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Amphibian occupancy and abundance in beaver ponds in Switzerland

Master thesis in Biology

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Abstract

As ecosystem engineers, beavers are capable of creating heterogeneous environments that have a positive impact on many species. They increase habitat availability that can be colonised by species (endangered or not) and reduce fragmentation. Amphibians, one of the most threatened groups of vertebrates, are part of the species that could use and colonise the beaver ponds. The aim of this study is to analyse the occupancy and abundance of amphibians in beaver ponds in Switzerland. This analysis addressed the following questions: 1) What is amphibian abundance and occupancy at beaver ponds, 2) Does *Rana temporaria* use beaver ponds as ovipositional sites, 3) What are the factors (e.g., dam age) that drive amphibian occupancy and abundance in beaver ponds, and 4) if beaver ponds increase connectivity. Results of the occupancy analysis revealed that there were some preferences for the type of beaver pond occupied, most of them being flooded forests. Then, results from both abundance and occupancy showed that the strongest predictor that always came up was the dam age. Indicating that the older the dam is, the better, with more individuals in middle aged dams. Results from the connectivity revealed that beaver ponds had higher diversity if there were at least two amphibian breeding ponds nearby (less than one kilometre). Meaning that beavers could extend the already existing amphibian network by creating new ponds. Consequently, they have a good potential for conservation goals by maintaining stable and increasing amphibian populations.

Keywords: Amphibians, Beaver ponds, occupancy, abundance, dam age, conservation

1.Introduction

1.1 Beavers as ecosystem engineers

Beavers are ecosystem engineers because they are able to modify environments in order to meet their own ecological needs. They convert the habitat by burrowing, cutting trees and building dams that can reduce the flow of water and create impoundments (Puttock et al., 2017; Rosell et al., 2005). Through these changes, beavers conceive a series of ponds, wetland patches varying in successional stage that inundate floodplains. Ponds can have emergent vegetation thanks to opening the canopy of riparian forests giving more sunlight. They also form deadwood habitats that can serve as refuges for different species. Additionally, they build canals, tunnels or ways that connect their territories and so enhance connectivity between the ponds (Brazier et al., 2021). Through all these modifications, they are able to generate whole new landscapes changing biotic properties and increase the structural heterogeneity of habitats (Brazier et al., 2021; Dalbeck et al., 2014; Rosell et al., 2005; Sommer et al., 2018; Vehkaoja & Nummi, 2015). A higher heterogeneity can provide more local richness (Gutiérrez, 2017). After the almost total disappearance of beavers in Europe (with only a few small populations of 1300 individuals left), multiple reintroduction plans were successfully carried out in different countries. In Switzerland, around the end of the 19th century, a national reintroduction programme resulted in the release of 141 individuals between 1956 and 1978 in the Rhine and the Rhone watersheds. Since then, the populations and territories have not ended to expand, making the wetland habitats come back, but also raising conflicts with humans. With the habitat modifications mentioned before, there lies a big potential in beaver activities by the benefits they can bring, increasing the ecological infrastructure in Switzerland for multiple species (Angst, 2014; Angst et al., 2023; Minnig et al., 2016).

Several species can benefit from the beaver ponds but in this study, we will focus mostly on amphibian populations, because it is still not completely clear to what extent they can benefit from beaver ponds. The study of the occurrence of amphibians in beaver ponds created by their dam impoundment is an under-researched area in Europe. There are a few studies that have been done, but not stating all the characteristics of the environment that could make them attractive for amphibians. The other species, the North American beaver (*Castor canadensis*) in North America has been studied a little more with interesting results (Dalbeck et al., 2014, 2020). However, the few studies made in Europe revealed that beavers are able to create conditions that favour many amphibian species to breed, by conceiving warm, shallow water, rich emergent vegetation and large amounts of woody debris (Vehkaoja & Nummi, 2015). Another study from (Romansic et al., 2021) also showed that multiple pond-breeding amphibians have a positive correlation with beaver habitats at a patch scale. There are studies from temperate Europe that have shown a general increase of richness for both anuran and urodele species in beaver habitats, mostly the common frog *Rana temporaria* (Dalbeck et al., 2014).

1.2 The situation of amphibians in the world and in Europe

Amphibians are the group of vertebrates that is considered the most threatened in the world from the IUCN red lists (International Union for Conservation of Nature's Red List of Threatened Species) having 41% of threatened species (IUCN,2024). The principal causes of this decline are: habitat destruction, as the main factor specially for breeding ponds, pollution, introduction of exotic and invasive species, diseases, climate change, and overexploitation. These causes can have cofactors that interact between them (Blaustein et al., 2011). In Europe, nearly a quarter of amphibian species (23%) is threatened with extinction, mostly reducing them through the threats on their habitats (freshwater) reducing or destroying them, additionally climate change and other threats are placing them under severe stress, mainly in the south of Europe (Temple & Cox, 2009).

Situation in Switzerland

The new recent red list of 2023 (Schmidt et al., 2023) revealed that from the 19 evaluated indigenous amphibian species, 15 species figured on the Red List (79%) instead of 14 as in 2005 and four species were no longer threatened following the IUCN criteria. Since 2005 the situation has slightly improved, even if there still is a deterioration, it is less than it was before, since the conservation efforts with multiple protection measures have helped to reduce this decline (Moor et al., 2022). These efforts have to be maintained though and even strengthened in order to increase the low number of populations.

Causes of population decline stayed the same, mostly because of reduction in the quality and quantity of adequate habitats due to human alteration. Modifications on their aquatic or terrestrial habitat can affect amphibians very negatively. A big threat that occurs more and more is drought, mainly the one that affects the forests, one of the most important habitats for them. A second very important habitat is the aquatic habitat, i.e. temporary or flooded bodies of water (Schmidt et al., 2015).

Before humans made modifications on a lot of water bodies and before the beaver (*Castor fiber*) disappeared from Europe, there were a lot more wetlands; reducing these habitats had a very negative influence on many species (Vehkaoja & Nummi, 2015). Beavers can alter vegetation and hydrology and could have some important impacts on other wetland, aquatic or riparian dependent species (Skelly & Freidenburg, 2000; Smith & Goldberg, 2022). The use of ecosystem engineer species has, since recently, gained more attention in order to restore ecosystems like wetlands (Vehkaoja & Nummi, 2015). From here a question came up whether beavers constructing dams with lentic water/ponds could help amphibians by reducing the threats when creating new freshwater habitats for them.

Additionally, amphibians, apart from being good bioindicators, are also good indicators of the impact beavers could have on the landscape, since their appearance depends on the availability of both water and suitable habitat (Dalbeck et al., 2007, 2020; Figueiredo et al., 2019).

The aim of this study will be the evaluation of the benefits that beaver impoundments/ponds can bring with their dam constructions to the Swiss amphibian population in a total of 33 sites. The specific addressed questions are:

1. What is amphibian abundance and occupancy at beaver ponds?
2. Does *Rana temporaria* use the beaver ponds as ovipositional sites?
3. Which factors, such as dam age, determine spatial variation in abundance and occupancy?
4. Could beaver ponds lead to a denser amphibian network enhancing the connectivity?

It was not known in advance which species would be found, just an assumption based on previous studies made on other beaver sites, making it interesting to know what the diversity of species is. Nevertheless, each species has some habitat preferences, thus it is predicted to see more forest type or ubiquitous species and less open country species that prefer more human modified habitats (e.g. gravel quarry with scarce vegetation) (Dalbeck et al., 2020). More details about these preferences will be explained in the discussion.

By answering these questions, beavers could become very important for managements and conservation actions to maintain hydroperiods and, through this, issue many benefits for the amphibians as they depend a lot on water to survive and, as such, prevent more populations decline (Ceballos et al., 2015 in Romansic et al., 2021).

2.Material and methods

2.1 Site selection

The selection of the sites (i.e., beaver territories) was made using QGIS (Quantum Geographic Information System) and the data provided by the database from Info Fauna (Biberfachstelle and Karch). These data included the beaver dams; their location, the year since they were present (age), the beaver territories; the year since the beaver territory was established at the site, the start (upstream), the middle and the end of the territory (downstream) and finally, the amphibian reproduction sites (including the species observations and the year).

To be selected the sites had to fulfil the following criteria:

a) there had to be at least one functional beaver dam with a pond or flooded area

b) beaver dams had to be of different ages (i.e. according to the time since the site was colonised by beavers, from different years, young and old ones).

c) an amphibian reproduction site (data from Karch) needed to be nearby (at a distance of no further than 1 km).

For the first criteria, a visit at daytime was made at the initially selected sites to confirm that there still was an intact beaver dam present with a pond or flooded area, equivalent to a beaver pond with not too much river flow behind the dam. Thirty-three sites met all three criteria and were elected. In this selection there were twenty-two sites with dams older than five years and eleven sites with dams aged from one to four years old. In some cases, sites contained both mature dams (>5 years) and young ones (< 4 years) in the same beaver territory.

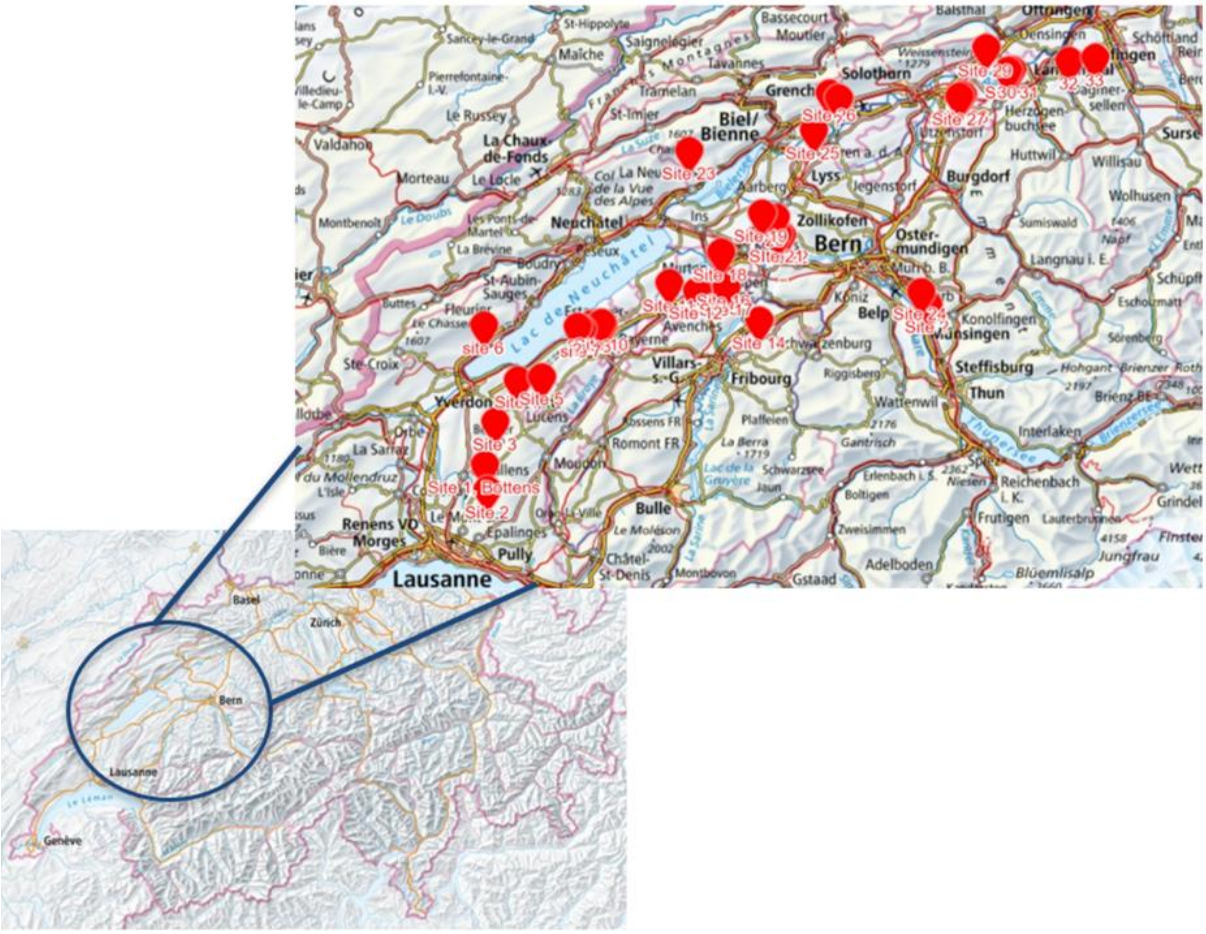


Figure 1: Map of Switzerland with the selected 33 sites, source: map.geo.admin.ch

2.2 Fieldwork and data collection

All the fieldwork was done between February and June 2023. A total of five visits, two by day and three by night, were made at each site. The first two visits meant to look for egg masses principally of the species *Rana temporaria*, because it is the only suitable species to ensure reliable counts of egg masses (Dalbeck et al., 2014). As the reproduction period and egg-laying of this species is between early or mid-February until end of March/April (depending on the temperature) the sampling was made during this period. If there was a low number, the egg mass count was made directly by eye and if there was a high amount, it followed the approximation of Griffiths & Raper (1994) setting that per 1x1 m there was an amount of 100 egg masses. If there were eggs of other species, it would be written down as well.

