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A landscape-level study on the breeding site characteristics of ten amphibian species in Central Europe

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Abstract. Temporary ponds are characterized as being in natural or close to natural states in Central and Eastern Europe, especially those located in forested landscapes. As these ponds function as breeding sites for many amphibians, they represent an ideal target to explore the terrestrial and aquatic habitat preferences of different species. We surveyed 133 small ponds in a forested, hilly region of North-Central Hungary. The occurrence of ten amphibian species and amphibian species richness were compared to six pond-related habitat variables and the extent of four terrestrial habitat types in the area surrounding the ponds. Our results suggest that most species' occurrence and species richness are chiefly related to pond characteristics, although terrestrial habitat variables could also be a determining factor in particular species. Whereas the majority of amphibian species prefer larger, hence more permanent water bodies with abundant aquatic vegetation, the common frog (*Rana temporaria*) chooses small, shallow wallow pits for breeding and has special requirements concerning terrestrial habitat composition. This could explain its restricted distribution in the area. Our results suggest that maintaining a diverse set of ponds and forestry management which facilitates habitats' structural heterogeneity are both important factors for the preservation of the rich amphibian fauna in Central Europe.

Keywords: breeding pond use, Hungary, landscape ecology, temporary ponds.

Introduction

Temporary ponds are important for a number of wildlife species (Williams et al., 2003; Scheffer et al., 2006; Scheffer and van Nes, 2007) and their persistence depends on various environmental factors. Having a relatively small size, their importance in ecosystems may be underestimated, and often their disappearance goes unnoticed (Semlitsch and Bodie, 1998). Temporary ponds fulfil a number of functions at both a local and landscape level. They act as breeding habitats for a number of organisms. Indeed, temporary ponds may have higher species richness than permanent ponds due to the absence of predatory fish (Scheffer et al., 2006). Further, temporary ponds may act as stepping stones for a number of wildlife species, increasing connectivity at the landscape level (Semlitsch, 2000; Williams et al., 2003; Roe and Georges, 2007).

Pond breeding amphibians are an important group to address the impacts of the globally threatening habitat loss on wildlife (Bender, Contreras and Fahrig, 1998; Fahrig, 2003) for a number of reasons, e.g. complex life cycles and dependence on both aquatic and terrestrial environments (Wilbur, 1980; Stuart et al., 2008); seasonal migration between habitats (Cushman, 2006); or sensitivity to environmental conditions due to their permeable skin (Feder and Burggren, 1992). As a consequence of these characteristics, amphibians are in global crisis (Alford and Richards, 1999; Houlahan et al., 2000), with habitat degradation and loss being the most important drivers of their decline in the Northern Hemisphere (Stuart et al., 2004).

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Considering their life history particularities, the habitat use and occurrence of pond breeding amphibians can be best understood by simultaneously examining pond-related and terrestrial habitat-related variables (Marsh and Trenham, 2001). An increasing number of studies use this approach to explore amphibian occurrence. In Europe, the majority of these studies were carried out in the western part of the continent where landscape fragmentation (e.g. due to intensive agriculture, increasing urbanization and road networks) was generally well pronounced, including Switzerland (Pellet, Guisan and Perrin, 2004; Van Buskirk, 2005; Zanini, Pellet and Schmidt, 2009), Italy (Ficetola and De Bernardi, 2004; Ficetola, Padoa-Schioppa and De Bernardi, 2009), Belgium (Denoël and Ficetola, 2007, 2008), Netherlands (Laan and Verboom, 1990; Vos and Chardon, 1998), England (Scribner et al., 2001), Ireland (Marnell, 1998), France (Joly et al., 2001; Denoël and Lehmann, 2006; Curado, Hartel and Anrtzen, 2011), and Sweden (Piha, Luoto and Merilä, 2007), but see Indermaur et al. (2010). The Central and Eastern European region is still scarcely covered by such studies, although some have been undertaken in Poland (Babik and Rafiński, 2001), and central Romania (Hartel et al., 2009, 2010a, 2010b). All these studies highlight the importance of traditional land use for the preservation of amphibians. Ecosystems and landscapes are considered to be generally less impacted by anthropogenic activities in this part of Europe (Palang et al., 2006; Hartel et al., 2008) therefore this region offers the opportunity to explore the ecology of amphibian habitat use (e.g. Hartel et al., 2010a, 2010b). Understanding environmental factors governing amphibian habitat use is important in Central Europe also because this region currently faces human-induced habitat changes, e.g. habitat fragmentation (Csorba, 2008; Kovács, Vági and Török, 2010) and climate change (Bartholy and Pongrátz, 2007). It is of great importance to know what features of an area with scarce human impact and especially what breeding pond characteristics are relevant for the maintenance of a diverse amphibian assemblage, as well as suitability for each species.

