Master’s thesis

Master’s degree programme in Environmental Sciences

THE FATE OF AMPHIBIANS IN AARGAU: EFFECT OF FUTURE LAND-USE SCENARIOS

Identifying Suitable Areas for Blue-Green Infrastructure

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The following R-scripts belong to this thesis:

- 0_Data_Formatting.R *(script written by Dr. Giulia Donati)*
- A_Generation_PA_matrix.R
- B_Environmental_Predictors.R
- C_biomod2.R
- D_Output_Analysis_Figures.R

Abstract

Biodiversity is essential to sustain various ecosystem services. The growing human population and associated land-use change through urbanization and intensification of agriculture result in degradation, loss, and isolation of habitats. Largely due to this land-use change, 40 % of amphibian species are considered to decline worldwide. The concept of Blue-Green Infrastructure (BGI) aims to alleviate conflicts between human and natural ecosystems. In this study, occurrences of 10 amphibian species with differing habitat requirements in the Canton of Aargau were modelled. With the aid of these species distribution models, the influence of five future land-use scenarios, which differed regarding human population growth and the degree of governmental interventions, was assessed. Two existing landscape inventories supporting biodiversity were regarded as starting points to identify regions with existing and missing BGI coverage. My findings revealed that scenarios with a higher degree of urbanization resulted in a higher change of modelled biodiversity hotspot areas, which resulted not only in losses but also in gains. The results suggest that gains on future urban areas can occur provided that the surrounding coverage within a focal window of 300 x 300 m remains on average below 70 % regarding urban land use and above 20 % concerning forest coverage. As urbanization in the included land-use scenarios is mostly predicted in flat areas near the main rivers of the Canton encompassing primary habitats for many amphibian species, biodiversity hotspot losses were mostly predicted in these areas. Therefore, a continuation of the displacement of amphibians into secondary habitats was predicted. As habitat requirements vary severely between amphibian species, BGI needs to be planned and managed as diversely as possible. For instance, the comparison of the two species with the most extreme predicted future changes suggested that *Epidalea calamita* might establish in urban areas, while *Salamandra salamandra* probably profits more from consistent protection of forests. This underlines the importance of deriving BGI in both urban and rural environments. 18 % of the modelled amphibian biodiversity hotspot areas in the study area resulted to be covered by existing landscape inventories with legally binding protection goals and can be regarded as already having a network of BGI. However, other regions like the Southwest of the Canton of Aargau, where additionally several models agreed on predicting biodiversity loss, were found to lack coverage. To sustain biodiversity and associated ecosystem services in the long-term, this finding could support decisions for additional legally binding conservation strategies in these areas.

Keywords: Amphibians, Biodiversity, Blue-Green Infrastructure, Human-dominated Landscapes, Land-use change, Scenarios, Species distribution models

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1. Introduction

Biodiversity is defined as the variety and diversity of life on the levels of genes, species, and ecosystems (Carreon-Lagoc et al. 1994). It is of fundamental importance to support diverse ecosystem services, as the efficiency of ecological communities to capture, produce and recycle nutrients increases with biodiversity (Cardinale et al. 2012). Ecosystem services include a wide range of processes from the purification of air and water, increasing soil fertility, mitigation of floods and droughts to the provision of recreational areas (Daily 2003). These services are globally essential for human civilization and well-being in both urban and rural environments (Bolund and Hunhammar (1999), Kroll et al. (2012)). Additionally, biodiversity increases the resilience of ecosystems, which may be an important foundation to ensure that future generations can continuously profit from ecosystem services under projected human-induced changes (Oliver et al. 2015).

However, intensification and expansion of human land use in the past decades have heavily influenced biodiversity (Foley et al. 2005) on all levels regarding genetic, species, and ecosystem diversity (Hansen, DeFries, and Turner 2004). The ongoing growth of the world's human population results in increasing land-use demand of both urban and agricultural areas (Döös 2002). Land-use change often occurred at the expense of areas like wetlands and forests, which provide important ecosystem services and are rich in biodiversity (Lindquist et al. (2012), Sica et al. (2016)). Concerning wetlands, an estimated 50 % were lost globally due to the conversion to urban and agricultural areas (Rijsberman and Silva (2006), Gardner, Barchiesi, et al. (2015)). Urbanization is usually linked with loss and fragmentation of habitats, alteration of water and nutrient cycles, and changes in the composition of species (Crooks and Soulé (1999), O'Driscoll et al. (2010), Lin et al. (2014), Liu, He, and Wu (2016)). Agricultural intensification often leads to high levels of nutrients, pesticides, monocultures, and intensive grazing or cutting of grasslands, which are all unfavourable to sustain a high level of biodiversity (Plantureux, Peeters, and McCracken (2005), Karp et al. (2012), Brühl et al. (2013), Tsiafouli et al. (2015), Raven and Wagner (2021)).
Amphibians are highly threatened through land-use change and associated habitat loss and fragmentation (Cushman (2006), Becker et al. (2007)). Among vertebrates, amphibians are the most threatened group in the world and over 40 % of the known species are considered in decline (Stuart et al. (2004), IUCN (2020)). Around 90 % of the threatened amphibians are impacted by urbanization (Baillie, Hilton-Taylor, and Stuart 2004). Depending on the season and stage of life, amphibians need both aquatic and terrestrial habitats. This requirement is in conflict with the decline of suitable semiaquatic habitats like wetlands. Amphibians have a key role regarding nutrient flow and recycling of both aquatic and terrestrial ecosystems, as they are predators and prey at the same time (Crump 2009). However, there are important differences between habitat preferences of amphibian species, for instance the degree of specialization. While some amphibian species like *Rana temporaria* are classified as generalists as they have few habitat requirements (Flory 1999), specialists like *Salamandra salamandra* are found in a narrower subset of ecological conditions (Küry 2003). Additionally, pioneering species like *Epidalea calamita* colonize dynamic habitats in an early successional state (Snep and Ottburg 2008). For the design of conservation strategies, species-specific requirements should be taken into account (Cushman (2006), Brown et al. (2012), Klaus and Noss (2016)).