Figure 2: Example image of common frog egg masses, counting the total number of egg masses like the circled one seen here. Source: ©P.Bolle

Each site was variable in size or in the type of pond (forested pond, canal pond, small or big pond etc, more precise information of the beaver ponds can be found in the appendix).

Thus, in each of them, if possible, the whole border flooded area/still water or "pond", created by the beaver dam, was checked once, in the first two visits for the egg mass count and then, by night, for the three other visits to carry out the species census. The aim of the visits by night was to look for and count the amphibian species present. This was done to assess and measure the amphibian abundance and diversity of each site, permitting to know the occupancy as well. For the night visits one single torch and a frontal light were used allowing to walk in the dark and facilitate the recognition of the species (recognising the reflections of the eyes or just a silhouette). If needed an amphibian guide was used to identify the species (mostly newts and juveniles). No nets or traps were needed to capture the individuals, only rarely, in case of doubt, the frog or newt was caught by hand to confirm the species, disinfecting the hands after the manipulation. Moreover, calls of the anurans were also used to know which species were present, even if not seen directly. If possible, a count of the number of calling individuals was made (this was done mostly for the species *Pelophylax* sp.*, Rana temporaria* and *Bufo bufo)*. At the edges where it was not too deep, close by aquatic vegetation and at the bottom of the ponds, newts could be found (for example, the alpine newt (*Ichthyosaura alpestris*) and the palmate newt (*Lissotriton helveticus*)). For each visit, I recorded the time spent at each site for the fieldwork. In case the temperature was too low, below four-five degrees and no amphibian activity was detected, the night visit was postponed for another day with better conditions.

In some cases, as for a small river, first one side was checked and then on the way back the other side, always looking upstream and downstream of the dam since the amphibians could be spread all over, sometimes even on the dam itself or just behind; before moving to the next one (if there was more than one dam close by). For some sites only part of it could be used for sampling because it was not possible to go around the whole area due to access difficulty (trees, brambles, holes, etc). For some others waders had to be used to walk around in the river or in wetlands, avoiding too deep areas. After each site, waders were disinfected before going to another site. It was done with a specific product, Virkon (Olson et al., 2021) mixing 5 grams of it with 0,5 litres of water, then spraying it on the waders and waiting between 30 minutes to 1 hour to be effective. This was important in order to avoid the transmission of pathogens to different beaver or amphibian populations.

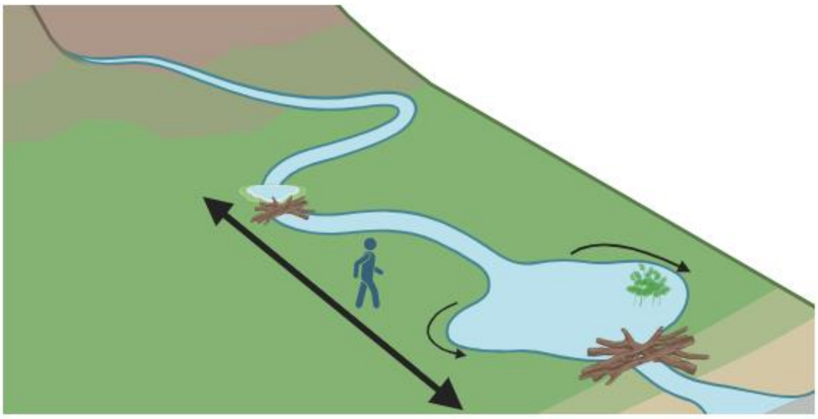


***Figure 3**:* Illustrative representation of the fieldwork with the example of two dams, one that created a pond and the other with just a small flooded/ still water area. The whole area by the edges and if possible, around the pond was checked for egg mass and species census.

2.3 Measured variables

In order to get a good description of each beaver pond and its characteristics, at each site I measured the following environmental variables, resumed in table 1.

The **air temperature**, based on the car thermometer read, to check whether it was right, the value given on the Swiss weather app (MeteoSwiss) at the precise location was checked for each night visit. Between these two values, the one considered most correspondent was kept.

Beaver territory size, this corresponds to the river section beavers occupy, with the help of QGIS mostly the centre of the sites was selected, then after the first visit to the site, only the section with dams was sampled. Thus, this sampled area was measured with the QGIS and called sampled territory size. Within these territories, one or several beaver **ponds** were also measured (in m^2) using the website map.geo.admin.ch.

Canopy, to calculate this variable, the estimation of the canopy from figure 4 was used, based on a document from Info Fauna (Biberfachstelle and Karch) looking at the quantity of trees present and estimating the percentage of shading they gave by their crown diameter during the second day visit and night visits, taking a final estimated percentage.

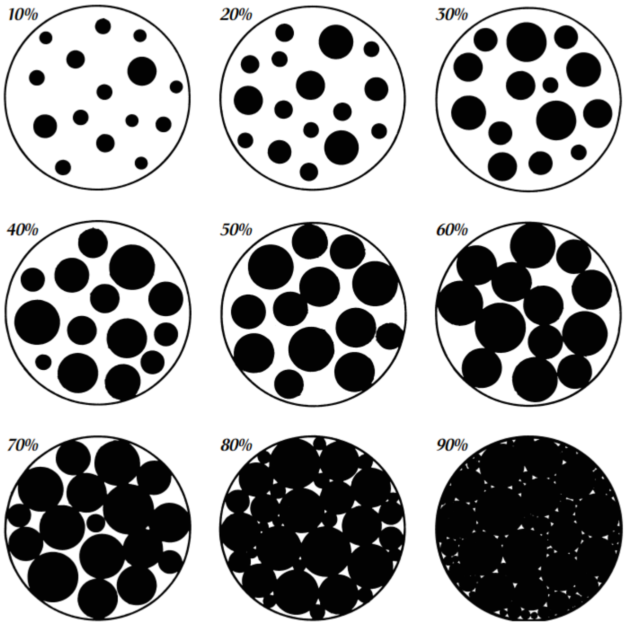


Figure 4: *Estimation of the canopy in percentage depending on the number of trees and crown diameter*

The vegetation inside the pond, referring to the emergent and aquatic vegetation in the ponds **and the vegetation outside** the pond/flooded area by the edges were qualified in estimated mean percentage by the quantity that was present, during the second day.

The **presence or absence of fish** in the ponds/river was checked at each visit, i.e. five times at all sites, by view, if one or more fish were seen, it was considered present. It was checked at each visit in order to be sure of their presence and no fish had been missed in a previous visit. The **water level** was monitored only if there was a significant difference between the first and last visit. No precise measure was taken, only by eye if it was dryer or a clear difference of lower water level seeing the marks of drought on the edges. And finally, **dam age**, that was selected as explained above for the site selection. Additionally, a categorisation of the dam ages was done, by young (less than five years old), middle aged (from 5 to 11 years old) and old ones (older than 12 years old). Moreover, during the first two visits, a description of each site served to uncover the environmental differences (type of ponds, forest or agricultural landscape, etc.) and to describe beaver pond characteristics. All these variables were measured in order to know if they had an impact on the abundance and diversity of amphibians.

Table 1*: Summary of the measured variables, how they were measured, the number of times it has been measured and the measuring unit at each site.*

Variable	How was it measured?	Number of times it has been measured	Measuring unit
Air temperature	Car thermometer + Swiss weather app (MeteoSwiss) at precise location, taking one corresponding value	5	Degrees (C°)
Beaver territory size	QGIS program, length of territory only with the dams	1	Metres (m)
Pond size	Using map.geo.admin.ch	1	Square metres (m^2)
Canopy	By eye with help of an estimation of canopy percentage (fig 4)	2 (second daytime visit and second night visit)	Percentage (%)
Vegetation inside the pond	Estimation by eye of the quantity of aquatic/emergent vegetation inside the pond	2	Mean percentage (%)
Vegetation outside the pond	Estimation by eye of the quantity of plants outside the pond	2	Mean percentage (%)
Fish	By eye, if one or more were seen, it was considered present	5 (to be sure none had been missed in the first visits)	Present (yes) or absent (no)
Water level	By eye at the last visit if there was a clear difference from the first visit	1	No units, just indication if lower or dryer pond.
Dam age	QGIS program with database from Info Fauna (Biberfachstelle)	1	Years

2.4 Data analysis

To do the analysis, the program RStudio version 4.3.1 was used, using principally the package unmarked for occupancy models with prediction of abundance and detectability (Fiske & Chandler, 2011; Kellner et al., 2023) and more packages for other tests. The package unmarked was used to make prediction of the occupancy for each species with the explanatory variables. To do so, the models were fitted first without an observation covariate and then with one (temperature) for the detection formula. Finally with the explanatory variables for the occupancy formula. For the predicted detection, only temperature was used and not the others, because it was the only variable measured at each visit from the beginning to the end.

For all species a set of candidate occupancy models were fitted to the data:

Model 1: occu(~1 ~dam_age, data)

Model 1.2: occu(formula = ~ temperature ~ dam_age + Fish + canopy + vegetation_inside + vegetation_outside + Territory_size + pond_size, data

Model 1.3: occu(formula = ~temperature ~ dam_age + Fish + canopy + vegetation_inside + pond_size, data)

Model 2: occu(~1 ~dam_age + Fish, data)

Model 3: occu(~1 ~ dam_age + canopy, data)

Model 4: occu(~1 ~ dam_age + vegetation_inside, data)

Model 5: occu(~1 ~ dam_age + vegetation_outside, data)

Model 6: occu(~temp ~ dam_age, data)

Model 7: occu(~temperature ~ dam_age + canopy,data)

Model 8: occu(~temperature ~ dam_age + vegetation_inside,data)

Model 9: occu(~temperature ~ dam_age + vegetation_outside,data)

Model 10: occu(~temperature ~ dam_age + canopy + vegetation_inside + pond_size ,data)

Model 11: occu(~temperature ~ dam_age + pond_size,data)

Model 12: occu(~1 ~ dam_age + pond_size, data)

Model 13: occu(~1 ~pond_size, data)

Before doing the analysis, the data had to be checked if the residuals of the linear model were normally distributed. This was done with the Shapiro Wilk test, revealing that they were all not normally distributed ($p<0.05$, rejecting the null hypothesis). Thus, the explanatory variables and the observation covariate had to be normalised before doing all the respective models, to do so, it was transformed into data frame and then scaled. Once the models were fitted, Akaike's Information Criterion (AIC) was used to rank the models and see which one would be the "best" or have more support (Burnham & Anderson, 2002).

Generalised Linear Model (glm) with Poisson regression, was done to predict an outcome variable representing counts from a set of continuous predictor variables (environmental ones). Having one count data response and many numerical or factor predictor(s):

I.e.: m1= glm (count data ~ (predictor factor 1/) + (predictor factor 2))

m1 = glm (egg mass ~ dam age + vegetation inside)

Different models with each environmental variable were made in order to see if the egg mass was significantly impacted by any environmental variable of the beaver ponds.

For the glm I fitted the following models:

Model 0: glm(max_eggmass~ max_dam_age + Fish, family = poisson, data)

Model 2: glm(max_eggmass~max_dam_age + Fish + Canopy, family = poisson, data)

Model 3: glm(max_eggmass~ max_dam_age + Canopy, family = poisson, data)

Model 4: glm(max_eggmass~ max_dam_age + Canopy + Vegetation outside + Vegetation inside, family = poisson, data)

Model 5: glm(max_eggmass~ max_dam_age + Canopy + Vegetation outside + Vegetation inside + Sampled territory size, family = poisson, data

Model 6: glm(max_eggmass~ max_dam_age + pond_size + Canopy + Vegetation inside + Sampled territory size, family = poisson, data)

And model 7: glm(max_eggmass~ max_dam_age + pond_size, family = poisson, data)

Models were fitted as well for each species, to have a look at which measured variables had a significant effect on them.

Model 0: glm(max_indiv~ max_dam_age + Fish, family = poisson, data)

Model 1: glm(max_indiv ~ Canopy + Vegetation inside + Vegetation outside, family = poisson, data)

Model 2: glm(max_indiv~ max_dam_age + Vegetation inside + Vegetation outside, family = poisson, data)

Model 3: glm(max_indiv ~ max_dam_age + Canopy + Vegetation inside+ Vegetation outside, family = poisson, data)

Model 4: glm(max_indiv ~ max_dam_age + Fish + Vegetation inside+ Vegetation outside, family = poisson, data)

Model 5: glm(max_indiv ~ max_dam_age + max_temp + Vegetation inside+ Vegetation outside, family = poisson, data)

Model 6: glm(max_indiv ~ max_dam_age + Canopy + Vegetation inside+ pond_size, family = poisson, data)

Model 7: glm(max_indiv ~ max_dam_age + Canopy + Vegetation inside + pond_size + max_temp, family = poisson, data)

Then for the data of egg mass with the "vegan" package (Oksanen J, *et al.,* 2022) a PCA (Principal Component Analysis) was done in order to have an idea of which environmental variables and reflecting the principal axes that explains the most the environmental variables that would have more impact on the quantity of egg mass. Additionally, for all the species a CCA (Canonical correspondence analysis) was done to see how the abundance of the species responded to the studied environmental gradients (dam age, temperature, pond size, vegetation inside and outside and the territory size. Other visualisation parameters like boxplots, qqplots and barplots were also used to have an idea on the effect of certain variables like dam age and pond size.

