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From ponds to pondscapes: habitat characteristics influencing the abundance of the threatened yellow-bellied toad (*Bombina variegata*)

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Abstract. Amphibians are the most endangered class of vertebrates globally, with approximately 40% of species threatened with extinction. Among them, the yellow-bellied toad (*Bombina variegata*) has experienced significant population declines due to habitat destruction, fragmentation, and the disappearance of dynamic aquatic environments. To provide effective insights for conservation practitioners, this study examines the ecological requirements of *B. variegata* by analysing habitat characteristics influencing the species presence and abundance across two spatial scales: pond clusters and ponds. Using generalized linear mixed models, we assessed the presence and abundance from 518 ponds spread across 33 pond clusters located in four regions of western Switzerland. Our results emphasize the importance of pond network density, with species presence and abundance increasing in pond clusters containing at least eight ponds. At the pond scale, occupancy was highest in sunlit ponds with sand/gravel or silt/clay substrates, while abundance was positively associated with populational connectivity and the availability of mineral shelters in the direct proximity of the breeding site. By integrating our finding with existing conservation guidelines, we recommend the creation of multiple small ponds within 150 m of occupied sites, ensuring high connectivity and maximising sun exposition. Terrestrial habitat management should incorporate structural refuges near breeding sites to enhance habitat suitability. Additionally, regular habitat renewal is crucial to sustaining dynamic breeding conditions. These insights reinforce the need for targeted habitat restoration to support *B. variegata* populations in human-dominated landscapes and, more generally, stress the importance of maintaining well-connected pond clusters with high-quality terrestrial habitat for spatially-structured populations of pond-breeding amphibians.

Keywords: amphibian, ecological requirements, conservation management, multi-scale effects.

Introduction

Amphibians are the most endangered class of vertebrates globally, with approximately 40% of species threatened with extinction (Houlahan et al., 2000; Luedtke et al., 2023; Re:wild et al., 2023). The primary drivers of amphibian declines include habitat destruction, fragmentation, and loss due to human activities, as well as climate change, invasive alien species and emerging infectious diseases (Grant et al., 2016; Jaureguiberry et al., 2022).

Among those threats, habitat degradation remains a major and ongoing factor contributing to population declines in freshwater ecosystems (Reid et al., 2019). Aquatic habitats are not only essential for pond-breeding amphibians, but also support a wide range of species by providing water, food, and shelter, thereby playing a crucial role in maintaining local and regional biodiversity (Hill et al., 2021).

To mitigate the freshwater biodiversity crisis in human-dominated landscapes, effective conservation measures must be implemented

(Sutherland et al., 2020; Grant et al., 2019). In this context, conservation guidelines and management recommendations are crucial for protecting threatened species and their habitats (Arlettaz et al., 2010; Hoffmann et al., 2010). For conservation actions to be effective, both practical and empirical evidence are required (Fabian et al., 2019). Bridging the persistent gap between conservation science and practice is therefore essential, ensuring that research-based recommendations are directly applicable to conservation practitioners (Arlettaz et al., 2010; Canessa et al., 2019).

Recent proof-of-concept studies have demonstrated the effectiveness of habitat creation in halting and reversing wildlife population declines (Smith and Sutherland, 2014; Svenning, 2020). In freshwater ecosystems, aquatic habitat restoration at both local and regional scales has proven to be a viable strategy for supporting declining pond-breeding amphibian species (Sutherland et al., 2020; Moor et al., 2022). Such measures have been shown to counteract population declines by enhancing habitat availability, restoring environment dynamics and improving connectivity between ponds (Hill et al., 2018, 2021; Moor et al., 2022).

Although aquatic habitat has traditionally received the most attention in amphibian conservation, surrounding terrestrial habitats are increasingly recognized for their importance (Clauzel et al., 2024). Terrestrial landscapes influence freshwater quality by affecting chemical and physical properties (Ficetola et al., 2011), ultimately impacting a wide range of taxa, including amphibians (Harper et al., 2008). Consequently, habitat creation must integrate both aquatic and terrestrial features (Semlitsch and Bodie, 2003; Nolan et al., 2023) to establish networks of well-connected, high-quality habitat patches capable of sustaining amphibian populations (Sutherland et al., 2020; Moor et al., 2024). Given their complex life cycles and their spatial structure in well-connected populations (Jeliazkov et al., 2019), pond-breeding amphibians rely on dispersal mechanisms to maintain spatially-structured populations (Revilla and Wiegand, 2008; Cayuela et al., 2020b), making them particularly vulnerable to habitat fragmentation and the loss of dispersal corridors (Falaschi et al., 2021). This highlights the need to incorporate connectivity metrics when designing conservation strategies for species with limited dispersal capabilities (Drake et al., 2022).

In the context of pond construction, incorporating species-specific habitat preferences has been shown to effectively support declining amphibian populations (Smith and Sutherland, 2014; Siffert et al., 2022). The importance of ecological knowledge in guiding habitat restoration and adaptive management has been well documented (Gann et al., 2019; Hill et al., 2021). However, our understanding of how specific habitat characteristics influence amphibian occurrence and abundance remains limited (Grant et al., 2019). This knowledge gap is particularly evident for the yellow-bellied toad (*Bombina variegata*), a species for which the influence of aquatic and terrestrial habitat features on population dynamics remains poorly understood (Cayuela et al., 2021).

The yellow-bellied toad is a European species, with a distribution spanning from France to Turkiye (Bülbül et al., 2016), covering Central Europe and the Balkan Peninsula (Dufresnes et al., 2025). Typically found at elevations between 300-800 m a.s.l. throughout the Alps (Gollmann and Gollmann, 2012), some populations use much higher habitats in Southern Europe, up to 2200 m in Albania (Haxhiu, 1994).

