ARTICLE

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Amphibian abundance is associated with reduced mosquito presence in human-modified landscapes

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Abstract

The impacts of landscape anthropization on mosquito abundance and diversity are already well studied, but the underlying ecological factors behind these effects are still poorly understood. One such underlying ecological factor may be related to the loss of amphibians in human-modified landscapes, providing ideal habitats for several mosquito species. In this study, we conducted a mosquito and amphibian larvae survey in 77 ponds along a gradient of landscape anthropization in western Switzerland. We used structural equation models to investigate the direct and indirect effects of building footprints and several local pond parameters on mosquito abundance and composition through amphibian abundance. We highlighted that landscape anthropization increases the presence probability of mosquito larvae and the proportion of *Culex pipiens* in mosquito communities. Our results also suggested that one of the ecological mechanisms underlying these effects is a reduction in amphibian abundance, limiting competition and predation experienced by mosquitoes in human-modified landscapes. In addition, we showed that several local pond characteristics prevent the presence and abundance of mosquito larvae. Indeed, deep ponds, which promote amphibian abundance, limit the probability of larval mosquito presence, and large and old ponds have a lower larval mosquito abundance. Amphibians appear to be effective control agents of natural mosquito populations. Therefore, the development of measures to protect amphibians in human-modified landscapes could help to reduce both mosquito-related nuisances and the risk of emergence of vector-borne diseases in humans and wildlife.

KEYWORDS
common frog and toad, *Culex pipiens*, deforestation, pondscape, spatial analysis, structural equation modeling, urbanization, wetlands

Philippe Christe and Olivier Glaizot are co-last authors.

INTRODUCTION

The incidence, resurgence, and outbreaks of several mosquito-borne diseases, including dengue, chikungunya, and yellow fever, have grown dramatically around the world these last decades (Gardner & Ryman, 2010; WHO, 2014, 2020). The treatment for these mosquito-borne diseases is mainly supportive, as there is no cure for most of them; the focus is on reducing the risk of infection (Lee et al., 2018). One of the risk reduction methods is vector control by different sterile and/or incompatible insect techniques (e.g., radiation-sterilized males or *Wolbachia*-based sterilization, respectively), which are not always successful (Zheng et al., 2019). Therefore, it is important to determine where and why certain areas are more at risk of mosquito proliferation than others and identify the underlying ecological mechanisms that limit this proliferation.

A large body of literature showed a link between landscape anthropization (i.e., urbanization, deforestation, and agricultural development) and both mosquito abundance and diversity. Overall, landscape anthropization leads to a general decline in mosquito diversity by reducing most mosquito abundance and favoring a few species adapted to human-modified landscapes that serve as vectors of human diseases (reviewed by Burkett-Cadena & Vittor, 2018; Perrin et al., 2022; Sallam et al., 2017). However, the ecological factors behind these landscape anthropization effects remain to be investigated.

One ecological process that deserves attention is the loss of mosquito predators and/or competitors in human-modified landscapes, which provide ideal habitats for mosquito breeding (Carver et al., 2015). Indeed, the larval stages of mosquitoes develop within a large panel of aquatic habitats, including human-made containers, tree holes, puddles, ponds, and wetlands. These habitats are discrete, and the limited food resources within them lead to many biotic interactions that impact the development of aquatic larvae (Mokany & Shine, 2003). These interactions can be negative when a species competes for resources and/or causes increased predation on mosquito larvae, but they can also be positive when a species consumes mosquito pathogens and/or reduces predation on mosquito larvae (Blaustein & Chase, 2007; Juliano, 2009). In this context, natural predators and competitors of mosquitoes are amphibians (Brodman & Dorton, 2006; DuRant & Hopkins, 2008), and several studies have already shown a negative effect of amphibian density on larval mosquito density (e.g., Brodman et al., 2003; Rubbo et al., 2011). At the same time, many studies reported strong impacts of landscape anthropization on amphibian community and composition, showing lower species richness and abundance in human-modified landscapes than

in natural environments (Cordier et al., 2021; Cushman, 2006; Hamer & McDonnell, 2008; Thompson et al., 2016; Thompson & Donnelly, 2018).

Here, we investigated the impacts of landscape anthropization on both amphibian abundance and larval mosquito communities. We considered the influence of several other biotic and abiotic parameters of ponds that are known to have significant impacts on mosquito abundance and/or community composition. We collected field data to characterize larval mosquito presence, abundance, and community composition as well as the presence and abundance of amphibians across 77 sampling sites in western Switzerland. Using path analyses, we then tested the direct and indirect effects through amphibian abundance of both landscape anthropization and local pond characteristics on larval mosquito communities. We hypothesized that because of a loss of amphibians, landscape anthropization modifies competition and/or predation pressures on mosquito species, resulting in a modification of larval mosquito community structure.

METHODS

Study area

The study was carried out in the canton of Vaud in several localities around the town of Lausanne in 2015. In this year, the canton of Vaud was the third most populous canton of Switzerland with 761,446 inhabitants (Demographic balance by canton—https://www.bfs.admin.ch/asset/fr/px-x-0102020000_101, accessed in January 2022). The population in this canton doubled between 1950 and 2015 (StatVD, 2018). This population growth conducted to an increase in expanding cities and artificial surfaces, as well as the increased use of chemical fertilizers and mechanization, which had negative impacts on biodiversity (Niwa et al., 2012). Now, more than half of the canton is covered by housing and infrastructure surfaces (10%), agricultural areas (42%), one-third by wooded areas (32%), and 16% by other unproductive surfaces (OFS, 2021).

