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Original article

Relative importance of dynamic and static environmental variables as predictors of amphibian diversity patterns

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ABSTRACT

In this study, we evaluated whether static approaches, such as including only habitat characteristics that do not change over time, are adequate for the assessment of diversity–habitat relationships. We assessed the contribution of habitat characteristics that change over time to the spatial pattern of diversity (variation in species richness and in assemblage composition) in comparison to those characteristics that do not change. We have also provided an integral analysis to evaluate the role of the hydroperiod in structuring amphibian assemblages at any diversity level, including variation in species richness, variation in assemblage composition (i.e., nested pattern or species turnover) and variation in beta diversity. We monitored 19 amphibian assemblages from 2003 to 2006 in a highly fluctuating ecosystem, the temporary ponds in Doñana National Park. Both sets of habitat variables (temporally fixed and temporally variable) were necessary to develop a realistic understanding of amphibian diversity patterns, both when considering data collected in particular years or over several years. We found that environmental attributes that are irrelevant for pond species richness (alpha diversity) might be responsible for the variation in assemblage composition among ponds (beta diversity) and, hence, contribute to species diversity in the entire study area (gamma diversity). Therefore, we illustrate the need for an integral analysis of diversity in order not to disregard any relevant habitat factor. Alternatively, the relevance of the hydroperiod was not constant across time and was negligible in the wet year, while, in the dry year, we observed a strong nested pattern along the hydroperiod gradient and small differences in species predominance among assemblages. Therefore, our results show two conservation priorities in the study area: the preservation of ponds along the wide hydroperiod gradient; and a particular concern for the preservation of ponds with a long duration because they will provide a breeding habitat for most species in unfavourable years.

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1. Introduction

A central question in ecology is explaining the spatial variation of diversity (Gaston, 2000). In a stable system, the spatial environmental variation largely explains the spatial variation in the incidence or abundance of species and the assembly of species in space (Stiling, 1999). However, stable systems are more the exception than the rule because both communities and habitats may change over time (Ricklefs and Schluter, 1993). In fact, temporal variation in communities and habitats are related processes in an ecosystem and, in many scenarios, temporal

changes in community composition can be attributed to temporal changes in environmental characteristics (Houlahan et al., 2007). Therefore, the spatial variation of diversity will not be constant over time in temporally variable ecosystems because it will be responding both to spatially fixed environmental variation (not changing over time) and to environmental characteristics that change both over time and space. If we could disentangle the role of fixed and fluctuating environmental characteristics as drivers of the spatial pattern of diversity, we would ascertain whether static approaches to the assessment of diversity–habitat relationships are adequate. From a practical standpoint, the main advantage of static approaches is the low data collection costs because they do not require simultaneous field sampling of habitat characteristics. Instead, these approaches are mostly based on cartographic environmental data.

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Ecological theory implicitly assumes that environmental variables determine, at least in part, species distributions across space (Hutchinson, 1957) and, thereby, promote the existence of different species assemblages (spatial diversity) along environmental gradients. Following Legendre et al. (2005) and Tuomisto and Ruokolainen (2006), the distribution of communities along environmental and spatial gradients can be evaluated at three different levels: (1) the community composition; (2) the variation in community composition (beta diversity), considering either species incidences or species abundances; and (3) the variation in the variation in community composition (variation in beta diversity). The relevance of differentiating the variation in species richness from the variation in community composition lies in the fact that two sites may have exactly the same number of species but completely different community compositions. In recent years, the interest in beta diversity has increased because of its contribution to the understanding of spatial patterns in diversity (Arponen et al., 2008; Baselga and Jiménez-Valverde, 2007; Soinin et al., 2007). A particular concern in many diversity studies has been the ability to differentiate the effects of spatial and environmental variation, both in richness gradients (Baselga, 2008; Lobo et al., 2001) and beta diversity (Baselga, 2008; Borcard et al., 1992; Parris, 2004). The purpose has been to discriminate the role of dispersion/migration processes and species ecological requirements. However, the assessment of the relative contribution of habitat characteristics that change over time in comparison to those that do not change remains untested. Partitioning the effect of temporally fixed and temporally variable habitat characteristics is relevant because it will help to clarify whether temporal environmental variability should be explicitly accounted for in diversity–habitat models. In this sense, it seems reasonable to expect that habitat characteristics changing over time (i.e., water physico-chemical characteristics) would influence diversity patterns at specific sampling dates, whereas habitat characteristics that do not change over time (i.e., geographical position) would mostly influence diversity patterns in the medium or long term.

The main aim of this study is to contribute to the understanding of the adequate time frame (annual or medium term) needed for diversity–habitat studies given the nature of the environmental data available (temporally fixed or temporally variable). We use an amphibian community breeding in Mediterranean temporary ponds as a model system. Several studies have investigated the influence of environmental gradients on amphibian richness gradients and/or the variation in assemblage composition by including both temporally fixed and temporally variable habitat characteristics (i.e., Beja and Alcazar, 2003; Brodman et al., 2003; Knutson et al., 2004); however, none of these studies have explicitly accounted for the temporal variability in the system. This point might be critical in diversity model outputs because wetlands are unstable and dynamic *per se* (Fjeldsa and Lovett, 1997), and many amphibian communities change from year to year (Hecnar and M'Closkey, 1996b; Trenham et al., 2003). Moreover, pond-breeding communities are partly structured on an annual basis by species responses to current hydrological conditions (Church, 2008). For all these reasons, our purpose is to discern whether amphibian communities are determined by stable habitat characteristics and/or particular annual conditions. In other words, we use amphibians breeding in temporary ponds as a model system to integrate the spatiotemporal dynamism of habitats with the spatial distribution of diversity.

