



**University of
Zurich**^{UZH}

**Zurich Open Repository and
Archive**

University of Zurich
University Library
Strickhofstrasse 39
CH-8057 Zurich
www.zora.uzh.ch

Year: 2024

Building pondscapes for amphibian metapopulations

Moor, Helen ; Bergamini, Ariel ; Vorburger, Christoph ; Holderegger, Rolf ; Bühler, Christoph ; Bircher, Nicolas ; Schmidt, Benedikt R

DOI: <https://doi.org/10.1111/cobi.14281>

Posted at the Zurich Open Repository and Archive, University of Zurich

ZORA URL: <https://doi.org/10.5167/uzh-259678>

Journal Article

Published Version



The following work is licensed under a Creative Commons: Attribution-NonCommercial 4.0 International (CC BY-NC 4.0) License.

Originally published at:

Moor, Helen; Bergamini, Ariel; Vorburger, Christoph; Holderegger, Rolf; Bühler, Christoph; Bircher, Nicolas; Schmidt, Benedikt R (2024). Building pondscapes for amphibian metapopulations. Conservation Biology: Epub ahead of print.

DOI: <https://doi.org/10.1111/cobi.14281>

CONTRIBUTED PAPER

Building pondscapes for amphibian metapopulations

Helen Moor^{1,2}  | Ariel Bergamini¹  | Christoph Vorburger^{2,3}  | Rolf Holderegger^{1,3}  |
 Christoph Bühler⁴ | Nicolas Bircher⁵ | Benedikt R. Schmidt^{6,7} 

¹Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Birmensdorf, Switzerland

²Swiss Federal Institute of Aquatic Science and Technology Eawag, Dübendorf, Switzerland

³Department of Environmental Systems Science, ETH Zurich, Zurich, Switzerland

⁴Hintermann & Weber AG, Reinach, Switzerland

⁵Sektion Natur und Landschaft, Kanton Aargau, Aarau, Switzerland

⁶info fauna karch, Neuchâtel, Switzerland

⁷Department of Evolutionary Biology and Environmental Studies, University of Zurich, Zürich, Switzerland

Correspondence

Helen Moor, Swiss Federal Institute of Aquatic Science and Technology Eawag, Überlandstrasse 133, CH-8600 Dübendorf, Switzerland.
 Email: helen.moor@eawag.ch

Article impact statement: Ponds built for amphibian conservation should have ≥ 100 m² of water, be temporary, be located in open land, and be situated within 0.5 km of ≥ 2 existing populations.

Funding information

Board of the Swiss Federal Institutes of Technology; Blue-Green Biodiversity Initiative, Grant/Award Number: (BGB2020)

Abstract

The success of ponds constructed to restore ecological infrastructure for pond-breeding amphibians and benefit aquatic biodiversity depends on where and how they are built. We studied effects of pond and landscape characteristics, including connectivity, on metapopulation dynamics of 12 amphibian species in Switzerland. To understand the determinants of long-term occupancy (here summarized as incidence), environmental effects on both colonization and persistence should be considered. We fitted dynamic occupancy models to 20 years of monitoring data on a pond construction program to quantify effects of pond and landscape characteristics and different connectivity metrics on colonization and persistence probabilities in constructed ponds. Connectivity to existing populations explained dynamics better than structural connectivity metrics, and simple metrics (distance to the nearest neighbor population, population density) were useful surrogates for dispersal kernel-weighted metrics commonly used in metapopulation theory. Population connectivity mediated the persistence of conservation target species in new ponds, suggesting source–sink dynamics in newly established populations. Population density captured this effect well and could be used by practitioners for site selection. Ponds created where there were 2–4 occupied ponds within a radius of ~ 0.5 km had > 3.5 times higher incidence of target species (median) than isolated ponds. Species had individual preferences regarding pond characteristics, but breeding sites with larger (≥ 100 m²) total water surface area, that temporarily dried, and that were in surroundings with maximally 50% forest benefitted multiple target species. Pond diversity will foster amphibian diversity at the landscape scale.

KEYWORDS

amphibian, blue–green ecological infrastructure, connectivity, evidence-based conservation, habitat quality, metapopulation

INTRODUCTION

Habitat loss and degradation due to land-use change have been the dominant drivers of recent anthropogenic biodiversity loss (Jaureguiberry et al., 2022), necessitating efforts to halt and reverse this trend (Grant et al., 2019). Given past and ongoing degradation, the protection of remaining high-quality habitat is, however, insufficient to halt biodiversity loss (Dobson et al., 1997; Perring et al., 2015). Instead, destroyed or degraded habitat must be restored or new habitats must be created to achieve a net gain in the extent and functioning of ecosystems (Bull et al., 2020; Gann et al., 2019). The UN Decade on Ecosystem

Restoration (2021–2030) emphasizes the importance of ecological restoration to prevent biodiversity loss (UN, 2019). The Kunming–Montreal Global Biodiversity Framework, adopted by the parties of the UN Convention on Biological Diversity, includes the ambitious goals to restore and conserve 30% of terrestrial, freshwater, and marine areas by 2030 (CBD, 2022). Habitat creation plays a vital role in achieving these goals, also by reinstalling lost habitat in human-modified landscapes. Treating habitat creation and restoration programs as large-scale experiments provides valuable data to improve the evidence base for future actions (Harper et al., 2021; Schmidt et al., 2019).

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial License](https://creativecommons.org/licenses/by-nc/4.0/), which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2024 The Authors. *Conservation Biology* published by Wiley Periodicals LLC on behalf of Society for *Conservation Biology*.

Ecological infrastructure, also referred to as green or blue-green infrastructure, is a key concept for restoration at the landscape scale (Bullock et al., 2022; Perring et al., 2015) and a cornerstone of the Swiss biodiversity strategy and action plan (FOEN, 2012, 2017). Ecological infrastructure refers to a network of interconnected natural and seminatural habitats of high-quality and sufficient quantity that enables the landscape-scale persistence of a rich and resilient biodiversity (FOEN, 2017). This landscape perspective is based on the need for a sufficient amount of well-connected high-quality habitat patches to support metapopulations and metacommunities (Perring et al., 2015). High-quality habitat is vital for local population growth and persistence. Complex landscapes with a greater variety of different habitat types benefit more species with different ecological requirements (Bullock et al., 2022; Török & Helm, 2017), and the quantity of habitat determines the landscape-scale carrying capacity and influences connectivity (Fahrig et al., 2022). Connectivity is essential for the colonization of restored or newly created habitat and for the perpetuation of sufficient gene flow between populations to maintain genetic diversity (Angelone & Holderegger, 2009).

Connectivity metrics can help determine optimal locations for the construction of habitat patches. Structural metrics, based on the spatial distribution of all available habitat patches in a landscape, have the advantage that they do not require information on the occurrence of target species. They could thus provide easily accessible guidelines for planners even in the absence of species distribution data. Potential population connectivity metrics, based on the connectivity to occupied habitat patches that might contain source populations, require more information but may be better predictors of colonization. Similarly, simple metrics, such as the distance to the nearest neighboring patch, are more accessible for practitioners compared with theory-based metrics that rely on assumptions about dispersal kernels (Hanski, 1994). Such theory-motivated metrics are often assumed to be superior to simple metrics because they integrate information on density and distance (Moilanen & Nieminen, 2002), but they are harder to calculate and implement for conservation planners. The same is true for resistance-based metrics and functional connectivity, which require data on landscape resistance, gene flow, or actual movements of animals (Keeley et al., 2021). Practitioners often rely on simpler measures, derived from observation or intuition, such as the distance to the nearest pond (e.g., Durrer, 2014; Oldham et al., 2000) or the density of ponds in a landscape (FOEN, 2023). If such simple metrics prove useful, this would be helpful to empower planners and managers to make better conservation decisions. Prugh (2009) suggested that simple metrics can be as effective as theory-based metrics in predicting colonization and occupancy, but evidence is still scarce. We evaluated simple and theory-based, structural, and potential population connectivity metrics to determine their usefulness in predicting colonization of and persistence in newly created habitat patches.

In freshwater ecosystems, habitat loss and degradation remain the leading proximate causes of recent population declines (Reid et al., 2019). Despite their small area, freshwater ecosystems, and ponds in particular, support numerous species

and contribute strongly to regional biodiversity (Dudgeon et al., 2006; Williams et al., 2020). Wetlands, including ponds, have suffered extensive losses in the past century, especially in Europe, the United States, and China, mainly due to conversion to agricultural land (Fluet-Chouinard et al., 2023; Gimmi et al., 2011). Ponds are small (1 m² to about 5 ha), natural or human-made, shallow water bodies that permanently or temporarily hold water (De Meester et al., 2005). These small ecosystems contribute disproportionately more to regional aquatic biodiversity than lakes or rivers, owing mainly to their high beta diversity (Davies et al., 2008; Williams et al., 2003). Alongside aquatic and semiaquatic species, many terrestrial species also rely on ponds for water, food, and habitat (e.g., insects, terrestrial birds, and bats) (Hill et al., 2021). Ponds thus boost regional diversity in otherwise intensively used landscapes by providing habitat for many rare and endangered species. Pond-breeding amphibians are directly dependent on ponds for reproduction and larval development (Semlitsch, 2002). Ponds are straightforward to build and can be integrated in intensively used landscapes, thus offering opportunities for habitat restoration for the benefit of amphibians and other aquatic and terrestrial species (Ilg & Oertli, 2017; Lewis-Phillips et al., 2019). Despite their benefits, ponds remain a low priority in international legislation, which tends to focus on the conservation of large water bodies (Hill et al., 2018).

Pond creation to support declining amphibian species is effective (Smith et al., 2020), especially when conducted at the landscape scale (Magnus & Rannap, 2019; Moor, Bergamini, et al., 2022; Rannap et al., 2009). Constructed ponds are readily colonized even by rare species as long as there are remaining source populations and pond characteristics and surrounding terrestrial microhabitat match species' preferences (Schmidt et al., 2019). Switzerland has a rare long-term monitoring program that accompanied the landscape-scale construction of hundreds of new ponds in an intensively used landscape. A recent analysis of this data set showed that all 12 extant pond-breeding amphibians readily colonized newly created ponds and that the regional number of populations stabilized or increased even for species that had been in decline for decades (Moor, Bergamini, et al., 2022).

We used these data to elucidate the factors that influence colonization and persistence probabilities and consequently the expected long-term occupancy probability (incidence) in newly created habitat. We considered pond and landscape characteristics and compared a range of different connectivity metrics in their ability to explain colonization and persistence probabilities of 12 pond-breeding amphibian species. We contrasted responses of conservation target species with those of common species and one invasive. To synthesize the effects of environmental variables on the dynamic rates of colonization and persistence, we approximated long-term occupancy with the expected site-specific incidence for each species (Hanski, 1994). We aimed to provide useful information for practitioners regarding how and where to construct new ponds to benefit as many species as possible.

We fitted species-specific dynamic occupancy models to explore the following questions: Does connectivity affect

colonization and persistence probability? Are structural connectivity measures, calculated irrespective of the occupancy status of ponds, useful surrogates for connectivity to occupied ponds? Are simple measures (distance to the nearest neighbor, density of ponds) comparable to theoretical (kernel-based) measures in their ability to explain colonization–persistence dynamics? With regard to pond and surrounding landscape characteristics, how should ponds be designed to optimize colonization and persistence probabilities and the resulting incidence?