Finally, the connectivity was calculated to see if close-by amphibian reproduction sites could be connected and influence the income of the species depending on the number of them. This was done with the help of the QGIS program, creating a circular buffer of a radius of one kilometre around the beaver pond site, because it is the distance that most amphibian species can disperse. Movements between ponds at more than one kilometre can be rare (Brooks et al., 2019; Drake et al., 2017; Wendt, 2017). Then, inside this buffer count how many amphibian breeding ponds there are, mark them and assemble in groups the beaver sites that have the same number of ponds nearby. Additionally, calculate the distance in metres from the breeding ponds to the beaver pond, take the mean of these distances and attribute it to each group. This mean distance would indicate the distance amphibians have to travel to get to the beaver ponds from other breeding ponds.

3.Results

3.1 Amphibian richness

A total of five amphibian species were found in the beaver ponds, three anuran (*Rana temporaria, Bufo bufo, Pelophylax* sp.) and two urodele species (*Ichthyosaura alpestris*, *Lissotriton helveticus*). There was at least one of these species present in 31 sites of the 33 as figure 5 shows, having an occupation of 93% from the amphibian populations at the beaver sites. Additionally, another anuran species, the yellow-bellied toad *Bombina variegata* was found, but only in two sites, so this one was not included in the data analysis because a meaningful analysis is not possible with only two occurrences.

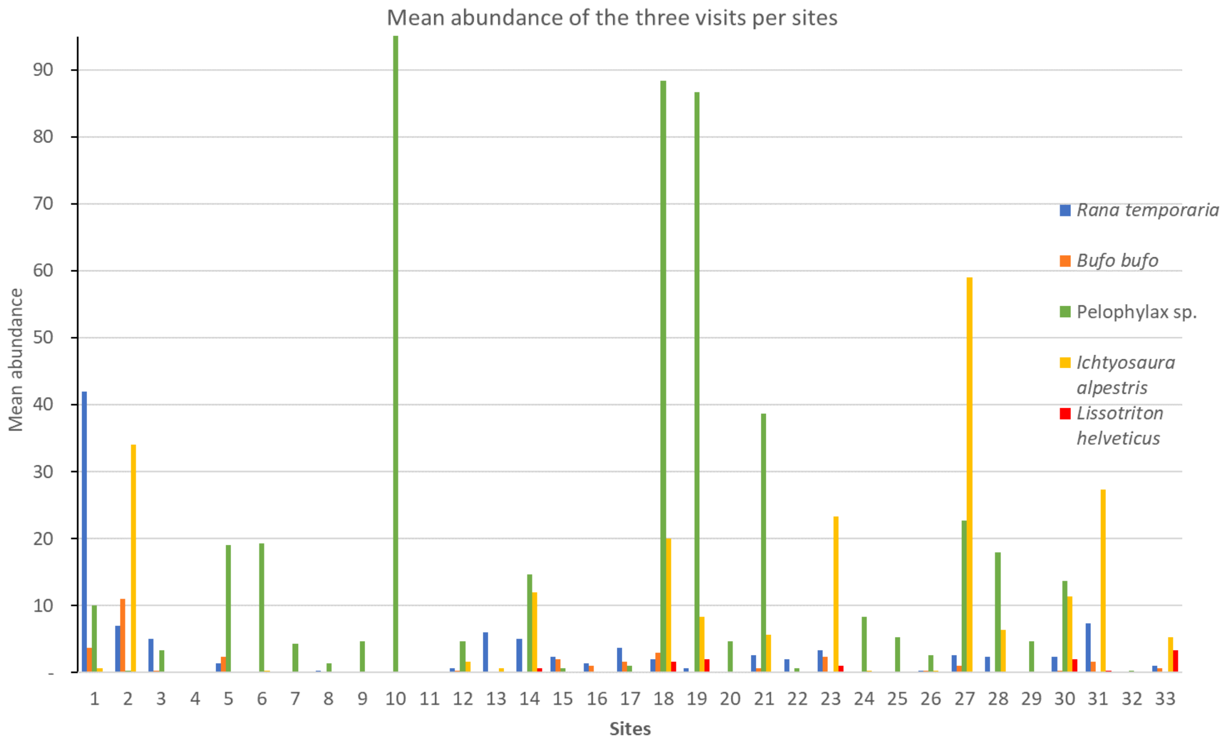


Figure 5: Graph showing the diversity and mean abundance of species among the 33 sites.

From the figure 5 above, we can observe that there are ten sites (1, 2, 14,18,19, 23,27,30,31,33) that have more individuals and diversity of species, see figure 6. Figure 7 shows some images of these more relevant sites.

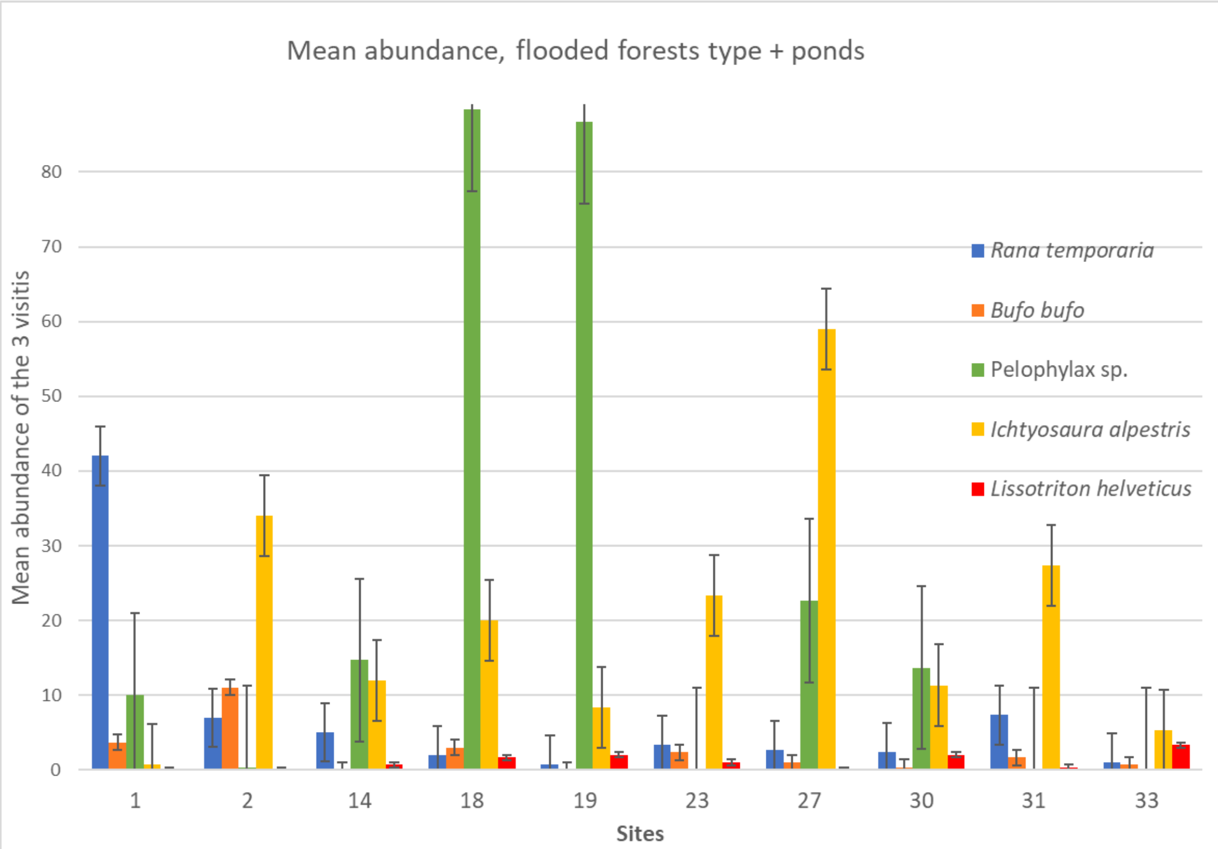


Figure 6: Graph showing the ten sites among the 33 that had a higher abundance and diversity of species represented as legend at the right indicates in different colours.

a)

b)

c)

Figure 7: Three images (a, b and c) showing some of the preferred sites, being in most cases, medium size flooded ponds in forest habitats, source: ©P. Bolle.

3.2 Environmental variables and the abundance.

From the glm models of each species listed in the materials and methods section, the best models with the lowest AIC and their corresponding variables are shown in table 2.

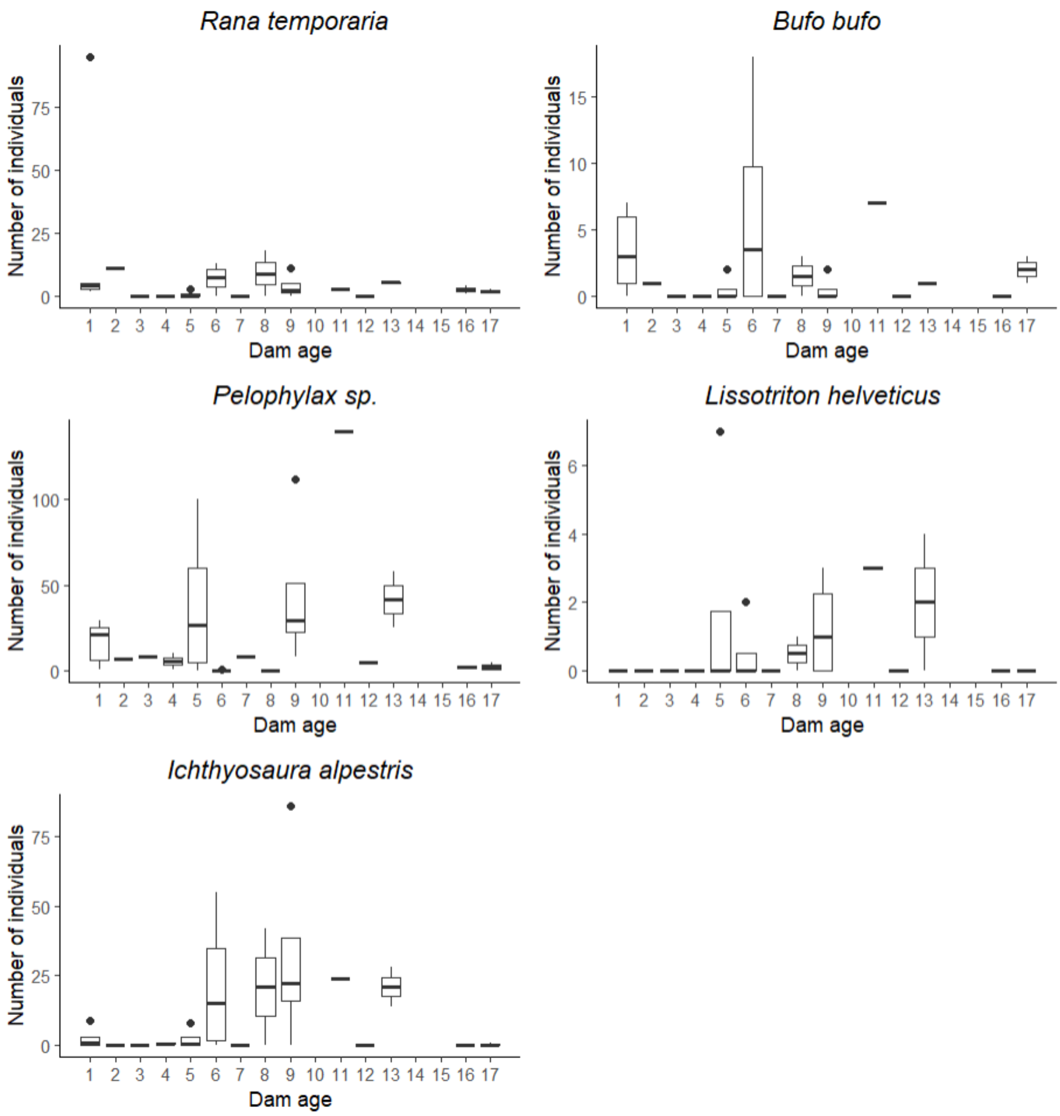
Table 2*: List of the best models with the lowest AIC of each species, with the variables and their corresponding regression coefficients.*