In particular, i) we assess the spatial distribution of diversity in the study area and ii) evaluate the relative importance of temporally fixed and temporally variable habitat characteristics as drivers of amphibian diversity. To do this, we assess the contribution of each set of habitat variables to explain ii (a) richness gradients and

ii (b) variation in assemblage composition among ponds. Both analyses were computed for annual fauna and for fauna observed over a four-year period (cumulative fauna).

In addition to these global analyses, we also conducted a specific set of analyses iii) to evaluate the unique contribution of the pond hydroperiod in structuring amphibian assemblages in the study area. The hydroperiod is regarded as a major force structuring pond communities (Wellborn et al., 1996) and, for that reason, its relationship with amphibians has been tested both experimentally (Leips et al., 2000; Maret et al., 2006) and in the field (Baber et al., 2004; Pechmann et al., 1989; Snodgrass et al., 2000b). We evaluated whether the hydroperiod explained species richness gradients and/or whether it was responsible for the variation in assemblage composition among ponds (beta diversity pattern). Moreover, we discriminated among different types of beta diversity patterns, such as a nested pattern or a species turnover pattern, which are opposite patterns (Leibold and Mikkelsen, 2002). A species turnover pattern reflects the tendency for species to replace each other (Leibold and Mikkelsen, 2002), while a nested pattern illustrates that the species composition of species-poor assemblages is a nested subset of species rich assemblages (see Patterson and Atmar, 1986; Ulrich et al., 2009). Similarly, we also tested if differences in the hydroperiod could explain the variation in beta diversity observed in the study area. Therefore, with this approach, we have assessed the extent to which we could use hydroperiod categories to discriminate ponds with different amphibian assemblages.

2. Material and methods

2.1. Study area

The study was conducted in an area of 6794 ha within Doñana National Park, in southwestern Spain (see Siljeström et al., 1994 for a geo-morphological description). The dominant vegetation in this area is Mediterranean scrub (*Halimio halimifolii*–*Stauracanthetum genistoides* and *Erico scopariae*–*Ulicetum australis* as defined by Rivas-Martínez et al., 1980) and isolated patches of pine (*Pinus pinea* L.) and juniper forests (*Juniperus phoenicea* L.).

Many temporary ponds of natural origin occur on the sandy area of the park (see Gómez-Rodríguez et al., 2008). The duration of flooding (or hydroperiod) varies among ponds, from pools persisting one month or less to ponds persisting up to 10 months in very wet years. The pond hydroperiods show large inter-annual variation depending on rainfall input and pattern (Gómez-Rodríguez et al., 2010a, 2009). We chose 19 temporary ponds, all of which are dry every summer (a detailed description of these ponds can be found in Gómez-Rodríguez et al., 2009). These ponds were selected to cover the hydroperiod gradient in amphibian habitats in the study area.

2.2. Amphibian sampling

From 2003 to 2006, an intensive monthly survey was conducted during each of the following sampling seasons: February–May 2003, January–May 2004 and March–May 2006. The ponds did not flood in 2005 and, therefore, could not be sampled. Additionally, reasons why some ponds could not be sampled include the following: two ponds were not accessible in 2004; in 2003, one pond was only accessible in May; and in 2006, two ponds were flooded for less than one month. We used dipnetting techniques (Heyer et al., 1994) to collect and identify larvae to the species level *in situ* (from hereafter referred to as “larval sampling”). We counted the number of larvae captured in each sampling unit (three consecutive sweeps on a stretch of approx. 1.5 m) and then released them in the pond. For most ponds, we set 12 sampling units as the

standard sampling effort. Sampling units were separated a minimum of 5 m to avoid interference between surveys. Small ponds were sampled in proportion to their size, so the number of sampling units could decrease to guarantee minimum separation (5 m). In large ponds, we tried to sample all different microhabitats and increased the number of sampling units performed. The effectiveness of larval sampling and the level of completeness of the pond inventories were high as evidenced by two non-parametric richness estimators (level of completeness estimated with ACE = 93.6% ± 11.7 [S.D.]; with Chao 1 = 98.6% ± 5.3 [S.D.]) computed with EstimateS (Colwell et al., 2004), and the fact that the probability of having detected each species was high after the sampling effort in each season (see Gómez-Rodríguez et al., 2010c).

Larval sampling was complemented with visual surveys in and around the pond to detect eggs, larvae and metamorphic individuals. Visual surveys were conducted regularly, starting when ponds filled (November 2002, November 2003 and January 2006). Because larval sampling was a standardised protocol, it provided data on species relative abundance, whereas the larval sampling combined with visual surveys provided data on species presence/absence and species richness.

2.3. Environmental and spatial variables

We selected habitat variables relevant for amphibian habitat selection based on the available ecological information. We differentiated between two types of habitat variables: (i) those changing over time (WATER), such as the hydroperiod and water physico-chemistry; and (ii) site/landscape variables (POND/LANDSCAPE), which do not vary with time. WATER variables are measured *in situ* because their values change between surveys and/or years, whereas POND/LANDSCAPE variables may be extracted from available cartographies or orthophotos.