METHODS

Study area and species

We used monitoring data (species detection and nondetection per site) from 1999 to 2019 for all 12 extant pond-breeding amphibian species (Appendix S1) in 5 regions in the canton of Aargau in the Swiss lowlands. In the 1990s, surveys in this canton showed widespread declines of 7 of these species, which became conservation target species (Meier & Schelbert, 1999; Schmidt & Zumbach, 2019). The 3 more dispersal-limited (adults rarely move >1 km) target species were midwife toad (*Alytes obstetricans*), smooth newt (*Lissotriton vulgaris*), and great crested newt (*Triturus cristatus*). The 4 more mobile (adults can move >1 km) target species were yellow-bellied toad (*Bombina variegata*), natterjack toad (*Epidalea calamita*), European tree frog (*Hyla arborea*), and water frogs (i.e., the *Pelophylax* species complex of the closely related and ecologically similar pool frog *P. lessonae* and edible frog *P. esculentus*). The authorities responded to the decline with an extensive pond construction program, focused on 5 regions with significant remnant populations of the target species (Meier & Schelbert, 1999). By 2019, 422 new ponds had been constructed in these regions, resulting in 856 sites in total. In many cases, a site consisted of a cluster of multiple small ponds (Siffert et al., 2022). The species, study area, and characteristics of old and newly constructed ponds are described in detail in Moor, Bergamini, et al. (2022). Data are publicly available from Moor, Bühler, et al. (2022).

The amphibian monitoring mainly aimed to survey populations of the 7 conservation target species, but all 12 pond-breeding amphibians occurring in this landscape were recorded (Bühler, 2020). Common species also recorded were the alpine newt (*Ichthyosaura alpestris*), palmate newt (*Lissotriton helveticus*), common toad (*Bufo bufo*), and common frog (*Rana temporaria*), as well as the invasive marsh frog (*Pelophylax ridibundus*) (multiple invasive *Pelophylax* species occur in Switzerland, here summarized as *P. ridibundus* [Dufresnes et al., 2018]). The monitoring focused on the same 5 regions as the pond construction program. All breeding sites potentially suitable for a target species were surveyed comprehensively and regularly in a rotating panel design. The regions were subdivided into subregions for annual surveys (Bühler, 2020). Within a survey year, each site of a surveyed subregion was visited on average 2.8 times (SD 0.5). We used these repeat visits within a breeding season to estimate detection probabilities. Between 1999 and 2019, each

subregion was surveyed on average 5.5 times with a mean period of 3.8 (SD 1.38) years between surveys. Potential breeding sites of common, nontarget species were not all visited. Note that this may affect estimates of connectivity for common species. Not all species occurred in all regions. Regions with less than 10 sites with detections were excluded from modeling for that species (Moor, Bühler, et al., 2022).

Explanatory variables

Environmental variables describing the ponds and their surrounding landscape were tested for effects on colonization and persistence probabilities (Table 1). Data on these variables were either available from the monitoring program or accessible through national geographical information systems (swissTLM3D 2021 swisstopo [5704000000] [Moor, Bühler, et al., 2022]).

In addition to pond and landscape characteristics, we explored the effects of 3 connectivity metrics, calculated in 2 different ways: as structural connectivity metrics that describe connectivity to all other ponds irrespective of their occupancy status and as potential population connectivity metrics (hereafter population connectivity) that quantify connectivity to ponds observed to be occupied during the last survey. For both connectivity types, we calculated 3 metrics: Euclidean distance to the nearest (occupied) neighbor and density of (occupied) ponds within 1 km² of the focal pond (excluding the pond itself) (Appendix S2) (both simple metrics) and kernel connectivity (theory-derived metric) calculated in 3 variants with different assumptions about dispersal distances. This kernel metric weights the contributions of neighboring (occupied) ponds to the connectivity of a focal pond by a negative exponential dispersal kernel, following metapopulation theory (Hanski, 1994; O'Hara et al., 2002). We tested 3 values of the scaling parameter α (Table 1), which is related to the average dispersal distance (Hanski, 1994; Moilanen, 2004; Moilanen & Nieminen, 2002). We did not include pond area in the kernel connectivity metric because we wanted to test for area effects separately (Table 1). Connectivity metrics were correlated with each other in ways that depended on habitat patch configuration (ponds were not evenly spaced) and, for population connectivity, on the species' prevalence (Appendix S3). Structural connectivity metrics correlated strongly with other structural metrics (mean: $r = 0.75$), and population metrics correlated strongly with other population metrics (mean across species: $r = 0.70$). Distance had the weakest correlations with other metrics. Correlations between structural and population metrics were moderate (mean across species: $r = 0.34$) and especially weak for the rare species midwife toad ($r = 0.15$) and natterjack toad ($r = 0.21$), and the invasive marsh frog ($r = 0.10$) (Appendix S3). Structural and population connectivity increased over time (Appendix S4). We tested for connectivity effects on both colonization and persistence. Persistence is the complement of local extinction in metapopulation theory (i.e., the probability that an occupied patch remains occupied in the next time step [year]).

TABLE 1 Explanatory variables describing all 856 ponds surveyed in the amphibian monitoring program of the Swiss canton of Aargau, their surrounding landscape, and metrics of structural connectivity and species-specific potential population connectivity (Moor, Bühler, et al., 2022).

Type	Variable	Definition	Mean (range)
Pond	Area	Total surface area of all water bodies in a site (m ²)	782 (0.4–65,000)
	Water table fluctuations	Strong water table fluctuations within a season (i.e., the possibility of temporary drying out [0 or 1])	0, 56% of ponds; 1, 44% of ponds
	Age	Years since construction (new ponds only)	7.5 (0–29)
Landscape	Elevation	Elevation above sea level (m)	404 (261–668)
	Forest cover	Forest cover (% area) in 100-m radius	37 (0–100)
	Road cover	Area of large roads (width ≥ 6 m) (m ²) in 1-km radius	35,600 (0–293,800)
Structural connectivity	Distance _{str}	Euclidean distance to nearest pond (m)	459 (20–3500)
	Density _{str}	Density of ponds (km ⁻²) regardless of species presence	3.1 (1–18)
	Conn _{str,α}	Kernel connectivity $\text{conn}_{\text{str},i,t} = \sum_{j \neq i} \exp\left(\frac{-d_{ij}}{\alpha}\right) E_{jt}^a$, dimensionless, assuming typical dispersal distances $\alpha = \{200, 500, 1000 \text{ m}\}$	Conn _{str,α200} 0.55 (0.0–4.9) Conn _{str,α500} 2.3 (0.0–11) Conn _{str,α1000} 6.3 (0.2–19)
Potential population connectivity	Distance _{pop}	Euclidean distance to nearest pond (m) with detected presence of same species during last survey	1709 (20–15,600) ^b
	Density _{pop}	Density of ponds (km ⁻²) with detected presence of same species during last survey	0.57 (0–14)
	Conn _{pop,α}	Kernel connectivity $\text{conn}_{\text{pop},i,t} = \sum_{j \neq i} \exp\left(\frac{-d_{ij}}{\alpha}\right) E_{jt} y_{jl}^c$, dimensionless, assuming typical dispersal distances $\alpha = \{200, 500, 1000 \text{ m}\}$, y_{jl} : detection and nondetection of same species in pond j in previous survey year l	Conn _{pop,α200} 0.11 (0.0–3.8) Conn _{pop,α500} 0.48 (0.0–8.6) Conn _{pop,α1000} 1.3 (0.0–17)

^aStructural kernel connectivity Conn_{str} was calculated as a function of Euclidean distance d_{ij} (m) between ponds i and j , the scaling parameter α , and the variable $E_{jt} = \{0, 1\}$, which indicates whether pond j existed in year t or not.

^bMean and range of population connectivity metrics across all species.

^cPotential population kernel connectivity Conn_{pop} considered only connectivity to ponds j with detections of the same species ($y_{jl} = 1$) in the previous survey year l .

Statistical analyses

For each species, we fitted 10 structurally identical dynamic occupancy models to species detection–nondetection data at the site level with Bayesian inference (Royle & Kéry, 2007). Occupancy models exploit repeat visits to the same site to estimate and account for imperfect detection (MacKenzie et al., 2002). Our observation model differentiated night- and day-time visits and accounted for individual observer bias (Schmidt et al., 2023; Tanadini & Schmidt, 2011) (model formulation in Appendix S5). The ecological part of the dynamic occupancy models relates the expected occupancy probability ψ_{it} of site i in year t to the site's occupancy status in the previous year ($z_{i,t-1}$) and the annual, site-specific probabilities of colonization (γ_{it}) and persistence (φ_{it}):

$$\psi_{it} = \left[(1 - z_{i,t-1}) \gamma_{it} + z_{i,t-1} \varphi_{it} \right] E_{it}, \quad (1)$$

where $E_{it} = \{0, 1\}$ indicates whether or not site i exists in year t . Effects of covariates on colonization and persistence probabilities were included as logit-linear models (Royle & Kéry, 2007; Sjögren-Gulve & Hanski, 2000) of the general form $\text{logit}(\gamma_{it}) = \alpha_R + \sum_k \beta_k X_{kit}$ with a region-specific

intercept $\alpha_R \sim N(\mu_\alpha, \sigma_\alpha^2)$ and slope parameters β_k estimating the effects of k covariates X_{kit} that could vary between sites and over time. The formulation for persistence, $\text{logit}(\varphi_{it})$, was equivalent (details in Appendix S5).

Each model tested for the effects of all pond- and landscape covariates and one connectivity metric at a time on both colonization and persistence probabilities (Table 1). The goal was to test for effects of environmental variables on colonization and persistence probabilities and to compare the effects of different connectivity metrics in an exploratory manner, rather than conducting model selection to aim at the highest predictive capacity (Tredennick et al., 2021). Therefore, all covariates (including one connectivity metric) were included in each model. All covariates were standardized to mean zero and unit variance to enable the comparison of parameter estimates as effect sizes of the different covariates and to facilitate interpretation of quadratic effects (Schielzeth, 2010). For surface area and forest cover, quadratic terms were included to allow for possible unimodal effects. Effects are reported by the median and the 95% equal-tailed credible interval (CI) of the posterior distributions of parameter estimates. We conservatively considered effects as important if the 95% CI of the posterior density of a parameter estimate did not include zero (i.e., importance corresponds to >95% certainty). Reported effect sizes of environmental covariates are

valid for all ponds (old and new). The partial dependence plots visualize these effects for new, constructed ponds by including a new-pond intercept (Appendix S5).

To compare models with different connectivity metrics, we compared model goodness of fit through the posterior mean deviance (Spiegelhalter et al., 2002). Deviance (D) is directly related to the log likelihood of the data given the model as $D(\theta) = -2\log[p(\theta)]$. Absolute values of deviance are not informative, but their comparison is: lower deviance corresponds to higher likelihood and better fit of a model to the data. Deviance was normalized by dividing through the number of detections for each species to facilitate model comparison among species.

We further compared the effects of the different connectivity metrics on colonization and persistence probabilities with their estimated slope parameters β_k in the logit-linear regression models (Appendix S5). Because all covariates were standardized, β_k can be interpreted as effect size.