Species	Model, AIC	Variables	Coefficients	Standard Error and p – value
Rana temporaria	Model 3 AIC = 427.5	Dam age Canopy Vegetation inside Vegetation outside	-0.46748 0.75472 -0.25214 -0.18882	SE=0.09594, p=-1.10e-06 SE=0.09247, p=3.29e-16 SE=0.11669, p=0.0307 SE=0.10913, p=0.0836
Bufo bufo	Model 1 AIC = 151.1	Canopy Vegetation inside Vegetation outside	0.1745 -0.9601 -0.6463	SE=0.1389, p=0.208929 SE=0.2637, p=0.000272 SE=0.1723, p=0.000176
Pelophylax sp.	Model 5 AIC = 943.2	Dam age Temperature Vegetation inside Vegetation outside	0.04139 0.82257 0.41683 -1.07001	SE=0.05375, p=0.441 SE=0.04834, p= <2e-16 SE=0.06920, p=1.71e-09 0.06920, p=< 2e-16
Lissotriton helveticus	Model 0 AIC = 77.8	Dam age Fish	0.45479 -18.61015	SE=0.23880, p=0.0569 1619.81135, p=0.9908
Ichthyosaura alpestris	Model 4 AIC = 730	Dam age Fish	0.56275 -0.97922	SE=0.07345, p=1.84e-14 0.13819, p=1.38e-12

		Pond size	0.23379	SE=0.04399, p=1.07e-07
		Vegetation inside	0.63741	SE=0.06912, p= < 2e-16
		Vegetation outside	-0.76460	SE=0.07305, p= < 2e-16

Table 2 showed that all species had the variable of dam age being significant ($p<0.05$) except *Pelophylax* sp. and *Bufo bufo.* Figure 8 below shows how it affected each species differently, having the same range of dam age which had more or less individuals.

a)



b)

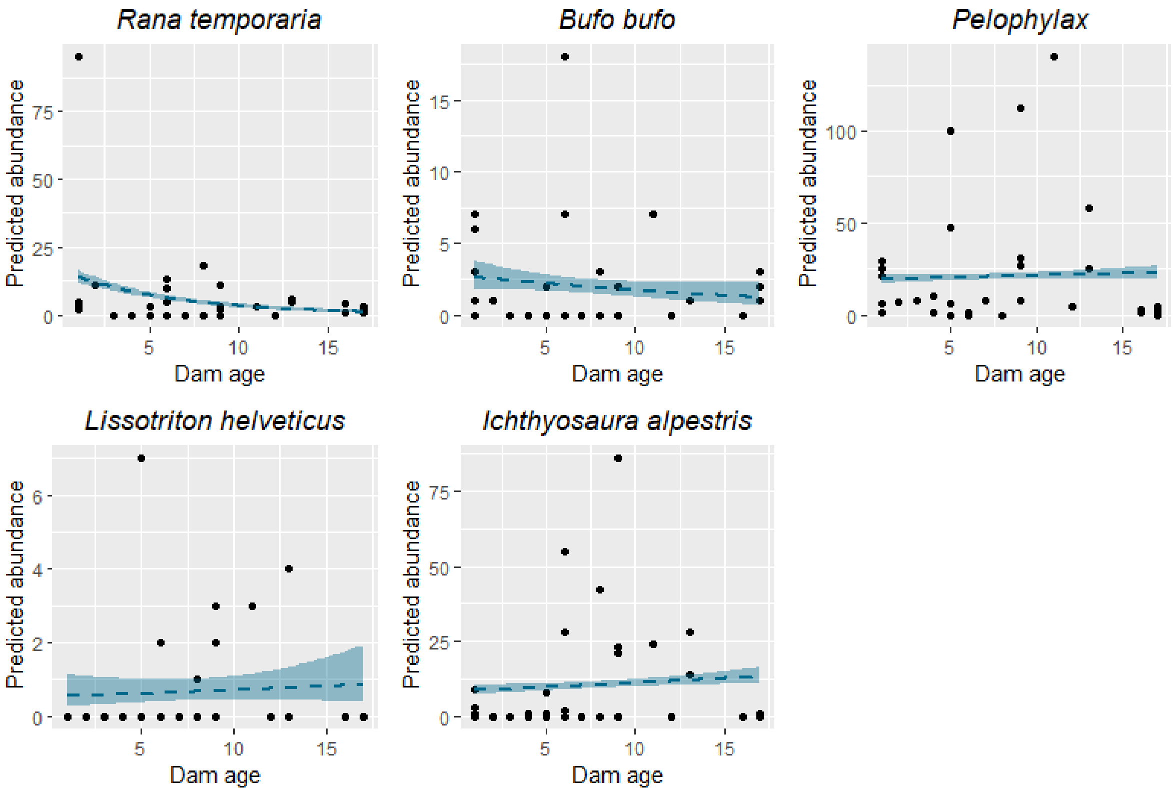


Figure 8: *a)* five boxplots showing the raw data and b) five other graphs with the output of the predicted abundance showing both which range of age of the dams had a greater number of individuals per species.

Another variable that had an effect on the abundance was the presence of fish. The pcount abundance analysis in unmarked gave the following results with the regression coefficients: -1.06 (SE = 0.182, p = 4.60e-09) for *Rana temporaria*, 0.24, (SE =0.247, p = 3.31e-01) for *Bufo bufo,* -0.842 (SE = 0.0911, p = 2.54e-20) for *Pelophylax* sp, -10.451 (SE = 50.430, p = 0.836) for *Lissotriton helveticus* and -0.894 (SE = 0.1317, p = 1.14e-11) for *Ichthyosaura alpestris*.

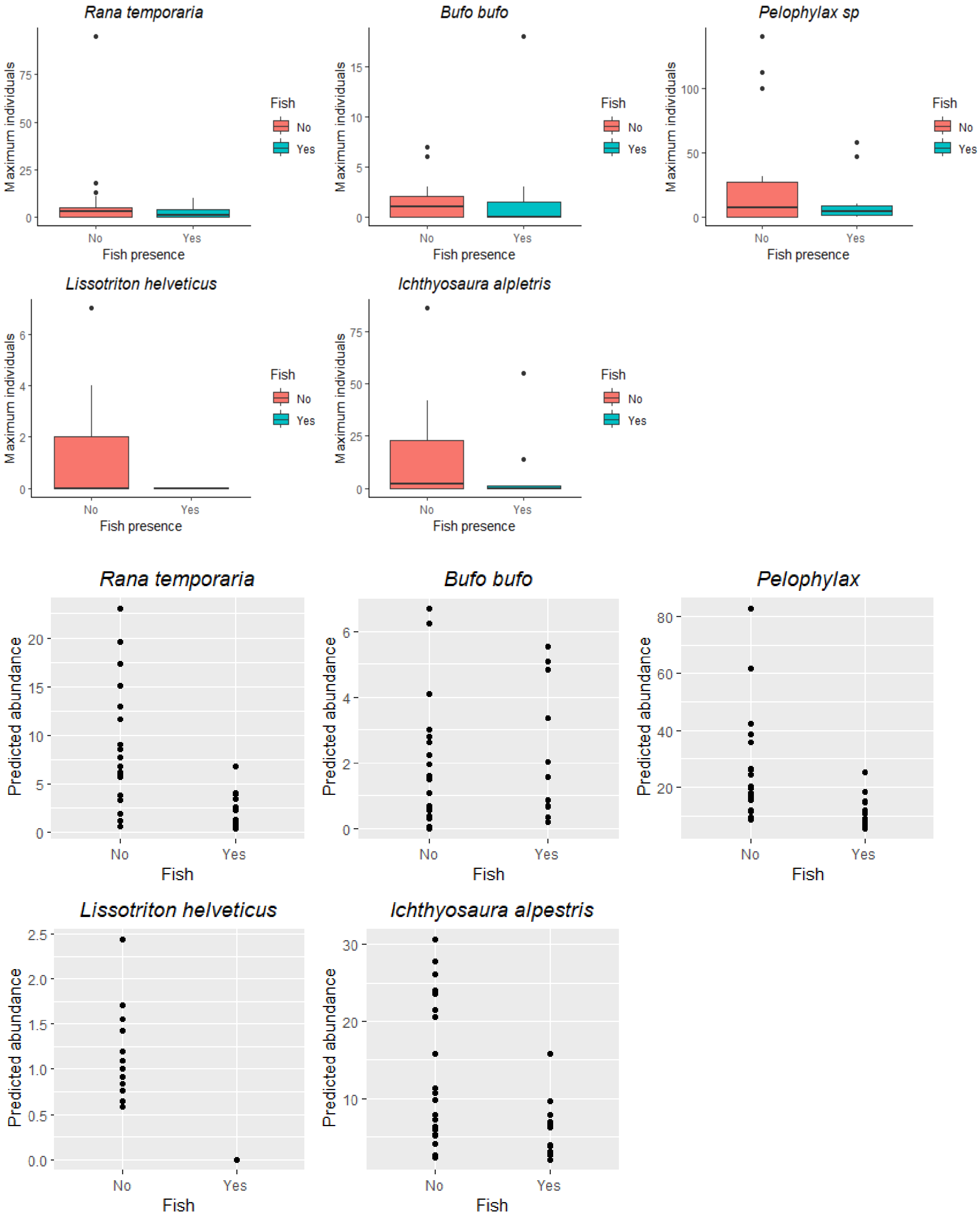


Figure 9: a) Boxplots with the raw data showing the effect of fish on the abundance and b) other five plots showing the predicted abundance.

Apart from fish some other aquatic species such as a crayfish from the genus *Austropotamobius* was also present at some sites, the precise species was not known.

The canonical-correlation analysis (CCA) revealed that the species were affected differently by the environmental variables, showing that the ones having some more correlated impact are the temperature, dam age and the vegetation inside. Moreover, the pond size did also have an impact, mostly for the newts and *Pelophylax* sp. The territory size seemed to be more important for *Rana temporaria and Bufo bufo* and the other two vegetation outside and canopy did not have much impact on the species as can be seen in figure 10.

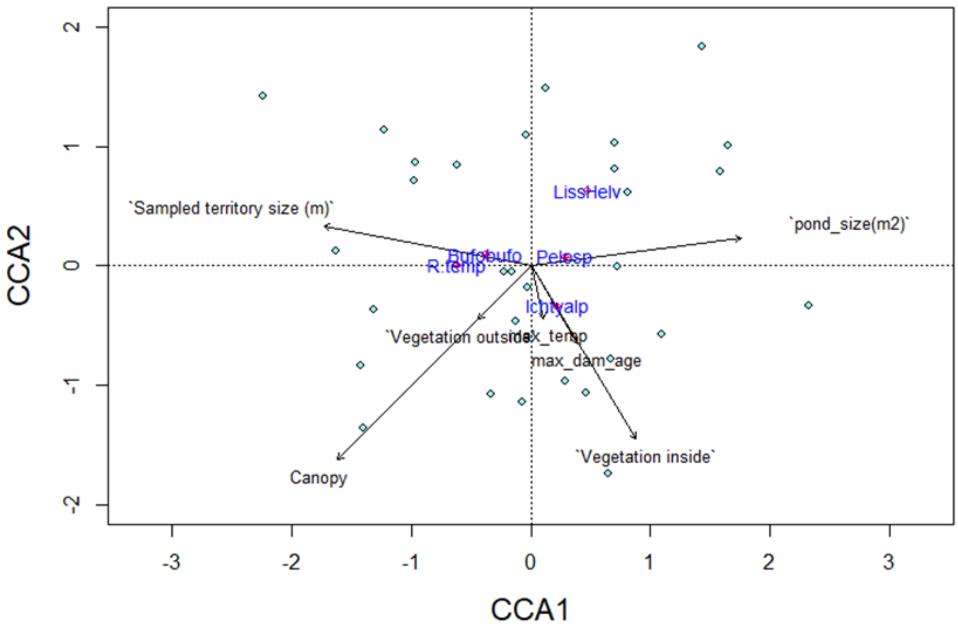


Figure 10: Representation of the CCA results having variable correlations but confirming the important impact of the dam age, pond size, vegetation inside and the temperature.

3.3 Breeding sites

Egg masses of *Rana temporaria* were found in 20 sites (1, 2, 4, 5, 12, 13, 14, 15, 16, 18, 19, 20, 21, 22, 23, 27, 28, 30, 31, 33) out of the 33, so 60% of the sites were used to breed. Moreover, only in one, there was a line of egg mass from *Bufo bufo*, but as it was the only case it was not significant for the analysis. No other egg masses from any other species were seen during the fieldwork.

The presence of fish had an impact on the quantity of egg mass present, there was a higher amount where fish were absent and lower if present, as it is represented in figure 10. Furthermore, juveniles of the common frog, alpine newt and crested newt were also seen at some sites.

