

In Switzerland, both rare and common amphibians declined strongly in the past and either continue to decline to this day or their populations linger at low levels (27–29). In the Swiss state Aargau, concern about these declines motivated a large-scale, ongoing pond-construction program (30). The state Aargau is a densely populated, highly urbanized landscape with managed forests and intensive farming, which is highly fragmented by traffic infrastructure and where few patches of natural ecosystems remain (31) (SI Appendix, Fig. S1). About 20% of the agricultural area is actively drained by drainage pipes (32). Pond-breeding amphibians are further affected by multiple stressors, such as nonnative fish, the amphibian chytrid fungus *Batrachochytrium dendrobatidis*, and pesticides (33–35). In this landscape, hundreds of ponds were added to the existing set of ponds and a monitoring program accompanied these measures.

Here, our aim was to evaluate whether this massive conservation effort benefitted declining amphibian species and whether negative trends could be reversed. To this end, we fitted dynamic occupancy models accounting for imperfect detection and observer bias to 20 y of monitoring data for all 12 pond-breeding amphibian species in the state Aargau (36). The data encompass thousands of surveys in 856 ponds, 422 of which were newly constructed between 1991 and 2019, distributed across five regions (Rheintal, Aaretal, Reusstal, Suhretal, and Wiggertal; SI Appendix, Fig. S2). The regions are geographically distinct and follow major river valleys separated by hills. We assumed that each region accommodates a distinct metapopulation, potentially connected by dispersal within (mean interpond distance within regions in 1999 was 420–800 m) but relatively isolated between regions. The 12 studied species included all extant pond-breeding amphibians (the stream-breeding salamander *Salamandra salamandra* was not part of the conservation and

monitoring program). They comprised eight anurans (toads and frogs) and four newts with different life histories, habitat requirements, and dispersal capacities (SI Appendix S1). Eight species are on the national Red List (27), and one is an invasive species (SI Appendix, Table S1). Our analyses aimed (i) to describe the trajectories of Nos. of occupied ponds across and within five major regions in the Swiss state Aargau, (ii) to assess whether and how the colonization of new ponds contributed to changes in metapopulation sizes, (iii) to test whether colonization-persistence dynamics differed between existing (i.e., old) and newly constructed ponds, and (iv) to identify characteristics of the ponds that were important for colonization.

Results and Discussion

State-Wide and Regional Trends in the No. of Occupied Ponds.

To assess changes in state-wide population sizes, we compared the estimated number of ponds across the five regions occupied in 2019 and 1999 and classified differences into increases, stable Nos., or declines (based on the proportion of the posterior distribution of differences below or above zero with a threshold of 90% certainty). At the scale of the entire state, the number of occupied ponds increased for 10 of the 12 species from 1999 to 2019, did not change for *Alytes obstetricans*, and declined for *Epidalea calamita* (SI Appendix, Table S2 and Fig. S3).

Trends in metapopulation sizes differed substantially between regions (Fig. 1). Across all species, the majority (65%) of the 43 regional metapopulations increased in size between 1999 and 2019, 21% remained stable, and 14% declined. Considering only the 25 metapopulations of the eight Red-Listed species, 52% increased, 32% remained stable, while 16% declined. The only species that consistently increased in all regions was the

