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Habitat matrix effects on the structure and dynamic of the metacommunity in two different regions

The metacommunity concept supposes that species occurrence depends on species dynamics and interactions at the local and the regional level via the movements of individuals among localities. For species with complex life cycles, such as several amphibian species, not all required resources are contained in the breeding habitat, and some species depend on terrestrial habitat to complete their life cycles. As animal movement can also be influenced by the physical quality of the matrix to be crossed to reach the breeding habitat and on the affinity of a species for specific terrestrial habitats, it is reasonable to expect that different matrix characteristics act either to enhance or to hinder dispersal success. These effects on dispersal success would logically be expected to impact on the species' composition of larvae assemblage at local level and, in consequence, to determine metacommunity structure and dynamic. We tested to determine whether two metacommunities with the same species pool along similar freshwater gradients exhibited different structures and dynamics in two regions that were well differentiated in terms of their respective terrestrial matrix. Our observation was that in the heterogeneous region all species showed lower co-occurrence than in the homogeneous region. Local extinction and colonisation rates were also higher in the homogeneous region. Abundances of tadpoles at local level in the homogeneous region were determined principally by the local process (pond permanence, predation risk and competition) whereas, in the heterogeneous region, abundances were explained in part by landscape factors. Differences observed in the structure and the dynamic of metacommunities between the two regions demonstrated the importance of inter-patch matrix heterogeneity for organisms with complex life cycles.

INTRODUCTION

Much recent work about the composition of local species inhabiting freshwater ponds has adopted a metacommunity point of view. Included in this recent work are studies of plankton (e.g. Leibold & Norberg 2004), invertebrates (e.g. Urban 2004), fishes (Shurin & Allen 2001), and amphibians (e.g. Joly et al. 2001; Marsh & Trenham 2001). Metapopulation approaches and, by extension, metacommunity approaches, are currently being applied to pond-breeding taxa, taking a "ponds-as-patches" view. This perspective is suggested because ponds are

spatially discrete habitats and are populated by many taxa with complex life cycles, including terrestrial adults that may move among ponds, as insects and amphibians do.

The metacommunity perspective differs from metapopulation perspectives, in that the principal issue in metapopulation theory is to address what determines the persistence of a metapopulation in a system of connected habitats, whereas metacommunity studies address what regulates the coexistence of multiple species in such a system (Leibold & Miller 2004). The metacommunity concept reconciles the recognition that assembly occurs at multiple scales and in joint regional and local dynamics (Mouquet & Loreau 2002). Metacommunity models consist of multiple local communities connected by the dispersal of at least some of the species involved (Appendix 2). However, these models differ in their assumptions concerning the importance of biotic and abiotic interactions, environmental heterogeneity, and dispersal constraints in regulating local species' persistence (Leibold et al. 2004). Closely spaced ponds frequently exhibit different abiotic and biotic factors, which affect local community structure (McPeek 1989; Urban 2004; Sanderson et al. 2005). Pond communities are often strongly associated with environmental gradients (Batzer & Wissinger 1996; Wellborn et al. 1996). Trade-offs to pond desiccation, competition abilities (Smith 1983) and predation risk susceptibility across the hydroperiod gradient (Batzer & Wissinger 1996; Wellborn et al. 1996) shape species assemblage at regional scale in terms of species-specific tolerance to pond desiccation, competition and predators (e.g. McPeek 1996; Richardson 2001; Stoks & McPeek 2003; Morey & Reznick 2004). The generality of community structure across the freshwater habitat gradient associated with different trade-offs suggests that metacommunity models which recognise patch heterogeneity (species-sorting and mass-effect models), will apply to these species assemblages (Urban 2004).

Both the species-sorting and the mass-effect models recognise the importance of patch heterogeneity and species-specific abilities in different habitats, but the two models differ in terms of the role of dispersal (Leibold et al. 2004). The species-sorting models assume that species partitioning operates according to individual adaptations and that interspecific fitness varies among patches (Leibold 1998). The mass-effect model assumes that dispersal rates exceed the rate at which environmental conditions exclude taxa such that migrants influence community composition in patches (Mouquet & Loreau 2002).

However, most adult amphibians spend little time in breeding ponds and spend the majority of their lives in terrestrial habitats that may or may not be directly adjacent to the breeding site (Wilbur 1984; Marsh & Trenham 2001; Smith & Green 2005). Dunning and co-workers (1992) coined the term "landscape complementation" to highlight the requirement for several species to link together different habitat types to complete their life cycles. Anura in general require two distinct habitats: a breeding pond and a terrestrial habitat. Some empirical studies showed that the evidence for terrestrial isolation or terrestrial matrix impermeability effects is stronger than the evidence for pond-to-pond isolation effects (Pope et al. 2000; Joly et al. 2001; Marsh & Trenham 2001). Thus, differences of adult habitat preferences and terrestrial matrix-surrounded ponds could restrict species assemblages at pond level (Van Buskirk 2005). The ability of an individual to cross a landscape is determined by the interaction between its movement behaviour and the landscape structure (Stevens et al. 2004). At regional level, the terrestrial inter-pond matrices could be heterogeneous (naturally or by human perturbation). If the juveniles or adults of the different species of a metacommunity show preferences for some terrestrial habitats or by patch boundary permeability (deMaynadier & Hunter 1999; Rothermel & Semlitsch 2002; Stevens et al. 2004), then we should reasonably expect that different matrix characteristics act either to enhance or to hinder dispersal success. These effects on dispersal success might be expected to impact on the species composition of larvae assemblage at local level. Under these circumstances, metacommunities assembled from the same species pool along similar freshwater gradients could exhibit different structures and dynamics in different regions as a function of their respective terrestrial matrices and their effects on animal movements.

The main goal of this study is to examine the relative contributions of local effects (abiotic and biotic factors) and terrestrial habitats' heterogeneity to amphibian metacommunity structure and dynamics. For this purpose we compare the same anuran community at two different regions: a heterogeneous region with different terrestrial habitats, and a second region with low terrestrial habitat variability (homogeneous region). We expect that in the region with different terrestrial habitats species remain separated into spatial niches because dispersal is not sufficient to alter their distribution in part by adults' terrestrial habitat preference, following a structure and dynamic as predicted by species-sorting model. By contrast, in a

region without different terrestrial habitats, dispersal among ponds is not influenced by adult terrestrial habitat preferences, and local (abiotic and biotic) factors determine species' assemblages and population dynamics. This situation is most similar to the mass-effects model, in which two species can be present in two different habitats and local coexistence is facilitated by dispersion.

MATERIAL AND METHODS

Study area

The study area comprises two natural parks near Barcelona, which are parts of the Catalan littoral sierra (NE Spain). The two parks comprise a similar area: 7628 hectares in the Parc Metropolità de Collserola and 10000 hectares in the Parc Natural del Garraf. Both areas have a similar Mediterranean climate with a dry winter and summer, preceded by important rainfall episodes in the autumn and spring, respectively. They are separated by a linear distance of only 15 kilometres, which constitutes the depression of the Llobregat river delta, a strong altered zone which comprises numerousness urban and industrial sites. Given their proximity and similar climate, these two parks differ greatly in their abiotic and biotic factors. Collserola is formed by a mosaic of landscapes, ranging from forests of Aleppo and nut pines, evergreen oaklands and riverside copses (a total forest surface of 67.45%), to maquis and scrublands (18.45%) and cultivated surfaces (7.49%). In Collserola, amphibians are found in watercourses, marshes, and permanent and temporal ponds. Garraf, on the other hand, is a typical karstic, semi-arid Mediterranean shrubland area (79.76%) with low forest coverage (13.77%) and with no surface waters except for temporal rain ponds and agricultural reservoirs (for a full description of landscape soil cover description see CREAF, 2000).

The community of native amphibians is the same in the two areas, and is formed by a total of 8 native species: 1 urodela (*Salamadra salamandra*) and 7 anura (*Alytes obstetricans, Pelodytes punctatus, Pelobates cultripes, Bufo bufo, Bufo calamita, Hyla meridionalis* and *Rana perezi*). To the present study we concentrated in anura species, but excluded *P. cultripes* to be a rare species in both regions.