Bombina variegata thrives in dynamic environments where new ponds frequently appear (Pichenot, 2008). It primarily breeds in small, temporary ponds that are sparsely vegetated and warm up rapidly (Gollmann and Gollmann, 2012), conditions that favour larval development while reducing aquatic predation pressure (Boualit et al., 2019). Reproduction occurs between late April and August, with females distributing their clutches across multiple sites

to enhance reproductive success (Barandun and Reyer, 1997). The species relies on a network of ponds spaced between 500 meters to 2 kilometres apart, where juvenile dispersal and population connectivity is guaranteed (Jacob et al., 2009). Additionally, terrestrial habitats with structurally rich forests and open areas offering shelters such as rocky structures, deadwood, and leaf litter have been found to support species occupancy (Harper et al., 2008).

Over the past century, the yellow-bellied toad has undergone significant declines across Western Europe mainly due to habitat destruction, fragmentation, and the loss of dynamic aquatic environments driven by human activities (Gollmann and Gollmann, 2012; Luedtke et al., 2023). Due to the marked decline of its primary habitats such as alluvial plains and near-natural watercourses, the species has shifted to substitute habitats of anthropogenic origin including extraction sites, military training grounds, agricultural fields, and managed forests (Gollmann and Gollmann, 2012; Cayuela et al., 2021).

Because of its alarming decline, *B. variegata* is protected at the European level under the EU Habitats directive (Annex II and IV). In Switzerland, the species was classified in the 2023 Red List as highly dependent on targeted conservation measures (Schmidt et al., 2023). Despite the urgent need to preserve and restore its breeding habitats to mitigate further declines, little is known about how specific habitat characteristics influence the species demography (Cayuela et al., 2021). In particular, the impact of the physical characteristics of ponds (e.g., surface area, depth), their spatial integration (e.g., connectivity with other ponds), and the composition of the surrounding landscape (e.g., presence of physical barriers to dispersal) remains insufficiently documented (Grant et al., 2019; Cayuela et al., 2021).

This study aims to identify the ecological requirements of *B. variegata* across aquatic and terrestrial habitats to provide effective insights for conservation practitioners. Species monitoring and habitat surveys were conducted to assess the influence of habitat characteristics on species presence and abundance. Since the yellow-bellied toad's distribution is shaped by landscape-scale factors extending over several kilometres from breeding sites (Zanini et al., 2009; Pröhl et al., 2021), conservation efforts must integrate multiple spatial scales. Research was therefore conducted at two levels (table 1): (1) pond clusters (i.e., networks of ponds and their surrounding matrix; Boothby, 1997), accounting for the spatial structure of regional populations; and (2) pond, where individuals were detected.

Given the pioneer character of the species (Gollmann and Gollmann, 2012), we expect *B. variegata* abundance to be higher in pond clusters with a greater number of ponds and higher connectivity (Hill et al., 2018; Jeliazkov et al., 2019). Likewise, forest and ruderal cover should positively influence abundance (Pichenot, 2008), while built areas are expected to have a negative impact (Cayuela et al., 2019a). At the pond level, temporary, sunlit, sparsely vegetated ponds with clay substrates and nearby wood or mineral terrestrial shelters are expected to support higher abundances as compared with other ponds (Mermod et al., 2010; Gollmann and Gollmann, 2012; Cayuela et al., 2021).

Materials and methods

Study area

We defined the study area using *Bombina variegata* occurrence data from the past 10 years in western Switzerland with a geographic precision of under 250 m, sourced from the Swiss Species Information Center (InfoSpecies). We then delineated two buffer zones around these occurrences. The first had a radius of 500 m (Herrmann, 1996; Laufer, 2014; Aletsee, 2023) and described the spatially-structured populations at the regional scale (i.e. groups of local populations connected by the exchange of dispersing individuals; Revilla and Wiegand, 2008), derived from natal dispersal (i.e. the movement of individuals between the completion of metamorphosis and first reproduction; Cayuela et al., 2020b). The second had a radius of 150 m (Jacob et al., 2009; Höppner et al., 2017; Aletsee, 2023) and reflected the local population structure at the pond cluster-scale, informed by breeding dispersal (i.e. the movement of

Table 1. Explanatory variables used in the models, categorized by spatial scale (pond cluster or pond level).

	Habitat model	Name	Description	Mean	SD	Range
Pond cluster scale	Aquatic	nb_p	Number of ponds within site	16.225	17.721	1-61
	Terrestrial	surface	Site total surface area (ha)	17.292	11.200	6.952-48.716
		prop_F	Forest area within site (%)	49.795	31.802	0-98.307
		prop_R	Ruderal area within site (%)	8.733	13.913	0-46.287
		prop_C	Built area within site (%)	1.953	0.905	0.489-6.079
	Connectivity	conn_str	Pond cluster structural connectivity	0.326	0.209	0.024-0.913
		conn_pop	Pond cluster populational connectivity	0.242	0.193	0.018-0.774
Pond scale	Aquatic	level	Temporal dry out of the pond outside of the breeding season	–	–	0 or 1
		surface	Total surface of the pond (m^2)	11.115	20.938	0.255-194.208
		depth	Median depth of the pond (cm)	10.639	14.534	1-120
		slope	Mean of the pond bank slope (%)	9.915	13.678	0.611-100.358
		sunshine	Sunlight at the vertical of the water surface between May and June (%) (at 10%)	91.640	20.790	0-100
		quality	Eutrophic (1): turbid water, floating filamentous algae. Oligotrophic (0): clear water, no floating filamentous algae	–	–	0 or 1
		hydrophytes	Pond coverage by submerged and floating hydrophytes (%) (at 10%)	3.691	9.131	0-80
		helophytes	Pond coverage by helophytes (%) (at 10%)	8.755	10.216	0-60
		substrate	Benthic substrate (liner/concrete (LC); leaves/peat (LP); silt/clay (SC); sand/gravel (SG))	–	–	–
	Terrestrial	mineral	Mineral shelter adjacent to the pond	–	–	0 or 1
		wood	Wooden shelter adjacent to the pond	–	–	0 or 1
	Connectivity	conn_str	Pond structural connectivity	15.490	9.654	0-33.655
		conn_pop	Pond populational connectivity	7.317	6.061	0-23.436

