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Impact of global warming on the distribution and dispersal of reptiles in the Western Swiss Alps

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Abstract

Global warming directly acts on species distribution and range shifts have already occurred in many taxa, as *Reptilia*. However, these shifts not only depend on climatic conditions, as species dispersal can be slowed down or stopped by physical barriers as highway or streams, and the ecology of the species plays a key role in dispersal. Here, we evaluate how expert characteristics for reptile dispersal, such as dispersal kernel and propagation probability, can modify predictions of current and future distributions of reptiles' habitat suitability in the Western Swiss Alps. Various dispersal simulations were conducted by including physical barriers and five dispersal scenarios to standard habitat suitability predictions. Without physical barrier and dispersal kernel, cold adapted species are predicted to lose large parts of their current distribution, whereas warm adapted species would gain surfaces. The effect of barriers was not strong in the simulations, but prevented the colonization of sites for some species. By comparing the five dispersal scenarios, more restrictive dispersal parameters lead to more pessimist scenarios. This study allows estimating future threats to reptile species in such a mountain landscape, and assisting conservation planning in this area.

Résumé

Le réchauffement climatique engendre des conséquences directes sur la distribution des espèces. Des changements de distribution se sont déjà produits dans beaucoup de taxons, tel que *Reptilia*. Cependant, ces changements ne dépendent pas seulement des conditions climatiques. La dispersion des espèces peut être freinée ou stoppée par des barrières physiques, telles qu'une autoroute ou une rivière. L'écologie de l'espèce joue aussi un rôle clé dans la dispersion. Dans cette étude, nous évaluons comment les caractéristiques de dispersion des reptiles, tels que le kernel de dispersion et la probabilité de propagation, peuvent modifier les prédictions des distributions actuelles

et futures de la qualité des habitats des espèces dans l'ouest des Alpes suisses. Différentes simulations de dispersion ont été générées, incluant des barrières physiques et cinq scénarios de dispersion, et sont basées sur des prédictions standards de qualité des habitats. En l'absence de barrière physique et de kernel de dispersion, les espèces adaptées au froid sont prédites à perdre de grandes surfaces de leur distribution actuelle, tandis que celles des espèces adaptées au chaud augmenteraient. L'effet des barrières dans les simulations n'est pas toujours très marqué, mais empêche la colonisation de sites par certaines espèces. En comparant les cinq scénarios de dispersion, plus les paramètres de dispersion sont restrictifs, plus le scénario est pessimiste. Cette étude permet d'évaluer les futures menaces des espèces de reptiles dans un milieu montagneux, et fournit une aide aux plans de conservation dans la zone d'étude.

List of abbreviations:

- CSCF: Swiss Center of Fauna Cartography
- ETP: Potential evapotranspiration
- GDD: Growing degree-days
- KARCH: Centre for the Coordination and Protection of reptiles in Switzerland
- LDD: Long distance dispersal
- SDD: Short distance dispersal
- SDD&LDD: Short and long distance dispersal

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Introduction

Global warming is one of the most considerable issues for nature conservation. Its impact on species distribution is large. It can modify species' habitat and ultimately affect their survival (Thomas *et al*., 2004). As climatic conditions may drastically vary in the coming decades, vulnerable species may not adapt fast enough to the new conditions and would have to migrate to survive (Malcolm *et al*., 2006). In particular, it is expected that species adapted to cold habitats would have to migrate to higher elevation or latitude (Chen *et al*., 2011).

Ectothermic species, as the *Reptilia* class, regulate their internal temperature with the temperature of their environment. Moreover, their sex-determination is temperature-dependent (Walther *et al*., 2002). Therefore, they should be particularly sensitive to climatic changes. In Switzerland, some species as *Natrix tessellata* (Laurenti, 1768) and *Zamenis longissimus* (Laurenti, 1768) live at low altitude, whereas *Zootoca vivipara* (Jacquin, 1987) can live up to 2'000m (Meyer *et al*., 2009). Therefore, the ecological niche varies a lot between reptile species. Swiss species can be grouped into three categories according to the expert assessment of the Centre for the Coordination and Protection of reptiles in Switzerland (KARCH): "Warm adapted species", "Cold adapted species" and "Transitional-species". Warm adapted species are species living in habitats with higher temperature, mainly at lower elevations. Oppositely, cold adapted species occupy cooler habitats. In Switzerland, they are found at higher elevations or at low altitudes but in humid habitats. Transitional-species are an intermediary group between the two previous ones.

Under climatic change, sites previously suitable can become unsuitable and vice versa. So, in the future, species' distribution can expand or shrink depending on the climatic conditions. However, physical barriers can slow down dispersal of species and prevent their colonization of potential sites (Driscoll, 2004). These barriers can be natural as a lake or human-made as a road.

Several studies have already described the future potential shift of species distribution for many different taxa (e.g. Araújo, 2006; Wiens, 2009). However, few studies have included physical barriers in the dispersal of species under climate change, and how these could impact future distributions (Engler & Guisan, 2009; Pflüger & Balkenhol, 2014), and existing studies mostly concentrated on plants. The aim of this study is to

predict dispersal of 12 reptiles species through different dispersal scenarios from 2010 to 2085 in the study area. We fitted topoclimatic models for the reptile species with the 'biomod2' package in R by taking into account changes in different climatic predictors by 2010, 2035, 2060 and 2085 in the Western Swiss Alps. By using the generated maps of topoclimatic models in the 'MigClim' package, we simulated 5 different scenarios of dispersal with presence or absence of physical barriers: No dispersal, universal dispersal, short-distance dispersal (SDD), long-distance dispersal (LDD) and short and long distance dispersal (SDD&LDD). No dispersal means no dispersal can occur, and so, the current occupied area cannot increase. Universal dispersal allows species to reach any potentially suitable sites. In SDD simulations, dispersal depends on the dispersal kernel of species and on physical barriers. The dispersal in LDD simulations depends on LDD frequency and LDD distance range. The SDD&LDD simulations take into account SDD, LDD and barriers. Following the recommendations of the KARCH, we respected as far as possible the ecology of reptiles. Each parameter in MigClim simulations was adapted to each species (i.e. dispersal kernel, initial maturity age and probability of propagation, LDD frequency and LDD distance range, and barrier types)

With these simulations, we investigated how the potential area covered by the distribution of reptile species in the study area are predicted to change with global warming. In particular, we observed if the area occupied by cold adapted species would decrease because of global warming, even without barriers, and inversely, if the one of warm adapted species would increase, with a conservation-related interest in two invasive species of the study area: *H. viridiflavus* (Lacépède, 1789) and *N. tessellata*. We observed if the presence of physical barriers and dispersal kernel would decrease the occupied area in comparison to a universal dispersal. Finally, by comparing the five dispersal scenarios, we tested if the more restrictive the dispersal parameters, the more the species would colonize areas.

Methods

Study area

The study area is the RECHALP priority research area of the University of Lausanne (*http://rechalp.unil.ch*). It has a size of 700 km^2 with altitudes from 372m to 3210m. This area encompasses the Western Swiss Alps from south of St-Maurice up to the

Lavaux and Pays-d'Enhaut regions. It includes a great diversity of environments and climates, with mountains, plains and banks of Geneva Lake. This diversity leads to many different habitats, which matches with the different ecological niches of a lot of species.

Species

We studied the distribution of 12 reptiles species, including 4 *Lacertidae*: *Lacerta agilis* (Linnaeus, 1758), *Lacerta bilineata* (Daudin, 1802), *Podarcis muralis* (Laurenti, 1768) and *Zootoca vivipara*, three *Colubridae*: *Coronella austriaca* (Laurenti, 1768), *Hierophis viridiflavus*, *Zamenis longissimus,* two *Natricidae*: *Natrix natrix* (Linnaeus, 1758), *Natrix tessellata,* two *Viperidae*: *Vipera aspis* (Linnaeus, 1758), *Vipera berus* (Linnaeus, 1758), and one *Anguidae*: *Anguis fragilis* (Linnaeus, 1758). *Natrix maura* (Linnaeus, 1758) and *Emys orbicularis* (Linnaeus, 1758) were not taken into account, because of the low rate of data occurrences in the zone. *Vipera berus* and *Zootoca vivipara* are distributed mainly in altitude and are considered as "cold adapted species", *Lacerta agilis* as a transitional species and the other ones as "warm adapted species". The KARCH provided occurrences data of Switzerland with a 100m resolution and of study area with a 25m resolution.

Field work

The aim of the field work was to prospect for the presence of all reptile species in zones, which were defined by the expert assessment of the KARCH (Fig. 1). These zones were defined either by the absence of observations, or by the possible distribution boundary of a species. Thus, the high quality of the collected data allowed to improve the validation of the models.

The field work lasted from April to August. Screes, rock slides, edges of forests and bushes were sites with the highest probabilities to find individuals. We used the smartphone application Webfauna of the Swiss Center of Fauna Cartography (CSCF) to measure the coordinates with a precision between 1 to 10 meters. Then, we recorded them and sent them to CSCF via the application. At the end of the field work, the KARCH, which is merged with CSCF, sent us our observations back in addition to the observations in study area of this year.

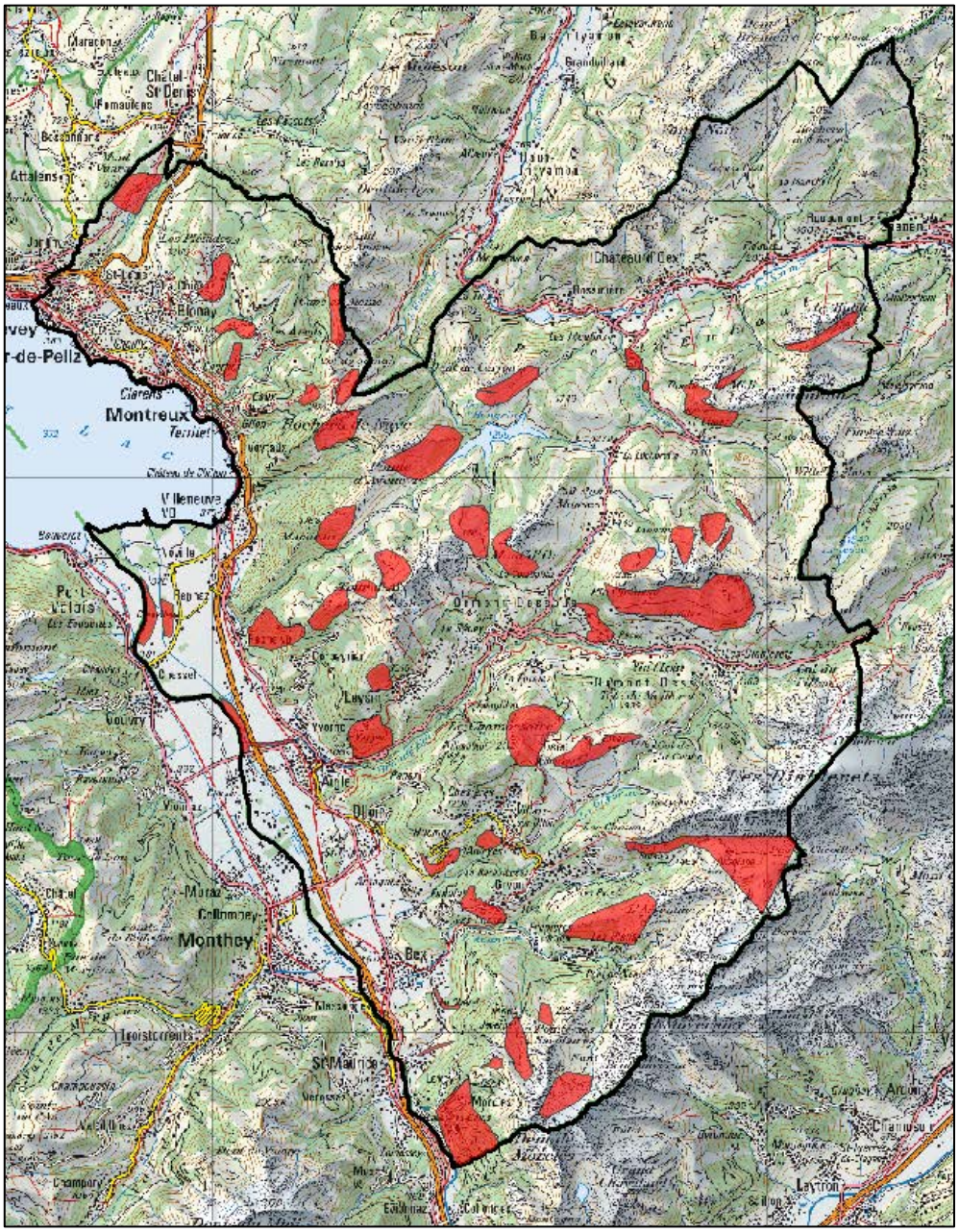

Figure 1: Study area and prospected zones. The study area is located in the Western Swiss Alps and is limited to the inside of the black line. The red polygons are the prospected areas provided by the expert assessment of KARCH.

Environmental predictors

We included four climatic and three topographic predictors in our models. The climatic predictors had a resolution of 25m and represented four years: 2010 (current), 2035, 2060 and 2085. In this study, the climatic scenario is the A1B, which predicts a balanced

use of fossil and non-fossil fuels. We chose this scenario because its predictions most closely match the evolution of current climate.

The climatic predictors are the average monthly temperature and precipitation, the sum of growing degree-days (GDD) with a base temperature of 3°C and the average daily potential evapotranspiration (ETP) calculated with the Turc method (1961), which is optimized to temperate climates. We calculated their mean from March to October (*tave_mar-oct*, *prec_mar-oct*, *gdd_mar-oct* and *etp_mar-oct*). This time period matches the average active period of reptile species. The topographic variables are the slope (*slope*), the exposition (*expo*) and the topographic position (*topo,* defines if a site is a hilltop, a flat plain or a valley bottom). All predictors for the current period come from the Federal Institute for Forest, Snow and Landscape Research (WSL, Zimmermann & Kienast, 1999), except GDD and ETP, which we calculated. The 2035, 2060 and 2085 temperature and precipitation variables were previously calculated by Pradervand *et al.* (2014).

We chose temperature and GDD variables to respond to the physiologic need of ectothermic species (Hofer *et al*., 2001; Zani & Rollyson, 2011). Precipitation and ETP variables are related to their environment. A habitat with lower precipitations and a higher ETP will be more suitable for some species (McKenney *et al.*, 1998; Rodríguez *et al*., 2005). The topographic predictors were used to improve the characterization of their habitat. Reptiles choose a strategic exposition to better warm up (Hofer *et al*., 2001). A certain slope and topographic position reflect a more suitable landform of the habitat (Guisan & Hofer, 2003).

Modelling

We used R via the software *Rstudio* (https://www.rstudio.com) for all modelling analyses. We used the occurrences data with 100m resolution at the Swiss scale and we disaggregated them by including a minimal distance of 250m to avoid spatial autocorrelation. Then, we used the R package "biomod2" (Thuiller *et al*., 2014), which allows running an ensemble of Species Distribution Models, for all the main modelling steps.

For the calibration of the models, we used predictors spatially aggregated at a resolution of 100m at the level of Switzerland to match the precision of the occurrence data. We did

this calibration at Swiss scale to include a larger part of the ecological niche of each species. To feed a presence-absence model, we sampled randomly five sets of 10'000 pseudo absences (PA). We split the data; 80% for calibration and 20% for evaluation. We used an ENSEMBLE modelling approach by calculating the average of four modelling techniques: Generalized linear model (GLM), which was set with linear and quadratic responses and an interaction level of one; Generalized additive models (GAM) with the algorithm mgcv *(Mixed GAM Computation Vehicle)*; Boosted regression trees (GBM) with a sequence of 1000 trees; and Random forest (RF). These models were run 5 times with each set of PA. In total, we thus performed 100 runs per species. The importance of each variable was calculated by comparing the original model with the variable untransformed to a second model with the variable randomized (by permutation). The evaluation of the models was done with the True Skill Statistics (TSS), Kappa, and the area under the curve (AUC) of a Receiver Operating Characteristics (ROC) plot. These evaluation metrics fit with the presence-absence models. Then, from the four modelling approaches, we performed an ENSEMBLE modelling. The ENSEMBLE modelling make an average of the four modelling approaches to generate more informative predictions (Araújo & New, 2007; Thuiller *et al*., 2009). The models evaluation methods were also done with KAPPA, TSS and AUC.

