



## Do habitat preferences of European fire salamander (*Salamandra salamandra*) larvae differ among landscapes? A case study from Western Germany

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**Abstract.** The European fire salamander (*Salamandra salamandra*) is a widespread species that occurs in a variety of habitats throughout its range. We studied if different environmental parameters influence presence as well as abundance of larvae within different local landscape units across a more than 5,000 km<sup>2</sup> large Central European study area. This knowledge is crucial to differentiate between habitat specific absence/low abundance and externally triggered extinctions or population declines, e.g. through newly emerging infectious diseases. Within our study area, the salamander plague, caused by the invasive fungus *Batrachochytrium salamandrivorans*, has recently been invoked as major factor for population declines in *S. salamandra*. We estimated larval habitat preferences of 135 European fire salamander populations (presence-absence only), and estimated larval abundances in 85 out of them. In the entire study area, regardless of landscape units, presence of European fire salamander larvae was positively affected by low elevation, a high number of pools (preferred larval microhabitats) and a high amount of consumable macrozoobenthos in the reproduction creeks as well as a high proportion of forest cover in the surrounding terrestrial habitats. Apart from some minor differences among landscape units when they were analysed separately, we observed in many cases a positive effect of a high number of pools (11 out of 56 overall models = 20%) and, furthermore, a negative effect of a late mapping date (mainly due to larval drift caused by heavy rainfalls in early summer and metamorphosis) on larval abundances (12 out of 56 overall models = 21%). Consequently, at least in this Central European study area, which includes mountainous regions up to 700 m a.s.l. ('West- and Osteifel', 'Hunsrück'), a mainly agriculturally used lime soil plateau ('Gutland') and a river valley ('Moseltal'), these habitat preferences can be used to differentiate between habitat-caused and disease-caused absence of European fire salamanders and also population declines using the larval population.

**Key words.** Amphibia, Caudata, chytridiomycosis, habitat suitability, *Batrachochytrium salamandrivorans* salamander plague, larval ecology, stream habitat.

### Introduction

Amphibians are dramatically declining at the global scale (STUART et al. 2004, 2010, WAKE & VREDENBURG 2008). Habitat change, environmental pollution, alien species, over-exploitation, global change and emerging infectious diseases are main factors for amphibian population declines and extinctions (e.g. DASZAK et al. 2000, COLLINS & STORFER 2003). This also applies to the European fire salamander, *Salamandra salamandra*, a common species in Western Europe (THIESMEIER 2004). Beside conversion of deciduous into coniferous forests (THIESMEIER 2004) or pollution of larval habitats (MANDRILLON & SAGLIO 2007), this species is now locally threatened by amphibian chytridiomycosis, an emerging infectious disease: While in

the Pyrenees, population declines were described due to the amphibian chytrid fungus *Batrachochytrium dendrobatidis* (BOSCH & MARTÍNEZ-SOLANO 2006), a second chytrid fungus, *B. salamandrivorans* (*Bsal*), is responsible for local population declines in Central Europe, especially Germany (MARTEL et al. 2013, 2014, SPITZEN-VAN DER SLUIJS et al. 2016, STEGEN et al. 2017, DALBECK et al. 2018, LÖTTERS et al. 2020 in this issue, SCHULZ et al. 2020 in this issue). Unfortunately, according to these authors, disease-driven declines of European fire salamander populations may occur unnoticed.

With the goal to better understand potential past declines in Germany, SANDVOß et al. (2020 in this issue) analysed the characteristics of larval habitats in a *Bsal*-free area. Using an ecological modelling approach, they then

compared their results with data from a mountain chain where, despite several former records, European fire salamanders are only sparsely found today. They focussed on the larval populations since European fire salamander larvae can be easily detected using standard methods within their mostly lotic freshwater habitats, while the strong cryptic behaviour of the terrestrial life-stages hampers a large-scale mapping of the species within a given area (cf. THIESMEIER 2004, SKELLY & RICHARDSON 2009). For this purpose, SANDVOß et al. (2020 in this issue) applied a standardised removal sampling approach proposed by SCHMIDT et al. (2015), which allows a rapid quantitative assessment of the larval population. SANDVOß et al. (2020 in this issue) then used a presence-absence habitat suitability model built upon data from the disease-free region to show that most creeks in the area where species is sparse today in fact constitute highly suitable larval habitats. They concluded that *Bsal* might have driven these populations to extinction, as in addition to their modelling results, the pathogen was observed in alpine (*Ichthyosaura alpestris*) and palmate newts (*Lissotriton helveticus*) and – most recently – in one of the last remaining European fire salamander populations in this area (SANDVOß et al. 2020 in this issue).

Habitat suitability models are frequently used in conservation planning to quantify a species' habitat requirements, to understand species-habitat relationships and to predict species occurrences (e.g. AHMADI-NEDUSHAN et al. 2006). They come in different methodological flavours, with mere presence-absence data being the simplest way to feed such models, often just to verify the use of a habitat by a species rather than the success of that use. Major input variables are local biotic and abiotic habitat characteristics, which affect the presence (e.g. SANDVOß et al. 2020 in this issue) and abundance and thus the range of a focal species (SCHMIDT et al. 2015, WAGNER et al. 2020 in this issue). Habitat suitability models based on local data may capture both general ecological and potential local adaptations. Hence, it may be questioned that they will assign meaningful suitability values to habitats outside this area, so in consequence they may lead to insufficient or even false management decisions.

