

## ARTICLE

## Animal Ecology

# Traditional water structures in villages support amphibian populations within a protected landscape

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**Abstract**

Amphibians are among the most globally threatened vertebrates, with habitat loss and degradation being the primary drivers of their decline. While natural waterbodies are essential for amphibian survival, artificial habitats can also serve as important refuges, particularly in human-altered landscapes. This study investigates the role of artificial waterbodies in supporting amphibian populations within villages and disturbed areas of Peneda-Gerês National Park (PNPG), a protected area in northern Portugal. We surveyed 162 waterbodies, 68 artificial (tanks, drains, fountains, and cave-like structures) and 94 natural (ponds, streams, stream pockets, and caves) sites within human-altered areas to assess community composition, species richness, Shannon diversity, relative abundance, proportion of occupied sites, and breeding activity. We recorded 10 amphibian species, with species composition showing moderate overlap between the two habitat types, indicating both shared and distinct species assemblages. Natural waterbodies had higher observed species richness (nine species) than artificial sites (seven species). Shannon diversity was greater in natural waterbodies for adults, while juvenile/larvae diversity was greater in artificial habitats. *Rana iberica* was the most widespread species, found across all waterbody types but predominantly in natural sites. *Salamandra salamandra* juveniles/larvae were also primarily found and bred in natural habitats, especially stream pockets. In contrast, *Lissotriton boscai* and *Triturus marmoratus* were more commonly found and bred in artificial waterbodies, particularly historic water tanks. Natural waterbodies had a higher proportion of their sites occupied (76.6%) compared to artificial ones (51.5%), with stream pockets having the highest at 96.6% and other natural sites around two-thirds. Among artificial sites, tanks were highest with 62.5% occupied. Breeding occurred in one-fifth of surveyed sites, with breeding events recorded in half of stream pockets and over a quarter of tanks. Tanks supported the highest

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number of breeding species (four of five), compared to three in natural habitats. These findings highlight the importance of water tanks, traditionally used for laundry and water storage, in supporting amphibians in PNPG. They underscore the need to conserve both natural and artificial habitats to protect amphibian biodiversity, especially in human-altered landscapes where artificial waterbodies provide crucial refuges as climate change reduces natural breeding sites.

#### KEYWORDS

amphibians, artificial habitats, Bosca's newt (*Lissotriton boscai*), cultural heritage, drainage systems (open channels and drains), fire salamander (*Salamandra salamandra*), Iberia, marbled newt (*Triturus marmoratus*), Peneda-Gerês National Park, Portugal, *Rana iberica* (Iberian frog), water tanks

## INTRODUCTION

Amphibians are the most globally threatened vertebrate group, with more than 40% of all species at risk of extinction, primarily driven by habitat loss and degradation, emerging infectious diseases, and the effects of climate change (Luedtke et al., 2023; Stuart et al., 2004). Habitat loss in particular poses the most critical threat impacting 93% of endangered amphibian species (Luedtke et al., 2023). The loss and alteration of both aquatic breeding grounds and terrestrial habitats play a significant role by disrupting the complex biphasic life cycles typical of most amphibians (Becker et al., 2007; Cushman, 2006). Their highly permeable skin also makes them particularly vulnerable to environmental changes, making them sensitive to fluctuations in moisture, temperature, and pollutant exposure in both aquatic and terrestrial environments (Alford & Richards, 1999). However, the impact of habitat changes on amphibian populations varies across species and habitats (Hamer & McDonnell, 2008; Pyron, 2018; Valdez et al., 2021). While pristine wetlands and forests provide ideal conditions, some artificial habitats can offer supplemental refuge when natural areas are lost or degraded.

Recent studies show that roughly one-third of the world's amphibian species use artificial habitats to some extent, even occupying heavily altered environments (Valdez et al., 2015, 2021; Warren & Büttner, 2008). Although not a substitute for natural habitats, constructed waterbodies like drainage ditches, rice paddies, agricultural ponds, and wastewater treatment ponds can provide vital alternative aquatic breeding grounds, helping to support and sustain populations of threatened amphibian species when natural habitats become scarce or degraded (Boissinot et al., 2019; Brand & Snodgrass, 2010; Caballero-Díaz et al., 2020; Conan et al., 2023; Knutson et al., 2004; Romano et al., 2023; Valdez

et al., 2015; Yu et al., 2022). Additionally, terrestrial habitats like plantations, pastures, gardens, and urban greenspaces can serve as habitats when forests become fragmented or degraded (Hartel, 2004; Holzer, 2014; Manenti et al., 2013; Valdez et al., 2021; Yu et al., 2022). Nevertheless, while some artificial habitats can support certain amphibian species, many others are less beneficial due to limitations such as altered hydrology, ecological traps, pollution, and invasive species, which can lead to lower survival rates and reduced biodiversity compared to natural areas (Băncilă et al., 2023; Cordier et al., 2021; Gordon et al., 2009; Hamer & McDonnell, 2008; Knutson et al., 2004; Price et al., 2011). Determining whether individual artificial habitats support or threaten particular amphibian populations is key to evaluating their long-term conservation value, especially in regions with a legacy of extensive anthropogenic landscape alteration.

In Europe, for example, approximately 80% of landscapes have been extensively transformed over the past centuries due to agricultural intensification, urbanization, and infrastructure expansion (European Environment Agency, 2023; Pedrolí & Meiner, 2017). These changes have led to the loss of over 50% of wetlands in many European countries due to the draining of floodplains and peatlands for agriculture and urbanization (Fluet-Chouinard et al., 2023). Meanwhile, since the 1990s, the expansion of artificial land has accelerated more than any other land cover type, driven by ongoing urbanization and infrastructure construction (Pedrolí & Meiner, 2017). Nevertheless, some artificial habitats such as stormwater ponds, highway drainage systems, and fish farms have been found to partly mitigate the impact of natural habitat loss for some species in certain areas (Conan et al., 2023; Kloskowski, 2010; Le Viol et al., 2012).

