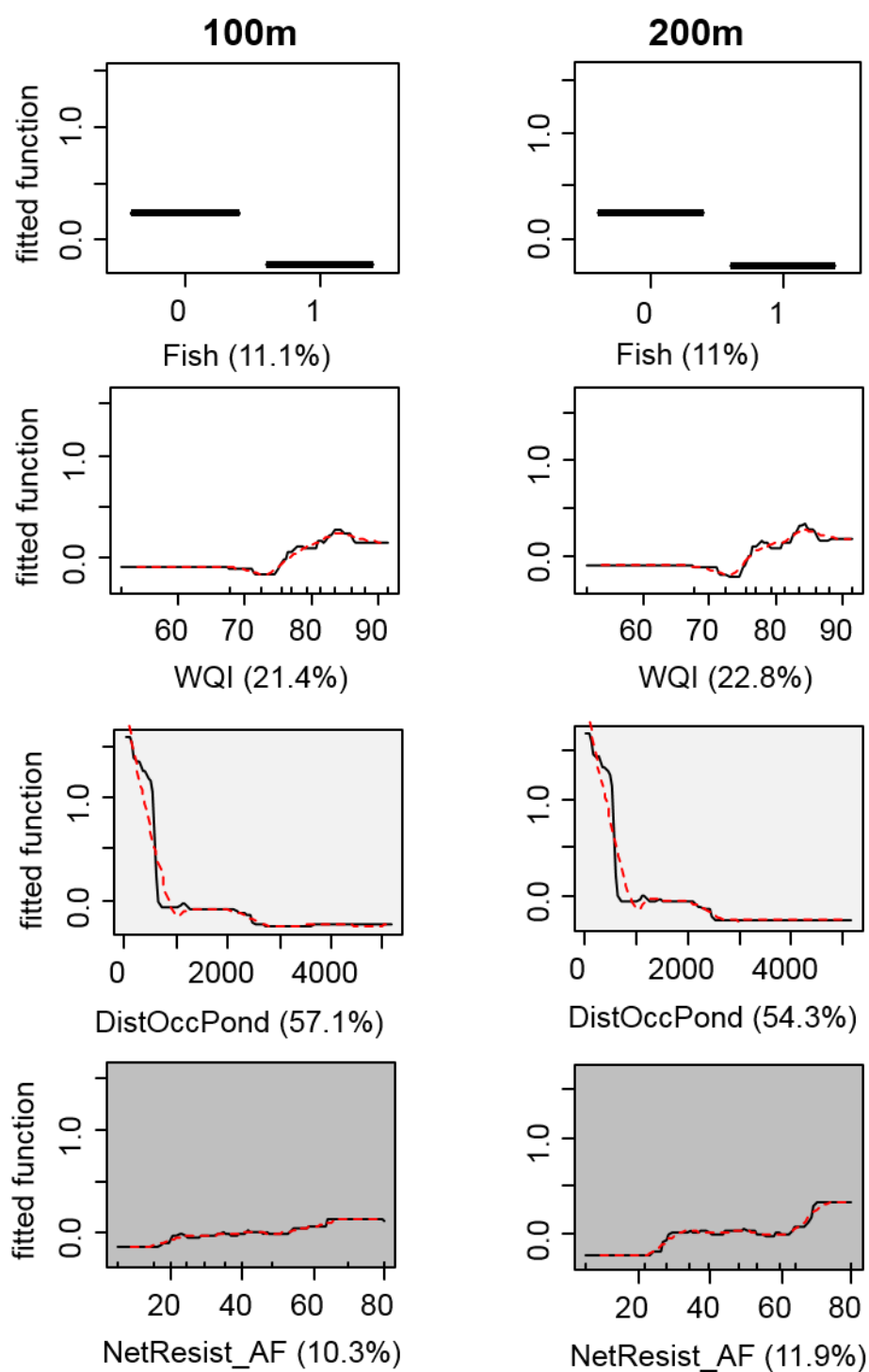
a) *B. bufo*



b) *R. dalmatina*



c) *T. vulgaris*



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APPENDIX S7

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

a)

Model	Predictor 1	Predictor 2	Interaction size	Type of cross-scale interaction
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

b)

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

N * N	1	5
Tot	20	100

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