We projected the ENSEMBLE models in the study area with predictors at a 25m resolution. The spatial projections were done for the current period and for 2035, 2060 and 2085. Binary projections were obtained from the probabilistic projections by applying a threshold yielding the best TSS. Then, we used the 2010 and 2035 habitat suitability maps to produce habitat suitability maps from 2011 to 2034 by taking values of both maps and weighted them according to which year (e.g. map_2011 = 0.96*map_2010 + 0.04*map_2035). This method was repeated to produce maps from 2036 to 2059 and from 2061 to 2084. We use these maps in the MigClim simulations. All these steps were repeated for each species. The whole procedure is shown in Fig. 2.

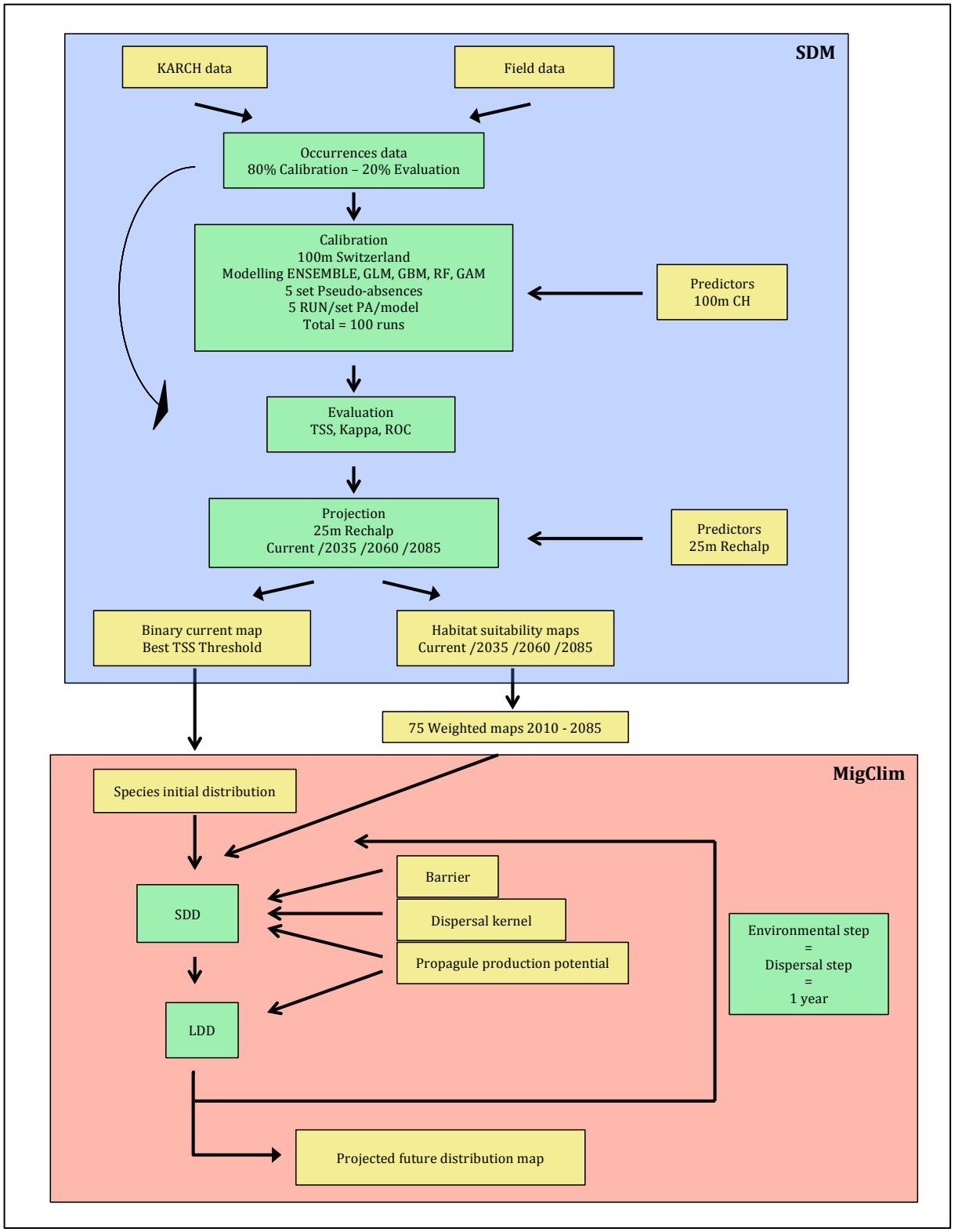

Figure 2: The whole procedure. The large blue square contains the species distribution modelling steps and the red one contains the MigClim steps. The green squares refer to the process steps and the yellow squares to needed or produced elements at each of these steps (e.g. data and maps).

Migclim simulations

We used the R package "MigClim" to simulate dispersal from species distribution models. This package allowed us to perform simulations of the dispersal of species under environmental changes with different dispersal scenarios and physical barriers. As a result, we could predict the change of species distribution and their limitation to colonize new areas. The explanations of the Migclim process are based on the user guide of the package (Engler *et al.*, 2013). To initiate the simulation, we used the current binary projection performed with "biomod2". The simulation starts in 2010 and lasts until 2085. Each year, a new habitat suitability map is imported in the simulation and a dispersal step is generated. We set a continuous threshold to define the invasion probability (P_{inv}) of a cell by taking its value on the habitat suitability maps. We had to define different parameters specific to the species, which were used to generate the dispersal steps. The dispersal kernel (Fig. 3) is the dispersal probability as a function of distance (P_{disp}). The propagule production potential is defined by the maturity age and propagation probability as a function of time (P_{prop}). P_{inv}, P_{disp} and P_{prop} defined the short-distance dispersal. Then, we set LDD frequencies and LDD distances, which were generated as a function of P_{prop}. In order to respect the ecology of species at best, these values were given for each species by the expert assessment of KARCH. The report of evaluation of dispersal and dispersal potential of western Switzerland reptiles is present in the supplementary material 1.

We created physical barrier layers, which were used in every simulation. The layers are available in the supplementary material 2. These binary layers could take into account: lakes, streams, highways, main and secondary roads, slope superior to 60°, dense forests (calculated from the minimum canopy height). We removed the intersection between streams and roads, which reflects the presence of ways to cross streams which can be used by reptiles. These layers were adapted to the different species; e.g. a stream did not limit an aquatic species or a slope did not limit a species, which can climb a steep surface (Table 1).

For each species, we performed 30 simulations of 3 dispersal scenarios: Short-distance dispersal, Long-distance dispersal and both of them. In each simulation, the output included, for each dispersal step, the occupied area with a universal dispersal scenario (i.e. all suitable areas are colonized), the occupied area with no dispersal, the occupied,

absent, colonized and decolonized areas with the kernel dispersal and the physical barriers. The number of LDD success was recorded too. The whole procedure is shown in Fig 2.

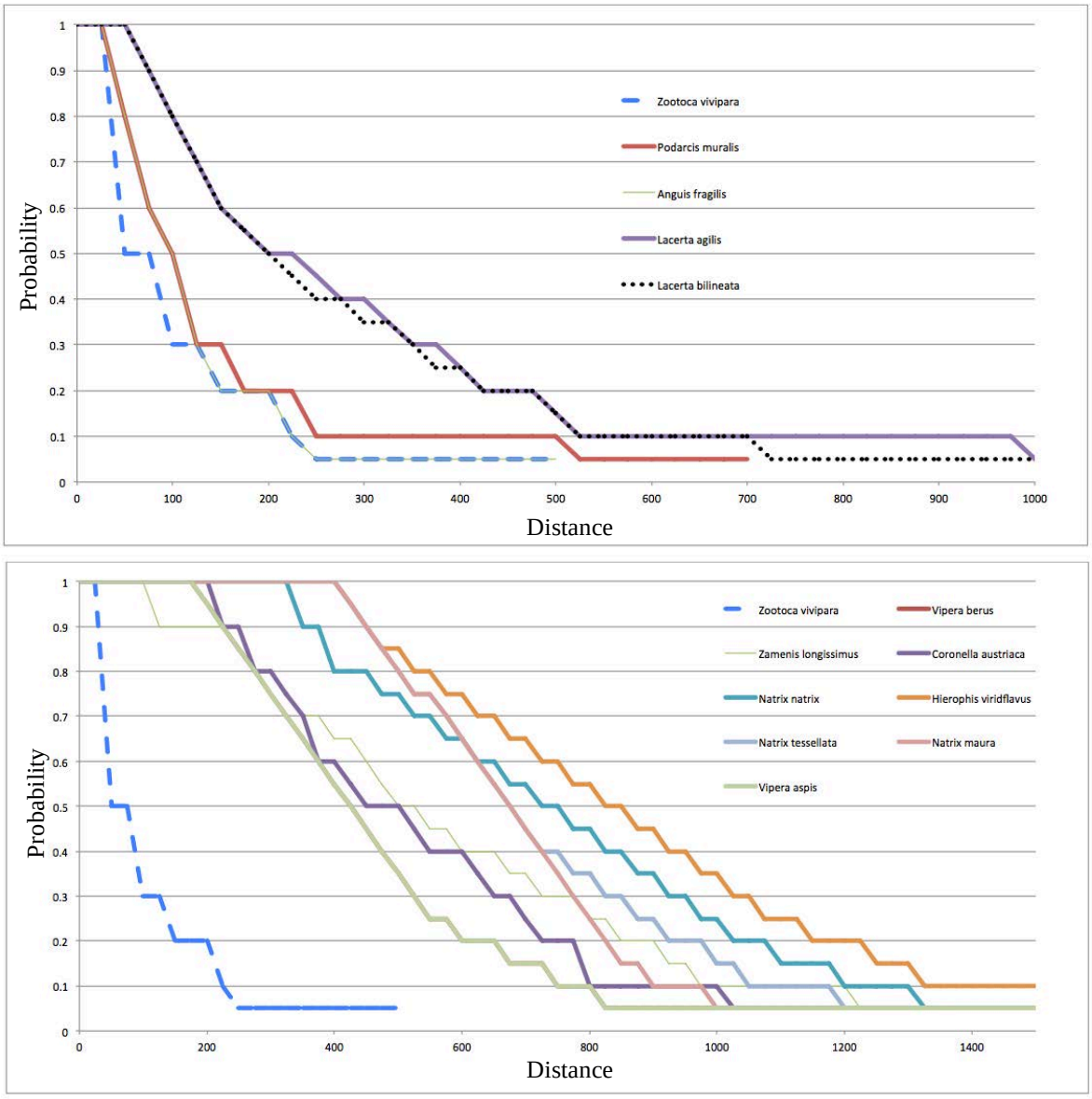

Figure 3: The dispersal kernel used in the simulations. It displays the probability to disperse as a function of distance. The upper graph refers to lizards species and the lower one to snakes species. These dispersal kernels come from the report of expert assessment of KARCH. *Z. vivipara* is present on both graphs, as a reference species.

Species	Highways	Main roads	Secondary roads	Streams	Lakes	Denses forests	Slope>60°
A. fragilis	x	x	x	x	x	x	x
C. austriaca	x	x	x	x	x	x	-
H. viridiflavus	x	x	-	x	x	x	x
L. agilis	x	x	x	x	x	x	x
L. bilineata	x	x	-	x	x	x	x
N. natrix	x	x	-	-	x	x	x
N. tessellata	x	x	x	-	x	x	x
P. muralis	x	x	-	x	x	x	-
V. aspic	x	x	x	x	x	x	x
V. berus	x	x	x	x	x	x	x
Z. Longissimus	x	x	-	x	x	x	x
Z. vivipara	x	x	x	x	x	x	x

Table 1: Specific physical barriers. Each species has specific physical barriers. A cross means that the element is a barrier for the species and a dash that is not.

Results

Importance of the predictor variables

The importance of each predictor variable was calculated for each modelling approach and averaged (Table 2). Values can vary between 0 (the focal variable does not change the predictions of the model) and 1 (the focal variable completely changes the predictions of the model). Globally, the climatic predictors prove more important than the topographic ones. Temperature and growing degree-days have the highest importance. Temperature has the highest values of importance for *V. berus* (0.683) and *Z. longissimus* (0.563). Growing degree-days has a higher importance on *N. tessellata* (0.715) and *H. viridiflavus* (0.615). Potential evapotranspiration follows in importance with the highest values for *C. austriaca* (0.53) and *V. aspis* (0.464).

Among the topographic predictors, slope is important for *V. aspis* (0.276) and *Z. longissimus* (0.224) and topographic position has a higher importance on *C. austriaca* (0.344) and *V. aspis* (0.3).

Species	temp mar_oct	prec mar_oct	gdd mar_oct	etp mar_oct	slope	topo	expo
A. fragilis	0.411	0.025	0.388	0.395	0.088	0.125	0.041
C. austriaca	0.386	0.055	0.324	0.53	0.142	0.344	0.03
H. viridiflavus	0.463	0.205	0.615	0.23	0.075	0.05	0.021
L. agilis	0.336	0.038	0.556	0.189	0.079	0.092	0.056
L. bilineata	0.505	0.174	0.443	0.2	0.179	0.112	0.022
N. natrix	0.480	0.036	0.474	0.043	0.042	0.098	0.015
N. tessellata	0.485	0.245	0.715	0.153	0.064	0.169	0.0177
P. muralis	0.254	0.04	0.568	0.375	0.105	0.123	0.021
V. aspis	0.385	0.037	0.515	0.464	0.276	0.3	0.049
V. berus	0.683	0.039	0.419	0.126	0.07	0.129	0.031
Z. longissimus	0.563	0.089	0.557	0.191	0.224	0.096	0.007
Z. vivipara	0.522	0.128	0.46	0.355	0.163	0.056	0.019

Table 2: Importance of environmental variables. Variables with their importance in the species distribution modelling for the twelve species.

Models TSS scores

To interpret the TSS scores, we used the same ranges than Zhang, L. *et al.* (2015): Poor models have scores lower than 0.4, useful are situated between 0.4-0.8 and good to excellent are higher than 0.8. For all species, TSS scores of ENSEMBLE models are all higher than their respective individual models (Table 3, Fig 4). Based on the ENSEMBLE evaluation, *N. tessellata* (TSS = 0.951), *H. viridiflavus* (TSS = 0.909), *Z. longissimus* (TSS = 0.878) and *L. bilineata* (TSS = 0.875) can be considered as good to excellent predictions. The other species are in the range 0.4-0.8 and their predictions are useful. No model has poor predictions (<0.4).

Species	GLM	GBM	RF	GAM	ENSEMBLE
A.fragilis	0.47	0.472	0.493	0.472	0.59
C. austriaca	0.547	0.554	0.588	0.555	0.664
H. viridiflavus	0.86	0.874	0.883	0.878	0.909
L. agilis	0.543	0.59	0.615	0.576	0.67
L. bilineata	0.772	0.828	0.83	0.818	0.875
N. natrix	0.559	0.581	0.593	0.561	0.647
N. tessellata	0.861	0.916	0.925	0.906	0.951
P. muralis	0.602	0.601	0.64	0.596	0.691
V. aspis	0.517	0.573	0.612	0.584	0.676
V. berus	0.666	0.659	0.675	0.662	0.742
Z. longissimus	0.793	0.829	0.848	0.838	0.878
Z vivipara	0.428	0.43	0.46	0.423	0.566

Table 3: Model evaluation by TSS scores. The table provides the TSS scores for each modelling approach - GLM, GBM, RF, GAM and ENSEMBLE - for each species.