2.3.1. Water-related characteristics (WATER)

We included hydroperiod, a major structuring factor of pond communities (Beja and Alcazar, 2003; Snodgrass et al., 2000b; Wellborn et al., 1996; Werner et al., 2007), and water-chemistry characteristics relevant for amphibians (Hecnar and M'Closkey, 1996a; Houlahan and Findlay, 2003; Knutson et al., 2004). To measure the pond hydroperiod, every pond was visited monthly to assess the months of filling and desiccation in two years with opposite hydrologic regimes (2003 and 2006). The annual rainfall, measured from September (previous year) to August, was 549.5 mm in 2003, with abundant autumn rainfall (326.4 mm); while it was 468 mm in 2006, a year of scarce autumn rainfall (149.3 mm). Water physico-chemistry was sampled on three different occasions (January 2003, May 2003, and March 2006). We measured the following: electrical conductivity, pH, chloride (Cl^-), sulphate (SO_4^{2-}), sodium (Na^+), potassium (K^+), magnesium (Mg^{2+}), calcium (Ca^{2+}), photosynthetic pigments (CHL-A), dissolved inorganic phosphate (i-P) and dissolved inorganic nitrogen (DIN) and the ratio between Na^+ and Mg^{2+} ($\text{Na}^+/\text{Mg}^{2+}$). We did not sample for water-related characteristics in 2004. A detailed description of the sampling methodology, parameter values and temporal variability are provided in Gómez-Rodríguez et al. (2009).

2.3.2. Site and landscape characteristics (POND/LANDSCAPE)

We included the following characteristics: i) pond location (geographic coordinates and altitude) and distance to key features (sea, marshland, and road) to account for spatial structures in the distribution of diversity; ii) pond area, which is a major structuring force in pond communities (Beja and Alcazar, 2003; Burne and Griffin, 2005; Werner et al., 2007), extracted from a pond

cartography built at a maximum inundation event (Gómez-Rodríguez et al., 2008); iii) pond morphometry, which conditions the availability of different microhabitats that each species may require in a selective manner (Smith et al., 2003). We measured pond slope and the percentage of different microhabitats within each pond (see Gómez-Rodríguez et al., 2009 for details); iv) percentage of pond shoreline immediately surrounded by dense scrub vegetation, which increases pond shade, an important habitat attribute for amphibians in some studies (Burne and Griffin, 2005; Sztatecsny et al., 2004); v) the characteristics of the terrestrial habitat because they provide refuge for amphibian species during the dry season (mostly adjacent habitat, i.e., <200 m) and also constitute the matrix that interconnects ponds (Gibbons, 2003). We measured the percentage of surrounding terrestrial habitat (dune, dune valley, rural path, xerophytic scrub, hygrophytic scrub, pine forest, palustrine area, human-transformed area, marshes and ecotone between the marshes and the aeolian sands) in two buffer areas (200 m and 1000 m radius) from the edge of each pond; vi) the distribution pattern of surrounding aquatic habitats, as a measure of ecological connectivity in metapopulations/patchy populations (Marsh and Trenham, 2001; Semlitsch, 2002). We measured the distance to the nearest water body and the percentage of flooded area and the number of ponds in the aforementioned buffer areas to discriminate complexes of ponds located within the dispersal range of most amphibian species (<1000 m) (Smith and Green, 2005) from those ponds located nearby (<200 m). The rationale is that individuals may frequently move among adjacent ponds, as Marsh et al. (1999) reported for tungara frogs, and, therefore, encompass them as a single breeding site (Petranka et al., 2004).

A detailed description of the sampling methodology and values of these characteristics, except for the distance to key features and terrestrial features, are provided in Gómez-Rodríguez et al. (2009). We measured the distance to key features and percentage of surrounding terrestrial habitat from orthophotos (Junta de Andalucía, 2003) using ArcView GIS 3.2.

2.4. Data analysis

First, we described the spatial variation in amphibian diversity. This first step is intended to demonstrate that biotic differences exist among ponds prior to determining whether those differences are related to environmental gradients. Since differences in the number of species detected in a pond (species richness) are provided elsewhere (Gómez-Rodríguez et al., 2010b), in this study we only described the variation in assemblage composition (beta diversity). We computed an unconstrained ordination of ponds, Non Metric Multidimensional Scaling (NMDS) (Legendre and Legendre, 1998) (command metaMDS, package vegan, R statistical package), using the Morisita–Horn dissimilarity index (Magurran, 2004) and the relative abundance of each species over the entire study period, which was measured as catch-per-unit-effort (number of larvae collected per sampling unit). We used this index because it is not influenced by species richness gradients (Magurran, 2004). To detect assemblage variation due to the replacement of species, we should address comparisons of the specific assemblage composition using dissimilarity indices independent of richness values (Baselga, 2010; Baselga et al., 2007; Koleff et al., 2003). Schmidt and Pellet (2005) recommend the use of abundance rather than presence/absence data because it provides more information. We set the number of dimensions in the NMDS ordination to two to reduce stress to values lower than 10%. We identified the species which significantly influenced the ordination (envfit command, package vegan, R statistical package) and tested the significance with 1000 permutations.

Second, we explored the relationships between environmental variation and amphibian diversity patterns. We summarised the environmental variation using Principal Components Analyses (PCAs) with a varimax rotation. Because we aimed to disentangle the effect of POND/LANDSCAPE and WATER variables and evaluate relationships in the short-term (annual data) and in the medium term (data from the entire study period), we computed the following four PCAs: on POND/LANDSCAPE variables, on all WATER variables, on WATER variables measured in 2003 and on WATER variables measured in 2006. Missing values were substituted by the mean value of the variable to maintain the size of the data set. In each analysis, we retained PCA components that contributed to an increase in explained variation higher than 10%.