The conceptual framework of Blue-Green Infrastructure (BGI) aims to balance conflicts between natural and human ecosystems (Benedict, McMahon, et al. (2002), Kowarik, Fischer, and Kendal (2020)). According to the European Commission (2013), BGI is defined as a strategically planned network of natural and semi-natural blue (aquatic) and green (terrestrial) areas. They are designed and managed to deliver a wide range of ecosystem services both in urban and rural settings. In urban areas, BGI might help to restore ecosystem services like microclimate regulation to reduce the urban heat island effect (Gunawardena, Wells, and Kershaw 2017), improve the air quality (Hewitt, Ashworth, and MacKenzie 2020) as well as human well-being (Völker and Kistemann 2013), and provide habitats for a surprisingly high diversity of species (McKinney 2008). Through strategical management of forests and agriculture, BGI can be combined with existing protected areas or landscape inventories, to enhance structural connectivity across the landscape and improve the provision of ecosystem services like pollination and carbon retention (Hermoso et al. 2020). Maes et al. (2015) underlines that substantial investments in the development of BGI are needed to offset land losses resulting from increasing human population, whereof both ecosystems and society might benefit. Due to their need for semiaquatic habitats, amphibians are one of the vertebrate groups that can profit from the establishment of BGI (Hamer and McDonnell (2008), Holzer (2014)). This is why I investigated how amphibian distributions might be affected by future land-use changes to identify regions with an increased need for BGI. Five future land-use scenarios developed by Price et al. (2015) for Switzerland were included for this purpose. These scenarios are based on forecasts of socio-economic developments expected until the year 2035. One of the aims of Price et al. (2015) was to identify regions with a high risk of urbanization, which provides a promising opportunity to investigate the influence on future biodiversity. The Canton of Aargau, located in the Swiss Central Plateau, was taken as a case study as it belongs to the most populated and fragmented regions of Switzerland (Jaeger, Bertiller, and Schwick 2007), but has at the same time a high responsibility for the national conservation of amphibians. Mainly the low, climatically mild locations along the rivers Aare, Reuss, Limmat, and Rhine are part of the distribution area of endangered species (Flöss 2009). Flory (1999) describes that primary habitats along the rivers were lost due to human land-use change to a large extent, which resulted in the displacement of species to secondary habitats.

Possible future distributions of 10 amphibian species differing in habitat preferences in the Canton of Aargau were modelled. Species distribution models (SDMs) allowed investigating the influence of five future land-use scenarios. This aimed to identify suitable starting points for the development of BGI to support the diversity of amphibian species by addressing the following research questions:

1. *How do different land-use scenarios influence amphibian biodiversity hotspot areas in the Canton of Aargau? Which land-use categories are the most important drivers of the change?* Based on the findings of Becker et al. (2007) and Hamer and McDonnell (2008), I expect scenarios with higher growth in economy and population (leading to more urban sprawl) and less support for environmental concerns (leading to more intensive agriculture and abandonment of pasture agriculture) to show higher losses in biodiversity. Urbanization was reported as a decisive driver of amphibian decline (Baillie, Hilton-Taylor, and Stuart (2004), Scheffers and Paszkowski (2012)). Therefore, I laid a special focus on urbanizing areas with the question *How does modelled biodiversity change on future urban areas?*

2. Hamer and McDonnell (2008) see the utility in combining both species-specific and community diversity approaches for amphibian conservation. This is addressed in the following questions: *Which species occur in current biodiversity hotspots and what are likely changes in the future given changing land use? Which species show most extreme changes given future land-use scenarios and why?*

3. *If existing landscape inventories are considered as starting point for a network of blue-green infrastructure (BGI): where are modelled amphibian biodiversity hotspots already covered and which regions require additional protection?* This question is based on the work of Hermoso et al. (2020), who designed a network of BGI across the European Union with protected areas as a starting point.

Deepening the understanding of how different land-use scenarios influence amphibian biodiversity, as well as individual species, could contribute to plan and implement BGI that supports amphibian conservation. This ultimately aims at supporting biodiversity and ensuring attached ecosystem services for future generations, which is in accordance with the Federal Council's Swiss Biodiversity Strategy (BAFU 2017a).

2. Material and Methods

2.1. Study Area

The study area consisted of the Canton of Aargau (1’404 km^2) located in the North of the Central Plateau in Switzerland. With elevations ranging from 261 to 903 m a.s.l., Aargau belongs to the least mountainous regions of Switzerland. Important national traffic routes and densely populated areas fragment the landscapes (Jaeger, Bertiller, and Schwick 2007). According to the areal statistics of 2004/09 computed by the Swiss Federal Statistical Office (SFSO 2013), the dominant land uses and land covers include agricultural land (44 %), forests (36 %) and settlement areas (17 %, see Figure 1a).

2.2. Landscape Inventories

There are several landscape inventories for the Canton of Aargau which are designed to preserve ecosystem services. To identify regions with existing or missing BGI, I used two landscape inventories. First, the Federal Inventory of Landscapes and Natural Monuments (Bundesinventar der Landschaften und Naturdenkmäler (BLN)) aims to preserve the most typical and valuable landscapes of Switzerland (BAFU 2017d). Among other functions, BLNs allow formulating legally binding strategies to protect biodiversity. For each BLN of the Canton, goals to preserve local fauna and habitats are formulated. 9 of the 12 BLNs encompass amphibian breeding sites of national importance (ALG n.d.). Second, I included the national ecological network (Réseau écologique national (REN)). It represents a vision of connected habitats on a national scale with no legal bindings (Berthoud, Lebeau, and Righetti 2004). The total network consists of five parts that cover different types of habitats and their associated species. Amphibians were included as indicator species for the "wetland" part.

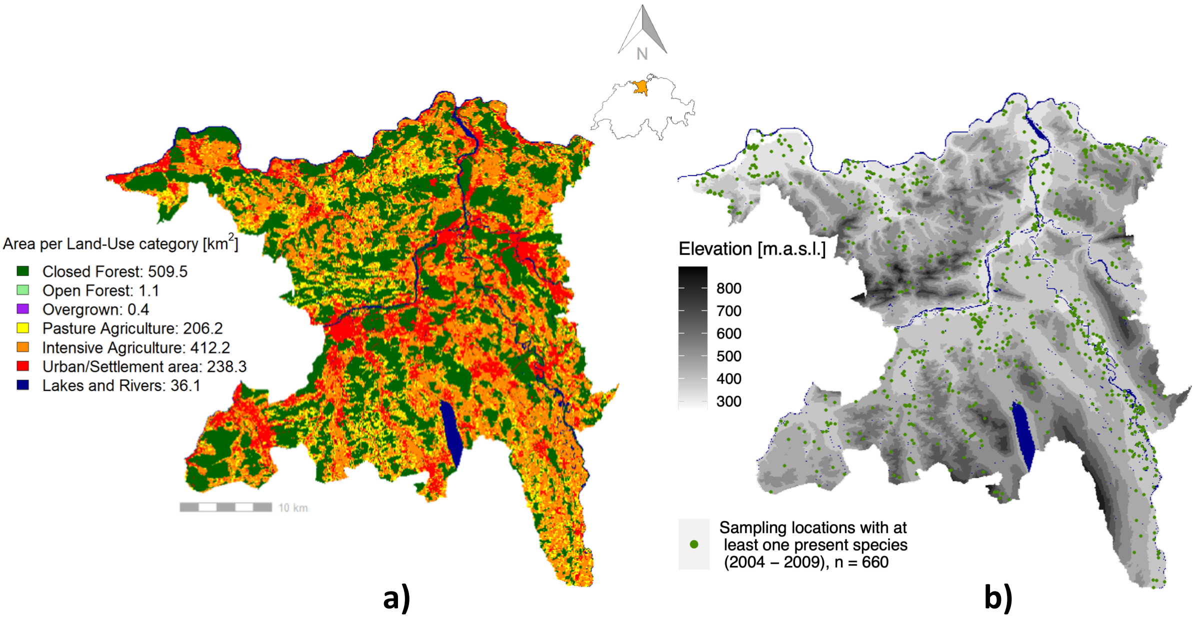


Figure 1: a) Land use and land cover of the study region (Canton of Aargau, 100 m resolution, areal statistics of 2004/09, SFSO). **b)** Occurrences of 10 selected study species were sampled at 660 locations of the Amphibian Monitoring Program of Canton Aargau. *Source of the elevation map in the background: swisstopo 2001.*

