

1 Amphibian communities are structured by local habitat quality 2 in garden ponds and spatial factors in urban ponds

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45 **Conflict of interest statement**

46 The authors declare no conflict of interest.

47 **Data availability statement**

48 The data associated with the manuscript will be available via the Figshare repository at
49 <https://doi.org/10.6084/m9.figshare.31812748>. Pond coordinates are available from the authors
50 upon reasonable request. To protect the privacy of private property owners participating in the
51 study, the coordinates of private ponds are provided only at reduced spatial precision.

52 **Abstract** [182 words]

53 Amphibians are among the most threatened vertebrates, and urbanisation contributes to their
54 decline through habitat loss, fragmentation, pollution, and the spread of invasive species. At
55 the same time, urban freshwater habitats, such as ponds, can serve as important refuges within
56 highly modified landscapes. While the role of urban ponds in supporting freshwater
57 biodiversity is increasingly recognised, the contribution of privately managed garden ponds
58 remains poorly understood. Here, we compared amphibian communities in 90 ponds across

59 Budapest, Hungary, including privately managed garden ponds and other urban ponds, to
60 evaluate the relative importance of local environmental conditions, landscape context, and
61 spatial connectivity. Amphibian communities differed less in taxonomic composition than in
62 the processes structuring them. Garden pond communities were primarily shaped by local
63 environmental filtering, whereas spatial configuration within the pond network played a
64 stronger role in structuring communities in larger urban ponds. These results highlight
65 contrasting mechanisms of community assembly across urban pond types. Urban amphibian
66 conservation can therefore benefit simultaneously from local stewardship of garden ponds and
67 strategic planning of connected urban pond networks that reduce dispersal barriers across the
68 urban landscape.

69 **Keywords:** biodiversity; urban ecology; conservation; freshwater ecology; metacommunity

70 **Introduction**

71 Urbanisation is an inevitable outcome of rapid population growth and associated economic
72 development (Seto, Güneralp & Hutyrá, 2012; United Nations, 2022). However, it remains one
73 of the major drivers of biodiversity loss worldwide (McKinney, 2002; Oertli & Parris, 2019;
74 McDonald *et al.*, 2020). Urban development exerts multiple stressors on ecosystems, including
75 habitat loss and fragmentation, pollution, altered hydrology, the spread of invasive species, and
76 increased human disturbance (Dudgeon & Strayer, 2025). These stressors modify the physical
77 environment in urban ecosystems and can act as strong abiotic filters for the local biota (Grimm
78 *et al.*, 2008; Francis & Chadwick, 2013).

79 Urban ponds have been increasingly recognised for their potential to conserve biodiversity
80 within cities, acting as valuable refuges and contributing to urban ecological networks (Hassall,
81 2014; Krivtsov *et al.*, 2022). These small water bodies can support diverse taxa (Oertli *et al.*,
82 2002; Hill *et al.*, 2017), including amphibians, which often rely on them for breeding, dispersal,
83 and shelter within otherwise fragmented urban landscapes (Parris, 2006). Different types of
84 urban ponds - such as stormwater ponds (Brand & Snodgrass, 2010; Scheffers & Paszkowski,
85 2013), drainage ponds (O'Brien, 2015), and garden ponds (Banks & Lavericki, 1986;
86 Butterworth, Van Helden & Close, 2025) - can all provide important habitats for amphibians,
87 even though they differ strongly in management regimes and environmental conditions (Oertli
88 & Parris, 2019; Hassall, 2014; Horváth *et al.*, 2025). Urban ponds may therefore function as
89 critical components of conservation networks, supporting metapopulation dynamics and

90 providing refugia for threatened taxa in heavily modified landscapes where many natural
91 aquatic habitats have been lost.

92 Urban ponds found in parks, natural reserves or other publicly accessible areas within an urban
93 landscape generally tend to be larger, older, and more heterogeneous (Hassall, 2014; Peeters *et*
94 *al.*, 2023), whereas garden ponds, as their specific subtype, tend to be smaller, younger, and
95 subject to more intensive management by their owners (Loram *et al.*, 2011; Hassall, 2014;
96 Hamer *et al.*, 2024). Urban ponds differ not only in their physical and environmental
97 characteristics but also in their origin, ownership, and management, creating distinct ecological
98 settings within the same urban matrix. Current understanding of biodiversity in urban pond
99 networks remains strongly biased toward larger, publicly accessible water bodies, whereas
100 privately managed garden ponds are still understudied, despite representing a substantial
101 proportion of potential amphibian habitat in urban areas (Horváth *et al.*, 2025). Garden ponds
102 can also increase habitat connectivity in the urban landscape and provide aquatic refugia for
103 multiple species during droughts, thereby stabilising metapopulation dynamics within urban
104 landscapes.

105 Pond-breeding amphibians are among the most endangered vertebrate groups, with
106 approximately 41% of species currently threatened by habitat loss and climate change (Luedtke
107 *et al.*, 2023). Beyond their conservation status, amphibians play key ecological roles in
108 freshwater and terrestrial ecosystems by regulating invertebrate populations and mediating
109 energy and nutrient fluxes between aquatic and terrestrial habitats, thereby contributing to
110 ecosystem structure and function (Hocking & Babbitt, 2014). Moreover, because of their
111 permeable skin, biphasic life cycles, and limited dispersal ability, amphibians are widely
112 regarded as sensitive indicator taxa for assessing habitat quality, pollution, and functional
113 connectivity in freshwater networks, including urban pond systems (Estes-Zumpf *et al.*, 2022).
114 Urbanisation generally exerts negative effects on amphibian assemblages, with increasing
115 levels of urban intensity often leading to declines in both species richness and functional
116 diversity (Pereyra *et al.*, 2021; Demartin, Ghirardi & Lopez, 2024). Their dependence on both
117 aquatic and terrestrial habitats makes them particularly sensitive to multiple urban stressors
118 operating across spatial scales (Hamer & McDonnell, 2008; Smallbone, Luck & Wassens,
119 2011).