We evaluated the PCA components as explanatory variables of richness gradients and, independently, of variation in assemblage composition, both on the medium term and on annual data. For the richness gradient analyses, we conducted multiple regression models (command "lm", R software) using the number of species recorded in a pond as the response variable. To explain the variation in assemblage composition, we conducted Constrained Analyses of Principal Coordinates (CAP) (Oksanen et al., 2007) with command capscale (package vegan, R statistical package) and preserved the Morisita–Horn dissimilarity and relative abundance data. Compared with traditional canonical analyses, such as redundancy analysis (RDA) or constrained correspondence analysis (CCA), CAP has the advantage of accommodating any dissimilarity measure through the use of principal coordinates analysis (PCoA) as an intermediate step, while also taking into account the correlation structure among variables in the response data (Arponen et al., 2008). In both statistical approaches (regression and CAP models), we tested as predictors POND/LANDSCAPE PCA components and, independently, WATER PCA components corresponding to the sampling period of the response variable (2003–2006, 2003 season or 2006 season). Variables were selected using a manual step-forward procedure and were based on significant contribution to the model. As an additional step, we partitioned the variance explained by each data set (POND/LANDSCAPE vs. WATER PCA) when all significant predictors were included in a global model. Variation partitioning is a way of estimating how much of the variation of the response variable can be attributed exclusively to one set of factors once the effect of the other set has been taken into account (Legendre and Legendre, 1998). In CAP analyses, we used a variant of the method ("partial CAP") for variance partitioning. The significance of each data set was tested using permutations of residuals under the reduced model (Legendre and Legendre, 1998).

Third, we conducted a specific set of analyses to evaluate the role of the hydroperiod in structuring amphibian assemblages by analysing its relationship with each type of diversity pattern as follows: i) *Richness gradient*: We conducted a Pearson correlation to assess the relationship between hydroperiod and species richness; ii) *Variation in assemblage composition*: We examined a potential nested pattern along the hydroperiod gradient by means of a Spearman correlation between the hydroperiod value and the nested rank of ponds. We measured nestedness using the Nestedness Temperature Calculator and empirically assessed its significance using 999 null models (commands nestedtemp and command oecosimu, respectively, package vegan, R statistical package). We also evaluated the role of the hydroperiod on species replacement and on the replacement in species abundance among ponds, using CAP analyses that tested the hydroperiod as a unique predictor. Species replacement was measured from presence/absence data and using the Simpson dissimilarity index, while the replacement in species abundance among ponds was measured

with the Morisita–Horn dissimilarity index. We used these dissimilarity indices because they are not influenced by species richness gradients (Magurran, 2004); iii) *Variation in beta diversity*: We assessed whether the hydroperiod categories explained the variation in beta diversity (i.e., analysis of beta diversity in the sense of Tuomisto and Ruokolainen, 2006) and whether the hydroperiod categories could be used to identify ponds with different amphibian assemblages. We conducted an analysis of similarities (ANOSIM) (Clarke, 1993) (anosim command, vegan package, R statistical package) for each dissimilarity matrix (presence/absence [Simpson] and relative abundance [Morisita–Horn]), with hydroperiod category as the grouping factor (see hydroperiod categories in Fig. 3 caption).

All hydroperiod analyses were conducted for both annual and cumulative values of species richness and assemblage composition. We related biotic data collected over the entire study period to both the hydroperiod values measured in 2003 and in 2006 because we hypothesised that the hydroperiod values for certain years (extremely dry or wet) could influence pond fauna in the medium term.

3. Results

3.1. Spatial variation in assemblage composition among ponds (beta diversity)

We detected eight species, and all of them attempted reproduction each year. The following larvae counts were measured for each species: *Bufo calamita* Laurenti, 1768, 1001 larvae; *Pelobates cultripipes* (Cuvier, 1829), 453 larvae; *Discoglossus galganoi* (Capula, Nascetti, Lanza, Bullini and Crespo, 1985), 74 larvae; *Pelophylax perezi* (Seoane, 1885), 7 larvae; *Hyla meridionalis* Boettger, 1874, 1541 larvae; *Pleurodeles waltl* (Michahelles, 1830), 107 larvae; *Triturus pygmaeus* (Wolterstorff, 1905), 1603 larvae; and *Lissotriton boscai* (Lataste, 1879), 176 larvae. We did not observe a marked segregation among ponds based on their assemblage composition (Fig. 1A). The ordination of ponds accounted for 90.13% of the variation in pond assemblage composition (first axis = 76.74%; second axis = 13.38%). Three groups of ponds were distinguishable: two small groups dominated by the abundance of species breeding in ephemeral ponds, such as *B. calamita* and *D. galganoi* [GROUP 1 and GROUP 2, respectively], and a larger group [GROUP 3], which seemed to depict a succession from pond assemblages with a high abundance of species breeding in ponds with a larger duration (i.e., *P. cultripipes*, following Díaz-Paniagua, 1990) to pond assemblages with a high abundance of species breeding in intermediate duration ponds (i.e., *T. pygmaeus* or *H. meridionalis*, following Díaz-Paniagua, 1990).