To summarize and visualize the effects of covariates on the net outcome of colonization and persistence dynamics, we calculated the expected incidence J_i from the marginalized site-specific colonization (γ_i) and persistence (φ_i) probabilities:

$$J_i = (1 - J_i)\gamma_i + J_i\varphi_i \Rightarrow J_i = \frac{\gamma_i}{\gamma_i + (1 - \varphi_i)}. \quad (2)$$

Incidence is the site-specific quasi-stationary probability of occupancy (Hanski, 1994; Royle & Kéry, 2007; ter Braak & Etienne, 2003), here used as an approximation of the long-term, site-specific equilibrium occupancy probability. This approximation holds under the assumptions of colonization and persistence probabilities that vary only with environmental variables and connectivity as well as under a long time to extinction of the entire metapopulation (ter Braak & Etienne, 2003). We used incidence as a qualitative summary of the combined consequences of site-specific colonization and persistence probabilities and their dependencies on pond and landscape conditions.

RESULTS

Model goodness of fit

Overall, the choice of connectivity metric did not strongly affect model fit when considering the uncertainty associated with the models given the data (Appendix S6). Population connectivity metrics explained colonization and persistence dynamics slightly better than structural metrics in all but one common species. For 11 species, a population connectivity metric resulted in the best fitting model (Appendix S6). Most frequently, this was the simple metric density of occupied ponds (6 species), followed by distance to the nearest occupied pond (3 species). For 2 species, the population connectivity kernel metric resulted in the best fit: smooth newt (assuming a mean dispersal distance $\alpha = 500$ m) and marsh frog ($\alpha = 1000$ m). For both species, population density resulted in an almost equally good fit as the best fitting population kernel connectivity metric. For one

species only, the widespread common frog, a structural connectivity metric resulted in the best fit: the simple metric distance to the nearest pond (Appendix S6). Median parameter estimates for the best fitting models are shown in Appendix S7.

Comparison of connectivity metrics

The ecological effect of connectivity on colonization and persistence probabilities was quantified by the effect size of different connectivity metrics (i.e., the slope parameter estimates in the logit-linear models for colonization and persistence probabilities) (Figure 1; Appendix S8).

Structural connectivity metrics had little influence on colonization probabilities (Figure 1; Appendix S8). One general exception was the target species yellow-bellied toad. Nearly all structural connectivity metrics, as well as all population connectivity metrics, increased both colonization and persistence probabilities of this species (population connectivity to occupied ponds always had a stronger effect than structural connectivity). Further exceptions were the crested newt and the alpine newt, which had increasing colonization probabilities with higher structural kernel connectivity (i.e., higher colonization probabilities in denser pond networks) (both for $\alpha = 1000$ m) (Figure 1).

Persistence probabilities more frequently depended on structural connectivity metrics, mainly in the common species. All common species had lower persistence probabilities with higher structural kernel connectivity (especially $\text{conn}_{\alpha = 200}$ m) (Figure 1). In the common alpine newt and palmate newt, the negative effect of increasing structural connectivity became stronger for larger values for α (i.e., for kernels considering larger areas around the focal pond). Common species also had higher persistence probabilities at greater distances to the nearest pond; this effect was >95% certain in alpine newt and in common frog. Some conservation target species, in contrast, had increasing persistence probabilities with increasing structural connectivity. Strong positive effects (albeit associated with broad uncertainty limits) were evident for the dispersal-limited target species smooth newt, for which higher structural kernel connectivity and higher density of ponds increased persistence probability (population connectivity metrics had similar effects on persistence).

Population connectivity metrics in contrast had positive effects on both colonization and persistence probabilities in most species. These effects were strong for the target species and less consistent or absent for common species (Figure 1; Appendix S8). The colonization probability of all target species was strongly affected by both simple population connectivity metrics: the distance to the nearest occupied pond and the density of occupied ponds in the surroundings (Figures 1 & 2). Increasing population density was also associated with higher persistence probabilities in all species but the water frog species as well as in common toad and common frog (Figures 1 & 2).

Although increasing structural connectivity decreased the persistence of common species, population connectivity did not have the same effect (except for negative effects of population

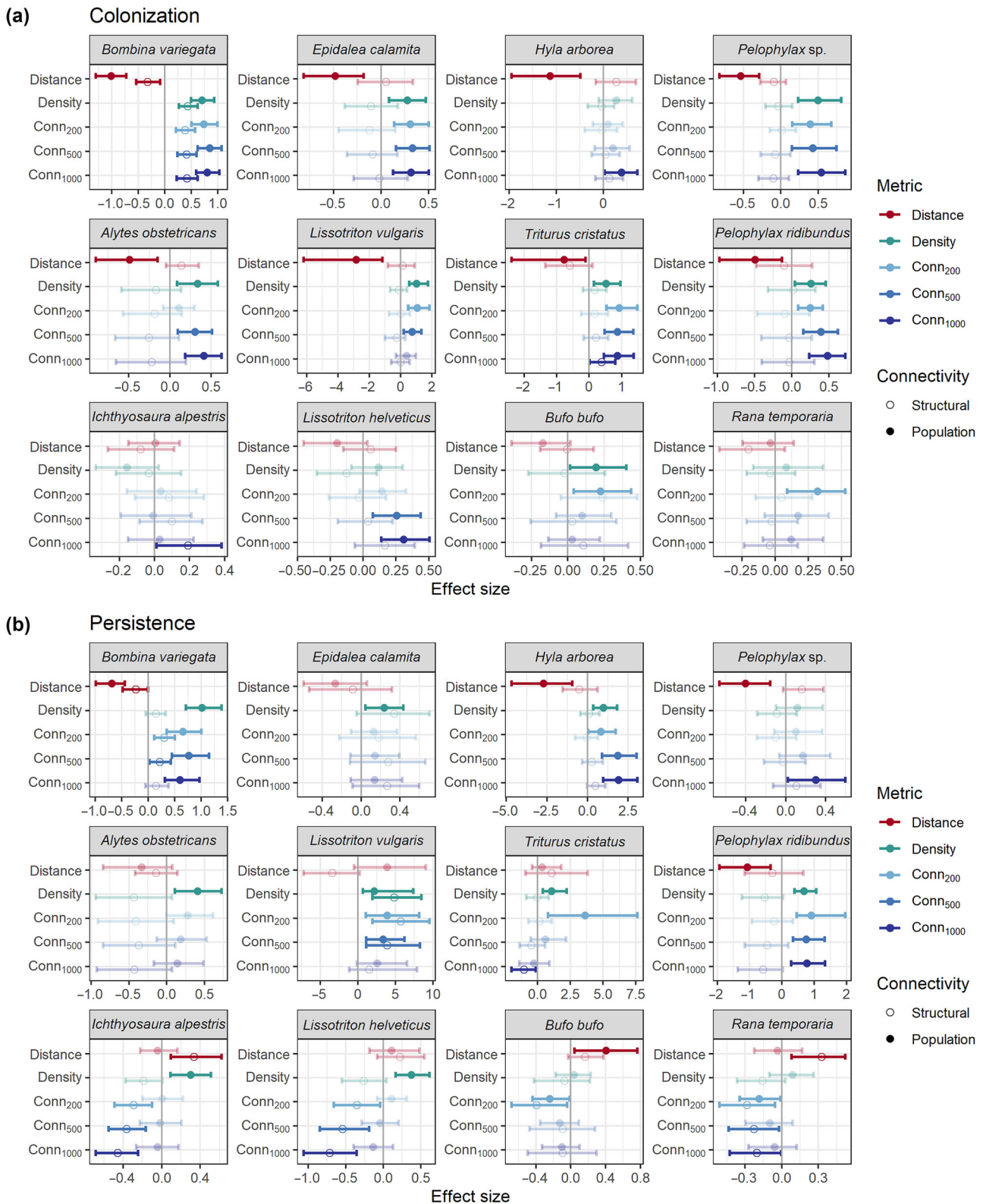


FIGURE 1 Effects of structural and population connectivity metrics on (a) colonization and (b) persistence probabilities of each amphibian species (conn_α, kernel connectivity for α = {200, 500, 1000 m}; colors, connectivity metric; open circles, structural connectivity metrics; closed circles, potential population connectivity metrics). Effect size is quantified by the slope parameter estimates for standardized covariates. Shown are median estimates and 95% equal-tailed credible intervals (CIs). Effects where the 95% CI overlaps zero are transparent.

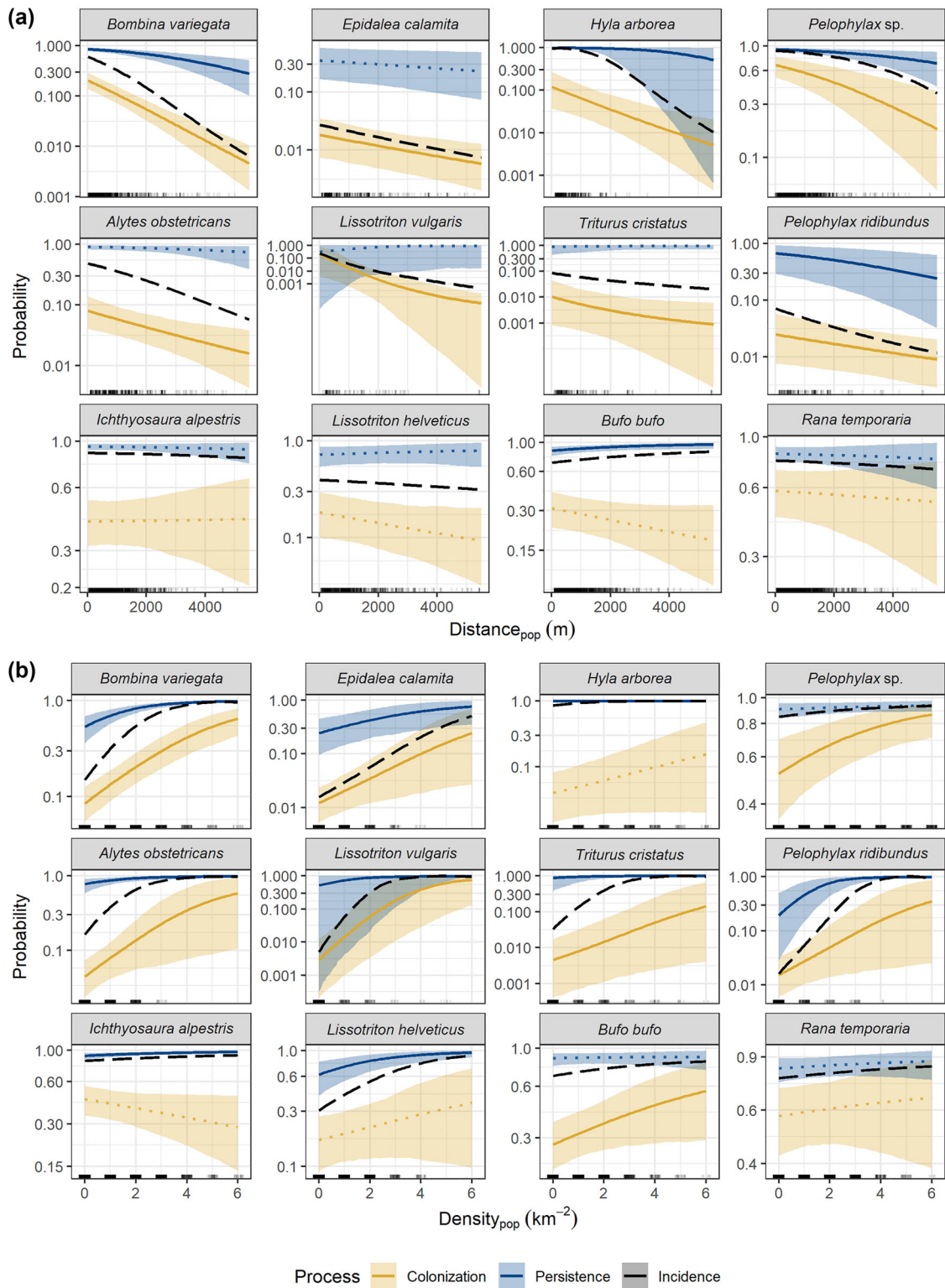


FIGURE 2 Mean change (with 95% credible interval [CI], shading) in colonization (yellow) and persistence (blue) probabilities in new ponds in response to the population connectivity metrics (a) distance to the nearest occupied neighbor and (b) density of occupied ponds (solid lines, effects are >95% certain; dotted lines, uncertain effects; black dashed lines, expected equilibrium pond occupancy [J_i , summarizing patch-wise colonization probability γ_i and persistence probability φ_i as $J_i = \gamma_i / (\gamma_i + (1 - \varphi_i))$]; data rugs, ponds with species detections).

kernel connectivity [$\alpha = 200$ m] for both common toad and common frog). The invasive marsh frog responded positively to connectivity to occupied ponds (Figure 1).