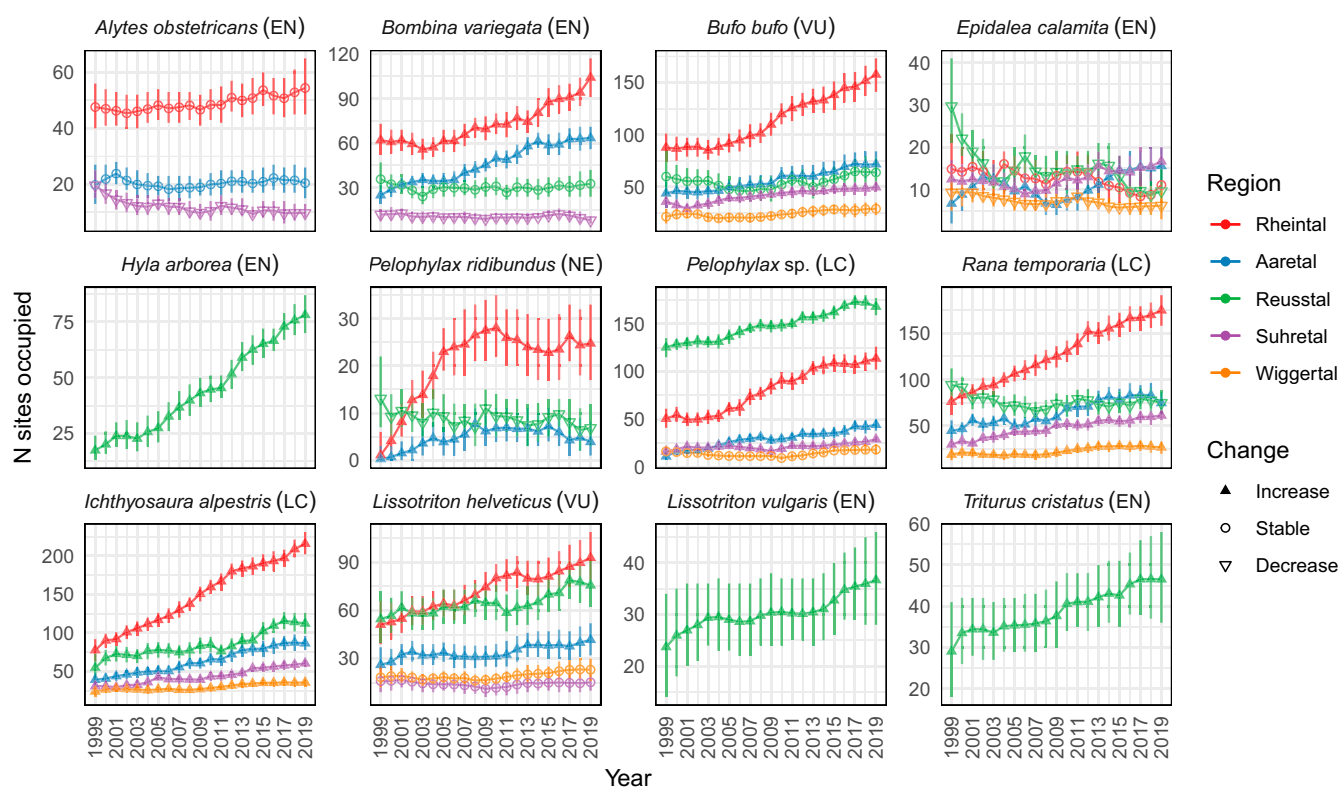


Fig. 1. Trajectories of estimated metapopulation size (number of occupied sites; mean with 95% CI) in five regions from 1999 to 2019. Not all species occur in all regions. Filled upward triangles indicate increases in metapopulation size (with certainty >90%), open circles no change, and open downward triangles decreases between 1999 and 2019. EN, VU, NT, LC, and NE in parentheses indicate the national Red List status following IUCN criteria and categories.

common and widespread *Ichthyosaura alpestris*. *E. calamita* showed the most variation between regions, with two declining, one stable, and two increasing metapopulations. There were thus some discrepancies between population change assessed at different spatial scales. The state-wide decline of *E. calamita* masked increasing trends in two regions (Fig. 1), even if these increases were small in absolute terms. Analogously, *A. obstetricans* has been declining at the national scale for decades (27) but has remained stable since 1999 in our study area. To assess progress toward large-scale conservation goals, national-, continental-, and even global-scale analyses are needed (9, 29, 37), but in order to evaluate conservation actions and their success, effects should be considered at the spatial scale where actions took place and are expected to have impact. Pond-breeding amphibians can maintain stable metapopulation sizes despite local extinctions if distances between ponds are shorter than typical dispersal distances. The relevant scale for long-term population management is therefore the metapopulation scale ((38–40); herein operationally defined as the regions).

