



RESEARCH PAPER

Spatial analysis of the potential exposure of amphibians to plant protection products at the landscape scale

Greg Churko^{a,*}, Erich Szerencsits^a, Annette Aldrich^b, Benedikt R. Schmidt^{c,d}

^a *Agroscope, Agroecology and Environment, Agricultural Landscape and Biodiversity, Reckenholzstrasse 191, Zürich 8046, Switzerland*

^b *Federal Office for the Environment FOEN, Biocides and Plant Protection Products, 3003 Bern, Switzerland*

^c *Info fauna Karch, Bellevaux 51, Neuchâtel 2000, Switzerland*

^d *Department for Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, Zurich 8057, Switzerland*

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ABSTRACT

Plant protection products (PPPs) are among the many drivers that lead to the loss of biodiversity in agricultural landscapes and they are a contributing factor to the global decline of amphibians. The aim of the present study is to estimate the potential exposure of amphibian population networks to PPPs. Specifically, our goal is to describe the spatial overlap of amphibian population networks with agricultural crops where PPPs are potentially used. We estimate terrestrial habitat suitability for eleven amphibian species using a multi-scale species distribution modelling approach. Using the suitability maps as the basis for estimating landscape resistance, we then calculate potential dispersal corridors between known breeding sites for each species. Where available, we use local landscape genetic studies from the literature to validate and select the most appropriate resistance model for each species. By comparing the locations of suitable habitat and dispersal corridors with a parcel-scale database on agricultural land-use, we locate and quantify potential hotspots for PPP-exposure within the core habitat around each species' breeding sites and along the movement routes between them. By highlighting differences among species, we identify species which are particularly at risk of exposure and gain insight into the mechanisms with which PPPs in terrestrial habitats may potentially influence these networks. Together, the maps provide policy makers with a flexible tool that can identify and prioritize regions for the implementation of locally adapted management strategies.

Introduction

Recent success stories bring new hope to conservation activities in intensively used landscapes (Chapron et al., 2014; Moor et al., 2022). Agricultural landscapes can have high value for biodiversity (Fischer et al., 2012; Hartel et al., 2020). However, if agriculture becomes too intense, then conditions for biodiversity deteriorate (Beckmann et al., 2019). To preserve and to promote biodiversity in agricultural landscapes, it is important to know which drivers adversely affect biodiversity and how their effects can be mitigated and compensated (Tschamntke et al., 2021). Plant protection products (PPPs) are among the many drivers that lead to the loss of biodiversity in intensively used agricultural landscapes. There are strong negative correlations between the use of PPPs and biodiversity (Gibbs et al., 2009; Geiger et al., 2010; Leenhardt et al., 2022).

As part of the overall biodiversity crisis, amphibians are undergoing

a global decline (Houlahan et al., 2000; Stuart et al., 2004). The many drivers of amphibian population declines include habitat loss and degradation, pollution, overexploitation of populations, invasive species, and emerging infectious diseases (Collins & Storfer, 2003; Stuart et al., 2004; Grant et al., 2020). The relative importance of those drivers varies among populations (Grant et al., 2016). It is well known that amphibian populations can be found in agricultural areas (Knutson et al., 2004; Salazar et al., 2016; Swanson et al., 2019; Smalling et al., 2015) and PPPs are also thought to contribute to amphibian population declines. Research has shown that some PPPs can be highly toxic to amphibians (Relyea, 2005; Brühl et al., 2013), that amphibians can be exposed to PPPs in both terrestrial and aquatic habitats (Lenhardt et al., 2013; Hua et al., 2015; Smalling et al., 2015) and that PPPs have likely caused the extirpation of populations at the landscape scale (Davidson et al., 2002; Davidson, 2004) even though the population-level consequences of PPPs on amphibians are not always straightforward to

* Corresponding author.

E-mail address: gregory.churko@agroscope.admin.ch (G. Churko).

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predict from toxicity data (Schmidt, 2004).

Despite decades of research into amphibian ecotoxicology, there are still many gaps in our knowledge (Ockleford et al., 2018). The risk for amphibians posed by PPPs depends on toxicity and exposure. Acute toxicity in the aquatic stages of amphibians is comparatively well characterized. Toxicity of PPPs in their terrestrial stages can also be high (Reylea, 2005; Brühl et al., 2013), but this needs further research (Ockleford et al., 2018). The second component of risk, exposure, is not well characterized for amphibians in the terrestrial environment. While ponds can be found in agricultural landscapes, it is the terrestrial stages which use agricultural fields (Sinsch, 1988; Miaud & Sanuy, 2005; Leeb et al., 2020) where they may be directly exposed to PPPs, either by direct overspray or through other pathways (Weltje et al., 2018; Ockleford et al., 2018). There is a need to better understand and quantify the exposure of amphibians to PPPs in the terrestrial environment and the effects thereof on individuals and populations (Wagner et al., 2014; Aldrich et al., 2016; Ockleford et al., 2018). Wagner et al. (2014) showed that amphibians may be exposed to PPPs even in ‘special areas of conservation’ because ‘land use with regular PPP applications’ according to CORINE land cover classes overlapped with these conservation areas.

The aim of the present study is to characterize the potential exposure of amphibians to PPPs. Specifically, our goal is to describe the spatial overlap of amphibian population networks with agricultural crops where PPPs are regularly used. We estimate terrestrial habitat suitability for eleven amphibian species using a multi-scale species distribution modelling approach. Using the suitability maps as the basis for estimating landscape resistance, we then calculate potential dispersal routes between known breeding sites for each species. Where available, we use data from local landscape genetic studies to validate and select the most appropriate resistance model for each species. By comparing the locations of suitable habitat and dispersal corridors with a detailed database on agricultural land-use, we locate and quantify potential hotspots for PPP-exposure within the core habitat around each species’ breeding sites and along the dispersal routes between them. By highlighting differences among species, we identify species which are particularly at risk and gain insight into the mechanisms with which PPPs in terrestrial habitats can potentially influence these networks. The products of the analysis, three types of high-resolution maps, can inform the conservation and promotion of amphibians in the agricultural landscape.

Materials and methods

Study region

We conducted the analysis over the entirety of Switzerland and Liechtenstein. With the exception of the common frog (*Rana temporaria*), the common toad (*Bufo bufo*) and the Alpine newt (*Ichthyosaura alpestris*), the distributions of the study species occur below an elevation of

1500 m in Switzerland (Grossenbacher, 1988). These are generally hilly regions intersected by the major river systems and former flood plains of the Rhine, Aare, Rhône, Reuss, Ticino and others. They are also the most populated and developed areas of the country, and where the majority of arable farmland exists. Open land cover within the region occupies 40–45 % of the landscape, split roughly equally between arable land and pasture/meadow; forest 35 %, waterbodies 3 %, and roads and settlements occupy the remaining 20 % (swisstopo, 2022).