In the drought-prone Mediterranean climate of the Iberian Peninsula, encompassing Spain and Portugal, artificial water bodies may be especially valuable for

amphibian species. Evidence suggests that structures such as irrigation canals, farm ponds, water tanks, ditches, and abandoned quarries can serve as habitats, providing critical network connectivity for dispersal and additional breeding habitats for many amphibian populations in this water-scarce and heavily altered region (Caballero-Díaz et al., 2020, 2022; Ferreira & Beja, 2013; Galvez et al., 2018; Garcia-Gonzalez & Garcia-Vazquez, 2011; Gutiérrez-Rodríguez et al., 2023). Understanding amphibian use of artificial habitats is vital to support populations now reliant on these man-made habitats, especially in the Iberian region, which contains the highest concentration of endemic and threatened amphibian species in Europe (Luedtke et al., 2023; Temple & Cox, 2009).

While many studies have explored the importance of specific artificial habitats for amphibians, there appears to be a lack of studies on the use of these habitats within protected areas. Peneda-Gerês National Park (PNPG) in northern Portugal, the oldest protected area and the only national park in the country, offers an ideal setting to investigate amphibian use of artificial habitats within a protected area (Soares et al., 2005). Established in 1971 and part of the “Natura 2000” network of European priority conservation areas, PNPG is situated at the crossroads of Euro-Siberian and Mediterranean zones, creating a unique climatic transition from Atlantic to Mediterranean conditions (Soares & Brito, 2007). This blending of 2 distinct bioclimatic regions enables the park to serve as a biodiversity hotspot, hosting 13 amphibian species and 4 Iberian endemics that thrive in its pristine montane streams, rivers, and ponds (Soares et al., 2005). However, the park also encompasses traditional mountain villages, home to centuries-old artificial waterbodies like historic stone fountains, communal laundry and water tanks, and drainage channels that were once vital to traditional village life (Cabral et al., 2017; Martins, 2022; Simões et al., 2019; Soares & Brito, 2007). These historically significant structures not only serve as cultural landmarks but also present a valuable opportunity to explore their potential as biodiversity refuges for amphibians within this unique protected area. Understanding the role of artificial habitats in PNPG is crucial for managing and protecting amphibian populations within this ecologically rich landscape shaped by natural and cultural elements.

In this study, we investigated the role of artificial waterbodies in supporting amphibian populations within PNPG, focusing on villages and other human-altered areas within its protected landscape. We compared amphibian community composition, species richness, species diversity, relative abundance, proportion of occupied sites, and breeding activity between artificial

waterbodies (tanks, drains, fountains, and cave-like structures) and natural habitats (ponds, streams, stream pockets, and caves). Additionally, we used principal components analysis (PCA) to examine the differences and similarities in habitat characteristics across the various waterbody types. This study aims to understand the ecological significance of artificial waterbodies in supporting amphibian populations within this unique protected area, where natural and cultural heritage intersect.

## METHODS

### Study area

The study was conducted over two survey periods: May 17–21, 2023, and May 6–12, 2024, covering a total of 162 waterbodies (68 artificial and 94 natural) within 11 villages and human-disturbed areas of PNPG, located in northern Portugal. The surveyed areas included Alcobaca, Assureira, Barreiro, Castro Laboreiro, Couscadas, Dorna, Lamas de Mouro, Mareco, Pousios, Ribeiro de Beixo, and Ribeiro de Cima. During the first survey period, 36 artificial and 50 natural waterbodies were surveyed. To account for sites that dried up or became inaccessible and to ensure comprehensive habitat coverage, additional sites were surveyed during the second period, resulting in a total of 67 artificial and 91 natural waterbodies. Approximately half of the waterbodies (37 artificial and 47 natural) were resampled and surveyed in both periods.

### Waterbody types

We categorized the various waterbodies into natural and artificial types (Figure 1). For natural habitats, we identified four categories: ponds, streams, stream pockets, and caves. Ponds (Figure 1a) are small natural standing bodies of freshwater, while streams (Figure 1b) are small, shallow, naturally flowing bodies of water typically originating from springs or rainfall. Stream pockets (Figure 1c) are localized areas within deeper and wider stream systems where water flow is more concentrated or pooled. Caves (Figure 1d) refer to naturally formed hollow spaces or chambers within rock formations that contain bodies of water. Within the artificial category, we identified four types of waterbodies: tanks, drains, fountains, and cave-like structures. Tanks (Figure 1e) are artificial containers historically used for storing water, often for laundry or troughs. Drains (Figure 1f) are man-made structures typically located at ground level, such as open drainage channels, designed to redirect excess rainwater and runoff, preventing water accumulation in village streets and agricultural areas.



**FIGURE 1** Types of waterbodies surveyed within Peneda-Gerês National Park. Natural waterbodies include (a) ponds, (b) streams, (c) stream pockets, and (d) caves. Artificial waterbodies are represented by (e) tanks, (f) drains, (g) fountains, and (h) cave-like structures. Photo credit: Jose Valdez.

Fountains (Figure 1g) are ornamental features with flowing water situated at higher elevations. Cave-like structures (Figure 1h) are artificial, enclosed spaces that mimic the appearance and environment of natural water-containing caves.

