

Integrating Multiple and Fine Scale Predictors of Habitat Selection and Landscape Resistance for Amphibian Distribution Modelling at Large Scale

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Research Article

Keywords: Species Distribution Models, friction-based predictor, accessibility, multi-scale, animal movements, functional grain, functional connectivity

Posted Date: March 9th, 2021

DOI: <https://doi.org/10.21203/rs.3.rs-181948/v1>

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Version of Record: A version of this preprint was published at Landscape Ecology on August 22nd, 2021.
See the published version at <https://doi.org/10.1007/s10980-021-01327-2>.

Abstract

Context – Species distribution modelling is a common tool in conservation biology but two main criticisms remain: (1) the use of simplistic variables that do not account for species movements and/or connectivity and (2) poor consideration of multi-scale processes driving species distributions.

Objectives – We aimed to determine if including multi-scale and fine-scale movement processes in SDM predictors would improve accuracy of SDM for low-mobility amphibian species over species-level analysis.

Methods – We tested and compared different SDMs for nine amphibian species with four different sets of predictors: (1) simple distance-based predictors; (2) single-scale compositional predictors; (3) multi-scale compositional predictors with *a priori* selection of scale based on knowledge of species mobility and scale-of-effect (4) multi-scale compositional predictors calculated using a friction-based functional grain to account for resource accessibility with landscape resistance to movement.

Results - Using friction-based functional grain predictors produced slight to moderate improvements of SDM performance at large scale. The multi-scale approach, with *a priori* scale selection led to ambiguous results depending on the species studied, in particular for generalist species.

Conclusion - We underline the potential of using a friction-based functional grain to improve SDM predictions for species-level analysis.

Introduction

Species distribution models (SDMs) are currently the most widely used models for making spatially explicit predictions of the suitable environment of a species in a given area (Guisan and Zimmermann 2000; Guisan and Thuiller 2005; Elith and Leathwick 2009; Franklin 2010) based on the relationships between species observations and environmental variables. Careful selection of variables can improve model performance and limit multi-collinearity and over-fitting problems (Araújo and Guisan 2006; Austin and Van Niel 2011; Dormann et al. 2013; Fournier et al. 2017). It is therefore necessary to rigorously select predictors based on species ecology, geographical context and ecological processes, at the appropriate spatial extent and resolution (Guisan and Thuiller 2005; Austin and Van Niel 2011; Araújo et al. 2019). However, problems of variable selection (Tulloch et al. 2016; Fournier et al. 2017) underly two major criticisms of SDMs: (1) the use of simplistic variables that do not account for fundamental ecological processes such as biotic interactions and species movements or connectivity (Franklin 2010; Barve et al. 2011a; Boulangeat et al. 2012; Decout et al. 2012; Foltête et al. 2012; Holloway and Miller 2017) and (2) a lack of consideration of the multi-scale character of the processes driving species distributions (Mayor et al. 2009; McGarigal et al. 2016; Fournier et al. 2017; Hallman and Robinson 2020). Indeed, most SDM studies use simple distance layers and/or map all predictors at the same grain (Fournier et al., 2017), whereas the interactions between species and landscape operate at a variety of spatial and temporal

scales (Wiens 1989; Levin 1992; Mayor et al. 2009; Jackson and Fahrig 2012; McGarigal et al. 2016; Miguet et al. 2016).

Variable scale-effect, or the scale at which species perceive and interact with the landscape (Miguet et al. 2016), is often related to species mobility and movement processes (Mayor et al. 2009; Jackson and Fahrig 2012, 2015; Thornton and Fletcher 2014). Movements are essential for animal survival, especially in fragmented human-dominated landscapes (Wiens et al. 1993; Hanski 1998; Sinsch 2014). They can be defined as regular and local movements (e.g. daily foraging movement); migration (i.e. seasonal movement inside the species annual home range) or dispersion (e.g. larger scale punctual unidirectional movement) (Pittman et al. 2014; Sinsch 2014; Holloway and Miller 2017). These movements can involve different levels of biological organization, e.g. from the individual moving from a daily roosting site to a foraging site within its home range, to the metapopulation characterized by dispersing individuals between more or less isolated sub-populations (Sinsch 2014). Thus, movements influence distribution patterns through processes acting at different scales and hierarchical levels, such as resource accessibility, colonisation of new suitable habitats, gene flow between populations and recruitment of new individuals (Levin 1992; Hanski 1998; Mayor et al. 2009; Pittman et al. 2014). It is therefore essential to consider movements in SDM (Soberon and Peterson 2005; Richard and Armstrong 2010; Boulangeat et al. 2012; Brotons et al. 2012) though they are not always included (Foltête et al. 2012; Holloway and Miller 2017).

Several approaches can be used to integrate movements and landscape connectivity at different scales into habitat suitability studies. Some examples are (1) including structural and/or functional connectivity predictors by using simple metrics of landscape structure or more complex metrics derived from circuit or graph theory (e.g. Foltête et al. 2012); (2) applying dispersal kernel layers (Summers et al. 2012); (3) using complex hybrid approaches (i.e. correlative SDM combined with spatially-explicit population models; (Brotons et al. 2012); (4) using SDM outputs to define nodes used in connectivity analysis (Estrada-Peña 2005; Duflot et al. 2018; Foltête et al. 2020) or to apply spatial filters to constrain species dispersal from previously occupied areas (Cardador et al. 2014). However, all such methods mainly concern broad-scale processes such as migration or dispersal movements at population level (Franklin 2010; Barve et al. 2011b; Holloway and Miller 2017) while finer scale movements are neglected (Holloway and Miller 2017).