Study species and data

We focused on 11 indigenous, pond-breeding amphibian species of Switzerland with nation-wide population distributions (Table 1). All but three species (*B. bufo*, *R. temporaria* and *I. alpestris*) are considered threatened in Switzerland (Schmidt et al., 2023). The species data used in the analyses, including breeding site locations and all occurrence records, was provided by Switzerland’s info fauna karch biological records center, which holds a collection of presence records data from systematic field surveys, monitoring programs and citizen submissions (<https://www.infofauna.ch/de/beratungsstellen/amphibien-karch#gsc.tab=0>; Schmidt & Zumbach, 2019). There are over 15,000 breeding site locations recorded in the database and the list can be considered reasonably exhaustive at lower elevations because systematic surveys of amphibian breeding sites were conducted decades ago and regularly updated (Grossenbacher, 1988; Schmidt & Zumbach, 2019). To focus suitability model outputs on the terrestrial phase of amphibians, all occurrence records contained within the hectare of a breeding site were excluded from the analysis. Thus, our suitability models differ from previous studies based on observations predominantly made at the breeding sites (Van Buskirk, 2005; Ortiz-Rodríguez et al., 2019; Donati et al., 2022). Occurrence records were extracted from the data base at a hectare resolution, consequently limiting the grid size of the analyses to 100 m (higher resolutions might be misleading because amphibians use relatively large home ranges; Indermaur et al., 2009). Any data older than 25 years was also excluded from the analysis. Most species have undergone strong declines in Switzerland and may therefore not be present anymore at sites where they were recorded in the past (Cruickshank et al., 2016).

Modeling habitat suitability

To calculate terrestrial habitat suitability maps for each species, we built multi-scale species distribution models (SDMs; McGarigal et al., 2016; Zeller et al., 2018; Lee-Yaw et al., 2022) with the R package BioMod2 (Thuiller et al., 2021). SDMs explain and predict the distributions of species by examining relationships between known records of species occurrence and the environmental characteristics associated with them (Hao et al., 2020). There are numerous approaches used to fit the models, from algorithms based on statistical regression to those on

Table 1

List of the eleven study species in the analysis including their status on Switzerland’s Red List, maximum recorded elevation, and the number of records available in the info fauna karch dataset in total, and after removing the records associated with a breeding site. ‘Max Elevation’ is the maximum elevation of an observation within the database. ‘n records (total)’ is the total number of records in the database and ‘n records (on land)’ is the number after removing breeding site locations.

Common Name	Taxon	Order	Family	Red List (CH)	Max elev. (m)	n records (total)	n records (on land)
Midwife toad	<i>Alytes obstetricans</i>	Anura	Alytidae	VU	1665	4308	724
Yellow-bellied toad	<i>Bombina variegata</i>	Anura	Bombinatoridae	VU	1297	6567	1516
Common toad	<i>Bufo bufo</i>	Anura	Bufoidea	LC	2375	15,981	3697
Natterjack toad	<i>Epidalea calamita</i>	Anura	Bufoidea	EN	940	3105	1052
European tree frog	<i>Hyla arborea</i>	Anura	Hylidae	VU	883	3449	795
Alpine newt	<i>Ichthyosaura alpestris</i>	Urodela	Salamandridae	LC	2485	15,815	3227
Palmate newt	<i>Lissotriton helveticus</i>	Urodela	Salamandridae	VU	1480	4847	581
Smooth newt	<i>Lissotriton vulgaris</i>	Urodela	Salamandridae	EN	1122	1263	272
Agile frog	<i>Rana dalmatina</i>	Anura	Ranidae	EN	1117	969	160
Common frog	<i>Rana temporaria</i>	Anura	Ranidae	LC	2827	25,535	4892
Northern crested newt	<i>Triturus cristatus</i>	Urodela	Salamandridae	EN	1115	1149	146

machine-learning decision trees, and the best approach is usually unclear as this can differ with every species and landscape. As such, SDMs are commonly modelled across a range of different algorithms, with the best approach selected after the fact using an independent dataset. An advantage of this method is that it allows the creation of ensemble models, which combine the predictions from each algorithm together into an average of all models (Hao et al., 2019). In some studies, ensemble models have been shown to have greater predictive power of habitat suitability than any model fit from a single algorithm (Hao et al., 2019).

For each species, we created SDMs from eight competing algorithms included in the BioMod2 analysis suite, along with a weighted ensemble SDM combining their results (nine SDMs in total; Lee-Yaw et al., 2022). The eight algorithms tested included Generalized Linear Models (GLM), Generalized Additive Models (GAM), Generalized Boosted Models (GBM, also known as Boosted Regression Trees), Multivariate Adaptive Regression Splines (MARS), Classification Tree Analysis (CTA), Artificial Neural Networks (ANN), Random Forests (RF), and Maximum Entropy (MAXENT).

To control for geographic sampling bias, we evaluated the spatial autocorrelation of the occurrence records for each species with a variogram (Ver Hoef et al., 1993). We set a grid size equal to the asymptote of the variogram and randomly selected a maximum of five records per grid cell to include in the analysis. Species presence locations were compared to an equal number of randomly generated pseudo-absences, which were placed using a disk strategy with a bounding limit of 10 km (Koldasbayeva et al., 2022). The presence and pseudo-absence dataset was then split with a 70:30 ratio into training and testing datasets for the suitability analysis.

Since the habitat requirements of the eleven species are diverse and distinct (Van Buskirk, 2005; Zanini et al., 2009), we considered a wide range of landscape attributes possibly associated with amphibian presence. In total, we evaluated 22 different explanatory environmental variables (Appendix A.1), including nineteen land cover and land use types, elevation, and local wetness potential, a combined metric estimating the potential for surface-flooding based on topological relief, precipitation, and geological qualities (Szerencsits et al., 2018). With 11 species in the analysis, the large number of land cover categories ensures granularity across environmental variables and allows drawing out distinctions between their habitat preferences. We also consciously avoided excessive pooling of features, like different water body types (e.g., flowing water) or road types together as these can have contradictory effects at their extremes (i.e., streams are prime habitat for some amphibians, but rivers can be strong barriers).

Each species can potentially respond to different landscape attributes at varying scales (McGarigal et al., 2016). They may require a landscape feature being in their immediate surrounding (e.g., primary hunting/foraging habitat), or require that at least one such feature is somewhere available within their movement range (e.g., overwintering habitat). As such, each variable was evaluated at multiple scales to determine its optimum scale of effect. Using a base resolution of 20 m, we applied a smoothing disk kernel transformation to each layer at scales of 100 m, 200 m, 500 m, 1000 m, and 2000 m with the R package *smoothie* (Gilleland, 2013). The results were then mean aggregated to the 100 m resolution of analysis. Each pixel thus describes the ratio of the amount of a landscape attribute within the kernel and, in effect, can capture the effects of both predictor prevalence and distance.