Larval mosquito and amphibian collection

We selected 77 ponds along a gradient of landscape anthropization (Figure 1). Each pond was sampled every 15 days from mid-May to beginning of August, for a total of six samplings per pond. Small thin-wired dippers of 6×6 cm were used for sampling mosquito larvae and nets of 45×30 cm for amphibian larvae. A sampling consisted of five dipping moves in the middle range and at the side of ponds. During the five dipping moves, the dipper
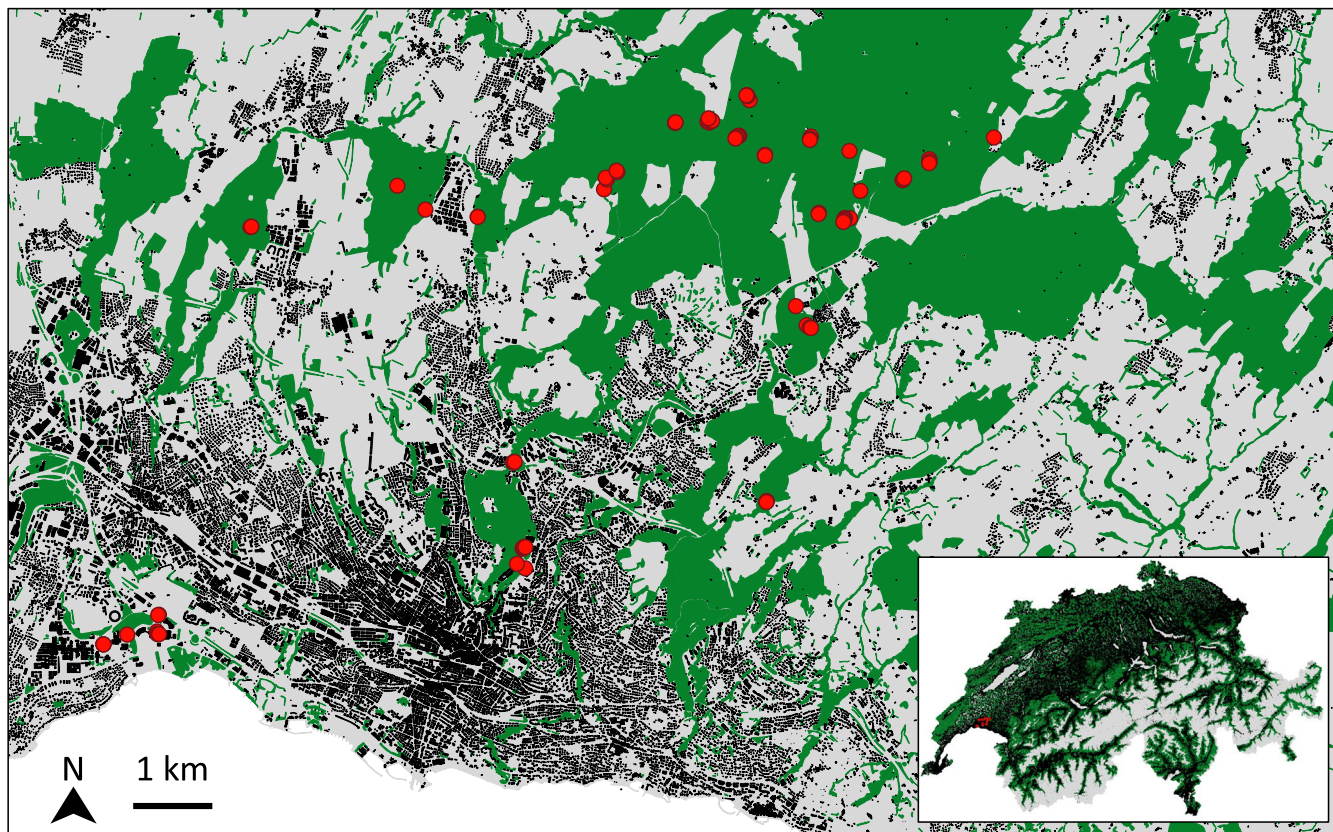
FIGURE 1 Map of the distribution of sampling ponds (red dots) in the canton of Vaud, Switzerland. The green, black, gray, and white colors represent the forest, building footprint, other surfaces, and undefined surfaces, according to the swissTLM3D geodata provided by the Federal Office of Topography swisstopo, respectively.

was placed at approximately 20 cm under the surface and quickly led upward to catch surface and middle-water mosquito larvae. For amphibian larvae, the net was placed at the bottom of the water column, at 2 m of the border, and on the sides of the pond to ensure a catch of bottom-dwelling amphibians. The number of samplings of each pond was directly correlated with the size of the pond following a standardized protocol provided by the IBEM pond diversity evaluation method (Appendix S1).

Mosquito larvae were placed in 20-mL Eppendorf tubes containing 70° alcohol and taken back to the lab for counting and identification. We identified mosquitoes at species level using Becker et al. (2010). All identified mosquito larvae were deposited in the collection of the Museum of Zoology in Lausanne, Switzerland. Identification of amphibian larvae at species level was made on the field, and all amphibians were released directly into the pond after the manipulation.

Landscape characteristics around pounds

To define the landscape anthropization level around each pond, we calculated the percent building cover (building footprint) and the percent of forest area within a 200-m-radius buffer surrounding ponds using the swissTLM3D geodata provided by the Federal Office of Topography swisstopo (https://www.swisstopo.admin.ch, accessed in January 2022). A 200-m-radius buffer was chosen because the bulk of the field sampling consisted of larvae of *Culex* sp., which have flight distances of around 400 m (Verdonschot & Besse-Lototskaya, 2014; Vinogradova, 2000). In addition, this buffer area allowed for sufficient landscape variability surrounding a pond and avoided huge overlap among buffers. The building footprint and the forest cover were defined with the *Gebaeude_Footprint* shapefile and the entities "Gebueschwald," "Wald," "Wald offen," and "Gehoelzflaeche" from the *Bodenbedeckung* shapefile, respectively. We used the 1.8 version of the geodata since the flight year of the aerial images used as a basis for these geodata corresponds to 2015.