To differentiate between naturally caused absence or low abundance of European fire salamander larvae (e.g. due to unsuitable aquatic or terrestrial habitats) and extinctions/population declines due to emerging infectious diseases caused by invasive pathogens, especially *Bsal*, we here present the results of a presence-absence mapping and abundance estimations of European fire salamander larvae based on standardized removal sampling in a more than 5,000 km<sup>2</sup> large study area in Western Germany. To test the performance of local models, we divided our study area into natural landscape units (Fig. 1) to compare local habitat preferences of the study species. We conducted presence-absence mapping in the German federal state of Rhineland-Palatinate in different regions including mountainous areas ('Eifel', 'Hunsrück'), a mainly agriculturally used plateau ('Gutland') and the river valley of the Mo-

selle between 2016 and 2019. Furthermore, we included the presence-absence data from SANDVOß et al. (2020 in this issue) from the 'Eifel' and the 'Gutland' from 2016 in the analysis to get an even larger data set. The goal of the study was to identify the main biotic and abiotic variables, which explain presence-absence as well as abundances and detection probabilities of European fire salamander larvae. Since *S. salamandra* has colonized Central Europe only after the last ice age (VEITH 1992) and thus constitutes a genetically rather uniform population here (STEINFARTZ et al. 2000), we expected that local habitat suitability models developed from different areas would identify similar biotic and abiotic predictors of the species' occurrence and abundance.

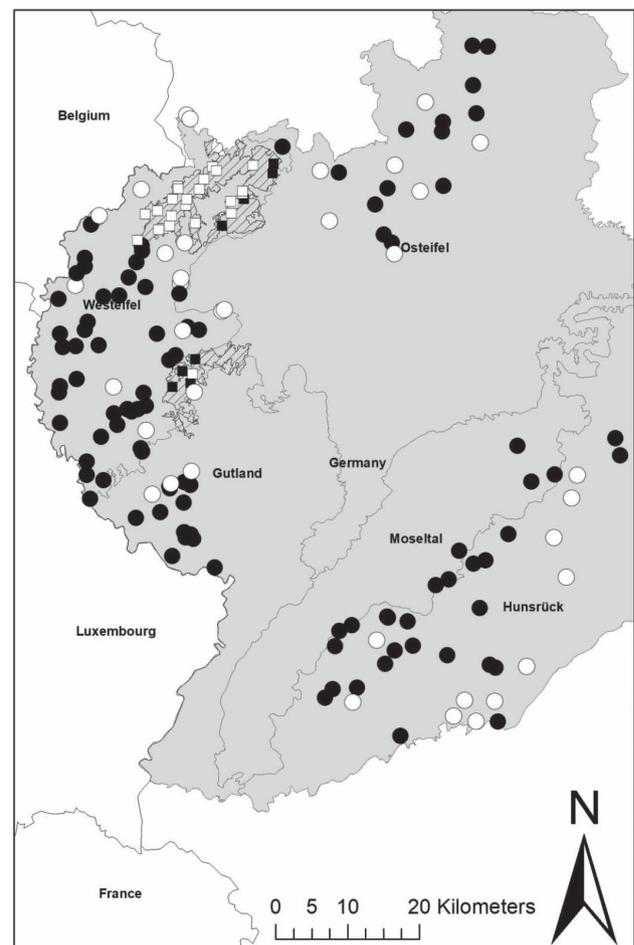


Figure 1. Study area in western Germany, divided into five landscape units. Hatched polygons indicate the continuous forest areas in which *Bsal* was detected and no creeks were considered for neither habitat suitability nor abundance modelling. Solid symbols indicate the localities of European fire salamander reproduction creeks, and open symbols creeks, where larvae of the species were not found. Circles indicate creeks, which were used in the analysis; squares those from the *Bsal*-affected forest areas that were excluded from the analysis.

## Materials and methods

### Study area

We conducted our study in the north-western part of the German federal state of Rhineland-Palatinate. The study area encompasses more than 5,000 km<sup>2</sup> and, according to MEYNEN & SCHMITHÜSEN (1962), can be divided into five landscape units: ‘Hunsrück’, ‘Moseltal’ (Moselle valley), ‘Gutland’, ‘Westefel’, ‘Ostefel’ (Fig. 1). The landscape units ‘Ostefel’ and ‘Westefel’ are the northern highlands of the study area and are part of the Rhenish Slate Mountains, with elevations up to ca. 700 m a.s.l. and with high proportions of planted coniferous forests (mainly *Picea abies* or *Pseudotsuga menziesii*). However, especially at the western slopes with red sand stone, at the border to Luxembourg, deciduous and mixed forests as well as large *S. salamandra* populations are found (WAGNER et al. 2017). The ‘Gutland’ is a plateau with mainly lime soils; therefore, agricultural land use is predominant here, but with several remaining deciduous or mixed forest, especially at the western part (partly red sand stone) into the direction of Luxembourg. The ‘Moseltal’ and the ‘Hunsrück’ are also parts of the Rhenish Slate Mountains. The ‘Moseltal’ is characterised by high proportions of vineyards on its steep slopes, but also residual forest patches and creeks that flow into the Moselle. In the ‘Hunsrück’, the southern highland of the study area with elevations up to above 600 m a.s.l., natural forests have been replaced by exotic *P. abies* and partly *P. menziesii*.

### European fire salamander occurrences

In suitable habitats within the entire study area (especially deciduous forests with small first and second order creeks; THIESMEIER 2004), large and stable populations of *S. salamandra* have continuously been reported in all five landscape units (BITZ et al. 1996, WAGNER et al. 2017). However, the amphibian pathogen *Bsal* was recently detected in two forest areas of the region, which are almost entirely situated in the ‘Westefel’ (Fig. 1). Twenty-four creeks with absence and eight creeks with presence of salamander larvae from these two sites were therefore excluded from habitat suitability analysis and abundance modelling (Fig. 1) because absence or low abundances could be already disease-caused here.