The expected incidence of all conservation target species, but not the common species, tended to decrease with increasing population distance and to increase with increasing population density (Figure 2).

Effects of pond and landscape characteristics

Effects of pond and landscape characteristics other than connectivity were largely consistent among models (Figure 3). Total pond surface area of a site and forest cover were important predictors for most species (Figure 3). Most species colonized sites with larger total water surface area more frequently (except yellow-bellied toad, which preferentially colonized smaller ponds) and had higher persistence probabilities with larger surface area. Only for crested newt, total pond surface area had no effect. The resulting incidence of all species except yellow-bellied toad either increased monotonically with total pond surface area or had an optimum at a total surface area of ~ 1000 m² (Figure 4). Increasing forest cover in the surroundings of the ponds was positive for the colonization probabilities of yellow-bellied toad and all 4 common species but decreased the colonization probabilities of 3 target species (natterjack toad, smooth newt, and crested newt), as well as of the marsh frog. Also, the persistence probability of multiple target species (midwife toad, tree frog, and natterjack toad) decreased with increasing forest cover, whereas it increased for smooth newt (Figure 3). The resulting incidence was lower at high forest cover for the target species natterjack toad, tree frog, and midwife toad (Figure 4).

Fluctuating water levels increased both colonization and persistence of yellow-bellied toad and natterjack toad, as well as the colonization probability of crested newt and the persistence of smooth newt. No species was negatively affected by fluctuating water levels. Pond age had important effects for crested newt and common toad (higher persistence in older ponds) and common frog and marsh frog (lower colonization of older ponds). Large roads in the wider surroundings negatively affected the colonization probabilities of tree frog, crested newt, and all *Pelophylax* species, as well as the persistence probabilities of midwife toad and water frogs. At higher elevation (>400 m asl), midwife toad and alpine newt had both higher colonization and higher persistence probabilities, natterjack toad persisted more frequently, and smooth newt had higher colonization probability. At lower elevation (<400 m asl), tree frog and water frogs had higher colonization and persistence probabilities, and crested newt colonized more frequently. Among common species, common frog more frequently colonized ponds at higher elevation, whereas common toad had higher persistence probability at higher elevation (Figure 3).

To facilitate comparisons across the 7 target species, we summarized the effects of the 2 important environmental variables (total water surface and forest cover in the surroundings) and the 2 simple population connectivity metrics on the inci-

dence of the 7 target species (Figure 5). Population density had the strongest effect on the average incidence across the target species. Compared with a situation with no other occupied ponds within a radius of 564 m around the centroid of the focal pond (density_{pop} = 0 km⁻²), the average incidence increased by 30% with one (density_{pop} = 1 km⁻²) and by 90% with 2 other occupied ponds (density_{pop} = 2 km⁻²). This effect began to saturate at density_{pop} ~ 4 km⁻² (Figure 5).

Results from the observation model (species-specific detection probabilities and observer variability) are given in Appendix S9.

DISCUSSION

Pond creation is a local conservation action that contributes to landscape-scale habitat availability and connectivity, thus supporting the recovery and viability of amphibian metapopulations. Declining species, as well as species expanding into new habitat, are not in equilibrium with their surroundings. To understand long-term occupancy dynamics under such conditions, the underlying processes of colonization and persistence must be understood (Yackulic et al., 2015). Our findings show that both the pond characteristics as well as their spatial location play important roles in mediating the natural colonization and persistence of amphibian conservation target species and therefore in the success of setting up an ecological infrastructure.

Connectivity metrics

Population connectivity metrics based on connectivity to known species occurrences were better performing than structural metrics, especially for conservation target species with fewer remaining populations. A recent comparison of structural versus population (i.e., “demographically weighted”) connectivity in explaining metapopulation dynamics of a small mammal similarly showed strong support for the importance of weighting connectivity based on the actual occupancy state of sites (Drake et al., 2022). Put simply, connectivity to empty sites does not increase colonization or persistence because empty sites do not contribute dispersing individuals. Building dense pond networks without considering the proximity of existing potential source populations thus will not benefit conservation target species in the short term. In the long term, however, once potential source populations get established closer by, such investments might nonetheless pay off and should therefore not be strictly disregarded (Moor, Bergamini, et al., 2022). For immediate conservation benefit though, the current distribution of the usually rare conservation target species must be considered when extending habitat networks.

The simple metrics distance to the nearest occupied pond and density of occupied ponds captured connectivity effects on colonization and persistence dynamics well. Effects of these simple metrics were comparable to or stronger than effects of kernel connectivity. These metrics can be useful for practitioners

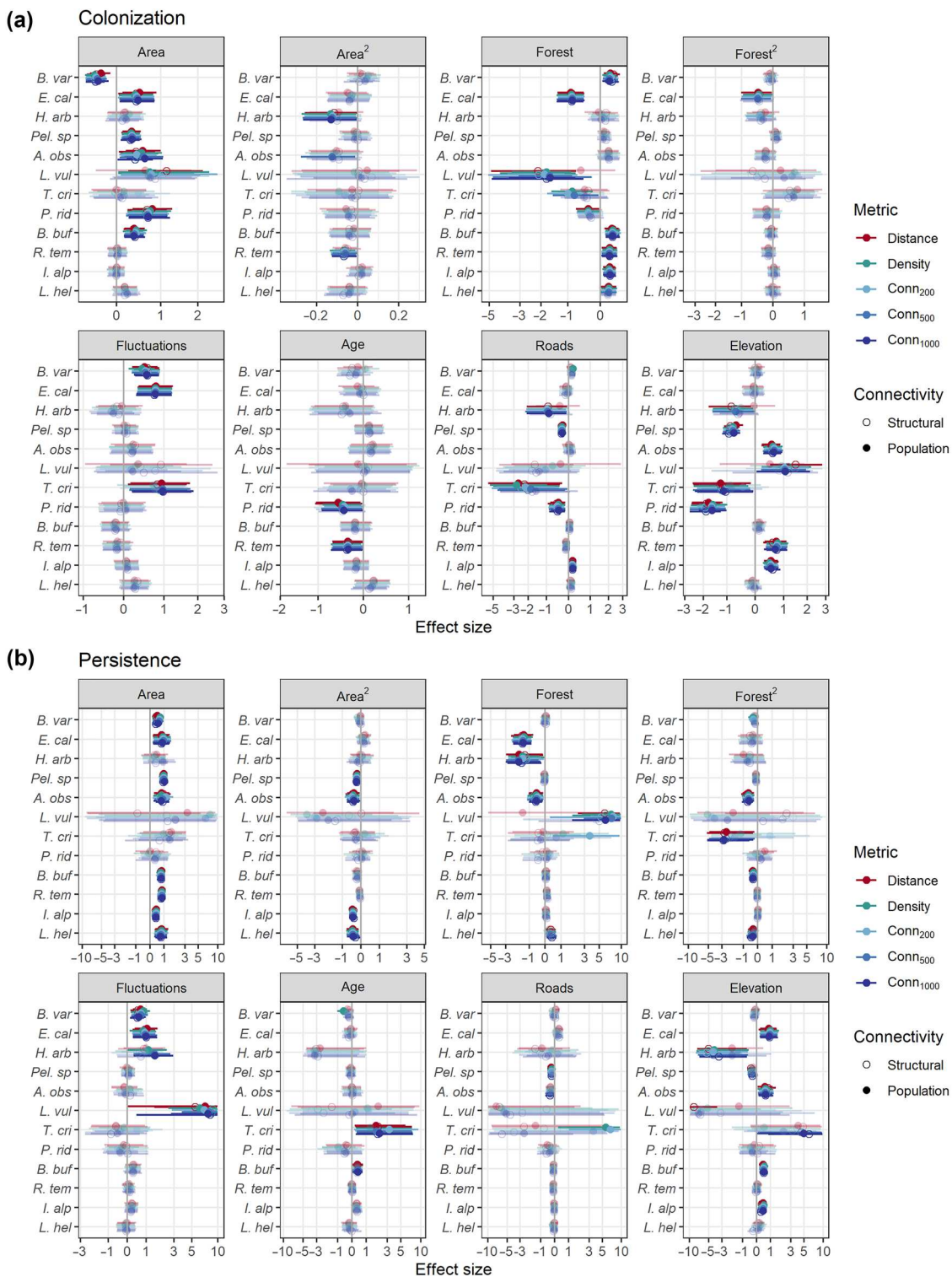


FIGURE 3 Effects (median and 95% credible interval [CI]) of pond and landscape variables on (a) colonization and (b) persistence probabilities from all models (colors and symbols, connectivity metric included in each model) ($\leq 95\%$ certain effects are transparent). Species abbreviations in Appendix S1.

because they are more easily calculated, and the interpretation is easier than kernel connectivity metrics.