## Survey sampling

To ensure comprehensive amphibian detection, we conducted both diurnal and nocturnal surveys. During daylight hours, we searched for and characterized waterbodies, recording GPS coordinates, dimensions (area, depth), turbidity, flow, and the percentage cover of key habitat features (rocks, mud, leaf litter, and aquatic vegetation). Amphibian sampling was conducted through systematic nocturnal surveys between 20:30 and 02:00. We first employed auditory sampling by playing back calls of all amphibian species known to occur in the area and recorded any vocal responses. A team of five trained observers then conducted visual encounter surveys by

walking along the perimeters of waterbodies to detect amphibians (Eekhout, 2010). Most surveyed waterbodies were relatively small (median area: 4 m<sup>2</sup>, range: 0.5–20 m<sup>2</sup>) and shallow (median depth: 25 cm, range: 5–75 cm), with clear water that made amphibians readily visible. In these conditions, dip nets were primarily used to capture amphibian larvae and adults for species identification of observed individuals. For deeper and less clear waterbodies, such as some artificial tanks, we employed systematic figure-8 dip-net sweeps across accessible edges and central zones to ensure thorough coverage. The presence of larvae was taken as evidence of breeding at the waterbody.

## Statistical analyses

Statistical analyses were performed using R version 4.2.2. Species composition was evaluated using the Jaccard similarity index (J) to determine community overlap between artificial and natural habitats. J was calculated by

dividing the number of species shared between artificial and natural habitats by the total number of unique species found across both habitat types. Species diversity was then quantified for adults and for non-adults (juveniles and larvae) separately using the Shannon-Wiener diversity index ( $H'$ ) across all sites to understand differences in species richness and evenness.

Pearson's chi-square test ( $\chi^2$ ) was also conducted to compare the proportion of occupied sites, defined as the number of waterbodies where at least one individual was observed, across habitat types (artificial vs. natural), individual waterbody types, and species. Similarly, we used chi-square tests to analyze the proportion of waterbodies with breeding activity (identified by the presence of eggs or larvae), comparing between artificial and natural habitats and among different waterbody types. Juveniles were excluded from this analysis, as their mobility between habitats makes them less reliable for indicating reproductive activity within a specific waterbody.

We also conducted a PCA using the FactoMineR package in R to explore the relationship between waterbody characteristics. Continuous variables were standardized for comparability, and categorical variables were converted into dummy variables. Rows with missing data were removed to create a clean dataset. After an initial PCA, we applied a contribution threshold of 5% to focus on the most significant variables contributing to the variation in the first two principal components. Variables exceeding this threshold were retained, and the PCA was rerun using the reduced dataset. The results were visualized with the factoextra package, using a gradient color scale to highlight the contribution of each variable and identify the key characteristics differentiating the waterbodies.

## RESULTS

### Community composition

We found 10 amphibian species within our study sites, comprising 6 frog species (Order: Anura) and 4 salamander species (Order: Urodela). Among the frogs, we recorded the Iberian frog (*Rana iberica*), Perez's frog (*Pelophylax perezii*), Spiny toad (*Bufo spinosus*), Common midwife toad (*Alytes obstetricans*), Natterjack toad (*Epidalea calamita*), and Iberian painted frog (*Discoglossus galganoi*). The salamander species included the Fire salamander (*Salamandra salamandra*) and three newt species within the subfamily Pleurodelinae: Marbled newt (*Triturus marmoratus*) and Bosca's newt (*Lissotriton boscai*), along with the Iberian ribbed newt (*Chioglossa lusitanica*). The Jaccard Similarity Index revealed a moderate similarity in species composition between artificial and natural

waterbodies ( $J = 0.6$ ). This suggests that while there was some overlap in the species present in both waterbody types, each supported relatively distinct species assemblages.

