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Fire Salamander, *Salamandra salamandra*, niche selection in Central European conditions

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Abstract. We analyzed data from 3,546 occurrence records of Fire Salamanders (*Salamandra salamandra*) from the territory of the Czech Republic where it has a heterogeneous distribution pattern. Its occurrence in terrestrial habitats adjacent to breeding streams is characterized by a mean distance of 103 m, maximum 1,321 m, from the nearest stream. Based on a logistic GLM (generalized linear model) analysis we determined the Fire Salamanders' climatic and habitat associations at landscape scale in the Czech Republic. The main limiting factors for its dispersal include the proximity of small shallow streams in rolling landscapes, the pH of these streams, the presence of broad-leaf or mixed forests, humidity, solar irradiation, and severity of winters. While the absence of suitable breeding habitats is the main limiting factor for their occurrence in more expansive lowlands, factors such as lower temperatures, lower humidity, and the absence of broad-leaf and mixed forests begin to play a role with increasing altitude. Unlike cold temperatures, low amounts of precipitation and higher temperatures do not act as limiters in the Czech Republic. Fire Salamanders respond to the colder climate of higher altitudes with intensified summer activity and the purely bimodal nature of their activity (with spring and autumn peaks) tends to fade at higher altitudes.

Key words. Amphibia, Caudata, Salamandridae, climate preferences, habitat preferences, logistic regression, niche modelling.

Introduction

The terrestrial environment surrounding water bodies plays a fundamental role in the ecology of terrestrial salamanders (e.g., Taylor & Scott 1997, Semlitsch 2003) and the Fire Salamander, *Salamandra salamandra*, is no exception in this regard (e.g., Manenti et al. 2017). It is a highly adaptable species of caudate amphibian, exhibiting high variability in its survival strategy (e.g., Buckley et al. 2007, Denoël 1996, Velo-Anton & Cordero-Rivera 2017) across its vast distribution range (Sillero et al. 2014, Sparreboom 2014). Fire Salamanders are known to tolerate low temperatures (Catenazzi 2016), but at the same time are able to persist even in warm, arid areas (Egea-Serrano et al. 2006). This species prefers moist broad-leaf forests across most of its range (e.g., Joly 1968, Egea-Serrano et al. 2006, Bani et al. 2015), however, Fire Salamanders have also been documented from a pastoral landscape with a network of hedges (Arntzen & van Belkom 2020) and are able to live in environments without woody cover (Veith 1997), or in scrublands and grasslands (Salvador & García-París 2001). They only avoid dry forests, especially spruce monocultures (Manenti et al. 2017).

In contrast to more western populations (Weitere et al. 2004), their reproduction within the territory of the Czech Republic is linked mostly with upper sections of small oligotrophic streams (Thiesmeier 1994, Caspers et al. 2009), often situated at the bottom of deeply carved and forested valleys (Ficetola et al. 2011). For salamanders, this is an attractive area because of the increased humidity levels (Gustafson et al. 2001). The occurrence of Fire Salamanders in the Czech Republic is not homogeneous (Fig. 1). As has been found in neighbouring Slovakia (Balogova et al. 2015) or Austria (Meikl et al. 2010), Fire Salamanders avoid more expansive lowlands and high mountain locations here. Without immediately obvious causes, however, they are absent also from many large areas with a low degree of anthropogenization that match well the general scheme of habitat and climatic requirements of this highly adaptable caudate.

Our research objective was to identify extrinsic abiotic factors that significantly influence the occurrence of Fire Salamanders in the Czech Republic, namely at landscape scale and by computing logistic regression models. The results enabled us to define an alternative hypotheses about the significance of the effects of these explanatory variables through several sets of a-priori models (see details in Appendix 1).

Materials and methods

Study area and salamander location data

Our study was focused on the Czech Republic, i.e., a territory in Central Europe covering 78,866 km². Here, weather conditions are determined by interpenetration and intermixing of oceanic and continental forces and are characterized by westerly winds and intense cyclonal activity, causing frequent exchanges of air masses and relatively high amounts of precipitation. The weather is greatly affected by the country's altitude and the relief of the landscape. Most of the area consists of rugged terrain, with a mean altitude of 450 m (115–1,602 m a.s.l.).

Data on Fire Salamander occurrences in the Czech Republic were adopted from the Species Occurrence Database, managed by the governmental Nature Conservation Agency of the Czech Republic (NCACR 2020). This database stores records of animal and plant occurrences that have been verified by NCACR experts. We obtained data from 3,546 such occurrence records for the Fire Salamander (larvae and salamanders in terrestrial habitats) from the period 1980–2019 (Fig. 1).

According to Greenwald et al. (2009) and Romero et al. (2012), the initial choice of variables to be included in a distribution model should be based mainly on the knowledge of the biology of the species concerned. These explanatory variables should then be used to test a-priori hypotheses about the relationships between species and habitat conditions. Therefore, our first step in selecting explanatory variables was to scour the literature for explanatory variables affecting the presence of Fire Salamanders within the chosen territory (see caption in Appendix 2) followed by defining the land cover types that most likely do not meet the requirements of Fire Salamanders. By overlapping salamander records from the NCACR database with the CORINE vector layer (Copernicus Land Monitoring Service 2018), we effectively removed areas with these land cover types. CORINE Land Cover is an inventory of European land cover and land use split up into 44 different land cover classes, ranging from broadly forested areas to individual vineyards. At the same time, this step filtered out disputable records of salamanders (3% of the total number of sightings). As potentially suitable, we kept only the sightings of larvae and salamanders after metamorphosis found within the following CORINE (as of 2018) classes: mixed forest (313), broad-leaf forest (311), coniferous forest (312), land principally used for agriculture, but including significant areas with natural vegetation (243), discontinuous urban fabric (112), non-irrigated arable land (211), and pastures (231) (Table 1). Within the Czech Republic, these CORINE classes cover 71,706 km² and include 3,446 Species Occurrence Database sightings of larvae and post-metamorphic salamanders (97% of the total number of sightings). We considered sightings logged in discarded CORINE 2018 classes 'water courses' (511), 'natural grasslands' (321), 'fruit and berry plantations' (222), 'green urban areas' (141), 'continuous urban fabric' (111), 'road and rail networks and associated land' (122), 'water bodies' (512), 'industrial or commercial units' (121), 'sport and leisure facilities' (142), 'complex cultivation patterns' (242), and 'transitional woodland-shrub' (324) erroneous due to possible inaccuracies in the localization of salamander sightings, inaccuracies in the spatial definition of the CORINE 2018 boundaries, or as a consequence of changes in land use during the period from which these sightings originate.

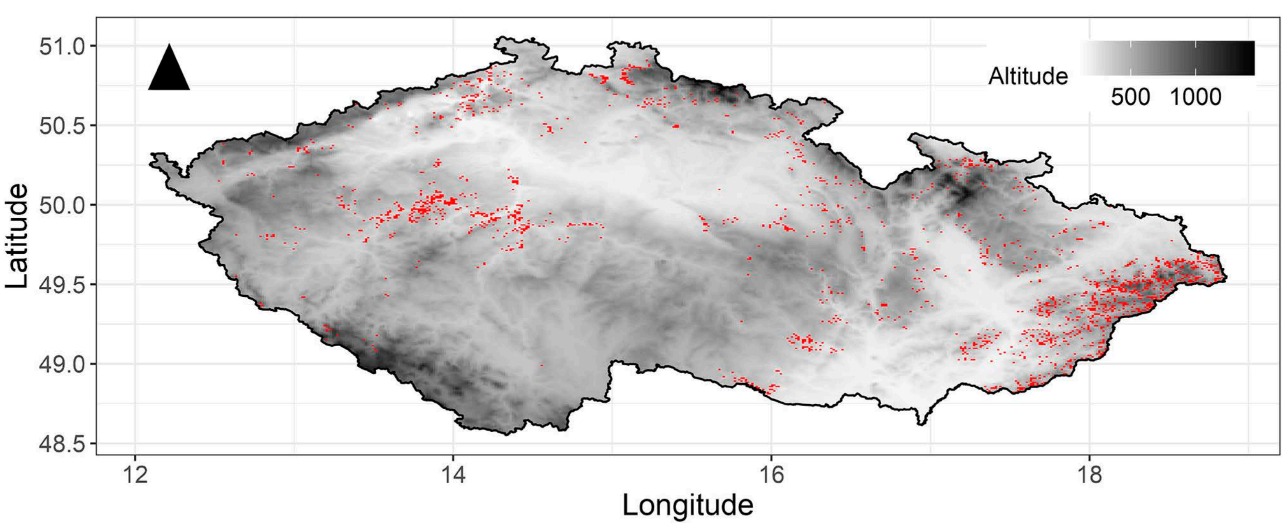

Figure 1. 1×1-km pixels with recorded occurrences of the Fire Salamander, *Salamandra salamandra*, (altitude range: 115–1,602 m) based on the Species Occurrence Database maintained by the Nature Conservation Agency of the Czech Republic. The red dots mark occurrences of Fire Salamanders.

