RESEARCH ARTICLE

The pond network: can structural connectivity reflect on (amphibian) biodiversity patterns?

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Abstract Landscape connectivity is a very recurrent theme in landscape ecology as it is considered pivotal for the long term conservation of any organism's populations. Nevertheless, this complex concept is still surrounded by uncertainty and confusion, largely due to the separation between structural and functional connectivity. Amphibians are the most threatened vertebrates around the globe, in Europe mostly due to habitat alteration, and to their particular life cycle. Pond breeding amphibians are considered to be organised in metapopulations, enhancing the importance of landscape connectivity in this group of animals. We sampled the amphibian species present in two pond groups in Central Western Spain. We applied the graph theory framework to these two pond networks in order to determine the importance of each pond for the entire network connectivity. We related the pond importance for connectivity with the species richness present in each pond. We tested if connectivity (partially) determined the presence of the amphibian species sampled using logistic regression. The results show that the structural connectivity of the pond network impacts on the amphibian species richness pattern and that the importance of the pond for the connectivity of the network is an important factor for the presence of some species. Our results, hence, attest the importance of (structural) landscape connectivity determining the pattern of amphibian (functional) colonization in discrete ponds.

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Introduction

Landscape connectivity definitions abound in landscape ecology literature (Crooks and Sanjayan 2006), but this complex concept is still surrounded by uncertainty and confusion (Tischendorf and Fahrig 2000). This is largely due to the incongruence between structural and functional connectivity. Structural connectivity approaches are centred on the physical

characteristics of the landscape, neglecting the behavioural response of the organisms to these characteristics. Such responses constitute the focus of functional connectivity, deals with the actual flux of organisms through the landscape (Taylor et al. 2006). These concepts often overlap partially, leading to complex relationships. Since it addressed to the level of organisms, conservation biology should be mainly interested in functional connectivity (Lindborg and Eriksson 2004; Broquet et al. 2006; Arens et al. 2007; Jordán et al. 2007). However, it is structural connectivity that is generally used in conservation and ecological literature and even for management plans as an equivalent of functional connectivity. This may lead to inaccurate and unsuccessful conservation schemes (Taylor et al. 2006). This bias derives from the relative simplicity in determining the structural connectivity with modern GIS tools, whereas, functional connectivity demands more funding, time and research effort. However, examples of functional connectivity assessments using different techniques may be found in the literature: (a) capture–mark–recapture (e.g. Sutcliffe and Thomas 1996; Baguette 2003); (b) genetic markers (e.g. Neville et al. 2006; Walker et al. 2007) and (c) landscape resistance (e.g. Stevens et al. 2004; Watts et al. 2010). Nevertheless, as a species, and landscape, specific measure it is highly challenging to assess functional connectivity beyond particular cases of species and regions (but see Watts et al. 2010).

Habitat connectivity of a given landscape can be determined using the graph theory framework (also known as network analysis) (Urban and Keitt 2001). This theory (Harary 1969) has been taken from its original mathematical context and is nowadays applied to many diverse disciplines (computer sciences, social sciences, etc.) (e.g. Gross and Yellen 2006), including understanding biological process as food webs, community stability and gene and protein networks (Proulx et al. 2005). The application to landscape ecology is not new (Risser et al. 1984) but it was not until recently that it started to be used in real-world situations, mostly for conservation practices (Jordán et al. 2007; Minor et al. 2009; Vasas et al. 2009). Briefly, a set of discrete habitats (usually favourable habitat patches) can be represented in a graph as nodes connected with each other by edges and the linkages between the nodes implying connectivity (for more detailed information see Cantwell

and Forman 1993; Urban and Keitt 2001; Bodin and Norberg 2007; Minor and Urban 2008).

In conservation terms, amphibians are the most endangered vertebrates worldwide (Wake and Vredenburg 2008). The drivers for this situation are diverse but, in Europe, the greatest threats are those related with habitat alteration: loss, fragmentation and degradation (Stuart et al. 2004; Becker et al. 2007; Temple and Cox 2009). Amphibians are extremely dependent on the surrounding environment due to their particular life cycle involving both aquatic (eggs and larvae) and terrestrial (adults) stages and different trophic levels (herbivorous aquatic anuran larvae and carnivorous terrestrial adults and aquatic urodele larvae) (Blaustein et al. 1994). These specificities, combined with restricted dispersal ability (Bowne and Bowers 2004; Russell et al. 2005), demand a landscape level approach when planning for amphibian conservation measures and habitat management. Pond breeding amphibians have reproductive populations associated with ponds distributed over the landscape and, because of that, are often considered to follow metapopulation dynamics (but see Smith and Green 2005). Thus, landscape connectivity and, specifically, pond connectivity is of extreme importance for the long term persistence of these populations, since it may buffer the stochastic events to which ponds (particularly Mediterranean ponds) are extremely prone (Cushman 2006; Compton et al. 2007).