### Species richness

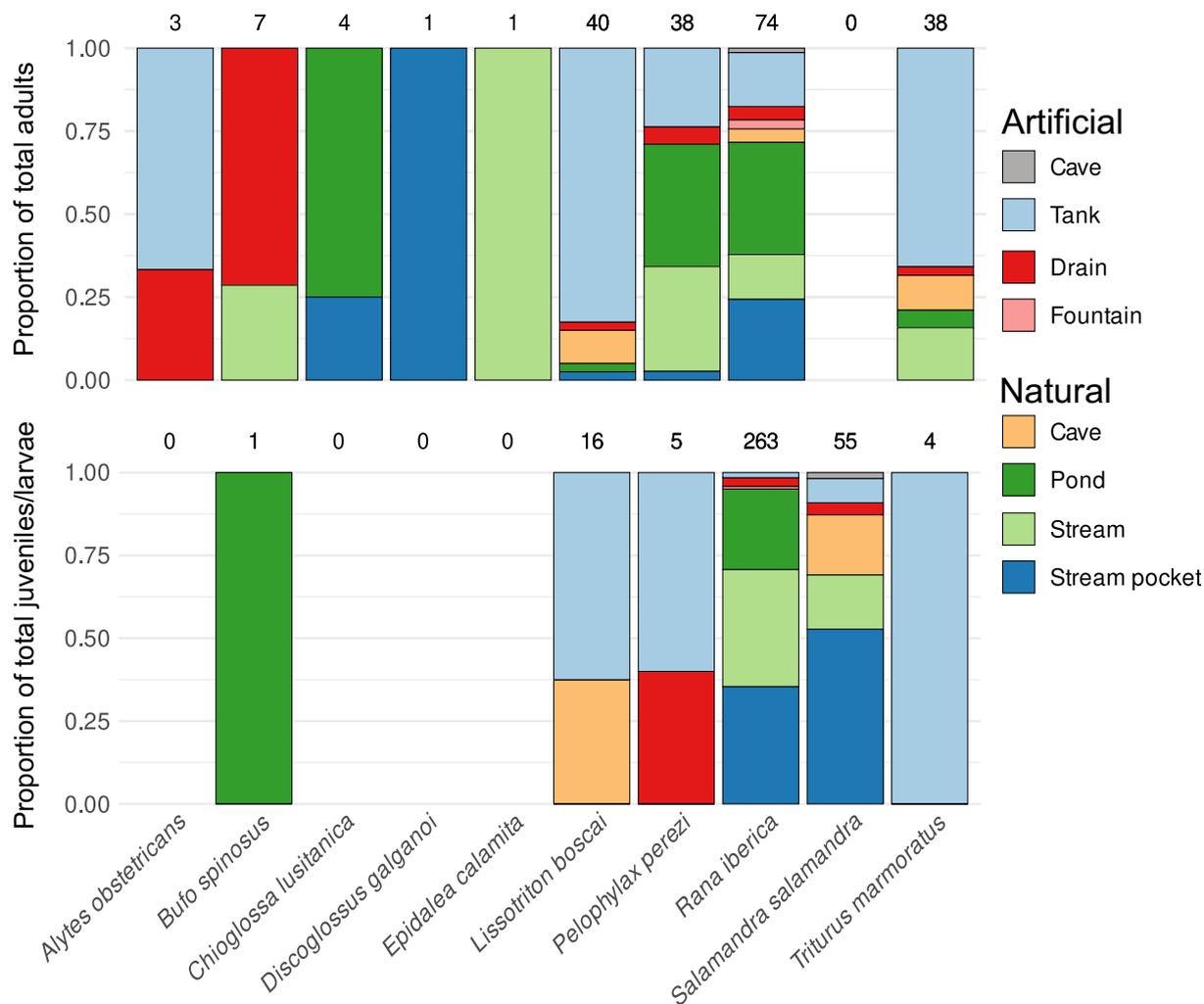
Natural waterbodies had the highest amphibian species richness, with 9 out of the 10 amphibian species observed, whereas artificial waterbodies hosted only seven species (Appendix S1: Figure S1). *D. galganoi*, *E. calamita*, and *C. lusitanica* were exclusively found in natural habitats, while *A. obstetricans* was only observed in artificial water bodies (Appendix S1: Figure S2). Species richness also varied across different waterbody types (Appendix S1: Figure S2). Within natural waterbodies, stream pockets, ponds, and streams each had six species, while caves had four species (Appendix S1: Figure S2). In contrast, drains had the highest richness among other types of waterbodies, with seven species, followed closely by tanks with six species (Appendix S1: Figure S2). Artificial caves and fountains were less diverse, containing only two and one species, respectively (Appendix S1: Figure S2).

### Species diversity

The Shannon-Wiener diversity index ( $H'$ ) showed distinct differences in amphibian diversity between natural and artificial sites for adults and non-adults. Adult amphibian diversity was higher in natural sites ( $H' = 2.37$ ) than in artificial sites ( $H' = 1.88$ ), indicating greater species richness and evenness. In contrast, non-adult amphibian diversity was higher in artificial sites ( $H' = 2.11$ ) than in natural sites ( $H' = 1.59$ ).

### Relative abundance

The most relatively abundant species was *R. iberica*, comprising 61.3% of all individuals observed across all life stages. Specifically, they accounted for 91.2% of all juveniles (95/104 individuals) and 69.1% of larvae (59/110 individuals), and 35.9% of adults (26/74 individuals). This species was strongly associated with natural habitats, with 95.1% of adults and 75.7% of juveniles/larvae recorded in natural ponds, streams, and stream pockets (Figure 2). *L. boscai* was the second most relatively abundant species (56 individuals; 40 adults, 16 larvae) with individuals predominantly (78.6%) found in tanks across life stages (82.5% of adults and 62.5% of larvae individuals) (Figure 2). *S. salamandra* was also a relatively



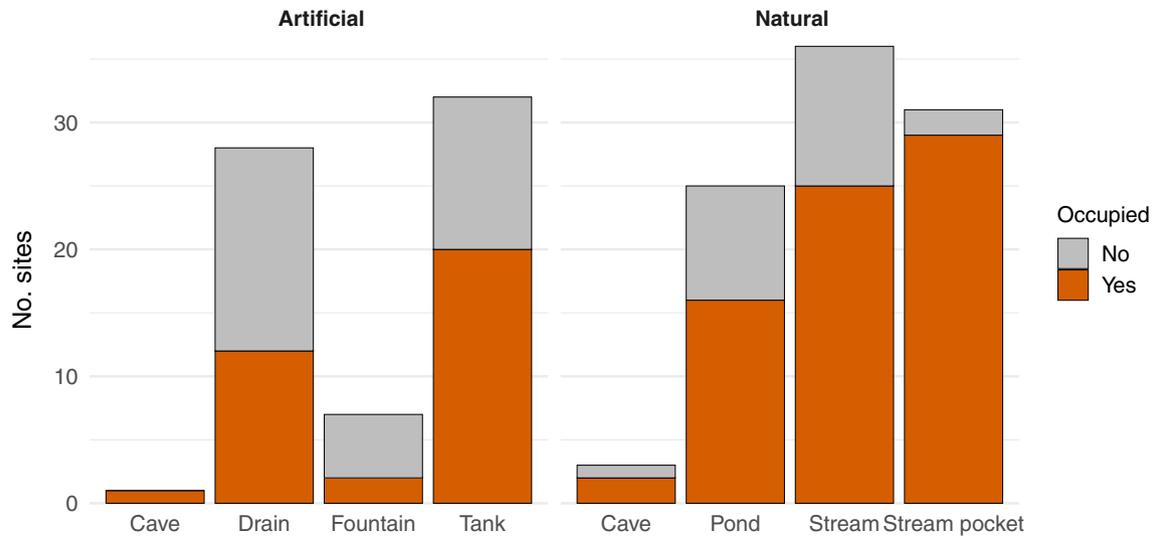
**FIGURE 2** Stacked bar plot of the proportional relative abundance for each amphibian species across different types of artificial and natural waterbodies in Peneda National Park, separated by adults (top) and non-adults (juveniles and larvae; bottom). The numbers above each bar indicate the total number of individuals recorded for each species.