Table 1. Representation of CORINE 2018 land cover types with numbers of Fire Salamanders (*Salamandra salamandra*) found in the total territory of the Czech Republic (CR) and in all salamander records.

CORINE 2018	Area in CR (km²)	% of the whole CR area	Number of salamanders found	% of salamanders found
313 – Mixed forest	6,132.65	7.8	1,135	32.0
311 – Broad–leaf forest	2,750.59	3.5	738	20.8
312 – Coniferous forest	16,533.40	21.0	689	19.4
243 – Land principally used for agriculture	6,878.45	8.7	471	13.3
112 – Discontinuous urban fabric	3,703.34	4.7	161	4.5
211 – Non–irrigated arable land	28,038.20	35.6	145	4.1
231 – Pastures	7,669.51	9.7	107	3.1
other	7,159.86	9.0	100	2.8

Explanatory variables

DIBAVOD is a vector database of watercourses for the territory of the Czech Republic (DIBAVOD 2019). It is a national-reference geographic database, created and managed by the governmental T. G. Masaryk Water Research Institute. It contains the majority of watercourses in the Czech Republic, including the smallest starting from their springs. Although Fire Salamander larvae have developed some predator-avoidance strategies with respect to fish (Bylak 2018), adult salamanders show a strong reproductive affinity to the uppermost parts of small streams, often small tributaries of other streams, in a quest to pre-empt larval predation (Thiesmeier 1994). Therefore, we selected only the uppermost sections of streams, i.e., first- and second-order streams (Baumgartner et al. 1999, Ficetola et al. 2008, Reinhardt 2014). We chose the second confluence, amongst others, to take into account the fact that even small streams can have two springs. Using the R function "geosphere::dist2Line()" (Hijmans et al. 2022), we calculated the shortest 2D distance of all sightings of postmetamorphic Fire Salamanders (n = 2498) from these sections of streams (Fig. 2). We subsequently created a buffer zone of 409 m along both sides along the uppermost sections of

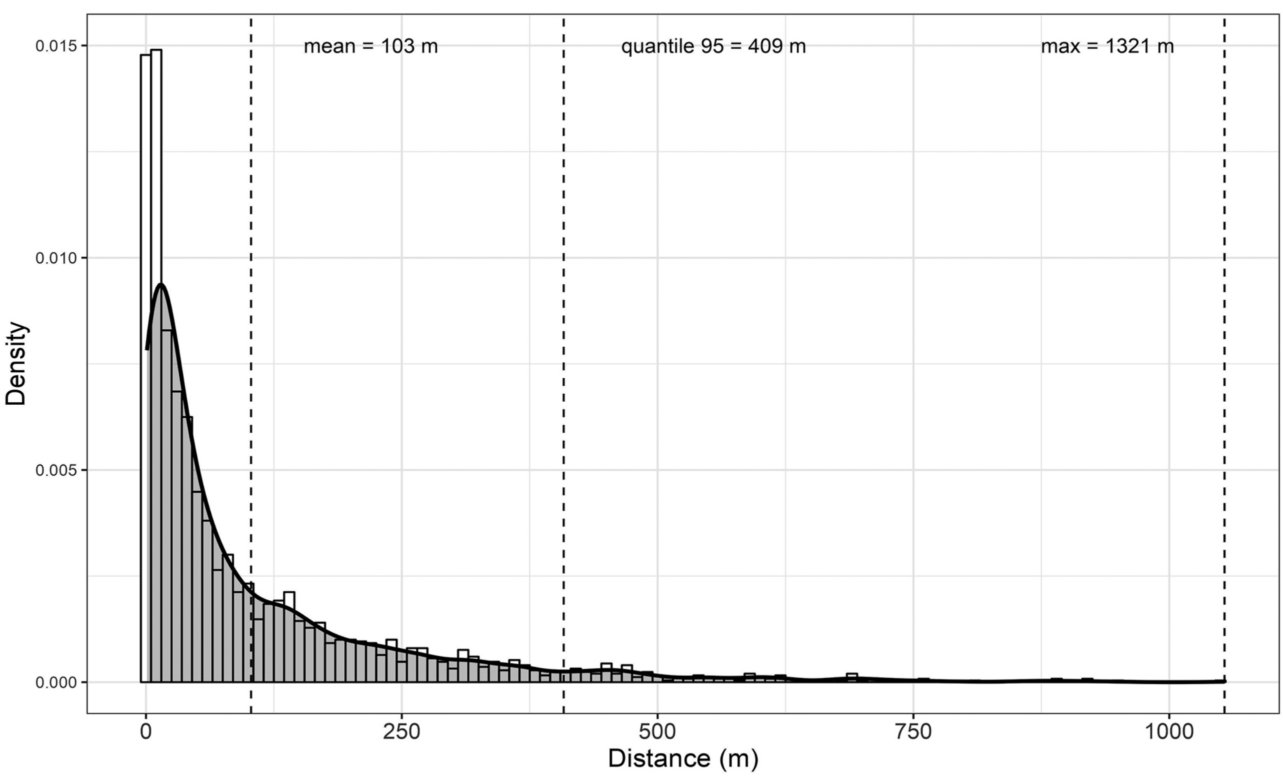

Figure 2. Distribution of Fire Salamanders (*Salamandra salamandra*, n = 2,498; excluding larvae) in terrestrial habitats adjacent to breeding streams as estimated from sightings recorded in the NCACR Species Occurrence Database. Mean = 103 ± 144 m, max = 1,321 m, median = 44 m, percentile 9 % = 409 m, percentile 7 % = 137 m.

these streams. This distance encompasses 95% of all sightings of postmetamorphic salamanders (n = 2377). Similar distances were reported also by Crawford & Semlitsch (2007), Schulte et al. (2007), Ficetola et al. (2009) and Tanadini at al. (2011). Outside more expansive lowlands, the network of small watercourses and their upper sections is very dense within the territory of the Czech Republic and the buffers thus covered 62% of it (49,067.8 km²). After removing areas with unsuitable habitats and the areas outside of the buffers, we related our explanatory and dependent variables to the remaining territory.

Explanatory variables for the creation of a-priori salamander models are related either to the aquatic habitats of larvae (e.g., Manenti et al. 2009a, Tanadini at al. 2011) or to the sightings of salamanders in terrestrial habitats (e.g., Dillard et al. 2008, Romero et al. 2012). Primarily in the case of land cover variables, some authors in their models compare the areas of the given categories with sightings and without sightings (e.g., Egea-Serrano et al. 2006, Ryan & Calhoun 2014), whereas others take into account the distances of sightings from individual land cover classes (e.g., Blank & Blaustein 2012, Olivero et al. 2016), and yet others quantify every land class as 'present' (1) or 'absent' (0) (e.g., Guerry & Hunter 2002, Greenwald et al. 2009, Farallo et al. 2018). We used this last approach and the only dependent variables were used to build our models (considering both larvae and individuals in the surrounding terrestrial habitats) in 57,947 pixels of a 1×1 km grid, regardless of the actual number of sightings within a given pixel. In particular, their presence (1) means that at least one Fire Salamander was found in the given pixel in at least one year within the period 1980–2019. These were pixels spreading over our stream buffers described above. Within these stream buffers, salamanders were present in 3% of the pixels and absent (or pseudo-absent) in 97%. One of the advantages of the described aggregation and gridding procedure is that it reduces spatial autocorrelation to 'present' in raw sightings.

Our explanatory variables came from the following sources: (1) 34 climatic variables 1×1 km (Fick & Hijmans 2017; here abbreviated as BIO), (2) 84 directly calculated and derived climatic variables 1×1 km generated with the ClimateEU v4.63 software package, (3) 87 directly calculated and derived climatic variables 1×1 km E-OBS (Copernicus Climate Change Service 2018), (4) three geomorphological variables 1×1 km derived from the European Digital Elevation Model (EU-DEM), version 1.1, (5) CORINE land cover types (Copernicus Land Monitoring Service 2018), (6) 11 soil variables (Panagos et al. 2012), (7) pH of surface water (9 categories) (Czech Geological Survey 2020), and (8) lithological variables (metamorphic, igneous and sedimentary rocks) (Onegeology 2017).

The level of availability of suitable breeding habitats is described as the length of the first- and second-order streams calculated for each 1×1 km pixel of our grid. Such a large number of explanatory variables would inflate the number of a-priori models beyond the number that can be reliably analyzed (Burnham & Anderson 2002) so that, besides CORINE filtering (CORINE classes potentially suitable for the salamanders occurrence), we preselected also the rest of the variables (see Dillard et al. 2008). This preliminary selection of explanatory variables, in accordance with Guthery et al. (2005) and Heinze & Dunkler (2017), was based on our previous experience with the study species and a review of similar studies (e.g., Egea-Serrano et al. 2006, Bani et al. 2015). This pre-selection was also necessary because many of the explanatory variables were strongly collinear.