individuals after first reproduction; Cayuela et al., 2020b). These buffer distances are further supported by empirical data on the species dispersal, obtained through Capture-Mark-Recapture (Hartel, 2008; Aletsee, 2023) and telemetry studies (Alleman et al., 2024, unpublished data; Łaciak et al., 2024, unpublished data), alongside evidence from genetic analyses (Hantzschmann et al., 2021; Pröhl et al., 2021).

Next, we selected regions containing at least five non-overlapping pond clusters. We established the land cover of the pond clusters within the selected regions by visualising the open access map of Switzerland's habitats (Price et al., 2021) based on the hierarchical Swiss Habitat Typology (TypoCH; Delarze et al., 2015) in QGIS (v.3.36). We then classified the pond clusters based on the proportion of (i) forest and (ii) pioneer -alluvial plains- or ruderal -extraction sites and military training grounds- cover in the following categories: forest-dominated (>50%), pioneer/ruderal-dominated (>50%) or mixed. To accurately represent the variation in habitat composition at the pond cluster scale, we selected four regions encompassing the following gradient: only forest pond clusters, mixed (forest-dominated pond clusters>pioneer/ruderal-dominated pond clusters; forest-dominated pond clusters<pioneer/ruderal-dominated pond clusters), only pioneer/ruderal pond clusters. In total, we collected data from 518 ponds across 33 pond clusters in four regions of western Switzerland, fitting varying degrees of land use (fig. S1 in the Supplementary materials). The locations of these four studied regions are shown in fig. 1.

Data collection

We conducted a preliminary daytime survey in each pond cluster to identify all ponds potentially suitable for the

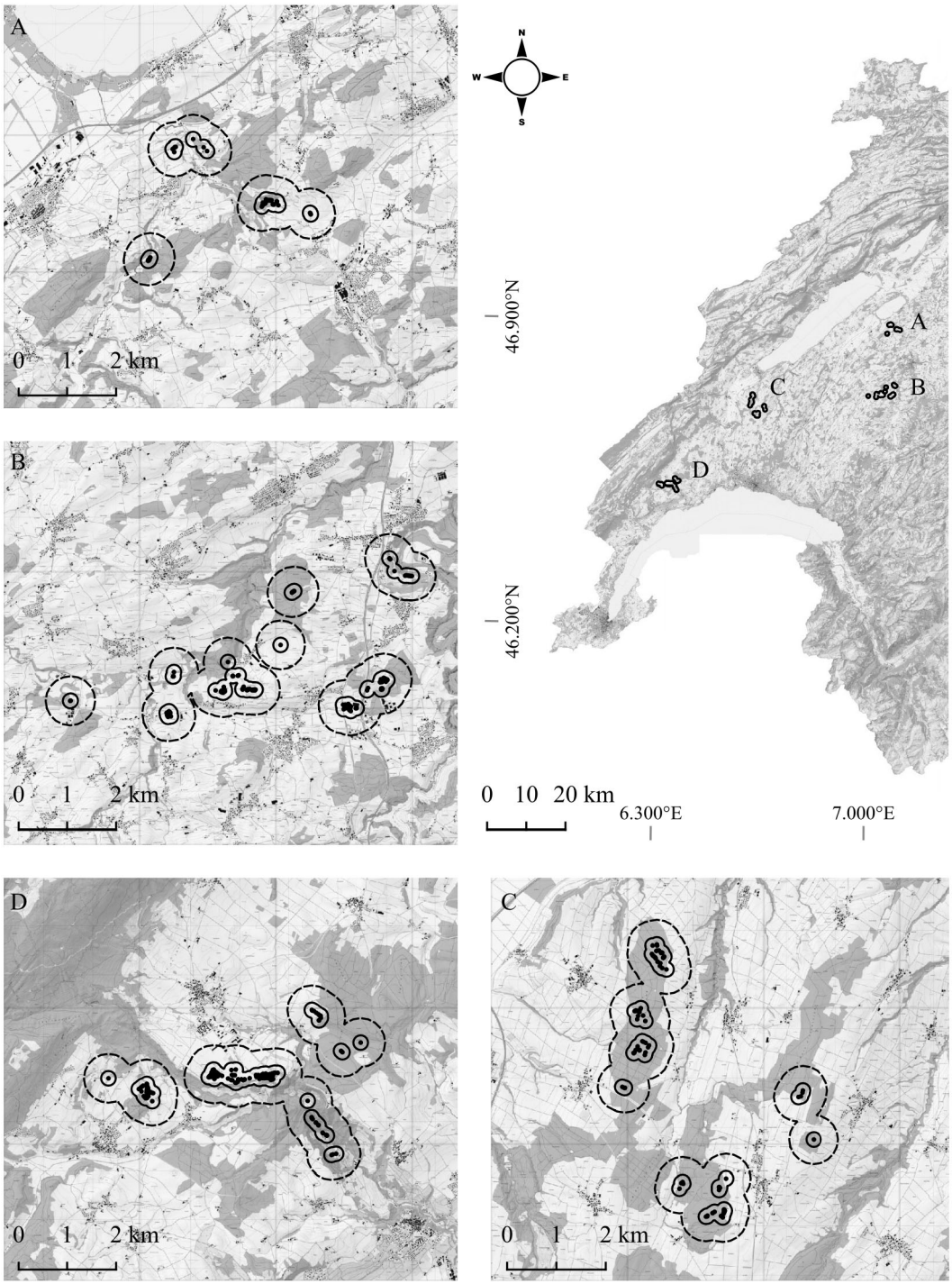

Figure 1. Map of studied regions at a 1:50 000 scale. The top right image displays an overview of regions distribution in western Switzerland: Courtepin (A), Ecuvillens (B), Suchy (C) and Aubonne (D). Buffers indicate surveyed pond clusters. Black dots indicate monitored ponds. The background map of Switzerland at a 1:10 000 scale highlights forested areas (dark grey) and human-made structures (black).