The building footprint and the forest cover around ponds were highly correlated (Pearson's $r = -0.9$ and $p < 0.0001$), we therefore only considered the percent building footprint as a landscape anthropization gradient in further analyses (hereafter called building footprint).

Local pond parameters

To determine the effect of pond-local attributes on mosquito abundance and composition, we measured a series of environmental parameters for each pond. First, the amount of vegetation in mosquito larval habitats is considered an important factor for the presence and development of mosquito larvae. The vegetation cover can serve as shelter against predation (Chirebvu & Chimbari, 2015) and several species of mosquito larvae have a biological need for aquatic vegetations (i.e., several species use plant tissues instead of the air/water interface to obtain their oxygen; Russell, 1999). However, vegetation cover can also act as a barrier to spawning females, support a high diversity of predators, and reduce the amount of sunlight reaching the water surface, which negatively affects mosquito larvae growth (Muturi et al., 2008). We thus estimated the percentage of pond surface covered by plants (mainly composed of *Lemna* sp., *Nuphar* sp., and *Nymphea* sp.) once per month and took the mean percentage value for each pond (hereafter called pond surface covered).

The second important factor for the presence and the development of mosquito larvae is the hydroregime of ponds (i.e., permanent or temporary; Vanwambeke et al., 2007; Yazdi et al., 2017). Temporary ponds represent refuges for mosquitoes since mosquitoes have much more rapid population dynamics than predators, allowing them to escape control by these predators (Chase & Knight, 2003), even if the risk of drying out is high in very dry seasons. Ponds were classified as permanent or temporary (hereafter called hydroregime) based on the likelihood of drying out in summer considering depth and water supply of ponds.

Third, we recorded the age of ponds (hereafter called age) as not all ponds in this study were created in the same year (i.e., the year of creation varied between 1998 and 2014). Several studies already explored predation and competition pressures on mosquitoes from amphibians in laboratory conditions, mesocosms created during a few weeks or ponds without accounting for age (e.g., Brodman & Dorton, 2006; Mokany & Shine, 2003; Rubbo et al., 2011; Smith & Petranka, 1987), which can bring a valuable information for the management of wetlands, particularly if recent ponds have less species that can have predation or competition interactions with mosquitoes than older ponds.

Finally, we took into account the size of ponds, because it determines the community structure of mosquitoes and other aquatic insects, including predators (Sunahara et al., 2002). We thus recorded the maximum depth (in May) and the surface of each pond (hereafter called depth and surface, respectively).

Statistical analyses

We considered three response variables to characterize larval mosquito communities in ponds. First, we recorded the presence of larval mosquitoes in all ponds, and then, given that they were present, we counted the number of larvae and calculated the proportion of *Culex pipiens*. The proportion of *Cx. pipiens* is an important measure of the larval mosquito composition in ponds. Indeed, *Cx. pipiens* is associated with many important vector-borne pathogens for humans (e.g., equine encephalomyelitis virus, Sindbis virus, West Nile virus, Japanese encephalitis virus, Usutu virus, Rift Valley virus, or lymphatic filariasis; Becker et al., 2020; Wilkerson et al., 2021). This species can live in a large panel of habitats, from natural to anthropized areas, and feeds opportunistically from a wide variety of blood hosts (Becker et al., 2020; Gad et al., 1995; Wilkerson et al., 2021). Therefore, the identification of environmental factors that drive the relative abundance of *Cx. pipiens* is a first step to understand the global drivers of vector-borne disease dynamics.

The analyses were conducted on two different datasets, one including all sampling ponds (for the presence/absence of larval mosquitoes) and the other including only the sampling ponds containing larval mosquitoes (for the abundance of larval mosquitoes and the proportion of *Cx. pipiens*). We used generalized linear mixed models (GLMM) to identify environmental parameters contributing most to the variability in presence, abundance, and composition of larval mosquito communities in wetlands. The $\log(x + 1)$-transformed abundance of amphibians, pond surface covered, age, hydroregime, depth, surface, and building footprint were included as fixed factors. The sector of the pond was included as a random factor to consider the potential spatial autocorrelation as several ponds are sampled in the same area (see Appendix S1). We also used GLMM to test the effect of landscape characteristics and local pond parameters on the abundance of amphibians. In these models, pond surface covered, age, hydroregime, depth, surface, and building footprint were included as fixed factors, and the sector of the pond was included as a random factor. GLMM with Gaussian (on the log-transformed abundance of mosquito larvae, the log-transformed abundance of amphibians, and the proportion of *Cx. pipiens*) and binominal (on larval mosquito presence) distributed errors were implemented, respectively, with the lme and glmer functions of the R packages "nlme" and "lme4." We used variance inflation factors (VIFs) implemented with the vif function of the R package "car" to check the absence of collinearity among the explanatory variables. We did not find any collinearity with all VIFs < 5 (Zuur et al., 2009). The dredge function of the R package "MuMIn" (Bartoń, 2020) was used to identify

the best candidate model, based on the Akaike information criterion corrected for small sample sizes (AIC_c), among all possible combinations of explanatory variables.