The use of functional grain including landscape resistance might be relevant to consider finer-scale movements (i.e. within grain movements) in broader scale SDM (Baguette and Van Dyck 2007; Romero et al. 2009; Galpern and Manseau 2013a). These movements define the functional grain, defined as the perceptual range (i.e. the minimum distance from which a resource may be detected), which is related to species mobility, with or without landscape resistance (Lima and Zollner 1996; Baguette and Van Dyck 2007; Galpern and Manseau 2013a). Functional grain then describes a set of functionally connected resource patches in an continuous area within which an animal may move freely according to its mobility (Galpern and Manseau 2013b). Awareness of functional grain may greatly enhance the ability to predict species distributions (Romero et al. 2009) especially for species like amphibians, with low movement capacities and which are highly affected by landscape features, composition, and configuration.

Movements through heterogeneous landscapes are crucial for amphibian survival (Pittman et al. 2014; Sinsch 2014). Amphibians have biphasic life cycle (i.e. with aquatic and terrestrial stages) means they seasonally travel relatively long distances despite their low locomotion capacity and sensitivity to desiccation (Janin et al. 2012). The distance between aquatic and terrestrial sites inside their annual home range can exceed several hundred meters (Marsh and Trenham 2001; Smith and Green 2005) and dispersal movements can reach a few kilometres (Pittman et al. 2014; Sinsch 2014). Consequently, amphibians are particularly sensitive to landscape permeability defined by landscape structure and composition at different spatial scales (Cushman 2006; Denoël and Lehmann 2006; Youngquist and Boone 2014; Collins and Fahrig 2017). Modelling their distribution over large scales (i.e. a scale with an effect of both climate and landscape variables) is particularly challenging and under-investigated although of high relevance for regional conservation, especially in a context of global change (Holloway and Miller 2017; Préau et al. 2019; Matutini et al. 2020). Hence, amphibians are an interesting focal taxon for testing whether functional grain analyses that integrate finer-scale movement processes improve SDM accuracy over large scales.

The aims of this study, at large scale and using low mobility amphibians as a focal taxon, were to compare the performance of (1) distance-based versus landscape composition predictors of species distribution (2) single-scale versus multi-scale models based on empirical knowledge of maximal mobility, and (3) multi-scale models using landscape composition within functional grains defined by fine-scale movements constrained or not by landscape resistance. We tested three associated hypotheses: (1) models using landscape composition predictors perform better than models using only distance layers as predictors; (2) a multi-scale approach based on prior knowledge of movement processes and the scale-of-effect improve model accuracy and (3) integrating fine-scale movements using a friction based functional grain improves prediction of amphibian habitat distributions at large scale.

Materials And Methods

1.1 Study species and area

Our study was performed in Pays de la Loire, a region of western France covering 32,082 km² where landscapes have been greatly modified by intensive agricultural activities over the last century. These have notably led to a decrease in forest cover, a homogenization of landscape mosaics and a degradation of wetlands. Traditional hedgerow network landscapes with small pastures delimited by hedgerows, ponds networks and small woods associated with extensive livestock farming have high, local conservation value (Baudry et al. 2000), especially for amphibians.

The 21 species of amphibians present in the region are protected and 12 of them are priority species for conservation. Among the nine studied species, *Pelodytes punctatus* (locally associated with open, sandy and pioneer environments), *Triturus marmoratus*, and *Rana temporaria* (both mainly forest specialists) have high conservation value. The other species, *Lissotriton helveticus*, *Bufo spinosus*, *Hyla arborea*,

Rana dalmatina, *Triturus cristatus* and *Salamandra salamandra*, are generalist and common species, except for *S. salamandra*, considered a forest specialist.

1.2 Habitat suitability modelling

1.2.1 Biological data for model calibration

We accessed high-resolution presence-only occurrences of 9 species of amphibian (1500 - 9000 presence data per species) from a regional database for the period 2013-2020 (see Matutini et al. 2020 and Appendix 1 for data description and selection procedure). After filtering out data points <500m apart to reduce autocorrelation, we projected remaining presence data on a 100m resolution grid. This presence data selection process was repeated for each modelling iteration.

1.2.2 Environmental variables

The environmental data used to establish predictor layers over the study area are described in Matutini et al. 2020 and in Annex 2. Each land cover type was rasterized at 10m or 20m resolution for metric calculations (see Table 1). We tested four different models performed with different sets of predictors (see Fig. 1):

- (1) *Distance-based predictors* calculated as the Euclidian distances from the grid-cell centroid to the nearest patch of a given land cover type. Predictors included in *DIST* model;
- (2) *Composition-based and single-scale predictors* calculated with a moving window analysis in a circular buffer around pixel centroids according to the species migration ability and home range size. Predictors included in *CIRC.SS* model;
- (3) *Composition-based and multi-scale predictors* calculated with a moving window analysis in circular buffers corresponding to different scales of landscape effects on the focal species (i.e. home range size and population levels). Predictors included in *CIRC.MS* model;
- (4) *Friction-based and multi-scale predictors* calculated in friction-based buffers or weighted distances to account for resource accessibility and landscape resistance to movement. These predictors were calculated only to assess the suitable resource accessibility. Predictors included in *FRIC* model (see Fig. 1).

Breeding sites (wetlands) and woodlands are strongly selected by amphibian species during different stages of their life-cycle (Laan and Verboom 1990; Guerry and Hunter 2002; Ficetola and De Bernardi 2004; Cushman 2006; Zanini et al. 2008; Hartel et al. 2010; Boissinot et al. 2019) and the true availability of these resources for individuals is conditioned by their accessibility. In *FRIC*, we calculated predictor layers of suitable resources with a sliding functional window analysis using a cost-distance method based on landscape permeability to obtain a functional grain including movement resistance (see Fig. 1) (Ray et al. 2002; Joly et al. 2003; Janin et al. 2009). A functional window is defined as a buffer around a

pixel centroid whose shape is determined by landscape resistance (i.e. a friction-based reachable zone, see Ray et al. (2002). Since ponds influence ecological processes at different levels (home range and meta-population levels), we used two pond variables: distance to the nearest pond, as the main breeding habitat requirement, and pond density within a potentially accessible area for dispersing individuals, as pond density is known to improve landscape connectivity (Cushman 2006; Ribeiro et al. 2011; Arntzen et al. 2017). In FRIC, these two variables were calculated using the friction cost methods described below.

