

HABITAT COMPLEMENTATION IN A SALAMANDER WITH A COMPLEX LIFE CYCLE

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Zusammenfassung

Habitatsergänzung wird definiert als die Nutzung verschiedener Habitate während eines Lebenszyklus einer Art über eine Landschaft verteilt, was wesentlich ist für Arten mit komplexen Lebenszyklen. Für Amphibien, welche sich im Wasser fortpflanzen, impliziert Habitatsergänzung, dass sowohl aquatische als auch terrestrische Habitate verfügbar sein müssen. Die relative Wichtigkeit von aquatischen und terrestrischen Habitatscharakteristika für Habitatsergänzung wird oft diskutiert, aber eine gewisse Unsicherheit verbleibt. Ferner ist über die relativen Effekte von den lokalen- sowie Landschafts-Skalen wenig bekannt. Wir haben Abundanzen von Larven des Feuersalamanders (*Salmandra salamandra*) in 50 Bächen in der Nordwestschweiz geschätzt, um die Wichtigkeit von terrestrischen und aquatischen Habitatscharakteristika zu beurteilen. Wir haben aquatische und terrestrische Habitatsvariablen wie z.B. Bachstruktur, Waldzusammensetzung und Wasserqualität im unmittelbaren Umfeld des Baches aufgenommen. Zusätzlich haben wir den Einfluss von Landschafts-Variablen wie Strassendichte und Landschaftszusammensetzung auf Abundanzen der Larven mittels eines Geoinformationssystemes auf einer Skala von 200m und 1km um die Bäche untersucht. Wir haben grosse räumliche Unterschiede in der Abundanz festgestellt, die am besten durch eine Kombination von Variablen auf verschiedenen Skalen erklärt werden konnten. Das aussagekräftigste Modell zeigte einen positiven Effekt der Länge von Kolken pro Bachabschnitt, einen negativen Effekt eines Fragmentierungsindex für Wald auf einer 200m Skala sowie einen negativen Effekt von engen, geteerten Strassen auf einer 1km Skala auf die Abundanzen der Larven. Unsere Resultate zeigen die Wichtigkeit des Einbeziehens mehrerer Skalen und Habitatsergänzung in ökologischen Studien über Arten mit komplexen Lebenszyklen. Des Weiteren diskutieren wir die Implikationen dieser Arbeit für den Artenschutz.

Abstract

Habitat complementation is defined as the use of different habitat patches throughout the landscape and life cycle and is crucial for species with complex life cycles. For aquatic-breeding amphibians, habitat complementation implies that both suitable aquatic and terrestrial habitats must be available. The relative importance of aquatic and terrestrial habitat characteristics for habitat complementation is often subject of discussion and uncertainty remains. Furthermore, the relative effects of local and landscape-level terrestrial habitats are poorly known. I estimated larval abundances of the fire salamander (*Salamandra salamandra*) in 50 streams in Northwestern Switzerland to assess the importance of terrestrial and aquatic habitat characteristics. I recorded both aquatic and terrestrial habitat variables such as stream structure, forest composition and water quality in the immediate (local) surroundings. I also investigated whether landscape-scale variables (e.g. road density and landscape) influence larval abundances by using a Geographic Information System on a 200m and 1km scale around the sampling location. I found strong spatial variation in abundance, which was best explained by a combination of variables at different scales. My top-ranking model showed a positive effect of the length of pools per stream section, a negative effect of a forest fragmentation index at the 200m scale, and a negative effect of narrow tarred roads at the 1km scale on salamander larvae abundance. My results show the importance of investigating multiple scales and the need for incorporating the concept of habitat complementation in ecological studies on species with complex life cycles. I further discuss implications for future conservation programs.