Distance to neighboring populations mediated colonization probability in all target species. Because these species are not currently widespread in the landscape, colonization probability

depends on a source population nearby. Negative effects of distance to the nearest occupied neighbor on pond colonization have previously been demonstrated for the pool frog (Sjögren-Gulve & Hanski, 2000) and the smooth newt and the common toad (Jeliazkov et al., 2019). Newts in particular can be expected

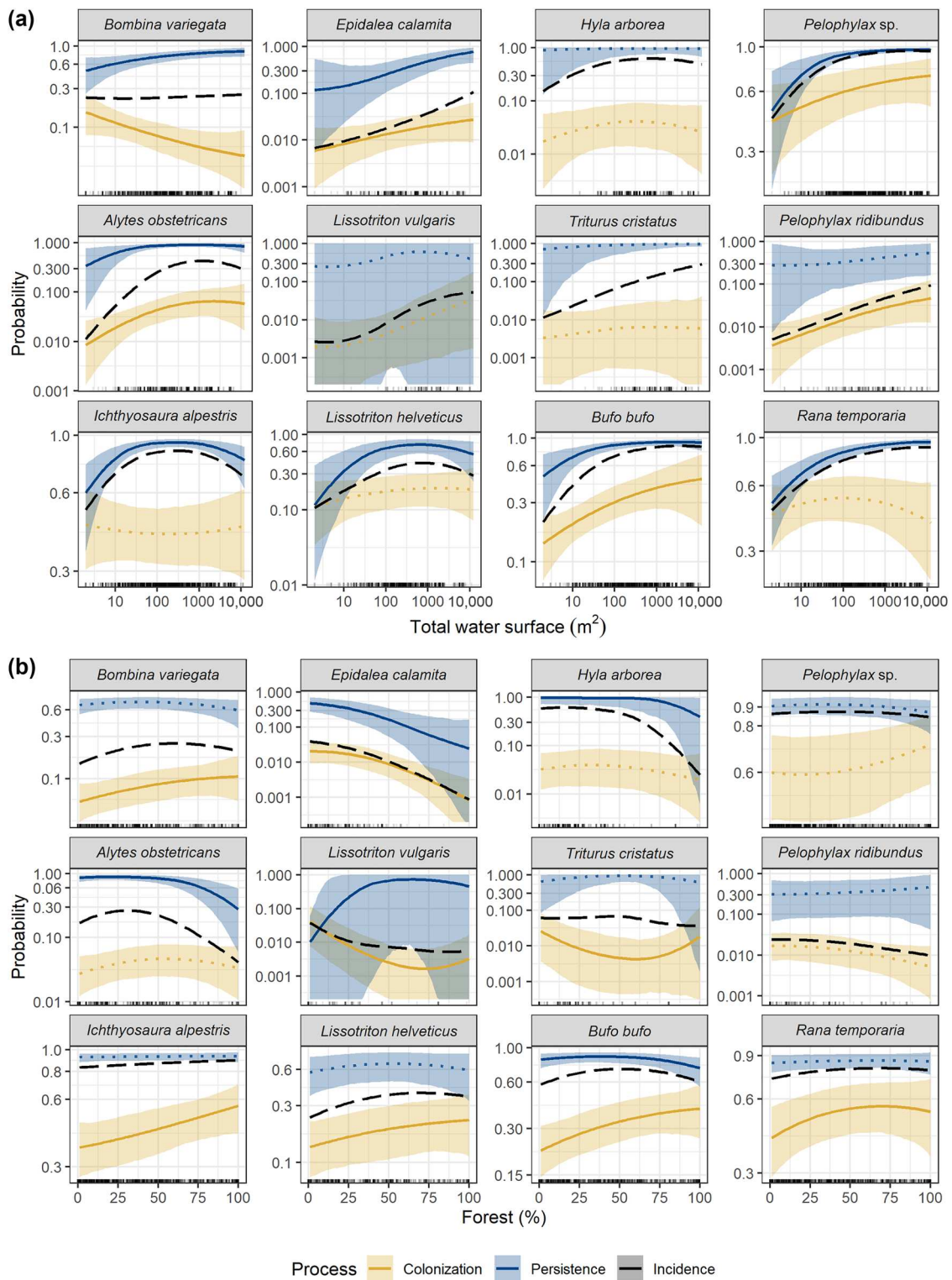


FIGURE 4 Mean change (with 95% credible interval [CI]) in colonization (yellow) and persistence (blue) probabilities in new ponds in response to changing (a) total water surface area and (b) surrounding forest cover under the best fitting model (solid lines, effects are >95% certain; dotted lines, uncertain effects; black dashed lines, summary of patch-wise colonization probability [γ_i] and persistence probability [ϕ_i] by the stationary pond-specific occupancy probability [incidence J_i , calculated as $J_i = \gamma_i / (\gamma_i + (1 - \phi_i))$]; data rugs, ponds with species detections).

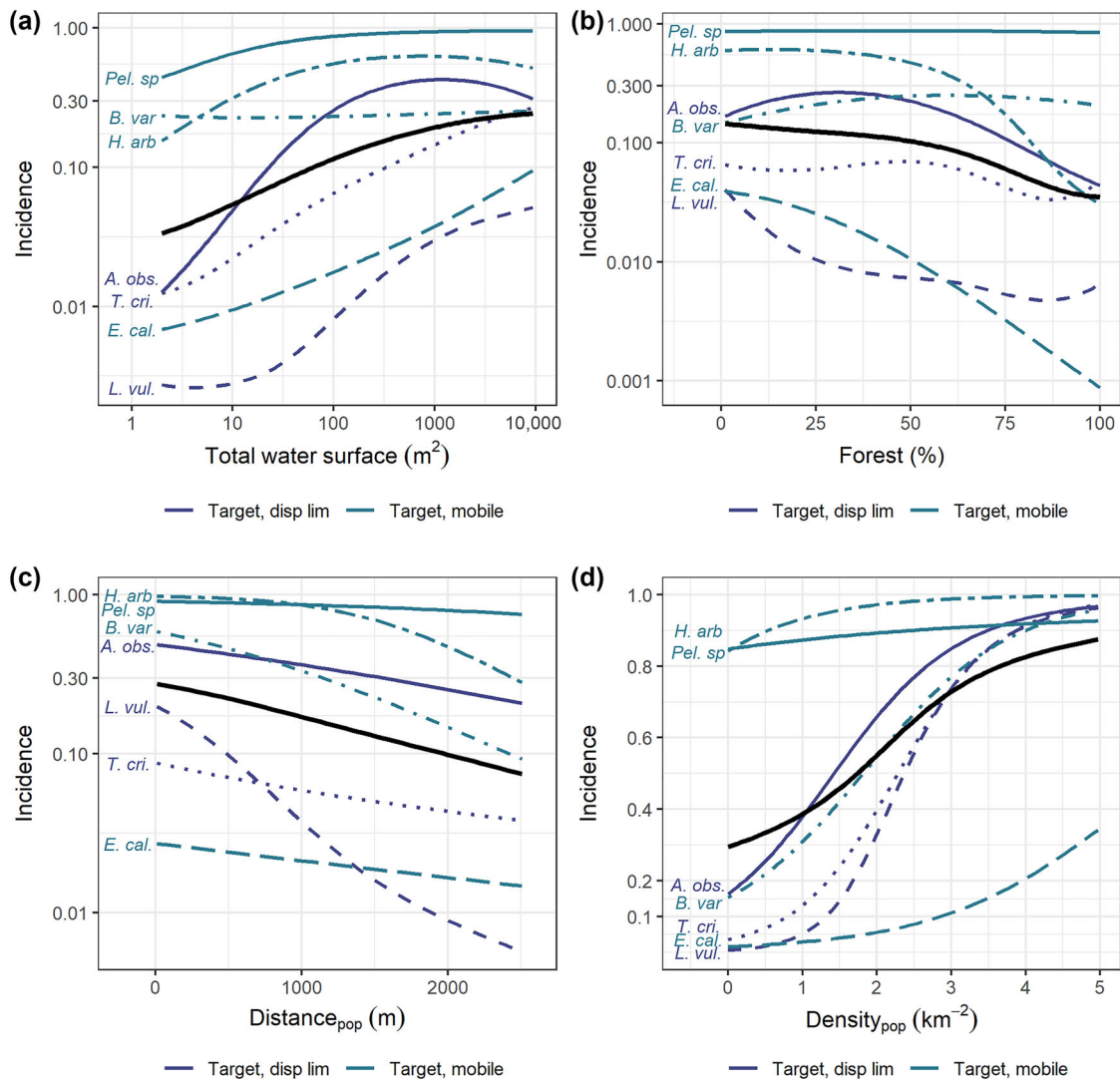


FIGURE 5 Site-specific incidence (i.e., long-term expected occupancy probability) of the 7 conservation target species in new ponds and in response to (a, b) 2 important pond and landscape variables and the 2 simple population connectivity metrics (c) distance to the nearest occupied neighbor and (d) density of occupied ponds (disp lim, dispersal-limited; pop, population). To optimize colonization and persistence probabilities simultaneously across target species, their average incidence (thick black line) could be maximized. Credible intervals are omitted for clarity and because incidence is used as a qualitative summary of colonization-persistence estimates. Species abbreviations in Appendix S1.

to be dispersal limited, moving rarely farther than ~500 m (Cayuela et al., 2020; Jehle & Sinsch, 2007; Unglaub et al., 2021). In our study, simple Euclidean population distance, irrespective of the type and quality of habitat that has to be traversed, was an important predictor for the colonization probability of all target species, even the more mobile species. Population distance, however, did not always also mediate persistence probability, which meant that overall, it was less important for incidence (Figure 5).

Higher population density, in contrast, was not only positive for colonization but also for the persistence of conservation target species (with the one exception of water frogs). Population density hence was a strong predictor of target species incidence (Figure 5), and we believe it can be a useful metric for practitioners. Across all target species, average incidence

nearly doubled at a population density of 2 other occupied ponds per square kilometer (i.e., within a radius of ~0.5 km) as compared with none. Colonization probability increases with density, since the number of potential source populations in an area likely correlates with the number of dispersing individuals that potentially could reach a new pond, thus potentiating the likelihood of a colonization event. Persistence probability also increased with increasing population density. This suggests the importance of rescue effects, where the persistence of local populations depends on immigration from nearby source populations (Brown & Kodric-Brown, 1977; Hanski & Gilpin, 1991), either because local conditions are suboptimal (leading to a lack of reproduction and therefore dispersing juveniles; Cruickshank et al., 2021) or owing to stochastic local extinction. Local population size also plays a role in such dynamics

because small populations are more prone to local extinction driven by environmental or demographic stochasticity (Pellet et al., 2007; Shoemaker et al., 2020). Pond-breeding amphibians exhibit generally more strongly fluctuating population sizes than species inhabiting more stable environments (e.g., streams), and population size variance is highest in the smallest populations (Green, 2003; Sjögren, 1991). Furthermore, a minimum number of calling males may be required in a pond to attract females and to ensure population persistence (Schmidt & Pellet, 2005). Newly established populations are initially small, and their maintenance may thus depend on frequent recolonization akin to source–sink dynamics (Pulliam, 1988). Population density seems to have captured this effect.

Kernel connectivity metrics integrate distance and density by calculating a weighted sum over occupied ponds in the surroundings, with distances as (negative exponential) weights. Positive effects of kernel connectivity have previously been demonstrated for colonization rates of amphibians (Cruickshank et al., 2020; Falaschi et al., 2020). These metrics are often regarded as superior to simpler metrics (Moilanen & Niemi, 2002), but we found effects of population density to be comparable to effects of population kernel connectivity metrics. Similarly, a comparison of effects of several connectivity metrics on occupancy and colonization probabilities in metapopulations of different taxa found the simple metric distance to the nearest occupied patch to be as good a measure as realized kernel connectivity (Prugh, 2009). Kernel metrics have their advantages, for example, the ability to weight patch contributions depending on species-specific dispersal ranges (the scaling parameter α). Nonetheless, their complexity makes them less amenable to practical application.

In summary, regarding conservation target species, population connectivity is preferable over structural connectivity, and simple metrics, especially population density, are useful surrogates for theoretical metrics.

Pond and landscape characteristics

Pond characteristics determine the (breeding) habitat quality for the different species and thereby are important mediators of persistence and long-term occupancy probabilities.