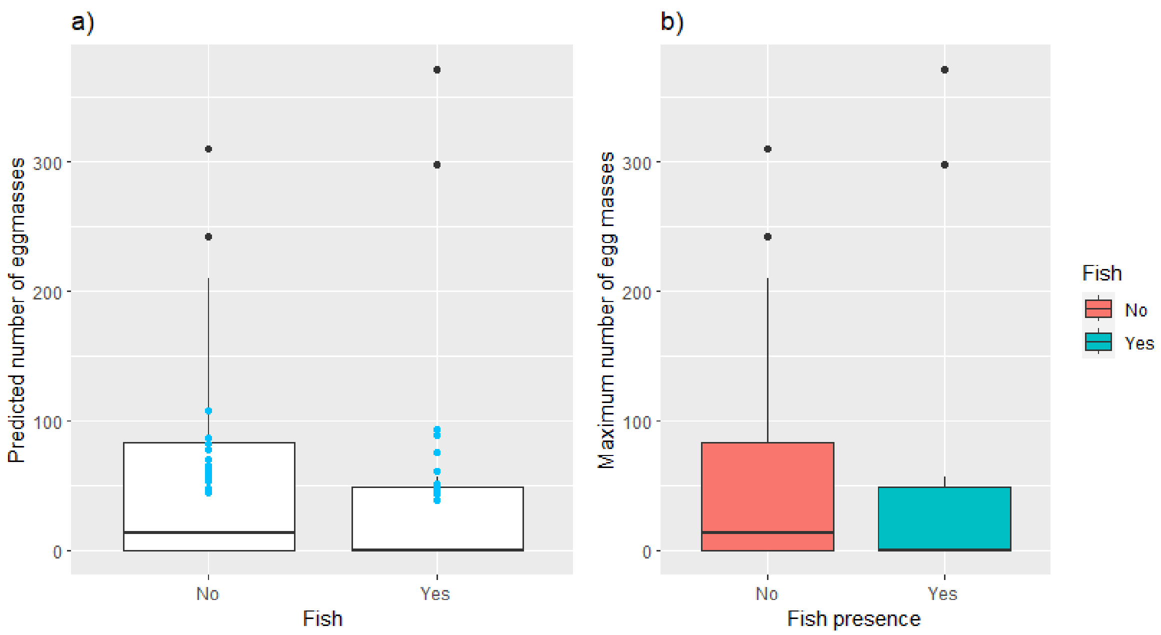


Figure 11*:* Graphics showing a) the predicted number of egg masses (blue dots) with the presence or absence of fish and b) the effect of the presence of fish on the raw data from the maximum number of egg masses, having a significantly higher amount without fish and less when it is present.

3.3.1 Environmental variables affecting the egg masses

After doing the PCA, the pond size seems to be the variable that is more correlated to the quantity of egg mass laid looking at figure 12. Furthermore, the dam age and territory size have an influence as well, looking at figure 13 with the correlations between each variable.

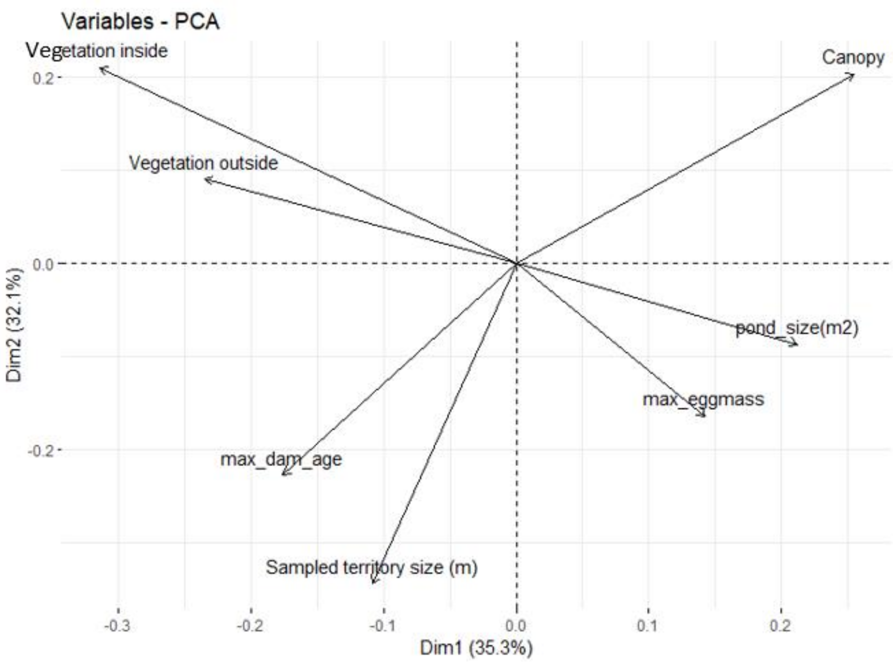


Figure 12*:* Graph showing the outcome of the PCA for the different variables, indicating that the pond size has more importance on the quantity of egg mass laid.

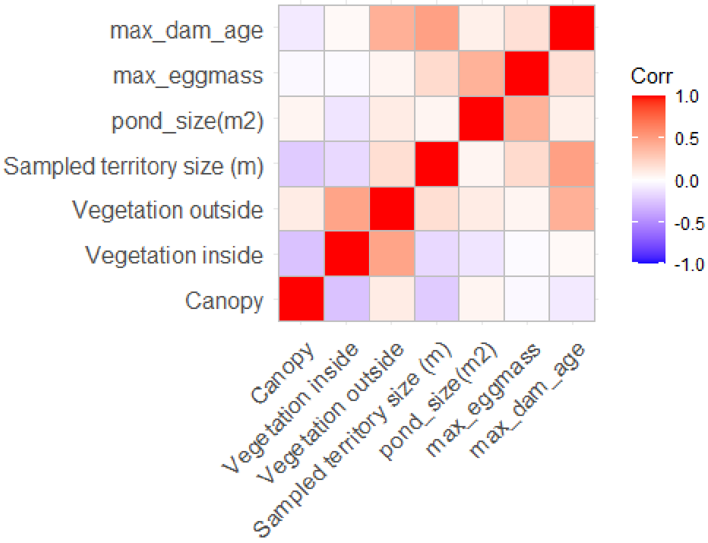


Figure 13: Representation of the correlation between the different variables showing that dam age, the territory size and pond size again are slightly correlated with the quantity of egg mass.

Table 3: *Summary of the model selection for the glm's*

Model	AICc	df	logLik	delta	weight
m6	4133.0	6	-2058.891	0.00	1
m7	4213.0	3	-2103.076	79.97	0
m5	4632.6	6	-2308.660	499.54	0
m0	4679.6	6	-2336.373	546.56	0
m2	4681.5	4	-2336.057	548.53	0
m3	4685.8	3	-2339.482	552.78	0
m4	4686.7	5	-2337.217	553.64	0

From the glm models, AIC values from table 3 above showed that model 6 was the best model (AIC = 4133), the regression coefficients were: 0.10114 (SE = 0.02769, p = 0.00026) for dam age, 0.31051 (SE = 0.01169, p = 2.2e-16) for pond size, 0.02141 (SE = 0.02671, p = 0.422) for canopy, 0.09980 (SE = 0.02438, p = 6.09e-05) for vegetation inside and 0.21342 (SE = 0.02385, p = <2.2e-16) for territory size. The relationship between the explanatory variables and the egg mass are shown in figure 14.

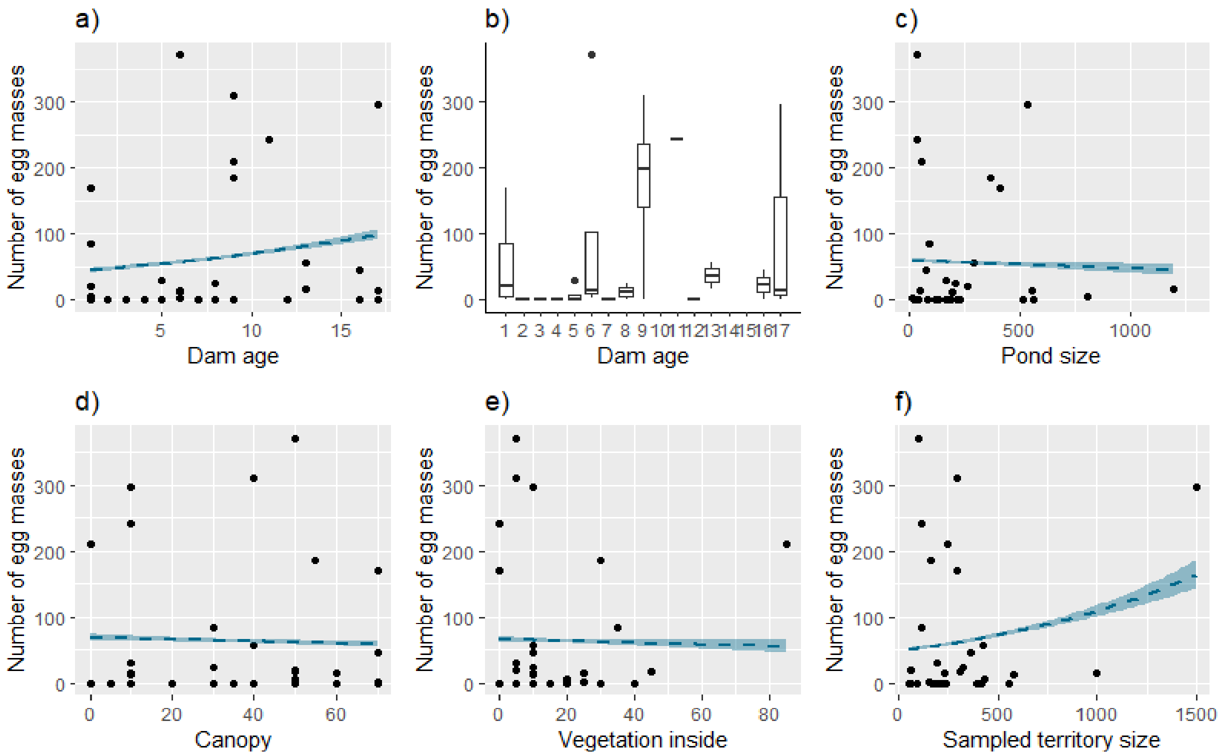


Figure 14 a, b, c, d, e and f: Relationship between the explanatory variables of the best model and the egg mass. The blue dotted line showing the regression line. Fig 14b shows in a boxplot how the number of egg masses vary among the different dam ages.

3.4 Occupancy models

For all five species, the variable of dam age was included in the best models, having a positive effect on the occupancy for all, the values of the regression coefficients are detailed in table 4. More information over the model selection (with the other AIC values, Akaike weight etc) can be found in the appendix.

Table 4: *Best occupancy models with the lowest AIC of each species with their regression coefficients and values.*

Species	**Model + Variables**	**Coefficient**	**Standard error (SE) and p-value**
Rana temporaria	Model 7 (AIC = 117.61) Dam age Canopy	 0,746 0,585	 SE= 0.501, p = 0.137 SE = 0.420, p = 0.164
Bufo bufo	Model 1 (AIC = 113.93) Dam age	 0.035	 SE=0.316, p = 0.912
***Pelophylax* sp.**	Model 6 (AIC = 107.04) Dam age	 0.189	 SE = 0.392, p = 0.6303
Lissotriton helveticus	Model 2 (AIC = 59.27) Dam age	 0.454	 SE= 0.409, p = 0.2677

	Fish	-9.463	SE = 39.414, p = 0.8103
Ichthyosaura alpestris	Model 11 (AIC=102.22) Dam age Pond size	 -0.54 3.24	 SE=0.400, p = 0.177 SE= 2.687, p = 0.228

The probability to detect the species form the previous occupancy models were: 74% for *Rana temporaria*, 51% for *Bufo bufo*, 85% for *Pelophylax* sp., 63% for *Lissotriton helveticus* and 74% for *Ichthyosaura alpestris*.

The relationship between the explanatory variables and occupancy for each species is shown in figures 15 to 25.

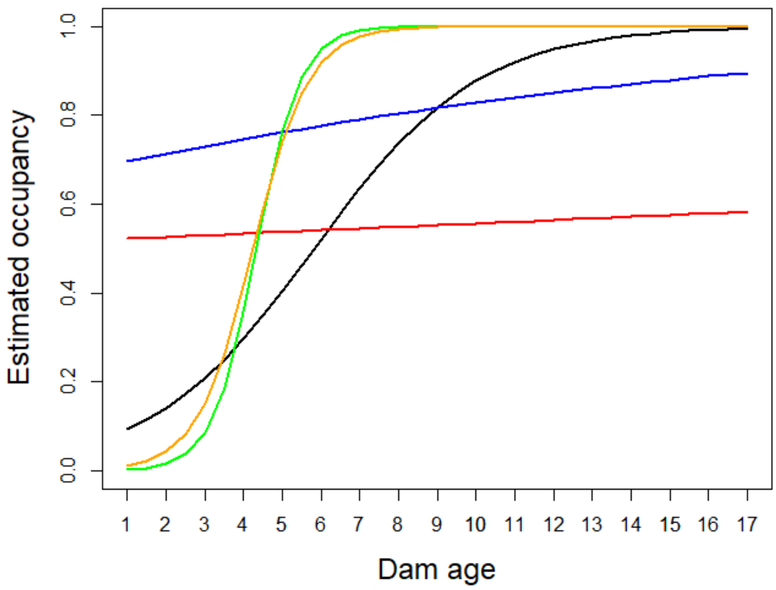


Figure 15*: Representation* of the estimated occupancy depending on the dam age (in real scale, years) for each species *(black: Rana temporaria, red: Bufo bufo*, blue: *Pelophylax* sp., green: *Lissotriton helveticus* and orange: *Ichthyosaura alpestris*) but non with a statistically significant effect.