3.2. Relationship between environmental variation and amphibian diversity patterns

3.2.1. Richness gradients

In the species richness analyses, we did not find a global model including variables from both data sets (WATER and POND/LANDSCAPE) for any sampling period; therefore, we did not conduct analyses of variation partitioning (Table 1). At least one WATER PCA component significantly explained species richness for the entire study period and in 2006; however, none was selected in the 2003 season. Conversely, a POND/LANDSCAPE PCA component significantly explained species richness in 2003, but no component was selected in the regression models for data collected in 2006 or over the entire study period. All models explained a low-moderate percentage of the variance ($R^2 < 0.33$).

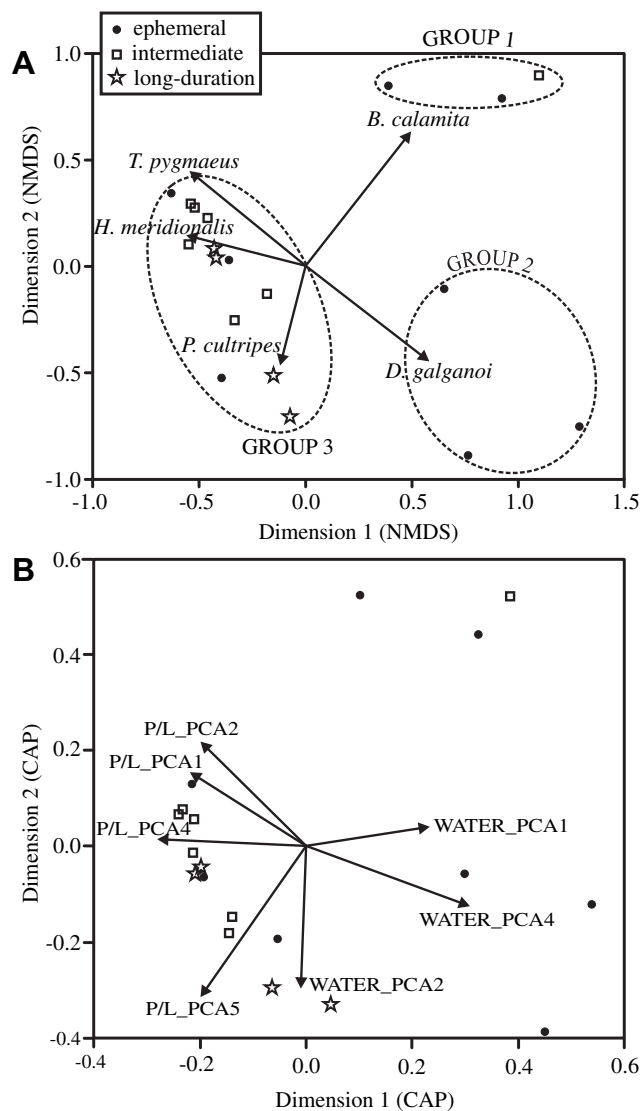


Fig. 1. Scaling of temporary ponds according to their faunal composition, measured as relative abundance, considering the three years of study. Pond hydroperiod (ephemeral, intermediate and long duration) is indicated with different symbols. A/NMDS ordination of ponds. Species vectors with significant squared correlation ($p < 0.05$) with the resulting ordination were added to the ordination plot. B/Constrained ordination of ponds (CAP analysis) showing PCA components that significantly explained differences in assemblage composition among ponds.

3.2.2. Variation in assemblage composition

Both WATER and POND/LANDSCAPE variable sets significantly explained the variation in assemblage composition computed for the entire study period (Table 2). The global model explained 58.4% of the total variation (Fig. 2). When pooling both predictor sets to compute partial CAPs, the POND/LANDSCAPE set alone significantly explained 24.4% of the variance (Fig. 2 and Table 2). The unique contribution of the WATER set was non-significant and resulted in 14.1% of the total variation explained. Fig. 1B shows that WATER variables mostly explained the differences in species composition among pond assemblages dominated by *D. galganoi*, while POND/LANDSCAPE variables were related to differences in assemblage composition in GROUP 3 (assemblages dominated by *P. cultripes*, *H. meridionalis* or *T. pygmaeus*).

We obtained different results in the analyses for annual data. The percentage of explained variation was lower than in the analysis for the entire study period (33.1% in 2003 and 40.3% in 2006;

Table 1

Explained variance (R^2) and significance (p) obtained in multiple regression analyses for species richness in 2003, in 2006 and in the entire study period. Predictor set (WATER vs. POND/LANDSCAPE) and number of predictors included in the final model are shown. NS = No potential predictor contributed significantly to explain species richness.

Sampling period	Variable set	Predictors	R^2	p
2003–2006	WATER	1	0.292	0.017
	POND/LANDSCAPE	NS		
2003	WATER	NS	0.328	0.013
	POND/LANDSCAPE	1		
2006	WATER	1	0.279	0.043
	POND/LANDSCAPE	NS		

Fig. 2). WATER and POND/LANDSCAPE variable sets significantly explained the variation in assemblage composition when tested independently (CAP analyses; Table 2). However, the unique contribution (partial CAP analyses) of both sets was significant in 2006, while only WATER variables showed a significant unique contribution in 2003. Notably, the fraction of explained variation shared by both sets of variables was very low in 2006 (0.04%; Fig. 2).