### Data acquisition

Presence-absence of larvae and larvae population size were used as response variables. Since the terrestrial life-stages show pronounced cryptic behaviour, they can only be detected during specific weather conditions at night (temperatures above 5°C, rainfall) (THIESMEIER 2004), and their terrestrial habitat can by quite large (SCHULTE et al. 2007). This is similar to many other amphibian species where larval sampling is a more effective way to monitor presence

and abundances (SKELLY & RICHARDSON 2009). Fieldwork was carried out from May to July 2016–2018. We consistently choose 75 m long sections next to the springs of 135 creeks, the preferred region where adult females of this larviparous species give birth to their offspring (mainly between March and May; THIESMEIER 2004). Hence, with beginning of our mapping, most larvae should have been deposited. We used the protocol described by SCHMIDT et al. (2015) to conduct a removal sampling in 85 of the creeks. Each 75 m section was subdivided into three 25 m subsections and in each subsection one person was capturing larvae using a dip net for 15 min. All larvae were removed from the creek and kept in plastic aquaria until the end of the sampling. Then, all persons rotated two times, so that finally nine capture events were conducted within 45 min. Subsequently, all larvae were released back to their subsections. For presence-absence monitoring in the remaining 50 creeks, data acquisition stopped when the first larva was discovered (confirmed presence); otherwise, after three unsuccessful capture attempts (i.e. a full removal sampling attempt without captures), a second 75 m section was chosen, and after another three unsuccessful capture events larvae were considered as truly absent. Several environmental variables were recorded in order to characterise each creek (larval habitat) and its surrounding terrestrial (adult) habitat (Table 1). After field work and when changing between localities, we carefully disinfected all boots and materials for at least 5 min using 0.5% Virkon S<sup>®</sup> solution to prevent transfer of potentially present zoospores (VAN ROOIJ et al. 2017).

### Statistical analysis

The software R 2.15.1 was used for all analyses (R Development Core Team 2012). In a first step, logistic regression models (function glm, Generalized Linear Models, GLMs, with logit link) were calculated for presence-absence data. We used the landscape unit as categorical variable and included it into all models (Fig. 1). Further potential predictor variables for presence and abundance of larvae (Table 1) include the record date because it is known that there are natural fluctuations in amphibian population sizes not only between years (e.g. MEYER et al. 1998) but also within a year due to, for instance, predation, but here mainly due to larval drift (especially catastrophic drift after heavy rainfalls: THIESMEIER & SCHUMACHER 1990, REINHARDT et al. 2018, VEITH et al. 2019). Elevation was used as a potential predictor because in the neighbouring federal state of North Rhine-Westphalia an elevational limit of 600 m a.s.l. for the European fire salamander is described (THIESMEIER & DALBECK 2011). With regard to the larval habitat, the number of pools within the creek, creek width, the water flow and the presence of predatory fish (especially salmonids; presence-absence coded) are important factors known to influence the abundance of larvae (BAUMGARTNER et al. 1999, WERNER et al. 2014, SCHMIDT et al. 2015). The tilt (°) parallel to the studied creek section influ-

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Table 1. Variables recorded at each studied creek to model presence-absence probabilities as well as larval abundances and detection probabilities.

Variable	Potential effect on detection probability	Reason	Potential effect on larval presence/abundance	Reason
Date	(Yes)	Indirectly over larval abundances	Yes	Larval drift, predation
Elevation	(Yes)	Indirectly over larval abundances	Yes	Due to known elevational limits of the species
Aquatic habitat				
Number of pools	Yes	Accumulation of larvae in pools	Yes	Preferred larval microhabitat
Creek width	Yes	Visibility of larvae, influence on water flow, larval drift	Yes	Influence on water flow, larval drift
Presence of predatory fish	(Yes)	Indirectly over larval abundances	Yes	Predation of larvae
Tilt parallel to creek section	(Yes)	Indirectly over larval abundances	Yes	Influence on water flow, larval drift
Tilt perpendicular to creek section	(Yes)	Indirectly over larval abundances	Yes	Accessibility of creek section for adult females
Quantity of prey items (ordinal, 1–3)	(Yes)	Indirectly over larval abundances	Yes	Obligate for survival (also decrease of cannibalism)
Substrate type (ordinal, 1–3)	(Yes)	Indirectly over larval abundances	Yes	‘Stony creeks’ with more hiding places
Terrestrial habitat				
Hiding places in 100 m buffer (ordinal, 1–3)	(Yes)	Indirectly over larval abundances	Yes	Core habitat preferences of adults
Land use (%) in 100 m buffer	(Yes)	Indirectly over larval abundances	Yes	Core habitat range of adults

ences the water flow and thereby larval drift (THIESMEIER & SCHUMACHER 1990, REINHARDT et al. 2018, VEITH et al. 2019). The tilt (°) perpendicular to the creek section is supposed to influence the accessibility for adult females, which are migrating to the reproduction waters for larvae deposition (MANENTI et al. 2009). The quantity of prey items for larvae, i.e. consumable macrozoobenthos (especially gammarids: RUFF & MAIER 2000) was estimated according to the by-catches during larval monitoring and in relation to all studied creeks (ordinal data: ‘low’, ‘medium’, ‘high’). The substrate type of the creek section (ordered according to increasing grain size, from mainly muddy over sandy to stony substrate) was included as a potential factor that influences larval abundance and detection probability. Regarding the terrestrial habitat, the quantity of potential suitable hiding places (dead wood, stones, etc.) for adult European fire salamanders was estimated in a 100 m buffer and in relation to all studied creeks (ordinal data: ‘low’, ‘medium’, ‘high’). Finally, the proportions of land use in a 100 m buffer was calculated using ArcMap 10 and the CORINE land cover data (see Supplementary documents 1–8, merged to ‘deciduous forest’, ‘mixed forest’, ‘coniferous forest’, ‘agricultural used land’, ‘grasslands’, ‘settlements’). The 100 m buffer around the reproduction creeks should cover the core area of the adult (and subadult/juvenile) population, although larger migratory distances are known (e.g. THIESMEIER 2004, SCHULTE et al. 2007).