120 Amphibian occupancy is typically shaped by factors across multiple spatial scales due to their
121 lifestyle: at the local scale, pond size, vegetation cover, water quality and predation pressure

122 play a key role (Hamer & Parris, 2011; Falaschi *et al.*, 2020; López-de Sancha *et al.*, 2025).
123 Landscape-scale features, including green space availability or the proximity to other ponds or
124 aquatic habitats, affect dispersal and long-term persistence within habitat networks (Collins &
125 Fahrig, 2017; Zhang, Li & Yang, 2022). In addition, amphibians often rely on temporary ponds
126 as stepping-stone habitats that facilitate movement between suitable breeding sites across
127 otherwise inhospitable matrices (Fortuna, Gómez-Rodríguez & Bascompte, 2006). In urban
128 ponds, human management can further modify local conditions by regulating vegetation, fish
129 or macroinvertebrate populations, or applying chemical treatments (Maerz, Blossey & Nuzzo,
130 2005; Oertli & Parris, 2019; Márton *et al.*, 2025). These local effects interact with landscape-
131 scale urbanisation processes that reshape ecological dynamics and constrain habitat quality for
132 amphibians (Kurz *et al.*, 2014; Mendenhall *et al.*, 2014; Thompson, Nowakowski & Donnelly,
133 2016). Despite growing research on urban freshwater systems, it remains unclear whether
134 amphibian communities in different types of urban ponds are structured by similar
135 environmental and spatial processes. Comparative studies disentangling environmental and
136 spatial drivers across different types of ponds remain scarce, limiting evidence-based
137 management in urban landscapes.

138 Here, we present the first comparative study of amphibian communities in privately managed
139 garden ponds and other urban ponds (in parks and nature reserves), evaluating how local habitat
140 quality and spatial connectivity jointly structure urban amphibian metacommunities. Using a
141 city-wide dataset from Budapest, Hungary, we tested whether amphibian species richness and
142 community composition differ between pond types and whether the relative importance of
143 environmental and spatial drivers varies between them. As garden ponds are typically smaller
144 and more intensively managed than other urban ponds, we expected stronger local
145 environmental filtering in these systems. However, given that amphibians frequently move
146 among ponds during their life cycle, we expected spatial connectivity within the pond network
147 to influence amphibian occurrence in both pond types. Understanding these mechanisms can
148 inform conservation strategies that integrate local habitat management with landscape-scale
149 connectivity in urban environments.

150 **Methods**

151 **Site selection**

152 Garden ponds were selected from the participant pool of the citizen science project called
153 MyPond (<https://mypond.hu/>) (Hamer *et al.*, 2024; Márton *et al.*, 2025; Huỳnh *et al.*, 2025), all
154 found within a 36 km radius of the centre of Budapest, covering a substantially larger area than
155 the city. The level of urbanisation around each pond was quantified as the proportion of urban
156 land cover (i.e., urban area including buildings and roads as well as other artificial surfaces but
157 not urban green spaces) within a 1 km radius, extracted from the Ecosystem Map of Hungary
158 (project KEHOP-430-VEKOP-15-2016-00001, Ministry of Agriculture, 2019). This index was
159 used solely for the stratified selection of garden ponds. The level of urbanisation surrounding
160 these ponds differed substantially; therefore, we divided the full gradient into ten equal-width
161 urbanisation categories (0-1 in 0.1 increments). We then randomly selected 6 ponds from each
162 of the ten categories using the ‘ddply’ function from the ‘plyr’ package (v1.8.9; Wickham,
163 2011a) and contacted their owners. As not all owners responded positively, we contacted
164 additional owners, which eventually resulted in 40 garden ponds.

165 In parallel, we compiled an inventory of publicly accessible urban ponds across the
166 metropolitan area of Budapest. The selection was based on field surveys and aerial imagery. In
167 addition, several ponds located within protected areas were included following consultations
168 with local nature conservation officers. Altogether, 54 urban ponds were identified. Although
169 some small or temporary ponds may have been overlooked, the dataset represents the vast
170 majority of urban ponds in Budapest (**Figure 1**).

171 Upon investigating the whole dataset compiled of 40 garden and 54 urban ponds, we decided
172 to exclude four ponds from the analysis. Two garden ponds were identified as agricultural
173 farmland ponds rather than actual ornamental garden ponds. From the urban pond subset, one
174 was excluded due to the lack of sampling permission, and another was also removed because
175 of its substantially smaller surface area (7 m²) compared to the rest (**Table S6**). This resulted
176 in a final dataset of 90 ponds in total, comprising 38 garden and 52 urban ponds.

177 **Field surveys and laboratory measurements**

178 Each pond was sampled once between April 4th and May 17th, 2022. At the beginning of each
179 survey, a 5-minute pre-disturbance acoustic survey was conducted to detect any anuran species
180 calling. Then, dipnetting was carried out with a net (mesh size 500 µm) to sample the water
181 body for larval stage anurans and newts. The number of sweeps was scaled to pond surface
182 area (**Table S1**) and allocated proportionally across microhabitats. We recorded species

183 presence and counted all visually encountered individuals during the surveys, including larvae
184 and adults. We recorded the presence of fish and the abundance of macroinvertebrates per litre
185 obtained during aquatic sampling. Macroinvertebrates were preserved in alcohol (70%) and
186 kept at 18-20°C until sorting and identification to the lowest taxonomic level in the laboratory.

187 Pond substrate (natural, concrete, plastic or rubber) was recorded, and data on approximate age
188 were collected from the pond owners. The percentage cover of water level, emergent,
189 submerged, fringing and floating vegetation, surface algae, open water, canopy cover and
190 woody debris was estimated visually at each pond. Pond depth was determined based on
191 information from their owners. The area of small ponds was measured with a measuring tape,
192 while the area of larger ponds was delineated and calculated using GIS (QGIS Development
193 Team, 2022). On-site measurements of physical and chemical parameters included
194 temperature, dissolved oxygen concentration (Hanna HI 9142N probe), pH, and electrical
195 conductivity (WTW 3620 IDS probe).