Here we present a case study of amphibian habitat in a forested area of Hungary. The ponds of this area have a temporary character and have a rich amphibian fauna. We focus both on individual amphibian species and species richness.

Materials and methods

Study area description

The study was conducted in the Pilis-Visegrád Hills (Pilis), located in North-Central Hungary within an area of $\sim$300 km^2 (fig. 1). Pilis is a moderately elevated range, the highest peak reaching 756 m above sea level, the altitude above 600 m representing less than 5% of total area. The Hills comprise two geologically different parts – Visegrád Hills on the northeast consist of mainly igneous rocks while the Pilis range at the southwest is made of limestone. As a consequence, surface water bodies and streams are more abundant in the northeastern part of the study area. The hydrology of the area is characterized mostly by temporary ponds, in addition to 10 small permanent streams.

The vegetation is mixed, consisting chiefly of deciduous forests although scattered hay meadows are also present. The oak forests of the lower altitudes are dominated by Turkey Oak (*Quercus cerris* L., 1753) and Sessile Oak (*Q. petraea* [Matt.] Liebl., 1784). The moderately elevated zones are covered mainly with mixed forests with oak species as above as well as Hornbeam (*Carpinus betulus* L., 1753). Pure Beech (*Fagus sylvatica* L.) stocks cover large parts of the northern slopes, the cooler valleys and the most elevated zones.

The Pilis ponds have either natural or artificial origin, those with the latter were established to provide drinking water for domestic animals and game at least 50 years ago. Due to the changes in land use and decreasing stockraising artificial ponds lost their significance in farming, hence their regular maintenance ceased. Nowadays all the ponds are governed primarily by natural processes. The pond maintenance activities of the forestry authority are restricted to occasional sediment removal in a few ponds.

Most of the ponds in Pilis Hills have a temporary character and, as a consequence, fish are absent; however, in years with above-average precipitation they retain water all year round. The surface of these small water bodies ranges from 10 to 6000 m^2 and their depth rarely exceeds 50 cm. Accumulating sediment could be significant in the ponds; sometimes the benthic sediment is 2-3 times deeper than the water column above. The average altitude of the ponds is $\sim$400 m, only five of them being above 600 m and none above 700 m.