In this study, we applied network analysis to two independent sets of ponds whose amphibian communities are known, in order to establish the structural importance of each individual pond to the connectivity of the entire network. With this procedure, we characterise each pond in terms of relative connectivity and the corresponding amphibian species richness. The latter has previously been related with landscape connectivity (Bailey et al. 2010) and, although, with constraints, it is a very straight forward measure of biological response to the environment. We scored presence or absence of each species at several ponds in central western Spain in order to disentangle the species-specific requirements in terms of pond connectivity. Since connectivity is not the only parameter that influences suitability of a pond for a species, we added several pond traits considered important for amphibians (namely depth, hydroperiod and vegetation) in the model. In this manner, we can contrast the importance of pond connectivity with those variables. With this

modelling approach, we formally test the importance of (structural) landscape connectivity on the pattern of amphibian (functional) colonisation of discrete landscape structures, here exemplified by ponds.
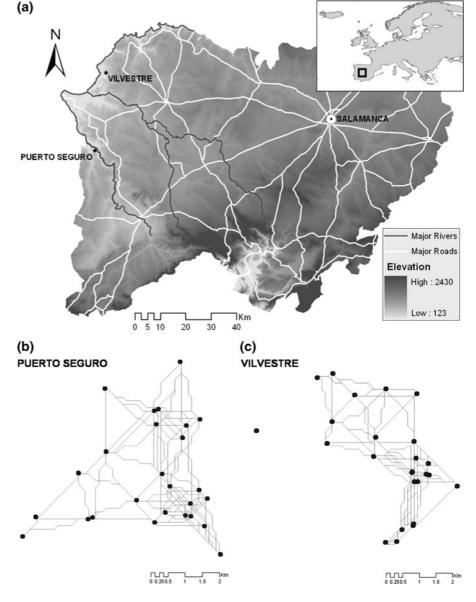
Methods

Study area and species

We sampled 51 ponds in two study areas: Puerto Seguro (26 ponds) and Vilvestre (25 ponds) both located in the Arribes del Duero Natural Park (Salamanca province, Central Western Spain; see Fig. 1). The region's climate is typically Mediterranean with low annual precipitation (average 400 mm per year), dry summers and cold winters (Peinado and Rivas-Marlinez 1987). The ponds sampled are used as water reserves for the cattle and all require some kind of human intervention in order to maintain water during at least part of the summer (mostly deepening the pond and partially uplifting the edges of the pond). Pond creation/alteration for water supply of cattle, a traditional management activity in

Fig. 1 **a** Location of the study areas (Puerto Seguro and Vilvestre) within the Salamanca province (Central Western Spain) in the Iberian Peninsula (Europe) together with major roads, rivers and altitude data. **b** and **c** Representation of the ponds networks executed with the freeware Pathmatrix (Ray 2005) over a regular matrix raster with the maximum distance of 2,000 m

Mediterranean landscapes, provides new/better breeding sites for amphibians benefiting their populations and increasing local biodiversity (e.g. Knutson et al. 2004; Miracle et al. 2010). The surrounding landscape, part of a protected area (Arribes del Duero Natural Park), is mainly constituted of a traditional rural matrix, allowing high permeability for the dispersal of amphibians, with low road density and other hostile land uses (Alarcos et al. 2003).

A total of 12 amphibian species are known to occur in the region: *Salamandra salamandra*, *Pleurodeles waltl*, *Lissotriton boscai*, *Triturus marmoratus*, *Alytes cisternasii*, *A. obstetricans*, *Discoglossus galganoi*, *Pelobates cultripes*, *Bufo bufo*, *B.calamita*, *Hyla arborea* and *Pelophylax perezi* (Pleguezuelos et al. 2002; Sillero et al. 2005). We used two methods to ascertain the presence of the amphibian species in each pond: (1) active search under all potential refuges (stones, logs, etc.) around the pond for amphibians in their terrestrial phase; and (2) dip-netting in the pond for amphibian eggs, larvae and adults in their aquatic phase. Every pond was sampled monthly during the reproductive periods from November 1999 to the autumn of 2002, resulting in a uniform sampling effort across the ponds. In order to minimize the observer error, all the sampling was conducted by the same person (G. Alarcos). We considered the species richness of each pond as the sum of all the species whose presence has been detected at the pond at least once during the sampling campaigns. This sampling effort during consecutive years is likely to detect any species present in all ponds.