196 Chlorophyll-a fluorescence was measured with an AquaPen (AP 100-C, Photon System
197 Instruments). Water samples were collected from each site within 1 m of the shoreline for
198 chemical analysis. We used a Multi N/C 3100 TC-TN analyzer (Analytik Jena, Germany) to
199 measure total organic carbon (TOC) and total nitrogen concentrations (TN). We used standard
200 spectrophotometric methods following the protocols of Eaton et al. (2005) to measure the
201 concentration of total phosphorus (TP) and additional water chemistry variables (major ions,
202 metalloids, and heavy metals) (**Table S3**).

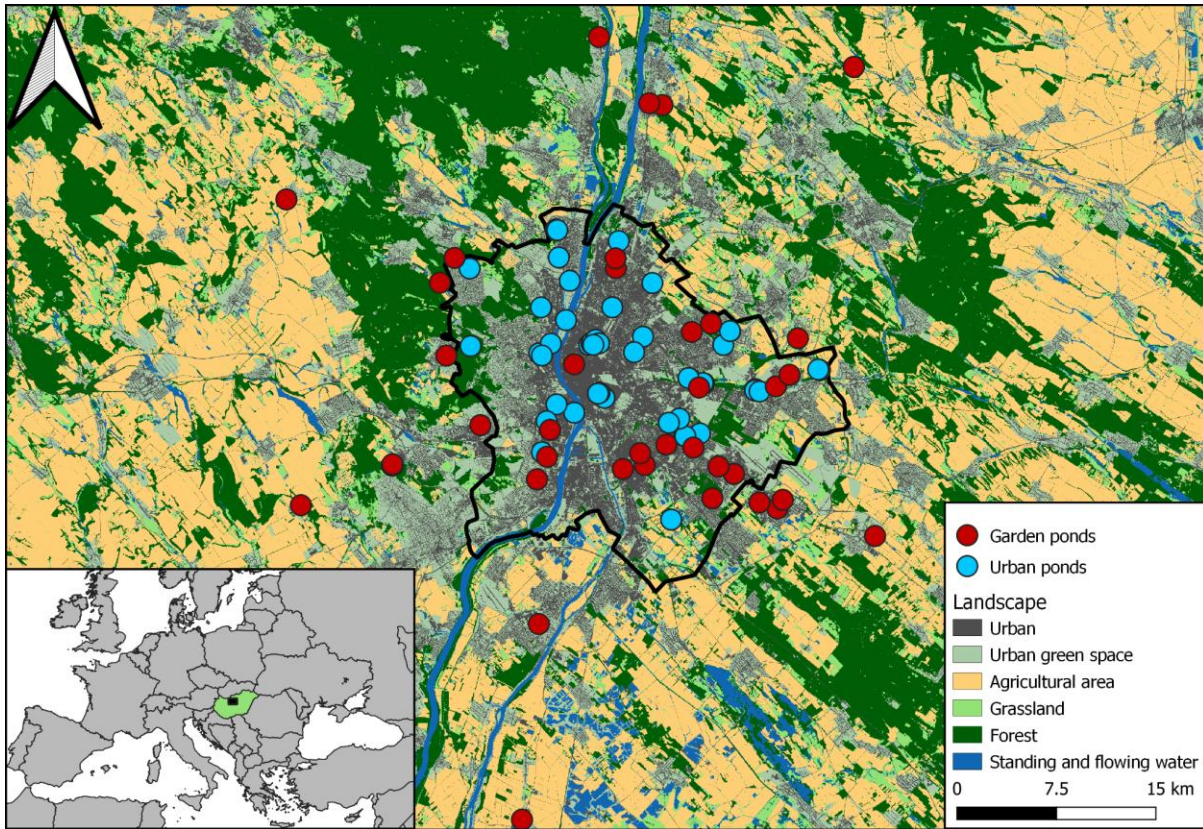
203 **Landscape and spatial data**

204 We used the Ecosystem Map of Hungary (project KEHOP-430-VEKOP-15-2016-00001,
205 Ministry of Agriculture, 2019) through QGIS 3.16.14 (QGIS Development Team, 2022) to
206 determine the effects of landscape cover on amphibian communities. A 1-km radius buffer was
207 mapped around each pond, which represents the maximal dispersal distance of most species
208 expected to occur in the study area (Smith & Green, 2005; Kovar *et al.*, 2009). Data on
209 landscape cover was extracted using the Zonal Histogram tool by counting the number of 20x20
210 m raster pixels of different landscape categories within the 1-km buffers. We recorded the
211 proportions of the urban land cover (tall buildings, short buildings, other artificial surfaces,
212 impermeable roads, railways), dirt roads, urban green space, agricultural area, grassland, forest,
213 and standing and flowing water (wetland, rivers) around the ponds. Tall, short buildings and

214 other artificial surfaces were merged into a single urban area variable, while impermeable roads
215 and railways were merged into the roads variable. Dirt roads were kept as a separate variable
216 since they are more permeable to amphibians than concrete roads or railways. We extracted
217 human population density from the JRC-GEOSTAT 2018 population grid (Joint Research
218 Centre, European Commission, 2021) using the Zonal Statistics tool to characterise
219 anthropogenic pressure around ponds, using population data from April 2021.