3.3. The role of pond hydroperiods on amphibian diversity patterns

The relevance of the hydroperiod to explain diversity patterns differed between the years of study. In 2006, it significantly explained species richness gradients, assemblage nestedness (Fig. 3) and species replacement among assemblages when measured with relative abundance data (Table 3). Conversely, we did not find any significant relationship between hydroperiod and amphibian diversity patterns in 2003 (Table 3). The hydroperiod was significantly correlated with species richness when considering data from the entire study period. Hydroperiod values in 2003 also explained the variation in assemblage composition measured during the entire study period. In particular, the hydroperiod significantly explained species replacement among ponds when measured with relative abundance data and showed a marginally significant relationship when it was measured with presence/absence data. In general, the percentage of explained variance was low in all beta diversity analyses (explained variance $\leq 20\%$) except in the nestedness analysis for 2006 (explained variance = 70%). The percentage of variance explained in the species richness analyses was higher (explained variance $\geq 48\%$).

We obtained a low, but significant, ANOSIM R value when analysing beta diversity in 2006 from relative abundance data. This result shows that the assemblage composition of ponds with the same hydroperiod were slightly similar, although we could not

Table 2

Pseudo-F and significance (p) obtained for each set of variables (WATER vs. POND/LANDSCAPE variables) in explaining variation in assemblage composition with Constrained Analyses of Principal Coordinates (CAP) for 2003, 2006 and the entire study period. Significance of unique contribution for each set of variables was tested with Partial CAPs. Number of axes is shown.

Sampling period	Variable set	Axes	CAP	Partial CAP
			Pseudo-F (p)	Pseudo-F (p)
2003–2006	WATER	3	2.567 ($p < 0.01$)	1.249 ($p = 0.18$)
	POND/LANDSCAPE	4	2.769 ($p < 0.01$)	1.614 ($p = 0.03$)
2003	WATER	1	5.638 ($p < 0.01$)	3.990 ($p < 0.01$)
	POND/LANDSCAPE	1	2.881 ($p = 0.02$)	1.570 ($p = 0.12$)
2006	WATER	2	2.601 ($p < 0.01$)	2.375 ($p = 0.01$)
	POND/LANDSCAPE	1	4.597 ($p < 0.01$)	3.872 ($p < 0.01$)

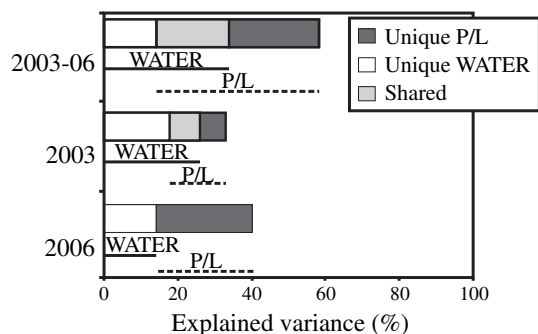


Fig. 2. Percentage of variation explained by Partial CAP analyses, identifying the total [lines] and unique contribution [bars] of each subset (WATER variables vs. POND/LANDSCAPE [P/L] variables) and the fraction of shared variation explained by both subsets [bars]. Independent analyses were conducted on pond assemblage composition in 2003 season; 2006 season and in the entire study period (2003–2006).

discriminate pond groups given the low value of the statistic. The ANOSIM R statistic should be above 0.75 to be relevant and, thereby, assume that ponds can be grouped based on the factor of interest (Clarke and Warwick, 2001).

4. Discussion

4.1. Relationships between hydroperiod and amphibian diversity

We observed inter-annual differences in the relationship between hydroperiod and pond diversity patterns, which would be in accordance with inter-annual differences previously reported in species–habitat relationships in the study area (Gómez-Rodríguez et al., 2009). The hydroperiod was not an important factor explaining amphibian diversity in 2003, when the pond hydroperiod was long (4–9 months). However, when the pond hydroperiod was shorter (≤ 4 months), in 2006, we observed a gain of species along the hydroperiod gradient but also observed small differences in species predominance among assemblages. We attribute the lack of relevance of the hydroperiod in 2003 to the fact that amphibian species did not face strong desiccation stress because the ponds were flooded for a longer period than the one required for successful metamorphosis of all species in the area. Additionally, inter-annual differences in the role of the hydroperiod might be related not only to habitat suitability but also to habitat availability. Given the strong intra-annual temporal segregation in larval communities in the study area (Díaz-Paniagua, 1988), the duration of a pond will also condition the number of species that may potentially breed in it, independent of their ecological requirements. Therefore, highly ephemeral pools (i.e., 1–2 months) may not be flooded at the time of reproduction of some species, while ponds with hydroperiod values above a given threshold (for example, 4 or 5 months) would be available habitats for all species. Additionally, we observed inter-annual stability in the nestedness patterns, as Azeria and Kolasa (2008) did in an aquatic invertebrate community in a similar dynamic system. However, we found different results in the associated hydroperiod gradient analyses. Therefore, we hypothesise alternative mechanisms that may lead to the observed nested pattern in amphibian assemblages in wet years (i.e., 2003). Taking into account that habitat heterogeneity is related to species richness in the study area (Gómez-Rodríguez et al., 2008), we hypothesise that a plausible driver for this pattern could be habitat nestedness, which is one of the main mechanisms leading to biotic nestedness in the literature (Ulrich et al., 2009).