2.3. Study Species

Ten amphibian species with differing characteristics and habitat requirements were selected as study species (Table 1). The dispersal ability and the ecological type are important characteristics that determine the species ability to colonize new habitats. The maximum migration distance was regarded as a proxy for dispersal ability based on the work of Dawideit et al. (2009). A species was regarded as present at a site if it was detected at least once in the years between 2004 and 2013. This period was chosen to match the land-use data (section 2.4) while providing a sufficient amount of observations for all focal species. In total, the data of 660 sampling sites (Figure 1b) of the volunteer-based Amphibian Monitoring Program of Canton Aargau were included. Since 1999, around 300 from a total of 1’500 breeding sites are monitored every year. Each selected breeding site is visited three times during the breeding season between April and June. Two visits occur at night and one at daytime (Hintermann & Weber AG 2019). The individual distributions of the sampling sites for each species can be found in Figure A.2.

Species richness is a component of biodiversity (Carreon-Lagoc et al. 1994) and was hence used as an indicator of biodiversity hotspots. Biodiversity hotspot areas were defined as areas where more than seven out of the ten species occur. This should ensure that at least two of the five endangered species occur, even if all five less threatened species ("least concern" or "vulnerable") occurred at the same site.

2.4. Environmental Predictors

The species presences were correlated to seven environmental factors (resolution of 100 x 100 m) that are relevant for the ecology of amphibians (Table 2 and Figure A.3). Four land-use predictors (Urban and settlement areas, pasture agriculture, intensive agriculture, and forests) originated from the areal statistics 2004/09 computed by the SFSO. The Swiss land use and land cover statistics were interpreted from aerial photographs with a periodicity of 12 years (SFSO 2013). The aerial photographs of Aargau for the statistic of 2004/09 were generated in 2006 and 2007 (SFSO 2004). Price et al. (2015) used six land use and land cover categories to project future land change for the whole of Switzerland that were considered to be affected by key land-use change processes in Switzerland: Closed forest, Open forest, Overgrown areas, Pasture agriculture, Intensive Agriculture, and Settlement and Urban areas. Unproductive areas like lakes and rivers were assigned as NoData (NA), as no changes are expected. Low frequencies of a category result in a high sampling error (SFSO n.d.). This is why I combined two categories with the most similar one: "Overgrown" with "Pasture agriculture" and "Open forest" with "Closed forest".

While the areal statistics of the SFSO of 2004/09 served to model the reference model, five future land-use scenarios (section 2.4.1) derived by Price et al. (2015) were used to compute future projections of species occurrences. I refer to the four land-use predictors as "dynamic" predictors. In order to include the dynamic predictors in the modelling process, the percentage of each land use within a moving window of 300 x 300 m was calculated for each pixel with the *focal* function of the raster package in R (Hijmans 2020). This window size was chosen in order to include the influence of the surrounding landscape, as amphibians migrate between different types of habitats. According to Semlitsch and Bodie (2003), the core terrestrial habitats that amphibians need for feeding and hibernation ranged within 160 to 290 m around aquatic sites.

Three predictors remained stable for the reference and the future scenarios: distance to water, the standard deviation of elevation, and the humidity of the soil. The predictors were tested for correlation and variance inflation (section A.1.3). Common climatic variables in SDMs, such as temperature (or elevation) and precipitation, were not included in these models because of the very restricted area with a homogeneous climate and no strong elevational gradients. Secondly, land use is argumented to be the more important small-scale driver of species distributions (Luoto, Virkkala, and Heikkinen 2006) and the highest available resolution for area-wide climate data of Switzerland is 1 km, which is 10 times higher than the resolution of the other environmental variables.

Table 1: Description of the 10 study species. The status of threats correspond to the abbreviations of the IUCN (2020): least concern (LC), vulnerable (VU) and endangered (EN). Based on Dawideit et al. (2009), the maximum migration distance was regarded as an indicator of dispersal distances.
(Sources: [1]Schmidt and Zumbach 2005, [2]Trochet et al. 2014, [3]Flory 1999, [4]Mermod, Zumbach, Borgula, Lüscher, et al. 2010, [5]Mermod, Zumbach, Borgula, Krummenacher, et al. 2010, [6]Mermod, Zumbach, Aebischer, et al. 2010, [7]Mermod, Zumbach, Lippuner, et al. 2010, [8]Grossenbacher 2014, [9]Küry 2003, [10]Scheuber 2014)

Taxon	Family	Status of Threat[1]	Number of sampling locations 2004 - 2009	Maximum migration distance [m] [2]	Ecological Type[3]	Distribution in the Canton of Aargau
Alytes obstetricans	Alytidae	EN	178	500	Specialist	In the Canton of Aargau, the species is found in hilly areas, but diminished on its original habitat on sunny areas of floodplains. Gravel pits and agricultural areas on slopes are important secondary habitats[3]. Suited terrestrial habitats have to be found in the immediate vicinity of spawning grounds[4].
Bombina variegata	Bombinatoridae	EN	322	3'800	Specialist, Pioneer	The species is found in floodplains and adjacent slopes. Gravel pits are important secondary habitats, while hill areas are avoided[3]. The species is specialized on dynamic habitats and colonizes temporary, small water bodies that have little vegetation[5].
Bufo bufo	Bufonidae	VU	468	4'000	Generalist	Particularly common on wooded slopes of river valleys if larger standing and persistent water bodies are present. If no wooded slopes are found in the vicinity of the spawning waters, long migration distances are possible. This can lead to conflicts on some street crossing points[3].
Epidalea calamita	Bufonidae	EN	118	2'600	Specialist, Pioneer	The toads use exclusively short-lived, temporary water bodies for reproduction. Therefore, it is not uncommon that the location is changed annually. The species is now only found in secondary habitats. Large construction sites are ideal habitats in the short term. Original ideal habitats would be found along of dynamic rivers[3]. Due to the usually static nature of garden ponds, they provide no suitable habitat for the species[6].
Hyla arborea	Hylidae	EN	79	12'570	Specialist, Pioneer	Typical inhabitant of natural river landscapes. All inventoried habitats are secondary habitats. Vital, but strongly isolated populations are for instance found in the Reuss valley[3]. In general, suitable habitats are not located in the vicinity of urban areas[7].
Ichthyosaura alpestris	Salamandridae	LC	624	1'000	Generalist	Very abundant and widespread species. It prefers stagnant waters[3]. Of all species, it can probably profit most from garden biotopes[8].
Lissotriton helveticus	Salamandridae	VU	298	400	Generalist	Very widespread species which prefers mild and sunny habitats[3].
Rana temporaria	Ranidae	LC	598	2'214	Generalist	The species is very abundant and can be found nearly in the whole canton. Especially common along rivers and creeks. It is the species with fewest habitat requirements[3].
Salamandra salamandra	Salamandridae	VU	124	30	Specialist	The forest is the typical habitat of the species[9]. Ideal spawning grounds are pristine and clean streams with no fish. Not found in urban and intensive agricultural areas[3].
Triturus cristatus	Salamandridae	EN	59	1'290	Specialist	The species occurs along streams and in bogs. It is very seldom in the Canton. It used to occur in flood plains. Streets and settlements isolate populations[3]. Ideal spawning grounds are about half a meter deep, rich in submerged vegetation and partially sunny[10].