220 To measure the effects of pond connectivity within the urban landscape, we calculated
221 closeness centrality and nearest-neighbour distance. We calculated the closeness centrality of
222 each pond based on the spatial distance matrix among all ponds, thereby quantifying each
223 pond's relative connectedness within the pond network. For this, we used the 'igraph' (v2.1.1;
224 Csárdi et al., 2026), 'fields' (v16.3; Nychka et al., 2021) and 'reshape2' (v1.4.4; Wickham,
225 2007) packages of the R software. Nearest-neighbour distance (distance to the closest pond)
226 was calculated using the 'fields' package (v16.3; Nychka et al., 2021). To calculate both
227 indices, we used a pond network with a larger dataset of 384 ponds from a citizen science
228 program (Hamer *et al.*, 2024). We then extracted the corresponding index values for the 90
229 sampled ponds used in the subsequent analysis.

230 To detect spatial patterns in the data, we used Moran's Eigenvector Maps (MEM) generated
231 with the R package 'adespatial' (v0.3.24; Dray et al., 2024). We only retained MEM
232 eigenvectors with positive autocorrelations as these represent broad- to intermediate-scale
233 spatial structures typically linked to ecological processes such as dispersal and spatially
234 structured environmental variation, whereas negative MEMs primarily capture fine-scale noise
235 or checkerboard patterns that are difficult to interpret ecologically (Dray, Legendre & Peres-
236 Neto, 2006). MEMs were calculated for the three datasets (for all ponds, only for garden ponds,
237 and only for urban ponds), matching the community datasets (i.e., we only used locations of
238 garden ponds for the garden pond dataset), resulting in three different sets of MEMs for the
239 three datasets.



240

241 **Figure 1:** Location of the study sites within the urban landscape of Budapest, Hungary. The
 242 map illustrates the spatial distribution of surveyed garden and urban ponds across the
 243 metropolitan area, providing the spatial context for subsequent environmental and spatial
 244 analyses.

245 **Response variable preparation**

246 Species data of all detected larvae and adult individuals were converted to presence–absence
 247 (0/1) before analysis. Sites at which no amphibian species were detected were removed.
 248 Multivariate community analyses were conducted on the remaining 14 garden and 19 public
 249 ponds.

250 For species-level habitat-use analyses, we employed an analogous modelling framework using
 251 all ponds of each dataset. To ensure robust estimation, model convergence and adequate
 252 representation, analyses were restricted to species recorded at least four times in each pond
 253 type (*Pelophylax* spp., *Rana dalmatina*, *Bufo bufo*, *Bufo viridis*).

254 **Predictor data preparation**

255 Some of the measured variables were excluded before analysis: water temperature and
256 dissolved oxygen due to high short-term variability. Water depth was removed from the
257 analysis due to having a high proportion of missing values. Some of the other environmental
258 variables (submerged vegetation, surface algae, predatory threat index and fish) were also
259 missing a smaller share of data (1 to 6 out of 61 ponds) due to field or lab measurement issues.
260 Here, missing values were imputed using the ‘mice’ package (v3.16.0; Buuren and Groothuis-
261 Oudshoorn, 2011), employing predictive mean matching (pmm) with five imputations. The
262 imputation model was based on correlations among the remaining environmental variables.

263 The four substrate categories were represented by three dummy variables, with the rarest
264 category (plastic) used as the reference level and therefore coded as 0 across the other three
265 variables. Fish presence was used as a binary variable. Pond age was transformed into an
266 ordinal variable based on the following formula: ponds aged 1 - 5 years = 1, 6 -10 years = 2, >
267 10 years = 3.

268 To account for biotic interactions with predatory macroinvertebrates, we constructed a
269 predatory threat index (Van Buskirk, 2005; Hamer & Parris, 2013). Predator abundances were
270 weighted by their relative risk to amphibian larvae and subsequently summed into a single
271 composite variable (**Table S2**).

272 To approximate Gaussian distributions (assessed using the Shapiro–Wilk test) for the analysis,
273 variables were subjected to various transformations (**Table S3**). Following transformations, all
274 predictors were standardised using z-score. We ran a principal component analysis (PCA) on
275 the water chemistry variables (ionic components only), extracted the site scores of the first
276 principal axis (PCA1), and proceeded to use these values as a single water chemistry variable
277 for the analysis. Variance inflation factors (VIFs) were used to assess multicollinearity among
278 the predictors independently for each pond subset (**Table S4**). Variables displaying high
279 collinearity ($VIF > 5$; Kim, 2019) were removed iteratively. All substrate types were removed
280 from the analysis due to having high variance inflating power in all subsequent analyses.

281 **Community analysis**

282 We tested for overall differences in amphibian community composition between garden and
283 urban ponds using a PERMANOVA based on Jaccard dissimilarities using the ‘vegan’ package
284 (v2.6.8; Oksanen et al., 2024). Differences in species richness were tested using a generalized
285 linear model with a quasi-Poisson error distribution, which relaxes the equidispersion

286 assumption of the Poisson model. Pond type was included as a categorical predictor in all
287 models.

288 To identify the environmental and spatial drivers of amphibian community composition,
289 predictors were grouped into four categories: environment, landscape, connectivity and spatial
290 autocorrelations (MEMs). We conducted distance-based redundancy analysis (db-RDA) using
291 Jaccard dissimilarities to assess the proportion of community variation explained by each
292 predictor group. Then, we applied permutation-based stepwise model selection ('ordistep';
293 5000 permutations; bidirectional) to identify significant predictors using the 'vegan' package
294 (v2.6.8; Oksanen et al., 2024). Due to the lack of collinearity ($VIF > 5$; Kim, 2019),
295 connectivity and MEM variables were merged into a single category, space for subsequent
296 variance partitioning. Using these significant predictors, variance components were partitioned
297 among environment, landscape, and space using Jaccard dissimilarity as species distances with
298 the varpart() function of the 'vegan' package, and final diagrams were produced using the
299 'VennDiagram' package (v1.7.3; Chen, 2022). These analyses were performed separately for
300 garden ponds, urban ponds, and the combined dataset.