To build the eight SDMs for each species, we followed an iterative approach similar to that outlined in Zeller et al.'s (2018) comparison of common connectivity modelling approaches. Each environmental variable was first evaluated univariately to find the scale with the maximum effect for each algorithm as measured by area under the receiver-operating curve (AUC). All variables, each at their optimum scale, were then evaluated together. Any explanatory variable which was correlated with other stronger variables ($R > 0.60$) after the first run was dropped from the model. Next, any variables which exhibited a

variable importance factor (VIF) of 0 after the second run were removed. To encourage parsimony in the final models, for the following runs, any variable with a $VIF < 0.2$ was removed and the process was repeated until only the strongest explanatory variables remained. All runs were evaluated over five repetitions, and the environmental variables were evaluated based on their mean VIFs across repetitions. By taking the average of the results of the best SDMs under each algorithm weighted by their AUC-ROC scores, we also produced an ensemble projection of habitat suitability for each species. We selected the best species distribution model for each species by comparing the resulting AUC-ROC and Boyce-Index scores of the eight SDMs and their ensemble SDM (Hirzel et al., 2006) and used this model to generate a terrestrial habitat suitability map for each species. Based on raw environmental characteristics, the nationwide maps describe the probability of a species occurring within each hectare on a continuous scale from 0 to 1, disregarding any existing limitations of the species' current distribution and dispersal capabilities.

Validation of species distribution models with landscape genetic data

In lieu of empirically derived field-data that accurately relates the movement of dispersing animals to the landscape, habitat suitability is commonly used as a proxy to predict the movement patterns of dispersers, though some caveats apply (Bolliger & Silbernagel, 2020). A species' mere presence in a landscape contains, of course, no direct indication of its movement pathways. The habitats an individual lives in cannot be expected to overlap perfectly with those it moves through, as the motivations dictating their behaviour in either phase are likely to differ (Beier et al., 2008). Modelling dispersal from habitat suitability is thus ideally complemented by validation with alternative data sources, e.g., telemetry or genetic data, which can be used to separately infer connectivity between populations (Bolliger & Silbernagel, 2020). Population genetic data is the result of many interacting ecological phenomena occurring over multiple spatial and temporal scales, including dispersal (Cushman et al., 2006). Examining differences in the genetics of neighbouring populations allows us to infer how movement between the populations has contributed to gene flow, and we can link the degree of movement to variation in the landscapes that separate them (Bolliger & Silbernagel, 2020).

We took the models generated in the previous step and explored the relation of each species' suite of SDMs to the genetic differentiation seen between populations in local landscape genetic studies from the literature (Appendix A.2). The species distribution model that best describes habitat suitability will not necessarily best predict patterns in species dispersal across a landscape (Beier et al., 2008). As such, we determined the best SDM for modelling dispersal by testing the ability of landscape resistance rasters derived from each algorithm's SDM to predict gene flow between the study populations. We assumed that more suitable terrestrial habitat would also be preferred by dispersing individuals (Cayuela et al., 2020), and used the SDMs as the basis for calculating the landscape's resistance to movement (McRae et al., 2008).

Using the R package *ResistanceGA* (Peterman, 2018), we calculated dispersal routes between sample sites within each study with *Circuit-scape*, and measured the correlation between F_{st} values and the effective distances between populations. As a basic measuring stick of model performance, we also compared the results to the genetic differentiation predicted by a simple isolation by distance model (IBD, Cushman et al., 2006). For each algorithm and ensemble model, we tested three mathematical relations between habitat suitability and landscape resistance: a negative linear transformation and two negative exponential transformations (ne4 and ne8; Keeley et al., 2016), which penalize movement through less-suitable matrix habitat to increasing degrees. Using a bootstrap procedure that subsampled 80% of the populations over 1000 repetitions, the results generated by each algorithm's suitability model along with the ensemble model were validated against null and isolation by distance models. The algorithm and transformation that produced the

best-fitting corridors as measured by the Akaike Information Criterion (AIC) was then used to create the final Swiss-wide corridor maps for each species. For the five species lacking landscape genetic studies conducted within Switzerland, we used the results from their ensemble models with landscape resistance calculated from the ne8 transformation. To test our hypothesis that excluding breeding site locations from SDMs would improve dispersal model performance, we also compared results for SDMs created from all occurrence records to those with the breeding sites removed for the natterjack toad (*E. calamita*), the midwife toad (*A. obstetricans*), and the European tree frog (*H. arborea*).

Potential dispersal routes between breeding ponds

We used Circuitscape Julia to calculate the potential dispersal routes of each species across Switzerland based on the best-performing SDM with respect to dispersal (Anantharaman et al., 2020). Circuitscape equates movement patterns in landscapes to electricity moving across conductive surfaces, whereby highly permeable landscape types are assigned a low resistance and movement barriers a high resistance (McRae et al., 2008). Connecting electricity between two dispersal points, or nodes, generates a continuous map of electrical current representing the probability of a disperser moving through each pixel of the map to reach the other site. Combining the individual maps for each dispersal link generates a cumulative map describing the relative probability of movement within a pixel for all potential dispersal routes across a study region (McRae et al., 2008). For our study, we connected all breeding sites within 2.5 km of each other in a pairwise manner and summed the individual current maps together into a cumulative map showing the relative likelihood of movement across the country for each species. We extended the maximum dispersal range to 5 km for the natterjack toad and the European tree frog, two highly mobile species with evidence of farther dispersal capabilities in the literature (Angelone et al., 2011; Sinsch et al., 2012). To reduce calculation times and emphasize longer dispersal routes, breeding sites within two hectares of each other were agglomerated together and treated as a single dispersal node. The resistance rasters were buffered by 5 km with random cells at the Swiss border to minimize bias caused by the concentration of movement along the edges of the study area (Koen et al., 2014). Additionally, all areas higher than ten percent over the maximum observed elevation of each species were masked from the analysis to improve calculation times.

Overlays with PPP-relevant cropland

We generated a detailed, parcel-scale, agricultural land use map for Switzerland, by merging together newly publicly available data from the direct payment schemes of 26 Cantonal Authorities (KGG-CGC, 2022). The dataset includes the main crop type grown on each parcel starting in 2021, which we used to produce a dataset of PPP-relevant cropland approximating agricultural parcels where PPPs are likely used (Koch and Prasuhn, 2021; Sälle et al., 2022; see list of PPP-relevant crop types in Appendix A.3). As the dataset lacks information on actual PPP applications, the map of PPP-relevant cropland represents a potential worst case. Rotational grasslands were considered part of the crop rotation and therefore PPP-relevant, and we therefore expect limited dynamic in the prediction of PPP-relevant areas across the study period.