We used structural equation models (SEMs) to test the hypothesis that mosquito abundance and composition are indirectly affected by environmental conditions through the presence and abundance of amphibians (Figure 2A). We developed path models based on the best models selected in the previous analysis. SEMs were fitted using the psem function implemented in the R package "PiecewiseSEM" (Lefcheck, 2016). Standardized path coefficients and Fisher's C statistic with their associated
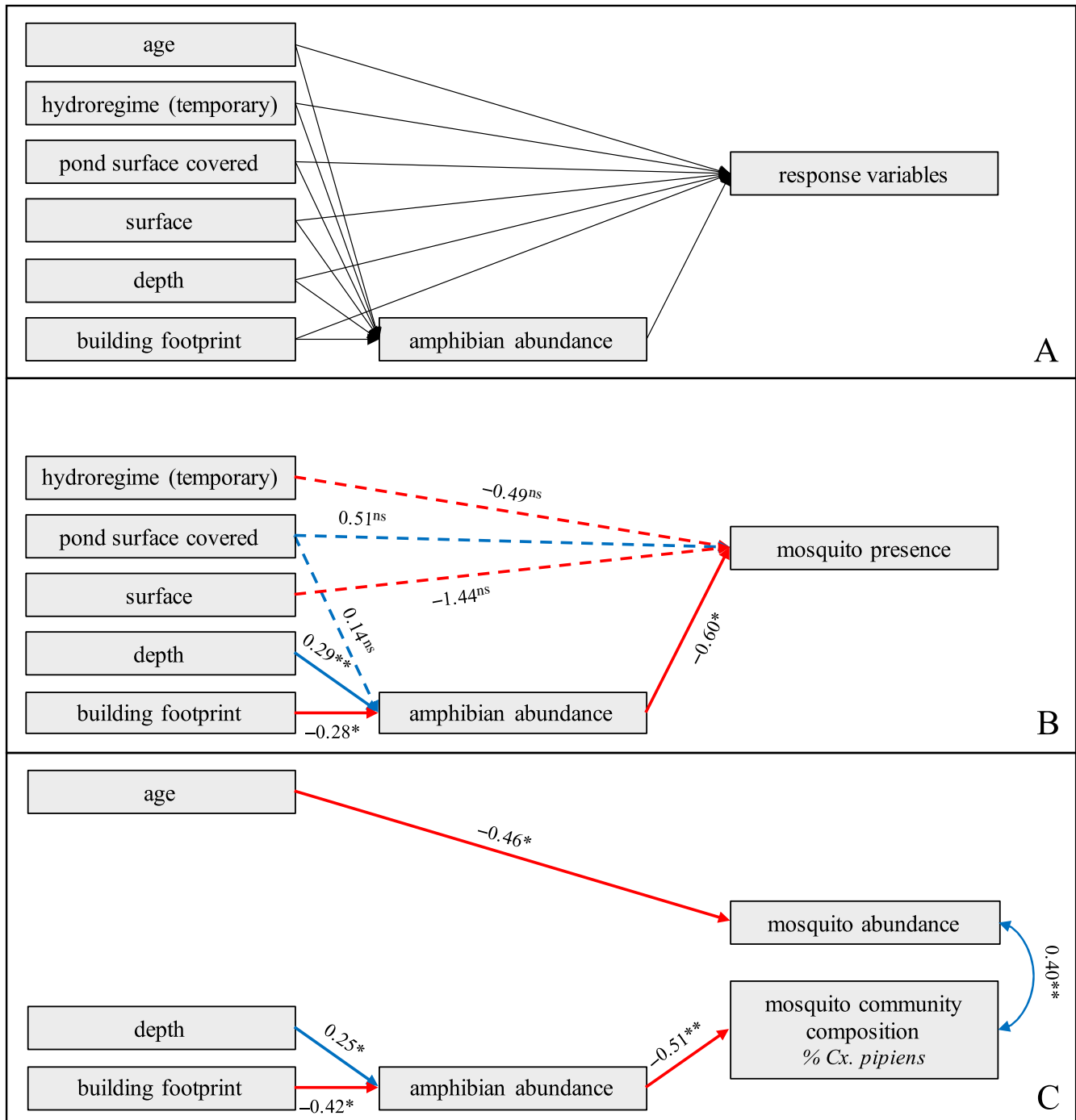
FIGURE 2 Conceptual structural equation models (A) as well as final path analyses for direct and indirect effects of environmental conditions on mosquito presence (B) and mosquito abundance and community composition (C). Blue and red arrows represent positive and negative relationships, respectively. Each path is labeled with its corresponding standardized coefficient. Solid and dashed arrows represent significant and nonsignificant relationships, respectively. ns, not significant; $*p \leq 0.05$; $**p \leq 0.01$.

p value were extracted. Fisher's C statistic tests the assumption that there was no missing path among the independent variables. We used the Shipley's test of directed separation to identify missing correlations. SEM was thus considered reliable (i.e., no missing links or explanatory variables) with the data when this test was not significant ($p > 0.05$).

RESULTS

Overall, 710 mosquito larvae belonging to 12 identified species were captured in 38 of the 77 sampling ponds (Table 1). *Culex hortensis* and *Cx. pipiens/torrentium* were the two most abundant species and correspond to 42% and 41% of all individuals, respectively. At the same time, we sampled 2044 amphibian larvae belonging to three species in 59 of the 77 sampling ponds (Table 1). Two species of

TABLE 1 Total number of mosquito and amphibian larvae per species captured in the 77 sampling ponds as well as number of positive ponds and mean abundance (SD) per positive pond for each species in the canton of Vaud in 2015.

Species	n	No. positive ponds	Mean abundance (SD) per positive pond
Mosquito larvae			
Aedes gr. cinereus	2	1	2 (−)
Anopheles claviger	20	10	2 (1)
Anopheles maculipennis	17	9	2 (2)
Anopheles sp.	2	2	1 (0)
Culex hortensis	301	9	33 (40)
Culex pipiens	294	14	21 (33)
Culex territans	39	13	3 (3)
Culiseta marsitans	4	1	4 (−)
Culiseta sp.	14	4	4 (2)
Ochlerotatus cantans	6	2	3 (3)
Ochlerotatus communis	1	1	1 (−)
Ochlerotatus flavescens	1	1	1 (−)
Ochlerotatus punctor	5	1	5 (−)
Ochlerotatus sp.	4	4	1 (0)
Total	710		
Amphibian larvae			
Bufo bufo	631	33	19 (17)
Ichthyosaura alpestris	355	41	9 (6)
Rana temporaria	1058	49	22 (14)
Total	2044		

Note: Positive ponds correspond to ponds that contain mosquito or amphibian larvae.