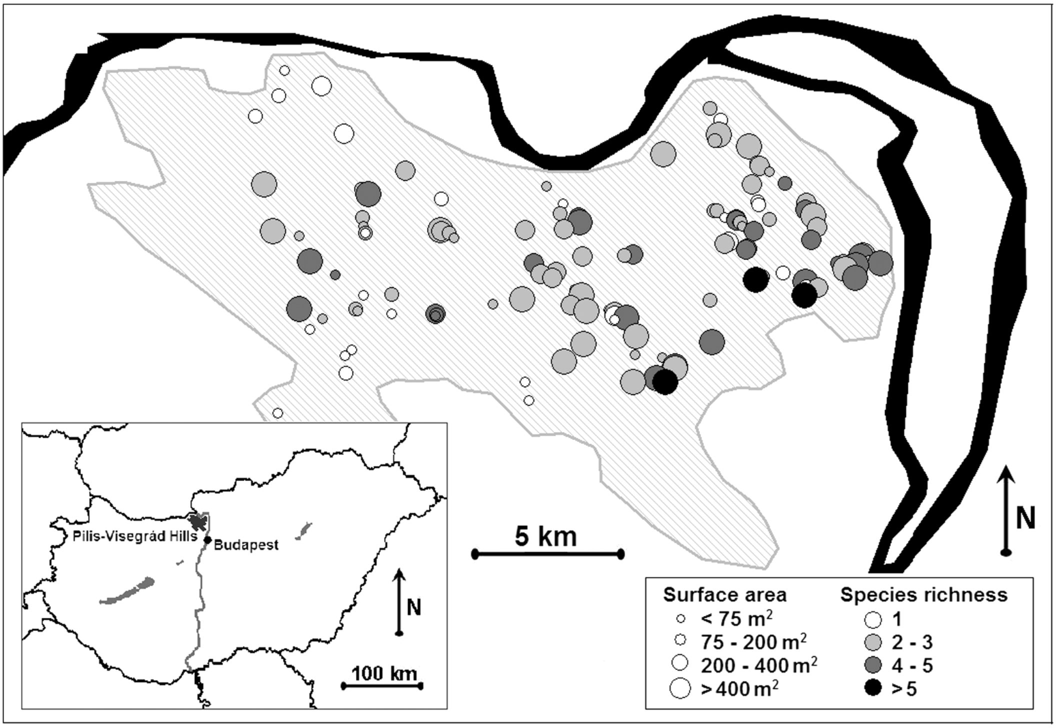

Figure 1. Location of the surveyed ponds in the region. The area with grey diagonal fill represents the area of Pilis-Visegrádi Hills. All the surveyed ponds are represented by circles, where the size of the circle represents the pond surface area, and the grey tone indicates the species richness (see legend). The thick black lines represent the Danube River. On the inset map: location of the study area in Hungary.

Amphibian surveys and variables selection

Surveys were made in 133 ponds in 2010. We included all known lentic water bodies of the area in our study, except those two large reservoirs, which contain fish. Each pond was visited at least twice between March and July: once during the breeding season of early-breeding amphibians (March and April), and a second time during May, June and July, when larvae of earlier breeders and adults of those species which reproduce later were present in the area. Amphibian presence was recorded by eggs, larvae, metamorphs or terrestrial life stages; in anurans supplemented with acoustic observations of calling adults. Arriving at a pond, we begun our survey with visual scanning of the whole surface area for egg clutches or strings, then we were dip-netting in the coastal area no longer than 20 minutes, changing our position every 2 minutes – we considered this interval was sufficient to detect all the species presented. Total sampling effort was related to the size of the pond; sometimes less than 20 minutes of dip-netting was considered enough due to the small size of the focal pond. Eggs and adults of frogs and toads were recorded by visual observation, larvae and adult newts by dip netting. As the ponds were isolated from each other (i.e. they were not connected to each other by streams) the presence of eggs and larvae was considered as an evidence for reproduction in the focal pond. Abundance of *Rana* species was estimated as the number of their egg clutches laid.

We characterized each site with 6 pond and 4 terrestrial variables (table 1). Approximate pond surface area was calculated from length and width measurements (to the nearest 1 m) taken by laser range finder (Precaster Enterprises Co., Taichung, Taiwan). On each study spot we drew an approximate line map of the pond and surface area was estimated by assuming an elliptic or rectangular shape. If it was necessary (as pond shape was too irregular), the approximate pond surface was divided into more than one elliptic or rectangular subunits and the total area was calculated by summing up the area of such subunits. Pond depth was measured at the deepest spot of the ponds by a measuring rod (to the nearest 5 cm). Sediment depth was calculated as the average of five measurements by a measuring rod (to the nearest 5 cm) at random locations in the ponds. Pond vegetation and shadow character of ponds were estimated by visual observation as presented in table 1. Elevation of the localities was recorded by GPS equipment (Garmin International, Olathe, Kansas, US), and all measures were validated using a detailed contour-map.