Field methods

From October 1999 until October 2003, we searched for water habitats as potential amphibian reproduction centres in the Collserola and the Garraf areas. During the first year, we monitored a total of 36 ponds in Collserola and 51 in Garraf, with ponds added until spring 2003, by which time a total of 181 ponds had been surveyed: 107 from Collserola and 74 from Garraf. All water bodies within the two study regions were located within a global positioning unit. Localities surveyed span the range of aquatic breeding habitats of the species studied, including ephemeral pools and temporary and permanent ponds. We assessed amphibian presence and successful reproduction in all of these ponds for different years by conducting dipnetting and egg searches. We sampled larvae amphibians for a minimum of four discrete periods during the species' spring breeding period (from February to July), after tadpoles had emerged using dipnets. Sampling time periods were dictated by preliminary sampling and accounted for temporal differences in breeding activity between species (unpublished data) and also ensured that all the species breeding were captured. Blind sweeps with dipnets were made in all mesohabitats (e.g. floating vegetation, open water) present. The duration of active sampling and number of dipnets varied depending on pond size at the time of sampling and the number of mesohabitats present. All tadpoles were identified in the field and returned to the pond. Throughout the same dipnetting period, egg searches were conducted. Egg searches consisted in searching clutches on water and submerged vegetation within 3 meters of the pond shore. Ponds were considered successful breeding sites only if eggs and larvae were found. The data thus gathered were used to construct a presence-absence matrix for species and locality in different years. The metapopulation analysis was then carried out using these data.

From March to August 2002, in addition to estimating presence-absence of species in the 181 ponds, we evaluated amphibian larvae and their potential invertebrate predators' abundance in four sampling periods during the spring and summer. Due to variation in the hydroperiod, not all sites were surveyed in all the sampling periods. Amphibian larvae and predacious invertebrates were sampled with dip-net sweeps (25 cm x 35 cm) to obtain relative species densities. This is a standardized technique used to sample these two groups (e.g. Heyer et al. 1994; Babbitt et al. 2003). A minimum of 5-10 dip-net sweeps were taken in each

possible tadpole mesohabitat, following standard techniques in terms of pond size (Heyer et al. 1994). All tadpoles were identified in the field and photographed with a grid background. The number of individuals of each species was counted and the tadpoles were then returned to the pond. Predacious invertebrates, demonstrated in previous studies to prey on tadpoles, were identified (e.g. as in Woodward 1983; Travis et al. 1985; Cronin & Travis 1986), counted, and photographed with a grid background. Three types of insects were considered potential predators: dragonfly larvae (considering aeshnid and libellulid odonate naiads as predators), heteroptera (notonectids and *Nepa* sp.) and diving beetles (Coleoptera). Fish presence was determined through visual surveys in addition to dip-net captures.

Total counts for each amphibian species and predacious invertebrate captured in each pond were divided by the number of dip-net sweeps taken in each pond, following the procedures described in previous studies (Babbitt et al. 2003). This yielded abundance on the basis of catch per unit effort, and could be compared across localities. Independently, for tadpole surveys, we visited ponds approximately every four weeks throughout the year to establish the date of drying and determine the position of the pond across the hydroperiod gradient. In this manner, we were able to evaluate the number of days (in 30 by 30 days) that ponds retain water. We visually classified overhead canopy cover and aquatic vegetation (macrophyte structure) by 20% categories after spring rain periods, when temporary and ephemeral ponds refilled and when the breeding period of species started (with the exception of *B. bufo* and *P. punctatus*, which breed at the end of winter). Data from this sampling period were used in the co-occurrence analysis and in the construction of predictive models.

Statistical analysis

Metapopulation analysis

To analyse and compare the community dynamics of the six species, we constructed a metapopulation model concept. For each species, we constructed an occurrence matrix in which each row represented a site and each column a year. We used the first 78 ponds monitored from spring 2000 until 2003. To explore metapopulation dynamics, p_e and p_c (the probability of extinction and colonization, respectively) between each pair of consecutive years were calculated. We used the models developed by Gotelli and Taylor (1999) as follows:

p_e = number of sites occupied in year (t) that were unoccupied in year (t+1)/number of sites occupied in year (t)

p_c = number of unoccupied sites in year (t) that were occupied in year (t+1)/the number of sites that were monitored in year (t).

As these values were expressed as probabilities, they were arcsine-transformed prior to statistical analysis. We compared these values between regions and species using ANOVA to detect any differences in the patterns of communities and species dynamics.

Predictive models and model selection

To test how regional heterogeneity can influence the abundances of amphibian species at local or landscape scale we used a model-selection approach to identify the model that is best supported by the data from among the candidate set (Appendix 1). We used the set of competing hypotheses and their respective mathematical functions previously defined by Van Buskirk (2005), a set which identifies variables that may be important at local and landscape scale to influence amphibian occurrence. Van Buskirk defined three categories of variables:

Local abiotic covariates: includes hydroperiod or the permanence of the pond, canopy cover and aquatic vegetation.

Local biotic covariates: includes invertebrate predators and tadpole competitors. We did not include fish as previous studies (Babbitt et al. 2003; Stocks & McPeek 2003; Van Buskirk 2003, 2005) had done because, in the system of isolated ponds studied, fish are not natural predators and few ponds (6 out of a total of 246 ponds in a high range area such as the present study) contained introduced fish that prey on tadpoles. Of these 6 ponds, only 3 were inside the range of the present study (one in Garraf and two in Collserola) and were not included in the study. Predation risk was a sum of the densities of all invertebrate predators weighted according to the degree of danger they presented. Previous studies have demonstrated that not all taxa and body size predators are equally dangerous and that the sum of the densities of all predators would be a poor measure of predation risk (Van Buskirk & Arioli 2005). To avoid this problem, potential predators were weighted according to their dangerousness. We measured the body lengths of predacious invertebrates from pictures,

and these invertebrates were classified into two groups: (1) small, above 5 mm until 15 mm, and (2) large predators over 15 mm body length. We used a modified model based on the Van Buskirk and Arioli (2005) estimations of predation risk. Thus, our model was calculated as $(4d_a + 2d_n + d_l + 0.5d_s)$, where d_a is the density of aeshnid larvae and diving beetles, d_n is the density of adults *Notonecta* (individuals over 15 mm body length), d_l is the density of libellulid odonate naiads, and d_s the density of all small predators which could predate over early stages of tadpoles and small tadpole species such as bufonids (unpublished data). Interspecific competition was represented by the density of all potentially competing amphibian larvae of other species. Experimental studies showed strong asymmetric competition among the species included in the study (unpublished data); however, as experimental conditions could not be extrapolated directly to nature (see discussion in Chalcraft et al. 2005; Skelly 2005) we opted for a sum of unweighted competitor species densities and assumed that all species are equally competitive.

Landscape covariates: This category includes five parameters obtained from free digital versions of 1:25000 ortophotomaps (Institut Cartogràfic de Catalunya: *www.icc.es*). The variables were the proportion of forest cover, the proportion of farmland cover, the proportion of urban area (including roads and stone quarries), the proportion of shrubland, and the density of ponds. The proportions of land covers were obtained with the help of GIS software from aerial photos, and pond density from a database of ponds georeferenced in the field with GPS. The selection of these covariates was suggested by earlier works which reported the sensitivity of amphibians to land use and fragmentation of terrestrial habitat for buffer zones around ponds (Pope et al. 2000; Semlitsch & Bodie 2003). All covariates were measured within a 1 km buffer from the pond based on previous revisions of dispersal and terrestrial habitat use of amphibians (Marsh & Trenham 2001; Semlitsch & Bodie 2003 but see Smith & Green for a discussion of this point). We reduced the five variables to four by grouping the proportion of shrubland and of farmland under a single category termed open landscape and which differed from forest cover. The amphibian assemblages are influenced by the continuum existing across the vegetation types, from shaded forest lands to agricultural lands (Welsh et al. 2005). The four variables revealed a correlation that would recommend the removal of highly redundant variables from the model. Due to this collinearity, we used principal component

	Correlation between factor and original variable	
Original variable	PC-1	PC-2
Proportion forest cover	0.9737	0.0022
Proportion openlands (shrubland + farmland)	-0.9207	0.3851
Proportion urban soil	-0.1191	-0.1189
Pond density (ponds/km^2)	-0.3869	-0.6437
Percent variance explained	48.99	32.89
Cumulative variance explained (%)		81.89

Table 1.- Results of a principal components analysis summarizing variation in landscape features within a 1-km radius of 181 ponds (Garraf + Collserola). Proportions were arcsin-square transformed and densities were log-transformed.
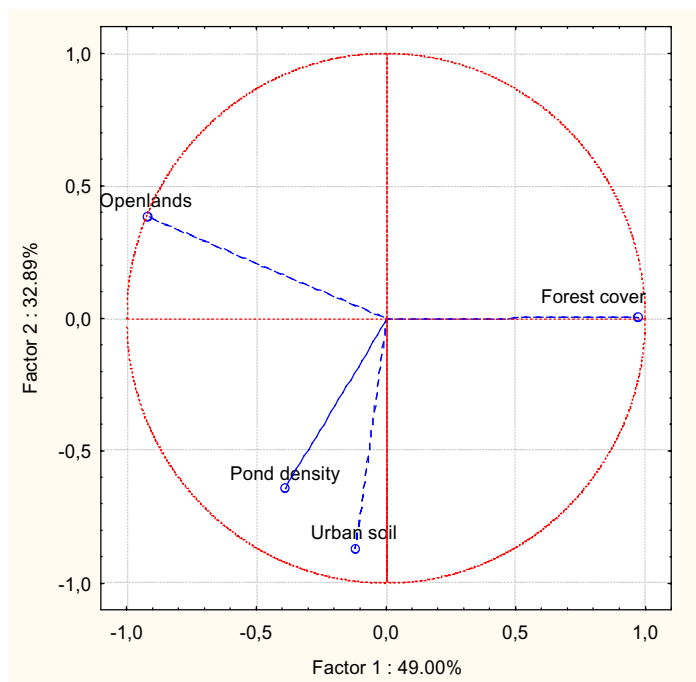

Fig. 1.- Axis represent Factor 1 and Factor 2 of the principal components analysis for the landscape covariates.