species (i.e. displaying water during the breeding season). Surveyed ponds encompassed all types of water bodies, ranging from small ruts (<1 m^2) to larger ponds approaching 200 m^2 in surface area. We then visited each pond three times at night within the breeding season (April to June 2024) to record the presence as well as the abundance of adults through both visual encounters and acoustic detections of calling males. Repeated visits to pond clusters allowed to account for imperfect detection while estimating species presence and abundance. Note that (i) we randomised the sequence of pond clusters visits to acknowledge for temporal and sampling bias, (ii) the order of pond monitoring varied across visits, (iii) all ponds within a pond cluster were surveyed on the same day to avoid bias caused by the movement of individuals, and (iv) all observations were gathered by only one observer.

To refine the analysis, we performed models integrating (i) presence and (ii) abundance data. Abundance-based models are known to provide deeper ecological insights, particularly into density-dependent demographic processes (Howell et al., 2020).

While the quality of breeding sites is crucial for local amphibian conservation, terrestrial habitat at the landscape scale and connectivity also strongly influence species distribution (Pichenot, 2008; Clauzel et al., 2024). Consequently, to evaluate the distinct influences of aquatic and terrestrial habitats, as well as connectivity on species presence and abundance, we designed the analysis by constructing separate models: (i) aquatic, (ii) terrestrial, (iii) connectivity, and (iv) a global model incorporating all variables. This approach allowed for a comprehensive assessment of the individual and combined effects of habitat characteristics on the species' occurrence and abundance at both the pond cluster and pond scales.

At the pond cluster scale, we gathered both aquatic and terrestrial habitat characteristics in QGIS (v.3.36) based on colour orthophotos obtained from the Swiss Federal Office of Topography (swisstopo) and on the open access dataset describing the habitats of Switzerland (see Study area above for more details). Altitude, temperature, and hygrometry were recorded at each pond cluster. Due to the geographical proximity of the sampled regions, climatic conditions were not considered in the statistical analysis. At the pond scale, we collected all data related to aquatic and terrestrial habitats directly in the field (July 2024) in accordance with the standardised protocol of the federal inventory of amphibian breeding sites of national importance (Ryser, 2002). Note that all ponds were checked for the presence of fish, a common threat to amphibian species (Falaschi et al., 2021). None were detected, which may result from the predominance of temporary ponds (approx. 90%) in the surveyed pond clusters.

Connectivity was calculated at both scales as proposed by Prugh (2009) and as implemented by Moor et al. (2024). Note that we distinguish structural connectivity (i.e. connectivity to all ponds/pond clusters, irrespective of their occupancy status) from populational connectivity (i.e. connectivity to ponds/pond clusters occupied by the species):

- Structural connectivity: $\text{conn}_{\text{str},i,t} \sum_{j \neq i} \exp(\frac{-d_{ij}}{\alpha}) E_{jt}$, where d_{ij} it the Euclidean distance (m) between ponds/pond clusters i and j, α a scaling parameter corresponding to the dispersal distance of the species (500 m at the pond cluster scale, 150 m at the pond scale), and $E_{jt} = \{0, 1\}$ indicates whether pond j existed in year t.
- Populational connectivity: $\text{conn}_{\text{pop},i,t} = \sum_{j \neq i} \exp(\frac{-d_{ij}}{\alpha}) E_{jt} y_j$, where y_j denotes the species presence in pond j during the field surveys (April-June 2024).

Pond cluster scale

Populations sampled at the pond cluster scale were considered closed to mortality, recruitment, and movement across visits. Single season occupancy models based on zero-inflated binomial models were fitted in RStudio (v.4.3.1) to estimate species occupancy within surveyed pond clusters (unmarked:occ; MacKenzie et al., 2006; Cruickshank et al., 2016). The negligible probability of false absence (0.03%) indicated high and consistent detectability across pond clusters. N-mixture models with negative-binomial family were then fitted to single-season spatially replicated count data to estimate detection probability of individuals abundance in each sampled pond cluster (unmarked:pcount; Royle, 2004; Kéry et al., 2005). Diagnostic evaluation of these models revealed systematic over- and under-prediction, with residuals pattern increase alongside predicted abundance, suggesting limited reliability of model-based abundance estimates. Therefore, subsequent analyses were performed using observed abundance within a generalized linear mixed-models framework.

Generalised linear mixed models were fitted at four hierarchical levels: aquatic, terrestrial, connectivity or global. Binomial family was used for occupancy models; zero-inflated negative binomial family for abundance. In abundance analyses, we chose to use the maximum adult abundance in a pond cluster as the response variable, which is recognized as being an appropriate proxy for carrying capacity (Gaston et al., 1997; Denoël and Lehmann, 2006). Note that to ensure model stability and parsimony given the limited number of regions ($n = 4$), the random effect of regions was excluded to avoid overparameterization and unreliable variance estimates (Groll and Tutz, 2014; McGillycuddy et al., 2024). Pearson correlation was calculated across variables (fig. S2 in the Supplementary materials), indicating no multicollinearity and associated bias (Mason and Perreault, 1991; De Winter et al., 2016).