A resistance map (20m resolution) was computed using friction cost values to account for resistance or barrier effects of different categories of roads, railways and urban areas (see Table 2). The cost values of impermeable barriers (i.e. high-density urban area, high-speed train line, highway and dual carriageways) were set as the maximum number of pixels that the species is able to cross, as required for analysis with Chloe 4.0 software (Boussard and Baudry 2017). Permeable features facilitating movement across barriers (e.g., viaduct, wildlife pass and others, see Table 2) were digitized from aerial photographs. The allocation of resistance values is strongly debated, can greatly affect model quality and scientific evidence is limited. In addition, the resolution of our resistance map was too coarse to consider fine linear elements of the landscape used by species for movements (e.g. hedges, field margins, ditches, road verges, channelized agricultural headwater streams). As a precaution, we allocated lower cost values than usually reported to permeable roads, railways and low settlement density areas, and other landcover classes were considered as permeable (i.e. with cost value equal to 1) (see Table 2).

Finally, for *CIRC.MS* and *FRIC*, maximum distances from the buffer centroid were based on species migration (i.e. seasonal movements in the annual home-range – *scale 1*) and dispersal (i.e. long-distance occasional movements – *scale 2*). These distances have been reviewed by Smith and Green (2005) and Boissinot (2009) and variable scale effects have been highlighted by Boissinot et al. (2019) in similar geographical and biological contexts. Pond density, road density, urban area and crops mainly influence population-level processes such as dispersal (Fahrig et al. 1995; Cushman 2006; Hartel et al. 2010; Ribeiro et al. 2011; Arntzen et al. 2017) and consequently related metrics were calculated at *scale 2*. *B. spinosus* and *H. arborea* are two species with higher mobility than other species so maximum distance considered for scale 1 (home range) was 600m and for scale 2 (dispersion) was 2000m. For all other species, we used a maximum distance of 300m for scale 1 and 1000m for scale 2 (see Boissinot et al. 2019 and Appendix 2).

All variables were mapped using R environment v. 3.5.3 (R Core Team 2019), QGIS 3.10 (Quantum GIS Development Team 2019) and Chloe 4.0 (Boussard and Baudry 2017). Variables used are described in Table 1. Final predictor resolution was 100m to match presence data resolution and was obtained by resampling original raster layers (value of the pixel centroid).

Table 1 Environmental variables used for species distribution modelling of each amphibian species in Pays de la Loire region. Variable names with an asterisk (*) were calculated inside a friction-based buffer or using least-cost distance in model *FRIC*. Scale 1 (migration / Home range): 600m (*Bufo spinosus* and *Hyla arborea*) and 300m (other species). Scale 2 (dispersion): 2000m (*Bufo spinosus* and *Hyla arborea*)

and 1000m (other species). See Appendix 2 for details on data sources, ecological justifications and associated references.

Model	Code	Scale range	Metric description
DIST	CLIM_1	4km	First axis from a PCA on 11 bioclim variables and altitude
	CLIM_2	4km	Second axis from a PCA on 11 bioclim variables and altitude
	D_BREED_SITE	distance	Distance to nearest “pond” or “pond + lake” or “pond + temporary stream” according to species ecology
	D_RIVERS	distance	Distance to nearest permanent rivers
	D_WOOD_DM	distance	Distance to nearest deciduous and mixed forest
	D_WOOD_C	distance	Distance to nearest coniferous forest
	D_PASTURE	distance	Distance to nearest permanent pasture
	D_HEDGE	distance	Distance to nearest hedgerow
	D_CROP	distance	Distance to nearest crop
	D_URBAN	distance	Distance to nearest urban area
	D_ROAD	distance	Distance to nearest primary road
CIRC.SS	CLIM_1	4km	First axis from a PCA on 11 bioclim variables and altitude
<i>Single-scale</i>	CLIM_2	4km	Second axis from a PCA on 11 bioclim variables and altitude
	WOOD_DM	scale 1	Area of deciduous and mixed forest
	WOOD_C	scale 1	Area of coniferous forest
	PASTURE	scale 1	Area of permanent pasture
	NB_HEDGE	scale 1	Hedgerow density
	CROP	scale 1	Area of crop
	URBAN	scale 1	Area of urban (settlements)
	NB_ROAD	scale 1	Roads density
	NB_PONDS	scale 1	Ponds density
CIRC.MS & FRIC*	CLIM_1	4km	First axis from a PCA on 11 bioclim variables and altitude
<i>Multi-scale</i>	CLIM_2	4km	Second axis from a PCA on 11 bioclim variables and altitude
	D_BREED_SITE*	distance	Distance from “pond” or “pond + lake” or “pond + temporary stream” according to species ecology

D_RIVERS*	distance	Distance to nearest permanent rivers
WOOD_DM*	scale 1	Area of deciduous and mixed forest
WOOD_C*	scale 1	Area of coniferous forest
PASTURE	scale 1	Area of permanent pasture
NB_HEDGE	scale 1	Hedgerow density
CROP	scale 2	Area of crop
URBAN	scale 2	Area of urban (settlements)
NB_ROAD	scale 2	Roads density
NB_PONDS*	scale 2	Ponds density

Table 2 Resistance values used in the functional model *FR/C* to define friction-based buffer in moving window analysis for predictor layer calculations. Maximum value *max* was defined for barrier elements (impermeable) according to maximal number of pixels that the species is able to cross in the 20m resolution resistance map.