Terrestrial habitat types were recorded around the ponds by visual observation within a 50 m radius. We estimated the coverage of each surrounding habitat types visually, and established a rank scale based on their relative dominance (table 1). We followed this method because the relative abundance of a certain habitat (comparing to other types) was

Table 1. Definitions and abbreviations for pond related and terrestrial habitat related variables measured at each pond.

Variable	Description
Pond-related variables	
Pond surface (S)	The surface area of the pond (m^2)
Pond depth (Dpt)	The maximum depth of the pond (cm)
Sediment depth (Sed)	The depth of the benthic sediment (the water column was not considered) (cm)
Pond vegetation (Veg)	Represented mostly by *Typha* spp., *Phragmites* spp. and *Carex* spp. 0 – no macrophyte vegetation was present, 1 – macrophyte cover ranged between 1-33%, 2 – macrophyte cover ranged between 34-66%, 3 – macrophyte cover ranged between 67-100%;
Shadow character (Shd)	If ponds were shaded by trees. In this respect we recorded: 0 – the pond was located in an open area 1 – the pond was surrounded by a discontinuous ring of trees 2 – the pond was surrounded by a continuous ring of trees 3 – the pond was located in a closed forest
Pond elevation (Alt)	The altitude above sea level of the pond (m)
Terrestrial habitat variables	
Mixed hornbeam and oak forest (HO forest)	The terrestrial habitat variables (in a circle with 50 m radius) were measured on a rank scale as follows: 0 – the habitat type was absent 1 – the habitat type was in a subordinate state (it was present, but there were more abundant other habitat types around the pond) 2 – the habitat type was in equal ratio with other habitat type(s) 3 – the habitat type was dominant (there were other habitats around the pond, but this was the most abundant) 4 – this was the only, exclusive habitat type around the pond
Beech forest (B forest)	
Oak forest (O forest)	
Hay meadow (meadow)	

easily and quickly detectable. The resulting rank scale was not additive to the terrestrial habitat ranks around one pond; e.g. if a pond was surrounded by 3 different habitat types, and all of them covered 33% of total terrestrial area, summing up their ranks result in 6; while in the case when a pond is surrounded by one type of habitat, it was assigned a rank of 4. All four habitat types were handled as separate variables. We are confident that our method represents the dominance ratios between terrestrial habitat types, hence their relative importance in the terrestrial environment around the ponds.

Data analysis

All continuous variables were z-transformed (standardized to an average of zero and a standard deviation of one) to increase comparability of predictors (Ćirović et al., 2008).

Principal Component Analysis (PCA) was used to remove strong inter-correlations inherently present within the explanatory variables and to reduce the number of predictors. Four principal components were considered significant under a broken-stick distribution (Jackson, 1993; Diniz-Filho, Sant'Ana and Bini, 1998) (table 2). The VARIMAX method with Kaiser normalization was used as a rotation method. The first principal component (Comp. 1) was represented by pond related variables (PRV) (correlation coefficients between Comp. 1 scores and environmental variables: S 0.571, Dpt 0.620, Shd -0.778, Veg 0.649) and reflected size and permanence of the pond; the second (Comp. 2) was in a negative association with oak forests and in a positive association with mixed oak and hornbeam forest and hay meadows (OHM) (correlation coefficients between Comp. 2 scores and environmental variables: O -0.769, HO 0.547, M 0.524), and it reflected the ratio of these latter two habitat types, which are mainly present in the middle altitudinal zone; the third (Comp. 3) was in a positive association with beech forest (BF) and elevation and in a negative one with mixed oak and hornbeam forests so it reflected the coolest climate zone (correlation coefficients between Comp. 3 scores and environmental variables: B 0.644, HO -0.626, Alt 0.473). In the fourth principal component (Comp. 4) all correlations with habitat variables had a value below 0.5, and those variables which had a correlation coefficient close to 0.5 were included in principal components 1-3 with a higher value, therefore we omitted Comp. 4 from further analysis. The three variables extracted by PCA axes were used to design models starting with univariate models (3) that included one variable, and continued with complex models that included all combinations of two (3) and global model that included all three variables (4).