We build the following models (Tabs. 2, 4, 6): (1) a ‘Global model’ containing all potential predictors; (2) the ‘Simplified global model’ using the stepAIC function from the

R-package ‘MASS’ (i.e. model simplification by stepwise removing variables without explanatory power using model selection according to their AIC values, BURNHAM & ANDERSON 2002); (3) a model only containing the variables of the larval habitats and the landscape units (‘Aquatic habitat model’); (4) a model only containing the variables of the terrestrial habitats and the landscape units (‘Terrestrial habitat model’); (5) a simple model only containing the elevation as potential predictor and the landscape units (‘Elevation model’). Because female European fire salamanders mainly deposit their larvae from March to May (THIESMEIER 2004) and catastrophic drift after heavy rainfall can substantially decrease larval abundance (and thereby detectability) in upper stream sections (THIESMEIER & SCHUMACHER 1990, REINHARDT et al. 2018, VEITH et al. 2019), we finally (6) built a simple ‘Time model’, only containing the date of field work occasions as potential predictor and the landscape units. All models were compared according to their AICc values (R package ‘MuMIn’). Models with  $\Delta AICc$  values  $< 2$  compared to the best model were considered as equally plausible (BURNHAM & ANDERSON 2002). Pairwise comparison of predictors of larval presence in presence and absence creeks from the different landscapes were conducted using t-tests or Wilcoxon-tests depending on normality of distribution and homogeneity of variances (tested with Shapiro-Wilk and F-tests).

Besides presence-absence mapping, we also collected abundance data in 85 out of the 135 studied creeks by removal sampling according to SCHMIDT et al. (2015). Hence, in a second analysis, we compared different hierarchical

models for removal sampling data (ROYLE 2004, DORAZIO et al. 2005, ROYLE & DORAZIO 2006). The categorical variable ‘landscape unit’ could not be integrated in these models; instead we first analysed the complete dataset from the whole study area (i.e. all 85 creeks were used for hierarchical modelling), and in a second step the dataset was analysed for each landscape unit separately (Fig. 1). All considered potential predictor variables (Table 1) were normalized prior to analysis. We built different generalized multinomial mixture models using pairwise combinations of the variables described above or a ‘constant’-intercept-model for both abundance and detection probability (R package ‘unmarked’). Survival probability was always kept constant as neither emigration/death nor immigration/birth was supposed to have taken place during the 45 min of data acquisition. All models were fitted to the data with either a Poisson or a negative binomial abundance model (see SCHMIDT et al. [2015] for details). The best fitting models were chosen according to the AIC values ( $\Delta AIC$  values  $< 2$ : BURNHAM & ANDERSON 2002) using the R package ‘AICcmodavg’.

### Results

We recorded presence-absence of larval European fire salamanders in 50 creeks including the data from SANDVOß et al. (2020 in this issue) to get a larger data set and conducted removal sampling in 85 additional creeks. Consequently, we used presence-absence data from 135 creeks and quantitative data from 85 creeks (Supplementary documents 1–2).

#### Logistic regression models

The best-fitting model was the ‘Simplified global model’ (Table 2). Only elevation of the creek above sea level had a highly significant negative effect on the presence of European fire salamander larvae, while the number of pools, the abundance of potential prey and the proportion of any forest type in a 100 m buffer around the creeks had a significant positive effect (Table 3).

The factorial variable ‘landscape unit’ did not explain variance and was, together with several other factors, excluded from the final best-fitting GLM. Comparing these predictors in presence and absence creeks from the different landscape units revealed that presence creeks were always lower in elevation, although highly significant only in the landscape unit ‘Westeifel’ (Fig. 2A;  $W = 121.5$ ,  $P < 0.001$ ). The number of pools was always higher in presence creeks; this difference was highly significant in the ‘Westeifel’ ( $W = 494.5$ ,  $P < 0.01$ ) and the ‘Hunsrück’ ( $t = 4.3$ ,  $df = 30.4$ ,  $P < 0.001$ ) and significant ( $t = 2.6$ ,  $df = 17.9$ ,  $P < 0.05$ ) in the ‘Osteifel’ (Fig. 2B). Likewise, the quantity of consumable macrozoobenthos was always higher in presence creeks; this difference was significant in the ‘Osteifel’ ( $W = 75$ ,  $P < 0.05$ ) and the ‘Gutland’ ( $W = 44$ ,  $P < 0.05$ ) (Fig. 2C). Moreover, the proportion of forest cover was al-

Table 2. Model selection overview of logistic regression models considering presence-absence data from 135 creeks in the study area.

Model	Degrees of freedom	Log Likelihood	AICc	Delta AICc	AICc weight
Simplified global model	9	-37.69	95.00	0.00	1.00
Global model	20	-32.68	113.60	18.61	0.00
Aquatic habitat model	11	-48.19	120.80	25.8	0.00
Elevation model	6	-68.54	149.80	54.79	0.00
Terrestrial habitat model	12	-62.52	151.60	56.66	0.00
Time model	6	-75.90	164.50	69.5	0.00

Table 3. Best-fitting logistic regression (‘simplified global’) model considering presence-absence data from 135 creeks in the study area.