301 **Species analysis**

302 To analyse species occurrence, we first used random forests with the 'randomForest' package
303 (v4.7.1.2; Liaw and Wiener, 2002) to rank predictor importance and reduce dimensionality,
304 thereby minimising overfitting. Following this pre-selection step, variance inflation factors
305 with the 'car' package (v3.1.3; Fox and Weisberg, 2019) were calculated to diagnose
306 collinearity. Due to the prescreening effect of the random forest, high VIF values were limited
307 to a subset of landscape predictors, in which case either urban area, roads, or agricultural area
308 was removed, depending on which exhibited the highest VIF (**Table S4**).

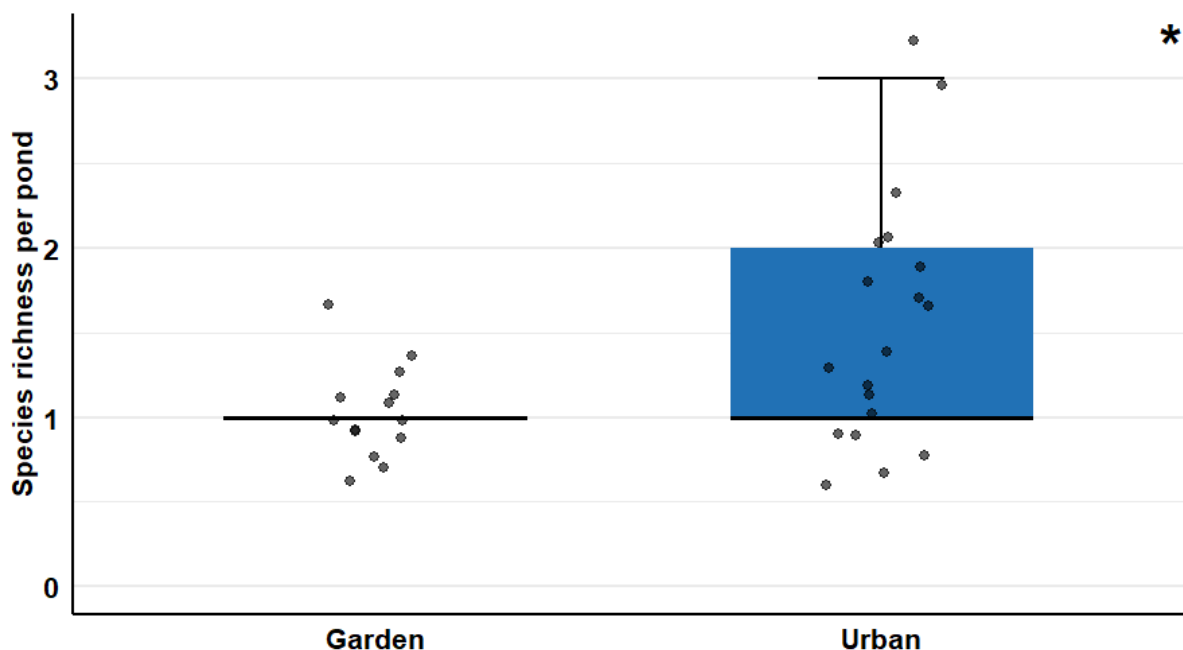
309 Then, we applied a similar framework using distribution-based generalized linear models to
310 identify the key drivers of species occurrence. We fitted binomial GLMs using the 'MASS'
311 package (v7.3.60.2; Venables and Ripley, 2002) with the selected predictors. To assess the
312 independent contribution of each predictor, we conducted likelihood ratio Type II analyses of
313 deviance using the 'car' package (v3.1.3; Fox and Weisberg, 2019). When complete or quasi-
314 complete separation was detected, we refitted models using Firth's bias-reduced penalized
315 likelihood logistic regression using the 'logistf' package (v1.26.1; Heinzer et al., 2010; Firth,
316 1993) to obtain stable parameter estimates. As in the community-level analysis, significant

317 variables were assigned to environmental, landscape, connectivity, and MEM groups;
318 connectivity and MEMs were later merged into a space group for comparability. Variance
319 partitioning was conducted using ‘vegan’, applying Euclidean distances on the binary data,
320 appropriate for univariate responses. Venn diagrams were produced using the ‘VennDiagram’
321 package (v1.7.3; Chen, 2022).

322 All the statistical analyses were carried out using the software R (v4.4.1; R Core Team, 2024),
323 plots were created using the ‘ggplot2’ package (v4.0.0; Wickham, 2011b).