Keywords

Salamandra salamandra, abundance, habitat complementation, conservation, amphibian decline, habitat fragmentation, roadkill, removal sampling, Switzerland

Introduction

Species with complex life cycles (CLCs) occupy different habitats in each life stage (Wilbur 1980; Pope et al. 2000; Van Buskirk 2005). They benefit from intraspecific niche partitioning during their life cycle and thus diminish competition (Wilbur 1980). The complexity arguably does not lie in the diphasic life cycle that most metamorphosing species exhibit *per se*, but in the multileveled interactions, dependencies and feedback-loops that emerge from it. Adding to this complexity is the fact that species with CLCs are often not spatially restricted during their life cycle (e.g. host plant and near surroundings) and depend on habitat complementation, i.e. the use of different habitat patches offering different resources throughout the landscape and the annual cycle (Dunning et al. 1992; Resetarits 2005; Dulaurent et al. 2011). Examples for species with CLCs depending on habitat complementation can be found in several taxa such as Lepidoptera (Ouin et al. 2004), Hymenoptera (Tscharntke et al. 1998) or Amphibia (Van Buskirk 2005). Habitat complementation is achieved in terrestrial habitats through migration of the adult and sub-adult life stages (Wilbur 1980). This means that not only the local (reproduction site) but also the landscape scale (complementary habitat) is crucial for the persistence of these species (Van Buskirk 2005; Ficetola et al. 2011). For habitat complementation to be achievable, the landscape needs to be intact and offer the resources needed for species with CLCs (Van Buskirk 2005, 2012). However, in the face of widespread anthropogenic land use intact landscapes become increasingly scarce

(Stuart et al. 2004). Amphibians display habitat complementation and strongly depend on both accessible water bodies for reproduction and terrestrial habitat offering foraging and hiding opportunities with suitable microclimate (Wilbur 1980; Sparreboom 2014). Due to this dependency, amphibians are especially affected to changes in land use, as their recruitment sites are being destroyed at an alarming rate and habitat connectivity is decreased as landscapes become increasingly fragmented (Stuart et al. 2004; Cushman 2006; Schmidt et al. 2007). In addition is movement ability in the Anthropocene adversely impacted by roads in anthropogenic landscapes, as they increase habitat fragmentation and cause high mortality rates (e.g. through roadkill) due to the high migratory activities of species with habitat complementation (Van Buskirk 2005; Marsh et al. 2017). However, when investigating landscape scale variables, the outcomes of studies strongly depend on the spatial resolution and it is important to investigate broad scales around reproduction sites of species with CLCs (Schmidt et al. 2005; Stoddard & Hayes 2005). It is not quite clear in many cases at which spatial resolution landscape scale processes affecting species with habitat complementation ultimately transpire as it depends on several factors such as migratory activity of adults and movement ability between microhabitats (Petranka et al. 2004; Cushman 2006; Bar-David et al. 2007; Van Buskirk 2012).

The fire salamander (*Salamandra salamandra*) is strongly affected by processes altering habitat suitability. It is declining steadily in Switzerland over the past decades and became listed as a threatened species in 2005 in the Swiss Red List (Schmidt & Zumbach 2005). The reasons for this are mostly unclear, but roadkill and the release of fish in formerly fishless streams have been suggested as possible causes (Schmidt & Zumbach 2005). *S. salamandra* have a unique ecology as they are the only ovoviviparous amphibians in central Europe with an aquatic larval stage (Sparreboom 2014). *S.*

salamandra are biological indicators and a keystone species as they are mid-level predators, strongly intertwined with several aspects of the ecology of broad leaved forests and connect aquatic with terrestrial energy and nutrient flows (Davic & Welsh, 2004; Nery & Schmera, 2016). For recruitment, they depend on natural first and second order streams with sections of reduced flow speed, located within or in proximity to broad leaved forests (Baumgartner et al. 1999; Manenti et al. 2009). In addition, landscape composition and the hydrological network also holds importance (Manenti et al. 2009; Ficetola et al. 2011; Manenti et al. 2013). However, more research is needed on this topic, especially regarding landscape composition, habitat fragmentation and the impact of roads.

To obtain further insights in this matter, I chose to estimate larval abundances of *S. salamandra* in several streams in Northwestern Switzerland. *S. salamandra* larvae are spatially restricted, which allows for accurate estimations of abundances (Schmidt 2004; Schmidt et al. 2015). For the investigation of landscape scale variables, I extracted data on two spatial scales via a geographic information system: 200m and 1km radii around the sampling location. 200m was chosen because adults are believed to migrate mostly within 200m (Ficetola et al. 2012). However, an organism does not perceive its habitat on a single scale (Kotliar & Wiens 1990; Stoddard & Hayes 2005). A 200m buffer might not capture large scale effects such as interpopulation dispersal (Semlitsch 2008). In addition, there is some evidence that migration ability of juveniles might be underestimated, as juveniles migrate on larger spatial scales when populations in the surrounding habitat are not at their carrying capacity (Cabe et al. 2007). For these reasons, I included a 1km buffer around the sampling locations in the analysis of landscape scale variables. Larvae are most certainly not as directly affected by most landscape scale variables (e.g. roads) as adults. However, a strong effect on adults will