Coefficient	Estimate $\pm$ SE	Z value	P value
y-intercept	-15.4 $\pm$ 8.6	-1.8	0.07
Elevation a.s.l. (m)	-0.0 $\pm$ 0.0	-3.4	< 0.001
Number of pools	0.1 $\pm$ 0.0	3.7	< 0.001
Substrate	0.5 $\pm$ 0.4	1.6	0.11
Prey	1.4 $\pm$ 0.5	2.6	< 0.01
Deciduous forest	0.2 $\pm$ 0.1	2.2	< 0.05
Mixed forest	0.2 $\pm$ 0.1	2.2	< 0.05
Coniferous forest	0.2 $\pm$ 0.1	2.0	< 0.05
Grassland	0.2 $\pm$ 0.1	1.8	0.06

ways higher in 100 m surroundings of the presence creeks; this difference was significant ( $W = 165$ ,  $P < 0.05$ ) in the ‘Hunsrück’ (Fig. 2D).

#### Hierarchical models

From the 85 creeks with quantitative data, two (‘Fersweiler2’ and ‘Watzbach’; Supplementary document 2) had to be excluded from analysis as outliers because of their high number of captured larvae (308 and 194, respectively; cf. overall average of only  $34 \pm 59$  larvae, see Supplementary document 2). All attempts to transform the removal data to include all creeks in hierarchical modelling failed. Furthermore, the environmental variable ‘substrate’ could not be used here due to missing data from the ‘Moeseltal’ and the ‘Hunsrück’. Hence, 512 candidate models were compared, and there was only one best-fitting, negative binomial model in which high larval abundances were best predicted by a high number of pools and detection probability was positively influenced by later mapping date (Fig. 3, Table 4).

Considering only the removal data of the 20 creeks from the ‘Osteifel’ (Fig. 1), there was neither agricultural land

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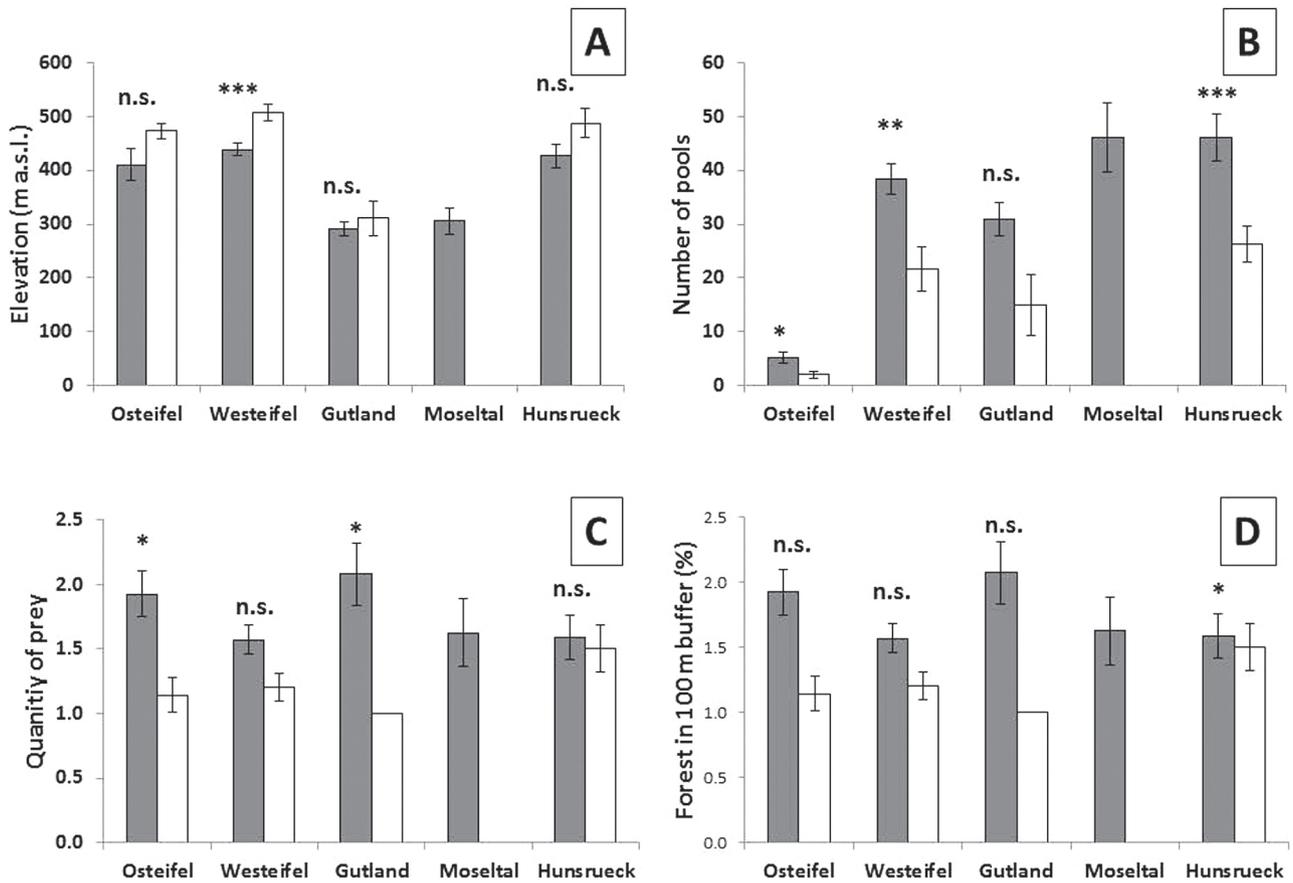


Figure 2. Pairwise comparison of predictor variables (A = elevation, B = number of pools, C = quantity of potential prey, D = proportion of forest cover within 100 m), which were significant in the best logistic regression model, between presence (grey bars) and absence (open bars) creeks and per landscape unit; all values are means  $\pm$  SE; significance levels are given:  $P < 0.001$  (\*\*\*),  $P < 0.01$  (\*\*),  $P < 0.05$  (\*) and  $P > 0.05$  (n.s.); absence creeks were missing in the Moseltal.