abundant species, represented by 49 larvae and 6 juveniles, with no adults observed. The species was mostly found in natural habitats (87.3% of observations), primarily in stream pockets (Figure 2). Another commonly found species was *P. perezi*, with adults (38 individuals) predominantly found in natural habitats (71.1%), especially ponds and streams. However, its juveniles (two individuals) were observed in drains, and its larvae (three individuals) in artificial tanks (Figure 2). Meanwhile, *T. marmoratus* had a similar relative abundance but different habitat preferences. Adults (38 individuals) were most commonly found in artificial habitats, particularly tanks (65.8%), while the juveniles (three individuals) and a single larva were exclusively recorded in tanks (Figure 2). The remaining species were much less relatively abundant, with *B. spinosus* (seven adults) and *A. obstetricans* (three adults) primarily found in artificial habitats (drains and tanks, respectively), while *C. lusitanica* (four adults), *E. calamita* (one adult), and

*D. galganoi* (one adult) were found exclusively in natural habitats (Figure 2).

### Proportion of occupied sites

There was a significant difference in the proportion of occupied sites, with 51.5% of artificial waterbodies (35 sites) and 76.6% of natural waterbodies (72 sites) having at least one species present ( $X^2 = 10.015$ ,  $p = 0.0016$ ). Among the resampled sites, species were detected in both survey years at only six artificial waterbodies (16.2%) and 16 natural waterbodies (34%). The proportion of occupied sites also varied significantly among all waterbody types ( $X^2 = 21.8$ ,  $p = 0.0013$ ). The natural waterbody types generally exhibited a higher proportion of occupied sites, with stream pockets showing the highest proportion occupied at 96.6%, followed by streams (69.4%), ponds (64%), and caves (66.7%) (Figure 3). In contrast, among



**FIGURE 3** Total number of waterbody sites with observed amphibian presence (Yes) or absence (No) across artificial and natural waterbody types in Peneda-Gerês National Park.

artificial waterbodies, the proportion of occupied sites was highest in tanks (62.5%), followed by drains (42.9%), fountains (28.6%), and caves (100%), although the cave was based on a single site (Figure 3).

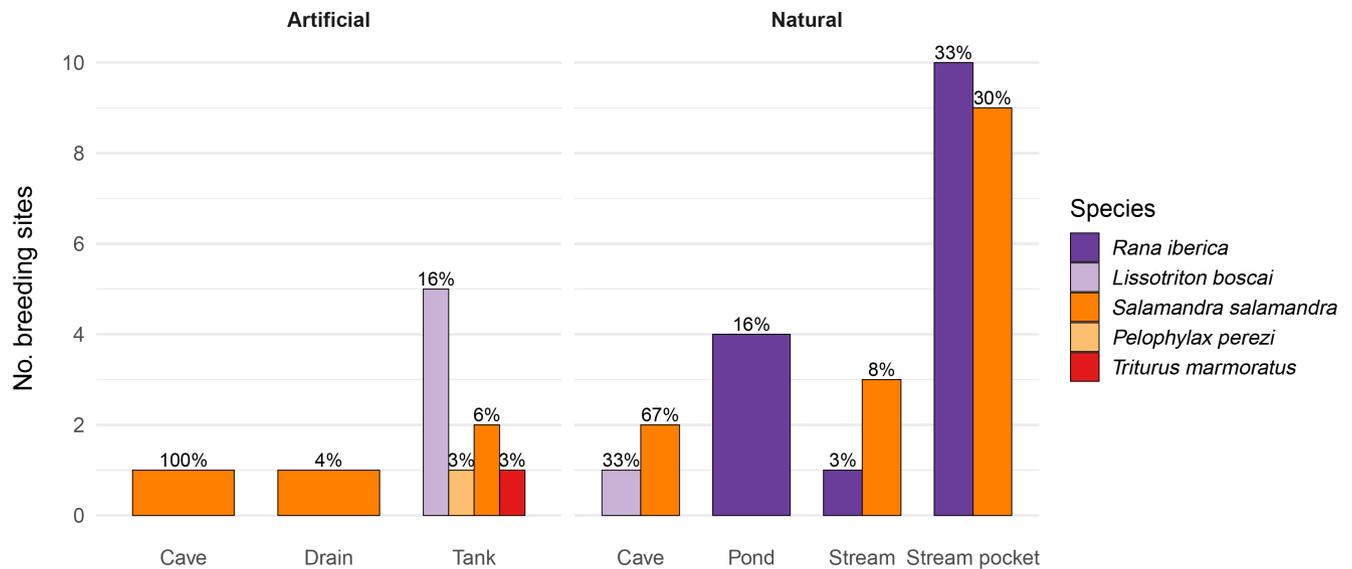
The proportion of occupied sites also significantly differed among species ( $X^2 = 357.9$ ,  $p < 0.001$ ). *R. iberica* was by far the most widespread species found in nearly half (48.1%) of all waterbodies surveyed, and the only species recorded in every habitat type (Appendix S1: Figure S3). It was present in over half of the waterbody types, with the highest proportion of occupied sites in stream pockets (83.3%), followed by streams (58.3%) and ponds (52.0%). In contrast, this species was found in about a quarter of all artificial waterbody types (Appendix S1: Figure S3). For *S. salamandra*, it was primarily found in natural habitats, with the highest proportion of occupied sites in caves (2/3 sites, 66.7%) and stream pockets (9/30 sites, 30.0%), although it was also detected in the only artificial cave (Appendix S1: Figure S3). Conversely, *T. marmoratus* and *L. boscai* each occupied one-fifth (7/32 sites, 21.9%) of all artificial tanks (Appendix S1: Figure S3). Meanwhile, *P. perezi* was recorded in both artificial and natural habitats, showing moderate proportions of occupied sites in streams (4/36 sites, 11.1%) and ponds (4/25 sites, 16.0%), while in artificial habitats, it was found in 7.1% of drains (2/28 sites) and 9.4% of tanks (3/32 sites). Each of the remaining species was found in very few or just one site (Appendix S1: Figure S3).