Regional Changes in Metapopulation Size Reflect Conservation Effort. Increases in metapopulation size were most common in Rheintal (seven out of nine species occurring there increased) and Aaretal (eight out of nine species; *SI Appendix*, Fig. S4). These are the regions where the most ponds were constructed (198 and 98 new ponds added to 131 and 72 pre-existing ponds in Rheintal and Aaretal, respectively). Increases were rarest and weakest in Wiggertal, where construction did not begin until 2009 and only 11 ponds were built in addition to 33 existing ponds. Here, only the two common species *Rana temporaria* and *I. alpestris* increased. Second was Suhretal, where 36 ponds were

added to 49 existing ponds, beginning in 2006. Three common species and two Red-Listed anurans (notably *E. calamita*) increased there, but two other Red-Listed anurans decreased (Fig. 1). Reusstal, which had the most old ponds (149), showed idiosyncratic patterns: all newts increased, while among seven anurans, three declined, two remained stable, and two increased. The latter included the spectacular recovery of *Hyla arborea*, which showed a nearly fivefold increase in metapopulation size, from 16 occupied sites in 1999 (95% CI: 12, 21) to 77 (95% CI: 70, 86) sites in 2019 (Fig. 1). Even though 79 new ponds were constructed in Reusstal, given the large initial number of ponds, the relative change in habitat availability was comparatively low. In summary, in regions where more new ponds have been built, more metapopulations increased and fewer declined (*SI Appendix*, Fig. S4).

Newly Constructed Ponds Contributed to Metapopulation Stabilization and Recovery. To further quantify the role of new ponds in changing metapopulation sizes, we split trajectories of regional metapopulation size into occupied old and new ponds and categorized changes therein based on differences between 1999 and 2019 (with >90% probability; *SI Appendix*, Table S3). Each metapopulation was assigned a pattern of change given the combination of its overall change with changes in old and new ponds (Fig. 2).

The contributions of new ponds to metapopulation recovery followed different patterns. Overall increases in metapopulation size (Fig. 2A) were always associated with the colonization of and persistence in new ponds, with the exception of *Pelophylax ridibundus* in Aaretal (Fig. 2A.1). This invasive species was present in Reusstal since 1970 but only started invading Aaretal and Rheintal in the late 1990s, where it occupied more old