Landcover type	Friction cost	References
Urban – high settlement density	max (barrier)	Compton et al. 2007; Safner et al. 2011; Van Buskirk 2012
Urban - low settlement density	2	Compton et al. 2007; Van Buskirk 2012
Highspeed train line	max (barrier)	Ray et al. 2002
Highway and dual carriageways	max (barrier)	Ray et al. 2002; Compton et al. 2007; Van Buskirk 2012
Other primary roads	5	Compton et al. 2007; Van Buskirk 2012
Secondary road	2	Compton et al. 2007; Van Buskirk 2012
Railway	3	Compton et al. 2007
Barrier underpasses (for road and train):		
- Pipe/tunnels	5	Jarvis et al. 2019; Testud et al. 2020
- Stream	1	/
- Path/track	2	/ (expert assessment)
- Wildlife bridges	2	/ (expert assessment)
- Viaduct	1	/
Other landcover types	1	/

The spatial correlation between environmental predictors was investigated using the variance inflation factor (VIF) as a measure of multicollinearity and Pearson correlation tests with VIF<6 and $|r|<0.6$, lower than advised by O'Brien, 2007 (see Appendix 2).

1.2.3 Statistical models

Detailed modelling methods are described in Matutini et al. 2020. We used one regression-based approach (Generalized Additive Models, GAM) and one machine learning algorithm (Random Forest, RF) to predict and assess habitat suitability within the studied region. We used random pseudo-absence selection constrained to take sampling effort into account as follows. We counted the number of dates with at least one amphibian observation on a 500m grid over the studied area. 500m-cells were considered as sampling units, i.e. if one species has been detected in the cell, we considered the 500m-cell as visited. Then, we proportionally sampled pseudo-absences according to sampling effort, with a minimum distance of 500m from a presence point of the target species. In addition, we randomly sampled 5% of pseudo-absences in unsuitable habitat (e.g. at least 75% of the cell area covered by urban and/or crops area without any tree or water in a cell). The number of pseudo-absences was fixed equal to

the number of presence data (Barbet-Massin et al. 2012; Liu et al. 2019) and we ran 20 replicates of the pseudo-absence generation processes.

Finally, we conducted ensemble modelling using the median value of all generated individual maps (i.e. 20 maps/algorithm) and extract a standard deviation map for each species.

1.2.4 Model validation

For independent model validation, we used two external independent presence-absence datasets from citizen sciences and field complementation (see Matutini et al. 2020). The first dataset, called *EVAL*, was filtered to increase independence from the training-set and robustness of evaluation as described in Matutini et al. 2020. For the second evaluation set, called *EVAL_STRAT*, we used a stratified sampling of *EVAL* on final predictive maps for each species (see Matutini et al. 2020).

We calculated different evaluation metrics to improve discrimination between models with 500 bootstraps each. We calculated a Symmetric Extremal Dependence Index (SEDI, Wunderlich et al. 2019) using the *sedWeighted* function in R from Wunderlich et al. (2019) and AUC values, Kappa, specificity (true negative rate) and sensitivity (true positive rate) of ensemble models with *EVAL* and *EVAL_STRAT* for each species (Allouche et al. 2006) using PresenceAbsence package (Freeman 2015). The threshold value for presence-absence discrimination were calculated for each permutation using the threshold function from dismo package (Hijmans et al. 2020) with sensitivity and specificity values optimisation strategy (i.e. True Skill Statistics, TSS).

In addition, we compared outputs from this modelling with final suitability maps obtained by Matutini et al. 2020 for the same species with coarse resolution (i.e. 500m) and single-scale SDM.

Results

The model accuracy varied among species, with AUC values from 0.63 to 0.89, Kappa from 0.29 to 0.63 and SEDI from 0.57 to 0.89. The accuracies were higher for specialist species models compared to those of generalist species. The models from this study performed better than the models from Matutini et al. (2020) for all species except *L. helveticus* (Table 3). In addition, the selected models are more similar and stable between evaluation methods for forest specialist species and Urodeles except for *T. cristatus*.

Distance versus compositional metrics (DIST vs CIRC.SS) – Hypothesis 1 (H1)

Using more complex landscape composition metrics generally improved model accuracy in comparison with simple distances to the nearest habitat. The predictive power of models using landscape composition predictors (*CIRC SS or MS* and *FRIC*) was better than models using distance-based predictors for all species except *R. dalmatina* and *R. temporaria*, with more ambiguous results depending on the evaluation method used (see Table 3 and Appendix 3).

Single-scale versus multi-scale models (CIRC.SS vs CIRC.MS) – Hypothesis 2 (H2)

Comparison between single-scale (SS) and multi-scale (MS) models shows more ambiguous results. MS models performed better for four species, *T. cristatus*, *B. spinosus*, *R. dalmatina* and *P. punctatus* while SS models performed better for *T. marmoratus*, *L. helveticus*, *H. arborea* and *R. temporaria* (see Table 3). Discrimination between the two models is not possible for *S. salamandra*.

Functional grain including fine-scale movements or not (CIRC.MS vs FRIC) – Hypothesis 3 (H3)

Using functional grain accounting for landscape resistance to fine-scale movements (*FRIC*) slightly improved model accuracy by comparison with *CIRC.MS* including predictors calculated used circular sliding windows. Indeed, differences between evaluation metrics vary from 0 to 0.02 for AUC, from 0 to 0.05 for SEDI and 0 to 0.07 for Kappa. *FRIC* models performed better for three species, *L. helveticus*, *H. arborea* and *R. temporaria* while *CIRC.MS* models performed better for *T. cristatus* only (see Table 3). Model discrimination is more difficult for other species but *FRIC* slightly improved predictions for *P. punctatus* and *S. salamandra*. In addition, *FRIC* model improved sensitivity (proportion of observed presences correctly predicted with TSS optimisation) for most species (see Table 3).

Table 3 Performance of discrimination capacity and accuracy of ensemble models for each studied species. Results obtained with stratified data for external evaluation (*EVAL_STRAT*) with 500 permutations. DIST: model with distance predictors only; *CIRC.MS*: model with compositional predictors calculated in different circular buffer sizes according to species migration or dispersal ability (multi-scale); *CIRC.SS*: same as *CIRC.MS* but using only one circular buffer size (single-scale); *FRIC*: same predictors as *CIRC.MS* but suitable resources are considered in a friction-based buffer according to landscape permeability. Best models: H1: distance vs composition-based models; H2: single-scale vs multiscale models; H3: including vs not including finer-scale movements using a friction-based functional grain. Brackets indicate high uncertainty for model selection (low discrimination). Bold values in “Best model” shows model selected using the two evaluation sets. Results for *EVAL* dataset are show Appendix 3. For each species, the bottom line shows the evaluation metrics calculated on the final maps obtain by Matutini et al. 2020.