## Reproduction

A total of 38 breeding events were observed across 35 waterbodies, representing 21.6% of all surveyed

waterbodies. Although a higher percentage of breeding events were recorded within the natural waterbodies (25.5%) compared to artificial ones (16.2%), this difference was not statistically significant ( $X^2 = 1.524$ ,  $p = 0.1085$ ). However, there were significant differences in breeding patterns across the various waterbody types ( $X^2 = 368.8$ ,  $df = 9$ ,  $p < 0.001$ ) (Figure 4). In artificial habitats, nearly all sites where breeding occurred were tanks, representing 28.1% of all surveyed tanks (Figure 4). For natural habitats, stream pockets were the most common breeding locations (15 sites), with 50% of stream pockets having breeding occurrences (Figure 4). Notably, 75% of all caves, both artificial and natural, showed breeding activity, although the sample size for all caves was only four sites (Figure 4). Breeding activity in artificial waterbodies remained relatively consistent across the two survey periods (13.9% and 9.0%). In contrast, natural waterbodies saw a significant decrease in breeding activity (40% to 7.7%).

Breeding was observed for 5 of the 10 species, with 4 species breeding in artificial waterbodies and 3 species in natural waterbodies during the two survey periods (Figure 4). *S. salamandra* exhibited the highest breeding frequency, with a total of 18 events, including 4 in artificial waterbodies and 14 in natural waterbodies (Figure 4). This species was found to breed in the widest range of waterbody types, except fountains, where no breeding events for any species were found to occur (Figure 4). *R. iberica* had 15 breeding events, all within natural habitats, specifically in caves, streams, and stream pockets (Figure 4). *L. boscai* had six breeding events, with five occurring in tanks and one in a natural cave (Figure 4). *P. perezi* and *T. marmoratus* each had one breeding event, both occurring in tanks (Figure 4).



**FIGURE 4** Number of waterbody sites with amphibian breeding events across artificial and natural waterbody types in Peneda-Gerês National Park. Percentages above bars indicate the proportion of sites within each waterbody type where breeding was recorded.

## Waterbodies characteristics

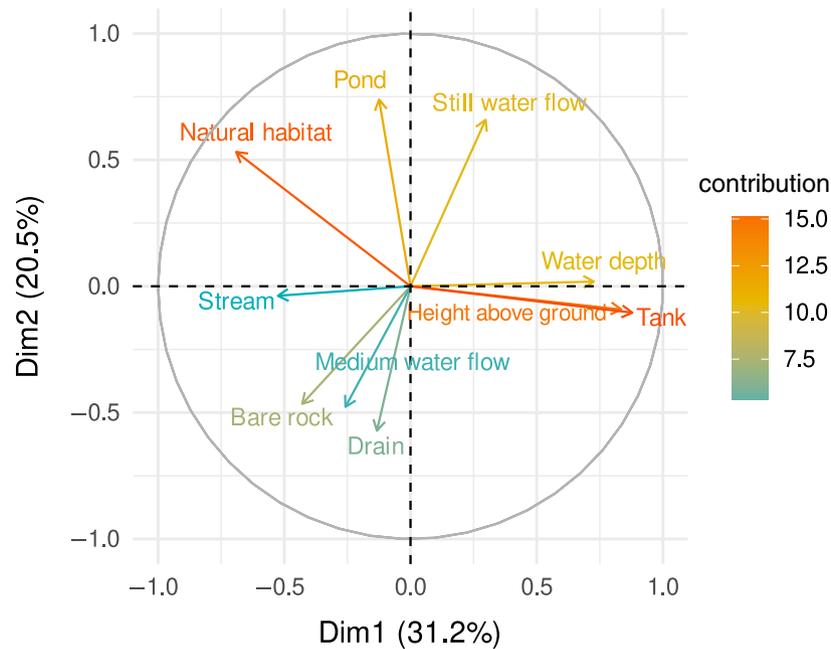
The PCA biplot shows the relationships between key environmental variables, with the first principal component (Dim1) explaining 31.2% and the second principal component (Dim2) accounting for 20.5% of the variance, together capturing 51.7% of the total variation (Figure 5). This analysis highlights clear distinctions between natural and artificial waterbodies, primarily defined by water flow and habitat characteristics. Natural habitats are on the upper left of the plot, closely associated with streams and ponds. Streams are linked to medium water flow, indicating their connection to dynamic environments, while ponds are associated with still water flow, reflecting stagnant conditions. Medium water flow and bare rock are positioned between streams and drains, suggesting that drains share similarities with natural flowing water systems. Although still water flow is positioned between ponds and tanks, indicating a shared characteristic of stagnation due to minimal water movement, tanks are distinctly located far to the right on the biplot. This positioning highlights their association with increased height above ground and greater water depth, highlighting their elevated and man-made nature, which further distinguishes them from natural waterbodies.