Variable	Abbreviation	Definition
Hydroperiod	Hy	Pond duration
Canopy cover	Cp	Proportion of pond area covered by canopy
Aquatic vegetation	Av	Proportion of pond area covered by aquatic vegetation
Predation risk	Pr	Abundance of predators by catch effort weighted by mortality they inflict upon tadpoles
Competition	Co	Density of all potentially competing tadpoles of other species (no./catch effort)
Forest cover PC-1	Fo	First axis from a PCA on proportion forest cover, proportion urban soil, proportion openland cover (shrub and farmland) and pond density
Urban cover PC-2	Ur	Second axis from a PCA on proportion forest cover, proportion urban soil, proportion openland cover (shrub and farmland) and pond density

Table 2.- Definition of the local habitat and landscape variables used in analyses of tadpole abundances and species composition.

analysis (PCA) to extract orthogonal measures of pond buffer landscape heterogeneity. The two principal factors of PCA explain 81.89% of the variation (Table 1). The first component represented forest landscape versus open landscapes, whereas the second represented open landscape versus urban settings and density of ponds (Fig. 1).

In the total for each pond we have three local abiotic covariates, two biotic covariates, and two landscape covariates resumed in Table 2. Correlations among all covariates were weak in both regions (Table 3) and could all be included in posterior analyses. Prior to analyses, proportions were arcsine square-root transformed, and the other values were log-transformed.

Formulating the model set

We used a series of models previously designed by Van Buskirk (2005), which represented different biologically plausible mechanisms at local and landscape scale. All models were designed to contrast the importance of groups of variables, or directly by testing specific ecological hypothesis (Table 4). Models that contained hydroperiod and predation risk were represented by two versions in which these covariates were entered as linear or quadratic terms. The nonlinear distribution of species along hydroperiod and predation gradients is supported by empirical field observations (Babbitt et al. 2002; Van Buskirk 2003), which showed that some species are more abundant in ponds of intermediate hydroperiod

	Hydroperiod	Canopy cover	Aquatic vegetation	Predation risk	Landscape forest PC-1	Landscape urban PC-2
Hydroperiod	----	0.162	0.233	0.291	0.039	-0.001
Canopy cover	0.218	----	-0.099	-0.043	0.479	0.273
Aquatic vegetation	0.049	0.094	----	0.274	0.115	-0.054
Predation risk	0.391	0.007	0.265	----	0.267	0.126
Landscape forest PC-1	-0.120	-0.108	0.050	-0.132	----	0.375
Landscape urban PC-2	0.047	0.268	-0.114	-0.006	-0.261	----

Table 3.- Pearson correlation coefficients matrix between habitat covariates. The variable "density of competitors" was not included because its value for each pond differs among species. Results for the Collserola region are above the diagonal (N=107 ponds), and the Garraf region data are below the diagonal (N=74 ponds).

or predator density. These models enabled us to compare the importance of landscape composition, species interactions and abiotic conditions (Van Buskirk 2005). We used this model set to check which conditions influenced how abundant a species was at a pond. A Generalized Linear Model (GLM) with the log of the density of tadpoles for each species was used to measure the influence of the covariates on each model.

Predictive models were ranked using Akaike's Information Criteria (AIC) bias-correction to rank models according to their strength of support from the data, and Akaike weights (Appendix 1). The goodness of fit of the most heavily parameterized model in the candidate set (Global model quadratic) was assessed (Johnson & Omland 2004), using conventional statistical test, estimating $\hat{c} = \chi^2/df$. Models with $\hat{c}$ value > 1.0, indicating overdispersion. Overdispersion can arise because there is a structural failure in the model, such as failing to include key predictor variables that are actually driving the response variable, or because the error model is inappropriate for the data (Rushton et al. 2004). We used a quasi-AIC (QAIC) corrected for small sample size because some models showed $\hat{c}$ > 1.0. Akaike weights estimate the relative competitiveness of the candidate models for fitting the dataset, given

Model name	covariates	Explanation
Core models		
Global model linear	Hy, Cp, Av, Pr, Pr^2, Co, Fo, Ur	all covariates important, linear
Global model quadratic	Hy, Hy^2, Cp, Av, Pr, Pr^2, Co, Fo, Ur	all covariates important, nonlinear
Local linear	Hy, Cp, Av, Pr, Co	only local covariates important, linear
Local quadratic	Hy, Hy^2, Cp, Av, Pr, Pr^2, Co	only local covariates important, nonlinear
Abiotic and landscape linear	Hy, Cp, Av, Fo, Ur	biotic interactions not important, linear
Abiotic and landscape quadratic	Hy, Hy^2, Cp, Av, Fo, Ur	biotic interactions not important, nonlinear effect of hydroperiod
Biotic and landscape linear	Pr, Co, Fo, Ur	abiotic factors not important, linear
Biotic and landscape quadratic	Pr, Pr^2, Co, Fo, Ur	abiotic factors not important, nonlinear effect of predation risk
Abiotic linear	Hy, Cp, Av	only local abiotic conditions important, linear
Abiotic quadratic	Hy, Hy^2, Cp, Av	only local abiotic conditions important, nonlinear effect of hydroperiod
Biotic linear	Pr, Co	only biotic interactions important, linear
Biotic quadratic	Pr, Pr^2, Co	only biotic interactions important, nonlinear effect of predation risk
Landscape	Fo, Ur	only landscape factors are important
Concept-oriented models		
Hydroperiod model	Hy, Co	hydroperiod and competition are important
Wellborn model	Hy, Pr	predator transitions are important
Wellborn extended model	Hy, Pr, Co	predator and competition transitions are important
Competition model	Co	only competition is important

Table 4.- The set of 17 candidate models used in analyses of abundance of tadpole species.

the models under consideration. Akaike weights were also used to estimate the relative importance of each variable in the selected models by summing the weights of those models in which that variable occurred (Appendix 1).

Co-occurrence indices and Community spatial autocorrelation

To test for the co-occurrence of species, we used a null model analysis of the presence-absence matrix, using data we collected in 2002, when a total of 181 ponds were surveyed. We considered ponds successful breeding sites for amphibian species only when eggs and larvae were found. Using these data, we constructed a presence-absence matrix for species (rows) and locality (columns).

We applied Stone and Robert's (1990) checkerboard score (C-score); this index also measures the degree to which species co-occur, but is not as stringent as others because it does not require perfect segregation among species (Gotelli 2000). For a community structured by species interactions, the C-score should be significantly larger than that expected to occur by chance. We used a Monte Carlo "null model" simulation to randomize each matrix in the data set. Gotelli's procedure (2000) with fixed sum row and column constraints and the sequential swap algorithm for randomization was followed. We conducted 10000 null matrices using EcoSim version 7.6 simulation software (Gotelli & Entsminger 2002). The software calculated the C-score for each null matrix, and the significance of the observed matrix was calculated as the frequency of simulated matrices that had indices that were equal to, or greater than, the index of the matrix observed (one-tailed test).

Mantel tests were used to test the hypothesis that community dissimilarity, measured as Jacard's coefficient, was spatially autocorrelated in both regions and if there are dispersal limitations, which may influence metacommunity dynamics such that communities close to each other are more similar than distant communities. In addition, partial Mantel tests were used to control the effect of the terrestrial matrix on communities composition. This statistic computes the degree of relationship between two distances matrices while controlling the effect of a third one (Fortin & Payette 2002). Partial Mantel tests were applied such that the relationship between community and geographic distance was conditioned on site landscape

heterogeneity (factor scores of PC1 from Landscape covariates) (Urban 2004). In both cases, the Mantel test correlation was evaluated via comparison normalized statistic z of 10000 permutations of the original matrix using PopTools v2.6 (Hood 2005).