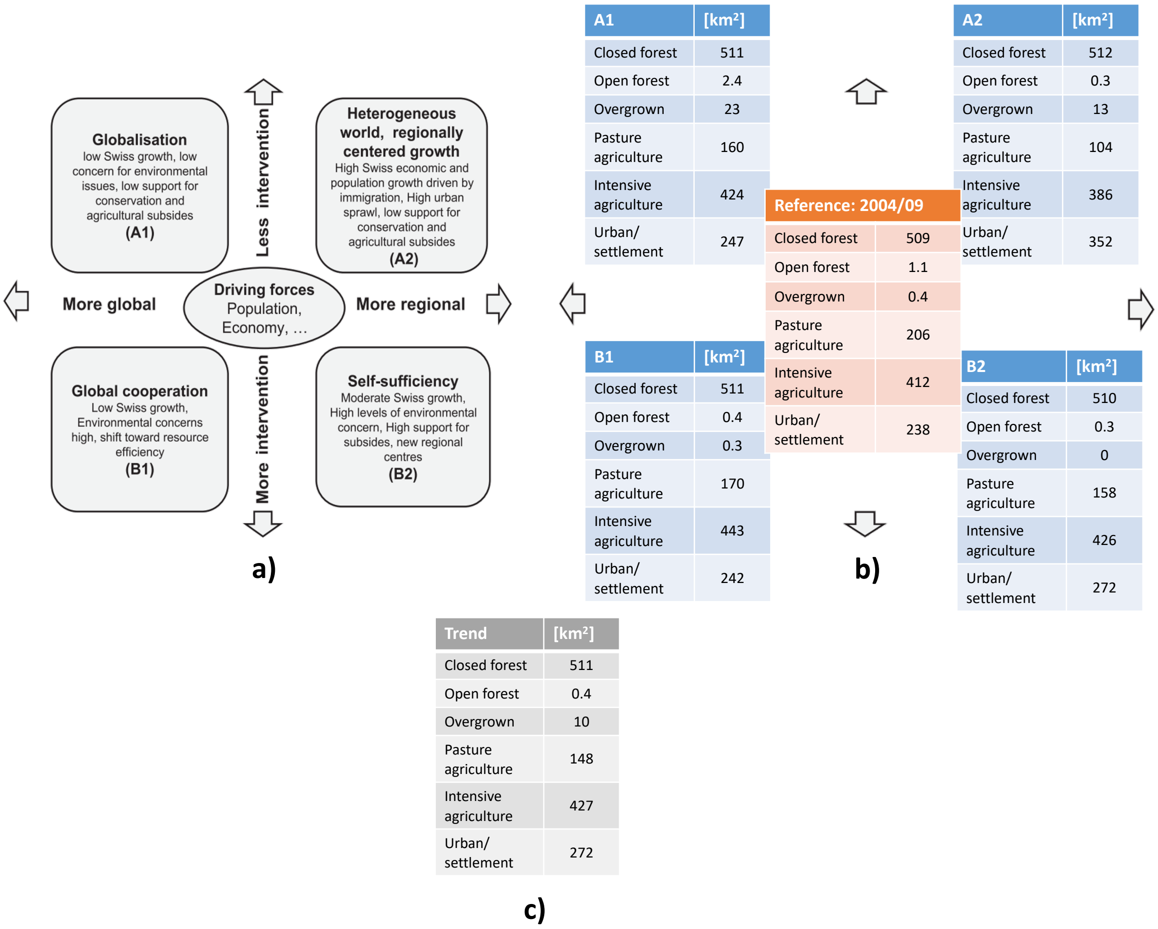
Table 2: Seven environmental predictors were used to model the occurrence of the 10 study species.

Type	Predictor	Unit	Ecological importance	Expected response of distribution	Geodata source	Processing steps
Dynamic predictors	Urban/settlement areas	Coverage in % within a focal window of 300 x 300 m around each pixel.	Urbanization changes the hydrology, modifies soils and can cause habitat fragmentation and loss (McKinney, 2006).	Decrease with higher values (Hamer and McDonnell 2008)	Areal statistics 2004/09 made by the SFSO. In the canton of Aargau, the aerial pictures were taken in 2007 and 2008 (SFSO 2004).	The land-use categories of the SFSO were aggregated by Price et al. (2015). For this thesis, the categories "Open Forest" and "Closed Forest" were combined. The category "Overgrown" was added to "Pasture agriculture". For each land use, the focal percentage within a moving window of 9 neighbouring pixels was calculated with the aid of the *focal* function of the raster package in R (Hijmans 2020).
	Forest		Forests influence the light availability, temperature and hydrology of a habitat (Schäfer and Dirk 2011).	Depending on the species: there are forest specialists, but some species prefer more open and sunny habitats (Halverson et al. 2003).		
	Intensive agriculture		Wet soils were often drained to create suitable agricultural land. This destructed amphibian primary habitats. However, agricultural ponds can serve as important secondary habitats for amphibians (Knutson et al. 2004) that prefer open and sunny habitats. High levels of nutrients and pesticides can harm amphibians (Brühl et al. 2013).	Increase for species that prefer open and sunny habitats. An important prerequisite are suitable water bodies or wet soils (Halverson et al. 2003).		
	Pasture agriculture					
Stable Predictors	Distance to water	m	Amphibian larvae develop in water. The dependency of adults depends on the species: some species are only at the water for mating while others spend the whole year in ponds (karch n.d.).	Increase with lower values	Cantonal cadastral map	Calculation of the euclidean distance to reed belts, stagnant and flowing water bodies (raster resolution 2 x 2 m) with the *distance* function of the raster package (Hijmans 2020). Aggregation to 100 x 100 m.
	Soil moisture (EIV_F)	Continuous gradient between 1 (dry soil) to 5 (plants growing in water)	Humidity is needed to prevent the moist skin of amphibians from drying out (karch n.d.).	Increase with increasing values	Descombes et al. (2020) modelled the soil moisture. It is based on the ecological indicator values (EIV) from Landolt et al. (2010).	–
	Standard deviation of elevation	m	Steeper soils can pose an obstacle for amphibian movement and drain quicker (Lowe et al. 2006, Ribeiro et al. 2018).	Increase with lower values	swisstopo (2001)	Calculation of the standard deviation of elevation within 100 x 100 m of pixels in the size of 25 x 25 m.