Models at coarse resolution may overestimate the exposure to climate variation that a species experiences, owing to the buffering effect of the microhabitat on temperature (Scheffers et al. 2014). We matched the geographic resolution of all data at a 1×1-km resolution, which is a scale often used in salamander habitat modelling (e.g., Romero et al. 2012, Olivero et al. 2016). Our results thus reflect Fire Salamanders´ preferences at landscape scale. The microhabitat characteristics such as the presence of moist leaf litter and coarse woody debris (Bragg & Kershner 1999), soil moisture and soil temperature (Hann et al. 2007), or stream water characteristics (Clipp & Anderson 2014) can seriously influence the presence of Fire Salamanders, but they cannot be studied with our data set.

Habitat suitability models

Regression models are a suitable tool to assess which environmental variables most accurately explain salamander species distribution (Romero et al. 2012). We used logistic regression analysis with an information theoretic approach (Burnham & Anderson 2002) to assess the effect of extrinsic factors (explanatory variables) on Fire Salamander occurrence and to develop a niche model from these predictors. Using purposeful selection (Hosmer et al. 2013) we thus set the most complex models, containing explanatory variables with acceptable multicollinearity. Applying stepwise backward elimination (Kleinbaum et al. 1998), we subsequently searched for the most parsimonious model(s).

Using the R function "stats::glm()" we computed generalized linear models (regressions) on binary (presence/absence) data (e.g., McCullagh & Nelder 1989). The ratios "events-per-variable" (events = our pixels with salamander sightings) of our a-priori variables (not variables in final model) were between 154 and 1,849 in our models, which seems to be more than sufficient (see Harrell 2015, Heinze & Dunkler 2017). Viewing such a high EPV ratio, we set a significance level of 0.05 for deciding whether or not to keep a given parameter in the model (Heinze & Dunkler 2017).

Strong multicollinearity among variables may bias regression analyses (Berry & Feldman 1985). To avoid unacceptable levels of multicollinearity in our models, we screened correlations between variables in R with the function "car::vif()" (Fox 2019) prior to model fitting. We checked each of the variables in the model for its possible correlation with other variables to meet the assumptions of logistic regression (Hosmer et al. 2013). Based on the recommendation by Zurr et al. (2010), we sequentially removed (or assessed in separate models) variables with high multicollinearity until all remaining variables had a variance inflation factor (VIF) of ≤ 4. This level seems to be conservative enough (comp. Manenti et al. 2009a, Olivero et al. 2016, Marquardt 1970, Montgomery et al. 2012, Romero et al. 2012).

We ranked all candidate models according to (sample size corrected) Akaike's Information Criterion (AICc) values (Hurvich & Tsai 1989, Burnham & Anderson 2002). The most parsimonious model has the smallest AICc value. AICc can be used to compare two models even if they are not hierarchically nested (Heinze & Dunkler 2017). We calculated the difference between the AICc value of a particular model and the lowest AICc value of all the models (ΔAICc). Following Burnham & Anderson (2002) and Greenwald et al. (2009), we considered a model with ΔAICc < 2 as having a strong support for making inferences. We considered models with ΔAICc > 7 being irrelevant (Suzuki et al. 2008). We calculated the Akaike weight ω (normalizing $\exp(-\Delta_i AICc/2)$ across the set of all models to be compared), which can be roughly interpreted as the probability at which that partial model is the best one. Finally, we used two metrics of predictive values for each model with ΔAICc < 2: McFadden's pseudo R^2 (McFadden 1974) and AUC. The area beneath the receiver operating characteristic (ROC) curve, known as the AUC, provides a single-number discrimination value across all possible ranges of variables and is independent of any favourability threshold (Hosmer et al. 2013). It indicates the degree to which a species is restricted to part of the variation range of the modelled predictors (Romero et al. 2012). We calculated McFadden's pseudo R^2 and AUC using the R functions "pscl::pR2()" (Jackman 2017) and "ROCR::performance()" (Sing et al. 2015). Larger values of McFadden's pseudo R^2 point out models with better predictive values. Quality of model-fitting ranging from 0 to 1 and values 0.2 to 0.4 indicate a very good model fit. AUC value ranges between 0.5 and 1. AUC = 0.5 suggest that the model accuracy is not better than the accuracy obtained by random assignment. AUC > 0.7 indicates useful performance, AUC > 0.8 indicates good performance, and AUC > 0.9 indicates excellent performance of the model (Manel et al. 2001, Baldwin 2009). We considered a model informative if the AUC value was > 0.7 (Lobo et al. 2007, Sutton et al. 2015). Its relevance as a general measurement of predictive accuracy of distributional models derived from presence/absence species data is debatable (Lobo et al. 2007, Jiménez-Valverde 2012). However, it is an effective measure for the comparison of the discrimination capacity of models in cases where they deal with the absence/presence of the focal species in a part of its known range (Lobo et al. 2007, Romero et al. 2012). If variables are to be ranked, comparisons based on AUC are recommended (Fielding & Bell 1997).

After choosing the best model(s), we investigated the relative relationship of each explanatory variable to each dependent variable. The final evidence of support was spread across more than one (sub)equally parsimonious top-model (Tables 3, 4). For this reason, we applied subset model averaging using the R function „MuMIn::model.avg" (Barton 2019). We weighted coefficients from different best-predictable models in each set by their AICc weights (Lukacs et al. 2010). Because the support for our top-one model was strong but not indisputable (AICc weight < 0.90), we averaged (and weighted by their AICc weights) parameter estimates for all variables from all four top candidate models (Lukacs et al. 2010, Burnham et al. 2011, Symonds & Moussalli 2011). Model-averaged estimates are more accurate than those generated from the top model alone (Hedlin & Franke 2017), and this method solves the problem of uninformative parameters, commonly present in the second-best model (Burnham & Anderson 2002).

We described model selection uncertainty by model-averaged coefficients with 85% confidence intervals (Arnold 2010). From these model-averaged statistics, we calculated the odds ratio with 85% confidence intervals for each variable (Table 2). We considered significant explanatory variables whose model-averaged 85% confidence intervals for the variable coefficient did not include 0 or whose model-averaged 85% confidence interval of odds ratio for the variable did not include 1 to explain the occurrence of salamanders. Besides the direction of association (±) of explanatory variables in our top models with ΔAICc < 2, we also briefly comment on the association of these variables in all other a-priori models with ΔAICc > 2 (Arnold 2010).

We obtained seasonal activity distribution profiles of Fire Salamanders from a single, comprehensive Poisson GAM model (Hastie & Tibshirani 1990, Wood 2017) of salamander presence as a function of altitude and position of day within a year (seasonal component), based on all available data.

We conducted all analyses in the R computing environment (Version 3.5.2) (R Core Team 2020); a CSV file with the source data and two main R scripts used in the analysis are available from the "Open Science Forum" at https://doi.org/10.17605/OSF.IO/M7NP4.

Results

Habitat suitability models

For model performance, see Table 3. The most strongly supported model was No. 55 (ω = 0.28, McFadden R^2 = 0.202) with CORINE land cover, terrain slope, terrain aspect, the length of streams, pH of surface water, soil depth to rock, absolute humidity, solar irradiation, number of warm daytimes, temperature seasonality, temperature difference between mean warmest and mean coldest month, precipitation seasonality, precipitation due to extremely wet days.

Three other models with ΔAICc < 2 also had strong support: No. 54 (ω = 0.28, McFadden R^2 = 0.202) with CORINE land cover, terrain slope, terrain aspect, the length of

Table 2. Numbers of positive (+), negative (-) and non-significant responses of variables in all our a-priori models (ΔAICc = the difference between the AICc value of a particular model and the lowest AICc value of all models).

Variables	All 59 models			Only the top-four models (ΔAICc < 2)		
	P < 0.01	P < 0.05	insignif	P < 0.01	P < 0.05	insignif
East aspect of slopes	57-			4-		
South aspect of slopes			57			4
West aspect of slopes			57			4
Slope	58+			4+		
CORINE112 – Discontinuous urban fabric	1-	20-	38		4-	
CORINE211 – Non-irrigated arable land	59-			4-		
CORINE231 – Pastures	59-			4-		
CORINE243 – Land principally used for agriculture			59			4
CORINE311 – Broad-leaf forest	59+			4+		
CORINE312 – Coniferous forest	27-	15-	17			4
CORINE313 – Mixed forest	59+			4+		
Soil depth to rock	1+	5+	48			4
Volume of stones in soil			1			
Sedimentary rock	1+					
Igneous rock		1+				
Metamorphosed sedimentary rock			1			
Sedimentary and metamorphic rock	1+					
Igneous and metamorphic rock			1			
Length of first- and second-order streams in each 1×1-km pixel	56+			4+		
pH of surface water	56+			4+		
Mean annual temperature	7+					
Autumn, mean temperature	2+					
Summer, mean temperature	2+					
Spring, mean temperature	2+					
Autumn, maximum mean temperature	1+					
Summer, maximum mean temperature	1+					
Spring, maximum mean temperature	1+					
Autumn minimum mean temperature	1+					
Summer minimum mean temperature	1+					
Spring minimum mean temperature	1+					
No. of warm nights			1			
No. of warm daytimes	17+			4+		
Days with temperatures below 0°C			1			
Days with temperatures above 5°C	1+					
Frost-free period	1+					
Julian date on the which frost-free period ends	3+					
Julian date on which the frost-free period begins	1-					
Temperature seasonality	14+	1+	5			2
Temperature difference between mean warmest month and mean coldest month	17+			4+		
Mean annual precipitation	2+, 2-	1-	1			
Autumn precipitation	1+					
Summer precipitation	1+					
Spring precipitation	1+					
Precipitation in wettest quarter	1+					
Precipitation in driest quarter	3-	3-	1	2-		
Precipitation in coldest quarter	4-					
No. of wet days (≥1 mm) (autumn)	2+					