eventually translate to the larval subpopulation and vice versa. Therefore, I expect a positive correlation between larval and adult abundance. My study takes a rather conservative approach regarding my investigation on terrestrial variables; meaning that false negatives might be obtained but false positives are rather unlikely. The goals of this study are to 1) identify the variables underlying the differences in larval abundances of *S. salamandra* and to 2) investigate at which scale population processes have the greatest impact.

Methods

Sampling of salamander larvae

S. salamandra larvae in fifty randomly selected streams from a pool of 187 known occurrences were sampled in the cantons Aargau and Basel-Landschaft, Northwestern Switzerland (Figure 1). A section of 25m length was defined for each stream with the centre being closest to the randomly selected coordinate. Sampling was conducted from April 28th to July 1st 2016, i.e. when salamander larvae abundances are typically high (Kopp and Baur, 2000). The number of larvae was estimated using removal sampling (White et al. 1982; Schmidt et al. 2015). Three subsequent removal sessions per stream section were done, each lasting 15 minutes. Sampling always started downstream towards upstream to maintain water clarity and only took place on dry days, to diminish discharge and water turbulence from rain. Every salamander larva found was put separately in a plastic cup and left nearby the stream. The larvae in the cups were covered with a leaf and left in the shade. After the three removal sessions were completed, the salamander larvae were counted and released at the site of capture. It

can be safely assumed that during this brief period neither downstream drift nor mortality occurred and that the populations were closed.

Recording of habitat variables in the field

Both biotic and abiotic variables that might influence larvae abundance were sampled in and around the streams directly after and during salamander sampling. Variables described both the aquatic and terrestrial environment. Abiotic factors included air and water temperature, pH, stream bed width, flow speed and number of pools. Both air and water temperature as well as pH were measured once in the middle of the stream section. Temperature impacts growth rate and activity in all animals, especially in ectotherms (Beachy 1995; vanderHave & deJong 1996; Grant et al. 2014). Although pH probably is not a primary factor for habitat selection of *S. salamandra* (Grant et al. 2014), it still can cause stress and mortality in some cases (Green & Peloquin 2008). Stream width was measured at four points along the stream section, spaced five meters from one another (Figure 2). Abundances might be lower in wider streams, because *S. salamandra* larvae particularly occupy first and second order streams (Baumgartner et al. 1999; Sparreboom 2014). Flow speed measurements were carried out in the middle of the stream outside of pools. These measurements were conducted through adding a drop methylene-blue ($C_{16}H_{18}ClN_3S$) to the water and determining the duration needed for it to flow one meter. Salamander larvae are stressed by turbulences, which increase with higher flow speeds (Baumgartner et al. 1999). Additionally, there is a strong downstream drift due to high flow speeds; floods in particular (Thiesmeier & Schuhmacher 1990; Baumgartner et al. 1999). To mitigate these effects, *S. salamandra* larvae often occur within pools, which serve as a refuge (Baumgartner et al. 1999;

Tanadini et al. 2012). For this reason, the lengths of pools for each 25m stream section were measured. Pools were defined as quiet sections of the stream with clearly reduced flow speed and turbulence due to stowage (Baumgartner et al. 1999). The pools were measured from the point where riffles waned to the barrage itself.

Biotic factors included presence of green algae which served as an indicator for nitrogen deposition. The abundances of several aquatic macroinvertebrates (i.e. Gammarus spp., Trichoptera spp., Plecoptera spp., Ephemeroptera spp., Diptera spp., Asellus spp., Hirudinea spp. and Plathelminthes spp.) were estimated, from which a saprobic index was calculated in accordance with the Naglschmid method (Czerniawska-Kusza 2005; Lubini et al. 2014) as a proxy of water quality. This was done thrice for the whole stream section simultaneously with the sampling of the salamander larvae, to improve estimates of their abundance.