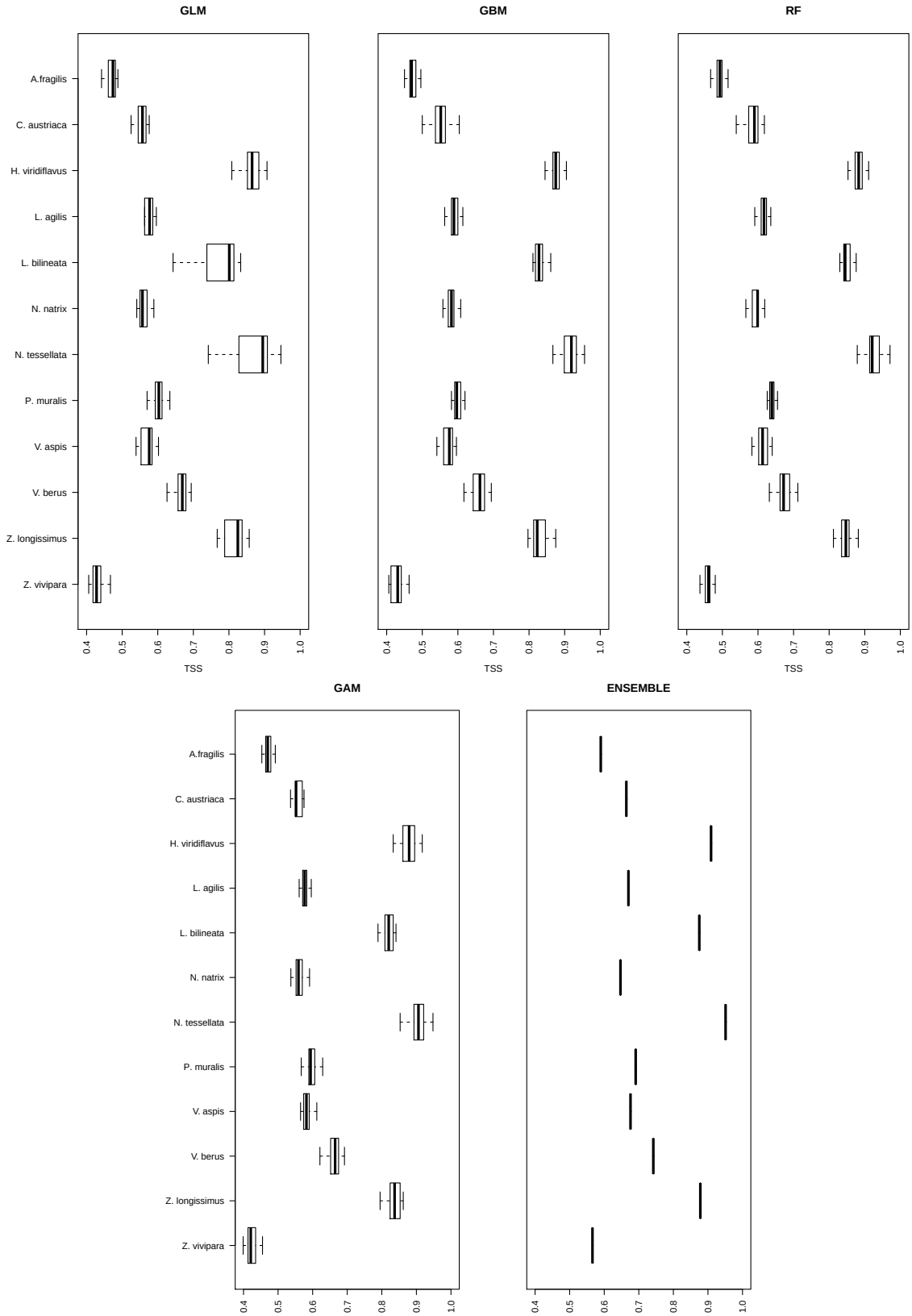

Figure 4: Model evaluation. The TSS score of each modelling approach are provided: GLM, GBM, RF, GAM and ENSEMBLE for each species.

MigClim

The results of the MigClim simulations are shown in Table 4 and in the supplementary material 3 and 4. One cell corresponds to one pixel of 25m resolution (thus 625 m^2). Here we mostly present the case of two species as illustrations: the expansion of a warm adapted and invasive species *H. viridiflavus* and the contraction of a cold adapted species *Z. vivipara*. Under a universal dispersal, the initial occupied area by *H. viridiflavus* in 2010 (105.64 km^2) strongly increases by 2085 (+346.5%). On the contrary, *Z.vivipara* has the highest occupied area both in 2010 (437.58 km^2) and in 2035 (367.64 km^2), but strongly decreases by 2085 (-54.34%). The species with the highest decrease is *V. berus*, which is cold adapted (-91.42%). Under no dispersal, the occupied area of *H. viridiflavus* doesn't change until 2085, whereas the one of *Z. vivipara* strongly decreases until 2085 (-60.98%), translating a decrease in habitats suitable for the species. Note the special case of *L. agilis* which initial suitable area has totally disappeared in 2085 (0 km^2).

The impact of barriers and dispersal kernel is shown by the difference of occupied area between a universal dispersal and a SDD&LDD simulation. Under universal dispersal, occupied area is always higher and, globally, the difference is not very large. For 5 warm adapted species including *H. viridiflavus*, this difference increases until 2060 (*H. viridiflavus*: +1.89%) and then, decreases until 2085 (*H. viridiflavus*: +0.23%). Note the highest impact of barriers on the warm adapted species *N.tessellata* (2060: +17.76%, 2085: +0.84%) For *L. bilineata* and *N. natrix*, the difference is only decreasing until 2085. For *C. austriaca*, *P. muralis*, *V. aspis*, *V. berus*, and *Z. vivipara,* the difference is very weak and can be omitted.

The colonized area strongly reflects the dispersal capacity of species to expand. This value varies between the three scenarios of dispersal; SDD&LDD, SDD and LDD (Table 4). Globally, the difference SDD&LDD/SDD is weak in comparison to the one between SDD&LDD/LDD, and SDD/LDD. In the case of the warm adapted species *H. viridiflavus* (Fig. 5), the difference of colonized area increases as a function of time between SDD&LDD/SDD (2035: +0.32%, 2060: +11.54%, 2085: +13.66%) and between SDD&LDD/LDD (2035: +99254.97%, 2060: + 64'058.15%, 2085: +43'017.94%). For the cold adapted species *Z. vivipara* (Fig. 6), the difference between SDD&LDD/SDD is weak and the one between SDD&LDD/LDD increases slightly (2035: +118'457.2%, 2060: +58'179.3%, 2085: +46'215.81%).

The decolonized areas reflect the loss of suitable habitat following climate change (Table 4). Most warm adapted species, such as *H. viridiflavus*, do not lose a large area. The only species, which does not lose area with the three dispersal scenarios, is the warm adapted species *P. muralis* (Fig. S1). In contrast, cold adapted species are very affected; *Z. vivipara* is the species losing the largest area in the three dispersal scenarios. Its highest loss is in 2085 with SDD&LDD dispersal (-268.81 km^2).

The number of successful LDD is higher in LDD simulations. The species, which have the highest number of LDD success in LDD simulations by 2085, are *P. muralis* (2050.8 LDD success) and *H. viridiflavus* (1258.1 LDD success). These numbers are lower in SDD&LDD simulations (resp. 15.9 and 56.5 LDD success). The cold adapted species *V. berus* has the least LDD success in 2085 in LDD (0.3 LDD success) and in SDD&LDD simulations (0.1 LDD success).

Hierophis viridiflavus								
Initial Distribution = 105.64		**No dispersal**	**Univ. dispersal**	**Occupied**	**Absent**	**totColonized**	**totDecolonized**	**totLDDsuccess**
SDD + LDD	**2035**	105.64	221.2	211.82	492.41	106.19	0	5.9
	2060	105.64	369.79	362.91	341.32	257.27	0	40.3
	2085	105.64	471.67	470.58	233.65	367.15	2.21	56.5
SDD	**2035**	105.64	221.2	211.49	492.74	105.85	0	-
	2060	105.64	369.79	336.3	367.93	230.66	0	-
	2085	105.64	471.67	426.65	277.58	323.01	2	-
LDD	**2035**	105.64	221.2	105.74	598.49	0.11	0	140
	2060	105.64	369.79	106.04	598.19	0.4	0	575.3
	2085	105.64	471.67	106.49	597.74	0.85	0	1258.1
Zootoca vivipara								
Initial Distribution = 437.58		**No dispersal**	**Univ. dispersal**	**Occupied**	**Absent**	**totColonized**	**totDecolonized**	**totLDDsuccess**
SDD + LDD	**2035**	349.57	367.64	367.58	336.65	18.01	88.01	0.1
	2060	226.05	247.05	247.01	457.21	22.87	213.44	0.1
	2085	170.72	199.76	199.71	504.52	30.94	268.81	0.2
SDD	**2035**	349.57	367.64	367.58	336.65	18.01	88.01	-
	2060	226.05	247.05	247.01	457.22	22.87	213.44	-
	2085	170.72	199.76	199.71	504.52	30.94	268.81	-
LDD	**2035**	349.57	367.64	349.59	354.64	0.02	88.01	6.7
	2060	226.05	247.05	226.08	478.15	0.04	211.54	21.4
	2085	170.72	199.76	170.78	533.44	0.07	266.86	38.5

Table 4: MigClim results of *H. viridiflavus* and *Z. vivipara*. Results of SDD&LDD, SDD and LDD simulations in 2035, 2060 and 2085. These results show the total occupied area under no dispersal, universal dispersal, SDD, LDD and SDD&LDD scenarios, the total area where the species is absent, the total colonized and decolonized areas and the number of LDD success. All the values are in km^2, except the number of LDD success, which has no unit.

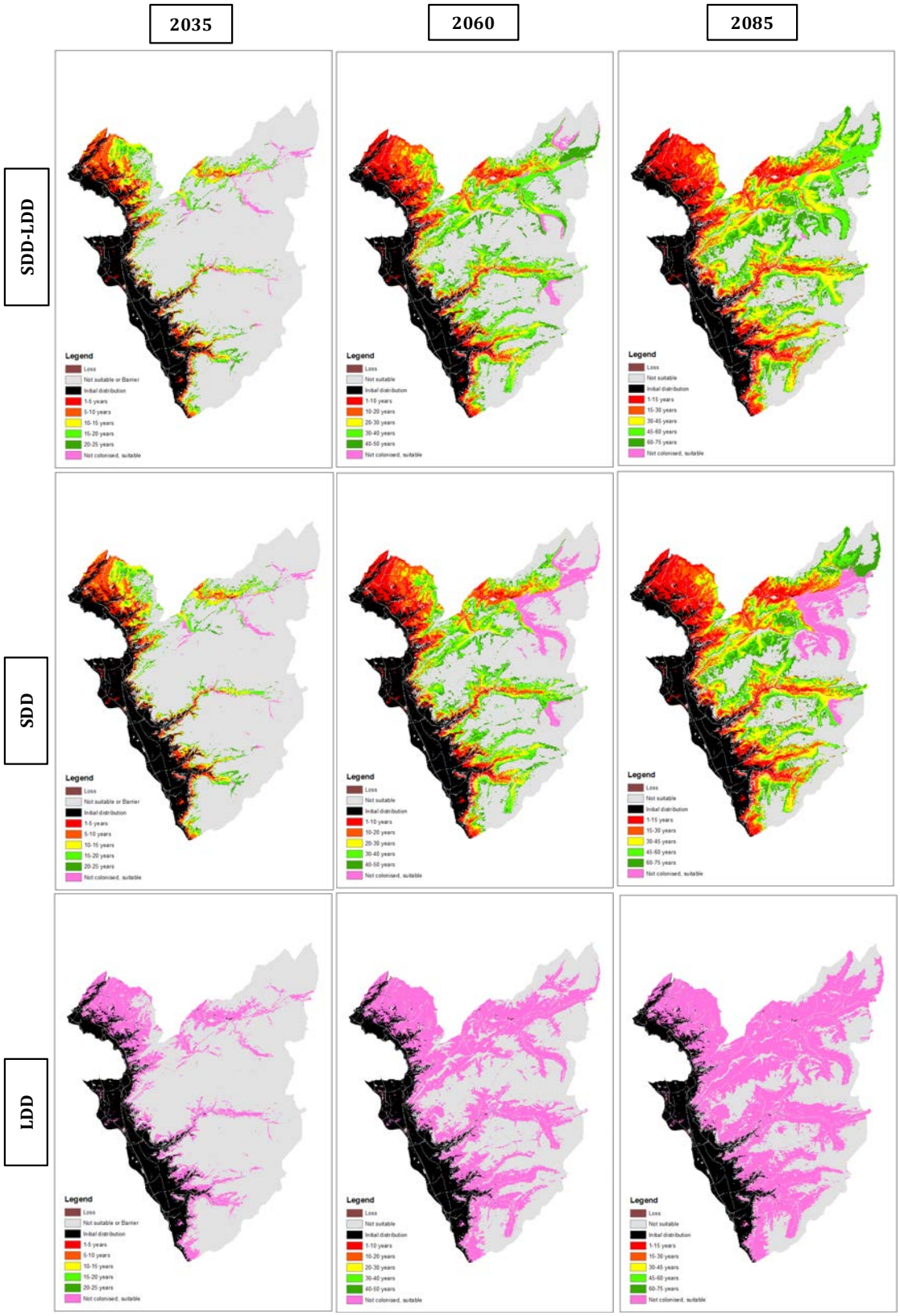

Figure 5: Migclim simulations of *H. viridiflavus*. The nine maps represent the three limited dispersal scenarios SDD&LDD, SDD and LDD in 2035, 2060 and 2085. Black refers to the initial distribution, brown to the decolonized areas, grey to the barriers or unsuitable areas, and pink to the not colonized and suitable areas. Colors red, orange, yellow, light and dark green refer to the period of colonization of areas (see legend in the figure).

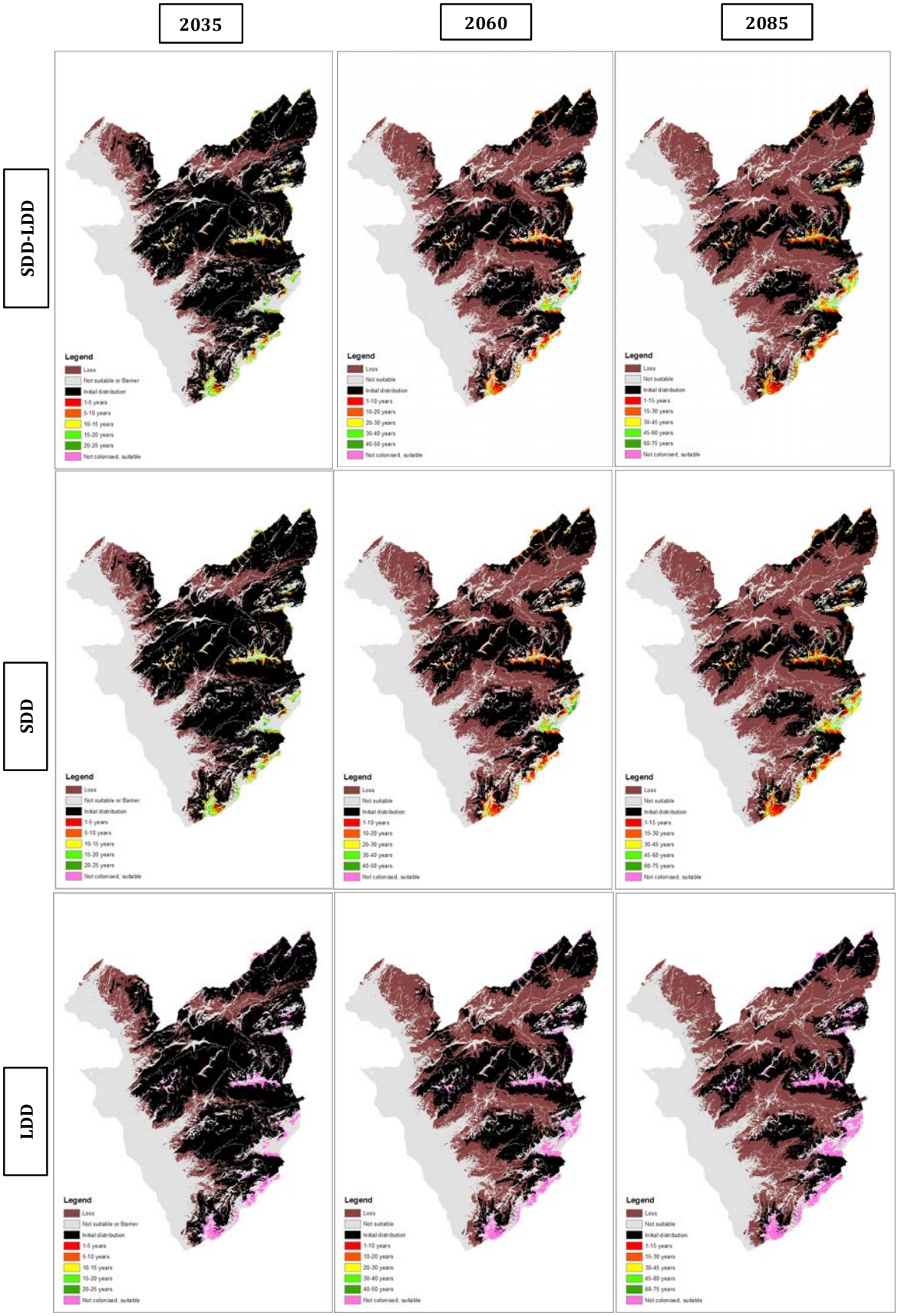

Figure 6: Migclim simulations of *Z. vivipara*. Description is the same as Figure 5.