Model selection was done by ranking the Akaike Information Criterion (AIC) obtained for each candidate model. All covariates were standardized to mean zero and unit variance to enable the comparison of parameters estimates. Visual inspection -DARMHa:simulateResiduals- was used in RStudio (v.4.3.1) to (i) assess standardised residuals overdispersion, (ii) check for outliers, and (iii) verify residuals variance homogeneity (Bolker et al., 2009). All assumptions were met for the presence analysis, while quantile-deviation was detected for the abundance analysis. Therefore, glmmTMB was used for better overdispersion handling (Brooks et al., 2017). Conditional inference trees were performed to identify partitioning threshold in variables significantly affecting species abundance, highlighting

their potential for ecological management (partykit::ctree; Hothorn et al., 2006). After excluding two pond clusters considered outliers due to their unsuitability -aquatic habitats lost due to the strong dynamics of the ponds used by the species- the final dataset comprised 33 pond clusters across four regions. Pond clusters where the species was not detected were excluded of the abundance analysis, which was thus conducted on 21 pond clusters instead of 33 for the presence.

Pond scale

A comparable approach was implemented at the pond scale, assuming populations were open across visits, precluding detection probability estimation (Kellner et al., 2023). Pearson correlations for all numeric variables were below 0.8 (fig. S2 in the Supplementary materials), indicating no multicollinearity and associated bias (Mason and Perreault, 1991; De Winter et al., 2016). To optimize model performance and prevent overparameterization, only the pond cluster random effect was included in the models, as the addition of the regional level introduced convergence challenges (Groll and Tutz, 2014; McGillycuddy et al., 2024).

Generalised linear mixed models were fitted and selected as in the pond cluster scale analysis. All covariates were standardized to mean zero and unit variance. All model assumptions were met for abundance, but quantile-deviation was detected in the presence analysis. Therefore, glmmTMB was used for better overdispersion handling (Brooks et al., 2017). After excluding 44 ponds considered outliers due to their unsuitability -drying out too early during the species' breeding season- data from 474 ponds across 33 pond clusters in four regions were included in the analysis. Ponds where the species was not detected were excluded of the abundance analysis, which was thus conducted on 218 ponds across 21 pond clusters instead of 474 ponds across 33 pond clusters for the presence.

Results

Pond cluster scale

Species presence at the pond cluster scale was best explained by the aquatic habitat model, which only included the total number of ponds as explanatory variable. Figure 2A illustrates the significant positive effect of pond density on occupancy probability ($P < 0.05$), showing

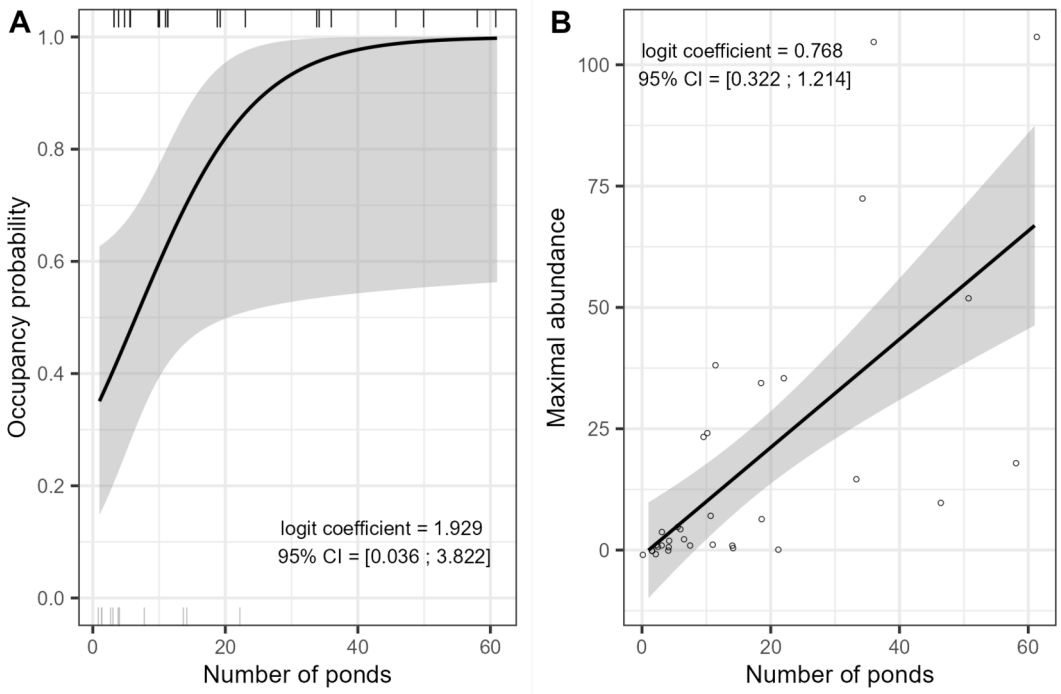

Figure 2. Influence of significant aquatic habitat variables on species presence (A) and abundance (B). (A) Occupancy probability of the species relative to the number of ponds within sampled pond clusters; tick marks represent the distribution of occupied (black) and non-occupied (grey) pond clusters by pond count. (B) Maximal species abundance in relation to the number of ponds within sampled pond clusters, with confidence intervals depicted in light grey. Logit-scale coefficients from the final model, along with their associated confidence intervals (95% CI), are shown directly on the graphs.

Table 2. Model selection table at the pond cluster scale. AICc: corrected Akaike information criterion.