2.4.1. Future land-use scenarios

Price et al. (2015) developed five different land-use change scenarios which are based on the same categories as the reference land use (areal statistics of the SFSO for 2004/09). The study was conducted to identify likely risk areas of urbanization and land abandonment in Switzerland. The Trend scenario is the linear projection to 2035 of observed land-use trends between the areal statistics from 1985, 1997, and 2009. Although no explicit time step was chosen for the modelling of the other four scenarios, 2035 served as a time horizon relevant to policy and planning and matching cantonal level growth scenarios. The four scenarios were modelled using the Dyna-CLUE land-use modelling framework (Verburg and Overmars 2009) by incorporating socio-economic and bio-geographical variables. The two main axes of driving forces were regional vs. global development and more vs. less intervention. This resulted in different proportions of the land-use categories (Figure 2). As described in Price et al. (2015), the "A" scenarios are considered as the market-driven scenarios, while the "B" scenarios are driven by high interventions. The urban and settlement areas increase in all scenarios due to population growth scenarios developed by the SFSO (2010). The highest increases in urban areas are predicted for scenario A2, followed by the scenarios Trend and B2. In line with general trends predicted for Europe (Rounsevell et al. 2005), agricultural land is expected to decrease between 9 (scenario B1) and 25 % (A2) by 2040, with lower losses of pasture agriculture than of the category of intensive agriculture. Concerning the forest areas, it was expected that the current restrictions that allow no net loss (FOEN 2013) would remain in the future. A1 shows high levels of agricultural land abandonment, which results in the highest increase of the Overgrown land-use category. Scenario A2 has the most extreme changes in land-use patterns. B1 has nearly no changes. A slight increase in the agricultural area is foreseen for the self-sufficiency scenario B2.

A spatial representation of the areas that changed in land use is shown in Figure A.6 for each scenario. Across all scenarios, urbanization is mainly occurring at the expense of agricultural areas. The changes in the Trend scenario are spatially more scattered than in the other scenarios.



A1	[km²]
Closed forest	511
Open forest	2.4
Overgrown	23
Pasture agriculture	160
Intensive agriculture	424
Urban/ settlement	247

A2	[km²]
Closed forest	512
Open forest	0.3
Overgrown	13
Pasture agriculture	104
Intensive agriculture	386
Urban/ settlement	352

Reference: 2004/09	
Closed forest	509
Open forest	1.1
Overgrown	0.4
Pasture agriculture	206
Intensive agriculture	412
Urban/ settlement	238

B1	[km²]
Closed forest	511
Open forest	0.4
Overgrown	0.3
Pasture agriculture	170
Intensive agriculture	443
Urban/ settlement	242

B2	[km²]
Closed forest	510
Open forest	0.3
Overgrown	0
Pasture agriculture	158
Intensive agriculture	426
Urban/ settlement	272

Trend	[km²]
Closed forest	511
Open forest	0.4
Overgrown	10
Pasture agriculture	148
Intensive agriculture	427
Urban/ settlement	272

Figure 2: Five land-use scenarios developed by Price et al. (2015) were used to project future species distributions. **a)** Four were modelled according to two axes (Figure extracted with permission by Price et al. (2015)), which resulted in different proportions of the land uses **b)**. The fifth scenario is a linear extrapolation of the changes observed between the SFSO areal statistics of 1985, 1997, and 2009 (Trend scenario, **c)**).

2.5. Species Distribution Modelling (SDM)

The species occurrence data and the environmental predictors were combined to model presence-only SDMs using the BIOMOD2 platform (Thuiller, Georges, et al. (2020), Version 3.4.6) in R (R Core Team (2019a), Version 3.6.1). An overview of the modelling process can be found in Figure 3.

1. **Reference model input:** For each species, four sets of randomly selected pseudo-absences were used for modelling. Barbet-Massin et al. (2012) showed that random distribution of the pseudo-absences yielded the most reliable predictions of species distribution for most model types. The pseudo-absence number was set to be three times higher than the presence frequency (Table 1). This is in line with the recommendation of Liu, Newell, and White (2019) to favor a small over a large multiplication factor between the numbers of presences and randomly distributed absence points. According to Barbet-Massin et al. (2012), the ideal ratio of presences to pseudo-absences differs between models. This is however not applicable for the generation of ensemble models (see step 4), as they rely on evaluating predictive power compared to the same data for each model type.
   Both presences and pseudo-absences were set to have a minimum distance of 100 m between each other to match the predictor resolution and to avoid spatial autocorrelation. The predictor data was prepared as described in Table 2.