Network analysis

We applied the graph theory to our landscapes considering the ponds as nodes and the connections between ponds as edges (Urban and Keitt 2001). The landscape analysis was made using the freeware Conefor Sensinode 2.2-CS22 (Saura and Torné 2009) and using the author's recommended binary connectivity index: integral index of connectivity (IIC) (Pascual-Hortal and Saura 2006). This approach classifies the ponds binarily as connected or not, with regards to a distance threshold which must be defined. This threshold should be similar to the dispersal ability of the studied species but dispersal information about Iberian amphibians is quite limited. However, studies carried out in Central Europe indicate that dispersal

distance is very variable among species (Kovar et al. 2009). We therefore, established three thresholds: 250, 500 and 1,000 m. Then, we tested at which higher threshold ($>1,000$ m) the relationship with species richness loses significance. For each threshold and study area, we calculated the overall value of connectivity of the entire network and used this value as reference for the following steps. Subsequently, we omitted one pond at time from the analysis and recalculated the overall value of connectivity for the study area. The overall connectivity was calculated while omitting one of the ponds at each iteration until all ponds had once been omitted from the dataset once. The more the omitted pond lowered the overall value, the greater its importance to the connectivity of the landscape. We used the difference between the overall value for the entire network of ponds and the same value for the landscape missing one of ponds (Pond importance$_{(node x)} = $ IIC$_{(entire network)} - IIC_{(network-node x)}$). The resulting value was an indicator of the deleted pond importance for overall landscape connectivity, the most important ponds attaining the highest values.

We used correlation analysis to relate the pond importance for connectivity to the species richness of the pond breeding amphibians. To test if the connectivity effect would remain after considering the individual pond traits relevant for amphibians, we applied logistic regression (backwards stepwise likelihood ratio design) for each species presence/absence with pond importance and four pond characteristics (area, depth, hydroperiod, and aquatic vegetation) as independent variables. Pond importance for connectivity at the distance threshold of 2,000, 1,000 and 500 m were the ones producing the more relevant relations with species richness for both areas and were selected to incorporate the logistic regression analysis. We tested the correlation of all the pond variables and decided to exclude pond area from the analysis since it was highly correlated with pond depth. All the other variables presented accepted levels of correlation (<0.70). The variable pond depth corresponds to the mean value of the depth measurement taken at approximately the center of the pond in every field campaign. This variable was log-transformed to ensure normality. Aquatic vegetation was a discrete ordinal variable with four levels: (1) none or low; (2) medium–low; (3) medium–high and (4) high. Hydroperiod classified the ponds in two categories: permanent (maintains
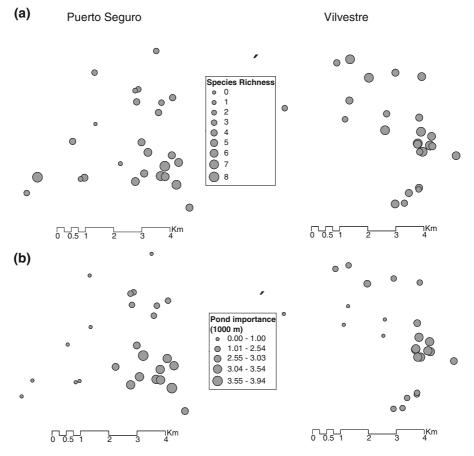
Fig. 2 Species richness (**a**) and pond importance using a distance threshold of 1,000 m (see Methods) (**b**) for each pond in both study areas. The selected method of classification was natural breaks (Jenks) and the size of the bubbles is proportional to species richness (**a**) and pond importance (**b**)

water all year) and temporary (presents a period of drought during the year).

Results

The values of species richness varied from none to eight amphibian species present at each pond on the study area Puerto Seguro and from three to seven species in the Vilvestre area (Fig. 2a). Overall, nine species of amphibians were found during the field work, *Pelophylax perezi* being the most ubiquitous species only absent from one pond in the Puerto Seguro area, whereas *Alytes cisternasii* was present in fewer ponds (Table 1).