We overlaid this dataset with the suitability and corridor maps to examine the amount of PPP-relevant cropland around and between each breeding site. For this analysis, we created binary maps of suitability from the best suitability models using the R package ecospat (Broennimann et al., 2022). The suitability threshold was set to the value above which 70 % of all species occurrences within our testing dataset were correctly predicted. We then calculated the amount of suitable habitat within 200 m, 500 m, and 1000 m buffers around each amphibian breeding site, the amount of PPP-relevant cropland, and the amount where they overlap. We also examined major land use types within the

same buffers classified as “Open” (pastures, arable land, and meadows), “Forest”, and “Settlement” (buildings buffered by 10 m and dissolved together). For the dispersal corridors, we generated polygons of high connectivity cells (top 25 %) for the individual current maps produced between each breeding site pair and calculated the percentage that occurred on PPP-relevant cropland.

Results

Performance of SDMs and dispersal models

Based on AUC-ROC and Boyce-Index scores, the ensemble species distribution models were overwhelmingly the most successful predictor of presence and absence across species compared to SDMs built from the eight individual model algorithms (Fig. 1). Only for the agile frog (*R. dalmatina*) was habitat suitability better described by a CTA-based model. Of 22 landscape variables in total, five were never relevant to predicting the presence or absence for any species. Included among them were notable barrier elements: rivers, highways, and railways. While wetness potential associated with water percolation, i.e., soil and geological characteristics, was rarely relevant, wetness potential associated with water accumulation, i.e., topological and meteorological characteristics, was an important determinant for a majority of species.

Interestingly, the best-evaluated SDMs for each species with respect to suitability never translated to the best dispersal model. In contrast to the suitability modelling, landscape resistance rasters generated by single algorithm SDMs nearly universally better explained the genetic differentiation between study populations versus the ensemble models (Table 2). This was not only due to the penalization of the greater number of parameters in the ensemble models under AIC evaluation, but was also seen in the marginal R^2 values. For every species with available landscape genetic data, the effective distances between populations generated by the best SDM-derived dispersal model were able to outperform the isolation by distance model. However, SDMs were not universally better predictors of genetic differentiation than IBD. Only for the common frog (*R. temporaria*) could all suitability-derived dispersal models better describe genetic differentiation than Euclidean distance in the IBD model. Additionally, the ensemble model failed to outperform distance for four of seven species. Generally, there were substantial differences in correlations to genetic data across suitability models and the best models needed to be parsimonious.

In our analysis of the performance of the midwife toad (*A. obstetricans*), the natterjack toad (*E. calamita*), and European tree frog (*H. arborea*) SDMs built using all available occurrence records versus those with the breeding sites excluded, we found that the latter models focusing on the terrestrial habitat better described genetic differentiation between populations (Table 2). Dispersal models built from SDMs with the breeding sites removed explained more genetic differentiation between populations using fewer model parameters, and this was seen in the majority of pairwise comparisons of each model algorithm.

Habitat suitability and dispersal maps

Fig. 2 shows the suitability and dispersal maps for the natterjack toad (*E. calamita*) (dispersal maps for four more species can be seen in Appendix A.4). As a species of open, warm, and high-disturbance habitats, we see in the upper maps how the SDM assigns a high suitability to the lowlands of the major river valleys, where the majority of arable land is located. The dispersal map, bound by the locations of existing populations, restricts the region of interest for this species to the middle plateau between the Jura mountains and the Alps. Zooming in, we see how movement is channelled along preferred habitat types, avoiding, for example, settlements and forest. Areas with many populations close together appear darker red, reflecting the higher chance of dispersal as multiple corridors between populations intersect each other. This

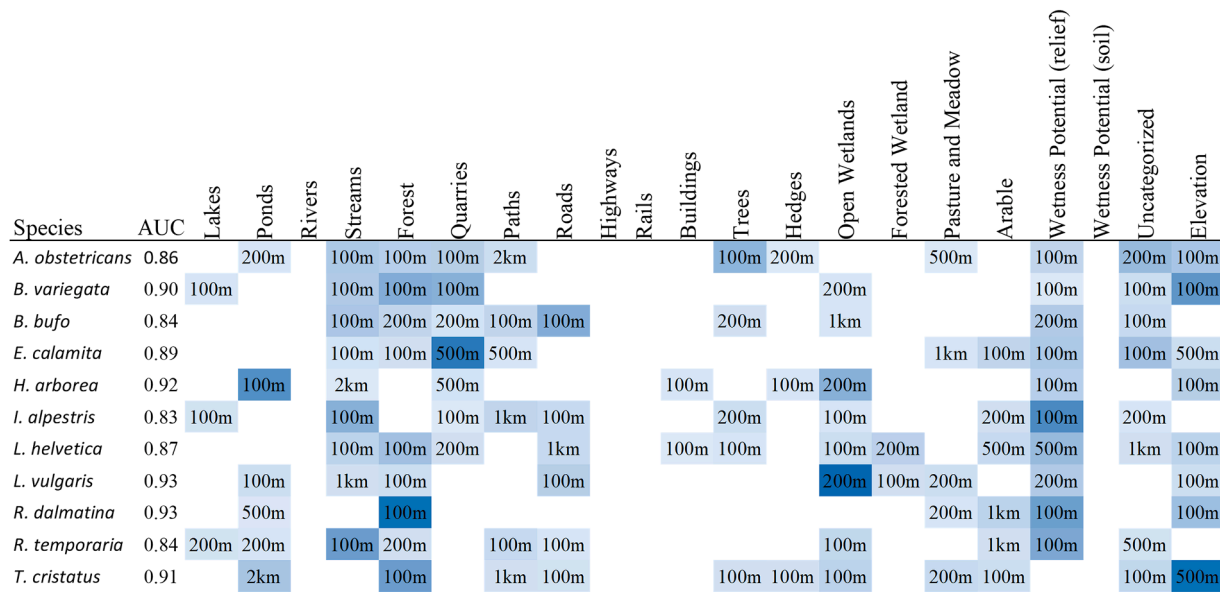


Fig. 1. Explanatory landscape variables for the best-performing species distribution models for each species, shaded according to relative variable importance (dark blue = high variable importance factor (VIF)). The AUC-value describes model performance as measured by the area-under-curve receiver operating characteristic (> 0.8 good, 0.9 excellent). The resolutions listed under each variable indicate the optimum kernel scale of analysis for that variable for each species (100 m, 200 m, 500 m, 1 km, or 2 km). Empty cells indicate landscape attributes that had no measured influence on species presence.

Table 2

Model performance for each species comparing the best dispersal models' capability of explaining genetic differentiation between populations with the isolation by distance model (IBD), and the 'Ensemble' model. For the *Alytes obstetricans*, *Epidalea calamita*, and *Hyla arborea*, we include a comparison to the best model produced by species distribution models using all species occurrence records, including those from breeding sites (bold). Models – RF = Random forests, MARS = Multivariate adaptive regression splines, CTA = Classification tree analysis, GBM = Boosted regression trees, GLM = Generalized linear model; k – number of model parameters; AIC – Akaike Information Criterion; LL – log-likelihood; RMSE – residual mean standard error.