Table 2 continued

Variables	All 59 models			Only the top-four models (ΔAICc < 2)		
	P < 0.01	P < 0.05	insignif	P < 0.01	P < 0.05	insignif
No. of wet days (≥1 mm) (spring)	2+					
No. of wet days (≥1 mm) (summer)	2+					
Total precipitation from wet days (>1 mm)	1+					
Precipitation total due to moderately wet days (>75th percentile)	1+					
Precipitation total due to very wet days (>95th percentile)	1+					
Precipitation total due to extremely wet days (>99th percentile)	18+			4+		
Precipitation seasonality	11+	3+	2	2+		
Absolute humidity	13+			4+		
Solar irradiation (annual mean)	9-			4-		

Table 3. Characteristics of selected regression models of Fire Salamander presence. For descriptions of the models see Appendix Table 1. Only models with ω > 0.02 are presented. K = number of explanatory variables; logLik = log likelihood, which is a measure of how well the model fits the data; AICc = Akaike's Information Criterion correlated to sample size; ΔAICc = difference between the AICc value of a particular model and the lowest AICc value of all models; ω = Akaike weight can be interpreted as the probability that a particular model is the best one; McFadden pseudo R^2 = quality of model fitting ranging from 0 to 1, with values 0.2 to 0.4 indicating a very good model fit; AUC = area under the curve calculated using the function "ROCR::performance()" (Sing et al. 2015).

Model	K	logLik	AICc	ΔAICc	ω	AUC	McFadden R^2
55	13	-7,428.73	14,907.48	0.00	0.30	0.886	0.202
54	13	-7,428.86	14,907.72	0.24	0.26	0.886	0.202
57	12	-7,429.95	14,907.91	0.43	0.24	0.886	0.202
56	12	-7,430.51	14,909.03	1.55	0.14	0.887	0.202
59	13	-7,430.86	14,911.73	4.25	0.04	0.885	0.202
58	12	-7,431.94	14,911.90	4.41	0.03	0.886	0.202

streams, pH of surface water, soil depth to rock, absolute humidity, solar irradiation, number of warm daytimes, temperature seasonality, temperature difference between mean warmest and mean coldest month, precipitation of driest quarter, precipitation due to extremely wet days; No. 57 (ω = 0.24, McFadden R^2 = 0.202) with CORINE land cover, terrain slope, terrain aspect, the length of streams, pH of surface water, soil depth to rock, absolute humidity, solar irradiation, number of warm daytimes, temperature difference between mean warmest and mean coldest month, precipitation of driest quarter, precipitation due to extremely wet days); and No. 56 (ω = 0.12, McFadden R^2 = 0.202) with CORINE land cover, terrain slope, terrain aspect, the length of streams, pH of surface water, soil depth to rock, absolute humidity, solar irradiation, No. of warm daytimes, temperature difference between mean warmest and coldest month, precipitation seasonality, precipitation due to extremely wet days.

In addition, model No. 59 (ω = 0.04, McFadden R^2 = 0.202) had an ΔAICc = 3,94 with CORINE land cover, terrain slope, terrain aspect, the length of streams, pH of surface water, soil depth to rock, absolute humidity, solar irradiation, No. of warm daytimes, temperature seasonality, temperature difference between mean warmest and mean coldest month, precipitation of coldest quarter, precipitation due to extremely wet days; and model No. 58 (ω = 0.03, McFadden R^2 = 0.202) had an ΔAICc = 4.23 with CORINE land cover, terrain slope, terrain aspect, the length of streams, pH of surface water, soil depth to rock, absolute humidity, solar irradiation, No. of warm day-times, temperature difference between mean warmest and mean coldest month, precipitation of coldest quarter, precipitation due to extremely wet days.

Beyond that, there was a sharp drop in model success. Within our a-priori models, these were the most complex, encompassing (a) climatic as well as (b) geomorphological and (c) habitat-related explanatory variables. Models made up of fewer explanatory variables, or those that did not contain some of these three groups, always scored significantly worse in terms of the metrics used (AUC and McFadden R^2). The discrimination capacity (AUC, ranging from 0.5 to 1) of our top four models was always higher than 0.885, and thus excellent according to Hosmer et al. (2013).

Leaving aside a few probably erroneous located sightings, sightings of Fire Salamanders come from the following CORINE land cover types: mixed forest > broad-leaf forest > coniferous forest > land principally used for agriculture > discontinuous urban fabric > non-irrigated arable land > pastures. Based on the averaged top-four models, Fire Salamanders were positively associated with broadleaf forest (CORINE311) and mixed forest (CORINE313) and negatively associated with non-irrigated arable land (CORINE211), pastures (CORINE231), and discontinuous urban fabric (CORINE112) in all our top-four models. Associations with coniferous forest (CORINE312) and land principally used for agriculture (CORINE243) were not obvious in any direction. They were positively associated also with terrain slope, the length of the hydrographic network, pH of these streams, humidity, seasonality of pre-

Table 4. Effects of explanatory variables on the occurrence of Fire Salamanders based on averaging the top four models with ΔAICc < 2 (ΔAICc = difference between the AICc value of a particular model and the lowest AICc value of all models, CI = confidence interval).

	Model averaged coefficient						
Variable	Estimate	85% CI		Odds ratio	85% CI of odds ratio		P
aspect_east	-0.303	-0.409	-0.198	0.738	0.665	0.820	< 0.001
aspect_south	0.094	-0.007	0.195	1.099	0.993	1.216	0.179
aspect_west	0.021	-0.074	0.117	1.022	0.928	1.124	0.757
BIO04	0.003	0.000	0.006	1.003	1.000	1.006	0.092
BIO15	0.014	0.007	0.021	1.014	1.007	1.021	0.003
BIO17	-0.004	-0.006	-0.002	0.996	0.995	0.998	0.002
CORINE112	-0.007	-0.011	-0.002	0.993	0.989	0.998	0.027
CORINE211	-0.029	-0.032	-0.026	0.971	0.968	0.975	< 0.001
CORINE231	-0.028	-0.032	-0.023	0.972	0.968	0.977	< 0.001
CORINE243	-0.004	-0.008	0.000	0.996	0.992	1.000	0.118
CORINE311	0.016	0.013	0.019	1.016	1.013	1.019	< 0.001
CORINE312	-0.003	-0.005	0.000	0.997	0.995	1.000	0.084
CORINE313	0.011	0.008	0.013	1.011	1.008	1.013	< 0.001
pH	0.625	0.526	0.724	1.868	1.691	2.063	< 0.001
r99ptot_yr	0.028	0.023	0.033	1.029	1.024	1.034	< 0.001
slope	0.202	0.183	0.222	1.224	1.201	1.248	< 0.001
soil02	0.184	0.010	0.358	1.202	1.010	1.431	0.132
SRADyear	-0.001	-0.001	-0.001	0.999	0.999	0.999	< 0.001
TD	0.622	0.528	0.716	1.863	1.696	2.047	< 0.001
tx90p_yr	0.802	0.698	0.906	2.229	2.009	2.474	< 0.001
humidity	1.364	1.101	1.626	3.911	3.007	5.086	< 0.001
water	22.226	15.909	28.544	4.4e+09	8.1e+06	2.5e+12	< 0.001

cipitation or, more precisely, the amount of precipitation on extremely wet days, the temperature difference between the warmest and coldest months, and the numbers of warm daytimes. They were negatively associated with solar irradiation, the eastern aspect of slopes, the amount of precipitation during the driest quarter (winter), and with the presence of the following land cover types: discontinuous urban fabric, non-irrigated arable land, and pastures (Table 4). Despite the negative association with these three types of habitat, Fire Salamanders occur there to a limited extent.

All the above explanatory variables scored in the same direction also in models that did not rank in the top four with ΔAICc < 2 (Table 2), oftentimes due to collinearity of the explanatory variables. Humidity, distance to small shallow streams, and the presence of broad-leaf and mixed forests were the explanatory variables most significantly increasing the discrimination capacity of all our models in terms of used metrics (AUC and McFadden R^2).