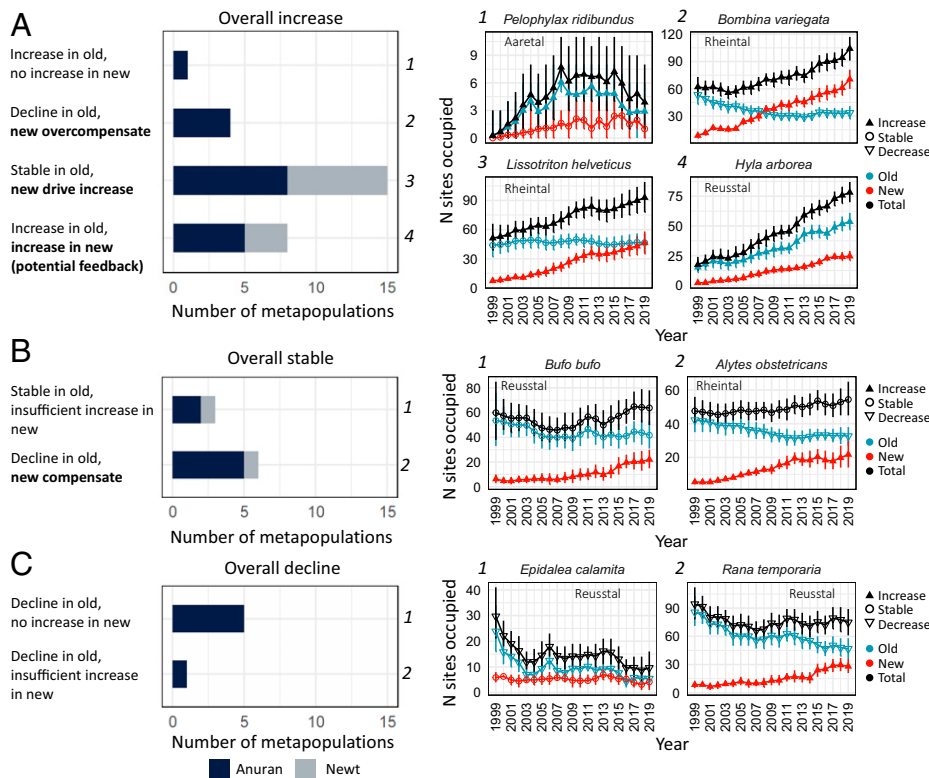


Fig. 2. Patterns of change in old and new ponds for 43 regional metapopulations with (A) increasing ($n = 28$ metapopulations), (B) stable ($n = 9$), and (C) overall declining ($n = 6$) metapopulation size from 1999 to 2019 (>90% probability). *Left* panels show the number of metapopulations that follow each of eight possible patterns. **Bold font** indicates patterns where the colonization of new ponds influenced the overall trend (33 or 77% of the 43 metapopulations). *Right* panels show one example per pattern of a corresponding trajectory of estimated total regional metapopulation size (black), split into the number of old (blue) and new (red) sites occupied. Symbols indicate increasing (filled upward triangles), stable (open circles), or decreasing (open downward triangles) Nos. of occupied ponds from 1999 to 2019 (with >90% probability). Error bars show 95% CI.

than new ponds (*SI Appendix*, Fig. S5). In all other increasing metapopulations, the occupation of new ponds caused an increase in total metapopulation size, either by overcompensation of declines in old ponds, by directly driving increases, or via concurrent increases in new and old ponds.

Overall stable metapopulation sizes (Fig. 2*B*) were associated either with stable Nos. of occupied old ponds or with the compensation of declines in old ponds by increasing Nos. of occupied new ponds. Overall declines (Fig. 2*C*) occurred where new ponds did not get colonized or not in sufficient Nos. to compensate for declines in old ponds.

Three nonmutually exclusive mechanisms are likely to be involved in the contributions of new ponds to changes in metapopulation sizes. First, the sheer number of new ponds increases the availability of breeding habitat for many species, of which highly mobile generalist species, such as *Bufo bufo*, *I. alpestris*, or *Pelophylax* frogs, should benefit most immediately. These common generalists were not the main conservation targets but profited as a side effect. Species with more-specific habitat requirements should also benefit, as long as structural and ecological variation in constructed ponds includes some suitable habitat for them as well. *E. calamita*, for example, prefers large shallow ponds with fluctuating water tables in open areas (41), while *A. obstetricans* needs terrestrial microhabitats, such as dry stone walls in the surroundings of ponds (23). An insufficient number of new ponds meeting such criteria might explain why these habitat specialists responded less to pond construction. Second, the constant addition of new, early successional ponds to some degree restores the dynamics of natural, undisturbed floodplains or temporarily flooded meadows and marshes. This should benefit pioneer species, such as *Bombina variegata* and *E. calamita*, that preferentially colonize ponds with short hydroperiods devoid of vegetation and predators (41). Successional changes likely explain declines of these species in old ponds (*SI Appendix*, Fig. S5; (41, 42)). This beneficial aspect of pond construction can therefore only be maintained if new ponds are constructed continuously or if active management periodically resets some ponds to early successional stages, which is already practiced (43). Third, the increasing density of and hence connectivity between ponds should benefit dispersal-limited species, such as newts, which rarely disperse farther than a few hundred meters (44). In mobile or already widespread species, increased habitat availability and increased connectivity could jointly cause a positive feedback, leading to higher occupancy of old and new ponds, as was potentially the case for *H. arborea*. The invasive *P. ridibundus* colonized new ponds readily (Fig. 2 and *SI Appendix*, Fig. S5); hence, it was also a beneficiary of pond construction. Similar to American bullfrogs (45), this large frog has negative impacts on native amphibians through predation or competition (46, 47). Nonetheless, most native species showed increased metapopulation sizes in response to pond construction, but the increase might have been even stronger in the absence of invasive species.

Higher Colonization Rates but Lower Persistence in New Compared with Old Ponds. The dynamics of colonization and persistence differed between old and new ponds (Fig. 3 and *SI Appendix*, Fig. S6). Colonization probabilities tended to be higher in new than in old ponds, especially in common species (*Pelophylax* sp., *R. temporaria*, and *I. alpestris*) but also for the rarer *B. variegata*, *Lisotriton helveticus*, or *Triturus cristatus*. This is expected, as new ponds start empty while suitable old ponds may already be occupied. New ponds also differ from old ponds in that they initially lack vegetation and predators