Anoura represented most of the sample (i.e., *Bufo bufo* and *Rana temporaria*; 83% of all individuals). Finally, the presence of both mosquito and amphibian larvae was recorded in 25 ponds.

Our piecewise SEM selection process yielded a final path model that represented the data well for mosquito presence (Fisher's $C = 5.21$, df = 8, and $p = 0.74$; Figure 2B) and for mosquito abundance and *Cx. pipiens* proportion (Fisher's $C = 15.10$, df = 14, and $p = 0.37$; Figure 2C). Hydroregime, pond surface covered, and surface are included in the final model for the presence of mosquito larvae, but the coefficients are not significant (Figure 2B). This suggests a nonsignificant trend whereby small temporary ponds with a low vegetation cover have a lower presence probability of mosquito larvae than large permanent ponds with a high vegetation cover. However, we found a significant negative effect of amphibian abundance on mosquito presence and *Cx. pipiens* proportion in the community, and we showed that amphibian larvae were more abundant in deep ponds and less anthropized areas (Figure 2C). This result suggests an indirect positive effect of landscape anthropization on mosquito communities (i.e., on the presence probability of mosquito larvae and on the proportion of *Cx. pipiens*) through a negative effect on amphibian abundance. We also found a positive correlation between the proportion of *Cx. pipiens* and the abundance of mosquito larvae in ponds (Figure 2C). Finally, our SEM analysis showed that the older the pond, the lower the abundance of mosquito larvae (Figure 2C).

DISCUSSION

Our results were in line with the large body of works showing worldwide negative effects of landscape anthropization on amphibian abundance and diversity (Cordier et al., 2021; Cushman, 2006; Hamer & McDonnell, 2008; Thompson et al., 2016; Thompson & Donnelly, 2018). In addition to a detrimental impact of landscape anthropization on the presence of European tree frog (*Hyla arborea*) calling males (Pellet, Guisan, & Perrin, 2004; Pellet, Hoehn, & Perrin, 2004), our findings indicate a negative effect on larval abundance of amphibians within ponds in western Switzerland.

Interestingly, our results showed that the reduction of amphibian abundance is responsible for an increase in the presence probability of larval mosquitoes in ponds. This is consistent with other studies that found reduced numbers of larval mosquitoes in ponds containing larval amphibians (Brodman et al., 2003; Rubbo et al., 2011). First, this negative link between amphibian and mosquito abundance could be explained by a significant

predation pressure exerted by amphibians, as already highlighted by many studies (e.g., Blaustein et al., 2014; Brodman & Dorton, 2006; DuRant & Hopkins, 2008). For instance, Watters et al. (2018) have shown that amphibian larvae were able to consume as many mosquito larvae as mosquitofish (*Gambusia* sp.), which are well-known predators used for mosquito biocontrol (Pyke, 2008). Second, numerous studies revealed a presence of both interference and exploitation competition between mosquito and amphibian larvae (e.g., Blaustein & Margalit, 1994, 1996; Mokany & Shine, 2002, 2003; Stav et al., 2010). If amphibian larvae are more competitive than mosquito larvae (e.g., for resource exploitation), this could explain the negative link between the abundance of mosquito and amphibian larvae. However, additional laboratory work must be conducted to validate this hypothesis. Third, this result could be linked to a choice of adult mosquitoes for an optimal egg-laying site (Rubbo et al., 2011). Although some studies have noted that oviposition avoidance is weak in response to amphibian presence (Blaustein et al., 2014; Vonesh & Blaustein, 2010), mosquitoes use chemical and biological cues to detect the presence of larval predators and/or competitors to avoid ovipositing in an unfavorable environment for their larvae (Blaustein et al., 2004; Herrera-Varela et al., 2014; Munga et al., 2006; Vonesh & Blaustein, 2010).

Moreover, the reduction of amphibian abundance is also responsible for mosquito community changes. We found a decrease in *Cx. pipiens* relative abundance in response to the increased amphibian abundance in ponds found in less anthropized areas. Our results were in line with studies that showed an increase of *Cx. pipiens* abundance in response to landscape anthropization (e.g., Deichmeister & Telang, 2011; González et al., 2020; Mayi et al., 2020; Reiskind et al., 2017; Trawinski & Mackay, 2010; Yazdi et al., 2017). Our results suggest that amphibians could be a factor regulating the abundance of *Cx. pipiens*, limiting its abundance in natural environments. Although no work to our knowledge has already demonstrated an amphibian feeding choice towards *Cx. pipiens* larvae, predation could only be linked to the relative abundance of the different species. Amphibian larvae would consume relatively more *Cx. pipiens* larvae in ponds where they are overrepresented, with a stabilizing effect on the diversity of the mosquito community. The absence or low presence of amphibians in anthropized environments could then explain the increase in *Cx. pipiens* in the community. However, at this stage, we cannot completely exclude a higher survival of *Cx. pipiens*, compared to other mosquito species, in small, temporary, and polluted ponds where amphibians are absent, explaining the negative link between amphibian abundance and *Cx. pipiens* proportion in the community.

In addition to landscape composition around sampling sites, our results suggest that some local characteristics of ponds influence mosquito community composition. First, we found that the first years following a pond creation is particularly productive for mosquito larvae. It could be due to the rapid colonization of newly constructed wetlands by mosquitoes (Schäfer, 2004) compared to their competitors and predators. Mosquitoes are opportunist aerial colonizers that can colonize a pond within a few days after its creation, while it can take several years for their predators (Batzer & Wissinger, 1996; Chase & Knight, 2003). Second, we found that water depth of ponds favors the abundance of amphibians and thus negatively impacts mosquito abundance. This result is not surprising considering the positive link already shown between amphibian reproductive effort and water depth (DiMauro & Hunter, 2002). Rubbo et al. (2011) also suggest that deeper ponds can have longer hydroperiods and that common amphibians, such as *R. temporaria* or *B. bufo*, breed preferentially in ponds with longer hydroperiods. Our results therefore suggest that the creation of deep ponds and the protection of older ponds both maximize amphibian abundance and limit mosquito-related nuisances in urban areas.