Species	Model	Threshold	Sensitivity	Specificity	Kappa	AUC	SEDI	Best model by hypothesis tested		
								H1	H2	H3
 <i>R. temporaria</i>	DIST	0.74	0.84	0.84	0.61	0.89	0.84			
	CIRC.SS	0.75	0.79	0.91	0.68	0.89	0.85	(x)	x	
	CIRC.MS	0.69	0.71	0.89	0.60	0.84	0.80			
	FRIC	0.74	0.74	0.92	0.66	0.86	0.84			x
	Matutini et al. 2020	0.51	0.97	0.70	0.56	0.84	0.86			
 <i>S. salamandra</i>	DIST	0.48	0.72	0.73	0.45	0.77	0.63			
	CIRC.SS	0.50	0.78	0.77	0.55	0.83	0.73	x	x	
	CIRC.MS	0.40	0.79	0.77	0.56	0.83	0.72		x	
	FRIC	0.43	0.85	0.72	0.58	0.83	0.74			x
	Matutini et al. 2020	0.42	0.80	0.67	0.47	0.79	0.65			
 <i>T. marmoratus</i>	DIST	0.44	0.80	0.61	0.38	0.73	0.57			
	CIRC.SS	0.55	0.82	0.70	0.49	0.79	0.69	x	x	
	CIRC.MS	0.59	0.82	0.69	0.47	0.77	0.66			
	FRIC	0.43	0.83	0.69	0.48	0.78	0.68			x
	Matutini et al. 2020	0.39	0.89	0.57	0.43	0.75	0.65			
 <i>P. punctatus</i>	DIST	0.43	0.90	0.63	0.46	0.78	0.74			
	CIRC.SS	0.51	0.81	0.77	0.55	0.81	0.75	x		
	CIRC.MS	0.56	0.80	0.80	0.58	0.84	0.77		x	
	FRIC	0.42	0.82	0.79	0.58	0.85	0.80			x
	Matutini et al. 2020	0.47	0.91	0.69	0.56	0.81	0.83			
 <i>T. cristatus</i>	DIST	0.48	0.84	0.70	0.46	0.79	0.74	(x)		
	CIRC.SS	0.66	0.83	0.65	0.42	0.78	0.73			
	CIRC.MS	0.58	0.93	0.67	0.48	0.83	0.85		x	x
	FRIC	0.66	0.91	0.65	0.46	0.80	0.82			
	Matutini et al. 2020	0.69	0.90	0.56	0.40	0.75	0.71			
 <i>L. helveticus</i>	DIST	0.32	0.70	0.76	0.34	0.71	0.70			
	CIRC.SS	0.49	0.79	0.72	0.44	0.74	0.71	x	x	
	CIRC.MS	0.54	0.72	0.72	0.33	0.71	0.66			
	FRIC	0.26	0.77	0.70	0.39	0.73	0.71			x
	Matutini et al. 2020	0.41	0.87	0.64	0.49	0.75	0.73			
 <i>R. dalmatina</i>	DIST	0.29	0.79	0.76	0.46	0.76	0.74	x		
	CIRC.SS	0.40	0.73	0.73	0.36	0.75	0.65			
	CIRC.MS	0.33	0.78	0.71	0.41	0.75	0.67	x		(x)
	FRIC	0.23	0.78	0.68	0.39	0.75	0.67			
	Matutini et al. 2020	0.28	0.76	0.62	0.29	0.69	0.57			
 <i>H. arborea</i>	DIST	0.38	0.88	0.69	0.57	0.79	0.73			
	CIRC.SS	0.41	0.86	0.74	0.60	0.82	0.76	x	x	
	CIRC.MS	0.36	0.81	0.71	0.51	0.79	0.69			
	FRIC	0.42	0.86	0.71	0.58	0.81	0.74			x
	Matutini et al. 2020	0.65	0.74	0.64	0.36	0.70	0.60			
 <i>B. spinosus</i>	DIST	0.43	0.63	0.67	0.29	0.63	0.59			
	CIRC.SS	0.21	0.88	0.55	0.43	0.66	0.74	x		
	CIRC.MS	0.46	0.94	0.71	0.63	0.80	0.88		x	(x)
	FRIC	0.43	0.96	0.70	0.63	0.78	0.89			
	Matutini et al. 2020	0.29	0.74	0.56	0.30	0.65	0.47			

Differences in habitat suitability predictions resulting from the four models (*DIST*, *CIRC.SS*, *CIRC.MS* and *FRIC*) are shown in Fig. 2 and Appendix 3. Absolute differences between suitability index values obtained through *DIST* and *CIRC.SS* modelling varied from 0 to 0.6, especially near cities. Absolute differences between *CIRC.MS* and *FRIC* were generally low, though in a few small areas scattered across the region the difference in suitability could be as high as 0.5. In addition, general patterns of suitable habitat differed between final maps of *DIST* and other models but were similar between *CIRC.SS*, *CIRC.MS* and *FRIC* (Fig. 2).

Discussion

For most species, model accuracy was satisfactory (AUC from 0.61 to 0.91) and higher and more stable for specialist compared to generalist species, as found in numerous empirical studies (Hernandez et al. 2006; McPherson and Jetz 2007) and simulations (Connor et al. 2018). Indeed, modeling the distribution of generalist species is particularly challenging (Brotons et al. 2004), especially because generalists are eclectic feeders, adaptable to various ecological contexts, use a large proportion of available habitats and are usually more mobile than specialist species. Hence, the statistical “signal” of the relationship between species’ occurrence and environmental conditions may be too weak to capture (Brotons et al. 2004; Connor et al. 2018). On the other hand, model accuracy of forest specialist species may be overestimated because forests are relatively scarce habitats and patchily distributed in the region (see Brotons et al. 2004).