	Model	Structure	AICc	Weight	Dev.	df res.
Presence	Aquatic	nb_p	38.73	0.428	34.3	31
	Terrestrial	surface+prop_F+prop_R+prop_C	39.12	0.352	26.9	28
	Global	nb_p+surface+prop_F+prop_R+prop_C+conn_pop+conn_str	40.09	0.216	18.1	25
	Connectivity	conn_pop+conn_str	48.15	0.004	41.3	30
Abundance	Aquatic	nb_p	176.7	0.996	22.8	18
	Connectivity	conn_pop+conn_str	187.7	0.004	23.7	17
	Terrestrial	surface+prop_F+prop_R+prop_C	192.8	0.001	23.3	15
	Global	nb_p+surface+prop_F+prop_R+prop_C+conn_pop+conn_str	200.8	0.000	22.3	12

Weight, Akaike weight; Dev., residual deviance; df res., degrees of freedom for residuals. See table 1 for abbreviations of variables.

Table 3. Model selection table at the pond scale.

	Model	Structure	AICc	Weight	Dev.	Df res.
Presence	Aquatic	level+depth+slope+surface+sunshine+ hydrophytes+helophytes+substrate+(1|site)	555.9	0.811	468	462
	Global	level+depth+slope+surface+sunshine+ hydrophytes+helophytes+substrate+mineral+ wood+conn_pop+conn_str+(1|site)	559.6	0.133	463	458
	Connectivity	conn_pop+conn_str+(1|site)	561.3	0.055	514	470
	Terrestrial	mineral+wood+(1|site)	570.5	0.001	499	470
Abundance	Global	level+depth+slope+surface+sunshine+ hydrophytes+helophytes+substrate+mineral+ wood+conn_pop+conn_str+(1|site)	933.6	0.979	198	200
	Connectivity	conn_pop+conn_str+(1|site)	941.5	0.019	191	212
	Terrestrial	mineral+wood+(1|site)	946.5	0.001	189	212
	Aquatic	level+depth+slope+surface+sunshine+ hydrophytes+helophytes+substrate+(1|site)	953.4	0.000	191	204

AICc, corrected Akaike information criterion; Weight, Akaike weight; Dev., residual deviance; df res., degrees of freedom for residuals. See table 1 for abbreviations of variables.

that an increase in pond number within a pond cluster favours the presence of *B. variegata*.

Species abundance at the pond cluster scale was best described by the aquatic model. Figure 2B illustrates that, once present, species abundance is significantly higher in pond clusters with a greater number of ponds ($P < 0.001$). Conditional inference trees revealed that the species abundance increased in pond clusters containing at least eight ponds and peaked when there are more than nineteen ponds (fig. S3 in the Supplementary materials).

Details of the candidate models for both presence and abundance at the pond cluster scale are provided in table 2.

Pond scale

Species presence at the pond scale was best explained by the aquatic model, which incorporated pond depth, slope, water level, surface, sun exposure, hydrophytes/helophytes coverage and benthic substrate. Among these, benthic substrate composition and sun exposure significantly impacted the species presence ($P < 0.05$; $P < 0.01$). The yellow-bellied toad presence was strongly enhanced in ponds where benthic substrate was sand/gravel or vase/clay. In contrast, leaves/peat substrates seemed to be less attractive for the species, while it was almost always absent in ponds with directly apparent liner/concrete. Additionally, increased sunlight exposure significantly