We tested for an association of the distribution of broad-leaf, mixed, and coniferous forests with altitude. Within forested areas, the proportions of broad-leaf (-0.25, P < 0.01 and mixed (-0.20, P < 0.01) forests, which were positively associated with Fire Salamander presence in our models, declined with rising altitude. On the other hand, there is an increasing proportion of coniferous forest (0.29, P < 0.01), which was otherwise negatively associated with Fire Salamander presence in our models. We also tested for an association of temperature (MAT), precipitation (MAP) and humidity (humid) with altitude. With rising altitude, there is a decline in air temperature (r = -0.93, P < 0.01) and absolute humidity (r = -0.97, P < 0.01), while the quantity of precipitation increases (e.g., BIO16: r = 0.63, P < 0.01, BIO17: r = 0.64, P < 0.01, BIO18: r = 0.63, P < 0.01, MAP: r = 0.78, P < 0.01). Ninety-five percent of locations with salamander sightings, equal to 95% of the Czech Republic's territory, show an identical mean annual precipitation of > 531 mm and a mean non-snow precipitation of > 493 mm, respectively. Therefore, the lack of precipitation does not seem to be a limiting factor here.

Using the function "WRS2::qcomhd()" (Mair & Wilcox 2020) we compared the lower (5%) and upper (95%) quantiles (Wilcox & Erceg-Hurn 2012, Wilcox et al. 2014) of mean annual temperatures (MAT) at the locations with salamander sightings and in all the areas within the 409-m buffer zones along streams. While the values of the lower quantiles were significantly different in favour of locations with salamander sightings (5.68 vs. 5.40, P < 0.001), this was not the case for the upper quantiles (8.52 vs. 8.50, P = 0.299). Thus, high temperatures do not seem to be a limiting factor for salamander presence in the Czech Republic either.

Seasonal salamander activity profile

Altitudes in the Czech Republic range from 115 to 1,602 m. Of the total area of the country, 67% lie at altitudes below 500 m and 32% between 500 and 1,000 m a.s.l.. Only 1% rises to altitudes higher than 1,000 m. Salamanders occur at altitudes ranging from 145 to 1,098 m (mean = 433 ± 147). Ninety-five percent of sightings come from altitudes above 254 and below 726 m, and 75% from above 321 and below 514 m (Fig. 3). While the average altitude of spring (< April) and autumn (> August) sightings was not significantly different (ANOVA, F = 0.49044, df = 1061.9, P = 0.4839), the average altitude of summer sightings (April–August) was significantly higher (ANOVA, F = 15.552, df = 870.45, P < 0.001) than that of sightings from the rest of the year. Figure 4 illustrates clearly that the seasonal (within-year) salamander activity profile is not the same for all altitudes. On the contrary, the within-year activity distribution shape changes relatively smoothly from low to higher altitudes. In fact, altitude modifies the activity distribution in several different ways. Firstly, the period when activity is non-negligible (when the normalized intensity exceeds some low threshold, e.g., 0.001, marked by the horizontal dotted line) is clearly uniformly longer for lower altitudes. The shortening of that period with altitude occurs at both ends: a later beginning and an earlier end of the main activity season. Another view of this phenomenon is that for a fixed time position (obtained as, say, 2.5th and 97.5th percentiles of salamander presence times – day positions 91 and 299, respectively), activity is much higher for lower elevations. Next, for a given altitude, the season start is more abrupt than the season's ending (steepness, or the profile curve derivative absolute value is generally higher on the left than on the right slope), but the difference decreases with altitude. Secondly, the seasonal distribution of activity is bimodal, expressing itself in spring and autumn activity peaks being interrupted by a summer depression. Proportions of the spring and autumn peaks differs systematically with altitude, however. For low altitudes, there is a complete dominance of the spring peak, but as altitudes increase, the proportion (and even local maximum) of the spring peak decreases. Moreover, the summer depression tends to be less pronounced, so that at higher altitudes there is a tendency towards unimodality (with the spring and autumn peaks joined by a somewhat flatter curve at the period of peak activity at higher altitudes).

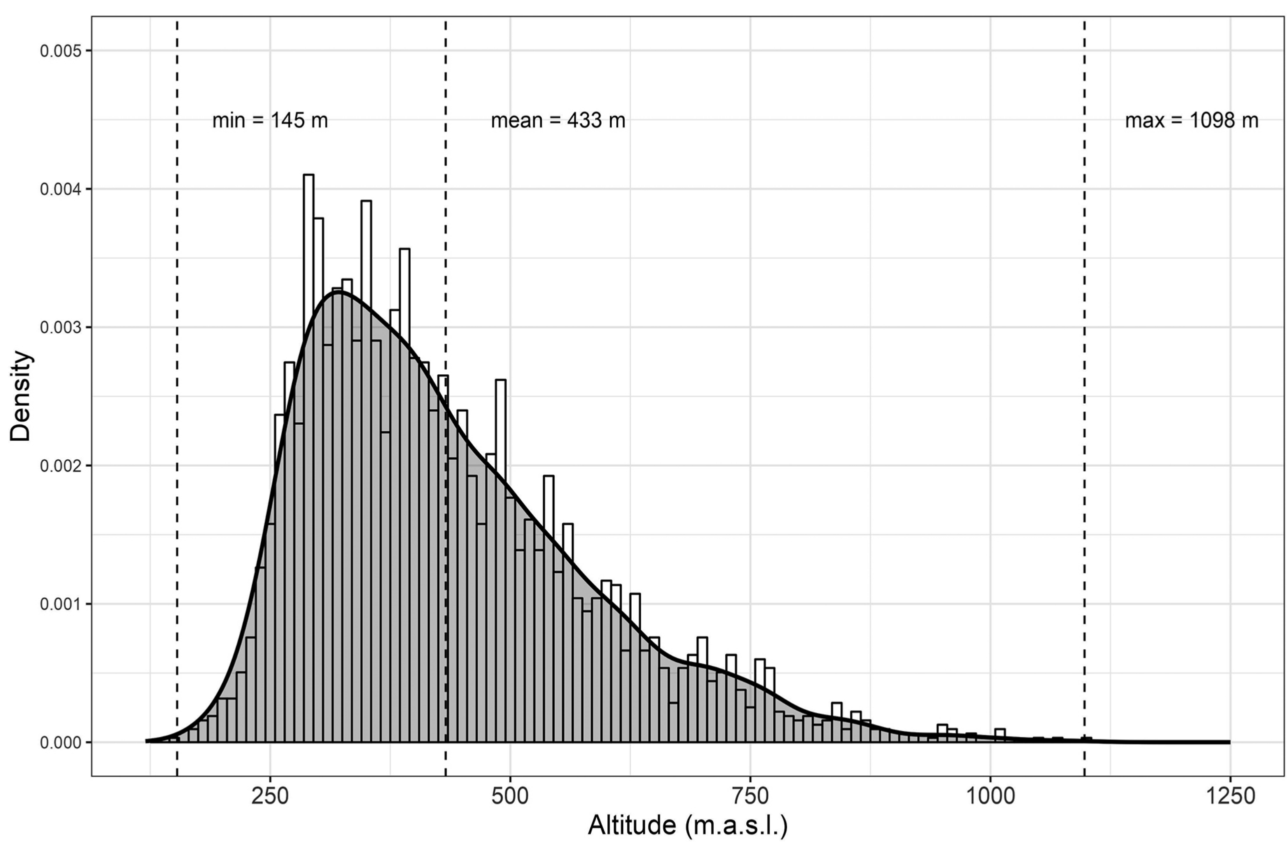

Figure 3. Altitudinal distribution of Fire Salamanders (*Salamandra salamandra*, n = 3,546; larvae and postmetamorphic salamanders in terrestrial habitats) as directly estimated from data in the Species Occurrence Database NCACR without reference to seasonality. Mean = 433 ± 147 m, max = 1,098 m, median = 400 m.

Discussion

Habitat suitability models

Our explanatory variables take into account the landscape scale (Mackey & Lindenmayer 2001). In the area studied here, salamanders very often inhabit deeply carved, shaded valleys, where locally specific microbiotope conditions prevail, and the microhabitat preferences of salamanders may therefore differ somewhat from landscape scale preferences (Romero et al. 2012, Sutton et al. 2015, Ficetola et al. 2018).

While in the southern parts of the species range, high summer temperatures and lack of precipitation, or the duration of the warm period, act as factors limiting the presence of Fire Salamanders (Egea-Serrano et al. 2006), in the area covered by this study the length of the winter period constitutes the limiting factor, which is demonstrated by its association with explanatory variables: Frost-free period, the Julian date on which the frost-free period begins, the Julian date on which the frost-free period ends, and days with temperatures above 5°C. However, compared with humidity (with which they are collinear) none of these explanatory variables were strong enough to be used in our top four models.

The Fire Salamander is generally considered a species that will prefer lower temperatures (Catenazzi 2016). Results from our models suggest that in the climatic conditions of the Czech Republic, higher temperatures do not constitute a limiting factor for the occurrence of Fire Salamanders, however. The presence of Fire Salamanders was positively associated with all our temperature variables in all our 22 a-priori models containing these variables. The only exception is the variable "number of warm nights" (tn90p_yr), which had no association with the presence of Fire Salamanders. Alternation of individual seasonal temperature variables in our models did not have much affect the scoring of these models in terms of the metrics used (AUC and McFadden R^2). Temperature is also strongly correlated with the humidity variable (e.g. MAT vs. humid, $r = 0.92$, $P < 0.01$), which was strongly positively associated with Fire Salamander presence in all of our top-four models. In unfavourable weather, salamanders hide underground, with at least some species retreating deeply underground (Riberon & Miaud 2000, Romano & Rugierro 2008). Fire Salamanders also spend only a very small part of their lives above ground, living most of their time underground (Rebelo & Leclair 2003). In these underground spaces, temperature conditions are very different from those above ground (Burda et al. 2007), and Fire Salamanders live there within a temperature range of 8–12°C, even during summer (Catenazzi 2016). The fact that they are not active above ground does not necessarily mean that they are inactive underground.