Although our study is a first step toward establishing a causal link between amphibians and mosquitoes in human-modified landscapes, future studies should test experimentally the real effect of competition and predation of amphibians on mosquito larvae. Studies have already shown that amphibian larvae were able to predate mosquito larvae (e.g., Blaustein et al., 2014; Brodman & Dorton, 2006; DuRant & Hopkins, 2008), led female mosquitoes to lay fewer eggs and was responsible for a lower survival of mosquito larvae when they are in a pond (Rubbo et al., 2011). However, we do not know which mosquito species and how many are consumed by amphibians in the 77 ponds of our study. This information could help identify which amphibian species is the most important and interesting from a management perspective in mosquito control and will confirm experimentally the causal pattern highlighted in this study between amphibians and mosquitoes in their natural habitats.

MANAGEMENT IMPLICATIONS

Our results, conducted at different times, with different predictors and response variables, showed a constant negative effect of landscape anthropization on amphibian communities, which adds to the lack of breeding ponds in western Switzerland (Pellet et al., 2002; Pellet & Neet, 2001). The underlying causes of these declines of amphibians in human-modified landscapes have long been identified and include the low vagilities and high vulnerability of

these species when they moved between seasonal habitats through inhospitable terrain, as well as their high vulnerability to pathogen, invasive species, and environmental pollution (reviewed by Cushman, 2006).

Although many wetlands have been destroyed in an attempt to reduce the habitat of mosquito larvae and therefore the associated disease risk, this destruction has been shown to lead to the isolation of ponds, which affects predators more negatively than mosquitoes (Chase & Shulman, 2009). This study highlights an alternative option to the destruction of wetlands; maintaining amphibian populations in human-modified landscapes might limit the presence and abundance of mosquito species of human concern. In addition, deep and old ponds that maintain a high abundance of amphibians could also be factors to consider in management plans to limit mosquito-related nuisances. Considering the widespread decline in amphibians these last decades, our study shows that their protection is essential since these species could act as biological control agents against mosquitoes and therefore be involved in ecological processes with important implications for human health.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT
Data and the R script (Perrin et al., 2023) used in the analysis are available from Mendeley: https://doi.org/10.17632/dfzfgytx5p.1.

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REFERENCES
Bartoń, K. 2020. "MuMIn: Multi-Model Inference." https://CRAN.R-project.org/package=MuMIn.

Batzer, D. P., and S. A. Wissinger. 1996. "Ecology of Insect Communities in Nontidal Wetlands." *Annual Review of Entomology* 41: 75–100.

Becker, N., D. Petrić, M. Zgomba, C. Boase, C. Madon, C. Dahl, and A. Kaiser. 2010. *Mosquitoes and Their Control*, 2nd ed. Heidelberg: Springer Berlin.

Becker, N., D. Petrić, M. Zgomba, C. Boase, M. B. Madon, C. Dahl, and A. Kaiser. 2020. *Mosquitoes: Identification, Ecology and Control*, 3rd ed. Cham: Springer.

Blaustein, J., A. Sadeh, and L. Blaustein. 2014. "Influence of Fire Salamander Larvae on Among-Pool Distribution of Mosquito Egg Rafts: Oviposition Habitat Selection or Egg Raft Predation?" *Hydrobiologia* 723: 157–65.

Blaustein, L., and J. M. Chase. 2007. "Interactions between Mosquito Larvae and Species That Share the Same Trophic Level." *Annual Review of Entomology* 52: 489–507.

Blaustein, L., M. Kiflawi, A. Eitam, M. Mangel, and J. E. Cohen. 2004. "Oviposition Habitat Selection in Response to Risk of Predation in Temporary Pools: Mode of Detection and Consistency across Experimental Venue." *Oecologia* 138: 300–5.

Blaustein, L., and J. Margalit. 1994. "Mosquito Larvae (*Culiseta longiareolata*) Prey upon and Compete with Toad Tadpoles (*Bufo viridis*)." *Journal of Animal Ecology* 63: 841–50.

Blaustein, L., and J. Margalit. 1996. "Priority Effects in Temporary Pools: Nature and Outcome of Mosquito Larva-Toad Tadpole Interactions Depend on Order of Entrance." *Journal of Animal Ecology* 65: 77–84.

Brodman, R., and R. Dorton. 2006. "The Effectiveness of Pond-Breeding Salamanders as Agents of Larval Mosquito Control." *Journal of Freshwater Ecology* 21: 467–74.

Brodman, R., J. Ogger, M. Kolaczyk, and R. A. Pulver. 2003. "Mosquito Control by Pond-Breeding Salamander Larvae." *Herpetological Review* 34: 116–9.

Burkett-Cadena, N. D., and A. Y. Vittor. 2018. "Deforestation and Vector-Borne Disease: Forest Conversion Favors Important Mosquito Vectors of Human Pathogens." *Basic and Applied Ecology* 26: 101–10.

Carver, S., D. P. Slaney, P. T. Leisnham, and P. Weinstein. 2015. "Healthy Wetlands, Healthy People: Mosquito Borne Disease." In *Wetlands and Human Health*, edited by C. M. Finlayson, P. Horwitz, and P. Weinstein, 95–121. Dordrecht: Springer Netherlands.

Chase, J. M., and T. M. Knight. 2003. "Drought-Induced Mosquito Outbreaks in Wetlands." *Ecology Letters* 6: 1017–24.

Chase, J. M., and R. S. Shulman. 2009. "Wetland Isolation Facilitates Larval Mosquito Density through the Reduction of Predators." *Ecological Entomology* 34: 741–7.