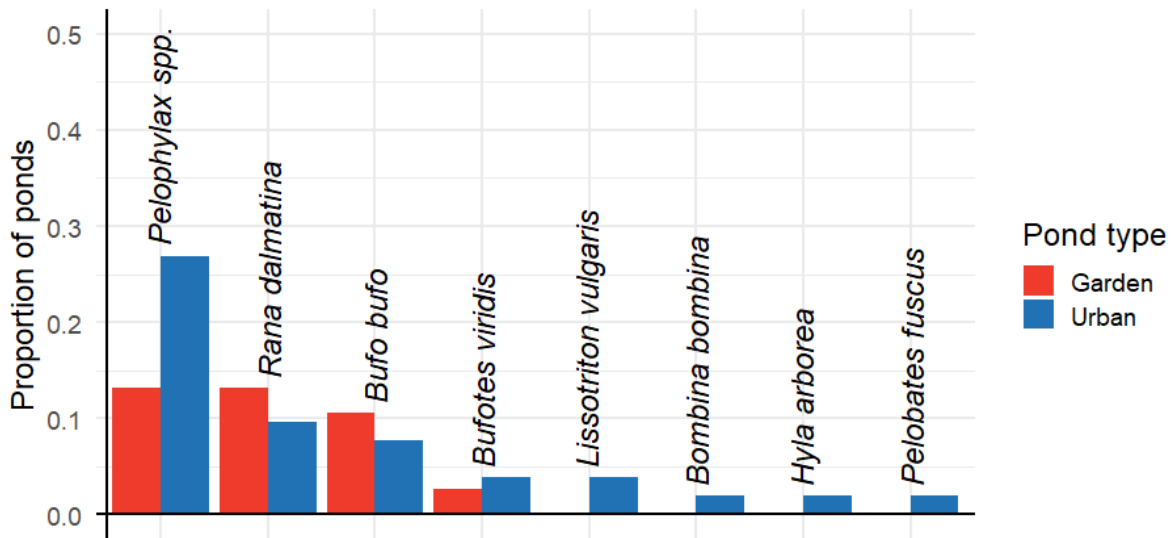
324 Results

325 We detected 1465 individuals of eight species in the 90 ponds: *Bufo bufo* (1170), *Bufo viridis*
326 (122), *Pelophylax* spp. complex (101), *Rana dalmatina* (43), *Hyla arborea* (11), *Bombina*
327 *bombina* (10), *Lissotriton vulgaris* (5) and *Pelobates fuscus* (3). In garden ponds, we recorded
328 207 individuals of four species, while in urban ponds, we recorded 1272 individuals of eight
329 species. Species richness differed significantly between pond types (quasi-Poisson GLM: $t =$
330 2.71 , $p = 0.011$), with higher richness in urban ponds (**Figure 2**).



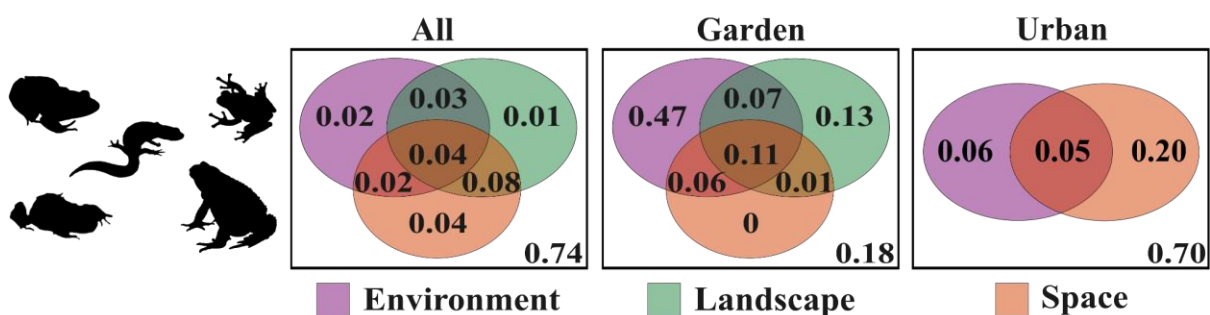
331
332 **Figure 2:** Boxplots displaying species richness for garden and urban ponds. An asterisk
333 indicates the significant difference between the two habitat types based on the generalized
334 linear model.

335 *Pelophylax* spp., *R. dalmatina*, *B. bufo*, and *B. viridis* were detected both in garden and urban
 336 ponds, while *L. vulgaris*, *B. bombina*, *P. fuscus* and *H. arborea* were only encountered in urban
 337 ponds (**Figure 3**). No significant difference was found in community composition between
 338 pond types (PERMANOVA, $F=1.549$, $R^2=0.048$, $p=0.201$).



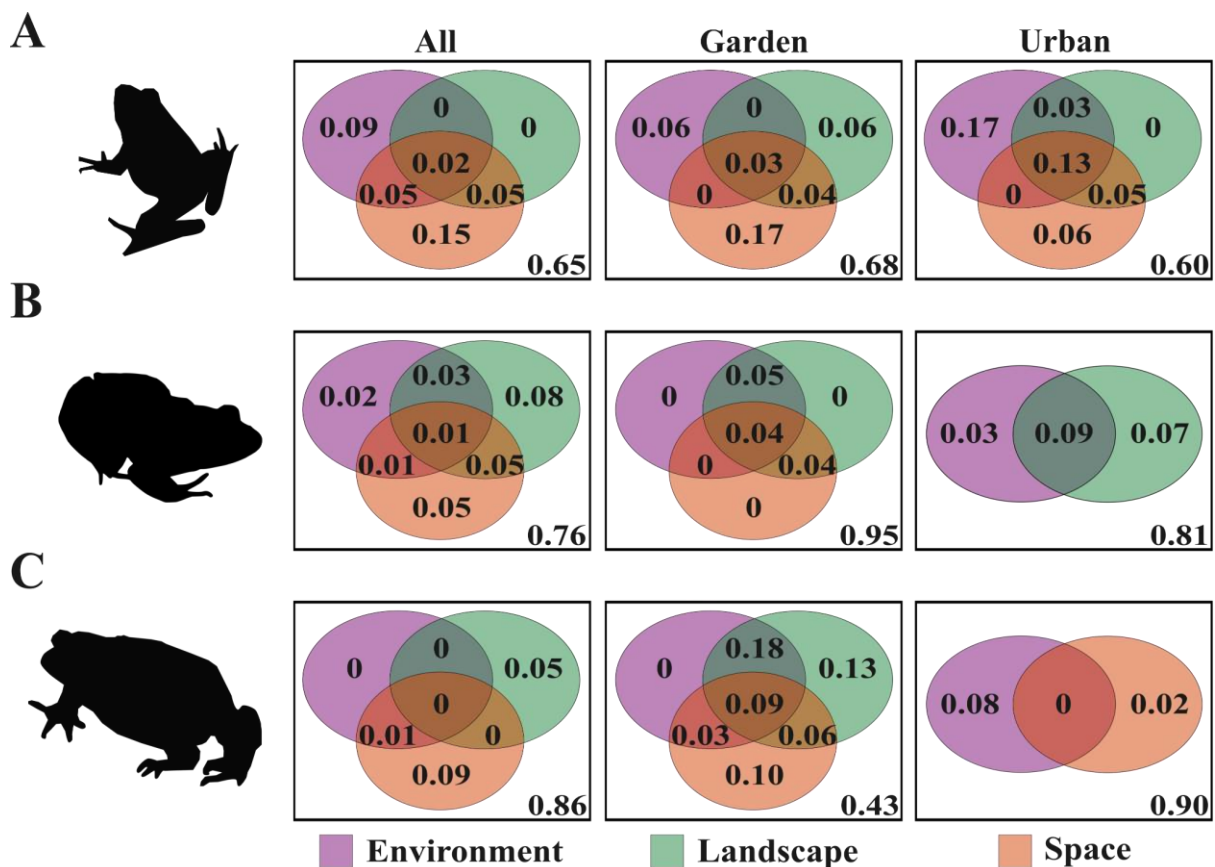
339
 340 **Figure 3:** Proportion of ponds in which each species was recorded in garden ponds (red, n=38)
 341 and urban ponds (blue, n=52).