Focusing on amphibian assemblages in the medium term, the pond hydroperiod correlated to species richness and explained some

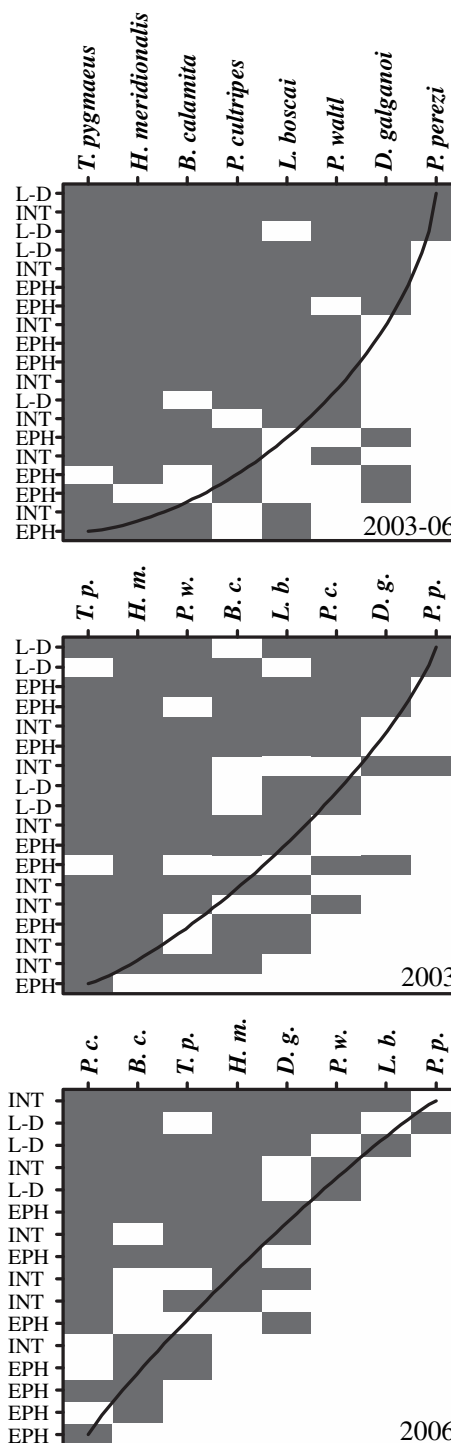


Fig. 3. Nested matrix of amphibian presence/absence in the entire study period (2003–2006), in 2003 and in 2006. Pond nomenclature corresponds to hydroperiod categories. L-D = long-duration temporary pond [8–9 months in 2003, 4 months in 2006], INT = intermediate temporary pond [6–7 months in 2003, 3 months in 2006], EPH = ephemeral [4–5 months in 2003, 2 months in 2006]. Hydroperiod nomenclature from 2003 is applied to the matrix for the entire study period (2003–2006).

of the variation in assemblage composition, both in species presence and relative abundance data. Even though the percentage of beta diversity explained was low, it was similar to the one obtained by Snodgrass et al. (2000a), who identified the hydroperiod as a major force causing spatial turnover. Focusing on the variation in beta diversity, the ANOSIM analyses proved that hydroperiod categories

Table 3
Relationships between hydroperiod and amphibian diversity patterns, both measured each year (2003 biotic data and 2006 biotic data) and over the entire study period (2003–2006 biotic data). For diversity data measured over the entire study period, relationships with hydroperiod values measured in 2003 and in 2006 are shown (year indicated in brackets).

Data	2003–06 biotic data	2003 biotic data	2006 biotic data
<i>Explaining alpha diversity</i>			
Richness gradients	Species richness Pearson $r = 0.482$; $p = 0.037$ [2003] Pearson $r = 0.486$; $p = 0.048$ [2006]	Pearson $r = 0.382$; $p = 0.107$	Pearson $r = 0.680$; $p = 0.003$
<i>Explaining beta diversity</i>			
Nestedness	Presence/Absence $T = 14.597$; $p = 0.503$ Spearman $r = 0.452$; $p = 0.052$ [2003] Spearman $r = 0.409$; $p = 0.082$ [2006] Explained variance = 10.75% [2003]	$T = 27.467$; $p = 0.043$, Spearman $r = 0.234$; $p = 0.350$	$T = 11.483$; $p = 0.005$, Spearman $r = 0.705$; $p = 0.002$
Species replacement	Presence/Absence Pseudo- $F = 2.047$; $p = 0.08$ [2003] Explained variance = 7.02% [2006] Pseudo- $F = 1.283$; $p = 0.25$ [2006]	Explained variance = 6.51%, Pseudo- $F = 1.115$; $p = 0.21$	Explained variance = 4.70%, Pseudo- $F = 0.690$; $p = 0.96$
	Relative abundance Explained variance = 14.12% [2003] Pseudo- $F = 2.797$; $p < 0.01$ [2003] Explained variance = 7.84% [2006] Pseudo- $F = 1.448$; $p = 0.13$ [2006]	Explained variance = 4.32%, Pseudo- $F = 0.723$; $p = 0.56$	Explained variance = 20.04%, Pseudo- $F = 3.259$; $p < 0.01$
<i>Analysing beta diversity</i>			
Similar assemblage composition	Presence/Absence ANOSIM $R = 0.043$; $p = 0.294$ [2003] ANOSIM $R = -0.041$; $p = 0.63$ [2006]	ANOSIM $R = 0.106$; $p = 0.11$	ANOSIM $R = -0.065$; $p = 0.757$
	Relative abundance ANOSIM $R = -0.008$; $p = 0.47$ [2003] ANOSIM $R = 0.000$; $p = 0.47$ [2006]	ANOSIM $R = -0.027$; $p = 0.55$	ANOSIM $R = 0.202$; $p = 0.047$

could not identify satisfactorily different species assemblages. This result was relatively surprising because the spatial variation in assemblage composition among ponds resembled spatial segregation of species according to the pond hydroperiod. Consequently, we attribute the lack of significance in the analyses of beta diversity to the fact that we faced gradual, instead of discrete, variation, both in the hydroperiod and faunal composition.