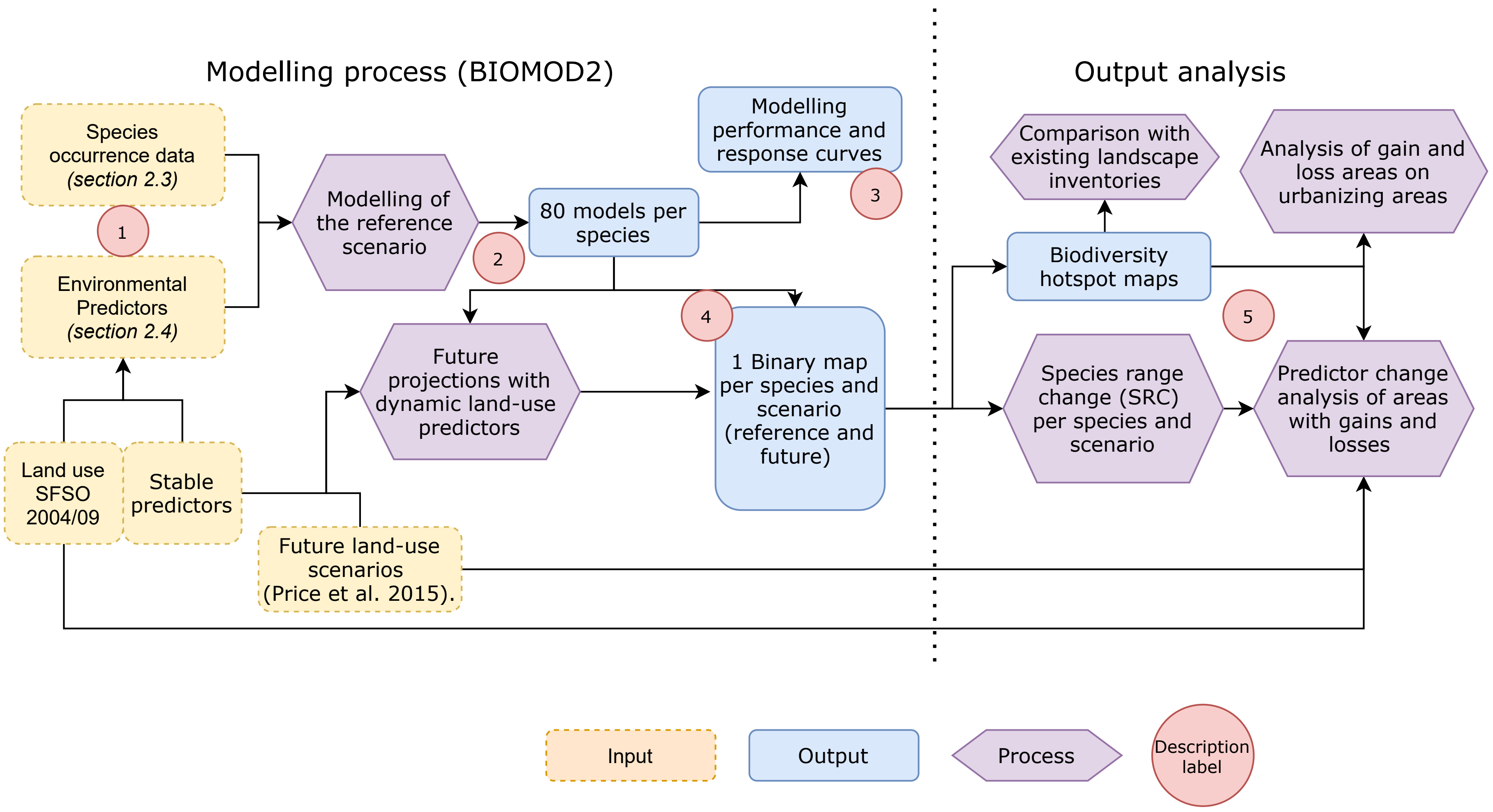


Figure 3: Overview of the modelling process *(created on diagrams.net)*

2. **Model set-up:** In this study, five models were applied: artificial neural networks (ANN, Ripley (1996)), flexible discriminant analysis (FDA, Hastie, Tibshirani, and Buja (1994)), generalized boosted models (GBM, also known as boosted regression trees, Ridgeway (1999)), generalized linear model (GLM, McCullagh (1989)) and random forest for classification and regression (RF, Breiman (2001)). For each focal species, 80 models were computed using the reference model predictors (5 model types x 4 sets of pseudo-absences (see step 1) x 4 evaluation runs (see step 3)). These models were rerun with the input data derived from the future land-use scenarios.

3. **Model evaluation:** As an alternative to evaluating a model on an independent dataset, Thuiller, Lafourcade, et al. (2009) propose data-splitting procedures. A user-defined proportion of the original data is randomly assigned as training data, while the other part is used to validate the model. To decrease the effect of the random assignment, the procedure can be repeated several times. For this study, 70 % of the presence data was used for training. Four repetitions of random classification into training and testing data were applied.
   The predictive power was assessed with the area under the curve (AUC) of the relative operating characteristic (ROC) curve (Hanley and McNeil 1982) and the true skill statistic (TSS, Allouche, Tsoar, and Kadmon (2006)). AUC is independent of prevalence as well as thresholds and considered as an effective evaluation indicator (Fielding and Bell 1997). The values range from 0 (model systematically wrong) to 1 (perfect model), where a value of 0.5 signifies that the model is not better than a random model. TSS is a threshold-dependent evaluation measure that ranges from -1 to 1. 1 signifies a perfect agreement of observations and predictors, while values below 0 indicate an agreement no better than a random classification. As applied by Zhang et al. (2015), subsequent ranges were used to interpret the evaluation values: AUC values < 0.7 were classified as poor, 0.7 - 0.9 as moderate and values > 0.9 as good modeling performance (Swets 1988). TSS values below 0.4 indicated poor, 0.4 til 0.8 useful and over 0.8 excellent models. In addition, the Boyce index was calculated which is particularly suitable for presence-only models (Hirzel et al. 2006). The values range from -1 to 1, where 1 indicates consistency between the predicted and observed presences.

4. **Ensemble modelling and binarization:** As described above, three sources introduce substantial randomness to the process of modelling: the random selection of pseudo-absences, the arbitrary assignment of the presences records into training and evaluation data as well as intermodel variance. To account for these variabilities, BIOMOD2 offers the possibility to form ensemble forecasts, where a range of different models generated by different methods and conditions is combined (Araújo and New 2007). Several options for this combination are available. For this study, the weighted mean method was chosen. In contrary to unweighted methods like committee averaging, weights are assigned depending on the predictive performance of the individual models. According to Marmion et al. (2009), the weighted mean method results in the most robust models and it is the most frequently used combination method (Hao et al. 2019). In this study, the weights were assigned based on the TSS and AUC values. In a pre-selection, models with a low predictive power (TSS < 0.4 and AUC < 0.7) were excluded.
   The binarization transforms continuous probabilities of occurrences into binary values for occurrences (presence or absence). I used the threshold that maximizes the TSS to define the threshold of binarization. According to Liu, White, and Newell (2013), it is a suitable method of binarization for presence-only data-sets.

5. **Output analysis:** In order to investigate the research topics defined in section 1, the modelling output was analyzed as follows:

   (a) To assess the influence of the different future land-use scenarios on the biodiversity hotspots, the values of changing areas were compared: This included the total area of change, as well as biodiversity hotspot gain and loss areas. Thereafter, the average change of the land-use predictors of biodiversity hotspot areas that changed between the reference and the future scenarios was calculated. This should provide insights into what land-use shifts drove the changes in biodiversity hotspots. As urbanization is expected to be an important driver of biodiversity loss (Scheffers and Paszkowski 2012), an additional analysis of the predictor change on areas that are predicted to be urbanized in the future was assessed, leading to the derivation of recommendations for the implementation of BGI.