RESULTS

Co-occurrence indices and Community spatial autocorrelation

For the co-occurrence indices estimated for the two regions studied, we observed two different patterns. The community in Collserola exhibited a species segregation distribution, with a larger *C*-score than would be expected by chance ($p_{(observed >= expected)}$ = 0.0411), whereas in the Garraf area species pairs did not show such a distribution ($p_{(observed >= expected)}$ = 0.2372) (Fig. 2). A non-parametric Kruskal-Wallis test showed that the ponds of Garraf concentrated a higher proportional number of species per pond than those of Collserola (U test = 2470; p < 0.001) (Fig. 3A). Also, tadpole abundance was higher in Garraf ponds than in Collserola localities ($F_{1, 179}$ = 15.07; p < 0.001) (Fig. 3B).
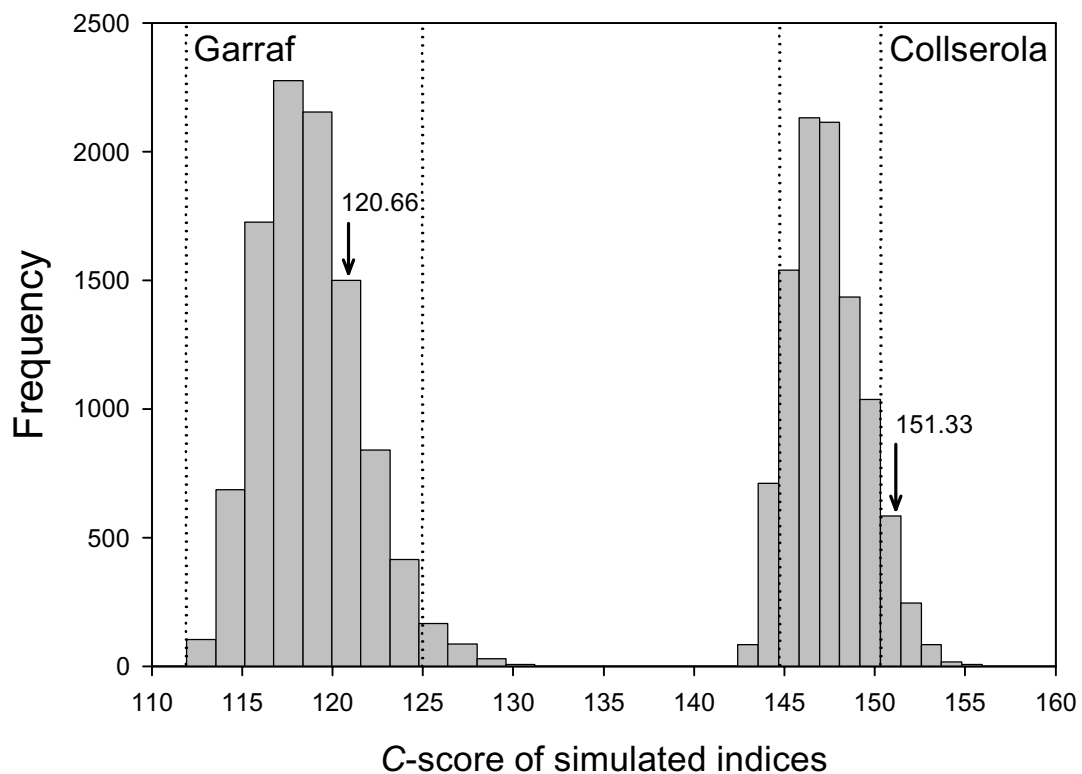

Fig. 2.- Frequency histograms for standardised effect sizes measured in presence-absence matrices. The standardised effect sizes for the *C* score for Garraf and for Collserola. In both cases dashed lines represented variance of simulated indices. Arrows indicate the *C* score for original community matrix (observed index for Garraf = 53.76190 and observed index for Collserola = 151.33330).

The mean distance to the nearby pond was very similar between the two regions, 0.55 km to Collserola and 0.78 km to Garraf (without statistical differences between regions: Mann-Whitney test $p = 0.177$) (Fig. 3C), but with differences in the density of ponds on the 1-km buffer area (Mann-Whitney test $p < 0.001$), where ponds of Collserola showed a major density than ponds of Garraf (Fig. 3D). However, the Mantel test for Collserola suggested that interpond distance was related to tadpole assemblage ($r = 0.13$; $p = 0.0014$). This relationship remained significant when the relationship between tadpole assemblage and geographic distance was conditioned on buffer terrestrial characteristic distance ($r = 0.13$; $p = 0.0011$). The test for the Garraf region also showed a relation between community dissimilarity and interpond distance ($r = 0.09$; $p = 0.0441$); however, this relationship disappeared when it was conditioned on pond landscape surround ($r = 0.07$, $p = 0.0624$).
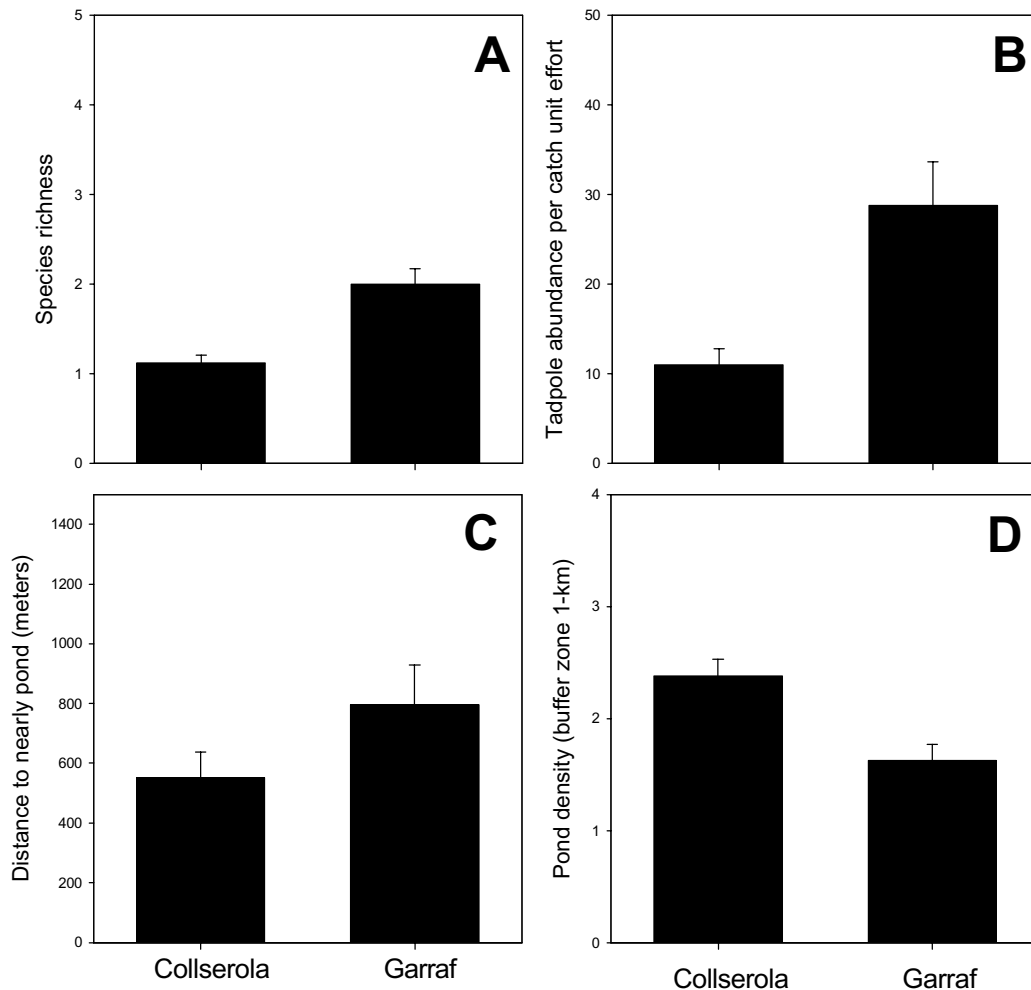

Fig. 3.- (A) Mean and standard error of species richness per pond, (B) mean and standard error tadpole abundance per pond, (C) mean and standard error distance to the closest pond, and (D) mean and standard error density of ponds on 1-km buffer area.