## DISCUSSION

Our study highlights the critical role that both natural and artificial habitats play in supporting amphibian populations within the protected landscape of PNPG.

While natural waterbodies supported higher overall species richness and proportion of occupied sites, our results revealed a moderate overlap in species composition between natural and artificial waterbodies, indicating shared species but also distinct assemblages. This was further emphasized by differences in Shannon-Wiener diversity, with natural habitats showing higher adult diversity and artificial habitats exhibiting greater non-adult (juveniles and larvae) diversity, suggesting artificial sites can be important for early life stages. Historical water tanks, in particular, supported species diversity comparable to natural waterbodies, with a significant proportion of these tanks being occupied or used for breeding, particularly by species such as the endemic *L. boscai* and *T. marmoratus*. These findings suggest that, despite their human-altered nature, artificial waterbodies can serve as valuable habitats for certain amphibian species, complementing natural habitats by providing essential breeding and refuge sites. This supports previous studies emphasizing the ecological value of artificial habitats in human-modified landscapes (Brand & Snodgrass, 2010; Caballero-Díaz et al., 2022; Knutson et al., 2004; Mazerolle, 2005; Romano et al., 2023; Valdez et al., 2015; Yu et al., 2022).

In total, we recorded 10 amphibian species during the study, including six of the eight Anura and four of the five Urodela species that are known to occupy the PNPG (Soares et al., 2005). The most common species was *R. iberica*, comprising over 60% of all individuals and 90% of juveniles. Other relatively abundant species included *L. boscai*, *S. salamandra*, *T. marmoratus*, and *P. perezi*. These abundance patterns align with previous



**FIGURE 5** Principal components analysis (PCA) biplot of environmental variables for waterbodies surveyed in Peneda National Park. The plot illustrates the contributions of environmental variables to the first two principal components (Dim1 and Dim2), which explain 31.2% and 20.5% of the variance, respectively. Arrows indicate the direction and strength of each variable's contribution and correlation to the components, with a color gradient showing higher contributions in warmer colors.

studies that have identified these species as common and widely distributed within the park (Godinho et al., 1999; Soares et al., 2005). Specifically, *R. iberica* and *S. salamandra* larvae and juveniles were predominantly found in natural habitats, particularly in stream pockets and ponds, while *L. boscai* and *T. marmoratus* were more widely distributed across artificial habitats, particularly water tanks. Additionally, while adult *P. perezi* were more commonly found in natural ponds and streams, non-adults were only found in artificial tanks and drainage channels. In contrast, *B. spinosus* and *A. obstetricans* were less numerous but more frequently found in artificial environments, whereas *D. galganoi*, *C. lusitanica*, and *E. calamita* were exclusively recorded in natural habitats, with only adults observed at one or two sites each, highlighting their small and fragmented distribution (Soares et al., 2005). Although *T. helveticus*, *P. cultripes*, and *H. arborea* were not observed, this was likely due to their scarcity in PNPG and preference for fossorial and arboreal habitats which were not covered in this study (Soares et al., 2005).

Overall, we found that natural waterbodies had higher proportions of occupied sites, greater species diversity, greater Shannon-Wiener diversity for adults, and more breeding events compared to artificial waterbodies. Specifically, three-quarters of the natural waterbodies were occupied by species at least once during the study, while only half of the artificial sites were

recorded as having a species present. Among the natural habitats, stream pockets were particularly crucial, with nearly all surveyed sites being occupied by species at least once. These pockets served as vital refuges and breeding sites, especially for *R. iberica* and *S. salamandra*, which bred in a third of all stream pockets. Notably, *R. iberica* bred exclusively in natural waterbodies, highlighting its reliance on these habitats for reproduction. In contrast, *S. salamandra* exhibited greater habitat flexibility, breeding in both natural and artificial waterbodies, although it did not breed in fountains. Despite higher breeding activity in natural habitats, artificial waterbodies supported a similar number of breeding events, suggesting that both types of habitats play an equally important role for reproduction.

While artificial waterbodies had a lower proportion of their sites occupied, they still played an important role in supporting amphibian diversity and reproduction. While there was some overlap in the species present in both artificial and natural waterbodies, each habitat type supported relatively distinct species assemblages, highlighting the unique role artificial waterbodies play in providing suitable habitats for certain amphibian species. Additionally, artificial habitats exhibited greater diversity in non-adults (juveniles and larvae), suggesting their significance as important sites for early life stages. Tanks were particularly important, with two-thirds being occupied at least once during the two survey seasons,

representing the highest proportion of their sites occupied among artificial waterbodies. These historical tanks supported breeding activity for four out of the five breeding species recorded (*L. boscai*, *S. salamandra*, *T. marmoratus*, and *P. perezii*). This species richness was greater than all types of natural waterbodies combined, which supported only the three most common species (*R. iberica*, *S. salamandra*, and *L. boscai*). These results demonstrate how these historical artificial waterbodies complement the park's natural waterbodies by providing vital refuges and additional breeding sites for a diverse range of amphibian species. Typically elevated and fish-free, such tanks provide stable hydrological conditions and protection from predators, significantly improving breeding success and larval survival (Arillo et al., 2022; Cabral et al., 2017; Ferreira & Beja, 2013; Garcia-Gonzalez & Garcia-Vazquez, 2011; Gould et al., 2024). Additionally, drainage channels were also found to be an important artificial habitat, consistent with previous studies (Mazerolle, 2005; Yu et al., 2022), with nearly 40% of them being occupied at least once and hosting the highest number of species among all waterbody types. Indeed, comparable studies have shown that artificial sites, such as water tanks and drainage channels, can provide important breeding habitats for amphibians, especially in landscapes altered by human activity (Brand & Snodgrass, 2010; Caballero-Díaz et al., 2020, 2022; Ferreira & Beja, 2013; Romano et al., 2023). The absence of breeding activity in fountains may be attributed to factors such as high water flow, lack of suitable substrates, chemical cleaning, or frequent human disturbance, making them less favorable for amphibian reproduction.