Larger water surface area in a breeding site was positive for most species (Figure 5). Note that this could be a single large pond or the combined surface area of multiple small water bodies. More aquatic habitat in a breeding site could theoretically support larger populations, which are less prone to stochastic extinction and can support higher recruitment rates (shown, e.g., for natterjack toad [Beebe et al., 1996]). Where water surface area stems from several smaller ponds, the heterogeneity of multiple ponds in close proximity to one another may support breeding success by distributing the risk of failed reproduction, through lower density dependence at the larval stage and higher recruitment rates (McCaffery et al., 2014). Across Swiss amphibian breeding sites of national importance, total aquatic surface area and local pond density were important predictors for the occupancy probability of most amphibian species,

and, importantly, a higher number of temporary ponds strongly increased occupancies of yellow-bellied toad and natterjack toad (Siffert et al., 2022).

Water level fluctuations indicate temporary water bodies with short hydroperiods (i.e., the potential to dry out in years with low precipitation). Fluctuations were positive for 5 conservation target species, confirming the critical importance of temporary ponds for many endangered amphibians in Switzerland (Schmidt et al., 2015; Siffert et al., 2022; Van Buskirk, 2003). A major positive effect of pond drying is via species interactions, specifically the elimination of potential predators such as fish (Wellborn et al., 1996). Population persistence of tree frogs and smooth newts in Northern Italy has been shown to be lower with fish present (Falaschi et al., 2020). Ponds can be constructed to allow for water level fluctuations (Cahoun et al., 2014; Schmidt et al., 2015), and more temporary ponds in a landscape would clearly benefit endangered amphibian species (especially yellow-bellied toad, natterjack toad, and smooth newt).

Forest cover in the surroundings of ponds was relevant for all but the *Pelophylax* species. Forest cover could be interpreted as a simple measure of terrestrial habitat availability near the aquatic breeding habitat and was overall positive up to ~50% cover (Figure 5). A notable exception was natterjack toad, which preferred more open surroundings. This species is adapted to early successional, unstable habitats, such as river flood plains, in open terrain supporting high ground level summer temperatures (Denton et al., 1997). The smooth newt similarly showed declining colonization and incidence in more forested habitat. Genetic analyses have found that population connectivity of this species is highest at forest edges, with forest cover values of 25–50% (Antunes et al., 2022). Although often difficult to quantify (Cruickshank et al., 2020), many species have unique requirements regarding aquatic and terrestrial habitat features. Midwife toad, for example, requires sunny embankments, stone piles, or dry stone walls close to the pond because of its parental care strategy, where males carry egg clutches on land until ready to hatch (Schmidt et al., 2019). An example for specific requirements with respect to the aquatic habitat is the crested newt, which prefers ponds with ~80% macrophyte cover (Oldham et al., 2000). A more detailed quantification of such features could further improve local habitat quality assessments.

Roads did not affect many species in our study notably, but their area decreased colonization probabilities of some of the more mobile species (tree frogs and *Pelophylax* species) and strongly affected crested newt. Roads can affect amphibians in different ways. The presence of infrastructure can represent a dispersal barrier (Zanini et al., 2008). Traffic causes direct mortality among migrating or dispersing individuals through collision with vehicles or stress (Beebe, 2013). European tree frogs are negatively affected by road density in a radius of 1 km around breeding sites, and this effect becomes stronger upon inclusion of traffic data, suggesting a role of direct mortality (Pellet et al., 2004). Furthermore, pollution from traffic affects habitat quality in the surrounding landscape: noise pollution can interfere with mating calls (Kunc & Schmidt, 2019) and chemical pollution can affect the success of reproduction (White et al.,

2017). Roads thus potentially affect amphibian populations via direct effects on dispersal, abundance, and reproduction (Cosentino et al., 2014). However, these effects might be more evident in local abundances rather than in presence/absence data and particularly in species where traffic causes mortality during seasonal migrations (Beebee, 2013).

Effects of elevation largely reflected general ecological preferences of species, with tree frog, crested newt, and smooth newt occurring more frequently in the lowlands and midwife toad more frequently at higher elevations. The natterjack toad is mainly found in the floodplains.

Common versus conservation target species

Common species are widespread in the studied region and had comparatively high average colonization probabilities in new ponds (ranging from 0.14 for palmate newt to 0.53 for common frog [Appendix S10]). Population connectivity was overall less important than in conservation target species, but some effects were present. Although higher population connectivity increased persistence in the common alpine and palmate newts, it lowered persistence probabilities of common toad and common frog. The mechanism for this effect is unknown, but similar effects were reported previously (e.g., Denoel & Lehmann, 2006). Conspecific attraction or biased dispersal toward sites with higher habitat quality might be explanations (Schmidt & Pellet, 2005; Unglaub et al., 2021).

Interestingly, also high structural connectivity decreased persistence in all common species. This suggests higher turnover in structurally dense pond networks. Common species might colonize readily but then not establish stable populations in such networks, subsequently abandoning ponds again, potentially toward already established, larger populations.

Larger water surface area was beneficial also for common species. Unlike conservation target species though, common species preferred more densely forested surroundings, were not dependent on temporary ponds, and were not adversely affected by roads. It is possible that we did not detect an effect of roads on common species because they occur overall more frequently and in greater abundances in the landscape, diluting the barrier effect and the impact of direct mortality of transport infrastructure.

The invasive marsh frog has been spreading in the studied landscape after the 1990s into 2 major river valleys (Moor, Bergamini, et al., 2022). During this expansion, connectivity to existing populations strongly mediated both colonization and persistence, in ways similar to recovering conservation target species. Otherwise, this robust generalist showed no sensitivity to pond characteristics beyond preferential colonization of sites with larger water surface. Large roads decreased its colonization probability, probably by presenting dispersal barriers or by reducing dispersal pressure through elevated individual mortality from traffic. If and how this invasive species modifies the positive effects of ecological infrastructure restoration remains an open question. This invasive frog reduces the abundance of conservation target species (Roth et al., 2016).

Outlook

Metapopulation models can forecast spatial dynamics and metapopulation viability under future scenarios of environmental change or management (Sjögren-Gulve & Hanski, 2000). A strength of Bayesian hierarchical models, such as the dynamic occupancy models used here, is that they can formally account for uncertainties stemming from parameter estimation and imperfect detection, on top of stochasticity in the ecological processes (O'Hara et al., 2002). Predictions of future dynamics from such models naturally account for important sources of uncertainty (Howell, Hossack, Muths, Sigafus, Chenevert-Steffler, et al., 2020). Bayesian metapopulation models are therefore valuable tools to transparently evaluate future restoration strategies through metapopulation viability analyses, as demonstrated for amphibian metapopulation management in Europe (ter Braak & Etienne, 2003), Australia (Heard et al., 2013), and the United States (Chandler et al., 2015; Howell, Hossack, Muths, Sigafus, Chenevert-Steffler, et al., 2020). Such models could be further improved by including, where available, data on local abundance or reproduction (Cruickshank et al., 2021; Howell, Hossack, Muths, Sigafus, & Chandler, 2020), to enable a deeper understanding of the relevance of local population sizes and demographic rates for source–sink dynamics. Finally, the combined analysis of multiple taxa, including invertebrates or plants, could help optimize pond construction for a broader range of species (Hill et al., 2021).

Syntheses and recommendations

Pond construction in this landscape has halted declines and initiated the recovery of declining metapopulations of endangered amphibians (Moor, Bergamini, et al., 2022). This pond construction program was successful for a number of reasons. First, amphibian conservation has a long history in Switzerland (Schmidt & Zumbach, 2019). A systematic mapping of amphibian breeding sites began in the 1970s, and repeated surveys in the canton of Aargau were key for the development of an amphibian conservation action plan (Meier & Schelbert, 1999). The action plan set priorities, but also took advantage of opportunities to build ponds. Pond construction was accompanied by a monitoring program with volunteers, which generated long-term data and helped build a community of amphibian conservationists. Conservationists also trialed different approaches to pond construction under different environmental conditions (soil types, hydrology) and shared the knowledge that they gained (e.g., Pellet, 2014).

We found that to optimally target individual species, connectivity to existing source populations and species-specific habitat requirements must be considered. Encouragingly, simple connectivity metrics were important predictors for both colonization and persistence. To optimize colonization probabilities, distances to the nearest source population can be considered. These should be viewed in the context of species-specific movement capabilities. Some target species have generally low average rates of colonization (Appendix S10). This includes the

more dispersal-limited species smooth newt and crested newt, but also the more mobile but rare natterjack toad. To optimize long-term occupancy (incidence), persistence in new habitat is more relevant. We therefore recommend considering the density of populations per square kilometer when deciding where to construct new ponds. Densities of 2–4 occupied ponds per square kilometer promote not only colonization of but also the persistence in new habitat for most target species (Figure 5). This implies that the distance to the nearest source population should be no more than ~0.5 km. This positive effect of population density saturated at around 4 occupied ponds per square kilometer, such that adding more ponds for a species in that situation would not improve its incidence much more. However, since population densities are species specific and species differ in their preferences for pond type, an even higher number of different ponds per square kilometer is needed to benefit multiple species.

Although species have individual preferences regarding pond characteristics, the 7 target species overall would benefit from breeding sites with larger total water surface area ($\geq 100 \text{ m}^2$) in more open surroundings ($\leq 50\%$ forest cover) (Figure 5). Especially the natterjack toad could benefit from large ($> 1000 \text{ m}^2$) shallow and temporary water bodies in open areas (Appendix S11). Lastly, temporary ponds with water level fluctuations and occasional drying out would be beneficial for most target species (Van Buskirk, 2003).

There is no ideal pond that is equally suitable for all species. A variety of different pond types, permanent and temporary, of different sizes and in different surroundings, in breeding sites and across the landscape, will likely have the largest benefit for amphibian diversity overall. Landscape heterogeneity begets species diversity (Tews et al., 2004). Reinstalling wetlands in the landscape at a higher density will not only contribute to an ecological infrastructure for amphibians but also foster a multitude of other taxa and ecosystem functions.

ACKNOWLEDGMENTS

We thank all field volunteers for their invaluable monitoring work and the canton Aargau for allowing us to use their data. We thank the ETH Board for funding through the Blue-Green Biodiversity (BGB) Initiative (BGB2020).

Open access funding provided by ETH-Bereich Forschungsanstalten.

OPEN RESEARCH BADGES

This article has earned an Open Materials badge for making publicly available the components of the research methodology needed to reproduce the reported procedure and analysis. All materials are available at <https://www.doi.org/10.16904/envidat.270>.