Metapopulations

To analyse the community dynamics we conducted MANOVA tests for region and species as independent variables with the arcsin-transformed probability of colonisation and extinction as dependent variables. The test revealed significant differences related to region ($\lambda = 0.693$, $F_{2, 23} = 5.088$; $p = 0.015$) and species ($\lambda = 0.179$, $F_{10, 46} = 6.276$; $p < 0.001$), but with no interaction between the two factors ($\lambda = 0.763$, $F_{10, 46} = 0.666$; $p = 0.749$). A Bonferroni *Post-Hoc* test applied to regions detected that Garraf exhibited a statistically significant, higher colonisation rate than Collserola ($p = 0.019$), without differences at extinction rate ($p = 0.570$). A Bonferroni test for species showed that *P. punctatus* and *B. calamita* differed in their probability of extinction from all the other species ($p < 0.05$) but not between each other ($p = 0.197$ between *P. punctatus* and *B. calamita*). The probability of colonisation did not show a clear pattern among species, and there were only statistical differences between *P. punctatus* and *B. calamita* (both with higher values) from *R. perezi,* the species with the lowest colonisation rate in our areas of study. In general, all species presented higher values of colonisation and extinction in Garraf than in Collserola (Fig. 4).
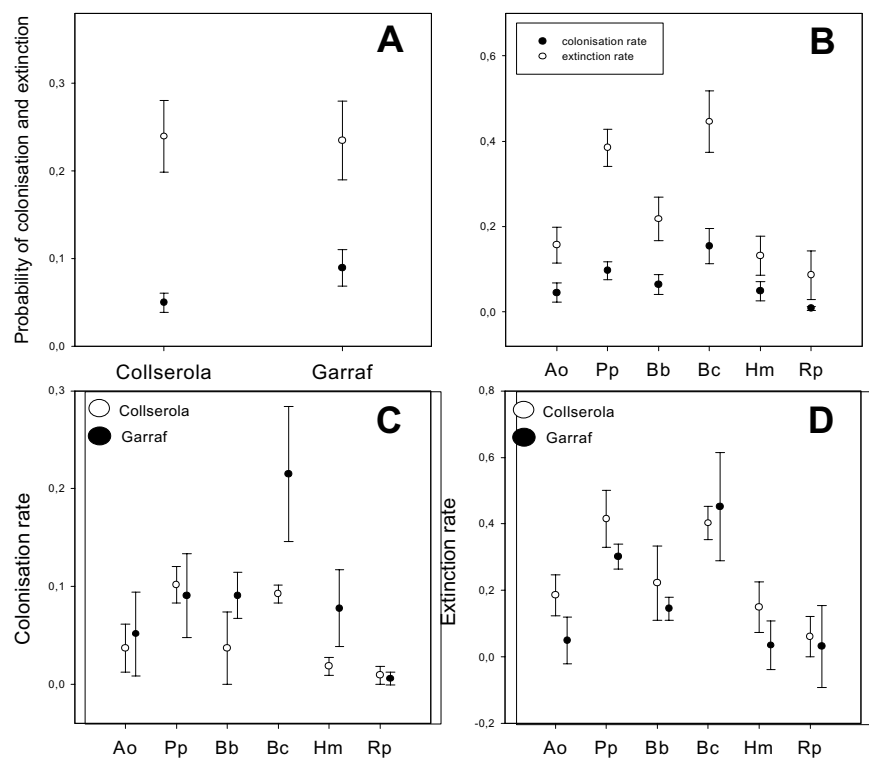

Fig. 4.- Mean and standard deviation of probability of colonisation (black circles) and extinction (empty circles) for all species in the two regions studied. Species abbreviations: Ao = *Alytes obstetricans*, Pp = *Pelodytes punctatus*, Bb = *Bufo bufo*, Bc = *Bufo calamita*, Hm = *Hyla meridionalis*, Rp = *Rana perezi*.

Predictive models and model selection

Tables 5A and 5B summarize the model-selection results, and Table 6 gives the parameter estimates for local and landscape covariates. The best-supported model was effective at predicting larval densities for most species in both regions (Table 5A for Collserola, R^2 values: 0.22-0.77; Table 5B for Garraf, R^2 values: 0.20-0.76). The kind of models selected differed among species within a region, and between regions.

In Collserola, most of the models selected showed influences for local and landscape level. In this region, models selected for five of the six species included the landscape covariates in combination with local parameters, with the exception of *R. perezi*. The density of amphibian larvae is often influenced by a combination of local and landscape effects. *B. bufo* and *H. meridionalis* were positively associated with forested landscape, whereas *A. obstetricans*, *P. punctatus* and *B. calamita* were more frequent in open landscape and in

Model	Anuran species abundance					
	A. obstetricans	P. punctatus	B. bufo	B. calamita	H. meridionalis	R. perezi
A) Collserola						
Global model linear	0	0	0	0	0	0
Global model quadratic	0	0	0	0	0	0
Local linear	0	0	0	0	0	0
Local quadratic	0	0	0	0	0	0
Abiotic and landscape linear	0	0	0	0	0	0
Abiotic and landscape quadratic	0.279** (0.78)	0	0	0	0	0
Biotic and landscape linear	0	0	0	0	0	0
Biotic and landscape quadratic	0	0.719** (0.14)	0.778*** (0.99)	0	0.633*** (0.31)	0
Abiotic linear	0	0	0	0	0	0
Abiotic quadratic	0	0	0	0	0	0
Biotic linear	0	0	0	0	0	0.675*** (0.89)
Biotic quadratic	0	0	0	0	0	0.713*** (0.10)
Landscape	0	0.224** (0.85)	0	0.187* (0.65)	0	0
Hydroperiod model	0.385** (0.21)	0	0	0	0	0
Wellborn model	0	0	0	0.366* (0.34)	0	0
Wellborn extended model	0	0	0	0	0	0
Competition model	0	0	0	0	0.633*** (0.69)	0
$\hat{c}$ of Global model	1.06	0.85	0.97	0.79	1.24	1.6

Table 5A.- Model selection results for predicting the abundance of amphibians in ponds in Collserola region. Value of R^2 and Akaike weights (in brackets) are given for all models with an evidence ratio > 0.1. (* $P < 0.05$; **$P < 0.01$; ***$P < 0.001$).

areas with a high density of ponds. Local influences also were important for species, especially biotic factors. The influence of abiotic factors was only detected in two species: *A. obstetricans* and *B. calamita*. The first species was associated with permanent ponds with low canopy cover and some kind of aquatic vegetation structure. However, *B. calamita* was more frequent in ephemeral and short-term temporary ponds. The effect of predation was detected in all species except in *A. obstetricans*. For the two bufonids, invertebrate predators influenced negatively on tadpole densities, but the rest of the species were positively associated with an increment of predation risk. This positive relationship between tadpoles and predation risk suggests the existence of other factors that positively influenced predators and several tadpole species, such as, for example, the hydroperiod and the quantity and quality of the resources (Van Buskirk 2005). On the other hand, the competition effects were negative for all species except for *A. obstetricans* and *B. calamita*, suggesting that the competitor density affects negatively the density of species.

In contradistinction to Collserola, the model selected for the same species in Garraf showed a clear preference for the local process, whereas models with landscape covariates were poorly supported. Only two species densities seem to be influenced by landscape covariates: *A. obstetricans* and *B. bufo*. The densities of species were related to open landscape, presumably to farmland areas, perhaps because man-made ponds tended to be permanent. In general, species densities were positive related to hydroperiod, except for *P. punctatus* and *B. calamita* which were related to short temporary ponds. *A. obstetricans* and *P. punctatus* also were related to sunny ponds with low canopy cover but with some kind of aquatic vegetation structure. As in Collserola, parameter estimates for predation risk were positive for some species and irrelevant for some others. None the less, competitor density was negatively associated with larvae density of four of the six species, especially for the two short-term temporary pond breeders (*P. punctatus* and *B. calamita*), and *B. bufo*. *A. obstetricans* and *R. perezi* densities seem not to be affected by the densities of the other species.