342 Models explained 26% of the total community variance when all ponds were analysed together
 343 (**Figure 4**). However, when garden and urban ponds were separated, different patterns emerged
 344 in the relative importance of environmental and spatial drivers. In garden ponds, environmental
 345 factors explained most of the variance (pure effect: 47%), which included pond area, total
 346 organic carbon, submerged vegetation, total phosphorus, and pH (**Figure 4, Table S5**). In
 347 contrast, spatial variables, including nearest-neighbour distance and MEM6 played a more
 348 prominent role in structuring amphibian communities in urban ponds (pure effect: 20%; **Figure**
 349 **4**).



351 **Figure 4:** Variance partitioning of amphibian community composition explained by
 352 environmental, landscape, and spatial predictors for all ponds, garden ponds, and urban ponds.
 353 Residual variance is displayed outside the Venn diagrams.

354 Species-level analyses of occurrence revealed contrasting patterns. *Pelophylax* spp. responded
 355 mostly to environment (pure effect: 9%) and space (pure effect: 15%) (**Figure 5a**) when
 356 analysing all ponds jointly. In garden ponds, however, spatial predictors were stronger (pure
 357 effect: 17%), while in urban ponds the strong influence of environment dominated (pure effect:
 358 17%). *Rana dalmatina* showed little response to environment and was instead affected by
 359 spatial factors and landscape cover when analysing all ponds together (**Figure 5b**). *Bufo bufo*
 360 exhibited largely unexplained variation (87%); however, when analysed separately by pond
 361 type, environment and landscape variables together explained most variance in garden ponds,
 362 while in urban ponds, residual variance remained high (**Figure 5c**).



363

364 **Figure 5:** Variance partitioning of the occurrence of three species: *Pelophylax* spp. (A), *Rana*
 365 *dalmatina* (B) and *Bufo bufo* (C) explained by environmental, landscape and spatial predictors
 366 for all ponds, garden ponds, and urban ponds. Residual variance is displayed outside the Venn
 367 diagrams for each variance partitioning.

368 Discussion

369 Here, we show that amphibian communities in garden and urban ponds differ more in the
370 processes structuring them than in their taxonomic composition. Urban ponds supported higher
371 species richness, yet the overall community composition did not differ significantly between
372 pond types. This indicates that garden ponds have the potential to support amphibian
373 communities comparable to those of urban ponds, despite their structural differences. However,
374 the drivers of community assembly differed between habitats. In garden ponds, local
375 environmental variables explained most of the variation in amphibian species composition,
376 indicating strong abiotic filtering at the pond scale. In contrast, spatial structure played a
377 stronger role in urban ponds, suggesting that dispersal processes and the spatial configuration
378 of the pond network more strongly influence amphibian communities in these systems.

379 Compared to garden ponds, urban ponds hosted higher amphibian species richness, yet both
380 pond types exhibited overall similar community composition. Urban ponds supported a wider
381 range of amphibian species, including species of higher conservation relevance, such as
382 *Bombina bombina* and *Pelobates fuscus*, which are typically less tolerant of habitat
383 modification and therefore less frequently recorded in highly urbanised environments
384 (Konowalik *et al.*, 2020; Kaczmarski, Benedetti & Morelli, 2020). In particular, *P. fuscus* has
385 experienced widespread population declines across Europe (Eggert *et al.*, 2006). Garden ponds,
386 on the other hand, hosted more common species, e.g. *Pelophylax* spp., *Rana dalmatina* or *Bufo*
387 *bufo*. This pattern is consistent with the smaller size, younger age, and higher levels of human
388 management typical of garden ponds, which can constrain colonisation and persistence (Gaston
389 *et al.*, 2005; Gledhill, James & Davies, 2008; Oertli, 2018; Márton *et al.*, 2025). Despite these
390 structural differences, the limited compositional separation suggests that both pond types draw
391 from the same regional species pool, dominated by urban-tolerant generalist species (Parris,
392 2006; Hamer & McDonnell, 2008; Hamer & Parris, 2011). Within this shared pool, rarer or
393 more sensitive species appear largely restricted to the larger and less intensively managed urban
394 ponds, compared to the smaller and more intensively managed garden ponds, which may
395 explain their higher species richness despite the overall similarity of community composition.