Discussion

This study has shown overall that the simulated dispersal pattern of species follows the elevation gradient in both expansion and contraction shifts. The effect of physical barriers and dispersal kernel during these shifts are not strong. This can be linked to not sufficiently restrictive dispersal parameters in the MigClim simulations. The five dispersal scenarios have shown that the more restrictive the dispersal parameters, the more the species would colonize areas. LDD does not allow large colonisations, whereas SDD do. These results are discussed in more details in the following sections.

General patterns in migclim simulations

Patterns revealed by the simulation are contrasted depending on the species. The shift affecting both cold and warm adapted species can be explained by the elevation gradient, which global warming is following (Colwell *et al*., 2008). As already observed by Engler & Guisan (2009), the presence of a plateau at low altitude (Rhone valley) and rather flat areas at medium altitude (Chateaux d'Oex, Les Diablerets, Les Mosses) in the study area can lead to an abrupt change in habitat suitability predictions. This, in particular, directly affects the species dispersal. Potential area of both cold adapted species *Z. vivipara* and *V. berus* strongly decreased in the future, even in simulations with a universal dispersal scenario (Table 4, Fig. 6). In our simulations, global warming would force these species to move higher in elevation, where suitable climatic conditions are present (Stevens, 1992). Knowing the sites that have the potential to be colonized in the future allows setting up conservation plans to prevent the potential future extinction of these species. On the contrary, the potential area of warm adapted species as *H. viridiflavus* or *N. tessellata* strongly increases in the future under universal dispersal (Table 4, Fig. 5). Global warming is thus favouring these species in our simulations. The suitable climatic conditions spread over a larger area with time. This spread allows the warm adapted species to colonize new sites at higher elevation while keeping their initial distribution in the majority of cases. The colonization of new areas by invasive species, such as *H. viridiflavus* and *N. tessellata*, can be of important conservation relevance.

Effect of physical barriers and dispersal kernel

The comparison of the outcome of the universal dispersal and SDD&LDD scenarios in the simulation allows to better understand the effect of barriers and dispersal kernel during climate change. For all species, the occupied areas in SDD&LDD simulation in 2035, 2060 and 2085, is lower, respectively, than simulations with universal dispersal. The barriers and dispersal kernel slow down the colonization. The effect of barriers is more visible in the case of warm adapted species, as exemplified by the case of *H. viridiflavus* which shows that some potentially suitable sites remains uncolonized (Fig. 5). In SDD&LDD simulations, the suitable but not colonized areas decrease as function of time. These suitable but not colonized areas are visible in 2035 and 2060, but less evident in 2085. Until 2060, some suitable sites remain unoccupied, because of the presence of a barrier or because the species did not have enough time to expand to them. The majority of these sites are occupied in 2085: the species had time to expand, to find a gap in the barriers or to use LDD to cross it. In the case of cold adapted species, however, the difference is very low. Fig. 6 shows that in the case of *Z. vivipara*, the difference is not visible (only some areas are not colonized). We can explain this weak difference by the fact that cold adapted species have a smaller area to colonize. This area is generally located closer from their initial distribution than warm adapted species. The distance to travel is shorter, with less barrier obstructing the dispersal of the species. We can underline the case of species, such as *C. austriaca* (Fig. S2), which spread towards higher areas and are thus in many places already present on both sides of the barriers. Globally, however, the effect of barriers and dispersal kernel is quite weak. This reduced effect was already observed by Engler *et al*. (2009) in the case of LDD. To increase this effect, we could include other pertinent elements of barriers, which can impact dispersal, such as intensive farming zones. Another possibility could be to modify the dispersal parameters. The dispersal parameters have been chosen by experts to respect the ecology of the different species. Experts may have described the maximum dispersal scenarios for each species. Taking average scenarios could decrease the dispersal capacity.

Five dispersal scenarios

The five dispersal scenarios (No dispersal, LDD, SDD, SDD&LDD and universal dispersal) give different results, although some of them are close. Under no dispersal, *H. viridiflavus*, *P. muralis* and *Z. longissimus* do not lose area until 2085. Both cold adapted species, *V. berus* and *Z. vivipara* are very affected. We note that the initial distribution of the transitional-species *L. agilis* totally disappears (Fig. S3). This species has a large shift in its distribution. It is cold-limited in higher elevation and suffers of competition with *L. bilineata* in lower elevation (Mole, 2010). These two factors shape the current distribution and explain such a change, through the increase of suitable area for *L. bilineata* (Fig. S4). In LDD simulations, the occupied area is not much higher than in the no dispersal simulation. The colonized area depends on two elements: the LDD frequency and the unoccupied and suitable area in the range of the LDD distance. The fact that the number of LDD success is higher in LDD than in SDD&LDD simulations is due to the higher unoccupied and suitable areas, which are not colonized by SDD. *H. viridiflavus* has a higher LDD frequency and more unoccupied and suitable area than *V. berus* (Fig. 5 and Fig. S5); the colonized area by LDD is much higher. However, one LDD success means only one colonized pixel of 25m resolution. In SDD simulations, although the barriers cannot be crossed, colonized areas per dispersal step are much higher. SDD simulations do not generate LDD to cross the barriers, which forces the species to bypass the barriers and find a gap to reach the other side. In the case of invasive species, such as *H. viridiflavus* and *N. tessellata* (Fig. S6), it avoids the colonization of several areas. In SDD&LDD simulations, both SDD and LDD are combined. We can observe that with a higher colonized area (Table 4). At the beginning of the simulation, SDD can start on one side of a barrier, then one LDD is generated to the other side. The colonized area by LDD can start to generate SDD when the initial maturity of the species will be reached. The difference of colonized areas is much lower between SDD&LDD and SDD simulations, than between SDD and LDD ones. We can note that the decolonized area is often higher in SDD&LDD than in SDD. SDD allows colonizing less area and, with time and as climatic conditions change, the area, which can potentially become unsuitable, gets smaller.

SDM accuracy

Globally, models were fairly accurate, with similarly high TSS scores for the four individual modelling techniques and for each species (Table 3, Fig. 4). One can note that RF models have significantly better scores than GLM, GBM and GAM, what had already been observed by Marmion *et al.* (2009). The TSS scores of the ENSEMBLE models are also higher than the individual models for all species, which confirms the power of the ensembling approach (Grenouillet *et al*. 2011; but see Crimmins *et al*. 2013). Species with best scores are *N. tessellata* and *H. viridiflavus*, followed by *Z. longissimus*, *L. bilineata* and *V. berus*. Species with narrow ecological niches have the best scores, whereas scores for opportunist (*A. fragilis*, *N. natrix*, *Z.vivipara*) species are worse, results also observed by Guisan & Hofer (2003) and Evangelista *et al*. (2008). Temperature and GDD have the highest variable importance in the models, followed by the potential evapotranspiration. This is not surprising considering that reptiles' physiology is regulated by external temperature (Hofer *et al*., 2001; Zanni & Rollyson, 2011). Additionally, ETP has an impact on the habitat and has already been described as important to explain reptiles' distribution (Rodríguez *et al*., 2005). Globally, climatic predictors have a higher importance than topographic ones, as already reported at the Swiss scale in the study of Guisan & Hofer (2003). It is also to be noted that exposure has the lowest importance, contrarily to expectations. This variable seems not to reflect the importance for reptiles of sunbathing to warm up their body and accelerate their metabolism. This could be due to a too large scale. Including solar radiations as a predictor in the models should increase the accuracy of the predictions. Here, topo-climatic models were exclusively performed, but including land-cover predictors would be important, especially for cold adapted species living in humid habitats at low elevations. Land-cover predictors, such as swamps, could allow better capturing the importance of these habitats for reptiles.

Conclusion

The scenarios shown in this study inform on potential future shifts in the distribution of reptile species, and are thus useful conservative tool in a prospective perspective. They allow indicating the future accessible refuge sites for threaten species and the ones that can be colonized by invasive species. The barrier layers and dispersal kernel had not a

very strong effect in the simulations. However, a difference in colonized areas was nevertheless visible for several species between SDD&LDD and universal dispersal simulations. This difference decreases as a function of time, because of dispersal parameters, which are not enough restrictive. Indeed, parameters such as dispersal kernel and LDD frequency values give a high dispersal capacity in MigClim simulations. Through the five scenarios of dispersal, we observed that restrictive or permissive parameters lead to different dispersal outputs, although some results in similar predictions. Perspectives for this type of study could be to apply these simulation methods to different taxa, at different scales, with more than one climate change scenarios, and adding landuse change scenarios.

Acknowledgment/Contribution

I would like to thanks Dr. Sylvain Ursenbacher and the KARCH for providing me the reptiles data, the dispersal distance data and the expert assessment on reptile ecology, Dr. Olivier Broenimann and Prof. Antoine Guisan for supervising the study, and advising on the written thesis, and the faculty of geosciences and the environment for financial support for the field sampling. This study was also part of and supported by the SNF project SESAM'ALP (grant 31003A-1528661).

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Supplementary material

Supplementary material 1: Expert assessment of KARCH: Report of evaluation of dispersal and dispersal potential of western Switzerland reptiles.

Supplementary material 2: Barrier layers. Six different barrier layers including specific elements adapted to species. These layers may include highway, main and secondary roads, lakes, streams, dense forests and slope superior to 60°. Barrier layer a) was used with *A. fragilis*, *L. agilis*, *V. aspis*, *V. berus* and *Z. vivipara*, b) with *H. viridiflavus*, *L. bilineata* and *Z. longissimus*, c) with *C. austriaca*, d) with *N. natrix*, e) with *N. tessellata* and f) with *P. muralis*. The detail of barriers components is shown in the table. A cross means that the element is a barrier for the species and a dash that is not.

Supplementary material 3: MigClim results. For each species, results of SDD&LDD, SDD and LDD simulations in 2035, 2060 and 2085. These results show the total occupied area under no dispersal, universal dispersal, SDD, LDD and SDD&LDD scenarios, the total area where the species is absent, the total colonized and decolonized areas and the number of LDD success. All the values are in km^2, except the number of LDD success, which has no unit.

Supplementary material 4: Migclim simulations. Nine maps representing the 3 limited dispersal scenarios SDD&LDD, SDD and LDD in 2035, 2060 and 2085. Black refers to the initial distribution, brown to the decolonized areas, grey to the barriers or not suitable areas, pink to the not colonized and suitable areas. Colors red, orange, yellow, light and dark green refers to the period of colonization of areas (see legend in the figures).
Figures 1 to 10 refers to reptiles species.

Supplementary material 1: Expert assessment of KARCH

Rapport: évaluation de la dispersion et des potentialités de dispersion des reptiles romands

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Introduction

Dans le cadre du travail de Master de Marc Pittet sur la répartition potentielle future des différentes espèces de reptiles sous l'influence du réchauffement climatique, il nous a été demandé de pouvoir fournir des approximations sur la distance et la probabilité de dispersion, ainsi que la potentialité de dispersion à longue distance pour les différentes espèces de reptiles présentes dans les Préalpes vaudoises (zone RECHALP). Or il n'existe, à notre connaissance, aucune donnée précise sur le déplacement régulier ou ponctuel des différentes espèces de reptiles présents en Europe. Dans la littérature, des informations de sources très diverses existent, souvent provenant d'observations isolées issues de suivis par capture-recapture, de suivis par télémétrie ou d'indices d'isolement génétique. Toutes ses données sont ponctuelles, et ne reflètent pas nécessairement les distances et les proportions réellement parcourues par les reptiles, aussi bien dans le cadre de leur déplacement régulier que dans le cadre de colonisation volontaire de nouveau territoire. Nous avons donc cherché à évaluer, grâce à des données de la littérature et de nos connaissances sur la biologie et l'écologie des espèces, la potentialité de dispersion des reptiles suisses.

Buts

Le but principal a donc été d'évaluer les distances et la probabilité de dispersion des différentes espèces de reptiles présents dans le canton de Vaud afin de pouvoir alimenter un modèle MigClim sur la colonisation de nouveaux sites en fonction des distances potentiellement parcourues pour chaque espèce, en fonction des connaissances actuelles de l'espèce.

Méthodes

L'évaluation de la distance de dispersion a été basée sur la littérature scientifique faisant mention de distances parcourues ou évaluées par télémétrie (voir tableau 1). Les fréquences de dispersion n'étant pas connues pour ces espèces, nous avons considéré la distance régulièrement parcourue par un individu au sein de son territoire habituel comme étant une dispersion à 100% sur cette distance. La fréquence entre cette distance et les distances maximales connues a été considérée comme suivant une courbe de type expoentiennelle. Seules les distances maximales semblant correspondre à des distances réalistes (hors distances parcourues par exemple suite à des déplacements volontaires ou involontaires) ont été considérées. Finalement, les connaissances de la biologie et de l'écologie des espèces ont aussi été prises en compte. Pour chaque espèce, la probabilité de disperser à une distance donnée est calculée comme le pourcentage qu'une espèce puisse atteindre cette distance à partir d'une population établie (selon la modélisation intégrée dans MigClim).

Concernant l'aspect déplacement à longue distance (propagules), les distances minimales ont été fixées sur la distance maximale de dispersion normale, alors que la distance maximale a été évaluée en fonction des connaissances de l'espèce basées souvent sur des observations ponctuelles en Suisse ou à l'étranger lors de très rares événements de colonisation.

Finalement, le modèle MigClim nécessite une évaluation de l'âge de la maturité des différentes espèces. Ces valeurs ont été reprises de la littérature citée dans le tableau 1 et dans la littérature mentionnée au sein de ces références.