Model	Anuran species abundance					
	A. obstetricans	P. punctatus	B. bufo	B. calamita	H. meridionalis	R. perezi
B) Garraf						
Global model linear	0	0	0	0	0	0
Global model quadratic	0	0	0	0	0	0
Local linear	0	0.709*** (0.10)	0	0	0	0
Local quadratic	0	0	0	0	0	0
Abiotic and landscape linear	0.321* (0.11)	0	0	0	0	0
Abiotic and landscape quadratic	0	0	0	0	0	0
Biotic and landscape linear	0	0	0.762*** (0.56)	0	0	0
Biotic and landscape quadratic	0	0	0	0	0	0
Abiotic linear	0.265* (0.87)	0	0	0	0	0
Abiotic quadratic	0	0	0	0	0	0
Biotic linear	0	0	0.745*** (0.37)	0.729*** (0.11)	0	0
Biotic quadratic	0	0	0	0	0	0
Landscape	0	0	0	0	0	0
Hydroperiod model	0	0	0	0.651*** (0.63)	0.217 (0.12)	0
Wellborn model	0	0	0	0	0	0.147 (0.45)
Wellborn extended model	0	0.708*** (0.88)	0	0	0	0
Competition model	0	0	0	0.644*** (0.29)	0.203* (0.86)	0
$\hat{c}$ of Global model	1.68	1.49	0.96	1.07	1.45	0.29

Table 5B.- Model selection results for predicting the abundance of amphibians in ponds in Garraf region. Value of R^2 and Akaike weights (in brackets) are given for all models with an evidence ratio > 0.1. (* $P < 0.05$; **$P < 0.01$; ***$P < 0.001$).

In general, in the two regions and for all species, models incorporating local covariates received somewhat more support overall than models with landscape covariates. In Collserola the weight of landscape covariates was greater than in models for Garraf, but local abiotic and biotic process clearly influences heavily larval species densities in the two regions (Fig. 5).

DISCUSSION

The main finding of this study is that the results suggest that terrestrial habitats impose a significant barrier to dispersal of some amphibian species and, consequently, affects metacommunity structure and dynamics in terms of landscape composition. Pond communities in the smaller region (Collserola 7628 hectares) were significantly affected by interpatch distance, whereas in Garraf (10000 hectares) species assemblages seem not to be conditioned by interpond distance. This correlation between local assemblage and distance was made greater in the heterogeneous region when it was conditioned with terrestrial characteristics. These results were in concordance with previous studies, which demonstrated that juvenile amphibians are capable of detecting and avoiding terrestrial unfavourable habitats (deMaynadier & Hunter 1999; Rothermel & Semlitsch 2002; Stevens 2004). Furthermore, landscape-level studies in fragmented landscapes suggest that local amphibian occurrence and species richness decline with increased isolation from other ponds, conversion of land to intensive uses such as agriculture, and road densities (Vos & Stumpel 1995; Findlay & Houlahan 1997; Gibbs 1998a, b; Joly et al. 2001 but see Gray et al. 2004). Theoretical and simulation models have demonstrated that changes in matrix heterogeneity show the potential to affect metapopulation dynamics (Gustafson & Gardner 1996; Vandermeer & Carvajal 2001).

The study demonstrates that a good knowledge of the landscape context in terms of both breeding habitat (local spatial scale) and complementary habitat (terrestrial matrix to complete their life cycles) may be required to understand the composition and dynamic of metacommunities of species with complex life cycles and complementary resource needs.

Landscape effects

Abundances of the different species at local level were principally conditioned by local factors more than by characteristics related to landscape surrounds. These results were in agreement with other studies performed with anurans and newts (Sztatecsny et al. 2004; Van Buskirk 2005). However, in the heterogeneous region (Collserola), several species were conditioned in part by landscape covariates, thus suggesting that terrestrial habitat may have some importance at the moment of choosing a pond. When we look at the map of Collserola and species distribution, distribution differences may appear on the surface to be directly

related to differences in vegetation structure. Suitable thermal environments are an essential element, determining fitness in population of ectotherms (Huey & Kingsolver 1989). The characteristics of forest and open-lands may originate physiological or ecological constraints on species, and these strongly influence their ability to forage, reproduce and survive. These physiological constraints have profound implications because they limit when and where species can exist and thrive on the landscape (Huey 1991). Modification of climate by forest structure differentially during vegetation succession, as temperature (air and water) and moisture (relative humidity) vary greatly (Chen et al. 1999; Welsh et al. 2005). In Collserola, some species showed a preference for ponds situated in open areas with high levels of sun irradiation (*A. obstetricans*, *P. punctatus* and *B. calamita*), whereas others preferred forest ponds (*B. bufo* and *H. meridionalis*). For example, the preferences of *P. punctatus* and *B. calamita* reflect the selection of open landscape and warmer ponds that enhance egg and larval development (Bregulla 1988, Toxopeus et al. 1993; Jakob et al. 2003). Differences in air and water temperature regimes among vegetation types may explain the poor presence of these species in forest areas, and their restriction to open areas dominated by shrubs.

Local effects

The results of the models of abundance in both regions showed that local processes are the most important factors to explain species abundance. The same factor can have a different consequence over the different species, drawing a trade-off scenario which is consistent with theoretical models and previous field studies (e.g. Smith 1983; Wellborn et al. 1996; Snodgrass et al. 2000; Richardson 2001, 2002; Van Buskirk 2005). In the two regions, pond permanence, predation risk, and competition were the factors identified as the most important ones to determine abundance of several species. Not all species, but a significant number of species, were restricted to a part of the hydroperiod gradient, with preference for temporary or permanent ponds, suggesting that species trade off adaptations to pond disturbance with those associated factors: predation risk and competition (Smith 1983; Wellborn et al. 1996). Taken together, these patterns argue for the non-equivalence of species and suggest that assumptions of the neutral model are not appropriate for these metacommunities (Urban 2004). Trade-off between the characteristics of ephemeral, temporary and permanent ponds
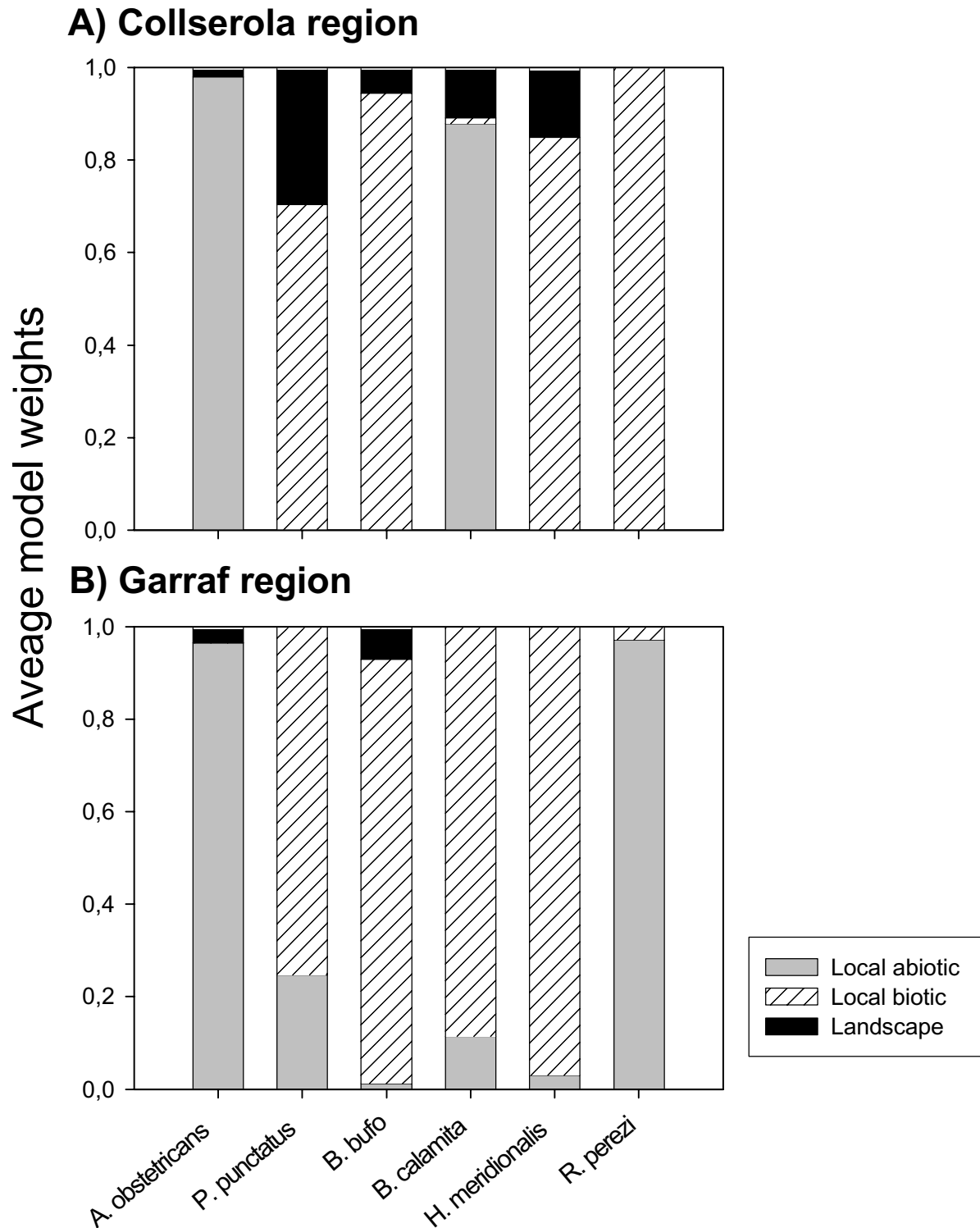
A) Collserola region