ORCID

Helen Moor  <https://orcid.org/0000-0002-1340-2039>

Ariel Bergamini  <https://orcid.org/0000-0001-8816-1420>

Christoph Vörburger  <https://orcid.org/0000-0002-3627-0841>

Rolf Holderegger  <https://orcid.org/0000-0001-7062-1759>

Benedikt R. Schmidt  <https://orcid.org/0000-0002-4023-1001>

REFERENCES

- Angelone, S., & Holderegger, R. (2009). Population genetics suggests effectiveness of habitat connectivity measures for the European tree frog in Switzerland. *Journal of Applied Ecology*, *46*, 879–887.
- Antunes, B., Figueiredo-Vázquez, C., Dudek, K., Liana, M., Pabijan, M., Zieliński, P., & Babik, W. (2022). Landscape reveals contrasting patterns of connectivity in two newt species (*Lissotriton montandoni* and *L. vulgaris*). *Molecular Ecology*, *32*, 4515–4530.
- Beebee, T. J. C. (2013). Effects of road mortality and mitigation measures on amphibian populations. *Conservation Biology*, *27*, 657–668.
- Beebee, T. J. C., Denton, J. S., & Buckley, J. (1996). Factors affecting population densities of adult natterjack toads *Bufo calamita* in Britain. *Journal of Applied Ecology*, *33*, 263–268.
- Brown, J. H., & Kodric-Brown, A. (1977). Turnover rates in insular biogeography: Effect of immigration on extinction. *Ecology*, *58*, 445–449.
- Bühler, C. (2020). *Amphibienmonitoring Aargau 2020: Methodenbeschrieb*. Kanton Aargau Abteilung Landschaft & Gewässer.
- Bull, J. W., Milner-Gulland, E. J., Addison, P. F. E., Arlidge, W. N. S., Baker, J., Brooks, T. M., Burgass, M. J., Hinsley, A., Maron, M., Robinson, J. G., Sekhran, N., Sinclair, S. P., Stuart, S. N., zu Ermgassen, S. O. S. E., & Watson, J. E. M. (2020). Net positive outcomes for nature. *Nature Ecology and Evolution*, *4*, 4–7.
- Bullock, J. M., Fuentes-Montemayor, E., McCarthy, B., Park, K., Hails, R. S., Woodcock, B. A., Watts, K., Corstanje, R., & Harris, J. (2022). Future restoration should enhance ecological complexity and emergent properties at multiple scales. *Ecography*, *2022*, Article e05780.
- Calhoun, A. J. K., Arrigoni, J., Brooks, R. P., Hunter, M. L., & Richter, S. C. (2014). Creating successful vernal pools: A literature review and advice for practitioners. *Wetlands*, *34*, 1027–1038.
- Cayuela, H., Valenzuela-Sánchez, A., Teulier, L., Martínez-Solano, Í., Léna, J.-P., Merilä, J., Muths, E., Shine, R., Quay, L., Denoël, M., Clobert, J., & Schmidt, B. R. (2020). Determinants and consequences of dispersal in vertebrates with complex life cycles: A review of pond-breeding amphibians. *The Quarterly Review of Biology*, *95*, 1–36. <https://doi.org/10.1086/707862>
- Chandler, R. B., Muths, E., Sigafus, B. H., Schwalbe, C. R., Jarchow, C. J., & Hossack, B. R. (2015). Spatial occupancy models for predicting metapopulation dynamics and viability following reintroduction. *Journal of Applied Ecology*, *52*, 1325–1333.
- Convention on Biological Diversity (CBD). (2022). Kunming-Montreal Global biodiversity framework. Decision adopted by the conference of the parties to the Convention on Biological Diversity. <https://www.cbd.int/meetings/COP-15>
- Cosentino, B. J., Marsh, D. M., Jones, K. S., Apodaca, J. J., Bates, C., Beach, J., Beard, K. H., Becklin, K., Bell, J. M., Crockett, C., Fawson, G., Fjelsted, J., Forsy, E. A., Genet, K. S., Grover, M., Holmes, J., Indeck, K., Karraker, N. E., Kilpatrick, E. S., ... Willey, A. (2014). Citizen science reveals widespread negative effects of roads on amphibian distributions. *Biological Conservation*, *180*, 31–38.
- Cruikshank, S. S., Bergamini, A., & Schmidt, B. R. (2021). Estimation of breeding probability can make monitoring data more revealing: A case study of amphibians. *Ecological Applications*, *31*, Article e02357.
- Cruikshank, S. S., Schmidt, B. R., Ginzler, C., & Bergamini, A. (2020). Local habitat measures derived from aerial pictures are not strong predictors of amphibian occurrence or abundance. *Basic and Applied Ecology*, *45*, 51–61.
- Davies, B., Biggs, J., Williams, P., Whitfield, M., Nicolet, P., Sear, D., Bray, S., & Maund, S. (2008). Comparative biodiversity of aquatic habitats in the European agricultural landscape. *Agriculture, Ecosystems and Environment*, *125*, 1–8.
- De Meester, L., Declerck, S., Stoks, R., Louette, G., Van De Meutter, F., De Bie, T., Michels, E., & Brendonck, L. (2005). Ponds and pools as model systems in conservation biology, ecology and evolutionary biology. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *15*, 715–725.
- Denoël, M., & Lehmann, A. (2006). Multi-scale effect of landscape processes and habitat quality on newt abundance: Implications for conservation. *Biological Conservation*, *130*, 495–504.

- Denton, J. S., Hitchings, S. P., Beebee, T. J. C., & Gent, A. (1997). A recovery program for the natterjack toad (*Bufo calamita*) in Britain. *Conservation Biology*, *11*, 1329–1338.
- Dobson, A. P., Bradshaw, A. D., & Baker, A. J. M. (1997). Hopes for the future: Restoration ecology and conservation biology. *Science*, *277*, 515–522.
- Drake, J., Lambin, X., Sutherland, C., & Gaillard, M. (2022). Spatiotemporal connectivity dynamics in spatially structured populations. *Journal of Animal Ecology*, *91*, 2050–2060.
- Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z. I., Knowler, D. J., Lévêque, C., Naiman, R. J., Prieur-Richard, A. H., Soto, D., Stiassny, M. L. J., & Sullivan, C. A. (2006). Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biological Reviews*, *81*, 163–182.
- Dufresnes, C., Leuenberger, J., Amrhein, V., Bühler, C., Thiébaud, J., Bohnenstengel, T., & Dubey, S. (2018). Invasion genetics of marsh frogs (*Pelodytes punctatus* sensu lato) in Switzerland. *Biological Journal of the Linnean Society*, *123*, 402–410.
- Durrer, H. (2014). Amphibienschutz im siedlungsnahen Raum um Basel (CH): 40 Jahre Erfahrung in Bau und Pflege von Weierbiotopen. *Mitteilungen Naturforschende Gesellschaften beider Basel*, *15*, 51–76.
- Fahrig, L., Watling, J. I., Arnillas, C. A., Arroyo-Rodríguez, V., Jörgen-Hickfang, T., Müller, J., Pereira, H. M., Riva, F., Rösch, V., Seibold, S., Tschantke, T., & May, F. (2022). Resolving the SLOSS dilemma for biodiversity conservation: A research agenda. *Biological Reviews*, *97*, 99–114.
- Falaschi, M., Giachello, S., Parrino, E. L., Muraro, M., Manenti, R., & Ficetola, G. F. (2020). Long-term drivers of persistence and colonization dynamics in spatially structured amphibian populations. *Conservation Biology*, *35*, 1530–1539.
- Federal Office for the Environment (FOEN). (2012). Swiss biodiversity strategy. <https://www.bafu.admin.ch/ud-1060-e>
- Federal Office for the Environment (FOEN). (2017). Action plan for the Swiss biodiversity strategy. <https://www.bafu.admin.ch/aktionsplan-biodiversitaet>
- Federal Office for the Environment (FOEN). (2023). *Biodiversität in der Schweiz*. Zustand und Entwicklung. <https://www.bafu.admin.ch/uz-2306-d>
- Fluet-Chouinard, E., Stocker, B. D., Zhang, Z., Malhotra, A., Melton, J. R., Poulter, B., Kaplan, J. O., Goldewijk, K. K., Siebert, S., Minayeva, T., Hugelius, G., Joosten, H., Barthelmes, A., Prigent, C., Aires, F., Hoyt, A. M., Davidson, N., Finlayson, C. M., Lehner, B., ... McIntyre, P. B. (2023). Extensive global wetland loss over the past three centuries. *Nature*, *614*, 281–286.
- Gann, G. D., McDonald, T., Walder, B., Aronson, J., Nelson, C. R., Jonson, J., Hallett, J. G., Eisenberg, C., Guariguata, M. R., Liu, J., Hua, F., Echeverría, C., Gonzales, E., Shaw, N., Decler, K., & Dixon, K. W. (2019). International principles and standards for the practice of ecological restoration. *Restoration Ecology*, *27*, S1–S46.
- Gimmi, U., Lachat, T., & Bürgi, M. (2011). Reconstructing the collapse of wetland networks in the Swiss lowlands 1850–2000. *Landscape Ecology*, *26*, 1071–1083.
- Grant, E. H. C., Muths, E., Schmidt, B. R., & Petrovan, S. O. (2019). Amphibian conservation in the Anthropocene. *Biological Conservation*, *236*, 543–547.
- Green, D. M. (2003). The ecology of extinction: population fluctuation and decline in amphibians. *Biological Conservation*, *111*(3), 331–343. [https://doi.org/10.1016/s0006-3207\(02\)00302-6](https://doi.org/10.1016/s0006-3207(02)00302-6)
- Hanski, I. (1994). Patch-occupancy dynamics in fragmented landscapes. *Trends in Ecology and Evolution*, *9*, 131–135.
- Hanski, I., & Gilpin, M. (1991). Metapopulation dynamics: Brief history and conceptual domain. *Biological Journal of the Linnean Society*, *42*, 3–16.
- Harper, M., Mejbøl, H. S., Longert, D., Abell, R., Beard, T. D., Bennett, J. R., Carlson, S. M., Darwall, W., Dell, A., Domisch, S., Dudgeon, D., Freyhof, J., Harrison, I., Hughes, K. A., Jähnig, S. C., Jeschke, J. M., Lansdown, R., Lintermans, M., Lynch, A. J., ... Cooke, S. J. (2021). Twenty-five essential research questions to inform the protection and restoration of freshwater biodiversity. *Aquatic Conservation: Marine and Freshwater Ecosystems*, *31*, 2632–2653.
- Heard, G. W., McCarthy, M. A., Scroggie, M. P., Baumgartner, J. B., & Parris, K. M. (2013). A Bayesian model of metapopulation viability, with application to an endangered amphibian. *Diversity and Distributions*, *19*, 555–566.
- Hill, M. J., Greaves, H. M., Sayer, C. D., Hassall, C., Milin, M., Milner, V. S., Marazzi, L., Hall, R., Harper, L. R., Thornhill, I., Walton, R., Biggs, J., Ewald, N., Law, A., Willby, N., White, J. C., Briers, R. A., Mathers, K. L., Jeffries, M. J., & Wood, P. J. (2021). Pond ecology and conservation: Research priorities and knowledge gaps. *Ecosystems*, *12*, Article e03853.
- Hill, M. J., Hassall, C., Oertli, B., Fahrig, L., Robson, B. J., Biggs, J., Samways, M. J., Usio, N., Takamura, N., Krishnaswamy, J., & Wood, P. J. (2018). New policy directions for global pond conservation. *Conservation Letters*, *11*, Article e12447.
- Howell, P. E., Hossack, B. R., Muths, E., Sigafus, B. H., & Chandler, R. B. (2020). Informing amphibian conservation efforts with abundance-based metapopulation models. *Herpetologica*, *76*, 240–250.
- Howell, P. E., Hossack, B. R., Muths, E., Sigafus, B. H., Chenevert-Steffler, A., & Chandler, R. B. (2020). A statistical forecasting approach to metapopulation viability analysis. *Ecological Applications*, *30*, Article e02038.
- Ilg, C., & Oertli, B. (2017). Effectiveness of amphibians as biodiversity surrogates in pond conservation. *Conservation Biology*, *31*, 437–445.
- Jaureguiberry, P., Titeux, N., Wiemers, M., Bowler, D. E., Coscieme, L., Golden, A. S., Guerra, C. A., Jacob, U., Takahashi, Y., Settele, J., Díaz, S., Molnár, Z., & Purvis, A. (2022). The direct drivers of recent global anthropogenic biodiversity loss. *Science Advances*, *8*, Article eabm9982.
- Jehle, R., & Sinsch, U. (2007). Wanderleistung und Orientierung von Amphibien: Eine Übersicht. *Zeitschrift für Feldherpetologie*, *14*, 137–152.
- Jeliazkov, A., Lorrillière, R., Besnard, A., Garnier, J., Silvestre, M., & Chiron, F. (2019). Cross-scale effects of structural and functional connectivity in pond networks on amphibian distribution in agricultural landscapes. *Freshwater Biology*, *64*, 997–1014.
- Keeley, A. T. H., Beier, P., & Jenness, J. S. (2021). Connectivity metrics for conservation planning and monitoring. *Biological Conservation*, *255*, Article 109008.
- Kunc, H. P., & Schmidt, R. (2019). The effects of anthropogenic noise on animals: A meta-analysis. *Biology Letters*, *15*, Article 20190649.
- Lewis-Phillips, J., Brooks, S., Sayer, C. D., McCrea, R., Siriwardena, G., & Axmacher, J. C. (2019). Pond management enhances the local abundance and species richness of farmland bird communities. *Agriculture, Ecosystems and Environment*, *273*, 130–140.
- MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, A. A., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, *83*, 2248–2255.
- Magnus, R., & Rannap, R. (2019). Pond construction for threatened amphibians is an important conservation tool, even in landscapes with extant natural water bodies. *Wetlands Ecology and Management*, *27*, 323–341.
- McCaffery, R. M., Eby, L. A., Maxell, B. A., & Corn, P. S. (2014). Breeding site heterogeneity reduces variability in frog recruitment and population dynamics. *Biological Conservation*, *170*, 169–176.
- Meier, C., & Schelbert, B. (1999). Amphibienschutzkonzept Kanton Aargau. *Mitteilungen Aargauische Naturforschende Gesellschaft*, *35*, 41–69.
- Moilanen, A. (2004). SPOMSIM: Software for stochastic patch occupancy models of metapopulation dynamics. *Ecological Modelling*, *179*, 533–550.
- Moilanen, A., & Nieminen, M. (2002). Simple connectivity measures in spatial ecology. *Ecology*, *83*, 1131–1145.
- Moor, H., Bergamini, A., Vorburger, C., Holderegger, R., Bühler, C., Egger, S., & Schmidt, B. R. (2022). Bending the curve: Simple but massive conservation action leads to landscape-scale recovery of amphibians. *Proceedings of the National Academy of Sciences of the United States of America*, *119*, Article e2123070119.
- Moor, H., Bühler, C., Bergamini, A., Vorburger, C., Holderegger, R., Schmidt, B. R., & Egger, S. (2022). Amphibian observation and pond data (Aargau, Switzerland). EnviDat. <https://doi.org/10.16904/envidat.270>
- O'Hara, R. B., Arjas, E., Toivonen, H., & Hanski, I. (2002). Bayesian analysis of metapopulation data. *Ecology*, *83*, 2408–2415.
- Oldham, R. S., Keeble, J., Swan, M. J. S., & Jeffcote, M. (2000). Evaluating the suitability of habitat for the Great Crested Newt (*Triturus cristatus*). *Herpetological Journal*, *10*, 143–155.
- Pellet, J. (2014). Temporäre Gewässer für gefährdete Amphibien schaffen—Leitfaden für die Praxis. *Beiträge zum Naturschutz in der Schweiz*, *35*, 1–25.