Information-theoretic approach was used to identify appropriate models for predicting the occurrence of individual amphibians species (Generalized Linear Model (GLM) assuming binomial error and a logit link function) and species richness (GLM assuming Poisson errors and a log link function); prior to analysis the assumptions required by GLM

Table 2. Habitat variables extracted by PCA, with eigenvalues, the percentage of variance explained before and after rotation, and the loadings (eigenvectors) of the original variables.

PC	1 (PRV)	2 (OHM)	3 (BF)	4
Initial eigenvalues	2.625	1.705	1.379	1.125
Total variance explained	26.254	17.048	13.787	11.251
Rotated eigenvalues	2.036	1.881	1.625	1.293
Total variance explained	20.357	18.809	16.245	12.928
Cumulative variance explained	20.357	39.167	55.412	68.340
Loadings for original variables				
Alt	−0.279	0.022	0.473	−0.425
S	0.571	0.145	−0.293	0.458
Dtp	0.62	0.488	0.075	0.276
Sed	−0.243	0.474	0.083	0.144
Shd	−0.778	−0.18	−0.171	0.214
Veg	0.649	−0.121	−0.164	0.055
O	0.448	−0.769	−0.113	−0.149
HO	−0.476	0.547	−0.626	−0.129
B	−0.315	−0.096	0.644	0.238
M	0.476	0.524	0.425	−0.378

were checked. The models were ranked according to their AICc values, the best model having the smallest AICc value. Delta (Δ) AICc was computed as the difference between each model and the best model. The Akaike weights (w_i) express the weight of evidence favouring the model as the best of all models. We calculated the percent deviance explained for each model by dividing the reduction in deviance for the full model by the deviance of the null model (Simon et al., 2009). We made species-level analysis on those species, which were present at least in 10% of the ponds. All statistical procedures were implemented in R 2.10.1 (R Development Core Team, 2009).

Results

Ten amphibian species were identified: *Salamandra salamandra* (Linnaeus, 1758), *Lissotriton vulgaris* (Linnaeus, 1758), *Bufo bufo* (Linnaeus, 1758), *Bombina bombina* (Linnaeus, 1761), *Bombina variegata* (Linnaeus, 1758), *Hyla arborea* (Linnaeus, 1758), *Pelobates fuscus* (Laurenti, 1768), *Pelophylax* spp. (Fitzinger, 1843), *Rana dalmatina* (Bonaparte, 1840) and *R. temporaria* (Linnaeus, 1758). The most common species was *R. dalmatina*, being identified in 128 of the 133 ponds (fig. 2). *R. temporaria*, *B. bufo*, and *L. vulgaris* occurred in 50-70 ponds while *H. arborea* was identified in 20 ponds. Other species were rare, being present in less than 10 ponds each.

The occurrence of three species (*R. dalmatina*, *B. bufo* and *L. vulgaris*) was best explained by models containing only pond related variables (PRV) while for species richness and the occurrence of the remaining species were best predicted by models containing both pond- and terrestrial habitat related variables (table 3). The explained deviance of the best models ranged between 5.51 (*B. bufo* occurrence) and 169.29 (*R. temporaria* occurrence), indicating a generally good predictive ability.

Most species of amphibians were positively associated with Comp. 1 (PRV) except *R. temporaria* occurrence, which was negatively influenced by PRV (table 4). The occurrence of *R. dalmatina* was positively associated with pond related variables but the relationship only approaches statistical significance ($P = 0.057$), and it has to be considered that *R. dalmatina* occurred in 128 out of 133 ponds (96%), which reduces the predictive value of the model for that widespread species. *Rana temporaria* was positively associated with Comp. 2 (OHM). Comp. 3 (BF) negatively influenced amphibian species richness and the occurrence of *H. arborea* (table 4). No significant associations were found between the occurrence of *B. bufo* and the measured variables (table 4).