Species	Model	Resistance Transformation	k	AIC	R ² m	LL	RMSE
<i>A. obstetricans</i>	RF (on land)	neg	4	−908.2	0.36	458.10	0.0498
	MARS (all data)	neg	6	−897.2	0.24	454.62	0.0499
	Ensemble (on land)	neg	8	−893.4	0.24	454.72	0.0500
<i>B. variegata</i>	IBD		2	−889.8	0.23	446.92	0.0515
	RF	ne8	3	−27.7	0.44	16.86	0.0459
	IBD		2	−27.6	0.28	15.80	0.0455
<i>E. calamita</i>	Ensemble	ne8	6	−20.6	0.37	16.31	0.0453
	RF (on land)	ne8	4	−113.1	0.83	60.55	0.0081
	IBD		2	−107.8	0.17	55.89	0.0072
<i>H. arborea</i>	Ensemble (on land)	ne8	6	−101.0	0.24	56.49	0.0071
	RF (all data)	ne8	8	−98.2	0.28	57.09	0.0071
	CTA (on land)	neg	3	−1255.6	0.42	630.78	0.0348
<i>I. alpestris</i>	Ensemble (all data)	ne8	5	−1244.9	0.38	627.44	0.0350
	Ensemble (on land)	ne8	7	−1241.2	0.38	627.59	0.0350
	IBD		2	−1239.8	0.36	621.90	0.0360
<i>L. vulgaris</i>	RF	ne8	4	−1970.5	0.08	989.27	0.0281
	IBD		2	−1965.6	0.02	984.80	0.0283
	Ensemble	ne8	6	−1964.2	0.07	988.09	0.0281
<i>R. temporaria</i>	GBM	ne8	3	−240.6	0.40	123.31	0.0271
	IBD		2	−236.9	0.18	120.44	0.0279
	Ensemble	neg	6	−233.0	0.23	122.50	0.0270
<i>T. cristatus</i>	Ensemble	ne8	10	−7559.7	0.42	3789.85	0.0366
	GLM	ne8	7	−7545.7	0.44	3779.87	0.0366
	IBD		2	−7399.9	0.11	3701.95	0.0387

property of the maps deserves special attention. Lighter shaded routes on the outskirts of species distributions do not necessarily imply weaker connectivity, but are rather a consequence of the lower breeding site density in the area. The colour scale must be considered within the context of the immediate surrounding landscape.

Some species have nicely defined corridors running between breeding sites (e.g., the yellow-bellied toad and the natterjack toad), whereas others appear as indistinct polygons around breeding sites that dissipate with distance (e.g., the midwife toad and the European tree frog; Appendix A.4). This comes from the different strengths of the

various landscape attributes and their scale of effect for the different species. The multi-scale mixed-model analysis allows this flexibility among the species and in the map products. The habitat suitability analysis suggests the common toad is more generalist, and maybe senses the landscape on a broader scale, whereas the yellow-bellied toad (*B. variegata*) has more stringent and local preferences. While the indistinct radiating corridors may not be very instructive, it is an interesting result that for some species 'distance to pond' is the dominant determining factor of their presence.

The southern-most Swiss canton, Ticino, is a rather cold spot in the

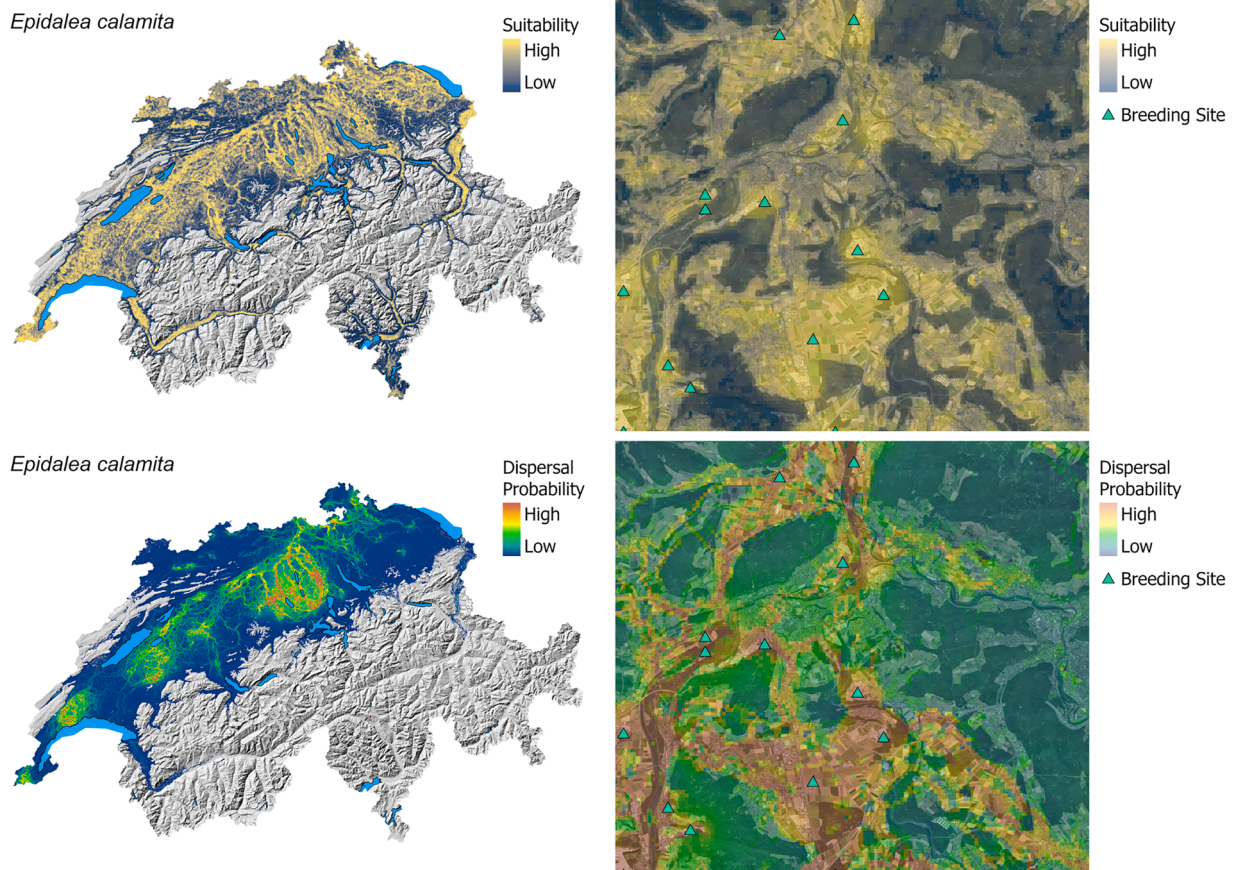


Fig. 2. Swiss-wide habitat suitability maps and dispersal maps (left) constructed from the best-performing species distribution models for the natterjack toad, *Epidalea calamita*, and the same maps zoomed into a portion of the Reuss valley in canton Aargau (right). Habitat suitability is indicated by increasing shades of yellow. Dispersal probability increases with shades of red. Map backgrounds: hill shade and lakes for the national maps; SwissImage aerial photographs for the zoomed images (blue), © swisstopo.

majority of the species maps. This does not reflect actual amphibian abundance and diversity but is rather due to the lack of Italian species in the analysis. A number of the study species are only encountered north of the Alps, and these species are functionally replaced by southern counterparts like the Italian agile frog (*Rana latastei*) and Italian crested newt (*Triturus cristatus*). These species were not included in the analysis due to their limited distribution ranges and datasets.