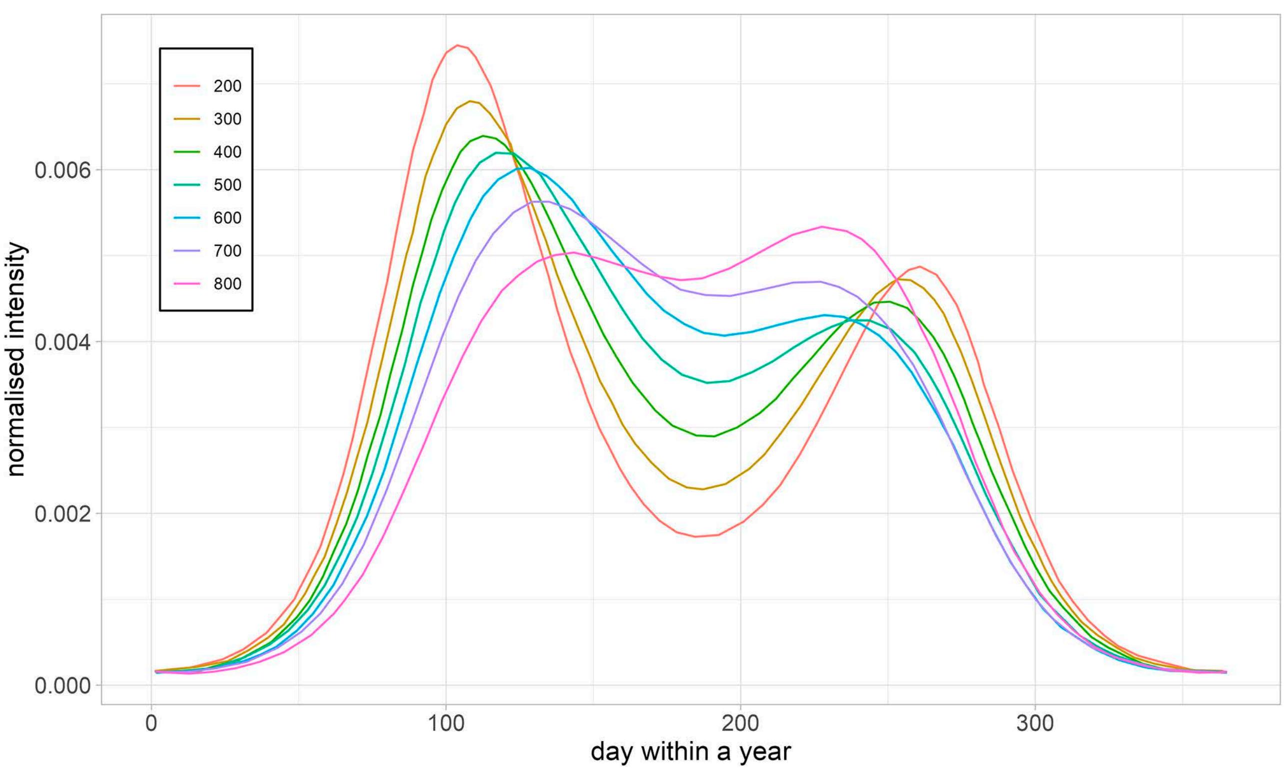

Figure 4. Seasonal salamander activity distribution profiles at different altitudes. Profiles are derived from a single comprehensive Poisson GAM model fitted to presence data from all locations. Estimated profile curves at selected altitudes are normalized to have unit integers to provide information on the seasonal distribution for a given altitude.

Fire Salamander presence was positively associated with the temperature difference between the mean warmest and the mean coldest month (TD) in all our 17 a-priori models containing these variables and in all our top-four models as well. The association with temperature seasonality (BIO4) was not so unambiguous, even though positive association prevailed or was not significant in some models. However, these associations are not a consequence of a preference for the continental climate, but reflect the fact that salamanders avoid higher cold altitudes, with temperature differences between the warmest and coldest months (TD) decreasing with increasing altitude ($r = -0.63$, $P < 0.01$), and the same applies to temperature seasonality (BIO4) ($r = -0.70$, $P < 0.01$).

The preference for broad-leaf and mixed forest we have found is in accordance with the general habitat preferences of Fire Salamanders from other parts of temperate Europe (e.g., Lanza et al. 2009, Bani et al. 2015). Arable land and pastures in any case are strong drivers of isolation for salamander populations (Greenwald et al. 2009, Romero et al. 2012). However, Fire Salamanders can persist in a high-intensity agricultural landscape (Baumgartner et al. 1999, Meikl et al. 2010, Tanadini et al. 2011), which is confirmed also by our results. In our models, they were negatively associated with discontinuous urban fabric, non-irrigated arable land, and pastures, but they can survive in some of those areas.

Due to the low willingness of most adult salamanders to move too far away from their breeding streams and the vulnerability of their larvae to fish predation, the presence of small, oligotrophic and heterogeneous streams with scarce periphyton, surrounded by woodlands, constitutes a generally appicable prerequisite for their occurrence (Manenti et al. 2009a), which is confirmed by the results from our models. As was found by Ficetola et al. (2008), the length of the hydrographic network ranked amongst the most important explanatory variables in all our top-four models. Topography and slope influence the amount of solar exposure and thus temperature, humidity and moisture of the substrate (Lookingbill & Urban 2004). Fire Salamanders were also positively associated with the slope of terrain in all our 58 a-priori models containing this variable. Their presence was negatively associated with the eastern aspect of slopes in all our 57 a-priori models containing this variable, and this negative association was significant in all our top-four models as well. Their association with the other aspects was not obvious. According to Werner et al. (2014), Fire Salamanders generally make use of sites with inclinations lower than 35°. Bani et al. (2015) mentioned that optimal slopes were angled at between 5 and 20°, while presence probability was close to zero for slopes steeper than 40°, where the runoff of water should be too strong to permit the formation of slow-flowing pools. Especially in mountainous landscapes, salamanders are ac-

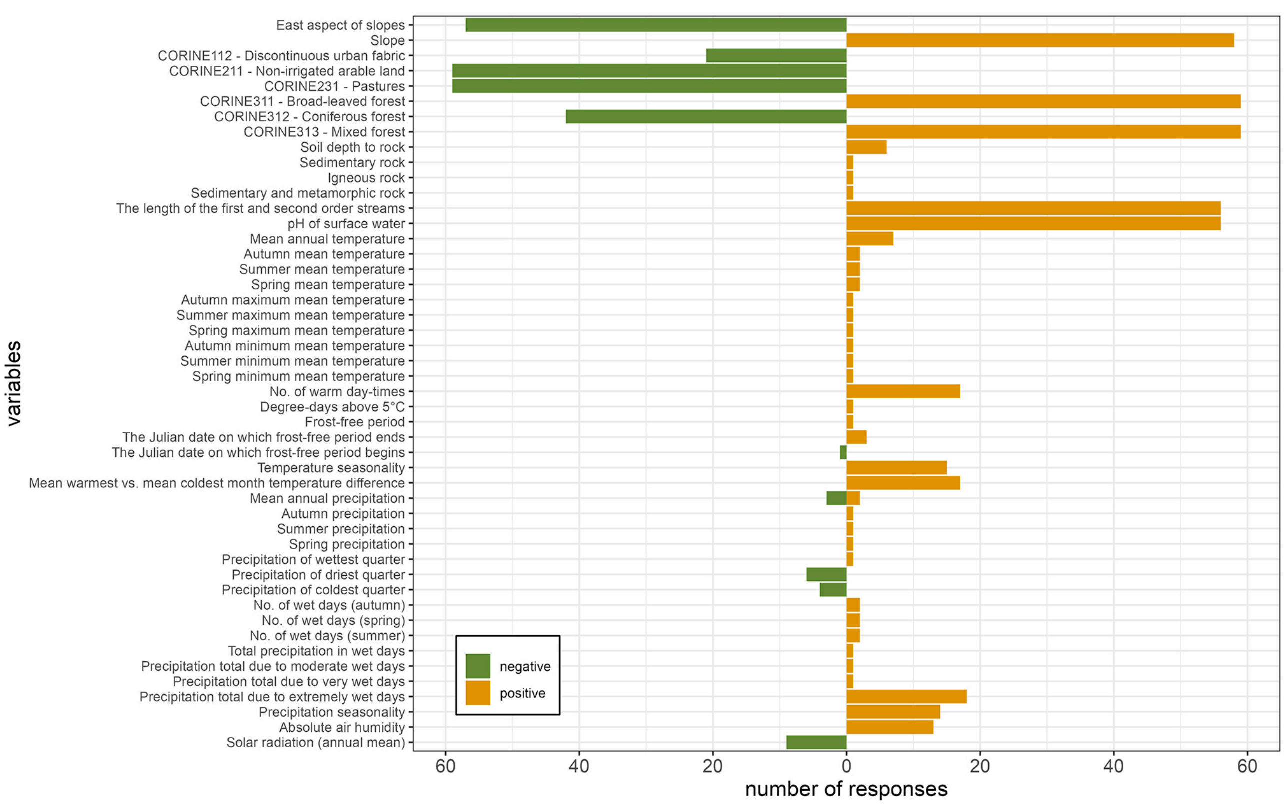

Figure 5. Numbers of positive and negative significant ($P < 0.05$) responses of explanatory variables in all our a priori models.

tive on paths with shallower inclinations (Denoël 1996, Manenti et al. 2017). These sightings are not in contradiction with the results of our models, though, because they describe microhabitat preferences. At the mesoscale, our models reveal an association of Fire Salamanders with small streams, flowing through rolling landscapes. Such aquatic and terrestrial habitats are missing in more expansive lowlands, which may explain the absence of Fire Salamanders in the lowlands of the Czech Republic. This is the main limiting factor for their occurrence in these areas.