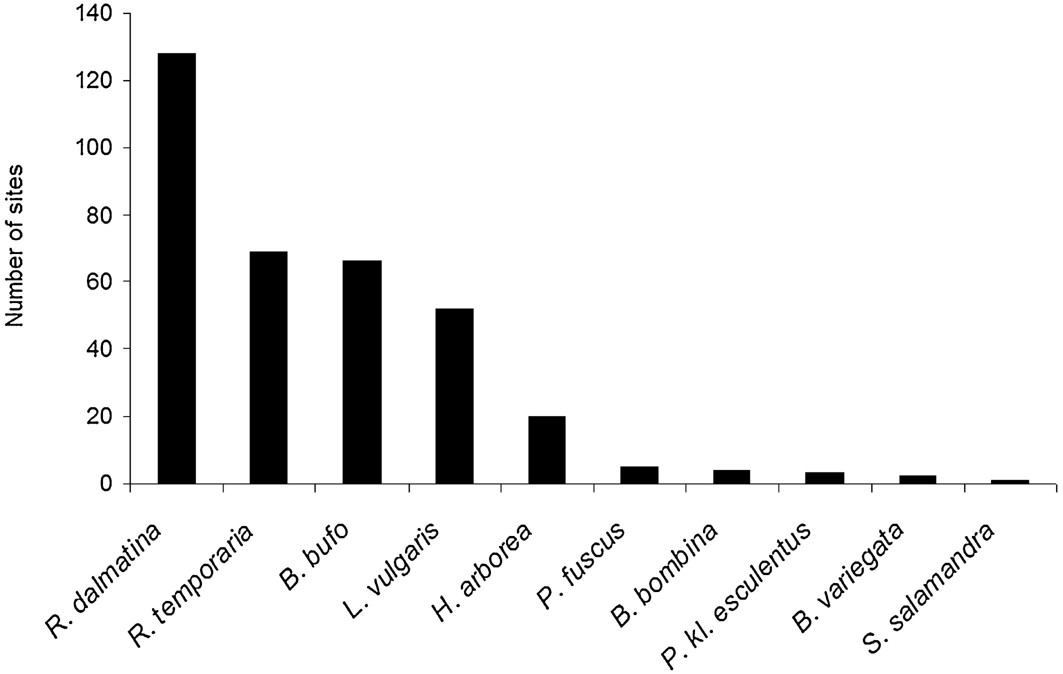

Figure 2. The number of ponds occupied by each amphibian species identified.

Discussion

Our study found that factors affecting amphibian occurrence and community richness in these ponds were mostly pond-related. However, for two species and the species richness the best habitat use models contained at least one terrestrial habitat variable, showing that both pond and terrestrial variables need to be considered to understand the occurrence of pond breeding amphibians (see also Van Buskirk, 2005; Hartel et al., 2010a). We found that pond area, depth and vegetation had generally positive effects on the occurrence of amphibians and the species richness. Such a result was not unexpected given that the pond system studied by us consists primarily of temporary ponds and both area and depth are indicators of pond size and permanence. Theory and empirical research predict that pond hydroperiod (i.e. the period of time ponds are filled with water) may impose various conditions, which may limit the occurrence of organisms with complex life cycles (Wellborn, Skelly and Werner, 1996) including pond-breeding amphibians (Weyrauch and Grubb, 2004; Herrmann et al., 2005; Vignoli, Bologna and Luiselli, 2007). In temporary ponds, a decrease of water volume negatively influences larval growth rates and body size at metamorphosis through a number of processes related to intra- and interspecific competition, resource depletion, the accumulation of metabolic waste and change of physical and chemical parameters of water (Wilbur, 1987). These in turn will influence larval survival, the success of metamorphosis and adult fitness (Wilbur, 1987). Although these ponds are of temporary character, we could not test the length of hydroperiod, as 2010 was an extremely wet year and none dried out during the sampling period.

In our study three species and species richness are positively associated with PRV, which reflects pond size, depth and vegetation. However, *R. temporaria* shows a negative association with this principal component. Although *R. temporaria* is a common species in Northern and Western Europe, in Hungary it has a restricted distribution (Dely, 1967), possibly be-

Table 3. Model selection results. Models are ranked in a decreasing Akaike weight (w_i) order. For clarity, models with Akaike weight < 0.03 are not shown. Statistics include the explained variance (D^2), the number of estimated parameters (K), the second order Akaike Information Criterion corrected for small sample sizes (AICc), AIC difference (Δi) and Akaike weights (w_i).