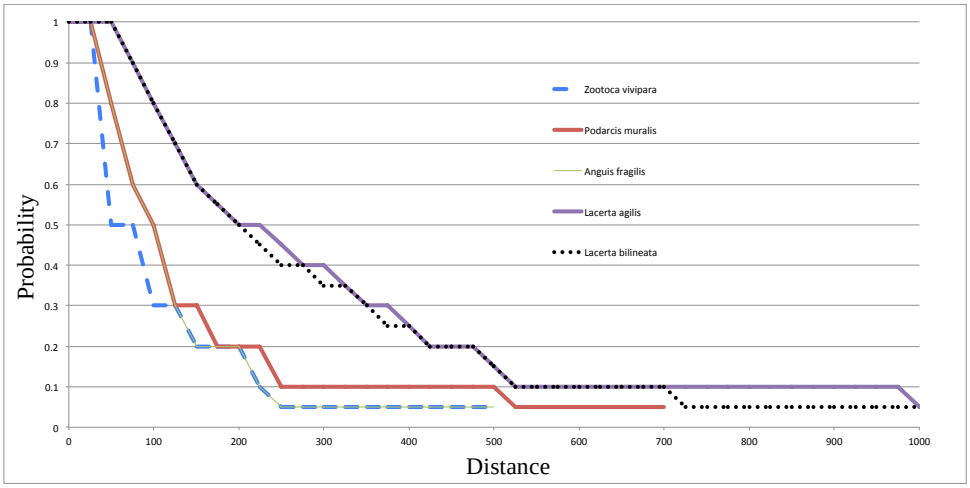
Résultats

Les courbes de dispersion sont disponibles dans la figure 1; elles correspondent aux valeurs indiquées dans l'annexe 1. Globalement, les distances de dispersion sont plus élevées pour les serpents que pour les lézards, à part pour l'orvet et le lézard vert. L'espèce de lézard le moins mobile est le lézard vivipare, alors que le serpent le moins mobile est, dans la zone concernée, la vipère péliade. Au contraire, la couleuvre verte et jaune est considérée comme l'espèce la plus mobile.

La distance maximale pour les déplacements à longue distance a été évaluée à 5000 m pour les lézards à l'exception du lézard des murailles (10000 m), espèce plus dynamique pour coloniser des sites très éloignés. La distance maximale de 5000 m a aussi été considérée pour les vipères et la coronelle lisse (Tableau 2). Les grandes couleuvres (*Hierophis viridiflavus* et *Zamenis longissimus*), ainsi que les couleuvres aquatiques (*Natrix sp*.) ont été évaluées comme ayant un plus grand potentiel de dispersion à longue distance (10000 m). Concernant les fréquences des événements de colonisation à longue distance, ce taux a été fixé entre 1 10^{-3} pour la couleuvre verte et jaune à une valeur de 5 10^{-5} pour la vipère péliade.

Finalement l'âge de la maturité à été évalué de 1.5 an pour le lézard des murailles à 4.5 ans pour les deux espèces de vipères et la couleuvre d'Esculape (Tableau 2).

Figure 1: courbes de dispersion supputées pour les différentes espèces de reptiles présents dans la zone des Préalpes vaudoises. Le graphique supérieur regroupe les lézards, le graphique inférieur les serpents. Le lézard vivipare est présent sur les deux graphes comme espèce de référence.



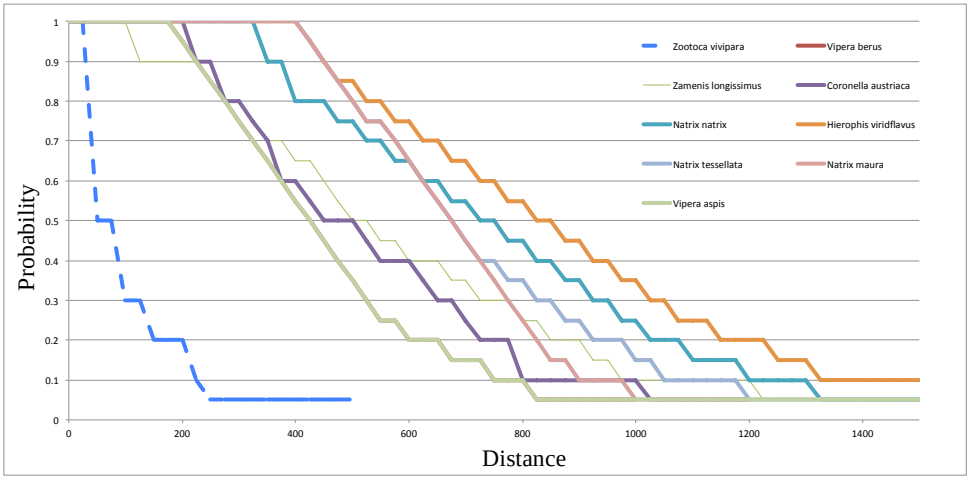


Tableau 1: liste des références utilisées pour les distances de dispersion pour chaque espèce

espèce	référence bibliographique utiliée
Lacerta bilineata	Kerstin Elbing (2010) Die Smaragdeidechsen Beiheft der Zeitschrift für Feldherpetologie 3, Laurenti Verlag
Lacerta agilis	Ina Blanke (2010) Die Zauneidechse, Beiheft der Zeitschrift für Feldherpetologie 7, Laurenti Verlag
Podarcis muralis	Ulrich Schulte (2008) Die Mauereidechse, Beiheft der Zeitschrift für Feldherpetologie 12, laurenti Verlag
Zootoca vivipara	Sylvia Hofmann (2005) Populationsbiologische Untersuchungen an der Waldeidechse, *Zootoca vivipara* (JACQUIN, 1787) in Sachsen-Anhalt und West-Sachsen, Dissertation, Mathematisch-Naturwissenschaftlich-Technischen Fakultät, Martin-Luther-Universität Halle-Wittenberg
Anguis fragilis	Wolfgang Völkl & Dirk Alfermann (2007) Die Blindschleiche, Beiheft der Zeitschrift für Feldherpetologie 11
Hierophis viridflavus	Lorenzo Rugiero, Massimo Capula, Leonardo Vignoli & Luca Luiselli (2013) Interpreting dispersal patterns of reproductive female *Hierophis viridiflavus* (Lacépède, 1789), around a communal nesting site, Herpetozoa 25 (3/4): 143-150
Zamenis longissimus	Axel Gomille (2002) Die Äskulapnatter *Elaphe longissima* - Verbreitugn und Lebenswise in Mittleeuropa, Edition Chimaira
Coronella austriaca	Wolfgang Völkl & Daniel Käsewieter (2003) die Schlingnatter, Beiheft der Zeitschrift für Feldherpetologie 6, Laurenti Verlag
Natrix natrix	Wolfgang Böhme (1999) Handbuch der Reptilien und Amphibiens Europas , Band 3/IIA: Schlangen (Serpentes), Aula Verlag
Natrix maura	Natacha Koller & Sylvain Ursenbacher (1996) Etude et estimation de l'effectif de Couleuvres vipérines (*Natrix maura*) et de Couleuvres tesselées (*N. tessellata*) dans le Lavaux, Travail de Diplôme, Université de Lausanne
Natrix tessellata	Konrad Mebert, Rafaqat Masroor & Muhammad Jamshed Iqbal Chaudhry (2013) The Dice Snake, *Natrix tessellata* (Serpentes: Colubridae) in Pakistan: Analysis of its Range Limited to Few Valleys in the Western Karakoram, Pakistan Journal of Zoology 45 (2): 395-410. Natacha Koller & Sylvain Ursenbacher (1996) Etude et estimation de l'effectif de Couleuvres vipérines (*Natrix maura*) et de Couleuvres tesselées (*N. tessellata*) dans le Lavaux, Travail de Diplôme, Université de Lausanne
Vipera aspis	Ulrich Hofer, Jean-Claude Monney (2001) Les reptiles de Suisse - répartition • Habitat • Protection, Birkhäuser Verlag
Vipera berus	Romain Sordello (2012) Synthèse bibliographique sur les déplacements et les besoins de continuités d'espèces animale - la vipère péliade, MNHN-SPN, Paris.

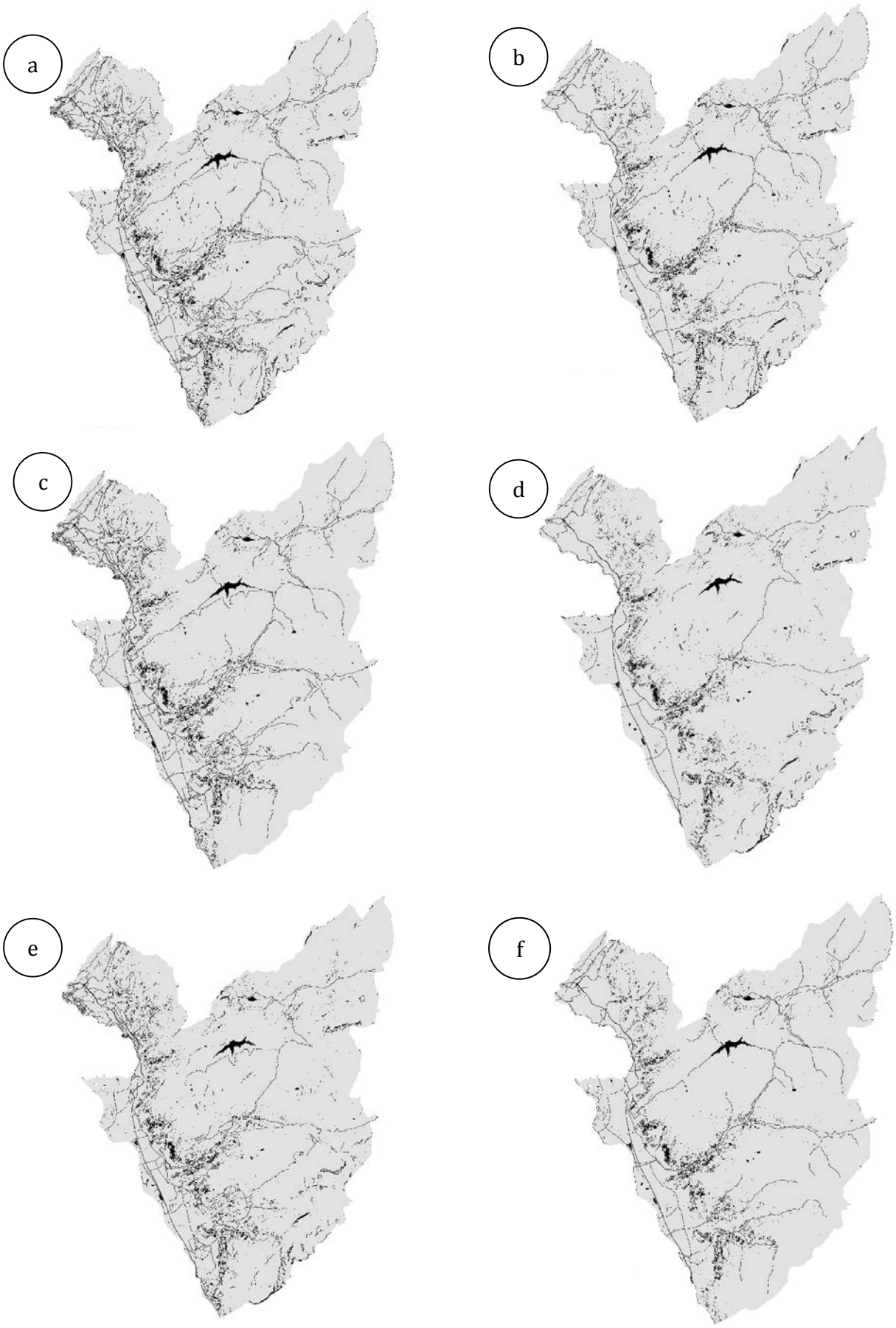
Tableau 2: distance maximale de dispersion des propagules, ainsi que leur fréquence et l'âge moyen évalué à partir de la littérature et des connaissances des différentes espèces.

espèce	distance maximale	fréquence de dispersion à longue	âge moyen de la maturité
Lacerta bilineata	5000	1.00E-04	2
Lacerta agilis	5000	1.00E-04	2
Podarcis muralis	10000	1.00E-03	1.5
Zootoca vivipara	5000	1.00E-04	2
Anguis fragilis	5000	1.00E-04	4
Hierophis viridflavus	10000	1.00E-03	4
Zamenis longissimus	10000	1.00E-04	4.5
Coronella austriaca	5000	1.00E-04	3.5
Natrix natrix	10000	1.00E-04	3.5
Natrix maura	10000	1.00E-04	3.5
Natrix tessellata	10000	1.00E-03	3.5
Vipera aspis	5000	1.00E-04	4.5
Vipera berus	5000	5.00E-05	4.5

Annexe 1: valeurs de dispersion supputées pour les différentes espèces de reptiles présents dans la zone des Préalpes vaudoises pour une échelle de 50 m.
Une représentation graphique est présente en figure 1.

Espèce	m	50	0	50	100	150	200	250	300	350	400	450	500	550	600	650	700	750	800	850	900	950	1000	1050	1100	1150	1200	1250	1300	1350	1400	1450	1500	1550	1600	1650	1700	1750	1800	1850	1900	1950	2000
Lacerta bilineata	1	1	1	0.9	0.8	0.7	0.6	0.55	0.5	0.45	0.4	0.4	0.35	0.35	0.3	0.25	0.25	0.2	0.2	0.2	0.15	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Lacerta agilis	1	1	1	0.9	0.8	0.7	0.6	0.55	0.5	0.45	0.4	0.4	0.35	0.3	0.25	0.2	0.2	0.2	0.15	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Podarcis muralis	1	1	1	0.9	0.8	0.7	0.6	0.55	0.5	0.45	0.4	0.4	0.35	0.3	0.25	0.2	0.2	0.2	0.15	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
Zootoca vivipara	1	1	0.5	0.5	0.3	0.3	0.2	0.2	0.2	0.1	0.1	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05
Anguis fragilis	1	1	0.8	0.6	0.5	0.3	0.2	0.2	0.1	0.1	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05
Hemorrhois viridiflavus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Coronella austriaca	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Zamenis longissimus	1	1	1	1	1	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9	0.9
Dolichophis caspius	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Natrix natrix	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Natrix tessellata	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Vipera aspis	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Vipera berus	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Supplementary material 2: Barrier layers



Species	Highways	Main roads	Secondary roads	Streams	Lakes	Denses forests	Slope>60°
A. fragilis	x	x	x	x	x	x	x
C. austriaca	x	x	x	x	x	x	-
H. viridiflavus	x	x	-	x	x	x	x
L. agilis	x	x	x	x	x	x	x
L. bilineata	x	x	-	x	x	x	x
N. natrix	x	x	-	-	x	x	x
N. tessellata	x	x	x	-	x	x	x
P. muralis	x	x	-	x	x	x	-
V. aspic	x	x	x	x	x	x	x
V. berus	x	x	x	x	x	x	x
Z. longissimus	x	x	-	x	x	x	x
Z. vivipara	x	x	x	x	x	x	x