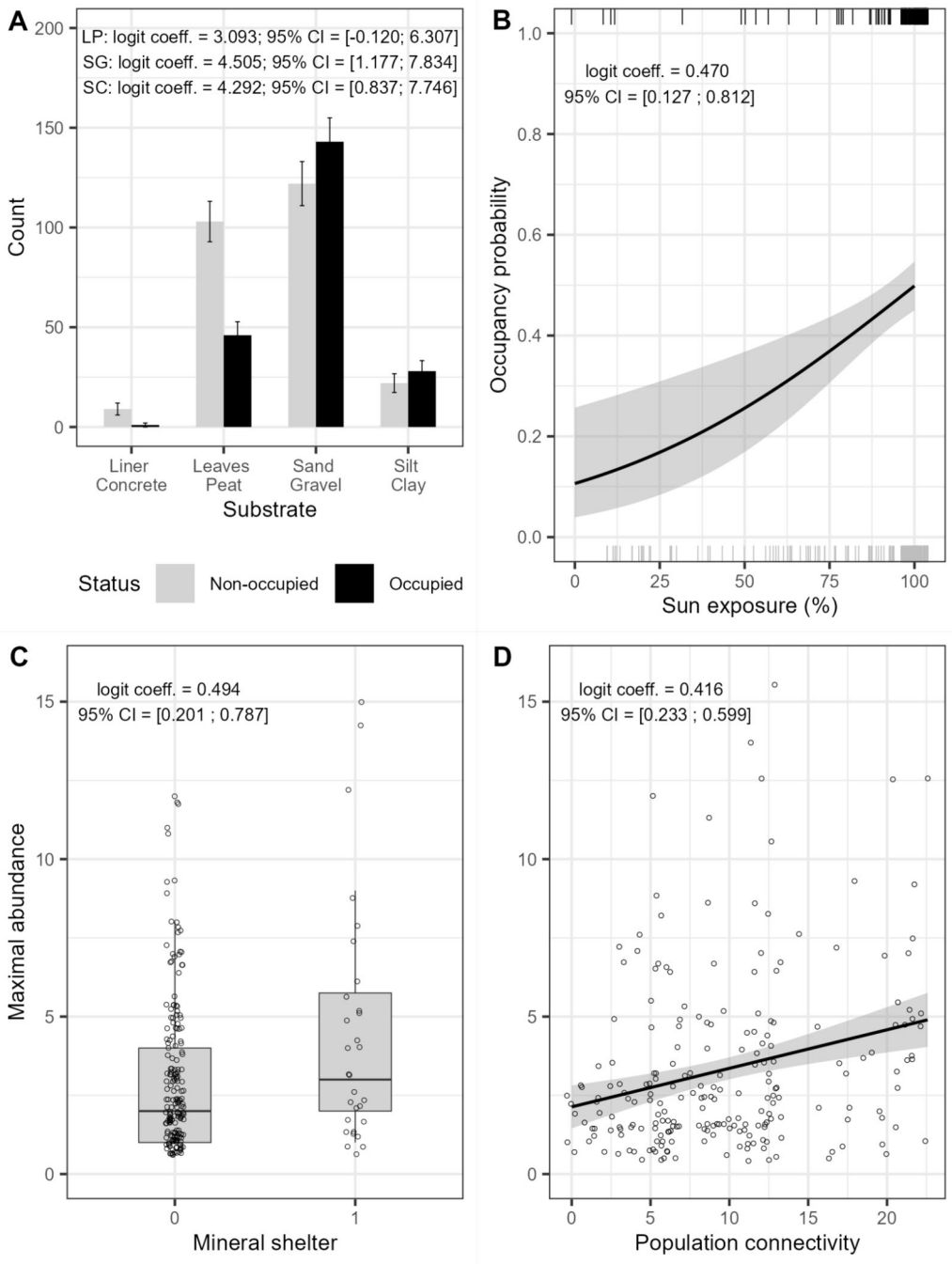

Figure 3. Influence of significant aquatic habitat variables on species presence (A, B) and of the global model significant variables on species abundance (C, D). (A) Number of ponds occupied (black) or non-occupied (grey) by the species depending on the substrate. (B) Species occupancy probability depending on the pond sun exposure (%); Tick marks represent the repartition of occupied (black) or non-occupied (grey) ponds sampled. (C) Maximal abundance of the species depending on the absence (0) or on the presence (1) of a mineral shelter in the direct surrounding of the pond. (D) Maximal abundance of the species depending on the pond population connectivity. Logit-scale coefficients from the final model, along with their associated confidence intervals (95% CI), are shown directly on the graphs.

enhanced species presence. Owing to the variations in sunlight exposure between ruderal areas and forest environments, the effect was more pronounced in forest habitats.

Species abundance at the pond scale was best explained by the global model. Once *B. variegata* was present in a pond, its abundance was significantly enhanced by connectivity to nearby occupied ponds ($P < 0.001$). Conditional inference trees revealed that the average abundance in a pond increased by 35% when $\text{conn}_{\text{pop},i,t} > 10.965$ (fig. S3 in the Supplementary materials). Furthermore, the yellow-bellied toad abundance was higher when mineral shelter was available in the direct proximity to the pond ($P < 0.001$).

Details of the candidate models for both presence and abundance at the pond scale are provided in table 3, while the corresponding results are illustrated in fig. 3.

Discussion

Our findings highlight the critical role of both pond cluster- and pond-scale habitat characteristics in promoting the presence and abundance of *B. variegata*. Specifically, we show that at the pond cluster scale, pond network density is a key driver of species presence and abundance, while at the pond scale, local connectivity, sunlit conditions, and substrates such as sand/gravel or silt/clay, combined with nearby mineral shelters are crucial for supporting populations. These results underscore the need for conservation strategies that combine high-quality aquatic and terrestrial elements within well-connected habitat networks.

Our findings align with existing conservation recommendations, where habitat creation is widely recognized as a simple and effective measure for mitigating the decline of pond-breeding amphibians in human-dominated landscapes (Magnus and Rannap, 2019; Moor et al., 2022). To ensure long-term persistence of spatially-structured populations (Howell et al., 2020; Pröhl et al., 2021), conservation measures should prioritize the establishment of well-connected pond networks that integrate high-quality terrestrial habitats (Drake, Lambin and Sutherland, 2022; Nolan et al., 2023). Our results build on these frameworks, reinforcing the importance of tailoring conservation planning to species-specific ecological requirements (Gann et al., 2019; Grant et al., 2019) while addressing both aquatic and terrestrial habitat needs.

Pond cluster scale

Our results demonstrate that species occupancy at the pond cluster scale is significantly enhanced by the number of ponds within a given pond cluster. This outcome is consistent with previous studies showing that *B. variegata* persistence is highly dependent on the availability of multiple breeding sites (Cayuela et al., 2020a; Clauzel et al., 2024). The presence of numerous ponds increases recruitment opportunities and enhances the stability of spatially-structured amphibian populations (Grant et al., 2016), a key factor for species that rely on highly dynamic habitats (Lowe et al., 2015).

In contrast, neither structural nor populational connectivity significantly influenced occupancy at the pond cluster scale. This observation contradicts earlier findings suggesting that connectivity between breeding sites plays a major role in amphibian distribution (Jeliazkov et al., 2019). Possible reasons for this trend include (i) barriers to individual movement causing discrepancies between measured connectivity and actual dispersal, and (ii) pond cluster-scale connectivity not accurately reflecting movement patterns, as individuals may disperse opportunistically across a broader landscape rather than strictly between adjacent patches. Future studies could refine connectivity assessments by incorporating finer-scale movement data (e.g. Capture-Mark-Recapture or telemetric data) and by performing sensitivity analyses to better determine the influence of buffer zone size on study outcomes.

Although the proportion of built-up areas was not included in the best-fitting model, it exhibited a strong negative impact on species presence. This finding aligns with existing literature, which indicates that road networks, urban infrastructure, and low-quality habitat create significant barriers to amphibian dispersal (Grant et al., 2019; Cayuela et al., 2019a). Consequently, conservation efforts should focus on minimizing habitat fragmentation and improving landscape permeability.