	Model structure	D^2	K	AICc	Δi	w_i
Species richness						
	PRV + OHM + BF	80.06	4	445.44	0.00	0.39
	PRV + OHM	84.49	3	447.75	2.31	0.12
	PRV + BF	84.87	3	448.13	2.69	0.10
	PRV	88.54	2	449.70	4.26	0.05
Rana dalmatina occurrence						
	PRV	37.80	2	41.89	0.00	0.33
	PRV + OHM	37.21	3	43.39	1.51	0.15
	PRV + BF	37.78	3	43.97	2.08	0.12
	PRV + OHM + BF	36.37	4	44.68	2.80	0.08
Rana temporaria occurrence						
	PRV + OHM	166.74	3	172.93	2.16	0.16
	PRV + OHM + BF	166.31	4	174.62	3.85	0.07
Bufo bufo occurrence						
	PRV	9.28	2	13.37	0.00	0.2
	PRV + BF	8.50	3	14.69	1.31	0.1
	PRV + OHM	8.87	3	15.05	1.68	0.09
	OHM	11.65	2	15.75	2.37	0.06
	BF	11.73	2	15.83	2.45	0.06
	PRV + OHM + BF	8.50	4	16.81	3.44	0.04
Hyla arborea occurrence						
	PRV + BF	77.74	3	83.93	0.00	0.34
	PRV + OHM + BF	75.84	4	84.15	0.22	0.3
Lissotriton vulgaris occurrence						
	PRV	159.23	2	163.32	0.00	0.22
	PRV + OHM	157.40	3	163.58	0.26	0.20
	PRV + BF	157.71	3	163.89	0.57	0.17
	PRV + OHM + BF	155.78	4	164.09	0.77	0.15

cause it is outcompeted from most breeding sites by other species. Our field experience confirms that this species often lays its eggs in small, shaded wallow pits without vegetation. One possible reason for this preference is that this species requires shallow water as it lays its egg clutches on the bottom of the ponds and does not attach it to plants or overhanging branches like *R. dalmatina* (personal observation). Another possible cause is that the reproduction of the two species coincides both temporally and spatially, which can result in reproductive interference (Hettyey et al., 2009), and further competition is possible among the tadpoles. According to this study, these small water bodies are suboptimal for *R. dalmatina* (however, due to the widespread occurrence of *R. dalmatina*, model performance is weaker for this species, but our unpublished data on abundance also confirms this assumption), hence in those breeding sites *R. temporaria* could avoid strong competition. If this assumption is true, the tadpoles of *R. temporaria* should be more adapted to develop in small ponds where the risk of desiccation could be higher. Contrarily, these small ponds also have a more shaded character due to the nearly continuous canopy cover, which can decrease the risk of desiccation. However, the lack of direct solar radiation also reduces the water temperature, and this can slow down the development of the tadpoles (Lillie and Knowlton, 1897).

Vegetation cover was also an important component of the pond related variables, positively influencing amphibians. Amphibians may benefit from aquatic vegetation through a number

Table 4. The relationship between amphibian species richness, occurrences and the three habitat variables extracted by PCA axes.

	Parameter estimate	SE	Test statistic (Wald χ^2)	p
Species richness				
PRV	0.213	0.046	4.599	<0.001
OHM	0.114	0.053	2.155	0.031
BF	−0.106	0.055	−1.924	0.054
R. dalmatina occurrence				
PRV	5.077	2.662	1.907	0.057
OHM	1.581	1.420	1.113	0.266
BF	1.024	0.845	1.211	0.226
R. temporaria occurrence				
PRV	−0.487	0.192	−2.539	0.011
OHM	0.649	0.205	3.164	0.002
BF	0.121	0.189	0.639	0.523
B. bufo occurrence				
PRV	65.852	83.474	0.789	0.430
OHM	−0.100	11.397	−0.009	0.993
BF	11.012	11.827	0.931	0.352
H. arborea occurrence				
PRV	1.777	0.422	4.208	<0.001
OHM	0.432	0.288	1.499	0.134
BF	−1.476	0.552	−2.676	0.007
L. vulgaris occurrence				
PRV	0.930	0.241	3.850	<0.001
OHM	0.263	0.191	1.374	0.169
BF	−0.269	0.215	−1.248	0.212