Supplementary material 3: MigClim results

Anguis fragilis								
Initial Distribution = 98.24		**No dispersal**	**Univ. dispersal**	**Occupied**	**Absent**	**totColonized**	**totDecolonized**	**totLDDsuccess**
SDD + LDD	**2035**	96.96	239.51	231.79	472.44	141.55	8.01	4
	2060	94.35	327.18	319.2	385.03	236.51	15.55	9.2
	2085	92.34	362.58	359.97	344.26	285.58	23.85	13.3
SDD	**2035**	96.96	239.51	231.47	472.76	141.16	7.92	-
	2060	94.35	327.18	317.73	386.5	234.95	15.46	-
	2085	92.34	362.58	357.4	346.83	282.73	23.57	-
LDD	**2035**	96.96	239.51	97.04	607.19	0.08	1.28	39.1
	2060	94.35	327.18	93.81	610.42	0.22	4.66	133.5
	2085	92.34	362.58	92.61	611.62	0.29	5.91	181.8
Coronella austriaca								
Initial Distribution = 277.26		**No dispersal**	**Univ. dispersal**	**Occupied**	**Absent**	**totColonized**	**totDecolonized**	**totLDDsuccess**
SDD + LDD	**2035**	268.71	351.54	351.42	352.81	82.71	8.55	0.2
	2060	253.49	385.56	385.4	318.83	135.2	27.06	0.2
	2085	248.94	373.64	373.52	330.71	150.29	54.03	0.7
SDD	**2035**	268.71	351.54	351.41	352.81	82.71	8.55	-
	2060	253.49	385.56	385.39	318.84	135.2	27.06	-
	2085	248.94	373.64	373.51	330.72	150.28	54.03	-
LDD	**2035**	268.71	351.54	268.77	435.46	0.07	8.55	27.5
	2060	253.49	385.56	253.68	450.55	0.19	23.77	107.5
	2085	248.94	373.64	249.25	454.98	0.33	28.34	198.7
Hierophis viridiflavus								
Initial Distribution = 105.64		**No dispersal**	**Univ. dispersal**	**Occupied**	**Absent**	**totColonized**	**totDecolonized**	**totLDDsuccess**
SDD + LDD	**2035**	105.64	221.2	211.82	492.41	106.19	0	5.9
	2060	105.64	369.79	362.91	341.32	257.27	0	40.3
	2085	105.64	471.67	470.58	233.65	367.15	2.21	56.5
SDD	**2035**	105.64	221.2	211.49	492.74	105.85	0	-
	2060	105.64	369.79	336.3	367.93	230.66	0	-
	2085	105.64	471.67	426.65	277.58	323.01	2	-
LDD	**2035**	105.64	221.2	105.74	598.49	0.11	0	140
	2060	105.64	369.79	106.04	598.19	0.4	0	575.3
	2085	105.64	471.67	106.49	597.74	0.85	0	1258.1
Lacerta agilis								
Initial Distribution = 31.84		**No dispersal**	**Univ. dispersal**	**Occupied**	**Absent**	**totColonized**	**totDecolonized**	**totLDDsuccess**
SDD + LDD	**2035**	7.04	73.72	57.51	646.72	55.85	30.18	0.9
	2060	0.03	112.25	88.97	615.26	125.25	68.12	6.4
	2085	0	127.4	124.19	580.04	191.44	99.09	12
SDD	**2035**	7.04	73.72	56.38	647.84	54.73	30.18	-
	2060	0.03	112.25	74.58	629.65	110.17	67.43	-
	2085	0	127.4	102.03	602.19	165.85	95.65	-
LDD	**2035**	7.036	73.72	7.05	697.18	0.01	24.8	2.3
	2060	0.033	112.25	0.03	704.2	0.02	31.82	3.4
	2085	0	127.4	0	704.23	0.02	31.86	3.4

Lacerta bilineata								
Initial Distribution = 64.41		**No dispersal**	**Univ. dispersal**	**Occupied**	**Absent**	**totColonized**	**totDecolonized**	**totLDDsuccess**
SDD + LDD	**2035**	64.28	238.28	223.2	481.03	158.93	0.14	3.3
	2060	64.27	377.91	370.81	333.41	307.15	0.75	11.8
	2085	64.27	399.93	398.14	306.09	350.55	16.82	16.3
SDD	**2035**	64.28	238.28	220.15	484.08	155.88	0.14	-
	2060	64.27	377.91	358.85	345.38	295.18	0.75	-
	2085	64.27	399.93	381.92	322.31	334.07	16.56	-
LDD	**2035**	64.28	238.28	64.32	639.91	0.05	0.14	26
	2060	64.27	377.91	64.42	639.81	0.14	0.14	100.5
	2085	64.27	399.93	64.52	639.7	0.25	0.14	200.8
Natrix natrix								
Initial Distribution = 97.59		**No dispersal**	**Univ. dispersal**	**Occupied**	**Absent**	**totColonized**	**totDecolonized**	**totLDDsuccess**
SDD + LDD	**2035**	96.6	197.54	185.82	518.41	90.41	2.18	1.3
	2060	84.37	293.42	282.8	421.43	208.56	23.34	5
	2085	37.84	304.95	303.74	400.48	284.39	78.23	7.5
SDD	**2035**	96.6	197.54	185.38	518.85	89.97	2.18	-
	2060	84.37	293.42	278.94	425.29	204.7	23.34	-
	2085	37.84	304.95	303.6	400.63	284.25	78.23	-
LDD	**2035**	96.6	197.54	96.65	607.58	0.05	0.99	20.3
	2060	84.37	293.42	84.45	619.78	0.1	13.24	62.8
	2085	37.84	304.95	37.93	666.3	0.15	59.81	103.7
Natrix tessellata								
Initial Distribution = 89.04		**No dispersal**	**Univ. dispersal**	**Occupied**	**Absent**	**totColonized**	**totDecolonized**	**totLDDsuccess**
SDD + LDD	**2035**	89.02	157.18	137.57	566.66	48.57	0.04	9.8
	2060	89.02	251.77	213.8	490.43	124.79	0.04	38.5
	2085	89.02	313.12	310.51	393.72	221.66	0.19	68.9
SDD	**2035**	89.02	157.18	136.35	567.88	47.35	0.04	-
	2060	89.02	251.77	183.34	520.89	94.33	0.04	-
	2085	89.02	313.12	218.25	485.98	129.38	0.17	-
LDD	**2035**	89.02	157.18	89.08	615.15	0.06	0.03	75.4
	2060	89.02	251.77	89.24	614.99	0.22	0.03	310
	2085	89.02	313.12	89.49	614.74	0.47	0.03	688.5
Podarcis muralis								
Initial Distribution = 180.52		**No dispersal**	**Univ. dispersal**	**Occupied**	**Absent**	**totColonized**	**totDecolonized**	**totLDDsuccess**
SDD + LDD	**2035**	180.52	290.32	288.77	415.46	108.25	0	2.7
	2060	180.52	407.46	407.46	296.77	226.93	0	10.5
	2085	180.52	466.65	466.28	237.95	285.76	0	15.9
SDD	**2035**	180.52	290.32	288.62	415.61	108.09	0	-
	2060	180.52	407.46	403.14	301.09	222.61	0	-
	2085	180.52	466.65	463.98	240.25	283.46	0	-
LDD	**2035**	180.52	290.32	180.71	523.52	0.18	0	226
	2060	180.52	407.46	181.21	523.02	0.68	0	948.7
	2085	180.52	466.65	181.95	522.28	1.43	0	2050.8

Vipera aspis								
Initial Distribution = 258.36		**No dispersal**	**Univ. dispersal**	**Occupied**	**Absent**	**totColonized**	**totDecolonized**	**totLDDsuccess**
SDD + LDD	**2035**	233.55	275.18	274.85	429.38	41.3	24.82	0.5
	2060	219.98	307.27	306.95	397.28	96.63	48.05	0.8
	2085	213.52	336.47	335.99	368.24	137.33	59.71	0.9
SDD	**2035**	233.55	275.18	274.85	429.38	41.3	24.82	-
	2060	219.98	307.27	306.95	397.28	96.63	48.05	-
	2085	213.52	336.47	335.98	368.25	137.33	59.71	-
LDD	**2035**	233.55	275.18	233.59	470.64	0.04	24.82	17.3
	2060	219.98	307.27	220.11	484.12	0.14	38.39	96.5
	2085	213.52	336.47	213.79	490.44	0.28	44.86	156
Vipera berus								
Initial Distribution = 187.1		**No dispersal**	**Univ. dispersal**	**Occupied**	**Absent**	**totColonized**	**totDecolonized**	**totLDDsuccess**
SDD + LDD	**2035**	51.38	54.29	54.28	649.94	2.91	135.73	0
	2060	12.57	18.93	18.91	685.32	7.92	176.11	0.1
	2085	11.07	16.05	16.03	688.2	9.77	180.84	0.1
SDD	**2035**	51.38	54.29	54.29	649.94	2.91	135.73	-
	2060	12.57	18.93	18.91	685.32	7.92	176.11	-
	2085	11.07	16.05	16.03	688.2	9.77	180.84	-
LDD	**2035**	51.38	54.29	51.38	652.85	0	135.73	
	2060	12.57	18.93	12.57	691.66	0	174.53	0.3
	2085	11.07	16.05	11.08	693.15	0	176.03	0.9
Zamenis longissimus								
Initial Distribution = 108.44		**No dispersal**	**Univ. dispersal**	**Occupied**	**Absent**	**totColonized**	**totDecolonized**	**totLDDsuccess**
SDD + LDD	**2035**	108.44	210.03	203.66	500.57	95.22	0	0.8
	2060	108.44	339.96	326.51	377.72	218.07	0	6.3
	2085	108.44	374.12	368.2	336.03	267.39	7.64	13.1
SDD	**2035**	108.44	210.03	203.58	500.65	95.14	0	-
	2060	108.44	339.96	323.84	380.39	215.41	0	-
	2085	108.44	374.12	362.03	342.2	261.1	7.51	-
LDD	**2035**	108.44	210.03	108.47	595.76	0.03	0	19.4
	2060	108.44	339.96	108.54	595.69	0.1	0	87.9
	2085	108.44	374.12	108.61	595.62	0.17	0	170.4
Zootoca vivipara								
Initial Distribution = 437.58		**No dispersal**	**Univ. dispersal**	**Occupied**	**Absent**	**totColonized**	**totDecolonized**	**totLDDsuccess**
SDD + LDD	**2035**	349.57	367.64	367.58	336.65	18.01	88.01	0.1
	2060	226.05	247.05	247.01	457.21	22.87	213.44	0.1
	2085	170.72	199.76	199.71	504.52	30.94	268.81	0.2
SDD	**2035**	349.57	367.64	367.58	336.65	18.01	88.01	-
	2060	226.05	247.05	247.01	457.22	22.87	213.44	-
	2085	170.72	199.76	199.71	504.52	30.94	268.81	-
LDD	**2035**	349.57	367.64	349.59	354.64	0.02	88.01	6.7
	2060	226.05	247.05	226.08	478.15	0.04	211.54	21.4
	2085	170.72	199.76	170.78	533.44	0.07	266.86	38.5