Weakness of distance predictors

Models using landscape composition predictors performed better than models with distance-based predictors. These results are consistent with numerous studies from Landscape Ecology (Moilanen and Nieminen 2002; Martin and Fahrig 2012). Distance-based layers only represent proximity to elements without considering the amounts of habitat which are important for species persistence (Moilanen and Nieminen 2002; Martin and Fahrig 2012).

Combining multi-scale predictors for a functional approach

Differences in accuracy between single-scale and multi-scale models were more ambiguous and varied among species, especially for generalist species. Hence, for *B. spinosus* and *T. cristatus* the multi-scale model performed best, while for *H. arborea* and *L. helveticus* the single-scale model was more accurate. For predictive approaches with SDM, the literature suggests that multi-scale or multi-level models are more accurate than single-scale models (Graf et al. 2005; Boscolo and Metzger 2009; Fournier et al. 2017; Bellamy et al. 2020; Hallman and Robinson 2020) but some authors have also found ambiguous results (Martin and Fahrig 2012). In our study, we used an *a priori* selection of appropriate scale for each predictor according to a species-specific known scale effects in similar geographical contexts but it might be misleading (Hallman and Robinson 2020). Indeed, even if species mobility and some associated species traits as body size might be a good indicator of potential variable scale of effect (Jackson and Fahrig 2012; Thornton and Fletcher 2014), scale-effects are much more complex and variable across large geographical extents. From simulation, Connor et al. (2018) demonstrates that scale-of-effect might vary between different landscapes (e.g. homogeneous vs heterogeneous), models and species and that statistical signal is difficult to capture for generalist species in homogeneous landscape and with increasing grain size.

In addition, multi-scale amphibian movements are still poorly understood (Pittman et al. 2014) and dispersal distances may be under-estimated (Sinsch 2014). According to Miguet et al. (2016), the scale of effect may be influenced by five groups of factors: species traits, landscape variables, biological

response, indirect influence (e.g. water quality or predator density) and regional context of the study. However, the determinants of the scale of effect are still only partly understood and empirical results tend to contradict theoretical predictions making *a priori* scale selection particularly complex (Jackson and Fahrig 2015; Moll et al. 2020). Therefore, even with good prior knowledge on species ecology in neighbour and/or similar regions, transferring results of previous studies may be erroneous and defining scale-of-effect using species mobility capacity might be not sufficient (Mayor et al. 2009; Zanini et al. 2009).

Furthermore, the model itself and the algorithm used might be sensitive to different scale-of-effect for the same variables (Connor et al. 2018; Hallman and Robinson 2020; Rose et al. 2020). Indeed, Rose et al. (2020) shows model-specific sensitivity to scale when predicting the distribution of a toad species in a large area in California using Random Forest, Point Process Models and Maxent. Some other algorithms such as Boosted regression trees (BRTs) are more robust to overfitting and collinearity than allow us to use several predictors at different scales (Hallman and Robinson 2020) and might better consider species functional response across scales.

Functional grain and finer-scale movements in SDM

Including landscape resistance to movement produced only slight to moderate improvements in model accuracy for six species. This may have been a consequence of the evaluation-set. Indeed, the majority of sites used to evaluate the models were far from potential barriers to movements (cities and roads) which are the main elements mapped in the friction map. As a result, the evaluation sites are mainly located in areas with similar environmental characteristics and low variability between predicted suitability values from models including or not landscape resistance (i.e *CIRC.MS* and *FRIC*).

Secondly, we mainly consider barrier elements in the friction map, which represent a small proportion of the total study area, also leading to low variation between predictors of *CIRC.MS* and *FRIC*. Many studies at local scale use several land-cover classes to generate resistance maps, in particular crops, forests, wetlands and edges (Ray et al. 2002; Joly et al. 2003; Compton et al. 2007; Buskirk 2012; Decout et al. 2012; Janin et al. 2012; Youngquist and Boone 2014; Jeliazkov et al. 2019). However, the integration of other land-cover classes to develop a more precise permeability map must be carried out at higher resolutions (e.g. 5 m). This relies on sufficient computational power for metric calculation at regional extent and on knowledge for resistance value estimations (see Zeller et al. 2012; Keeley et al. 2017). Indeed, amphibians can use small or narrow elements of the landscape such as hedgerows, ditches, field margins, road verges, channeled agricultural headwater streams for movements (Pope et al. 2000; Mazerolle 2005).

Considering these elements, the slight improvements observed indicate that using functional grain with a friction-based approaches might be relevant for predictions at large scales and merit further investigation, especially as crucial movement processes operate at fine-scale. Ray et al. (2002); Zanini et al. (2008) have underlined the interest of friction-based modeling approaches to improve the prediction of *B. bufo* presence or *B. bufo* and *R. temporaria* respectively compared to circular buffer zones around ponds.

Other studies underline the importance of considering true accessibility of habitat to explain species distributions or population dynamics and avoid incorrect conclusions (Eigenbrod et al. 2008; Hamer 2018). Our approach, for a larger number of species, highlights the potential of this method at any point of the landscape, i.e. not only around ponds.

General limits of our study

Finally, some ecological and methodological limits need to be mentioned. Firstly, the data we used are unstandardized presence-only data, from different sources and mainly collected by citizens. Data quality therefore limits the study of fine-scale processes and results need to be interpreted with caution (Guillera-Arroita et al. 2015); conversely, citizen science is a requisite to have data over large areas. Secondly, our large-scale study involves a diversity of landscapes that may present a high local level of variable collinearity un-detectable over a large extent. These different landscapes are the expression of different agricultural practices (e.g. cattle farming *vs* cereal crops; extensive practices *vs* intensive agriculture), which significantly affect amphibian distributions at different scales (e.g. water pollution, decrease and contamination of food resources, hedge management more or less suitable, spatial heterogeneity). The associated environmental data were not available at regional scale. In addition, the wide extent of our study implies the presence of sub-specific variations in habitat selection and movements (i.e. local adaptations) reducing model accuracy in species-level analyses (McPherson and Jetz 2007).