* SR = species richness; PRV = pond related variables; OHM = mixed oak and hornbeam forest and hay meadows; BF = beech forest and high altitude (cool microclimate).

of ways: refuge against predators (e.g. Teplitsky, Plénet and Joly, 2003), support for eggs (e.g. Ficetola, Valota and De Bernardi, 2006; Tóth, Hoi and Hettyey, 2011) and surface for algal development (that constitutes food for the tadpoles). This may allow amphibian larvae to grow and develop quicker and increase the chance for metamorphosis. In our study vegetation is particularly important for *Hyla arborea*, which make its choirs in dense vegetation and *Lissotriton vulgaris*, which wraps its eggs into the leaves of aquatic plants (Tóth, Hoi and Hettyey, 2011). Both species' occurrences are in a very significant positive association with PRV variable, which includes pond vegetation among its components. Species richness is also significantly correlated with PRV, therefore pond size and vegetation may be important factors also for the rare species we could not analyze.

Terrestrial areas such as forests can influence the quality of the pond habitats, e.g. by limiting light conditions and thus may indirectly influence amphibian occurrence and community structure in ponds (e.g. Werner, 2007). Previous studies conducted in traditionally managed farmlands of Eastern Europe (Hartel et al., 2010a, 2010b) showed that deciduous forest, where abundant, was not a limiting factor for amphibians. In more fragmented landscapes forests can even function as a driver of amphibian species occurrences (Herrmann et al., 2005). The present study showed that *H. arborea* tend to avoid high elevation ponds with increased beech cover in their surroundings. This is likely related to the thermal preferences of *H. arborea*, which prefers warmer ponds while the beech forests typically creates a colder microclimate. The species richness and *Rana temporaria* occurrence were positively associated with mixed oak and hornbeam forest and hay meadows (OHM). Hornbeam mixed with oak may create better habitat conditions for amphibians than the pure beech or pure oak stocks in the moderately mountainous landscape studied by us. Canopy cover in oak forests is generally more open than in beech forests (Hortobágyi and Simon, 1981) and this may result in warmer ground temperatures in mixed oak-hornbeam forests than in the compact beech forests. On the other hand, pure oak forests have substantially drier microclimates (Hortobágyi and Simon, 1981), which is also not favorable for most amphibian species. Mixed forests and hay meadows are situated at middle altitudes – where low elevation and high elevation species overlap in their occurrence – and this can result in a higher species richness.

In conclusion, our study found that pond related variables are the primary drivers of amphibian occurrence in this region. Pond loss may have serious consequences on amphibians at two scales: (i) the reduction of breeding habitat diversity and the opportunity to actively select ponds for reproduction (e.g. Sinsch and Seidel, 1995; Petranka, Smith and Scott, 2004); and (ii) the decrease of landscape connectivity by the destruction of ‘stepping stone’-like structures (Hartel et al., 2010a).

Our results suggest that for most species large ponds with dense vegetation are the most suitable breeding sites, but the common frog prefers shallow and shaded wallow pits. Hence the preservation and maintenance of a set of ponds of different size would be beneficial for the conservation of the whole amphibian assemblage in Pilis Hills. For some species and the species richness the terrestrial habitats in the close surroundings of the pond also were important in determining their breeding habitat use. Mixed forests had more positive influence on amphibians, and the mixing ratio of trees is mostly determined by forestry managing the Pilis area. Therefore proactive maintenance of the structural diversity assured by the diversity of native trees could be important in maintaining breeding sites attractive for amphibians.

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