Supplementary material 4: Migclim simulations

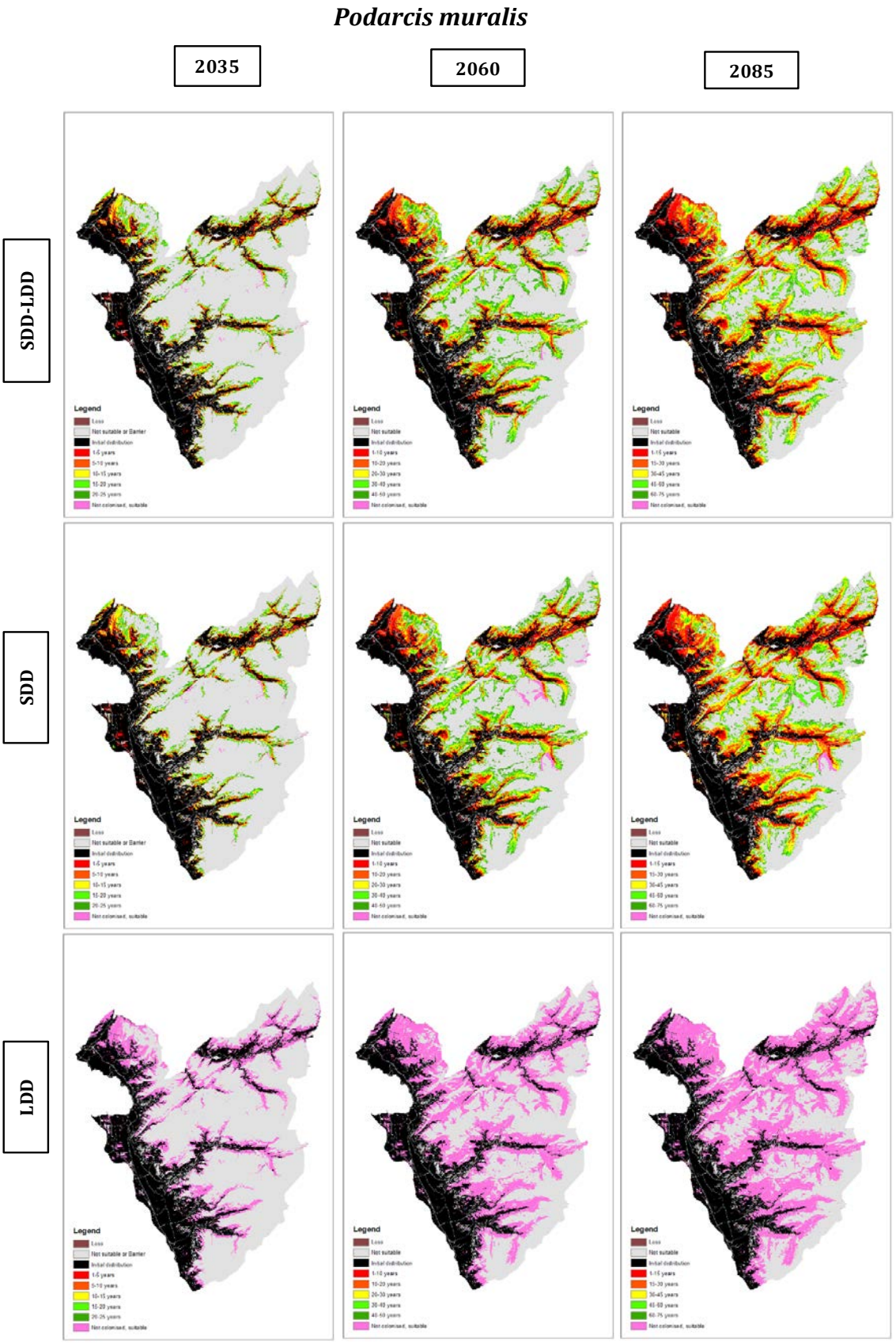


Figure 1: Migclim simulations of *P. muralis*

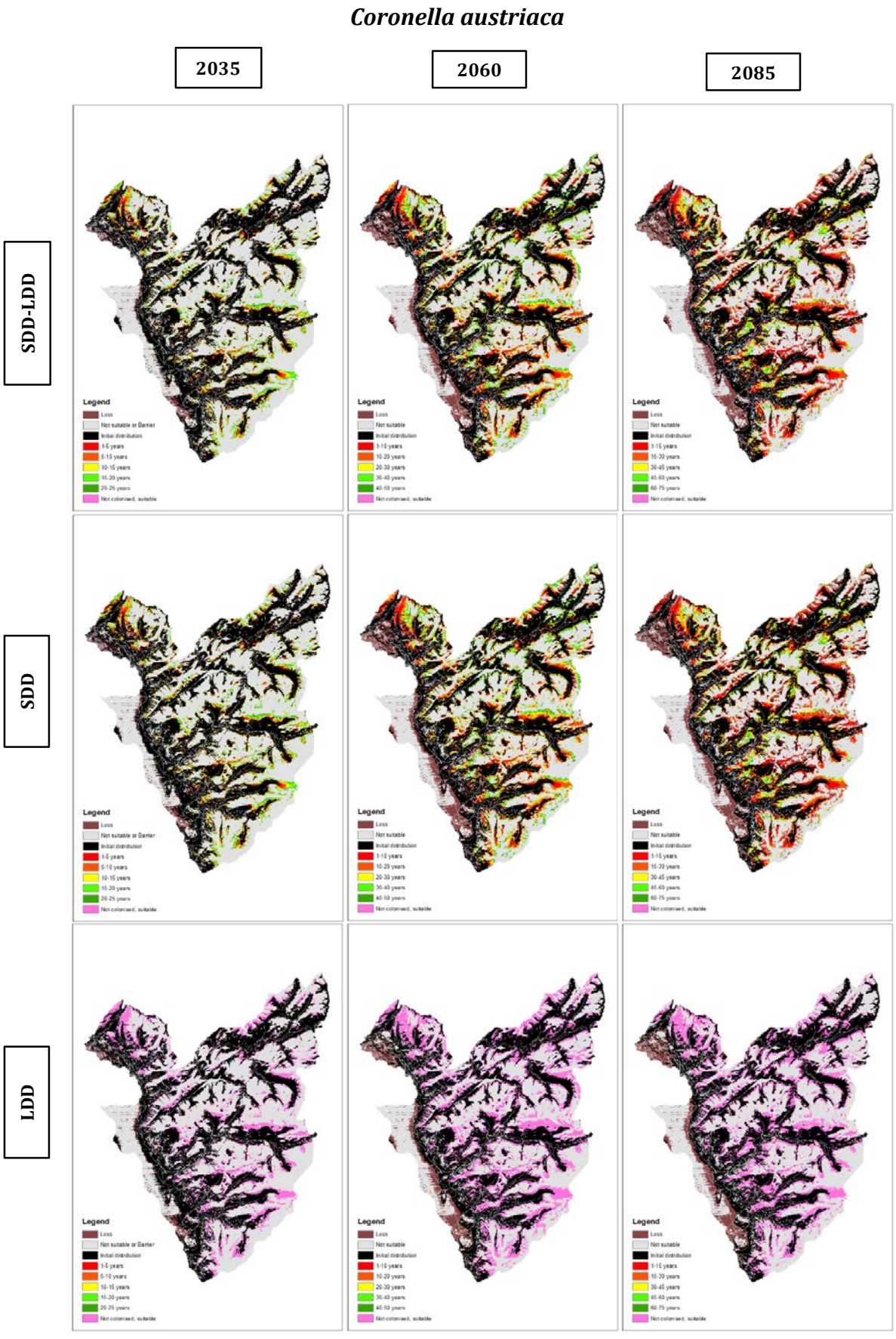


Figure 2 : Migclim simulations of *C. austriaca*

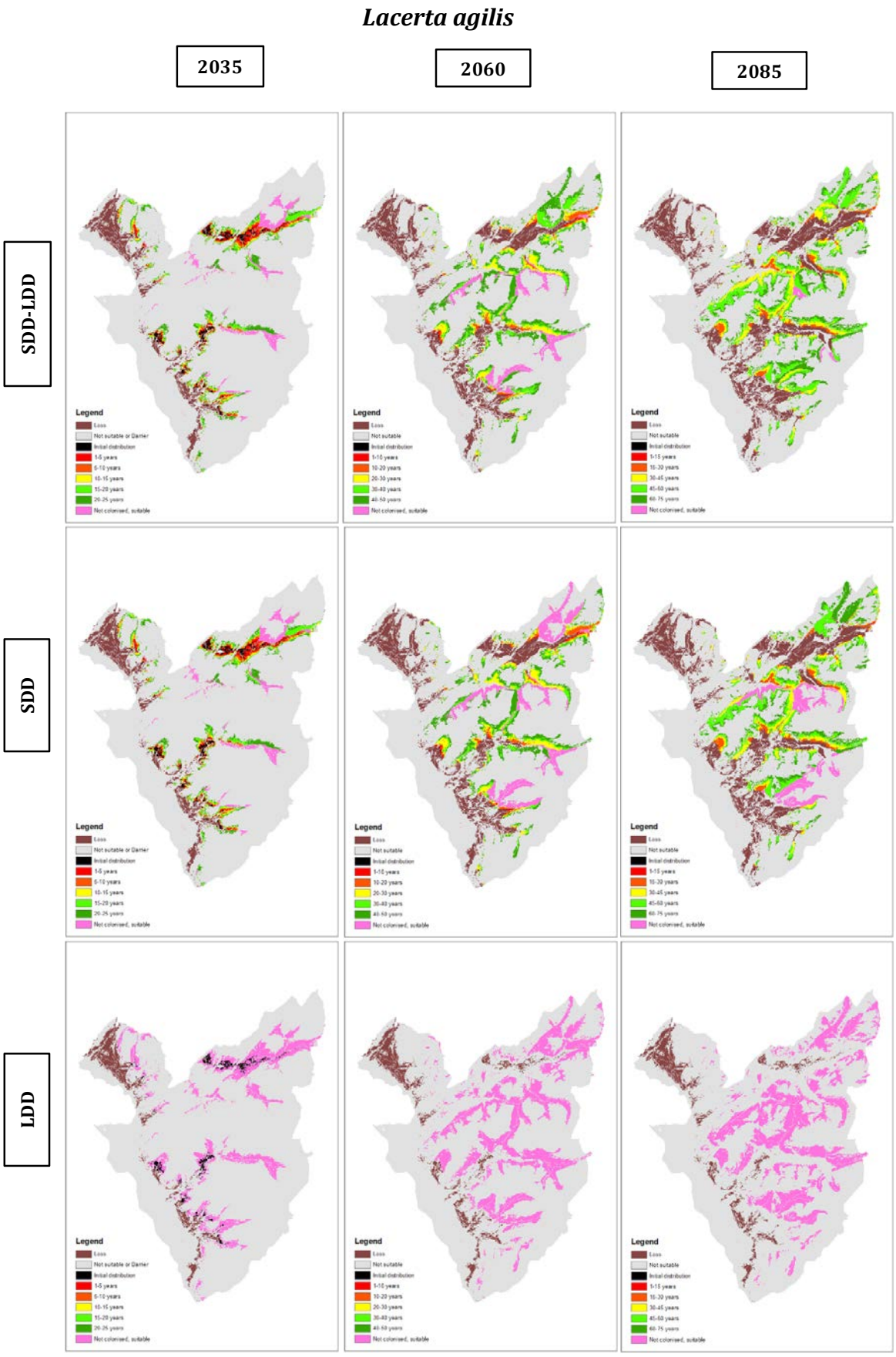


Figure 3 : Migclim simulations of *L. agilis*

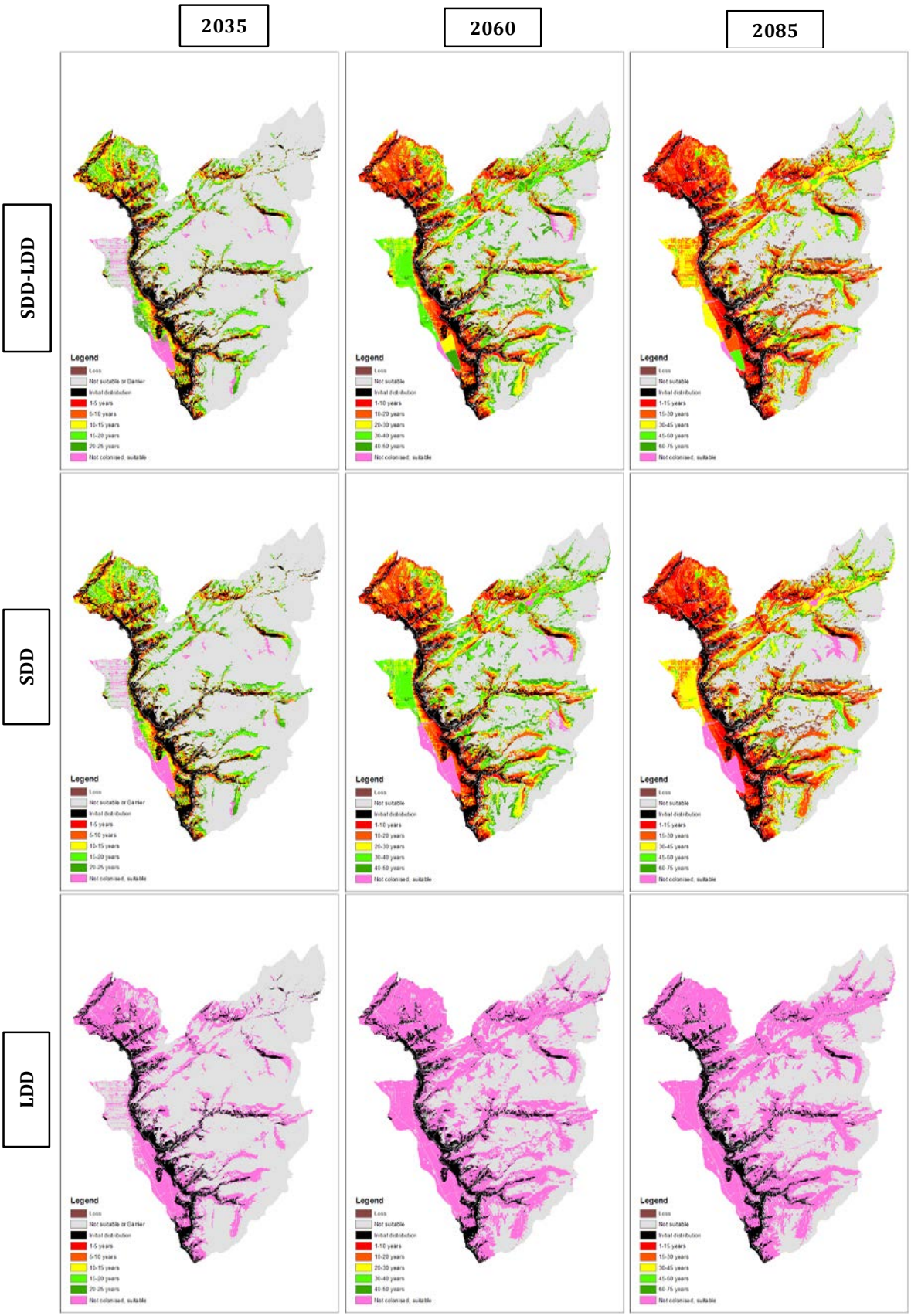


Figure 4: Migclim simulations of *L. bilineata*

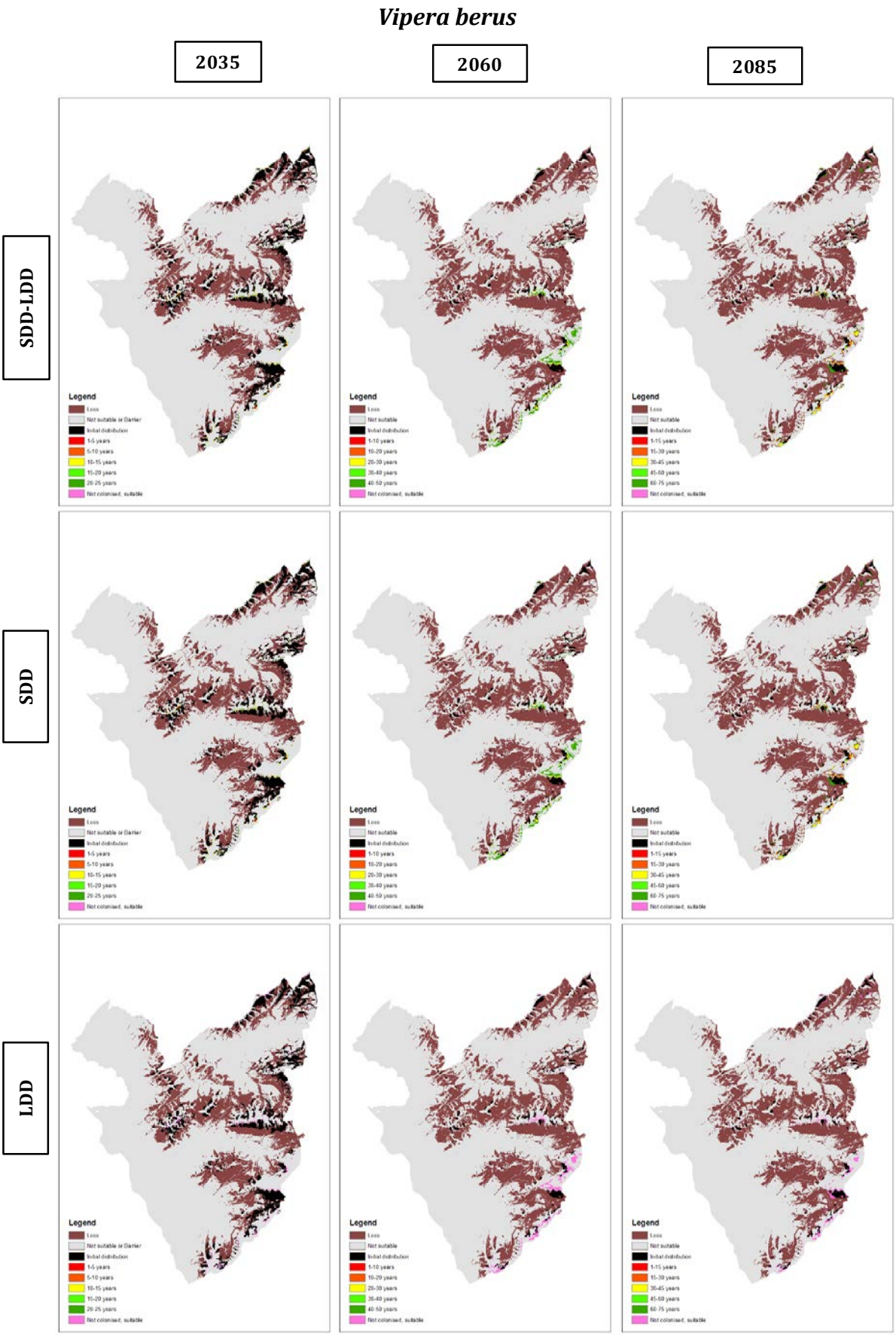