The species abundance was significantly correlated with the number of ponds within a pond cluster, whereas other habitat characteristics, including terrestrial and connectivity variables, were not significant. These results reinforce prior research indicating that increasing aquatic habitat availability is a key driver of species presence and should be a primary focus in conservation planning (Falaschi et al., 2021; Moor et al., 2024). The creation of artificial ponds in areas already occupied by the species is therefore a justified and effective strategy for population reinforcement.

Pond scale

Species presence was significantly favoured in sunlit ponds with benthic substrates such as sand/gravel or silt/clay. While the yellow-bellied toad occasionally occupied sunlit ponds with leaves/peat substrates, it was largely absent from shaded ponds or those with exposed liner/concrete bottom. This result is coherent with recent literature mentioning that the yellow-bellied toad's attraction to sun exposure may stem from increased water temperature, which tends to accelerate larval development (Morand et al., 1997), thereby favouring the species in strongly dynamic habitats where breeding patches availability is unpredictable and temporary (Cayuela et al., 2020a, 2021). Furthermore, competition with other species tends to be reduced in such harsh conditions, directly benefitting *B. variegata* progeny (Łaciak et al., 2022). Yet, under ongoing climate change, these advantages may be offset by more frequent droughts and heat waves, making it essential to maintain a landscape mosaic of temporary, permanent, shaded and sunlit waterbodies to buffer populations against climatic unpredictability and ensure long-term populations persistence (Lowe et al., 2015).

Surprisingly, pond physical characteristics such as surface area, depth, and the average slope of the banks, along with terrestrial features such as wood and mineral shelters, did not significantly affect species presence. This finding may reflect a lack of available breeding sites or conversely, a high population density, compelling the species to utilize suboptimal habitats.

Similarly, vegetation cover and water level fluctuations variables did not have a significant effect on species presence, despite expectations based on previous studies (Gollmann and Gollmann, 2012). This could be attributed to the fact that most of the sampled ponds were situated in highly dynamic pond clusters, which predominantly featured temporary ponds (approx. 90%), characterised by scarce vegetation.

Although population connectivity was not a significant predictor at the pond cluster scale, it had a strong positive effect on species presence at the pond scale. This finding aligns with previous studies emphasizing the necessity of incorporating connectivity to nearby source populations when designing habitat restoration efforts (Keeley et al., 2021; De Necker et al., 2025).

Species abundance within ponds was best explained by the global model. This result strongly supports previous statements on the importance of considering (i) aquatic habitat quality, (ii) surrounding terrestrial habitat, and (iii) connectivity to other occupied ponds, to broaden the number of individuals detected in a pond. These findings are in agreement with established conservation principles for pond-breeding amphibian conservation, which in addition to species-specific measures (Gann et al., 2019; Grant et al., 2019), require diverse habitat matrix, including breeding water bodies, summering sites, wintering

habitats, and movement corridors for population maintenance (Scheele et al., 2014; Semlitsch and Bodie, 2003).

Furthermore, increased population connectivity significantly enhanced species abundance, supporting frameworks in which breeding patches are interconnected through a flow of dispersing individuals (Cayuela et al., 2020b; Pröhl et al., 2021). These results reinforce the need to establish pond networks with short inter-pond distances to promote dispersal and recolonization opportunities (Jeliazkov et al., 2019; Moor et al., 2024).

Moreover, species abundance was significantly higher in ponds with nearby mineral shelters. This result aligns with existing knowledge advocating for the installation of small structures such as stone piles, branches and stumps to enhance habitat attractiveness for amphibians and small fauna (Semlitsch and Bodie, 2003; Indermaur and Schmidt, 2011; Pellet and Amstutz, 2014). Such microhabitats not only provide essential shelter but also serve as a food source for amphibians by attracting invertebrates (Harper et al., 2008).

Syntheses and recommendations

The creation of well-connected pond networks that integrate both aquatic and terrestrial habitat features effectively support pond-breeding amphibian populations in human-dominated landscapes (Magnus and Rannap, 2019; Sutherland et al., 2020). Our findings provide additional insights into the habitat characteristics shaping *B. variegata* presence and abundance, allowing for a more precise definition of the species' ecological requirements. This refined understanding aims to enhance the effectiveness of targeted conservation strategies across the species' range. Although highly dynamic streams were not included in the present study due to their scarcity in Switzerland, they are known breeding sites for the species and may serve as key refuges under climate change. Incorporating streams into conservation planning alongside forest and pioneer habitat helps form a comprehensive strategy to support population resilience. Hereafter, existing knowledge is presented alongside key findings from our study. As a complement, a visual summary is provided (fig. S5 in the Supplementary materials).

Pond clusters should be established within 500 m to 2 km of other populations to facilitate spatially-structured population dynamics (Laufer, 2014; Cayuela et al., 2019b; Aletsee, 2023). Our study indicates that effective pond clusters should contain at least eight temporary ponds, with an optimal target of more than twenty. To maintain strong functional connectivity between breeding patches, ponds should be located within 150 m of an occupied breeding site, aiming for a connectivity value of at least 10.96 between occupied ponds (fig. S4 in the Supplementary materials).

Optimal breeding ponds for the species are temporary (holding water for at least eight consecutive weeks between April and August), small (0.5-20 m^2), shallow (10-60 cm deep), vegetation-poor, and seasonally drying (Mermod et al., 2010; Gollmann and Gollmann, 2012). Our results further highlight the importance to prioritize sunny or semi-shaded ponds with canopy openness directly above the pond exceeding 75%, and benthic substrates of sand/gravel or silt/clay. Where artificial liner/concrete surfaces are used, they should be covered with these materials. Mineral or wood shelters adjacent to ponds (<50 m) should as well be favoured to enhance habitat suitability.

Supplementary materials. Data is available on https://doi.org/10.1163/15685381-bja10246 under Supplementary Materials.

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