Around the stream, the trunk circumferences of live and dead woody plants with a diameter larger than 7cm were recorded one meter above the ground along three 15m long transects (Figure 2). Only dead wood intersecting each transect was recorded, while live wood was measured within a one meter buffer around the transect. Dead wood serves as potential hiding opportunity for adults (Baumgartner et al. 1999). In addition, live wood was identified to species level as salamander abundances might depend on tree species composition (Sparreboom 2014). *S. salamandra* is strongly associated with forest cover (Manenti et al. 2009; Ficetola et al. 2011). Older forests might be more suitable to support larger populations of *S. salamandra*, for which reason the trunk circumference was measured.

Recording of habitat variables using GIS Analysis

To analyse the terrestrial habitat variables, 200m and 1km buffers were created around each sampling coordinate. For both buffers, data for the following was extracted: square meters of primary surface (forest, settlement and open area), distance of sampling locations to nearest forest, length of roads for each road class, length of hydrological network, length of streams in proximity to roads and finally length of hydrological network exclusively within forests. From the square meters of primary surface three indices for forest fragmentation were calculated in accordance with Jaeger (2000). The degree of landscape division index (DIVI, the likelihood that two random patches are not within the same unfragmented area), splitting index (SPLI, the number of patches obtained when dividing the total area into equal patch sizes without changing the DIVI) and effective mesh size (MSIZ, the size of patches when the total area is divided by the SPLI without changing the DIVI) were calculated (Jaeger 2000). These three indices are suitable for virtually all stages of habitat fragmentation (Jaeger 2000). To deposit the larvae, female *S. salamandra* need to be able to reach the streams. If no stream is available within the forest, they might be forced to cross open fields and settlement areas, which could cause high mortality (Guerry & Hunter 2002; Rothermel 2004; Cushman 2006). For this reason, the distance of the sampling location to the nearest forest edge was included as a variable. As mentioned above, roads reduce dispersal ability and increase amphibian mortality because of roadkill (Van Buskirk 2012; Marsh et al. 2017). The length of the hydrological network was calculated because habitat quality for *S. salamandra* should increase with more available streams (Manenti et al. 2009). When in search for suitable streams, salamanders are likely to cross a road. This probability is increased if the roads run parallel to a stream. As an approximation for this, the length of stream network within 50m distance to roads was calculated. To

do so, buffers of 50m for both stream network and roads were created. The intersect of these buffers was then in turn intersected with the hydrological network. The GIS Analysis was carried out with ArcGIS v10.5 and Vector25 maps from the Federal Office of Topography.

Statistical Analysis

The data was analysed using a hierarchical model framework to estimate abundances recorded via removal sampling (Royle & Dorazio 2006). The function *gmultmix* in the R-Package *unmarked* was used, as it provides a framework for fitting hierarchical models. It allows the analysis of removal sampling in closed populations and can account for imperfect detection (Kery & Schmidt 2008; Fiske & Chandler 2011; R Core Team 2016). In a first step, all variables were standardized. By means of a model selection approach, the model fitting the abundances best was identified. All models were fitted with either negative binomial or Poisson distribution. The model selection procedure was conducted using AIC-based methods (Burnham & Anderson 2002). Because the quantity of variables was quite high, generating a model including all variables and subsequently simplifying the model was unfeasible. Therefore, single covariate models for both abundance estimation and detection probability were created. The ten single covariate models with the lowest AIC values were retained and a general model was constructed including the explanatory variables from the selected models. A description of the best explanatory variables can be found in Table 1. Said model was then simplified by excluding single covariates to find the model with the lowest AIC value.

Results

In total, 598 larvae with an average of 11.96 (\pm 2.23) and a maximum of 55 individuals per stream were detected. In eleven out of the 50 visited streams (22%), no salamander larvae were found. Models with negative binomial distributions fitted my data better than Poisson distribution based on AIC values. Covariates for detection probability p did not improve AIC values. The following explanatory variables for estimating larval abundance (λ) were always present in the top-ranking models (Table 2): the amount of pools (0.455 ± 0.171 SE, p -value = 0.008), degree of landscape division index for forests (DIVI) at the 200m (-0.575 ± 0.186 , p -value = 0.002) and the length of “class 3” roads (-0.664 ± 0.163 , p -value < 0.001) at the 1km scale (the summary statistics were taken from the top-ranking model). The top-ranking general model contained exclusively these three covariates (Table 2). The next best models contain in addition up to three further covariates; however, without any consistency. The estimated abundance in relation to the three covariates contained in the top model can be seen in Figure 3.