Table 1 Number and percentage of ponds, for each study areas, with presence of each amphibian species

	Number of ponds	
	Puerto seguro	Vilvestre
Salamandra salamandra	11 (42.3%)	8 (32%)
Pleurodeles waltl	17 (65.4%)	25 (100%)
Triturus marmoratus	17 (65.4%)	23 (92%)
Lissotriton boscai	12 (46.2%)	17 (68%)
Alytes cisternasii	4 (15.4%)	1 (4%)
Pelobates cultripes	13 (50%)	11 (44%)
Bufo calamita	9 (34.6%)	10 (40%)
Hyla arborea	7 (26.9%)	14 (56%)
Pelophylax perezi	25 (96.2%)	25 (100%)
Total	26	25

The importance of each pond for connectivity, using a distance threshold of 1,000 m (the distance threshold with the strongest relation with species richness in both areas), is represented in Fig. 2b. As expected, the ponds located in the center of the network were the most important. However, as the two study areas present a different spatial distribution of the ponds (a more or less triangular shape in the Puerto Seguro area and a crescent shape in Vilvestre), the pattern of pond connectivity importance is also distinct in both areas.

The Pearson correlation analysis demonstrates that species richness is related with pond connectivity but not for all the distance thresholds (Fig. 3). Using the 250 m threshold, the pond importance is not related to the species richness in any area, but when applying the 500 m threshold the study areas diverge. Vilvestre does not show a significant relationship ($r = 0.21$ and $P = 0.32$) whereas, Puerto Seguro does ($r = 0.46$ and $P = 0.019$). In both study areas, the distance threshold producing the best correlation is 1,000 m ($r = 0.51$ and $P = 0.008$ for Puerto Seguro and $r = 0.53$ and $P = 0.006$ for Vilvestre). At this point, we decided to test at what upper threshold ($>1,000$ m) the relationship with species richness loses significance. The results show a divergence between study areas, the relationship loses significance at the

2,000 m threshold in Puerto Seguro and this only happens at the 4,000 m threshold in Vilvestre (Fig. 3).

The components of the final model selected by the logistic regression analyses for each species and study area are presented in Table 2. Once again, the influence of a connectivity factor determining the presence of amphibian species in the ponds is striking with a total of nine final models (five in Puerto Seguro and four in Vilvestre) including at least one threshold of pond importance. Nonetheless, there are some obvious differences between study areas as all the relations established in Vilvestre are positive (species presence in ponds with a high level of importance in terms of connectivity) whereas, Puerto Seguro shows both positive and negative relations.

Discussion/conclusion

The significant positive relationship between species richness and pond importance clearly demonstrates that there is an association between structural and functional connectivity in both study areas. It is remarkable that such an abstract and abiotical characterization of landscape structure would have a relation with the distribution pattern of pond breeding amphibians. Here we only state that landscape
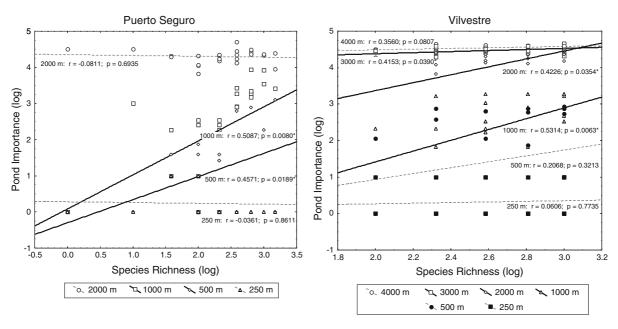

Fig. 3 Results of the pearson correlation analyses performed between species richness and pond importance for connectivity, using different distance thresholds (250, 500, 1,000 m and forward until losing significance) for both study areas

Table 2 Final models selected with the logistic regression analysis (backward stepwise likelihood ratio design): beta and standard errors for each independent variable