Chirebvu, E., and M. J. Chimbari. 2015. "Characteristics of *Anopheles arabiensis* Larval Habitats in Tubu Village, Botswana." *Journal of Vector Ecology* 40: 129–38.

Cordier, J. M., R. Aguilar, J. N. Lescano, G. C. Leynaud, A. Bonino, D. Miloch, R. Loyola, and J. Nori. 2021. "A Global Assessment of Amphibian and Reptile Responses to Land-Use Changes." *Biological Conservation* 253: 108863.

Cushman, S. A. 2006. "Effects of Habitat Loss and Fragmentation on Amphibians: A Review and Prospectus." *Biological Conservation* 128: 231–40.

Deichmeister, J. M., and A. Telang. 2011. "Abundance of West Nile Virus Mosquito Vectors in Relation to Climate and Landscape Variables." *Journal of Vector Ecology* 36: 75–85.

DiMauro, D., and M. L. Hunter, Jr. 2002. "Reproduction of Amphibians in Natural and Anthropogenic Temporary Pools in Managed Forests." *Forest Science* 48: 397–406.

DuRant, S. E., and W. A. Hopkins. 2008. "Amphibian Predation on Larval Mosquitoes." *Canadian Journal of Zoology* 86: 1159–64.

Gad, A. M., I. B. Riad, and H. A. Farid. 1995. "Host-Feeding Patterns of *Culex pipiens* and *Cx. antennatus* (Diptera: Culicidae) from a Village in Sharqiya Governorate, Egypt." *Journal of Medical Entomology* 32: 573–7.

Gardner, C. L., and K. D. Ryman. 2010. "Yellow Fever: A Reemerging Threat." *Clinics in Laboratory Medicine* 30: 237–60.

González, M. A., S. W. Prosser, L. M. Hernández-Triana, P. M. Alarcón-Elbal, F. Goiri, S. López, I. Ruiz-Arrondo, P. D. N. Hebert, and A. L. García-Pérez. 2020. "Avian Feeding Preferences of *Culex pipiens* and *Culiseta* spp. Along an Urban-to-Wild Gradient in Northern Spain." *Frontiers in Ecology and Evolution* 8: 568835.

Hamer, A. J., and M. J. McDonnell. 2008. "Amphibian Ecology and Conservation in the Urbanising World: A Review." *Biological Conservation* 141: 2432–49.

Herrera-Varela, M., J. Lindh, S. W. Lindsay, and U. Fillinger. 2014. "Habitat Discrimination by Gravid *Anopheles gambiae* Sensu Lato – A Push-Pull System." *Malaria Journal* 13: 133.

Juliano, S. A. 2009. "Species Interactions among Larval Mosquitoes: Context Dependence across Habitat Gradients." *Annual Review of Entomology* 54: 37–56.

Lee, H., S. Halverson, and N. Ezinwa. 2018. "Mosquito-Borne Diseases." *Primary Care: Clinics in Office Practice* 45: 393–407.

Lefcheck, J. S. 2016. "piecewiseSEM: Piecewise Structural Equation Modelling in r for Ecology, Evolution, and Systematics." *Methods in Ecology and Evolution* 7: 573–9.

Mayi, M. P. A., R. Bamou, B. Djiappi-Tchamen, A. Fontaine, C. L. Jeffries, T. Walker, C. Antonio-Nkondjio, A. J. Cornel, and T. Tchuinkam. 2020. "Habitat and Seasonality Affect Mosquito Community Composition in the West Region of Cameroon." *Insects* 11: 312.

Mokany, A., and R. Shine. 2002. "Pond Attributes Influence Competitive Interactions between Tadpoles and Mosquito Larvae." *Austral Ecology* 27: 396–404.

Mokany, A., and R. Shine. 2003. "Competition between Tadpoles and Mosquito Larvae." *Oecologia* 135: 615–20.

Munga, S., N. Minakawa, G. Zhou, O.-O. J. Barrack, A. K. Githeko, and G. Yan. 2006. "Effects of Larval Competitors and Predators on Oviposition Site Selection of *Anopheles gambiae* Sensu Stricto." *Journal of Medical Entomology* 43: 221–4.

Muturi, E. J., J. Mwangangi, J. Shililu, B. G. Jacob, C. Mbogo, J. Githure, and R. J. Novak. 2008. "Environmental Factors Associated with the Distribution of *Anopheles arabiensis* and *Culex quinquefasciatus* in a Rice Agro-Ecosystem in Mwea, Kenya." *Journal of Vector Ecology* 33: 56–63.

Niwa, N., D. Bourdin, and J. Mastrullo. 2012. "Which Agriculture Do you Want? Catalog of the Virtual Exhibition." http://www.vaud2030.ch.

OFS. 2021. "L'utilisation du sol en Suisse – 1985-2018." https://www.bfs.admin.ch/bfs/fr/home/statistiques/catalogues-banques-donnees/graphiques.assetdetail.19964677.html.

Pellet, J., S. Dubey, and S. Hoehn. 2002. "Les amphibiens du bassin de l'Aubonne: distribution et analyse d'habitat." *Bulletin de la Société vaudoise des Sciences Naturelles* 88: 41–57.

Pellet, J., A. Guisan, and N. Perrin. 2004. "A Concentric Analysis of the Impact of Urbanization on the Threatened European Tree Frog in an Agricultural Landscape." *Conservation Biology* 18: 1599–606.

Pellet, J., S. Hoehn, and N. Perrin. 2004. "Multiscale Determinants of Tree Frog (*Hyla arborea* L.) Calling Ponds in Western Switzerland." *Biodiversity and Conservation* 13: 2227–35.

Pellet, J., and C. Neet. 2001. "La Rainette verte (*Hyla arborea*; Anura) dans le canton de Vaud: un état des lieux." *Bulletin de la Société vaudoise des Sciences Naturelles* 87: 287–303.