(b) The influence of the land-use scenarios was assessed on the level of the species composition, as well as for individual species. For each species, the percentage of gained or lost area between the reference and future scenario was calculated. The difference between the gain and loss values is the species range change (SRC). It is an indicator if gains (positive values) or losses (negative values) are higher. The ten species were combined into groups of similar SRCs. Of the species with the most extreme changes, the changes in the predictors were calculated. Reasons for the extreme change were investigated with the help of ecological information of the species (Table 1) and the response curves. Response curves show how the species occurrence probability changes with increasing values of each predictor.

(c) In order to identify regions with existing or missing BGI coverage, the modelled amphibian biodiversity hotspots of the reference scenario were compared with the BLN regions and the "wetland" network of the REN (section 2.2).

3. Results

3.1. Model Assessment

For each species, ensemble models were generated and evaluated (Figure 4). They were computed with the weighted mean method based on 80 individual models per species (Figure A.8). The TSS values range between 0.5 and 0.8 and are classified as "useful" models (Zhang et al. 2015). The AUC values for *Triturus cristatus* and *Hyla arborea* are classified as "good" models, while the others rank "moderate" (Swets 1988). All Boyce indexes rank higher than 0.9, most even above 0.99 (Figure A.7). This indicates a high consistency between modelled and observed presences (Hirzel et al. 2006).

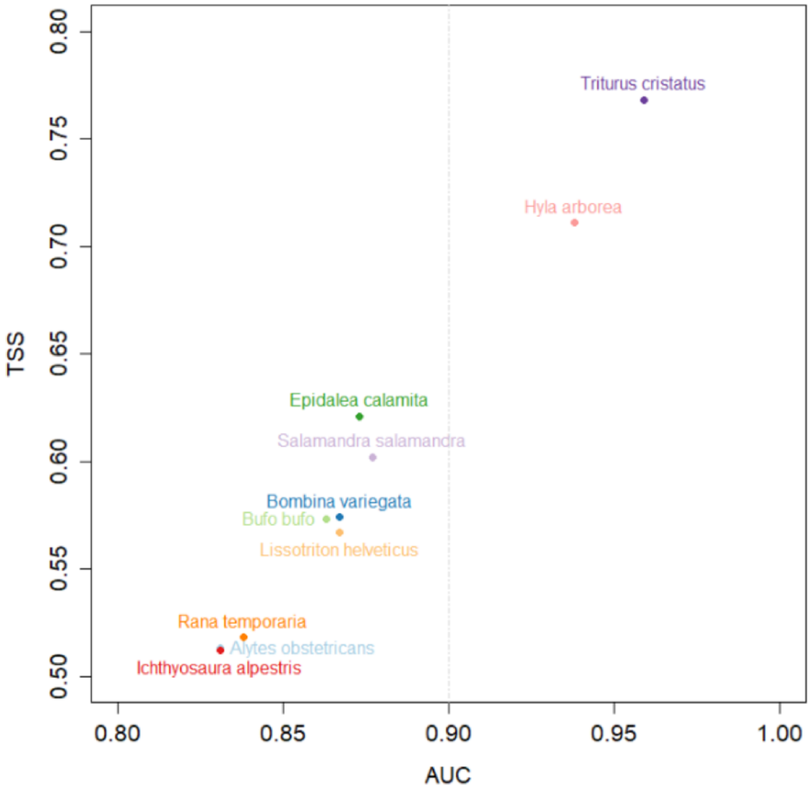


Figure 4: AUC versus TSS values of the ensemble models (reference scenario) that were calculated with the weighted mean method. The grey line corresponds to the AUC-threshold that separates “moderate” from “good” model performance (Swets 1988). The TSS values are all in the range of “useful” models (Zhang et al. 2015)

3.2. Effects of future land-use scenarios on amphibian biodiversity hotpots

Modelled biodiversity hotspots of the reference scenario encompassed 270 km^2. This corresponds to about one fifth of the Canton of Aargau. The total changes in biodiversity hotspot areas (Figure 5) ranged between 6 (scenario B1) and 32 km^2 (scenario A2). The highest absolute losses are observed in scenario A2 (19 km^2), followed by Trend (12 km^2) and scenario B2 (9 km^2). The highest absolute gains are observed in scenarios A2 (14 km^2), Trend (7 km^2), and A1 (5 km^2). Area loss was slightly higher than area gain in all scenarios. However, gains and losses contributed nearly equally to the total areas of change. At least two models agreed on predicting losses on 12 km^2 and gains on 7 km^2 (Figure 5, lower right panel).

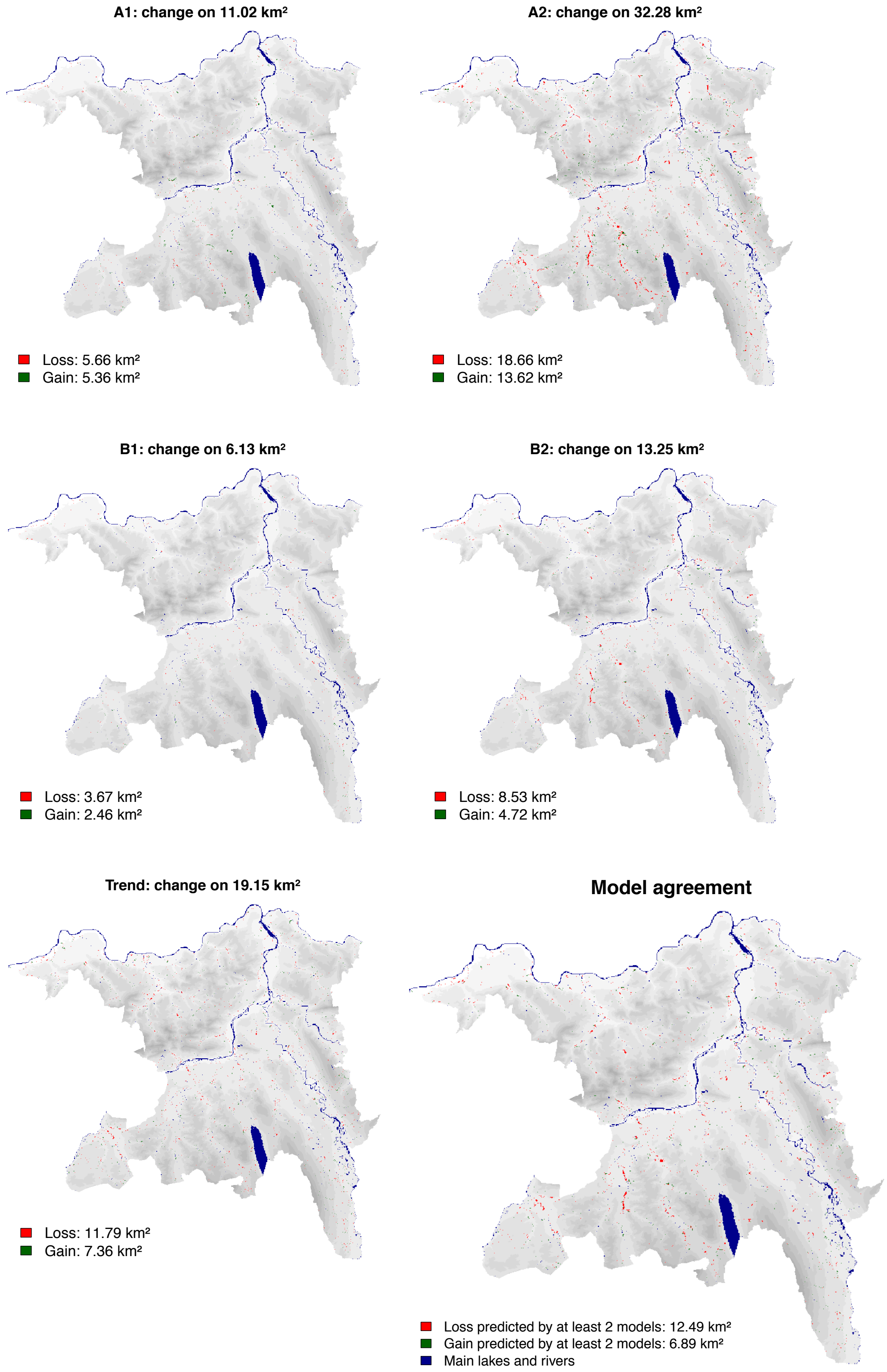
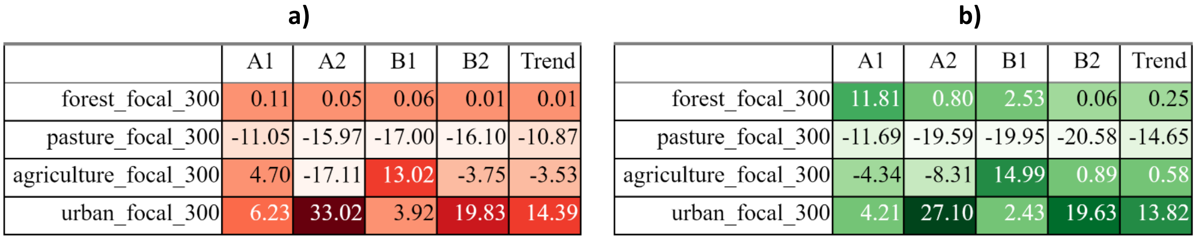