Conclusion

We highlight the potential of using a friction-based functional grain to improve SDM prediction at species level but further investigation is needed. Our results suggest that a multi-scale approach using *a priori* selection of scales, based on empirical data on species mobility and scale-of-effect, leads to ambiguous results depending on the species studied, in particular for generalists at species level. New methods are currently under investigation to propose a framework for multi-scale and multi-level SDM using specific scale-optimization or pseudo-optimization methods (Stevens and Conway 2019; Hallman and Robinson 2020) or post-modelling analysis (Miguet et al. 2016; Moll et al. 2020). Furthermore, spatial variability of scale-of-effect and species mobility through landscape matrices is a major limit for species-level analysis. Spatial structure of data according to landscape or sub-species variations induced by local adaptation is currently poorly included in SDM studies but should be considered explicitly, especially for high resolution studies over large extents (see Swanson et al. 2013; Crase et al. 2014). However, ecological relevance and final objectives of the study should remain the priority for model conceptualization and predictor selection. More complex models may be unreasonably computationally intensive for species-level analysis over large extents and could lead to difficulties in model interpretation, discrimination and evaluation (e.g. Bell and Schlaepfer 2016).

Decisions for biodiversity conservation often call for study of habitat suitability at large (regional) or global (national or European) scales. The ambiguity of certain results presented in this paper show that it can be difficult to include fundamental ecological processes linked to scales-of-effect and movements

over large areas (i.e. with sub-specific variability, diversity of landscapes and agricultural practices, mainly heterogeneous data from citizen science). As a result, a balance must be found between research and application objectives, availability and quality of data (environmental and biological) and model complexity with a strong consideration of ecological justifications.

Declarations

Acknowledgements

This work would not have been possible without the support of the Pays de la Loire Herpetological Group, the CPIE Regional Union and the French BirdLife partner (LPO). We are especially grateful to Morgane Sineau and Benoit Marchadour who coordinate regional naturalists' databases. We also acknowledge the many naturalists involved, for access to data and for additional fieldwork, especially Dorian Angot, Baptiste Gaboriau, Ludovic Aubry and Martin Bonhomme. We thank Andrew Chin, Jean Secondi and Aurélien Besnard for providing helpful discussion. Our work was supported by funding from Ecole Supérieure d'Agricultures d'Angers, Angers Loire Metropole, The French Society for Ecology and Evolution (SFE²) and "Humanité et Biodiversité".

Funding

PhD grant came from Ecole Supérieure d'Agricultures d'Angers and Angers Loire Métropole. Additional funding for field work provides from The French Society for Ecology and Evolution and "Humanité et Biodiversité".

Conflicts of interest/Competing interests

The authors of this preprint declare that they have no financial conflict of interest with the content of this article

Ethics approval

Access to citizen data is subject to a user agreement between our lab and the associations involved. We have done our best to involve volunteers and associations in this work with regular exchanges (attendance at meetings, reporting of results in different forms, organization of steering committees). In addition, all people involved in handling amphibians had specific ministerial authorization.

Consent to participate

All participants in this study consented

Consent for publication

All authors contributed critically to the drafts and gave final approval for publication.

Availability of data and material

Data sample and access procedure are available online: <https://doi.org/10.5281/zenodo.4358147>