Perrin, A., O. Glaizot, and P. Christe. 2022. "Worldwide Impacts of Landscape Anthropization on Mosquito Abundance and Diversity: A Meta-Analysis." *Global Change Biology* 28: 6857–71.

Perrin, A., J. Pellet, L. Bergonzoli, P. Christe, and O. Glaizot. 2023. "Data from: Amphibian Abundance Is Associated with Reduced Mosquito Presence in Human-Modified Landscapes." V1. Mendeley Data. https://doi.org/10.17632/dfzfgytx5p.1.

Pyke, G. H. 2008. "Plague Minnow or Mosquito Fish? A Review of the Biology and Impacts of Introduced *Gambusia* Species." *Annual Review of Ecology, Evolution, and Systematics* 39: 171–91.

Reiskind, M. H., R. H. Griffin, M. S. Janairo, and K. A. Hopperstad. 2017. "Mosquitoes of Field and Forest: The Scale of Habitat Segregation in a Diverse Mosquito Assemblage." *Medical and Veterinary Entomology* 31: 44–54.

Rubbo, M. J., J. L. Lanterman, R. C. Falco, and T. J. Daniels. 2011. "The Influence of Amphibians on Mosquitoes in Seasonal Pools: Can Wetlands Protection Help to Minimize Disease Risk?" *Wetlands* 31: 799–804.

Russell, R. C. 1999. "Constructed Wetlands and Mosquitoes: Health Hazards and Management Options—An Australian Perspective." *Ecological Engineering* 12: 107–24.

Sallam, M., C. Fizer, A. Pilant, and P.-Y. Whung. 2017. "Systematic Review: Land Cover, Meteorological, and Socioeconomic Determinants of *Aedes* Mosquito Habitat for Risk Mapping." *International Journal of Environmental Research and Public Health* 14: 1230.

Schäfer, M. 2004. "Mosquitoes as a Part of Wetland Biodiversity." Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology, Uppsala.

Smith, C. K., and J. W. Petranka. 1987. "Prey Size-Distributions and Size-Specific Foraging Success of *Ambystoma* Larvae." *Oecologia* 71: 239–44.

StatVD. 2018. "Population résidante permanente par origine, Vaud, 1950–2016." https://www.pisepub.vd.ch/PisePub/asp/Main.aspx.

Stav, G., B. P. Kotler, and L. Blaustein. 2010. "Foraging Response to Risks of Predation and Competition in Artificial Pools." *Israel Journal of Ecology & Evolution* 56: 9–20.

Sunahara, T., K. Ishizaka, and M. Mogi. 2002. "Habitat Size: A Factor Determining the Opportunity for Encounters between Mosquito Larvae and Aquatic Predators." *Journal of Vector Ecology* 27: 8–20.

Thompson, M. E., and M. A. Donnelly. 2018. "Effects of Secondary Forest Succession on Amphibians and Reptiles: A Review and Meta-Analysis." *Copeia* 106: 10–9.

Thompson, M. E., A. J. Nowakowski, and M. A. Donnelly. 2016. "The Importance of Defining Focal Assemblages When Evaluating Amphibian and Reptile Responses to Land Use." *Conservation Biology* 30: 249–58.

Trawinski, P. R., and D. S. Mackay. 2010. "Identification of Environmental Covariates of West Nile Virus Vector Mosquito Population Abundance." *Vector-Borne and Zoonotic Diseases* 10: 515–26.

Vanwambeke, S. O., P. Somboon, R. E. Harbach, M. Isenstadt, E. F. Lambin, C. Walton, and R. K. Butlin. 2007. "Landscape and Land Cover Factors Influence the Presence of *Aedes* and *Anopheles* Larvae." *Journal of Medical Entomology* 44: 133–44.

Verdonschot, P. F. M., and A. A. Besse-Lototskaya. 2014. "Flight Distance of Mosquitoes (Culicidae): A Metadata Analysis to Support the Management of Barrier Zones around Rewetted and Newly Constructed Wetlands." *Limnologica* 45: 69–79.

Vinogradova, E. B. 2000. *Culex pipiens pipiens Mosquitoes: Taxonomy, Distribution, Ecology, Physiology, Genetics, Applied Importance and Control.* Sofia: Pensoft Publishers.

Vonesh, J. R., and L. Blaustein. 2010. "Predator-Induced Shifts in Mosquito Oviposition Site Selection: A Meta-Analysis and Implications for Vector Control." *Israel Journal of Ecology and Evolution* 56: 263–79.

Watters, A. M., F. E. Rowland, and R. D. Semlitsch. 2018. "Larval Salamanders Are as Effective at Short-Term Mosquito Predation as Mosquitofish." *Canadian Journal of Zoology* 96: 1165–9.

WHO. 2014. *Vector-Borne Diseases.* New Delhi: WHO Regional Office for South-East Asia.

WHO. 2020. *Ethics and Vector-Borne Diseases: WHO Guidance.* Geneva: World Health Organization.

Wilkerson, R. C., Y.-M. Linton, and D. Strickman. 2021. *Mosquitoes of the World.* Baltimore, MD: JHU Press.

Yazdi, F., S. H. Nikookar, M. Fazeli-Dinan, S. A. Hosseini, M. Yazdi, S. P. Ziapour, and A. Enayati. 2017. "Diversity and Species Composition of Mosquitoes (Culicidae: Diptera) in Noor County, Northern Iran." *Tropical Biomedicine* 34: 14–21.

Zheng, X., D. Zhang, Y. Li, C. Yang, Y. Wu, X. Liang, Y. Liang, et al. 2019. "Incompatible and Sterile Insect Techniques Combined Eliminate Mosquitoes." *Nature* 572: 56–61.

Zuur, A. F., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed Effects Models and Extensions in Ecology with R.* New York: Springer New York.

SUPPORTING INFORMATION

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

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