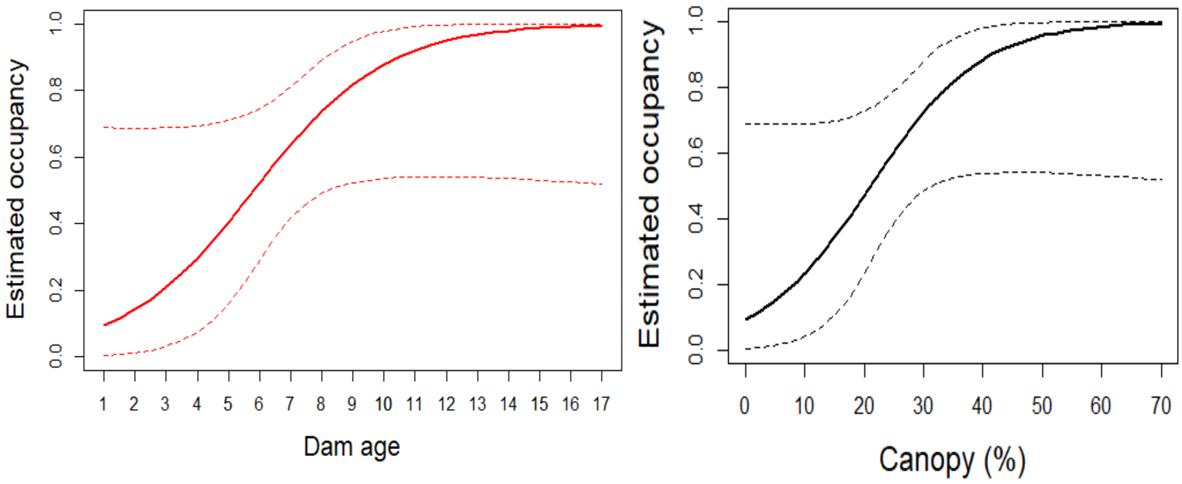


Figure 16*:* Relationship between the dam age (red), the canopy (black) and estimated occupancy of *Rana temporaria*. The dotted lines show the 95% confidence interval.

For *Rana temporaria* the model that had all variables was selected as well in order to see how they affect the predicted and estimated occupancy. This was the model 1.3: with the regression coefficients that were: 0.485 (SE=0.363, p = 0.181129) for temperature the detection variable, 1.1048 (SE= 0.626, p= 0.0777) for dam age, negative coefficient: -1.6934 (SE=1.137, p = - 0.1363) for the presence of fish that reduces the occupancy probability, 0.8365 (SE= 0.529, p = 0.1139) for canopy, -0.0303 (SE = 0.427, p = 0.9434) for vegetation inside, -0.4072 (SE = 1.741, p = 0.8150) for pond size as site covariates. The relationship between the explanatory variables and occupancy is shown in figure 17 and 18.

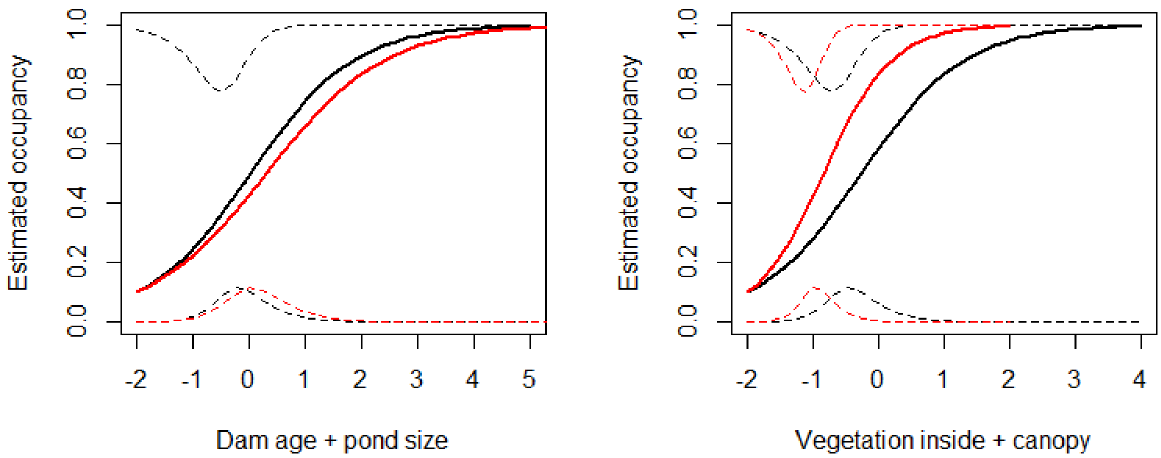


Figure 17*:* Representation of all standardised variables (dam age, vegetation inside in black and pond size, canopy in red) that have a positive effect on the estimated occupancy of *Rana temporaria*. The dotted lines show the 95% confidence interval.

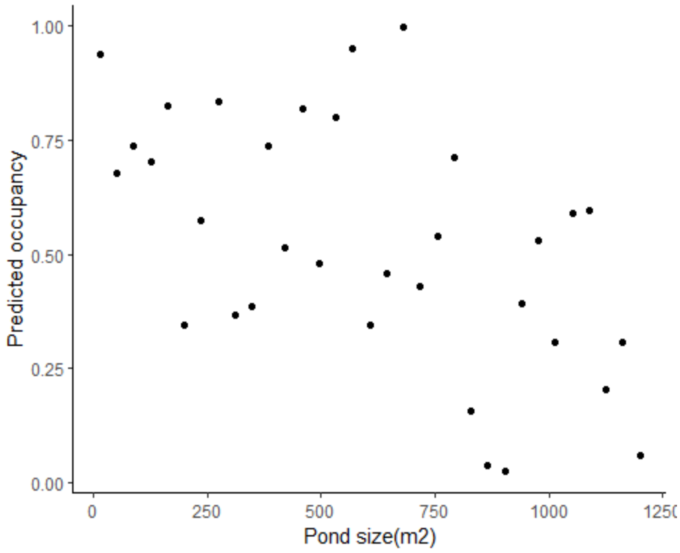


Figure 18: scatter plot showing that at a certain point if the pond size gets too big, the predicted occupancy decreases for *Rana temporaria*.

Figure 19 shows how some variables had not only positive but also negative effects on species (e.g. *Bufo bufo*).

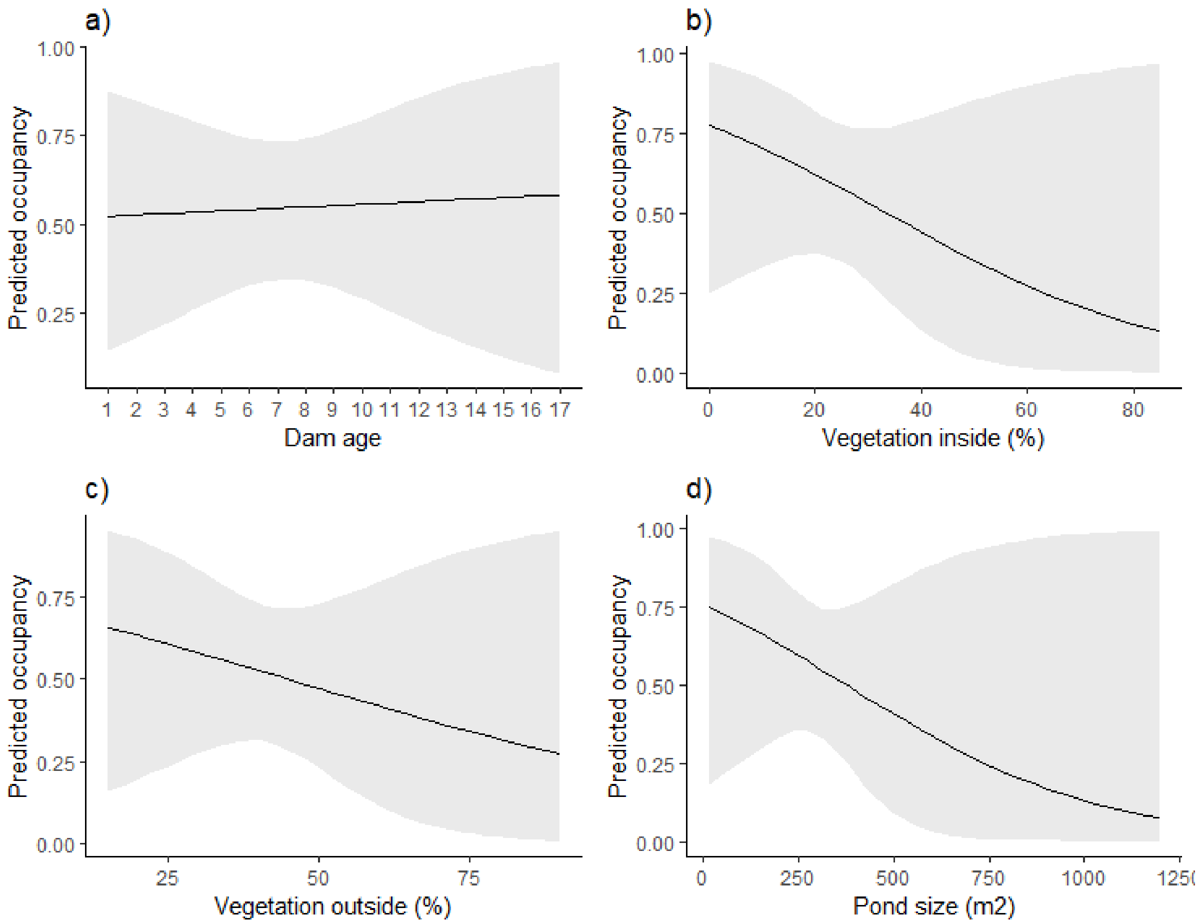


Figure 19: Relationship between the explanatory variables in real scale and predicted occupancy of *Bufo bufo*. a) increased predicted occupancy the older the dam gets. b and c show from the second-best model that the vegetation inside and outside has a negative effect on the occupancy, and d) with pond size, the areas in grey shows the 95% confidence interval.

The second-best model for *Bufo bufo* was number 6 (AIC = 114.26) the regression coefficients were: 0.0308 (SE= 0.346, p = 0.929) for the dam age and -0.5600 (SE = 0.474, p = 0.237) for vegetation inside. And third was number 7 (AIC=114.5) the regression coefficients were: 0.2567 (SE= 0.464, p= 0.580) for the dam age and -0.5725 (SE = 0.522, p = 0.273) for vegetation outside. I included these models to have a look at these variables as well.

The model which included the presence of fish (number 2) had a negative regression coefficient: -0.5362 (SE=0.854, p = 0.530)

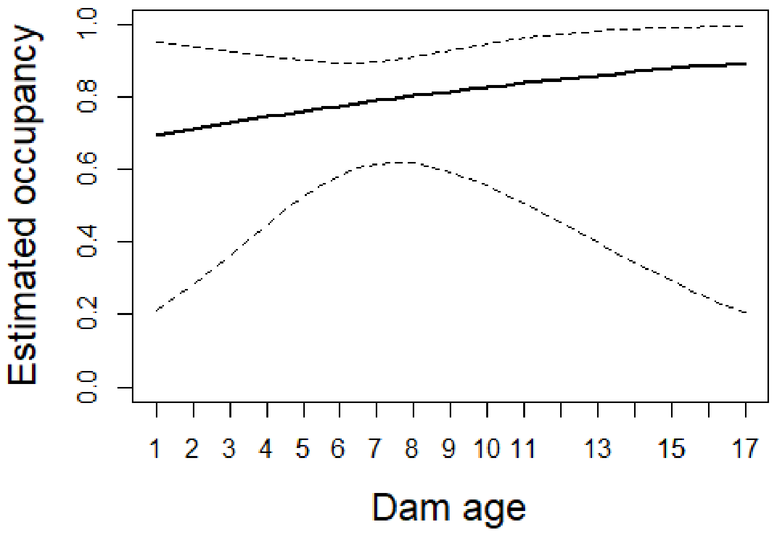


***Figure 20**:* Relationship between the dam age and the estimated occupancy of *Pelophylax* sp*.* The dotted lines indicate the 95 % confidence interval.

The second best was number eight with the same adding vegetation inside as the second site covariate, regression coefficient: 0.201 (SE = 0.376, p = 0.5924) for dam age and 0.511 (SE=0.606, p = 0.3994) for vegetation inside.

The third one was number eleven with the regression coefficients: 0.0152 (SE= 0.472, p= 0.9743) for dam age and 1.835 (SE=3.207, p= 0.5718) for pond size, size as second covariate, increasing the occupancy probability but not being significant.