B) Garraf region

Fig. 5.- Relative amounts of support provided by the data for local and landscape models of larval density for each species. Model weight is the Akaike weight averaged across all models that included variables of that category. Local abiotic covariates included pond permanence, vegetation cover, and canopy cover. Local biotic covariates included predation risk and potentially competing larvae. Landscape covariates were axes derived from a PCA of proportional land covers (Table 1 and Fig. 1).

species	Hydro-period	(Hydro-period)^2	Canopy cover	Vegeta-tion	Predation risk	(Predation risk)^2	Compe-tition	Forest cover PC-1	Urban cover PC-2
A) Collserola									
A. obstetricans	21.747	-4.633	-0.232	1.192	0.000	0.000	0.000	-0.585	0.326
P. punctatus	0.000	0.000	0.000	0.000	0.013	0.001	-2.496	-0.853	0.204
B. bufo	0.000	0.000	0.000	0.000	-0.195	0.023	-13.706	0.538	-0.270
B. calamita	-13.111	0.000	0.000	0.000	-0.172	0.000	0.000	-0.975	0.655
H. meridionalis	0.000	0.000	0.000	0.000	0.212	0.017	-8.290	0.319	-1.195
R. perezi	0.000	0.000	0.000	0.000	0.067	0.043	-5.063	0.000	0.000
B) Garraf									
A. obstetricans	2.812	-0.02	-3.28	1.698	0.000	0.000	0.012	-0.157	0.125
P. punctatus	-5.924	-0.086	-0.081	0.114	0.962	0.000	-17.934	-0.001	-0.002
B. bufo	-0.381	-0.016	0.014	-0.006	0.516	0.000	-32.502	-1.761	-0.764
B. calamita	-5.696	0.000	0.000	0.000	0.004	0.000	-43.842	0.000	0.000
H. meridionalis	0.142	0.000	0.000	0.000	0.000	0.000	-4.512	0.000	0.000
R. perezi	0.487	0.000	0.000	0.000	0.014	0.000	0.000	0.000	0.000

Table 6.- Coefficients of local habitat and landscape covariates predicting abundance, obtained by averaging across all models in the candidate set weighted by the Akaike weights.

provides evidences of mechanisms that may exclude species from one kind of habitat in function of their adaptations (Smith 1983; Wellborn et al. 1996). As in the work of Van Buskirk (2005), the results of the concept-oriented models do not favour any single model over the others. Contrary to the Van Buskirk results, we observed a negative influence of other tadpoles in several species, which was in concordance with competition models (Smith 1983). Competition effects seem to be especially strong in the two bufonids and *P. punctatus*, which showed as poor competitors in laboratory experiments (Richter-Boix et al. *unpublished*). The results reinforce local biotic interactions and time constraints imposed by hydroperiod, and the fact that in this system local extinction is not due to stochastic processes but to deterministic mechanisms (Skelly et al. 1999; Marsh & Trenham 2001; Sztatecsny et al. 2004). Species local extinction provides evidence for a low-fitness habitat that might also function as a population sink. These results agree with a growing number of studies that suggest the importance of colonisation and extinction dynamics in amphibian temporary pond communities (Sinsch 1992, 1997; Hecnar & M'Closkey 1996; Skelly et al. 1999; Trenham et al. 2003). The

degree to which habitat heterogeneity influences the fitness of community members will likely determine the applicability of traditional niche theories and neutral theories of communities. An integrated view suggests that joint processes of local niche assembly among heterogeneous habitats and regional dispersal lead to fitness equivalence at regional rather than local scales (Mouquet & Loreau 2002).

Metacommunity structure and dynamic

Evidence of interspecific trade-offs between local conditions from our data and from previous studies (Richards 2001; Urban 2004; Van Buskirk 2005) suggest metacommunity models (species-sorting or mass-effect model) for the application of niche-assembly. The species-sorting model suggested that partitioning of species among variable habitats operates according to individual adaptations and that interspecific fitness varies among patches (Leibold 1998). Dispersal rates are sufficient to distribute potential species among variable habitats, but not so fast that species sorting processes cannot selectively eliminate unfit species prior to recolonisation (Leibold et al. 2004). The mass-effect model differs from the species-sorting model by assuming that dispersal rates exceed the rate at which habitat conditions exclude species such that migrants influence assemblage composition in habitats (Mouquet & Loreau 2002). In our case the two regions seem to exhibit two different structures and dynamics.

In Collserola, the heterogeneous region with different terrestrial habitats, species showed a spatial segregation suggested by co-occurrence analyses, which is in concordance with predictions of species-sorting models, in which local factors and species-specific adaptations restrict the distributions of species. However, the same species pool showed a different structure and dynamic in Garraf. In Garraf, we detected no species segregation, and colonisation and extinction rates in general were higher than in Collserola, a scenario more similar to the one predicted by mass-effect models. These results suggest that the differences between both regions were mediated by variation in dispersion and animal movements. As animal movements can be determined by terrestrial habitat (Stevens et al. 2004), it is to be expected that in a landscape with different terrestrial habitats species restrict their movements to areas inside of or in close proximity to the adult habitat. Several species (e.g. *Bufo bufo,*

Rana dalmatina, *R. temporaria*, *Bombina variegata*, *Salamandra salamandra*) breed in sites which are near woodlands (Heusser 1968; Strijbosch 1979; Augert & Guyetant 1995). If species differ in adult terrestrial habitats, obviously co-occurrence at pond level is minimised and colonisation and extinction rates will be reduced. However, in a landscape without different terrestrial habitats, inter-pond movements are facilitated because animals don't have a place to which to restrict their movements, thus originating a community with a higher co-occurrence, local species richness, and with higher colonisation and extinction rates. These results are consistent with previous experimental studies. These studies of metacommunities have typically shown that increasing connectance among local communities increase diversity at the local scale (Warren 1996; Gilbert et al. 1998; Gonzalez et al. 1998).

The present study indicates the importance of terrestrial heterogeneity and their potential effect on species movement among ponds at regional level, and how this could determine the metacommunity structure and dynamic of the same pool of species. Accurate predictions of metacommunity dynamics depend on reconciling spatial scales of study with system-specific scales of environmental and landscape heterogeneity, interspecific variation, and dispersal limitations in terms of the permeability of matrix habitats (Urban 2004).

Searching a metapopulation concept for amphibians

Ecologists are becoming increasingly aware that processes affecting populations and communities do not stop at community boundaries and that issues of scale, in particular the interactions among processes operating at different scales, are of critical importance to understanding the dynamic of natural communities and assembled metacommunities (Leibold et al. 2004). However, defining meaningful scales for different organisms and different communities can be problematic, especially for organisms with complex life cycles (like amphibians) with two clearly different phases and which choose habitats at two levels: among terrestrial habitats from themselves and among aquatic sites for their offspring (Pope et al. 2000). A recurrent problem in pond-breeding amphibians and the application of metapopulation models for their conservation management is to be sure that each aquatic site represents a distinct population (Marsh & Trenham 2001). A recent fine-scale genetic study with newts

reveals that all individuals inhabiting a breeding site can indeed be regarded as a genetically panmictic unit (Jehle et al. 2005). In Jehle and coworkers study, individuals of one pond or a set of closer ponds can be distinguished genetically from relatively close neighbours. This observation is in agreement with metapopulation models which define three spatial scales: microsites, localities and regions (Appendix 2). In a recent, study Resetarits (2005) has proposed three scales for amphibians in terms of individual capacity of movement and choice of habitat for their offspring. Resetarits (2005) has defined a subdivided metapopulation consisting of "patches or microsites" (discrete communities or ponds), "localities" (local sets of discrete ponds), and large scale "regions" (group of localities). These categories were all defined as a function of the organism's perception of scale, and for management studies perception of scale and extension of "locality" must be adjusted to species-specific perception of scale. Resetarits' study has not considered terrestrial habitat choice by adults or juveniles. We think that this perspective will have to consider the terrestrial habitat. Hanski and Simberloff (1997) defined a patch as "a continuous area of space with all necessary resources for the persistence of a local population". According to this perspective, for amphibians and other taxa with complex life cycles, a patch must include the different habitats required by organisms to develop the different phases. Most studies on amphibians suggest that terrestrial habitats may also play an important role in population dynamics, by the presence of refuges, minor predators, low risk of desiccation or other resources (Loredo et al. 1996; Schwarzkopf & Alford 1996; Pope 2000; Rothermel & Semlitsch 2002) as well as the role of terrestrial habitat in determining local (within-pond) population dynamics (Skelly et al. 1999). The concept of "locality" of Resentarits (2005) must be amplified as a set of "ponds-as-patches" included in a terrestrial matrix capable of sustaining a population, distinguished genetically from close localities connected by dispersal individuals. The minimum geographical distance around a pond to configure a locality is impossible to specify (Jehle et al. 2005) because it depends on terrestrial habitats, to species capacity of dispersion (Smith & Green 2005), and because gene flow rates and animal movements can be determined by population size (Jehle et al. 2005).