Code availability

Scripts and codes are available online: <https://doi.org/10.5281/zenodo.4358147>

Authors' contributions

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Figures

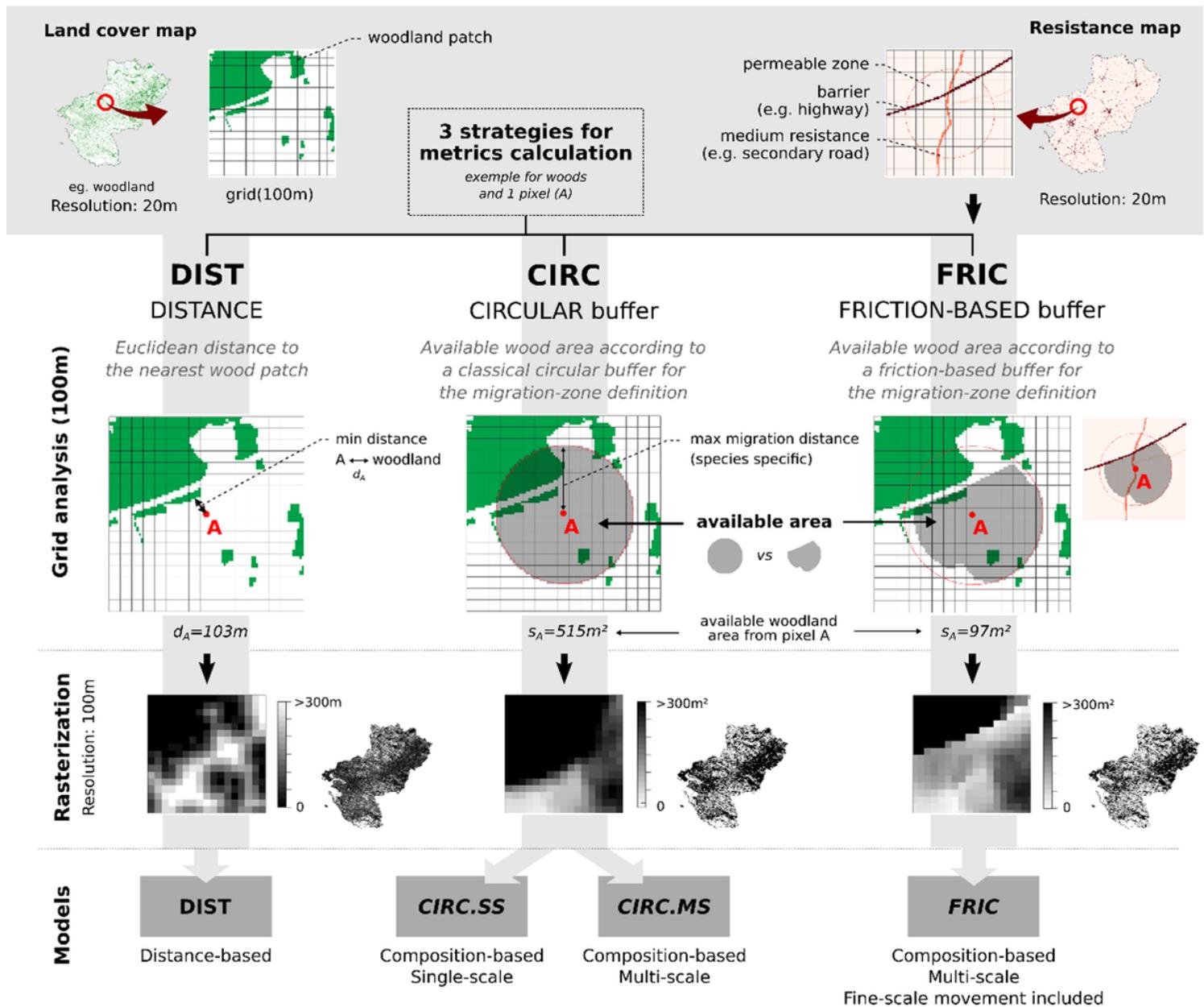


Figure 1

Method used for metric calculations for DIST, CIRC (SS and MS) and FRIC models. Example for metrics associated with deciduous and mixed woodlands. Here, the available area or distance calculation is shown for pixel A only.

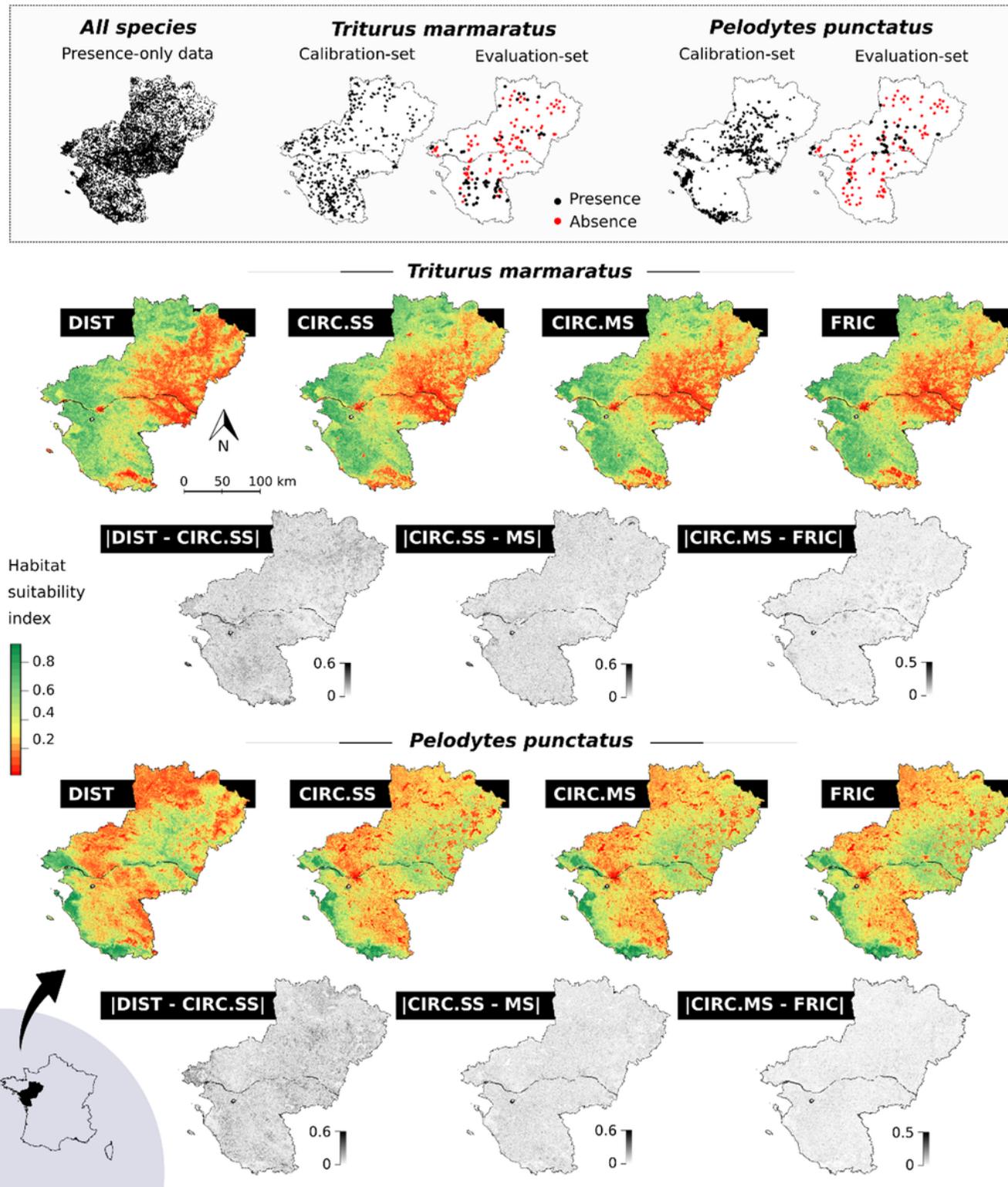


Figure 2

Differences between predictions of habitat suitability with DIST, CIRC (SS and MS) and FRIC models for two species of high regional conservation concern: *Triturus marmoratus* and *Pelodytes punctatus*. DIST: model with distance predictors only; CIRC: model with compositional predictors calculated in circular buffers (SS: single scale; MS: multi-scale); FRIC: same predictors as CIRC.MS but suitable resources are considered in a friction-based buffer according to landscape permeability. $|\text{model 1} - \text{model 2}|$ with

associated maps are absolute differences between the two final suitability maps of the two models. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

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