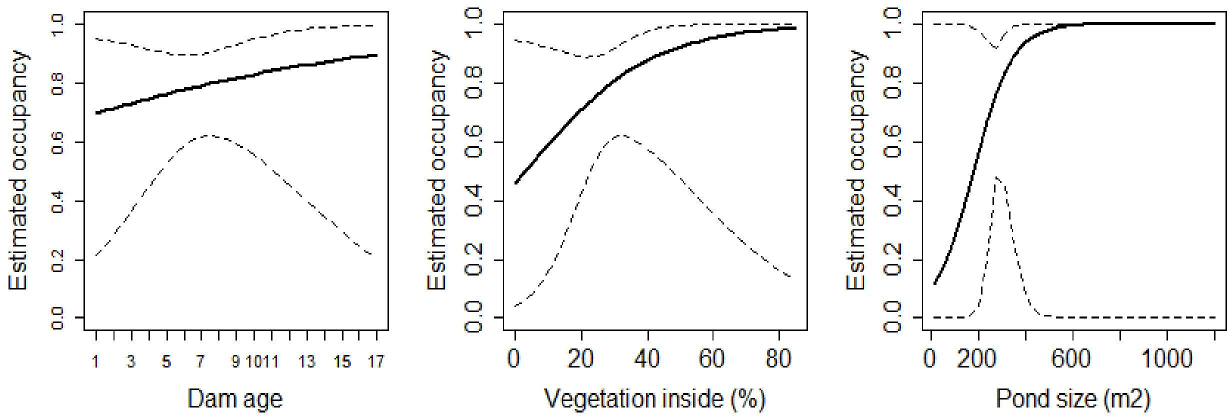


Figure 21: Representation of the increasing probability of the sites to be occupied by *Pelophylax* sp. with the variables dam age, vegetation inside and pond size in real scale. The dotted lines showing the 95% confidence interval.

The model 2 including the presence of fish revealed the regression coefficients: 1.480 (SE= 1.215, p = 0.2231)

For *Lissotriton helveticus* the second-best model was number m1.3 (AIC=61.73) having temperature as observation covariate for detection probability and dam age with the regression coefficients -664 (SE=0.816, p=0.611), fish with the regression coefficients -10.088 (SE=81.199, p=0.901), canopy with the regression coefficient -1.523 (SE=0.965, p=0.114), vegetation inside with the regression coefficient: 0.190, (SE=0.472, p=0.687) and pond size with the regression coefficients: 4.735 (SE=4.004, p=0.237) as site covariate for occupancy (see figure 22).

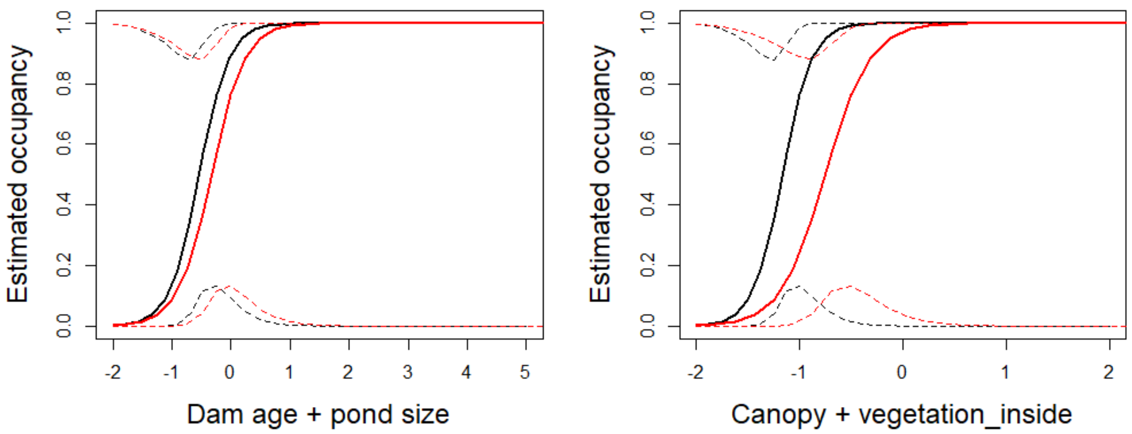


Figure 22*:* Relationship of the standardised variables (dam age and canopy in black, pond size and vegetation inside in red) from the second-best model with the estimated occupancy of *Lissotriton helveticus*. The dotted lines represent the 95% confidence interval.

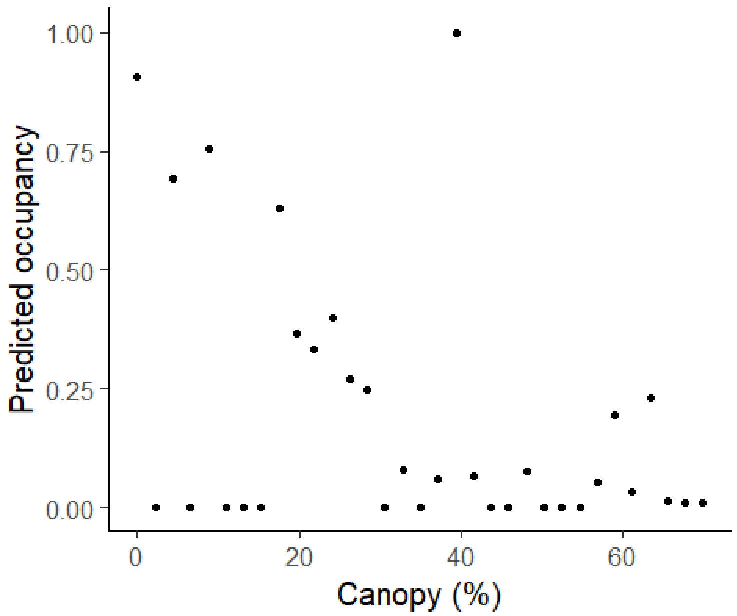


Figure 23: Scatter plot showing that canopy can increase the predicted occupancy but if there is too much canopy, the probability of the site to be occupied by *Lissotriton helveticus* will decrease.

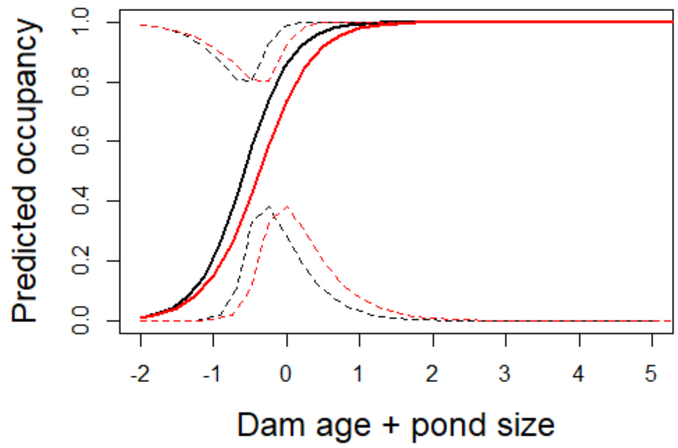


Figure 24: Relationship between the two variables (dam age in red and pond size in black, standardised) and the predicted occupancy of *Ichthyosaura alpestris*. The dotted lines represent the 95% confidence interval.

Ichthyosaura alpestris was also affected by fish with a negative regression coefficient: -0.6235 (SE=0.748, p = 0.404).

For all five species, the prediction for the effect of air temperature on detectability gave the same result that temperature has a positive effect, making the detection probability higher when it increases (see figure 25). The only exception was *Bufo bufo*, regression coefficients were a negative estimate -0.1973 (SE= 0.326 and non-significant p-value = 0.545) and *Lissotriton helveticus* regression coefficients were: -0.0511 (SE= 0.596, and non-significant p - value = 0.932).

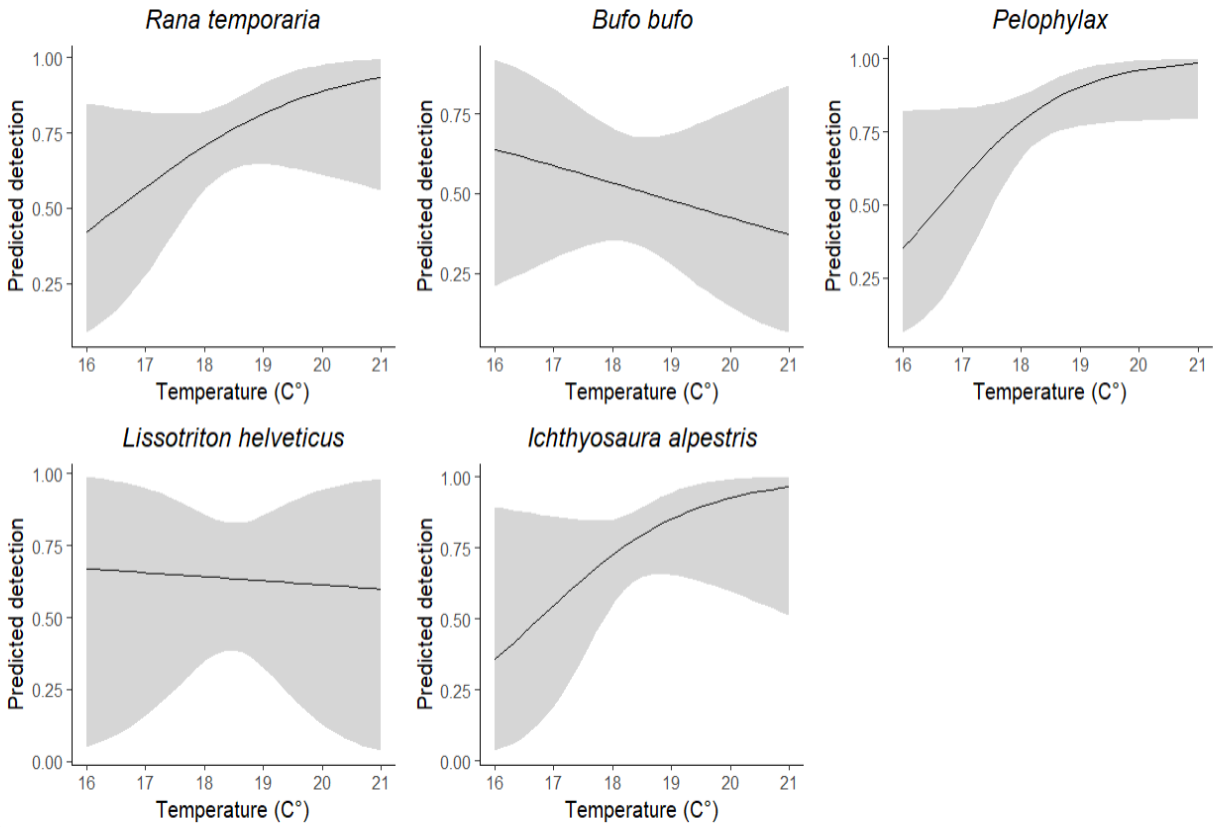


Figure 25: Representation of the predicted detection according to the temperature (C°) for each species.

3.5 Connectivity

The table 4 below shows how many amphibian breeding sites were close to the beaver ponds, the number of the corresponding beaver sites and the mean distance.

Table 4: *Indication of which sites had a corresponding number of breeding ponds nearby in the defined area and the mean distance. Numbers in green correspond to the sites shown in fig 6.*

Amphibian breeding ponds in the area of the beaver pond site	5	3	2	1	0
Number of beaver ponds sites	2	5	12	8	6
Sites (corresponding number)	**23**,32	**14**,20,24,26,**33**	6,11,12,15,**18**,**19**,21,22,**27**,28,**30**	**1**,**2**,5,7,9,10,16,**31**	3,4,8,17,25,29
Mean distance (m)	687	560	904	545	718

4. Discussion

Beavers are ecosystem engineers that are able to create heterogeneous environments thanks to their dams and their activities like cutting trees or digging burrows. These environments, modified by beavers, could have an important conservation potential for the decreasing amphibian populations, giving them the possibility to choose more convenient habitats to occupy and increasing their dispersal network (Zero & Murphy, 2016). The objective of this study was to analyse how the ponds created by the beaver dams affect the amphibian populations abundance and occupancy. Whether they establish successfully, if *Rana temporaria* breeds at beaver ponds, if there are any preferences. Which factors, such as dam age, determine spatial variation in abundance and occupancy, and if it could increase the connectivity between the different amphibian breeding sites network. After four months of fieldwork going to the different 33 selected sites in three cantons of Switzerland, the collected data could give some answers to the previous questions.

Amphibian abundance and occupancy at beaver ponds and as ovipositional site

Five species were found in all the visited beaver ponds and at least one species was present at 31 of the 33 sites as figure 5 shows, thus 93% of the beaver ponds were occupied by amphibians which indicates that they do establish there. To have a clear answer of this, a statistical analysis on species richness should be done in further studies. Having a look at the detection probabilities from the occupancy models, there might have been some missed occurrences, for example *Bufo bufo* with 51% and *Lissotriton helveticus* 63% of detection probability. However, as multiple visits have been done, the cumulative detection is high.

As mentioned in the results, there was one additional species found, *Bombina variegata*, that only had two occurrences. This might be due to the fact that it is a species highly subjected to fish predation or because most of the sites were not wooded enough (Dalbeck et al., 2020).