Figure 5: Migclim simulations of *V. berus*

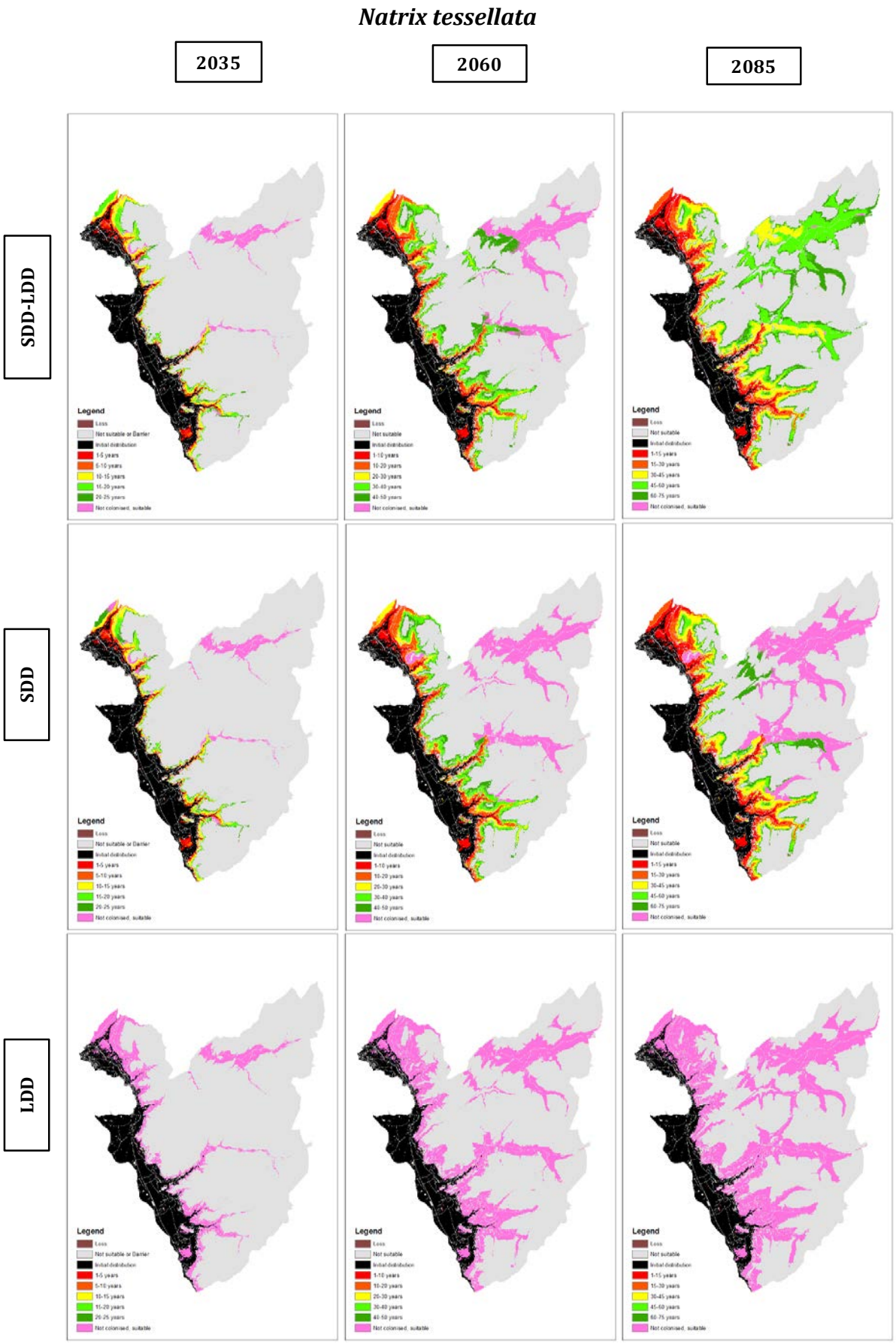


Figure 6: Migclim simulations of *N. tessellata*

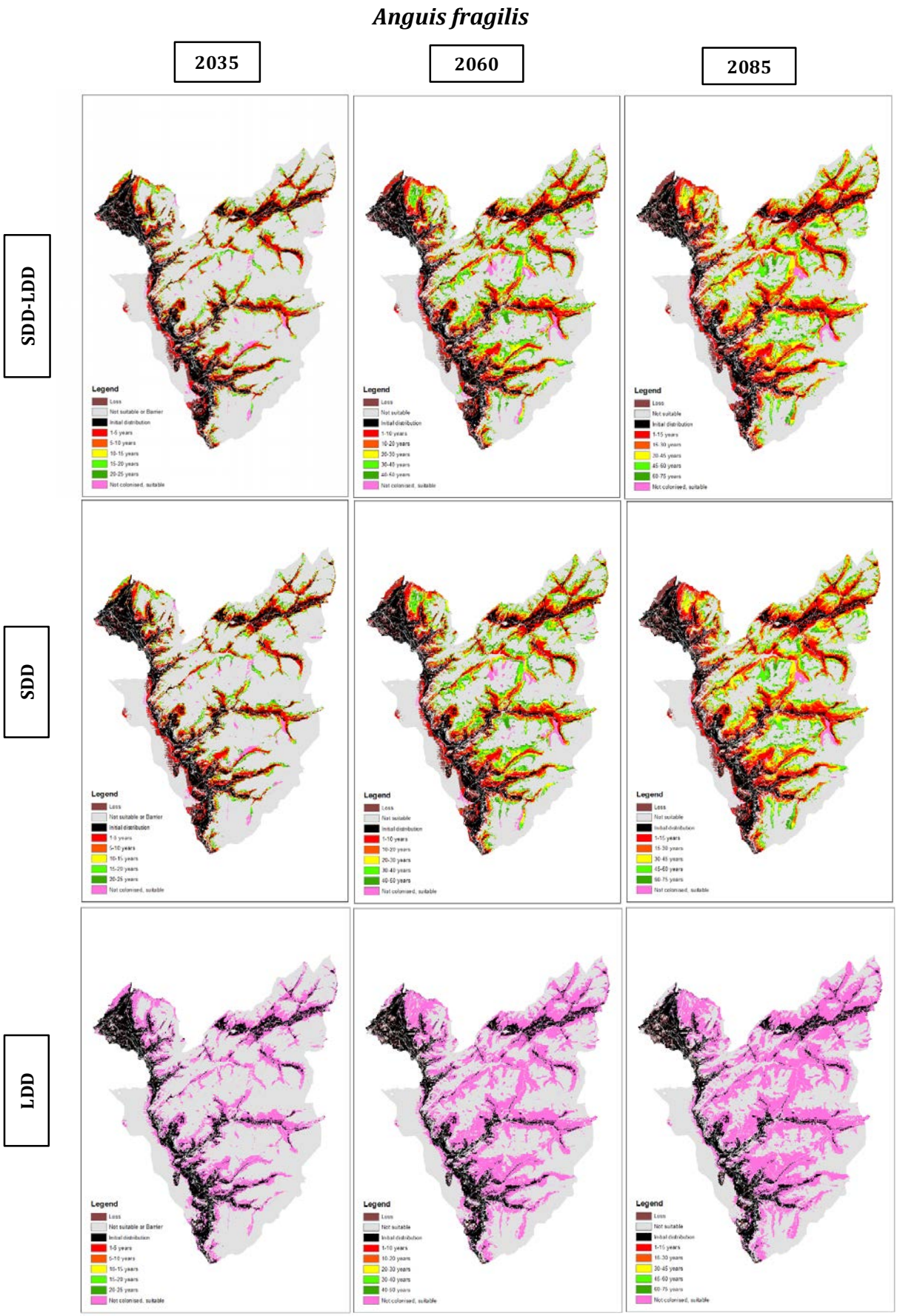


Figure 7: Migclim simulations of *A. fragilis*

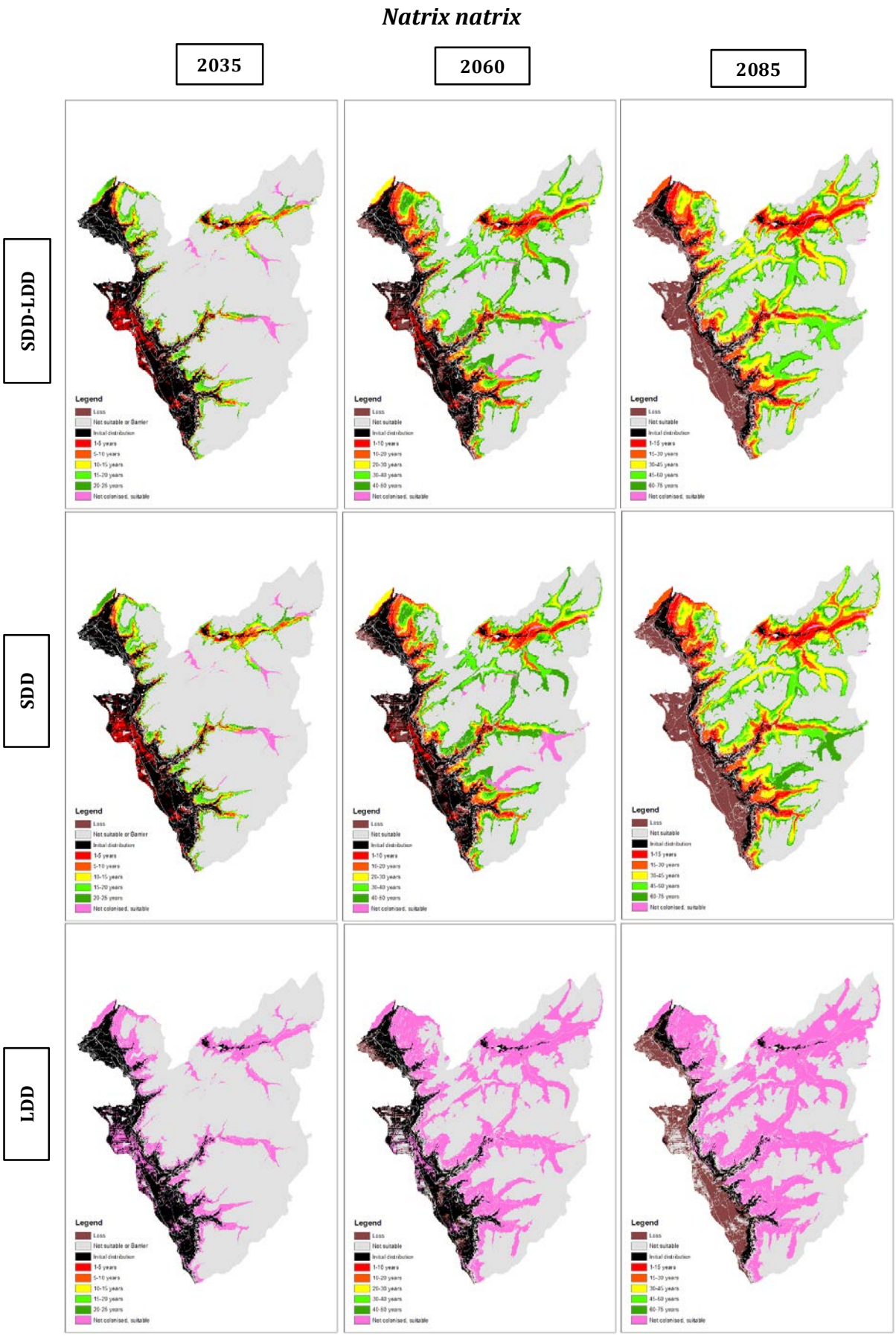


Figure 8: Migclim simulations of *N. natrix*

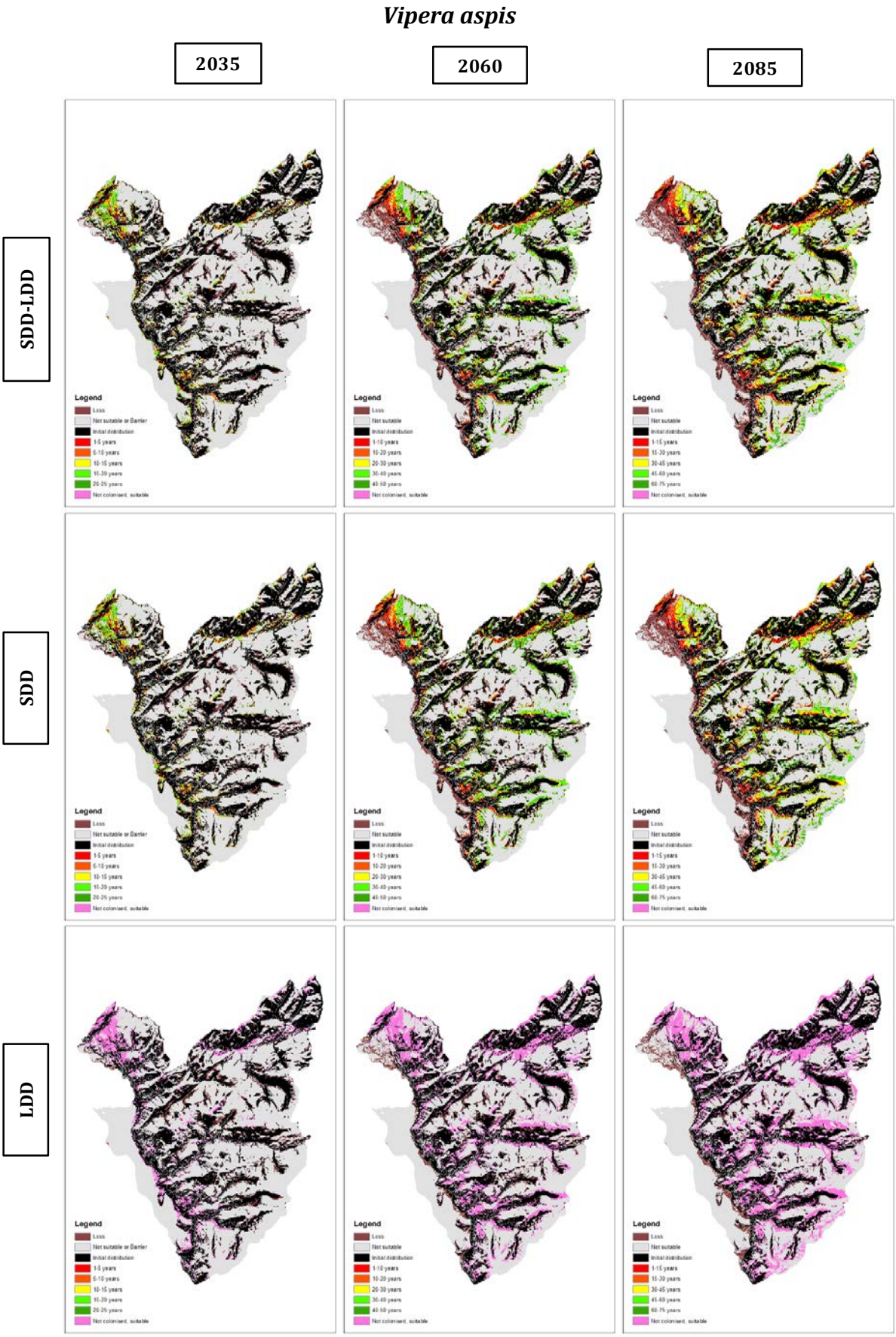


Figure 9: Migclim simulations of *V. aspis*

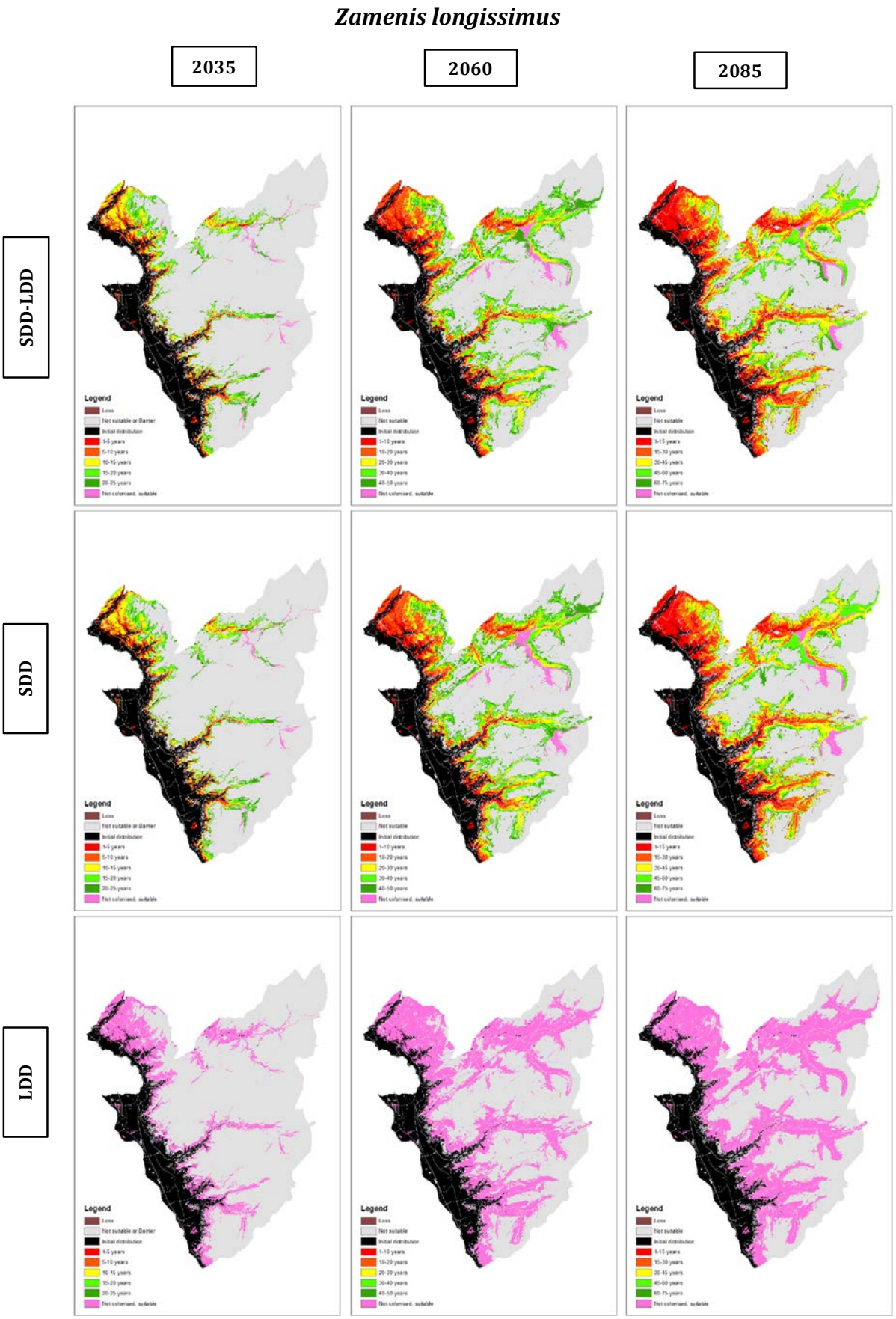


Figure 10: Migclim simulations of *Z. longissimus*