This study constitutes an important step towards the understanding of the hydroperiod's role in amphibian diversity patterns. We illustrate that the pond hydroperiod may be related to different diversity patterns, even to antagonistic patterns (nested pattern vs. species replacement), depending on the temporal time frame considered. The following studies have already addressed the role of the hydroperiod in some of these patterns: species richness (Beja and Alcazar, 2003; Werner et al., 2007), nestedness (Baber et al., 2004; Werner et al., 2007) and beta diversity (Snodgrass et al., 2000a). However, this study is the first to provide an integral analysis of the role of the hydroperiod at any diversity level, including variation in species richness, variation in assemblage composition and variation in beta diversity. This study also takes into account different types of variation in assemblage composition (beta diversity patterns), such as a nested pattern, turnover in species occurrence and turnover in species abundance. The overall conclusion is that the pond hydroperiod may be a major driver of pond-breeding assemblages only in years when the duration of the ponds is short, yielding a strong nested pattern along a hydroperiod gradient.

Our results describe two conservation priorities in our study area as follows: the preservation of ponds along the wide hydroperiod range, and a concern for the preservation of ponds with long duration because they will provide breeding habitats for most species in unfavourable years. Beja and Alcazar (2003) gave a similar recommendation for a different temporary ponds system. In general, it is widely acknowledged that a wide spatial variability in pond hydroperiods is required to maximise amphibian species diversity because it will provide habitat for different species (Semlitsch, 2003). For our study area, this variability also increases the overall abundance of species in the area, which results from the variability in species dominance along the hydroperiod gradient.

4.2. Relationship between environmental/spatial variables and amphibian diversity

We found inter-annual differences in the relevance of dynamic and static predictors to explain both the variation in species richness and in assemblage composition. WATER variables had a significant and unique contribution to the variation in assemblage composition in both years, but they only explained richness gradients in 2006, the drier year. Such inter-annual variability in the relationship between water-chemistry and amphibian richness gradients may explain why previous studies in different areas provided contradictory results (Babbitt et al., 2006; Beja and Alcazar, 2003; Brodman et al., 2003; Knutson et al., 2004). The relevance of WATER variables to explain diversity patterns in particular years is partially in agreement with our expectations because we hypothesised that temporally variable characteristics would be important drivers of annual diversity. However, we did not expect that POND/LANDSCAPE variables would be the only significant predictor of species richness in 2003. A plausible explanation might be that, in 2003, a hydrologically favourable year, there were no major environmental stresses precluding species breeding attempts in the study area. This fact would have favoured breeding of most individuals in the surroundings of a pond independent of the particular characteristics for that year. The presence of those individuals in the surroundings would be related to more stable characteristics of the habitat (such as terrestrial cover) because it would highly depend on the probability of adult survival in the medium term.

Focusing on amphibian assemblages in the medium term, the most remarkable result was the relevance of WATER variables to explain amphibian richness, while POND/LANDSCAPE variables did not. This result contradicts previous studies, which have reported that water-chemistry variables play a minor part in affecting amphibian species richness in the medium term (Hecnar and M'Closkey, 1996a; Weyrauch et al., 2004). In fact, it suggests that amphibian diversity in the medium term is also associated with environmental variability in time. Consequently, species diversity analyses should incorporate variables summarising the temporally

variable characteristics of ponds even when studying diversity over several years. A remarkable conclusion is that, despite the hydrology and water chemistry of ponds are supposedly governed by landscape features (Batzer et al., 2004), both sets of variables are necessary to develop a realistic understanding of amphibian diversity patterns in the study area, both when considering data collected in particular years and over several years. It should be clarified that we used dynamic predictors that intend to summarise the hydrologic conditions in two years with largely different hydrologic conditions. We avoided examining the relationships between temporally variable characteristics measured at a particular point in time (i.e., May 2003) and diversity over the entire study period because those would probably be spurious results and lack ecological meaning. In that case, we would have related a given invariant pond assemblage composition to a predictor that may show different and independent values depending on the sampling moment (see Gómez-Rodríguez et al., 2009). The inferred relationship would then depend on the date of habitat sampling. In other words, we have taken into account the temporal scale of variation in both habitat and biotic data to avoid spurious conclusions due to asynchrony between hypothesised causes (environmental characteristics) and the observed consequence (diversity).

Finally, our study also illustrates that environmental attributes irrelevant for pond species richness (alpha diversity) might be responsible for the variation in assemblage composition among ponds (beta diversity) and, therefore, contribute to species diversity in the entire study area (gamma diversity). These results reinforce the idea that beta diversity is a key concept for understanding the functioning of ecosystems, for conservation of biodiversity and for ecosystem management (Legendre et al., 2005). Previous authors have also argued the necessity of complementing species richness and community turnover assessments in conservation prioritisation (Arponen et al., 2008) or in the analysis of macroecological patterns (Gañan et al., 2008). We argue that such complements are also necessary in ecological studies relating species diversity to habitat attributes at small scales. These studies should include the various spatial scales at which relationships between diversity and habitat characteristics may become manifest. Many authors suggest multi-scale measurements of habitat attributes (Hazell et al., 2001; Van Buskirk, 2005); however, we should also include a multi-scale perspective of diversity to avoid disregarding environmental variables that may be relevant to the increase in species diversity for the entire area.

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Appendix. Supplementary material

Supplementary material related to this article can be found at doi:10.1016/j.actao.2010.10.002.

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