396 Amphibian communities in garden and urban ponds had a pronounced difference in the relative
397 importance of environmental and spatial drivers. When all ponds were analysed together, we
398 could only explain a relatively low share of community variation, with a weak spatial trend,
399 indicating that pooling obscured the type-specific patterns. This weak spatial structure reflected

400 a broad central–peripheral gradient across the study area, with garden and urban ponds
401 unevenly distributed along this gradient(**Table S5, S6**). When pond types were analysed
402 separately, contrasting assembly mechanisms emerged. In garden ponds, the community
403 structure was primarily driven by local environmental filtering. These ponds were smaller, had
404 higher submerged vegetation cover (**Table S6**), and are typically embedded within fine-scale
405 microhabitat settings (Hill *et al.*, 2021; Loram *et al.*, 2011; Hamer *et al.*, 2024). In line with
406 this, landscape variables had a weak effect, and no pure spatial effect was detected, suggesting
407 that suitable local pond quality might allow colonisation even in relatively isolated garden
408 ponds. In contrast, the amphibian community in urban ponds was structured mostly by spatial
409 processes. In urban landscapes, movement pathways are often constrained by infrastructure,
410 and connectivity depends heavily on the configuration of surrounding habitats (Johnson *et al.*,
411 2013; Guderyahn, Smithers & Mims, 2016). Urban barriers such as roads and built
412 infrastructure can reduce functional connectivity among water bodies (Cushman, 2006; Ribeiro
413 *et al.*, 2011), making ponds located within connected green corridors particularly important as
414 stepping-stone habitats (Lee *et al.*, 2022).

415 Our species-level analyses revealed contrasting habitat-use patterns among the three dominant
416 amphibians. For *Pelophylax* spp., fringing vegetation emerged as an important predictor,
417 consistent with existing evidence that emphasises the role of dense marginal vegetation in
418 increasing habitat heterogeneity, providing refuge from predators, and improving
419 microclimatic conditions (Buttemer *et al.*, 1996; Parris, 2006; Wassens *et al.*, 2010). In
420 contrast, *Rana dalmatina* responded more strongly to spatial and landscape-scale drivers when
421 all ponds were analysed together, reflecting its reliance both on surrounding aquatic habitats
422 (Dalpasso *et al.*, 2022) and permeable green matrices for its terrestrial movement (Hartel *et al.*,
423 2009). Finally, *Bufo bufo* showed more variable responses, broadly mirroring community-level
424 patterns. In garden ponds, local environmental and landscape predictors, particularly the
425 predatory threat index and proximity to rivers, were most influential. The positive association
426 with predatory macroinvertebrates likely reflects coexistence rather than direct facilitation,
427 while the river effect is consistent with existing evidence that riparian habitats enhance anuran
428 dispersal and occupancy (Birx-Raybuck, Price & Dorcas, 2010) and may also increase
429 macroinvertebrate abundance (Hill *et al.*, 2016), contributing to correlated patterns in the
430 variance partitioning.

431 While we included an extensive set of potential environmental, landscape, and spatial
432 predictors, a substantial proportion of the variation in community composition and species
433 occurrence remained unexplained in some models. Patterns generally became more
434 deterministic once garden and urban ponds were analysed separately, reflecting general
435 differences in how communities are assembled in these habitats. In garden ponds, the model
436 explained a large proportion of community variation, whereas lower explained variation in
437 urban ponds suggests that additional processes may influence amphibian communities in these
438 systems. Nevertheless, unexplained variation remained high in some species-specific models,
439 e.g. for *B. bufo* in urban ponds and *R. dalmatina* in garden ponds. Such residual variance is
440 common in amphibian metacommunity studies (Van Buskirk, 2005; Péntek *et al.*, 2017;
441 Knutson *et al.*, 1999; Dalmolin, Tozetti & Ramos Pereira, 2019), and may reflect unmeasured
442 predictors, including predators, pathogens, stochastic processes, legacy effects in terms of
443 population dynamics or local management, or fine-scale terrestrial habitat features relevant for
444 shelter or overwintering (Hamer & Parris, 2013; Parris & Cornelius, 2004; Green, 2003). In
445 addition, many landscape predictors covaried strongly along the urbanisation gradient (e.g.
446 urban cover, roads, and human population density versus forest or grassland cover), limiting
447 the attribution of effects to a single driver. Although correlated variables were removed for
448 statistical reasons, excluded predictors should not be interpreted as ecologically unimportant,
449 as their influence may be represented indirectly through the retained variables. Finally,
450 amphibian occurrences are inherently dynamic due to their frequent movements among ponds,
451 and our single-season sampling design may have resulted in imperfect detection for some
452 species (Gomes-Mello *et al.*, 2021), particularly under the unusually cold and dry spring of the
453 study period (Ficetola & Maiorano, 2016). Repeated surveys have been shown to substantially
454 improve detection probability and inference on habitat associations (Petitot *et al.*, 2014; Barata,
455 Griffiths & Ridout, 2017). Importantly, these limitations do not alter the consistent pattern that
456 local environmental conditions dominated community assembly in garden ponds, whereas
457 spatial processes were more influential in urban ponds.

458 Our results point to two complementary conservation pathways for urban amphibians:
459 improving local habitat quality in privately managed garden ponds and strengthening
460 connectivity within urban pond networks. Although based on a single city, the contrasting roles
461 of local habitat management and spatial connectivity are likely to apply broadly across urban
462 pond systems across temperate regions. For garden-pond owners, relatively simple measures -
463 such as retaining aquatic vegetation, avoiding fish stocking, minimising pollutant inputs, and

464 maintaining moderate hydroperiod - can substantially increase habitat suitability (Gledhill *et*
465 *al.*, 2008; Hassall, 2014; Oertli & Parris, 2019). As local environmental conditions were the
466 primary drivers of amphibian occupancy in these ponds, such local-scale management actions
467 can promote amphibian presence largely independent of the surrounding landscape context. At
468 the city scale, conservation planning should prioritise the retention and creation of ponds
469 embedded within green corridors and stepping-stone networks, while reducing dispersal
470 barriers such as concrete embankments, steep artificial shorelines, and other hard infrastructure
471 that restricts amphibian movement across the urban matrix (Gagné & Fahrig, 2007; Cayuela *et*
472 *al.*, 2019). Adaptive monitoring frameworks that track occupancy, species richness, and basic
473 habitat indicators (vegetation cover, fish presence, connectivity) could help evaluate the
474 effectiveness of these interventions. Engaging private pond owners through citizen science
475 initiatives could further support amphibian-friendly management while generating valuable
476 long-term data on how local actions influence urban amphibian communities.

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