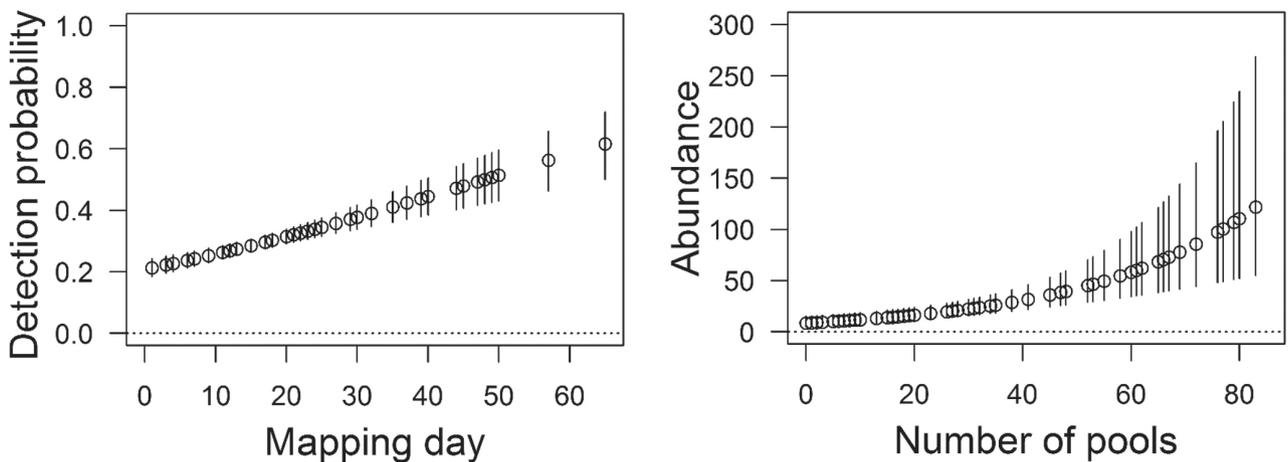


Figure 3. In the best fitting hierarchical model, detection probabilities of European fire salamander larvae increased with later capture occasions and the larval abundances increased with the number of pools in the studied creek sections. All values are predicted means  $\pm$  95% confidence intervals.

Table 4. Predictors of larval abundances and detection probabilities according to the best-fitting hierarchical model for the entire study area and for landscape units, respectively. All data were fitted to a negative binomial model. Arrows indicate positive (↑) or negative (↓) influence of factors on larval abundance. †, ‡

Landscape Unit	ΔAIC	Abundance (Lambda)	Detection probability (p)	Landscape Unit	ΔAIC	Abundance (Lambda)	Detection probability (p)
All data (N = 83)	0	Number of pools †	Mapping day †	Gutland (continued)	0.71	Agriculture ↓	Substrate †
Osteifel (N = 20)	0	Number of pools †	Coniferous forest ↓		1.05	Elevation a.s.l. ↓	Substrate †
	0.23	Number of pools †	Tilt parallel †		1.2	Agriculture ↓	Tilt parallel †
	0.28	Prey †	Coniferous forest ↓		1.52	Predatory fish ↓	Tilt parallel †
	0.46	Substrate †	Coniferous forest ↓		1.52	Coniferous forest ↓	Tilt parallel †
	0.51	Prey †	Tilt parallel †		1.53	Mapping day ↓	Substrate †
	0.64	Substrate †	Tilt parallel †		1.98	Grassland †	Substrate †
	0.74	Tilt perpendicular †	Tilt parallel †	Moseltal (N = 8)	0	Mapping day ↓	constant (.)
	0.76	Number of pools †	Hiding places ↓		0.25	Tilt perpendicular ↓	Width of creek
	0.86	Tilt perpendicular †	Coniferous forest ↓		0.25	Width of creek †	Tilt perpendicular ↓
	0.98	Prey †	Hiding places ↓		0.48	Mapping day ↓	Hiding places ↓
	1.22	Substrate †	Hiding places ↓		0.78	Prey †	constant (.)
	1.39	Number of pools †	Deciduous forest †		1.15	Prey †	Hiding places ↓
	1.42	Tilt perpendicular †	Hiding places ↓		1.16	Mapping day ↓	Width of creek
	1.64	Prey †	Deciduous forest †		1.24	Prey †	Tilt perpendicular ↓
	1.76	Substrate †	Deciduous forest †		1.27	Agriculture ↓	Tilt perpendicular ↓
Westeifel (N = 16)	0	Number of pools †	Width of creek †		1.34	Mapping day ↓	Tilt perpendicular ↓
	0.55	Number of pools †	Tilt perpendicular ↓		1.79	Mapping day ↓	Width of creek
	0.56	Number of pools †	Hiding places ↓		1.83	Mapping day ↓	Number of pools †
	0.89	Number of pools †	Number of pools †		1.85	Tilt perpendicular ↓	Agriculture
	1.56	Number of pools †	constant (.)		1.86	Mapping day ↓	Coniferous forest
Gutland (N = 7)	0	Predatory fish ↓	Substrate †		1.88	Mapping day ↓	Deciduous forest
	0	Coniferous forest ↓	Substrate †		1.96	Mapping day ↓	Agriculture
	0.35	Deciduous forest †	Substrate †		1.99	Mapping day ↓	Prey
	0.55	Number of pools †	Substrate †		1.99	Mapping day ↓	Mapping day
	0.58	Width of creek ↓	Substrate †	Hunsrück (N = 32)	0	Number of pools †	Width of creek ↓
	0.6	constant (.)	Substrate †		1.44	Agriculture ↓	Width of creek ↓
	0.69	Hiding places ↓	Substrate †		1.48	Mapping day ↓	Width of creek ↓
					1.89	Settlement ↓	Width of creek ↓