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APPENDIX 1

Model selection

Model selection is one way to identify the model (referred to as the "best model") that is best supported by the data from among the candidate set. Model selection offers a way to draw inferences from a set of multiple competing hypotheses. The first step lies in articulating a reasonable set of competing hypotheses. These hypotheses, which originate in verbal or graphical form, must be translated to mathematical equations before being fit to data. Translating hypotheses to models requires identifying variables and selecting mathematical functions that depict the biological processes through which those variables are related.

Once a set of candidate models is specified, each model must be fitted to the observed data. At an early stage of the analysis, one can examine the goodness of fit of the most heavily parameterized model (e.g. the global model). Such goodness of fit in our case was assessed using a chi-square procedure, and the goodness of fit was estimated as $\hat{c} = \chi^2/df.$ If the global model provides a reasonable fit to the data, then the analysis proceeds by fitting each of the models in the candidate set to the observed data using the method of maximum likelihood.

Model selection criteria can then be used to rank competing models and to weigh the relative support for each one. To do this we used the maximum likelihood scores as a measure of fit (more precisely, negative log-likelihood as a measure of *lack* of fit) and a term that, in effect, penalizes models for greater complexity. Thus, Akaike's Information Criteria (AIC) aids in identifying the most parsimonious model amongst a set. We used the AIC, which considers fit and complexity of models.

$$AIC = -2\ln(likelihood) + 2p$$

where *p* is the number of free parameters of the model. Because in our case some Global models showed values of $\hat{c}$ > 1.0, we used a quasi-AIC (QAIC) corrected for small samples.

$$QAIC = -2\ln(likelihood) + 2p(\frac{n}{n-p-1})$$

where *n* is the sample size. This procedure is more appropriate than techniques which maximize fit alone (e.g. adjusted R^2 value), because these techniques have clear limitations with regard to parsimony. The advantage of using model selection criteria is that such criteria can be used to make inferences from more than one model, something that cannot be done using the fit maximization or null hypothesis approaches.

To know which models are best supported by the data, AIC provides an easy way for making this determination. The best model is the one with the lowest AIC. Differences in AIC (Δ_i) can be used to interpret strength of evidence for one model versus another.

$$\Delta i = AIC_i - AIC_{min}$$

where AIC_{min} is the AIC value of the "best" model. A Δ value within 1-2 of the best model has substantial and should be considered along with the best model. Values within 4-7 of the best model have considerably less support, and values > 8 have virtually no support and can be omitted from further considerations. Model likelihood values can also be normalized across all R models so that they sum to 1. This value is referred to as the Akaike weight (w).

$$w_i = \frac{\exp(-0.5\Delta i)}{\sum\limits_{r=1}^{R} \exp(0.5\Delta r)}$$

Akaike weights can be interpreted as the probability that model i is the best model for the observed data, given the particular candidate set of models. They are additive and can be summed to provide a confidence set of models, with a particular probability that the best approximating model is contained within the confidence set.

To estimate parameters that are of particular biological interest, we can use maximum likelihood parameter estimates when there is clear support for one model. However, when no single model is overwhelmingly supported by the data ($w_{best} < 0.9$), then model averaging can be used. This entails calculating a weighted average of parameter θ estimates.

$$\theta = \sum_{i=1}^{R} w_i \theta_i$$

where θ_i is the estimate value of parameter θ from the ith model.

APPENDIX 2

The concept of the metacommunity is mostly theoretical and has received little empirical attention (Leibold et al. 2004). These authors define a metacommunity as a set of local communities that are linked by dispersal of multiple potentially interacting species. This definition posits that there are at least two fairly discrete levels of community integration: (1) the local level, with a great deal of classic literature on species interactions (competition, prey-predator dynamics, trophic structure, etc.), and (2) the regional level. Variable rates of dispersion among species and local communities affect community structure and dynamics at local and regional level. Metacommunity thinking has already led to its own terminology which is in part presented in Table 1 following the definitions of Leibold and coworkers (2004).

Term	Definition
Ecological scale of organization	
Population	All individuals of a single species within a habitat patch
Metapopulation	A set of local populations of a single species that are linked by dispersal
Community	The individuals of all species that potentially interact within a single patch or local area of habitat
Metacommunity	A set of local communities that are linked by the dispersal of multiple interacting species
Descriptions of space	
Patch	A discrete area of habitat. Patches have been variously defined as microsites or localities
Microsite	A site that is capable of holding a single individual. Microsites are nested within localities
Locality	An area of habitat encompassing multiple microsites and capable of holding a local community
Region	A large area of habitat containing multiple localities and capable of supporting a metacommunity
Types of dynamics	
Spatial dynamics	Any mechanisms by which the distribution or movement of individuals across space influences local or regional population dynamics
Mass effect	A mechanism for spatial dynamics in which there is net flow of individuals created by differences in population size (or density) in different patches
Rescue effect	A mechanism for spatial dynamics in which there is the prevention of local extinction of species by immigration
Source-sink effects	A mechanism for spatial dynamics in which there is enhancement of local populations by immigration in "sink" localities due to migration of individuals from other localities where emigration results in lowered populations
Colonisation	A mechanism for spatial dynamics in which populations become established at sites from which they were previously absent
Dispersal	Movement of individuals from a site (emigration) to another site (immigration)
Stochastic extinctions	A mechanism whereby established local populations of component species become extinct for reasons that are independent of the other species present or of deterministic change in patch quality. Among other possibilities, these changes include stochastic components associated with small populations and extinctions due to stochastic environmental changes that can affect large populations
Deterministic extinctions	A mechanism whereby established local populations of component species become extinct due to deterministic aspects of patch quality or in the composition of the local community
Types of model population or community structure	
Classic metapopulation (Levins)	A group of identical local populations with finite and equal probabilities of extinction and recolonization – no rescue effects occur
Source-sink system	A system with habitat-specific demography such that some patches (source habitats) have a finite growth rate of greater than unity and produce a net excess of individuals which migrate to sink patches. Populations in sink habitats have finite growth rates of less than one and would decline to extinction in the absence of immigration from sources
Mainland-island system	A system in which variation in local population size influences the extinction probability of populations. Systems are usually described as consisting of extinction-resistant mainland populations and extinction-prone island populations
Open community	A community which experiences immigration and/or emigration
Closed community	A community that is isolated, receiving no immigrants and giving out no emigrants
Patch occupancy model	A model in which patches contain either individuals or populations of one or more species and where local population sizes are not modeled
Spatially explicit model	A model in which the arrangement of patches or distance between patches can influence patterns of movement and interaction
Spatially implicit model	A model in which the arrangement of patches and/or individuals does not influence the dynamics of the system. Movement is assumed equally likely between all patches
Metacommunity paradigms	
Patch dynamic perspective	Assumes that patches are identical and that each patch is capable of containing populations. Patches may be occupied or unoccupied. Local species diversity is limited by dispersal. Spatial dynamics are dominated by local extinction and colonization
Species-sorting perspective	Emphasizes the resource gradients or patch types that cause sufficiently strong differences in the local demography of species and the outcome of local species interactions such that patch quality and dispersal jointly affect local community composition. This perspective emphasizes spatial niche separation above and beyond spatial dynamics. Dispersal is important because it allows compositional changes to track changes in local environmental conditions
Mass-effect perspective	Focuses on the effect of immigration and emigration on local population dynamics. In such a system, species can be rescued from local competitive exclusion in communities where they are bad competitors, by immigrate from communities where they are good competitors. This perspective emphasizes the role that spatial dynamics affect local population densities
Neutral perspective	A perspective in which all species are similar in their competitive ability, movement and fitness. Population interactions among species consist of random walks that alter relative frequencies of species. The dynamic of species diversity is then derived both from probabilities of species loss (extinction, emigration) and gain (immigration, speciation).