Stream acidification (Pough & Wilson 1977) and low pH of forest soil (Clip & Anderson 2014, Anderson & Johnson 2018) can restrict the distributions of salamanders. Fire Salamander presence was positively associated with water pH values in all our 56 a-priori models containing this variable and in all our top-four models as well.

Water vapour pressure (VAPRyear), or more precisely the absolute humidity of the air calculated from it, was a variable with a significant effect on the quality of model fit. Fire salamander presence was positively associated with water vapour pressure in all our 13 a-priori models containing this variable and in all our top-four models (comp. Velo-Anton & Cordero-Rivera 2017).

The amounts of precipitation and their even distribution throughout the year were variables, for which we expected a strong positive association with the presence of Fire Salamanders. However, this a-priori expectation was only partly fulfilled. The variables describing the amount of precipitation (the number of wet days in spring, summer and autumn, the amount of precipitation in spring, summer and autumn) mostly scored positively in our a-priori models. However, their manifestation was not strong enough for them to be used in our top four models. The alternation of individual seasonal precipitation variables in our models (r1mm: models 24, 25, 26 and PPT: models 28, 29, 30) did not have much effect on the scoring of these models in terms of the metrics used (AUC and McFadden R^2). All variables related to the amount of precipitation are strongly correlated with altitude, which from a certain level begin to act as a limiting factor for Fire Salamander occurrence because of decreasing temperatures, even if the amount of precipitation remains high. The association with the amount of precipitation in the driest quarter (winter) was negative, and this relationship was manifest also in our top-four models. The variable "precipitation of the coldest quarter" scored in the same direction. The negative association with winter precipitation (which falls in the shape of snow across most of the Czech Republic's territory and is an attribute of the harshness of winter) is reflected also in an ambiguous association of Fire Salamander presence with the variable of mean annual precipitation; it is an expected trend. The association with uneven distribution of precipitation, both in the course of a year (BIO15), as well as in the form of a smaller number of heavy rain events (r99ptot_yr) was always positive in our models including our top-four models. Although both variables are not so strongly dependent on altitude as temperature or the amount of precipitation, their values still depend on altitude, although each in a different direction. With increasing altitude, the differences between the amount of winter and summer precipitation narrow (BIO15: $r = -0.50$, $P < 0.01$), but on the other hand, the amount of precipitation (rain, snow) falling in torrential events (r99ptot_yr: $r = 0.57$, $P < 0.01$) increases. As is the case in other parts of the species' range (e.g., Joly 1968), Fire Salamanders in the Czech Republic prefer areas with abundant precipitation or with a lot of precipitation falling at once, albeit in less frequent events, but not areas with abundant precipitation that are at the same time cold (mountain areas).

Seasonal salamander activity profile

Fire Salamanders avoid more expansive lowlands and higher altitudes in the Czech Republic. Nevertheless, their absence there is not caused by the higher altitudes themselves, but rather by the environmental conditions prevailing in these situations. In the southern parts of their range, Fire Salamanders prefer higher altitudes than in the northern parts (e.g., Egea-Serrano et al. 2006, Olivero et al. 2016), and in larger mountain areas such as the Alps (Meikl et al. 2010) or the Carpathians (Balogova et al. 2015) they also occur at higher levels. In the area studied in this paper, Fire Salamanders respond to colder conditions at higher altitudes by shifting their above-ground circannual activity. The purely bimodal character of activity seen at lower and medium altitudes becomes compromised at higher altitudes, the spring peak disappears, and their summer activity (April to August) is more pronounced. It is not surprising that with increasing altitude, the start of activity in spring is delayed to an increasing extent, but this onset also blurs with altitude, with salamanders at lower altitudes leaving their overwintering shelters in a more explosive manner. The autumnal decline in activity copies that in spring in reverse, but differences between altitudes are less pronounced, i.e., altitude plays a smaller role in autumn than in spring.

Conclusion

The results of our models clearly show that in the conditions of the Czech Republic at a landscape scale the presence or absence of Fire Salamanders in an area is not due to the effect of one dominant factor, but rather is the result of a combined effect of multiple factors affecting these caudates in both their terrestrial and aquatic habitats. Manenti et al. (2009a) and Tanadini at al. (2011) arrived at similar conclusions when they analyzed comparable climatic conditions in France and Switzerland, respectively. The factors always coming to the forefront in the Czech Republic include distance to small shallow streams (-) in a rolling landscape (+), water pH of these streams (+), presence of broad-leaf or mixed forest (+),humidity (+), solar irradiation (-), and temperature (+). In various areas, for example depending on altitude or the degree of landscape anthropogenization, the order of influential importance of these main factors changes. In more expansive plains, which are mainly encountered at low altitudes in the Czech Republic, the main limiting factor for the occurrence of Fire Salamanders is the absence of suitable breeding habitats (shallow streams). With increasing altitude, decreasing temperatures, decreasing humidity levels, and the absence of broadleaf and mixed forests, which are the preferred habitats of Fire Salamanders, begin to play a role. At higher altitudes, the forests are substituted by coniferous (mainly spruce) monocultures, which are not attractive for Fire Salamanders (Manenti et al. 2017). Their typical association with shallow clean lotic water bodies could be a consequence of these not hosting predatory fish rather than a real selection (Montori & Herrero 2004). Low pH and higher solar irradiation are limiting factors regardless of altitude.

Fire Salamanders prefer areas with higher amounts of precipitation (especially non-winter precipitation). However, in terms of precipitation, the entire portion of the Czech Republic analyzed in this study seems to suit Fire Salamanders well. The amount of precipitation (total or non-snow precipitation) does not appear to be a limiting factor for their presence anywhere in the studied area. In contrast to cold, high temperatures here are not the limiting factor for their occurrence in the vast majority of areas they are a able to reach. If need be, they can avoid high temperatures locally by selecting cooler and more humid places at a microhabitat scale (e.g., the vicinity of streams at the bottom of deeply carved valleys within forests). Within the range of temperatures prevailing at a mesoscale in the Czech Republic, rather than being a cryophilic species, the Fire Salamander appears to be a species capable of tolerating lower temperatures. It responds to the colder climate of higher altitudes with an increase in summer activity, and the purely bimodal character of its activity (spring, autumn) disappears in higher altitudes, mainly at the expense of the spring maximum.

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Appendix 1

Explanatory variables included in each a-priori model.

Model No.	Variables
Habitats, geomorphology, water (= non-climatic variables)	
1	CORINE
2	CORINE, slope
3	CORINE, slope, aspect
4	CORINE, slope, aspect, water, pH
5	CORINE, slope, aspect, water, pH, soil02, soil08
6	CORINE, slope, aspect, water, pH, litho
Non-climatic variables and temperature in the period of Fire Salamander activity	
7	CORINE, slope, aspect, water, pH, soil02, Tave_at
8	CORINE, slope, aspect, water, pH, soil02, Tave_sp
9	CORINE, slope, aspect, water, pH, soil02, Tave_sm
10	CORINE, slope, aspect, water, pH, soil02, MAT
11	CORINE, slope, aspect, water, pH, soil02, Tmin_at
12	CORINE, slope, aspect, water, pH, soil02, Tmin_sp
13	CORINE, slope, aspect, water, pH, soil02, Tmin_sm
14	CORINE, slope, aspect, water, pH, soil02, Tmax_at
15	CORINE, slope, aspect, water, pH, soil02, Tmax_sp
16	CORINE, slope, aspect, water, pH, soil02, Tmax_sm
Non-climatic variables and winter climate influence	
17	CORINE, slope, aspect, water, pH, soil02, FFP