nor settlements around the studied creeks and no predatory fish were found, so these three variables were excluded from further analysis. Consequently, 392 candidate models were compared, from which 15 negative binomial models with ΔAICc values < 2 were considered as plausible (BURNHAM & ANDERSON 2002). The best-fitting model estimated again more larvae in creek sections with more pools and, furthermore, an (indirect) negative effect of the terrestrial habitat (here, proportion of coniferous forest in 100 m buffer) on the detection probability (Table 4). Each of the four remaining 14 plausible models estimated a positive effect of number of pools, a high amount of prey or stony substrate on larval abundances (Table 4). Similarly, in four models, detection probability was negatively influenced indirectly by the proportion of coniferous forest in the vicinity of 100 m (Table 4).

When only the 17 creeks from the landscape unit ‘Westeifel’ (Fig. 1) were considered, again, neither predatory fish nor agriculture nor settlement around the creeks could be observed, so these variables were again excluded from further analysis. In addition, the ‘Watzbach’ once more had to be excluded as outlier. 392 candidate models were compared, and in all four plausible negative binomial models the number of pools positively affected larval abundance, while no or varying factors influenced detection probabilities (Table 4).

Also from the dataset ‘Gutland’ (eight creeks only), ‘Ferschweilerz’ had to be excluded as outlier (see above). Here, no settlement was in the 100 m surroundings of creeks, so this variable was excluded. 512 candidate models were fitted, and 14 negative binomial models were considered plausible. Varying factors influenced larval abundanc-

es, in two models each, presence of predatory fish, agriculture and proportions of coniferous forest around creeks negatively affected abundance (Table 4). In eleven models, stony substrate enhanced detection probability (Table 4).

Data from eight creeks only were available in the 'Moseltal' (Fig. 1). No predatory fish, mixed forest, grasslands and settlements could be observed, and for half of the creeks no data on substrate was available. Hence, only eleven factors were considered in modelling. Among the 18 plausible models, larval abundances mostly decreased with increasing date (ten times), and detection probability was most often negatively affected by the perpendicular tilt (Table 4).

From the landscape unit 'Hunsrück', 32 creeks could be considered for abundance modelling (Fig. 1), but the variable 'substrate' had to be excluded due to missing data, so that 512 candidate models were compared. Among the four plausible models, different variables affected abundances, but creek width always negatively influenced detection probabilities (Table 4).

## Discussion

### Presence-absence of European fire salamander populations

With regard to habitat suitability, no influence of the natural landscape units could be observed, suggesting that only the predictors identified by our best model should influence the occurrences of European fire salamander larvae in the entire study region. Elevation a.s.l. had a negative effect on European fire salamander presence (Table 3). This is in accordance with THIESMEIER & DALBECK (2011), who found an elevational distribution limit of 600 m a.s.l. of the species in the federal state of North Rhine-Westphalia, which adjoins our study area to the north. In the 'West-eifel', presence creeks were significantly lower in elevation compared to absence creeks (Fig. 2A). THIESMEIER & DALBECK (2011) described the elevational limit of 600 m a.s.l. in North Rhine-Westphalia on the basis of more recent distribution data; however, in the 1990s, single European fire salamanders in this region were also found at higher elevations. Moreover, FELDMANN & KLEWEN (1981) reported European fire salamander populations in Westphalia from even above 800 m a.s.l. In Rhineland-Palatinate, several European fire salamander records from the 1980/90s were above 600 m a.s.l. (BITZ et al. 1996). Nevertheless, a preference of the European fire salamander for lower elevations in mountainous areas is consistent in both federal states. Therefore, we assume that the European fire salamander populations at high elevations of our study area (BITZ et al. 1996, WAGNER et al. 2017) live under sub-optimal conditions. Moreover, such areas are almost completely covered with conifers (WAGNER et al. 2017).

An increasing number of pools, which can serve as a proxy for the heterogeneity of a study creek, is known to positively affect the aquatic habitat of European fire salamander larvae (BAUMGARTNER et al. 1999, WERNER et

al. 2014, SCHMIDT et al. 2015, WAGNER et al. 2020 in this issue) (Table 4). This could be observed in all our landscape units (Fig. 2B), although not always significantly. The higher the estimated amount of prey, in our creeks mainly *Gammarus fossarum*, the more likely European fire salamander larvae were present (Fig. 2, Table 3), which also makes sense biologically. Finally, high proportions of forest around the creeks led to high presence probability, but without an observed negative effect of coniferous forests (Table 3), although land-use change from deciduous into coniferous forests in the terrestrial habitat of European fire salamanders is listed as a major threat for the species (e.g. THIESMEIER 2004). When comparing predictor variables of presence and absence creeks from different landscape units separately, obvious differences are found (Fig. 2). To sum up, a typical reproduction creek for *S. salamandra* in this case study across our study region is at low elevation, contains a high number of pools and consumable macrozoobenthos, and is situated inside a forest. This statistically confirms the well-known preferences of the species (e.g. THIESMEIER 2004, THIESMEIER & DALBECK 2011).