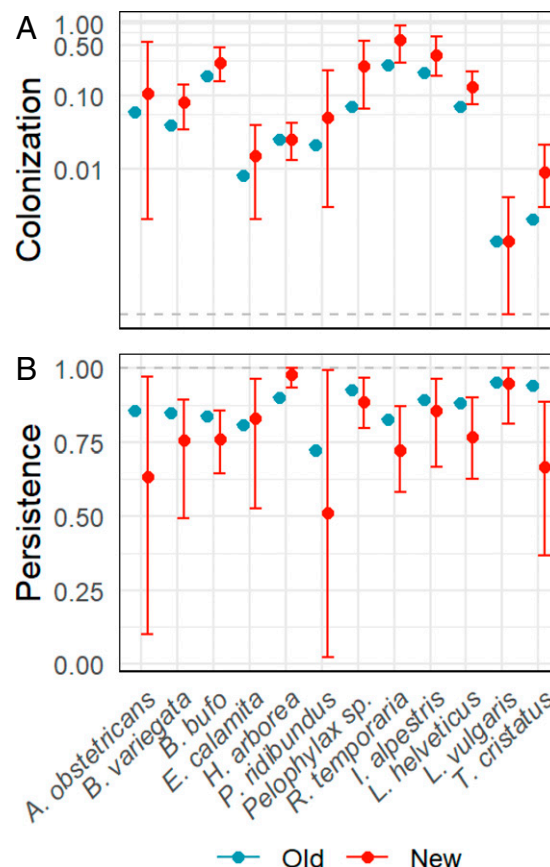


Fig. 3. Probabilities of (A) colonization and (B) persistence in new ponds (red, with 95% CI) compared with mean probabilities in old ponds (blue, point estimates as baseline without associated uncertainty) across all regions. Note the log scale y axis for colonization probability. Estimated probabilities in old and new ponds in individual regions are shown in *SI Appendix*, Fig. S6.

and are thereby more attractive to early successional species, such as *B. variegata*.

In contrast, persistence probabilities were lower in new ponds than in old ponds for the majority of species (Fig. 3). Immigrants may not always be able to establish persistent populations. Small initial population sizes render newly established populations prone to local extinction, be it due to Allee effects, local inbreeding, or environmental or demographic stochasticity (48). Lower persistence probabilities can also be expected for early successional species that become locally extinct, once vegetation becomes denser and populations of tadpole predators increase (e.g., *B. variegata*). *H. arborea* was the only species with higher persistence probability in new than in old ponds, which likely contributed to the exceptional increase in metapopulation size of this species.

Effects of Local and Landscape Variables on Colonization Probabilities. To inform future conservation practice (23), we assessed the influence of the age of ponds and of environmental variables describing the ponds and the surrounding landscape on colonization probabilities. Colonization rates depended on both pond and landscape characteristics, suggesting complementary effects of both aquatic and terrestrial habitat for completing the complex amphibian life cycle ((44, 49); Fig. 4 and *SI Appendix*, Table S4). Colonization probability increased with pond surface area continuously or unimodally for all species but *B. variegata*, which had a higher colonization probability in smaller ponds.

Water-table fluctuations, indicating variation in pond hydroperiod length and the potential for pond drying, increased colonization probabilities of *B. variegata* and *E. calamita*, as well as all newt species. This constitutes important information for practitioners, as both the surface area of ponds and water-table fluctuations can be specified during pond construction (23, 50). In our study landscape, for example, only 3% of newly constructed ponds had a surface area >1,000 m² and fluctuating water tables. A lack of large ponds with variable hydroperiod lengths may be a limiting factor for the recovery of *E. calamita* in this landscape.

Landscape complementation is important when selecting locations for new ponds, as amphibians require both suitable aquatic habitat for larvae and terrestrial habitat for adults (23, 49). *Epidalea calamita*, *P. ridibundus*, and *Lissotriton vulgaris* had higher colonization probabilities in ponds with less forest cover in the surroundings, while most other species showed unimodal or positive responses to forest cover (Fig. 4). Roads can have negative effects on dispersing or migrating amphibians (44). Here, we found negative effects of roads on colonization probabilities that were significant for the frog species and the strongly affected newts *L. vulgaris* and *T. cristatus*, which generally had low colonization

probabilities (Fig. 4). Structural connectivity, integrating the density and vicinity of other ponds, increased colonization probability of *B. variegata*, *H. arborea*, and, to some extent, *T. cristatus*, while *R. temporaria* more frequently colonized more isolated ponds. Pond age distinguished the early and fast colonizers (*B. variegata*, *P. ridibundus*, and *R. temporaria*) from species preferring late successional stages (*T. cristatus*).