- Pellet, J., Fleishman, E., Dobkin, D. S., Gander, A., & Murphy, D. D. (2007). An empirical evaluation of the area and isolation paradigm of metapopulation dynamics. *Biological Conservation*, *136*, 483–495.
- Pellet, J., Guisan, A., & Perrin, N. (2004). A concentric analysis of the impact of urbanization on the threatened European tree frog in an agricultural landscape. *Conservation Biology*, *18*, 1599–1606.
- Perring, M. P., Standish, R. J., Price, J. N., Caig, M. D., Erickson, T. E., Ruthrof, K. X., Whiteley, A. S., Valentine, L. E., & Hobbs, R. J. (2015). Advances in restoration ecology: Rising to the challenges of the coming decades. *Ecosphere*, *6*, Article 131.
- Prugh, L. R. (2009). An evaluation of patch connectivity measures. *Ecological Applications*, *19*, 1300–1310.
- Pulliam, H. R. (1988). Sources, sinks, and population regulation. *American Naturalist*, *132*, 652–661.
- Rannap, R., Löhmus, A., & Briggs, L. (2009). Restoring ponds for amphibians: A success story. *Hydrobiologia*, *634*, 87–95.
- Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T. J., Kidd, K. A., MacCormack, T. J., Olden, J. D., Ormerod, S. J., Smol, J. P., Taylor, W. W., Tockner, K., Vermaire, J. C., Dudgeon, D., & Cooke, S. J. (2019). Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biological Reviews*, *94*, 849–873.
- Roth, T., Bühler, C., & Amrhein, V. (2016). Estimating effects of species interactions on populations of endangered species. *American Naturalist*, *187*, 457–467.
- Royle, J. A., & Kéry, M. (2007). A Bayesian state-space formulation of dynamic occupancy models. *Ecology*, *88*, 1813–1823.
- Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, *1*, 103–113.
- Schmidt, B. R., Arlettaz, R., Schaub, M., Lüscher, B., & Kröpfl, M. (2019). Benefits and limits of comparative effectiveness studies in evidence-based conservation. *Biological Conservation*, *236*, 115–123.
- Schmidt, B. R., Cruickshank, S. S., Bühler, C., & Bergamini, A. (2023). Observers are a key source of detection heterogeneity and biased occupancy estimates in species monitoring. *Biological Conservation*, *283*, Article 110102.
- Schmidt, B. R., & Pellet, J. (2005). Relative importance of population processes and habitat characteristics in determining site occupancy of two anurans. *Journal of Wildlife Management*, *69*, 884–893.
- Schmidt, B. R., & Zumbach, S. (2019). Amphibian conservation in Switzerland. In H. Heatwole & J. W. Wilkinson (Eds.), *Amphibian biology, Volume 11: Status of conservation and decline of amphibians: Eastern Hemisphere, Part 5: Northern Europe* (pp. 46–51). Pelagic Publishing.
- Schmidt, B. R., Zumbach, S., Tobler, U., & Lippuner, M. (2015). Amphibien brauchen temporäre Gewässer. *Zeitschrift für Feldherpetologie*, *22*, 137–150.
- Semlitsch, R. D. (2002). Critical elements for biologically based recovery plans of aquatic-breeding amphibians. *Conservation Biology*, *16*, 619–629.
- Shoemaker, L. G., Sullivan, L. L., Donohue, I., Cabral, J. S., Williams, R. J., Mayfield, M. M., Chase, J. M., Chu, C., Harpole, W. S., Huth, A., HilleRisLambers, J., James, A. R. M., Kraft, N. J. B., May, F., Muthukrishnan, R., Satterlee, S., Taubert, F., Wang, X., Wiegand, T., ... Abbott, K. C. (2020). Integrating the underlying structure of stochasticity into community ecology. *Ecology*, *101*, Article e02922.
- Siffert, O., Pellet, J., Ramseier, P., Tobler, U., Bergamini, A., & Schmidt, B. R. (2022). Where land and water meet: Making amphibian breeding sites attractive for amphibians. *Diversity*, *14*, Article 834.
- Sjögren, P. (1991). Extinction and isolation gradients in metapopulations: The case of the pool frog (*Rana lessonae*). *Biological Journal of the Linnean Society*, *42*, 135–147.
- Sjögren-Gulve, P., & Hanski, I. (2000). Metapopulation viability analysis using occupancy models. *Ecological Bulletin*, *48*, 53–71.
- Smith, R. K., Meredith, H. M. R., & Sutherland, W. J. (2020). Amphibian conservation. In W. J. Sutherland, L. V. Dicks, S. O. Petrovan, & R. K. Smith (Eds.), *What works in conservation 2020* (pp. 9–64). Open Book Publishers.
- Spiegelhalter, D. J., Best, N. G., Carlin, B. P., & Van Der Linde, A. (2002). Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society Series B: Statistical Methodology*, *64*(4), 583–639. <https://doi.org/10.1111/1467-9868.00353>
- Tanadini, L. G., & Schmidt, B. R. (2011). Population size influences amphibian detection probability: Implications for biodiversity monitoring programs. *PLoS ONE*, *6*, Article e28244.
- Ter Braak, C. J. F., & Etienne, R. S. (2003). Improved Bayesian analysis of metapopulation data with an application to a tree frog metapopulation. *Ecology*, *84*, 231–241.
- Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M. C., Schwager, M., & Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. *Journal of Biogeography*, *31*, 79–92.
- Török, P., & Helm, A. (2017). Ecological theory provides strong support for habitat restoration. *Biological Conservation*, *206*, 85–91.
- Tredennick, A. T., Hooker, G., Ellner, S. P., & Adler, P. B. (2021). A practical guide to selecting models for exploration, inference, and prediction in ecology. *Ecology*, *102*, Article e03336.
- Unglaub, B., Cayuela, H., Schmidt, B. R., Preißler, K., Glos, J., & Steinfartz, S. (2021). Context-dependent dispersal determines relatedness and genetic structure in a patchy amphibian population. *Molecular Ecology*, *30*, 5009–5028.
- United Nations (UN). (2019). United Nations General Assembly (UN) Res 73/284 (6 March 2019) UN Doc A/RES/73/284. <https://digitallibrary.un.org/record/379431?ln=en>
- Van Buskirk, J. (2003). Habitat partitioning in European and North American pond-breeding frogs and toads. *Diversity and Distributions*, *9*, 399–410.
- Wellborn, G. A., Skelly, D. K., & Werner, E. E. (1996). Mechanisms creating community structure across a freshwater habitat gradient. *Annual Review of Ecology and Systematics*, *27*, 337–363.
- White, K. J., Mayes, W. M., & Petrovan, S. O. (2017). Identifying pathways of exposure to highway pollutants in great crested newt (*Triturus cristatus*) road mitigation tunnels. *Water and Environment Journal*, *31*, 310–316.
- Williams, P., Biggs, J., Stoate, C., Szczyr, J., Brown, C., & Bonney, S. (2020). Nature based measures increase freshwater biodiversity in agricultural catchments. *Biological Conservation*, *244*, Article 108515.
- Williams, P., Whitfield, M., Biggs, J., Bray, S., Fox, G., Nicolet, P., & Sear, D. (2003). Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. *Biological Conservation*, *115*, 329–341.
- Yackulic, C. B., Nichols, J. D., Reid, J., & Der, R. (2015). To predict the niche, model colonization and extinction. *Ecology*, *96*, 16–23.
- Zanini, F., Klingemann, A., Schlaepfer, R., & Schmidt, B. R. (2008). Landscape effects on anuran pond occupancy in an agricultural countryside: Barrier-based buffers predict distributions better than circular buffers. *Canadian Journal of Zoology*, *86*, 692–699.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Moor, H., Bergamini, A., Vorburger, C., Holderegger, R., Bühler, C., Bircher, N., & Schmidt, B. R. (2024). Building pondscapes for amphibian metapopulations. *Conservation Biology*, e14165. <https://doi.org/10.1111/cobi.14281>