Potential exposure to PPPs on agricultural land

Including open croplands, fruit production, and rotational grassland, there are over 412,000 hectares of PPP-relevant cropland in Switzerland according to land use surveys from 2021. Of these, parcels that are considered suitable habitat for at least one species and are within 200 m of a breeding site make up roughly 4 %, 15 % are within 500 m, and 39 % are within 1 km. 35 % of this area is located on high connectivity dispersal routes between the breeding site locations for at least one species (Fig. 3). The spatial distribution of potential PPP-exposure varies strongly with geography, however, and has a clear skew to the lowlands. In the canton of Aargau to the north of Switzerland, for instance, where 10 of our 11 study species are present, these numbers increase substantially: 10 %, 39 % and 62 % is considered suitable habitat within 200 m, 500 m, and 1000 m of breeding site locations and 59 % of PPP-relevant land lies on potential dispersal corridors.

Our suitability models show that all species have at least some part of the suitable habitat around their breeding sites located within PPP-relevant cropland (Fig. 4 and 5). For most species, however, the proportion of PPP-relevant cropland that is considered suitable habitat is

low, ranging from 10 to 20 % (Fig. 4). Comparing the proportion of suitable habitat on cropland to the total amount of cropland within the buffers around their breeding sites, we also see that most species actually appear to choose other habitats (Fig. 4). The major exception is the natterjack toad (*E. calamita*) which shows an active preference for cropland as habitat in the analysis and for which ~40 % of its suitable habitat occurs on cropland. Furthermore, suitable cropland and total PPP-relevant cropland ratios are about equal and comparatively high for the European tree frog (*H. arborea*), and the northern crested newt (*T. cristatus*) suggesting that these species will use these habitats where available.

Though these species have different scales of perceiving and using the landscape, we see little variation in trends across buffer sizes (Fig. 5). Of note, however, is the difference in the distributions of the results across scales. The upper whiskers in the suitability box plots in Fig. 5 indicate that nearly all species have portions of their breeding sites located in areas where the surrounding landscape is dominated by PPP-relevant cropland. Even if the species is averse to using cropland, in these areas their options are limited. Examining the distribution of the co-occurrence of breeding sites with PPP-relevant cropland for the three species most often found on cropland, we find a substantial proportion of populations where exposure risk is especially high. 36 % of all natterjack toad breeding sites are embedded in landscapes where PPP-relevant cropland makes up over half of the suitable habitat within 500 m. For the European tree frog and the northern crested newt, 20 % and 11 % of their breeding sites are similarly exposed, respectively.

While PPP-relevant cropland is under-represented in the suitable habitat of most species, we see a very different pattern when we look at

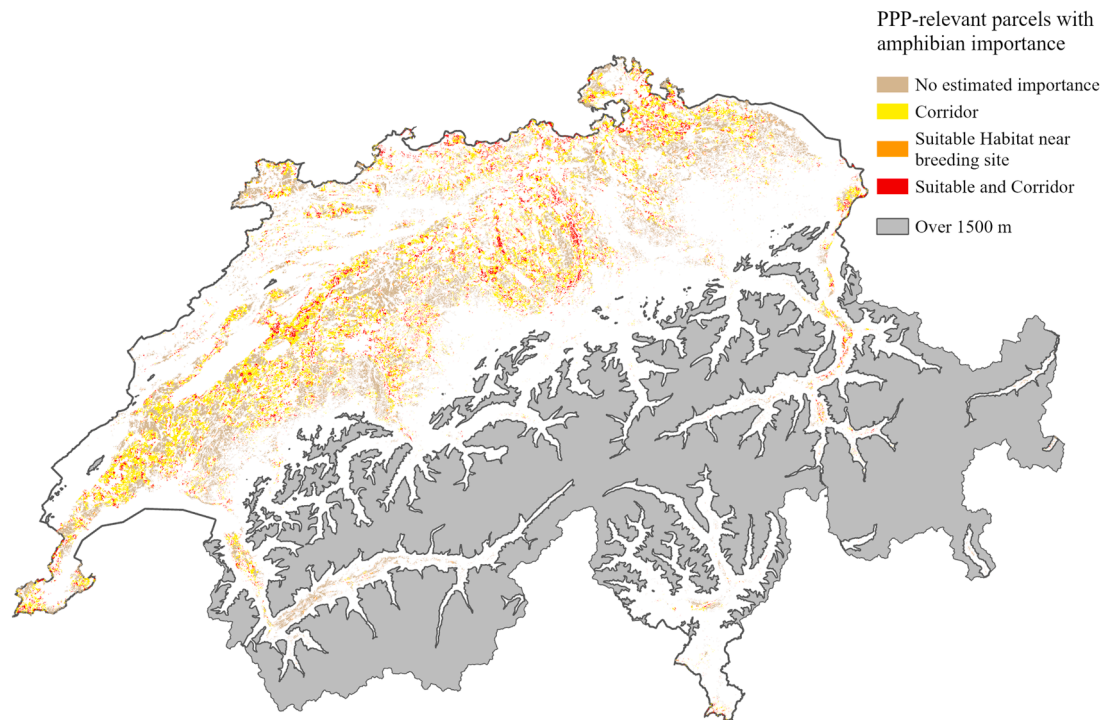


Fig. 3. The national distribution of PPP-relevant parcels which amphibians are likely to use as home-range habitat and/or dispersal corridors. Yellow parcels are located on corridors for at least one species. Orange parcels are suitable habitat for at least one species and within 500 m of a breeding site. Red parcels are both suitable habitat close to breeding sites and within dispersal corridors.