Summarizing landscape effects at the most general level, our results show that the rapid colonization of new amphibian breeding ponds is aided by constructing them close to forest, far from roads, and in proximity to other ponds. However, some species showed idiosyncratic responses, and for most species, the effects of landscape variables and structural connectivity were relatively weak. This supports the encouraging conclusion that no effort in pond construction is really wasted. Some species will benefit, and diverse landscape settings are ultimately required to maintain a heterogeneous community of species.

Pond Construction as a Conservation Tool for Amphibians: Lessons Learned. Large-scale and long-term surveys provide invaluable information on population trends (7, 51) and their

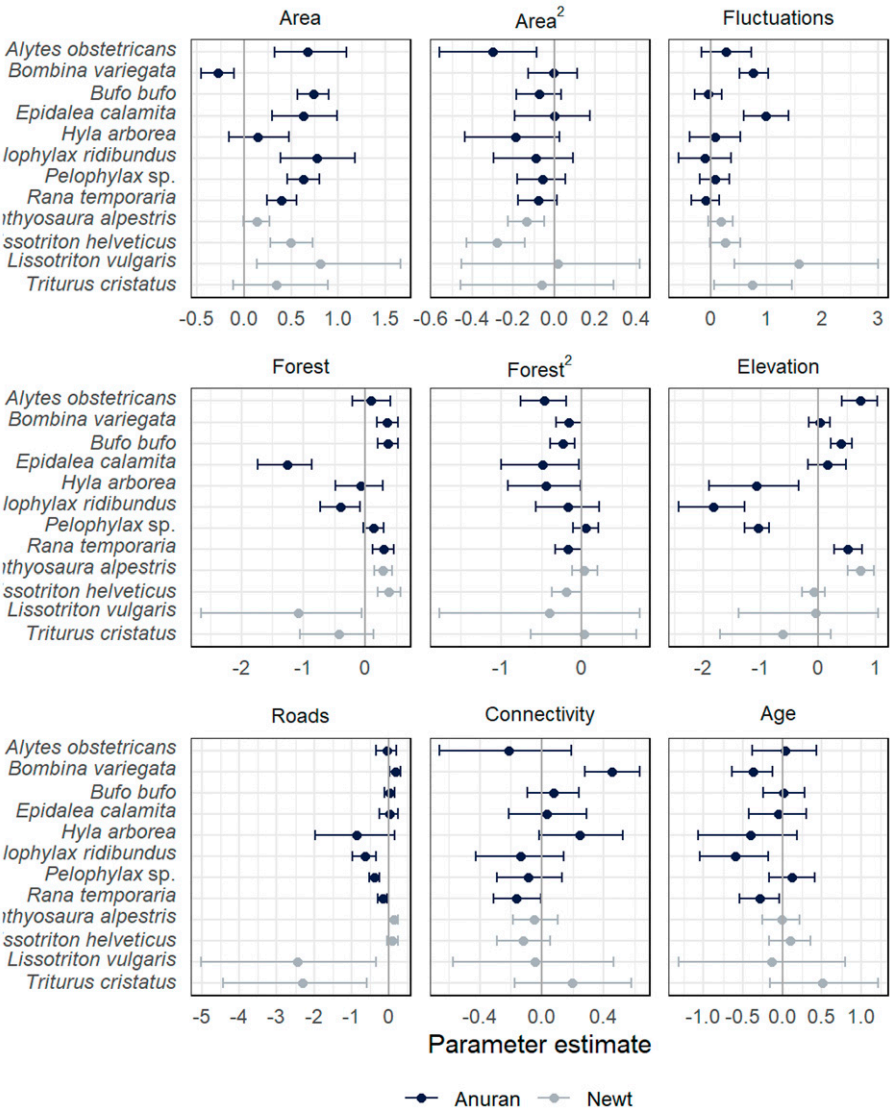


Fig. 4. Estimates (logit scale) of the effects of environmental variables on colonization probability (mean, 95% CI). Environmental variables were pond surface area, fluctuations of the water table, the percent area of forest within 100 m of the pond, elevation, the area of large (width ≥6 m) roads within 1 km of the pond, connectivity, and the age of newly constructed ponds. Absolute values of parameter estimates indicate effect size, as all covariates were standardized to mean zero and unit variance prior to analysis.