Discussion

The goals of this study were to identify habitat variables underlying spatial variation in salamander larvae abundance and the scales at which population processes have the greatest impact. I successfully identified several crucial habitat variables explaining variation in salamander larvae abundance. Both local (stream and its immediate surroundings) and landscape (at 200m and 1km radius around the sampling locations) scale variables proved to be important, as my top-ranking general model included a variable of each. While many variables explained much of the variation, the top-ranking model only included the length of pools within a stream section, the forest division index

within a 200m and the length of narrow tarred roads within a 1km radius around the sampling location (Table 2).

It seems that, except for pools, the most important drivers behind salamander larvae abundance are of anthropogenic origin. It is known that pools positively influence salamander larvae abundance (Thiesmeier & Schuhmacher 1990; Tanadini et al. 2012). My result showing that the negative effect of degree of landscape division for forests (DIVI) was more important than the actual area covered by forest was striking. Even though natural forests with good foraging and hiding possibilities for adults as well as natural streams for completing the larval stage probably are the main fundamental determinants for *S. salamandra* abundance, their populations are impacted so severely by roads and habitat fragmentation that these variables lose some of their relevance. Therefore, it seems likely that small forest patches are not suitable for *S. salamandra* populations and that forest patch-size is more important than the total amount of forest around the breeding locations. Higher habitat division increases mortality during migrations and limit dispersal, further promoting isolation (deMaynadier & Hunter 2000; Cushman 2006). Increased isolation in turn has a negative impact on demographic, genetic and stochastic processes (Gulve 1994; Rothermel 2004). The finding that *S. salamandra* is severely impacted by forest fragmentation has been shown before (Bani et al. 2015; Pisa et al. 2015). A negative effect regarding isolation is in my study more noticeable on the 200m than on the 1km scale. Juvenile and adult *S. salamandra* migrate mostly within 200m per year (Schulte et al. 2007; Ficetola et al. 2012). This might explain the greater impact of the smaller scale regarding fragmentation as it is the scale where the actual individual migrations occur.

Large scale processes can be seen in my results on the negative impact of narrow tarred roads ('class 3'), as their effect was especially pronounced on the 1km scale. Class 3 roads were among the most common road types in my study area and most likely have higher traffic densities compared to other narrow roads, as they are often the sole mean to reach a village by car. The underlying mechanisms behind the negative impact of narrow tarred roads driving salamander population sizes are debatable as I cannot confirm causality in this study. One explanation could be that road construction cause habitat fragmentation by incising forests. However, this did not seem to be the case here as these two variables were not strongly correlated (correlation coefficient = 0.31 between DIVI and class 3 roads at 1km scale). The greatest impact of roads on amphibians most likely lies in causing direct mortality through roadkill (Marsh & Jaeger 2015; Marsh et al. 2017). Unfortunately, there are no data on the amount of *S. salamandra* killed by roadkill, to my knowledge. Roads within suitable habitat act as a constant drain on adults. This loss of adults within *S. salamandra* populations has a profound impact as they are the main drivers behind population trends (Schmidt et al. 2005). If roads are present on a small scale, the loss of adults might be mitigated through immigration by surrounding source habitats. Only if roads are present on a large scale, an overall decline might become noticeable. Further research is needed to understand the negative impact of roads on *S. salamandra* and the role it is playing on population decline.

In summary, processes stemming from forest division act on a small scale, possibly due to direct dependence on the migratory ability of the focal species, but variables causing direct mortality such as traffic must be widespread on a large scale to affect this species adversely. Both variables impede the migratory ability within and between populations and indicate the dependence of *S. salamandra* on habitat complementation.