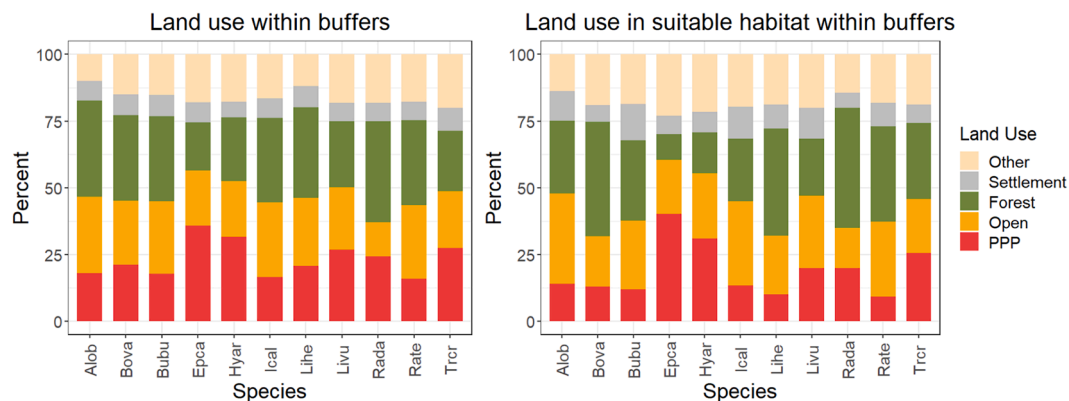


Fig. 4. Mean percentage of major land use types found within the vicinity of the breeding sites of each species (left), and within the suitable habitat that occurs within the same range (right). The mean percentages are averaged across 200, 500, and 1000 m radii. PPP: Cropland where PPP-relevant crop types were grown in 2021. Open: all pasture, meadow, and arable land after removing the PPP-relevant crop parcels. Species names denoted as a combination of the first two letters of their genus and species names, e.g., Alob = *Alytes obstetricans*.

its spatial overlap with high connectivity regions between breeding sites (Fig. 5). For all species, a substantial amount of the high connectivity regions between breeding sites runs through PPP-relevant land. Between 25–50 % of dispersal corridors occur on PPP-relevant cropland for the majority of study species, and that number climbs to over 60 % for the three target species mentioned above.

Discussion

Despite the prevalence of species distribution modelling of amphibians based on presence-only data in the literature (Ashrafzadeh et al., 2019; Donati et al., 2022; Matutini et al., 2023), this is the first study that we are aware of that attempts to focus the model building on data collected from the terrestrial phases of amphibians. The majority of existing amphibian occurrence data stems from surveys at breeding

sites, because this is the easiest method to encounter individuals and monitor existing populations (Denoël & Ficetola, 2015; data on terrestrial habitat use are usually collected at relatively small spatial scales, e.g., Indermaur et al., 2009). Naturally, suitability estimates derived from this data are more suitable to predict the waterbodies they choose to breed in rather than the terrestrial habitats through which they move. We instead sacrificed some of the statistical power of the large datasets on amphibian occurrence provided by info fauna karch to generate results representing habitat requirements outside of the aquatic phase.

In our investigation of the predictive power of SDMs built from species occurrences including and excluding data from breeding sites, we found that the genetic differentiation between populations of natterjack toad, midwife toad, and European tree frog were substantially better correlated with effective distances derived from SDMs built with breeding site data excluded. Markedly so for the natterjack toad

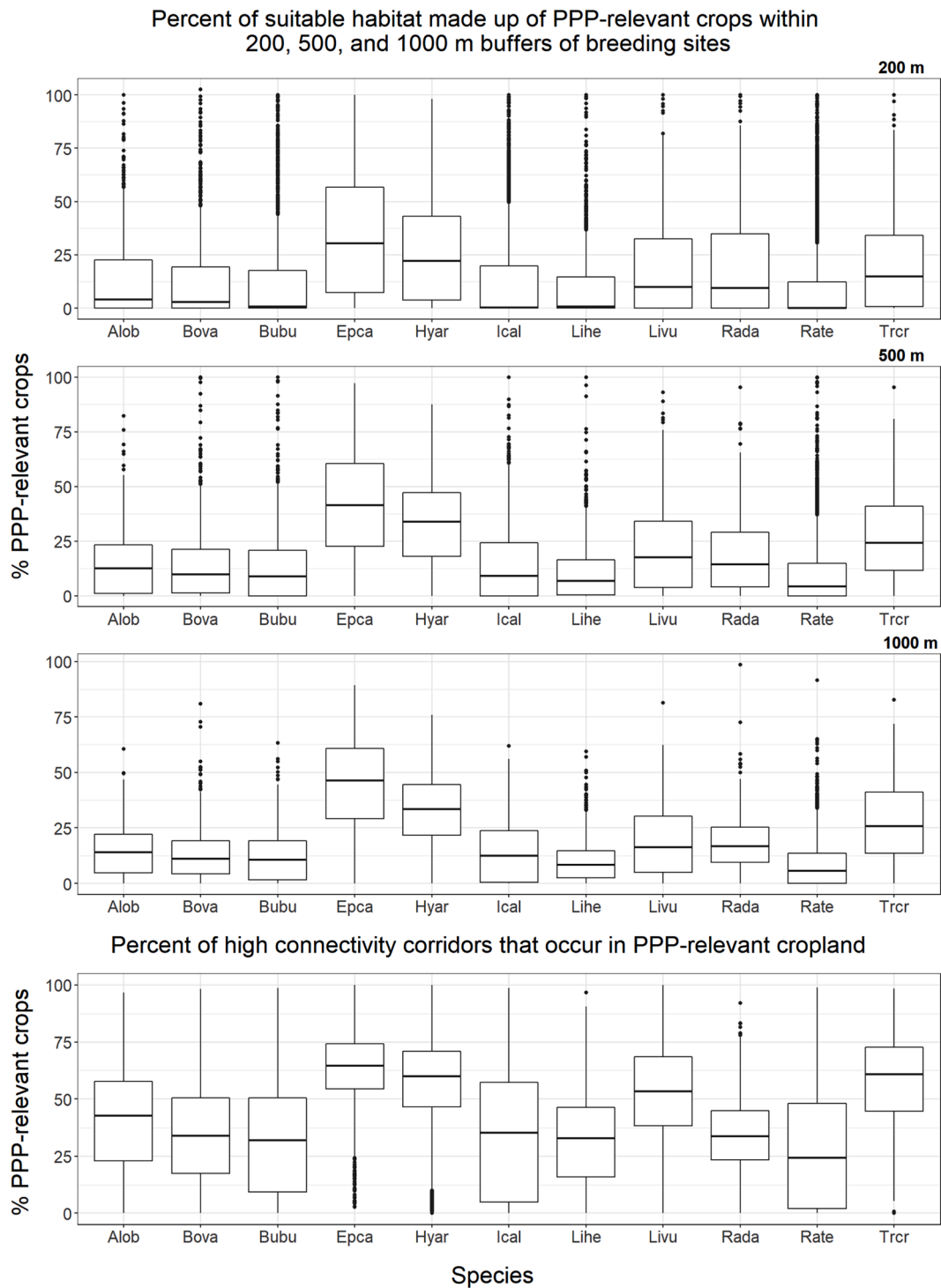


Fig. 5. Boxplots depicting the percentage of suitable habitat (top three) and high connectivity corridors (bottom) that occurs on PPP-relevant cropland for each species. Percentages for suitable habitat are shown for buffer sizes of 200, 500, and 1000 m around each breeding site.

(*E. calamita*), for which the best SDM built with breeding site data included could not even outperform the isolation by distance model. The natterjack toad is a far-ranging disperser, making use of small ephemeral waterbodies where they appear (Sinsch, 2009; Schmidt et al., 2015), and we presume that their unique relationship with the landscape is poorly explained by the habitats found within the direct vicinity of their major breeding site locations.