Regarding the breeding, a total of 60% of the sites had egg masses from *Rana temporaria*, which suggests that beaver ponds are used as ovipositional sites. Thus, confirming what other studies found about this species by showing that it can establish well and have high egg masses densities in northern, central and eastern European beaver ponds (Dalbeck et al., 2020; Romansic et al., 2021). A few juveniles were also observed, not only of this species but also of *Pelophylax* sp. and the two newts (*Lissotriton helveticus* and *Ichthyosaura alpestris*). However, having data only for egg masses belonging to a single species and a few observations of juveniles, present at some sites, cannot give us a clear answer that they successfully breed there. To ascertain this, another study should be done following the whole evolution of the cycle from egg, toad to juvenile over a longer period of time.

Variation in the type of beaver ponds (how and where it is constructed) selected by the amphibians

Having a look at figure 5, we can see that not all sites were occupied with the same number of species, some had more, less or no species. Suggesting that there is a preference for the amphibians to select their habitat, with some that prefer open water ponds and others more forested types (Anderson et al., 2019; Dalbeck et al., 2020; Hernández-Ordóñez et al., 2019). Figure 6 shows the sites with more diversity and abundance, which could be considered as the preferred sites. Although it varies among species, because each of them has different preferences, as the columns in the same figure show. Most of these sites were **small head water streams**, a similar type of environment as Dalbeck et al. (2020)

found, and **flooded forests beaver ponds** habitats (see images fig 7). These flooded areas were variable in sizes but generally big (from 4 x 1 m, 8 x 4, 13 x 4m, 16 x 2.5m, 15 x 18 m, 28 x 2.8 m, 53 x 8 m, 1380 m^2 up to 256 x 35 m). However, it was not always a forest type habitat but also for some cases, like site number 23, a habitat consisting of large canals that, with the beaver dam, create a long stagnant water canal which ends at a point, well used by newts (mostly *Ichthyosaura alpestris*, see figure 6) that go into the deeper areas of the pond with sand to hide in.

There was also another type of beaver pond (site 14) with more open water, being a **bog** habited by the beavers. The beaver ponds on the edges close to canals were the preferred spots colonised by newts. The dams inside the bog were not accessible but assumed to be occupied from hearing the calling sounds of the amphibians. Nearly all selected sites were the ones that had multiple ponds or stagnant water created by the beavers (e.g. site 1 and 5), making it possible for the different species to occupy the most convenient one. The majority of the considered preferred sites had the possibility to give refuge to amphibian species, going into the sand in the canals or some ponds, hiding in the submergent plus emergent vegetation, wood debris etc. This gives them good suitability for overwintering and protective refuges (Brazier et al., 2021; Dalbeck et al., 2007; Sommer et al., 2019; Vehkaoja & Nummi, 2015).

Causes for sites to show less abundance or no species at all (see figure 5) might be the following:

- Only few or non-lentic habitats, where the beaver dam laid within the canal with a high river flow that might have been too strong and non-convenient for amphibian species
- Canals around agricultural landscapes with not much aquatic vegetation
- Edges with too much inclination
- Beaver ponds near infrastructures like a water treatment plant

However, even if during the visits no individual was seen, at least they used the ponds next to the dams to breed. For example, site 4 which did have some egg masses in small ponds that might have originated thanks to the beavers, as their lodge was next to it. About the sites that had egg masses, some of them corresponding to the sites from figure 6, thus having the same habitat characteristics as the preferred ones mentioned before. The sites where there were no egg masses had the same facts as mentioned before for the ones without any species. Some sites even had artificial ponds created for amphibians next to the beaver ponds, but even there, no eggs were found, showing that amphibians prefer to go to the beaver ponds, which gives them more opportunities of having refuges to lay eggs (Dalbeck et al., 2020).

Which factors, such as dam age, determine spatial variation in abundance and occupancy?

The results in table 2 show that the variables that were the strongest predictors or that came out most significant in the best models of the glm's for each species were dam age, vegetation inside and outside. Those three elements are thus important features to attract amphibians (being variable for different species), making sense as, the older the dam is, the more heterogeneous the habitat will be, this being mostly the case in flooded forests beaver ponds. Having more emergent and submergent vegetation to offer support for eggs, shelter and food for amphibian adults and larvae, decreasing predation risks, less canopy because of the beaver cutting trees, wood stamps and a variation of ponds depth, size etc (Brazier et al., 2021; Hartel et al., 2007a; Vehkaoja & Nummi, 2015). This is not the case for sites in canals without any lentic habitat. Many studies showed that environmental heterogeneity was revealed to be the leading factor to increase local richness of amphibians and to be fundamental for biodiversity at different scales (Couto et al., 2017; Figueiredo et al., 2019). As beavers are able to create this type of habitat attracting amphibian populations, they have a big potential in a conservational way to help them to reduce their decrease. Additionally, results showed that every species had its own variables (see table 4) related to the occupancy (temperature, fish, canopy or pond size) as mentioned before, every species has its preferences, but for all species dam age was important, being the strongest predictor. Further, other predictors that showed up in the results of occupancy models for all the species, were vegetation cover inside the beaver pond (aquatic, emergent vegetation) and the one outside (see fig 17,19,21 and 22). These being the same as the strongest predictors for the glms on the abundance analysis.

Some of these variables had both positive and negative effects on the occupancy, for example canopy (see fig 23) for *Lissotriton helveticus* and *Ichtyosaura alpestris* too much canopy not being favourable, decreasing the occupancy of certain species. Therefore, beavers play an important role by cutting the surrounding trees consequently reducing a high percentage of canopy and creating more open-air ponds. Pond size for *Rana temporaria* (see fig 18), vegetation inside, outside the pond and pond size (see fig. 19 b, c and d) for *Bufo bufo*. Concerning the pond size, the majority of studies have observed that in middle-sized ponds (between 200-4000 m^2) there is a higher richness as amphibians have more space to establish (Semlitsch et al., 2015; Werner et al., 2007). Thus, the small, middle-sized ponds (in this case mean beaver pond sizes from 14,6 m^2 to 1195 m^2) are ideal to occupy and breed as figure 14 c shows. There was an exception with one site, number 19 that was very big (8960 m^2) but, as it was very long and wider from the water retention of the dam, the amphibians were mostly seen on the edges by the forest and in the shallower part, with wood piles and emergent vegetation.

Results from the abundance analysis in fig 9, egg masses (fig 11) and the occupancy, revealed that beaver ponds without fish are more attractive. As fish affect negatively on egg masses, on the abundance of all species except *Bufo bufo* and negatively on the occupancy probability on all species except *Pelophylax* sp. This exception might be explained since some studies revealed that tadpoles secrete a substance that fish do not like, avoiding predation. Moreover, there is a supposition that species lacking chemical defences like *Rana temporaria* started to respond to the predation risk by going to complex habitat refugia (like beaver habitats) (Hartel et al., 2007; Kats et al., 1988 in Kloskowski et al., 2020). Even so, there were some cases which did have fish and still populations that occupied the site. Mallards were also present at some sites and could have eaten some of the egg masses. Although, during the fieldwork, it was not each time reported where the mallards were present, thus no result can be shown.

The independent variable of air temperature made the occupancy probability increase the higher it was (see fig 25) except for *Bufo bufo*, regression coefficients were a negative estimate -0.1973 (SE = 0.326, p-value = 0.545) and same for *Lissotriton helveticus*, -0.0511 (SE= 0.596, p-value = 0.932). Some visits confirmed that if the air temperature was lower than four degrees, there was no amphibian activity or they were all hidden deep in the pond under the sand.

In both cases, for the individuals and occupancy analysis, the variable that always came up as the strongest predictor was the dam age, indicating that it does have an influence on the amphibian populations to establish at the beaver ponds. In general, the older the dam is, the higher probability there is that a beaver pond will be occupied (see fig 15), even though it cannot be totally confirmed as the results were not statistically significant. Moreover, for some species like *Rana temporaria, Pelophylax* sp., *Lissotriton helveticus*, the relationship between the variables and the predicted occupancy in figures 17,21 and 22, had a wide confidence interval which show that it is harder to tell the occupancy of these species. The results in table 2 revealed that the dam age had more significant impact on the abundance of the species *Rana temporaria*, *Lissotriton helveticus* and *Ichthyosaura alpestris* rather than *Bufo bufo* and *Pelophylax* sp. Having a look at table 4, we can see that dam age had a positive effect, but looking at the regression coefficient, small effect on the occupancy of *Bufo bufo*. This might be due to less individuals of this species seen at each site.

Results from figure 8, show that there was a variation in the abundance depending on the dam age. Dams aged between five and nine years old, had more individuals for all species, this being the same for the egg masses (see fig 14 a and b), the older the dam is the more eggs, but having more quantity in this range of dam ages, considered as mature dams/ponds. These results were similar to what other studies have shown (Dalbeck et al., 2014; Sommer et al., 2018) having a certain dam age range (middle aged dams), where there was a higher occupancy. Nevertheless, young dams (one or two years old) also had an important effect on the abundance for some species (*Rana temporaria, Bufo bufo, Pelophylax* sp. and *Ichthyosaura alpestris*) and on the amount of egg masses (see fig 8 and 14 a, b), meaning that they are also occupied and attractive for the amphibians. This could be due to a new fresh open water habitat interesting for amphibian juveniles that are on exploration for new ponds to breed in (Karraker & Gibbs, 2009). Nonetheless, to have a precise answer of the preferred dam age, another study should be done with more sites having this range of dam age to compare if there are more individuals in older dams than in mature ones, because in this study there is a possible bias by lacking more sites having dams aged more than 14 or 15 years old. The older the dam is, the more impoundment with stagnant water there is. This way, maintaining a more stable hydroperiod, even if the water level can go lower, as it happened in certain sites of this study. The water level mostly decreased in the period of May and June when the temperatures were higher, but still, they did not lose all the water. Beaver dams could help amphibian populations to have a guarantee of breeding success with the water level staying stable and surviving droughts (Karraker & Gibbs, 2009).

Connectivity

The connectivity is an important factor to maintain a high number and stable value of amphibian populations. The more patches of small or medium sized ponds there are, not too isolated with small distances between them (less than 1.2 km) the better, as it facilitates the species dispersion (Nowakowski et al., 2015). In this study there was a mixed result for the connectivity, table 4 shows the number of other breeding ponds close to the beaver ponds each site had and the average distance amphibians should travel from these other breeding ponds. Results in this table show that if there are at least one or two amphibian breeding ponds nearby, the sites numbers in green, with more diversity of species (fig 6), were included. If there was no breeding pond around, these beaver sites had a low number or no species present. Thus, it gives an idea that beaver ponds had a positive impact increasing the already existing pond network of the amphibians. However, as the beaver territories-colonies are closely connected and have multiple dam ponds it increases the possibility for the amphibian species to disperse, using in some cases stream corridors (Cunningham et al., 2007). Further studies would be interesting following the movements of amphibians and look if they stay by the beaver ponds or if they move on somewhere else.

5. Conclusions

After four months of fieldwork going to the different 33 selected sites in three cantons of Switzerland all the beaver ponds, except two, were all occupied by at least one amphibian species. Meaning that amphibian populations are able to establish at the beaver ponds. Additionally, some of the beaver ponds were used by the common frog (*Rana temporaria*) to breed there and potentially by other species, as both anuran or urodele juveniles were also seen. However, it wasn't in just any type of beaver pond, some sites had more abundance and diversity of species. These types of beaver ponds, considered as preferred ones, were the flooded forests, bogs and some adequate canals with stagnant water. In these types of habitats beaver created environments with multiple ponds or stagnant water making it possible for the different species to occupy the most convenient one. The ponds that were abandoned or had no beaver activity were less attractive for amphibians since, if there is no beaver activity, then the habitat loses its heterogeneity maintained by them. This heterogeneity being more important the older the beaver dam is and mostly the case in flooded forests beaver ponds. Having more emergent and submergent vegetation to offer support for eggs, shelter and food for amphibian adults and larvae, decreasing predation risks, less canopy because of the beaver cutting trees, wood stamps for refuge etc. Although young dams (from one or two years old) are also important (with stagnant water ponds), expanding the connectivity of the already existing amphibian ponds network. With the results obtained from this study, beavers could have a very important role to play in conservation efforts. Maintaining beaver ponds, mostly mature ones or young ones, could help increase or keep stable Swiss amphibian populations offering opportunities to restore their habitats and aid in their long-term conservation. Thus, management and agreements with farmers or municipalities should be made to be able to keep these very important environments for other species as well.

To get even more details about the importance of beaver ponds, further studies could be done comparing them with other amphibian breeding ponds nearby to see if there is a variation on the abundance and diversity between these ponds. Checking more beaver sites in other parts of Switzerland, to see if there are more variable preferences depending on the region. And finally, revisit the same 33 sites in five or ten years to state the evolution of the sites. This will involve determining whether the habitat has become richer, whether the same abundance and diversity are still present, and whether the dams have remained unchanged or been destroyed by human modifications or floodings.

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