Study area	Species	Independent variables												
		Pond importance 2000		Pond importance 1000		Pond importance 500		Depth		Temporality		Vegetation		Constant	
		Beta	SE	Beta	SE	Beta	SE	Beta	SE	Beta	SE	Beta	SE	Beta	SE
Puerto seguro															
	Pelophylax perezi	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Pelobates cultripes	−8.639**	4.284	0	0	0	0	2.828	1.470	0	0	0	0	25.585	14.866
	Hyla arborea	0	0	0	0	0	0	11.905	5.507	0	0	0	0	−52.291	23.907
	Bufo calamita	0	0	0	0	0	0	0	0	0	0	0	0	−.575	.417
	Alytes cisternasii	0	0	0	0	0	0	0	0	−20.510	11147.524	0	0	−.693	.612
	Triturus marmoratus	42.054*	32.889	−4.994**	3.952	0	0	15.288	11.128	0	0	7.111	4.889	−236.118	179.677
	Lissotriton boscai	−710.976**	112098.175	0	0	0	0	281.192	27894.261	0	0	109.168	8352.449	1786.670	375926.519
	Pleurodeles waltl	−21.722**	11.733	0	0	7.307*	3.891	0	0	−11.392	5.785	0	0	93.316	50.215
	Salamandra salamandra	0	0	.836*	.446	0	0	0	0	0	0	0	0	−2.306	1.251
Vilvestre															
	Pelophylax perezi	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Pelobates cultripes	0	0	.976*	.573	0	0	0	0	0	0	0	0	−2.619	1.514
	Hyla arborea	0	0	1.991*	.838	0	0	2.464	1.614	0	0	1.437	.770	−16.113	8.044
	Bufo calamita	0	0	0	0	0	0	0	0	0	0	0	0	−.405	.408
	Alytes cisternasii	0	0	0	0	0	0	211.450	22776.168	0	0	0	0	−1037.997	111370.652
	Triturus marmoratus	243.235*	9094.858	0	0	36.827*	7988.9	155.987	49093.130	0	0	495.060	17852.697	−1723.705	238061.434
	Lissotriton boscai	7.622*	4.748	0	0	0	0	10.285	4.914	7.925	3.870	1.572	.924	−78.897	36.826
	Pleurodeles waltl	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	Salamandra salamandra	0	0	0	0	0	0	0	0	−20.797	17974.843	0	0	−.405	.456

The models selecting pond importance are signalled with asterisks (single-positive relationships and double-negative relationships)

connectivity, even unattached from biological support, could provide relevant information on biological patterns. We are not diminishing the role of any biotic (e.g. dispersal behaviour, competition, predation) or abiotic (e.g. landscape permeability, pond characteristics) factors recognized as drivers in the colonization of ponds by amphibians. We are simply adding one more component that should be entered into the equation.

The relation of the landscape connectivity with species richness is unambiguous in both areas indicating that the accumulation of amphibian species in the ponds is, even if partially, related to the spatial position of the pond in relation to the other ponds nearby. Our results are concordant with those found by Cunningham et al. (2009) who described wetland connectivity as "the best variable in distinguishing wetlands with high amphibian species richness from those with low species richness". However, cunningham and co-workers measured the connectivity using the presence or absence of stream in-let or out-let connecting wetlands which is quite different from our approach here.

Species richness is an elementary measurement of regional diversity and it is extremely useful in conservation planning. On the other hand, it could be misleading when considering species with a different conservation status. The populations of amphibians in the study area are not considered endangered, as the human intervention in these landscapes is minimal and controlled (i.e. part of a Natural Park) and amphibian populations are healthy (Alarcos et al. 2003). Still, over 40% (four out of nine) of the species found in the study have a conservation status of some concern in Spain (*S. salamandra* – Vulnerable; *P. waltl, A. cisternasii* and *H. arborea* –Near Threatened) (Pleguezuelos et al. 2002). Our attempt at unravelling the species richness phenomenon using a species-specific approach cannot be considered completely successful. The logistic models of species did not provide a clear picture of the influence of pond connectivity on the presence of each species: *Hyla arborea* models selected a connectivity variable in Vilvestre but not in Puerto Seguro and the opposite situation occurred with *Salamandra salamandra*. However, the fact that the models for the presence of three out of the four species, having a conservation status of some concern, selected at least one variable of

connectivity for at least one area should not be considered frivolously. As stated before, the dispersal distances of the studied species are unknown but there is a general trend that anurans have higher vagility than salamanders (Green and Smith 2005). In the study area of Puerto Seguro, the logistic regression models show that for all the species of salamanders, a pond importance variable is included. This finding gives some support to the review carried out by Green and Smith (2005) that concluded that, in general, salamanders are less vagile than anurans and therefore should be more menaced by connectivity issues. However, the models corresponding to the Vilvestre study area shows pond importance variables for two anurans and two salamanders.

Even if we were not able to clearly establish which species was most affected, the effect of pond connectivity was evident for the whole amphibian community and should be considered when planning management strategies for this animal group.

Our approach of network analysis, using the structural connectivity directly obtained from the topology of the pond network exclusively, can be considered the simplest model (Euclidean distance and no weighing of the different ponds) and cannot be generalised to other cases without caution. We assumed that pond connectivity was limited by the distance between ponds. This assumption provides a good approach for relatively undisturbed areas as in this case, but it may prove inefficient when landscape connectivity is expected to be low [generally highly disturbed areas where the matrix surrounding the habitat patches along with other non-landscape factors plays an important role (e.g. Prevedello and Vieira 2009)]. However, when considering a conservation plan for organisms occupying discrete habitats, it is an extremely straightforward way for considering the connectivity aspect, which is absolutely fundamental for the long term survivorship of natural populations.

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