Even though only data on abundances of the larval stage was collected, I found that most main drivers underlying the differences in abundance are of terrestrial origin. Due to the conservative approach of this study to the examination of landscape scale variables the effect might be even greater when investigating the adult subpopulation. My results emphasize the importance of investigating both local and macro scale variables as key processes go unnoticed when only focusing on one spatial resolution, as has been suggested by several other studies (Kotliar & Wiens 1990; Stoddard & Hayes 2005). I found that the main reasons behind the decline of *S. salamandra* are of anthropogenic origin, namely habitat fragmentation and road network. This offers some implication for future conservation projects as *S. salamandra* is classified as vulnerable and its decline is still ongoing (Schmidt & Zumbach 2005). Steps need to be taken to restore streams, decrease forest fragmentation in the long term and restrict traffic in suitable habitat. However, these measures might prove difficult, but not impossible, to implement. Restoring streams might be the most applicable option. Streams have been increasingly channelled and straightened in the past decades. This is suboptimal for *S. salamandra* larvae, as it uniformes water flow and prevents the formation of pools (Baumgartner et al. 1999). To mitigate the negative effects of roads on amphibians more long-term solutions must be found, such as reducing road traffic in general (e.g. via public transport), restrict road construction or confine traffic during the breeding season in vicinity of crucial reproduction sites. Regarding forest fragmentation, policies must be found to decrease urbanization and promoting sustainable agriculture next to high quality habitat, as there is evidence that amphibians are not affected by traditionally managed pastures (Manenti et al. 2013).

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Statement of Authorship:

I declare that I have used no other sources and aids other than those indicated. All passages quoted from publications or paraphrased from these sources are indicated as such, i.e. cited and/or attributed. This thesis was not submitted in any form for another degree or diploma at any university or other institution of tertiary education.

Zurich, 30.03.2017

A handwritten signature in blue ink, reading "Oliver Dorsch". The signature is written in a cursive style with a large initial 'O'.

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Tables and Figures

Table 1: Description of the variables used in the top ten ranking models.

Variable	Abbreviation	Description
Meter Pools	Pools	Summed length of pools in a 25m stream section
Stream Width	StrWid	Average stream width, measured at four locations
Stream Assessment	StrAssess	Classification of the degree of naturalness of a stream
Degree of Forest Division 200m	DIVI.200	Degree of Forest Division in a 200m buffer
Length "Class 1" roads 200m	str1.200	Length of roads > 6m width in a 200m buffer
Area Forest 1km	AreaFo.1k	Total area covered by forest in a 1km buffer
Area Settlement 1km	AreaSe.1k	Total area covered by settlement in a 1km buffer
Degree of Forest Division 1km	DIVI.1k	Degree of Forest Division in a 1km buffer
Forest Mesh Size 1km	MSIZ.1k	Effective mesh size of forested area in a 1km buffer
Length "Class 3" roads 1km	str3.1k	Length of roads ≥ 2.8 m; <4m width in a 1km buffer
Length of streams in proximity to roads	Para.1k	Length of streams in a buffer around roads. Approximation for parallelism.

Table 2: Results of the removal sampling model selection procedure. λ stands for abundances of *S. salamandra*. The best models all showed negative binomial distribution and did not contain covariates for detection probability p and were set at $p \sim 1$. The models are ranked by their lowest AIC values. ω shows the Akaike weight. Only models with an Akaike weight of $\omega \geq 0.02$ are listed.

Model	ΔAIC	ω
$\lambda \sim \text{Pools} + \text{DIVI.200} + \text{str3.1k}$	0.00	0.18
$\lambda \sim \text{Pools} + \text{DIVI.200} + \text{str3.1k} + \text{DIVI.1k}$	0.11	0.17
$\lambda \sim \text{Pools} + \text{DIVI.200} + \text{str3.1k} + \text{StrAssess}$	0.37	0.15
$\lambda \sim \text{Pools} + \text{DIVI.200} + \text{str3.1k} + \text{AreaMesh.1k}$	1.14	0.10
$\lambda \sim \text{Pools} + \text{DIVI.200} + \text{str3.1k} + \text{AreaFo.1k}$	1.58	0.09
$\lambda \sim \text{Pools} + \text{DIVI.200} + \text{str3.1k} + \text{StrWid}$	1.99	0.06
$\lambda \sim \text{Pools} + \text{DIVI.200} + \text{str3.1k} + \text{AreaFo.1k} + \text{StrAssess}$	2.22	0.06
$\lambda \sim \text{Pools} + \text{DIVI.200} + \text{str3.1k} + \text{MSIZ.1k} + \text{DIVI.1k} + \text{str1.200}$	3.38	0.03
$\lambda \sim \text{Pools} + \text{DIVI.200} + \text{str3.1k} + \text{AreaFo.1k} + \text{Para.1k}$	3.47	0.04
$\lambda \sim \text{Pools} + \text{DIVI.200} + \text{str3.1k} + \text{Para.1k}$	3.96	0.02