Although this study offers valuable insights into the role of human-modified waterbodies for amphibian communities within the PNPG, it has several limitations. Surveys were conducted in a short time period of a week or less during just two consecutive breeding seasons, which may not capture the full temporal dynamics and seasonal variations that could influence amphibian relative abundance, breeding activity, habitat preferences, and life stage-specific use of waterbodies. Additionally, the study was limited to waterbodies that exist within human-disturbed areas, such as villages and roads, within the northern part of the park. As a result, the findings may not be fully representative of the amphibian communities and waterbodies across the broader, more remote, and pristine areas of the national park. We also recognize the limitations associated with not distinguishing between true absence and pseudo-absence and the lack of species-specific detection probability corrections, which could affect our data interpretation. Despite extensive systematic surveys, some species, particularly

those exhibiting cryptic behaviors, low population density, or life stage-specific habitat use, may have been overlooked, leading to an incomplete representation of community biodiversity. To address these limitations, future studies should incorporate detection-based approaches that account for life stage differences and explore amphibian use across a wider range of habitats, including larger or more pristine landscapes. Expanding geographic and temporal coverage and employing more comprehensive survey techniques will enhance our understanding of amphibian diversity and conservation within PNPG.

Looking ahead, the integration of artificial waterbodies into broader conservation strategies will be essential for sustaining amphibian populations not only within PNPG but also in the face of global challenges such as climate change and habitat loss (Brand & Snodgrass, 2010; Briggs, 2001; Garcia-Gonzalez & Garcia-Vazquez, 2011). While artificial waterbodies, such as historic water tanks and drainage channels, typically have lower species richness compared to natural ones, they often serve as the only viable breeding and refuge sites in human-altered landscapes (Brand & Snodgrass, 2010; Buono et al., 2019; Plăiașu et al., 2012; Valdez et al., 2021). As climate change intensifies, leading to more frequent and severe droughts in the Iberian Peninsula (Alvarez et al., 2024; Soares et al., 2023), artificial waterbodies will become increasingly crucial in sustaining biodiversity in the region. Such waterbodies will be important to support not only species like *T. marmoratus*, which are highly vulnerable to climate-induced range contractions (Préau et al., 2022) but also serve as essential refuges and connectivity stepping stones for all species as natural habitats continue to diminish and their availability becomes more unpredictable. Indeed, our study found that while breeding events in artificial waterbodies remained stable, natural waterbodies saw a dramatic decline during the second breeding season, underscoring the crucial role of artificial waterbodies as reliable refuges amid fluctuating conditions. This hydrological stability is particularly important for less mobile species such as newts, which are more sensitive to habitat changes and climate impacts, potentially reducing the persistence of all but a few mobile and opportunistic species (Ficetola & De Bernardi, 2004).

To maximize the benefits of artificial waterbodies, it is important to integrate their management with natural ecosystems, especially in areas like PNPG where land abandonment has led to the deterioration of these structures. Similar impacts have been observed in northern Italy, where land abandonment has negatively impacted the breeding sites of endangered amphibians (Arillo et al., 2022; Canessa et al., 2013). While fountains are more likely to be preserved for their historical and aesthetic value, they offer little support for amphibian conservation. In contrast, water tanks, which provide crucial

breeding habitats for several amphibian species, receive less conservation attention due to their lower cultural significance and are more vulnerable to neglect as traditional village life and agricultural practices decline. Effective management must not only conserve these structures but also address threats such as physical deterioration from land abandonment, chemical cleaning, and the introduction of non-native species (Chiacchio et al., 2024). Incorporating traditional and environmentally friendly land management practices can help maintain a mosaic of natural and human-altered landscapes that support optimal amphibian habitats (Briggs, 2001; Plăiașu et al., 2012). Additionally, incorporating key habitat characteristics, such as ramps in artificial habitats, has also proven effective in enhancing amphibian conservation efforts (Arillo et al., 2022; Yu et al., 2022). By integrating artificial waterbody management with natural ecosystems and holistic conservation practices, we can ensure that these habitats remain critical refuges for amphibians, preserving both cultural heritage and local biodiversity amid ongoing environmental challenges.

## CONCLUSION

This study underscores the often-overlooked yet crucial role of artificial habitats in sustaining amphibian populations within PNPG. Centuries-old water tanks and irrigation channels, remnants of traditional village life, not only offer essential refuges and breeding sites for amphibians but also reflect the region's rich cultural heritage. As natural wetlands decrease and environmental conditions grow more unpredictable, especially with the rising frequency and intensity of droughts in the Iberian Peninsula, many of these man-made structures will become increasingly critical for maintaining local biodiversity. By integrating the management of artificial habitats with broader conservation strategies, we can better support amphibian populations, improve ecological resilience, and preserve the cultural landscapes that are intrinsic to the region's heritage.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

## DATA AVAILABILITY STATEMENT

Data (Valdez, 2024) are available from Figshare: <https://doi.org/10.6084/m9.figshare.27304026.v1>.

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## SUPPORTING INFORMATION

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