Appendix 1 continued

Model No.	Variables
18	CORINE, slope, aspect, water, pH, soil02, bFFP
19	CORINE, slope, aspect, water, pH, soil02, eFFP
20	CORINE, slope, aspect, water, pH, soil02, DD<0
21	CORINE, slope, aspect, water, pH, soil02, DD>5
Non-climatic variables and severity of summer climate	
22	CORINE, slope, aspect, water, pH, soil02, tn90p_yr
Non-climatic variables and climate (temperature, precipitation) seasonality	
23	CORINE, slope, aspect, water, pH, soil02, BIO4, BIO15
Non-climatic variables and precipitation in the period of Fire Salamander activity	
24	CORINE, slope, aspect, water, pH, soil02, r1mm_spring_seas
25	CORINE, slope, aspect, water, pH, soil02, r1mm_summer_seas
26	CORINE, slope, aspect, water, pH, soil02, r1mm_autumn_seas
27	CORINE, slope, aspect, water, pH, soil02, MAP
28	CORINE, slope, aspect, water, pH, soil02, PPT_sp
29	CORINE, slope, aspect, water, pH, soil02, PPT_sm
30	CORINE, slope, aspect, water, pH, soil02, PPT_at
31	CORINE, slope, aspect, water, pH, soil02, BIO16
32	CORINE, slope, aspect, water, pH, soil02, BIO17
Non-climatic variables, temperature and temperature seasonality	
33	CORINE, slope, aspect, water, pH, soil02, MAT, BIO4
Non-climatic variables, temperature, temperature seasonality, precipitation, and precipitation seasonality	
34	CORINE, slope, aspect, water, pH, soil02, MAT, BIO4, MAP, BIO15
Non-climatic variables, temperature, temperature seasonality, precipitation, precipitation seasonality, and distribution of precipitation	
35	CORINE, slope, aspect, water, pH, soil02, Tave_at, BIO4, BIO15, r1mm_autumn
36	CORINE, slope, aspect, water, pH, soil02, Tave_sp, BIO4, BIO15, r1mm_spring
37	CORINE, slope, aspect, water, pH, soil02, Tave_sm, BIO4, BIO15, 1mm_summer
38	CORINE, slope, aspect, water, pH, soil02, MAT, BIO4, BIO15, MAP, r99ptot_yr
39	CORINE, slope, aspect, water, pH, soil02, MAT, BIO4, BIO15, MAP, r95ptot_yr
40	CORINE, slope, aspect, water, pH, soil02, MAT, BIO4, BIO15, MAP, r75ptot_yr
41	CORINE, slope, aspect, water, pH, soil02, MAT, BIO4, BIO15, MAP, prcptot_yr
Non-climatic variables, severity of climate, climate seasonality, humidity, solar irradiation, precipitation, and distribution of precipitation	
42	CORINE, slope, aspect, water, pH, soil02, air humidity
43	CORINE, slope, aspect, water, pH, soil02, eFFP, tx90p_yr, BIO4, TD, BIO17, r99ptot_yr
44	CORINE, slope, aspect, water, pH, soil02, eFFP, tx90p_yr, BIO4, TD, BIO15, r99ptot_yr
45	CORINE, slope, aspect, water, pH, soil02, humidity, tx90p_yr, BIO4, TD, BIO17, r99ptot_yr
46	CORINE, slope, aspect, water, pH, soil02, humidity, tx90p_yr, BIO4, TD, BIO15, r99ptot_yr
47	CORINE, slope, aspect, water, pH, soil02, SRADyear, tx90p_yr, BIO4, TD, BIO17, r99ptot_yr
48	CORINE, slope, aspect, water, pH, soil02, SRADyear, tx90p_yr, BIO4, TD, BIO15, r99ptot_yr
49	CORINE, slope, aspect, water, pH, soil02, humidity, tx90p_yr, TD, BIO15, r99ptot_yr
50	CORINE, slope, aspect, water, pH, soil02, SRADyear, tx90p_yr, TD, BIO15, r99ptot_yr
51	CORINE, slope, aspect, water, pH, soil02, humidity, tx90p_yr, TD, BIO17, r99ptot_yr
52	CORINE, slope, aspect, water, pH, soil02, humidity, tx90p_yr, TD, BIO19, r99ptot_yr
53	CORINE, slope, aspect, water, pH, soil02, humidity, tx90p_yr, BIO04, TD, BIO19, r99ptot_yr
54	CORINE, slope, aspect, water, pH, soil02, humidity, SRADyear, tx90p_yr, BIO4, TD, BIO17, r99ptot_yr
55	CORINE, slope, aspect, water, pH, soil02, humidity, SRADyear, tx90p_yr, BIO4, TD, BIO15, r99ptot_yr
56	CORINE, slope, aspect, water, pH, soil02, humidity, SRADyear, tx90p_yr, TD, BIO15, r99ptot_yr
57	CORINE, slope, aspect, water, pH, soil02, humidity, SRADyear, tx90p_yr, TD, BIO17, r99ptot_yr
58	CORINE, slope, aspect, water, pH, soil02, humidity, SRADyear, tx90p_yr, TD, BIO19, r99ptot_yr
59	CORINE, slope, aspect, water, pH, soil02, humidity, SRADyear, tx90p_yr, BIO04, TD, BIO19, r99ptot_yr

Appendix 2

Summary of sightings related to the effect of various explanatory variables on Fire Salamander presence. Expected positive (+), negative (-) and uncertain (?) response of salamanders to the variable based on a review of relevant literature (Gustafson et al. 2001, Thiesmeier & Grossenbacher 2004, Arntzen & Teixeira 2006, Egea-Serrano et al. 2006, Dillard et al. 2008, Ficetola et al. 2008, 2011, Suzuki et al. 2008, Greenwald et al. 2009, Manenti et al. 2009a, Tanadini at al. 2011, Blank & Blaustein 2012, Romero et al. 2012, Barrett & Maerz 2014, Olivero et al. 2016, Bani et al. 2015, Sutton et al. 2015, Ahsani et al. 2018, Cosentino & Brubaker, 2018, Arntzen & van Belkom 2020). [1] Fick and Hijmans (2017); [2] Hamann et al. (2013); [3] Copernicus Climate Change Service (2018); [4+5] Copernicus Land Monitoring Service (2018); [6] Panagos et al. (2012); [7] Czech Geological Survey (2020); [8] DIBAVOD (2019).

Abbreviation		Variable	Abbreviation		Variable
Tave_sp[2]	(?)	Spring (Mar.–May) mean temperature	r75ptot_yr[3]	(?)	Precipitation total due to moderately wet days (> 75^{th} percentile) (year)
Tave_sm[2]	(-)	Summer (Jun.–Aug.) mean temperature	prcptot_yr[3]	(?)	Total precipitation from wet days (> 1 mm) (year)
Tave_at[2]	(?)	Autumn (Sep.–Nov.) mean temperature	BIO15[1]	(-)	Precipitation seasonality (coefficient of variation)
MAT[2]	(?)	Mean annual temperature	BIO16[1]	(+)	Precipitation in the wettest quarter
TD[2]	(-)	Temperature difference between mean warmest month and mean coldest month	BIO17[1]	(+)	Precipitation in the driest quarter
DD<0[2]	(-)	Days with temperatures below 0°C	BIO19[1]	(?)	Precipitation in the coldest quarter
DD>5[2]	(+)	Days with temperatures above 5°C	PPT_sp[2]	(+)	Spring precipitation
FFP[2]	(+)	Frost-free period	PPT_sm[2]	(+)	Summer precipitation
bFFP[2]	(-)	Julian date on which the frost-free period (FFP) begins	PPT_at[2]	(+)	Autumn precipitation
eFFP[2]	(+)	Julian date on which the FFP ends	humid[1]	(+)	Absolute humidity (g/m^3) calculated by R function "humidity::AH" (Cai 2019) from VAPRyear (water vapour pressure, annual mean)
BIO4[1]	(-)	Temperature seasonality (standard deviation ×100)	SRADyear[1]	(-)	Solar irradiation (annual mean)
tn90p_yr[3]	(-)	No. of warm nights	CORINE[5]		Portion of CORINE 112, 211, 231, 243, 311, 312, 313 in each pixel
tx90p_yr[3]	(-)	No. of warm daytimes	water[8]	(+)	Lengths of the first- and second-order streams in each 1×1-km pixel
MAP[2]	(+)	Mean annual precipitation	pH[7]	(+)	pH of surface water
r1mm_spring[3]	(+)	No. of wet days (≥ 1 mm) (spring)	slope[4]	(+)	directly calculated from altitude
r1mm_summer[3]	(+)	No. of wet days (≥ 1 mm) (summer)	aspect[4]	(?)	N, E, S, W (4 categorical variables) directly calculated from altitude
r1mm_autumn[3]	(+)	No. of wet days (≥ 1 mm) (autumn)	soil02[6]	(+)	Depth to rock (5 categorical variables)
r99ptot_yr[3]	(?)	Precipitation total due to extremely wet days (> 99^{th} percentile) (year)	soil08[6]	(+)	Volume of stones (5 categorical variables)
r95ptot_yr[3]	(?)	Precipitation total due to very wet days (> 95^{th} percentile) (year)	litho[7]	(?)	6 lithological rock categories (metamorphic, sedimentary, igneous, metamorphosed sedimentary, sedimentary and metamorphic, igneous and metamorphic)