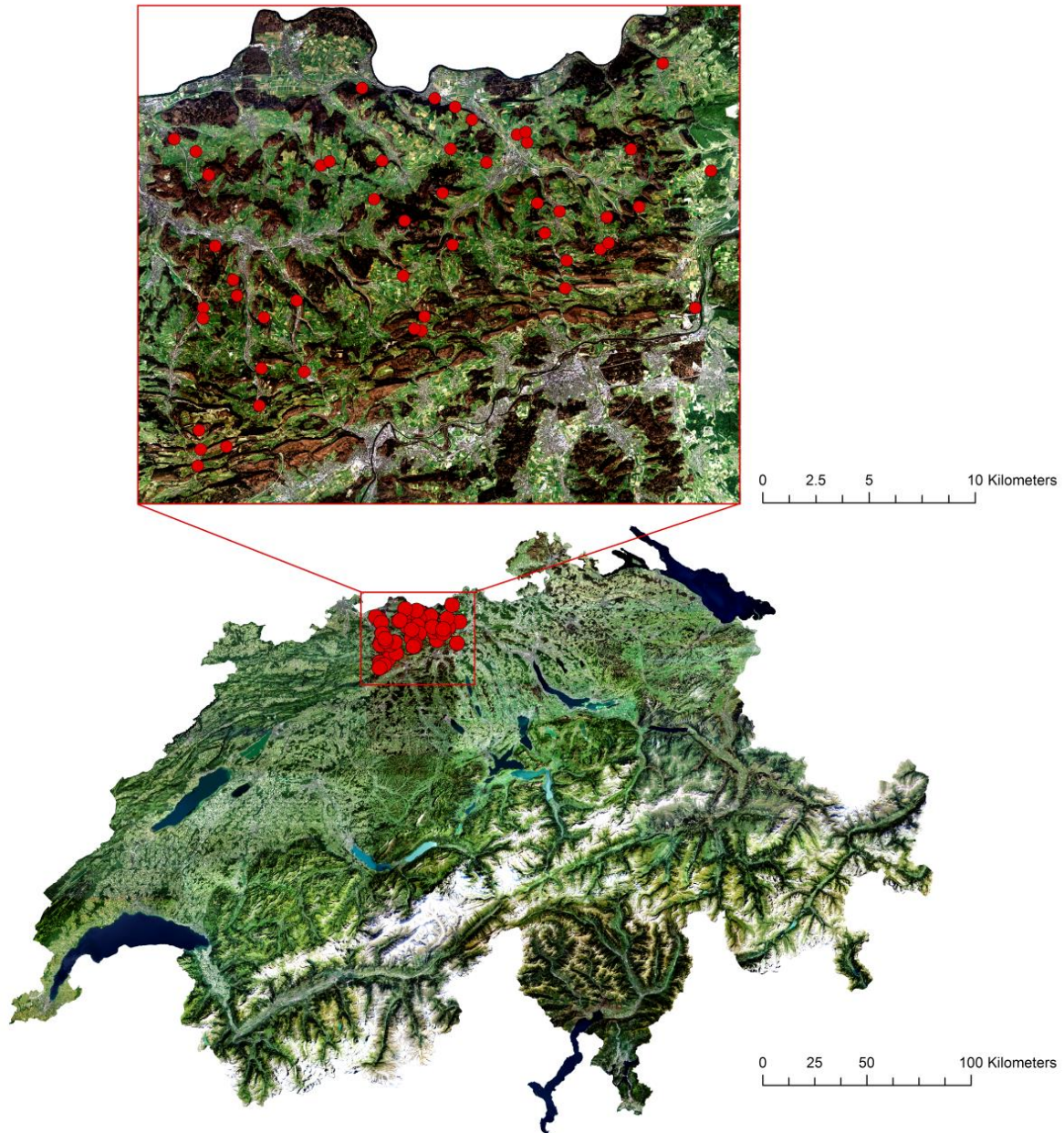


Figure 1: Map depicting the 50 sampling locations in the cantons Aargau and Basel-Landschaft in Switzerland.