### Larval abundance and detection probability

With regard to larval abundance, we found both similarities and differences in predictors among landscape units (Fig. 3, Table 4). Like for presence probability, there was a positive influence of increasing number of pools on larval abundance (Table 4) when creeks from the entire study area were included in hierarchical modelling (Fig. 3, Table 4) as well as for the landscape units 'Osteifel', 'West-eifel' and 'Hunsrück' (Table 4). Similarly, the later the capture occasion the lower the estimated larval abundance was estimated in our respective likely models (Table 4). Later in the field season, numerous larvae are likely to have been drifted down-stream, out of the studied creek sections (cf. THIESMEIER & SCHUMACHER 1990, REINHARDT et al. 2018, VEITH et al. 2019). In early summer 2016 and 2018, heavy rainfalls increased water flow in many study creeks. In addition, larval abundance will decrease with time due to the onset of metamorphosis. The positive effect of higher quantities of consumable macrozoobenthos on the abundance of European fire salamander larvae (Table 4) seems plausible; it should reduce cannibalism of earlier larvae by older conspecifics (see DEGANI et al. 1980 for *S. infraimmaculata*). Increasing agricultural land-use near creeks negatively affects larval abundance of European fire salamanders in the landscape units 'Gutland', 'Moseltal' and 'Hunsrück' (Table 4). Apart from the absence of suitable forests as terrestrial habitats (historical agricultural expansion), the application of agrochemicals may affect larval European fire salamanders. They may affect terrestrial and aquatic life-stages (reviewed by MANN et al. 2009). In a laboratory study, environmentally relevant herbicide concentrations led to lethargy and decreased predatory behaviour in larval European fire salamanders (MANDRILLON & SAGLIO 2007). In the field, herbicide contamination of creeks may result

in decreased body size of European fire salamander larvae, which vice versa can increase drift rates of smaller larvae into creek section with predatory fish (cf. VEITH et al. 2019). Hence, long-term agrochemical contamination of creeks could affect populations of European fire salamanders via the larval stages in direct and indirect ways. Finally, in the 'Osteifel' four out of 15 plausible models suggest a positive effect of stony substrate on larval abundance (Table 4). This may have an immediate positive effect on the aquatic habitat (i.e. the slate stones in creeks from this landscape unit forms suitable hiding places for larvae, which could also lower predatory pressure) or an indirect effect (capturing larvae under slate stones is easier and results in a higher detection probability). Further predictors are plausible (e.g. decreasing abundances with increasing elevation [see above] or presence of predatory fish: Table 4), while others may be non-causal artefacts (e.g. increasing abundance with increasing perpendicular tilt: Table 4).

When creeks from the entire study area are considered, detection probabilities increase with later field season (Fig. 3, Table 4). At first sight, this seems counterintuitive to the often observed negative effect of later capture occasions on larval abundances (Table 4). However, this may be explained by the larger body size of later larval stages or lower water levels in later season, which both increase detection, or the simple fact that at least some field workers improved their detection efforts. The negative effect of coniferous forest and the positive effect of deciduous forest surrounding the creeks should primarily affect the adult population, so their effect on larval abundance is indirect. The adult European fire salamander populations are usually smaller in coniferous and larger in deciduous forests (THIESMEIER 2004), and consequently less or more larvae will be deposited in the respective creeks. Likewise, increasing perpendicular tilt lowers accessibility of creek sections for females (MANENTI et al. 2009), and likewise the positive effect of the (parallel) tilt of the creek section could be indirect. A faster water flow throughout the year could force larvae to accumulate in pools and under stones/dead wood, where they are easier to detect. In the 'Gutland', a positive effect of a coarse, stony substrate on the detection probability is observed (Table 4; cf. discussion above on effects on abundance). In the 'Hunsrück', increasing width of the creek section decreased detection probability, which could be explained with widths up to 2–3.5 m in this landscape unit (Supplementary documents 1–2). In such wide streambeds many larvae should be overlooked.

### Conclusions

In our study, local habitat suitability models developed from different areas mostly identified the same biotic and abiotic parameters as major predictors of the abundance of larval European fire salamanders. Presence of European fire salamanders in north-western Rhineland-Palatinate, Germany, is positively affected mainly by low elevation, high numbers of pools, abundant consumable macrozoo-

benthos within creeks and high proportions of forest cover around creeks. Larval abundance is usually positively affected by higher number of pools (11 out of 56 overall models = 20%) and negatively by later mapping dates (12 out of 56 overall models = 21%). Detection probability is explained by various factors in the best fitting models, but using all data sets, again later mapping day had a negative effect. Consequently, such preferences of this wide-ranging urodelan species, which are easy to determine, can be used to differentiate between naturally caused absence or low abundance of European fire salamander larvae (e.g. due to unsuitable aquatic or terrestrial habitats, heavy rainfalls causing catastrophic drift) and extinctions/population declines due to emerging infectious diseases caused by invasive pathogens.

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### Supplementary data

The following data are available online:

Supplementary document 1. Raw data from presence-absence mapping of larval European fire salamanders.

Supplementary document 2. Raw data from removal sampling of larval European fire salamanders.

Supplementary document 3. Proportions of different land use in a 100 m buffer around all studied creeks, divided into presence and absence sites.

Supplementary document 4. Proportions of different land use in a 100 m buffer around the studied creeks from the 'Westeifel', divided into presence and absence sites.

Supplementary document 5. Proportions of different land use in a 100 m buffer around the studied creeks from the 'Osteifel', divided into presence and absence sites.

Supplementary document 6. Proportions of different land use in a 100 m buffer around the studied creeks from the 'Gutland', divided into presence and absence sites.

Supplementary document 7. Proportions of different land use in a 100 m buffer around the studied creeks from the 'Moselta'.

Supplementary document 8. Proportions of different land use in a 100 m buffer around the studied creeks from the 'Hunsrück', divided into presence and absence sites.