Based on our comparisons to landscape genetic data from the literature, SDMs provided a satisfactory, if limited, foundation for calculating dispersal corridors between breeding populations. Thanks to the

multi-scale mixed model approach, we were always able to find a combination of landscape variables, scales, and algorithm that improved our estimation of the landscape's effect on species dispersal over Euclidean distance. However, our habitat suitability analyses could not generate any estimates for notable barrier elements like rivers and highways (though their isolating effects may be overstated; see Luqman et al., 2018). This reflects an inherent drawback to building dispersal models based on habitat use – the habitats an individual lives in cannot be expected to overlap perfectly with those it moves through (Beier et al., 2008). Furthermore, for most species, only a handful of the tested

models outperformed Euclidean distance. This highlights the importance of having an independent dispersal-related dataset to validate the SDMs. Dispersal data from studies involving telemetry, capture-recapture, or genetics is generally rare, time-consuming and expensive to collect (Beier et al., 2008; Cushman et al., 2013). In absence of this data, scientists often rely on the best-fitting SDMs based on opportunistic observation data (Zeller et al. 2012), frequently ensemble models. We found, however, that the best performing suitability models – nearly universally ensemble models – were almost never the best at predicting the landscape's influence on the genetic differentiation of populations. In fact, for four of our seven study species with available landscape genetic data, effective distance derived from the ensemble SDM proved no better at describing genetic isolation than Euclidean distance between populations. Perhaps this is because by taking the average of multiple models we weaken the strength of contrast between habitat types determined by the individual models, diminishing the influence of strong corridors and barriers of movement. Alternatively, due to their increased complexity, ensemble models are more likely to overfit spatial patterns in observational data to spatial autocorrelation in the environmental variables (Roberts et al., 2017; Hau et al. 2020). While we took precautions to stratify and cross-validate the datasets during model-building, evaluating the SDMs with an independent dataset and methodology may have revealed this bias in the ensemble models which escaped the conventional evaluation of SDMs.

From our overlap analysis of amphibian population networks and PPP-relevant cropland, we see that PPPs potentially play a prevalent role across nearly all study species with respect to dispersal. This is likely due to the heavily-developed and patchy structure of the Swiss landscape, which cycles through settlement, agriculture, and forest across hill and river valley. Unused land is an exception and continuous habitat rare, and for dispersers to travel between breeding sites, they are inevitably forced to traverse PPP-relevant cropland. Adverse effects due to PPP exposure during dispersal can thus be expected to contribute to the fragmentation and decline of populations for these species (Cushman, 2006; Lenhardt et al., 2017). Focusing on terrestrial habitat use, we identify three species of particular consideration for risk mitigation measures: the natterjack toad (*E. calamita*), the European tree frog (*H. arborea*), and the northern crested newt (*T. cristatus*). For the natterjack toad (*E. calamita*), the modelling results confirm the results of radiotelemetry studies which show that the species uses agricultural fields during the summer months (Frei et al., 2016; Schweizer, 2016). The three species are, in fact, the same species recommended as model species to consider in the EFSA Panel report on PPPs (Ockleford et al., 2018). Despite the prevalence of breeding populations of other species in agricultural landscapes (e.g., the agile frog (*R. dalmatina*), the smooth newt (*L. vulgaris*), and the yellow-bellied toad (*B. variegata*), our models suggest that they tend towards other habitats besides cropland where available. Availability is the keyword, however: we see in Fig. 5 that all species have portions of their populations where cropland parcels make up the majority of the suitable habitat within their vicinity. As a future study, a time-series analysis comparing the historical development of these highly PPP-exposed populations using monitoring data could also provide interesting insights into the population-scale effects of PPP-exposure in the terrestrial habitats of amphibians. The detailed, parcel-based agricultural land use dataset we use in the analysis has only been available since 2021, relegating our work to a broader overview of potential PPP-exposure. As that dataset grows, however, and a longer time series of crop types grown on each land parcel develops, a detailed spatial comparison between specific crop types, their associated PPPs, and the development of neighbouring amphibian populations would also be very insightful.

Our models identify highly PPP-exposed breeding sites and their avenues for dispersal, providing information to help the prioritization of mitigation efforts. A detailed evaluation of potential risk mitigation and compensation measures was carried out alongside this project (Aldrich et al., in preparation). Mitigation might focus either on the terrestrial

habitat or the breeding site (the aquatic habitat). In the terrestrial habitat, one might provide incentives to farmers to reduce the use of PPP in suitable habitats (i.e., agricultural fields; Schweizer, 2016) or may provide terrestrial microhabitats which may be used as refuges and shelter from direct exposure to PPP (Indermaur & Schmidt, 2011; Schweizer, 2016). At the breeding site, no-spray buffers may prevent contamination of breeding sites with PPP (Jeliakov et al., 2014). However, models of amphibian population dynamics suggest that the terrestrial life history stages (juveniles and adults) are more important for population viability than the aquatic stages (larvae; Petrovan & Schmidt, 2019), and thus mitigation in the terrestrial habitat may be more fruitful if resources are limited.

The products of this analysis provide numerous potential benefits to efforts in PPP risk mitigation as well as compensatory measures which conserve or promote amphibian populations. Following the recent success story of the recovery of threatened amphibian populations after the mass construction of ponds in the Swiss canton of Aargau (Moor et al., 2022), the maps can identify suitable locations along the dispersal corridors for new ponds to efficiently connect separated populations. In a step towards precision farming, the integration of dispersal routes with weather forecasts and temporal observation data could enable the establishment of an alert system for farmers to refrain from spraying PPPs along dispersal routes at certain times (Peer et al., 2021; Lenhardt et al., 2015). The maps can also inform the design of biodiversity promotion areas, implemented as part of agricultural direct payment schemes, allowing the provision of species-specific shelter and resources along dispersal routes and near breeding sites (Collins & Fahrig, 2017). Similarly, they can be used to guide promising developments in integrated water management (Allouche, 2016), whereby water retention, reservoirs for irrigation, flood prevention, and intelligent drainage systems can be used to enhance amphibian habitat, and ecological infrastructure in general, in the agricultural landscape (van Rees et al., 2021).

Conclusions

Together, the maps of habitat suitability, potential dispersal routes, and potential PPP exposure provide policy makers with a flexible tool that can identify and prioritize regions for the implementation of locally adapted management strategies. The maps offer a national overview, as they show the populations and metapopulations of the individual species and the gaps and potential dispersal routes in between. This can help to define priorities, to mitigate conflicts and enhance the efficiency of conservation efforts. Experts who know the local situation must then develop specific measures in cooperation with farmers and policy makers.

Appendix A. supplementary data

Supplementary data associated with this article can be found in the online version, at XXXXX.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.baae.2024.02.004](https://doi.org/10.1016/j.baae.2024.02.004).

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