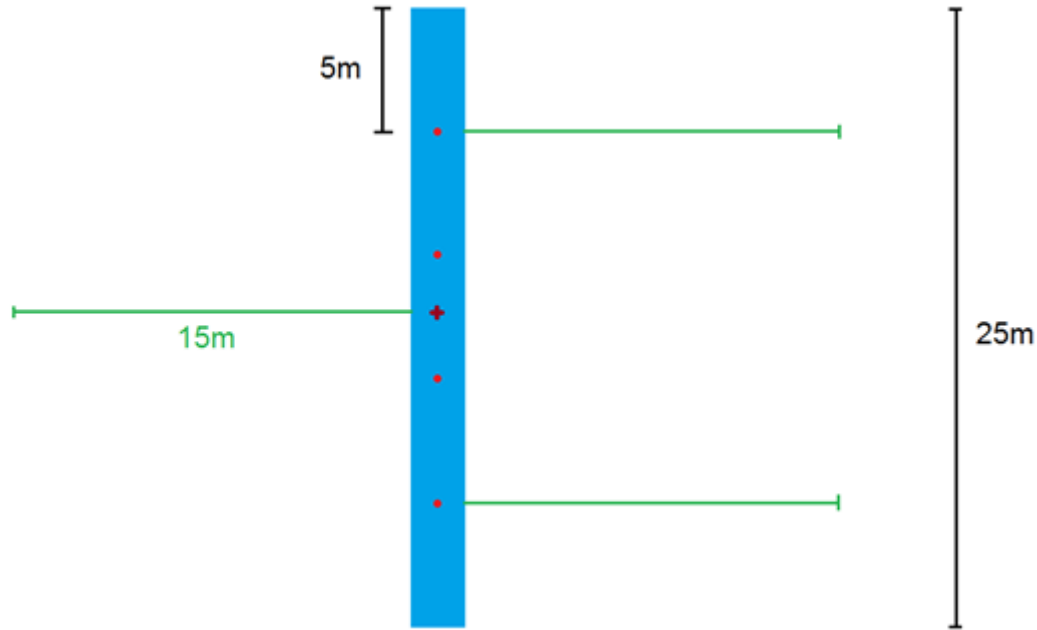


Figure 2: Sampling design of the removal sampling and recording of local habitat variables. The stream is symbolized by the blue area, the green lines show the transects for the local forest covariates and the red dots the locations where stream width was measured

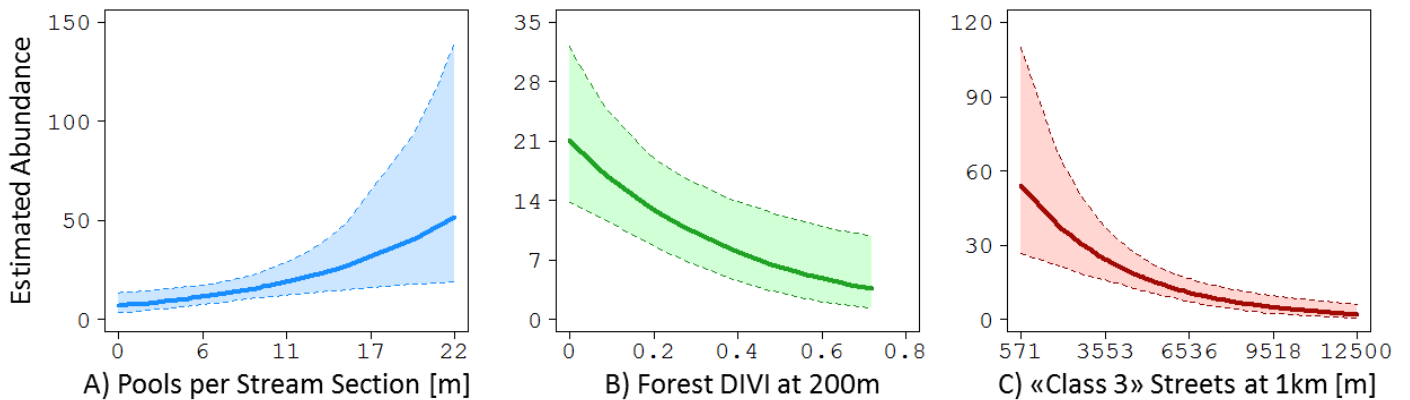


Figure 3: Plots showing the relationship between salamander larvae abundance and the three covariates of the top-ranking model. A) shows the length of pools per 25m stream section, B) the degree of landscape division for forests at a 200m radius and C) the length of narrow tarred roads ($\geq 2.8\text{m}$, $\leq 4\text{m}$) within a 1km radius around the sampling location.