Figure 5: Changes in modelled amphibian biodiversity hotspot areas: the total changes (indicated in the figure titles) ranged between 6 and 32 km^2. Gain and loss areas contributed nearly equally to the total areas of change. The panel on the bottom right shows the areas where at least two models agreed on predicting gains or losses.

3.2.1. Land-use predictor change on areas of biodiversity hotspot changes

The change of the four dynamic land-use predictors was analyzed to gain insights into which categories drove the change in modelled biodiversity hotspots. The dynamic predictors consisted of the percentage that was covered by the corresponding land-use category within a focal window of 300 x 300 m (Table 2). Table 3 shows the average change of all pixels with hotspot gains or losses between the reference and the future scenarios.
Modelled biodiversity hotspot loss areas showed nearly no change in the percentage of forest areas, while pastures decreased in all scenarios. In scenarios A1 and Trend, pastures decreased by around - 11 %. Given A2, B1, and B2 pastures decreased by around - 16 %. Furthermore, the change in share of intensive agricultural area showed no consistent trend between the scenarios: while scenarios A1 and B1 showed a moderate (+ 4.7 %) or strong (+ 13 %) increase, scenarios B2 and Trend showed a moderate (- 3.6 %) and A2 a strong decrease (- 17 %) of intensive agriculture. The highest values of change were usually found in the percentage of urban change. A2 showed the highest increase (+ 33 %). B2 and Trend showed intermediate increases (+ 14 and + 19 %), while A1 and B1 showed lowest increases (+ 4 and + 6 %, Table 3a).
Modelled biodiversity hotspot gain areas showed similar trends like the loss areas: pasture agriculture decreased and no consistent change is shown in the change of intensive agriculture. Urban areas increased as well, however less than in areas with losses. While the percentage of forest areas did nearly not change on loss areas, the values increased on all gain areas. The highest increases were observed in scenario A1 with + 12 % and in B1 with + 2.5 % (Figure 3b).

Table 3: Average percentage change in land-use of modelled biodiversity hotspots between the reference and future scenarios on **a)** biodiversity hotspot loss areas and **b)** gain areas.



a)

	A1	A2	B1	B2	Trend
forest_focal_300	0.11	0.05	0.06	0.01	0.01
pasture_focal_300	-11.05	-15.97	-17.00	-16.10	-10.87
agriculture_focal_300	4.70	-17.11	13.02	-3.75	-3.53
urban_focal_300	6.23	33.02	3.92	19.83	14.39

b)

	A1	A2	B1	B2	Trend
forest_focal_300	11.81	0.80	2.53	0.06	0.25
pasture_focal_300	-11.69	-19.59	-19.95	-20.58	-14.65
agriculture_focal_300	-4.34	-8.31	14.99	0.89	0.58
urban_focal_300	4.21	27.10	2.43	19.63	13.82

3.2.2. Amphibian biodiversity hotspot change on future urban areas

Urbanization is regarded as a decisive land-use change factor that decreases biodiversity (section 1) and was therefore subject of particular interest. I focused on areas that were predicted to become urbanized between the reference and the future scenarios and additionally showed changes in biodiversity hotspot areas. Several differences could be observed when comparing the dynamic predictors (coverage per land-use category within 300 x 300 m) of biodiversity hotspot gain and loss areas. The percentage of surrounding urban coverage increased in all scenarios compared to the reference (Land-use (LU) 04/09). However, urban coverage was lower for biodiversity hotspot gain areas compared to loss areas. All medians of urban percentage on gain areas remained below 70 % in the future scenarios (Figure A.9a). All biodiversity gain areas showed a higher forest percentage (medians > 20 %) compared to loss areas (medians ∼ 0 %, Figure A.9b). The change of the two predictors representing surrounding coverage of agricultural land use was not ambiguous. Generally, the coverage of intensive and pasture agriculture decreased between the reference and the future scenarios. However, the percentages of biodiversity hotspot gain and loss areas were not significantly different from each other (Figure A.9c and d).
Modelled biodiversity hotspot loss on future urban areas mostly occurred at lower distances to water (< 200 m), a lower standard deviation of elevation (< 3 m), and higher soil moisture

(value ∼ 3) than biodiversity hotspot gain areas (upper panels of Figure 6). These values can be compared to the frequency distribution of all areas that are predicted to be urbanized in the future (lower panels of Figure 6). Similar values are observed for the most frequent future urban areas as well as for areas predicting biodiversity hotspot loss.

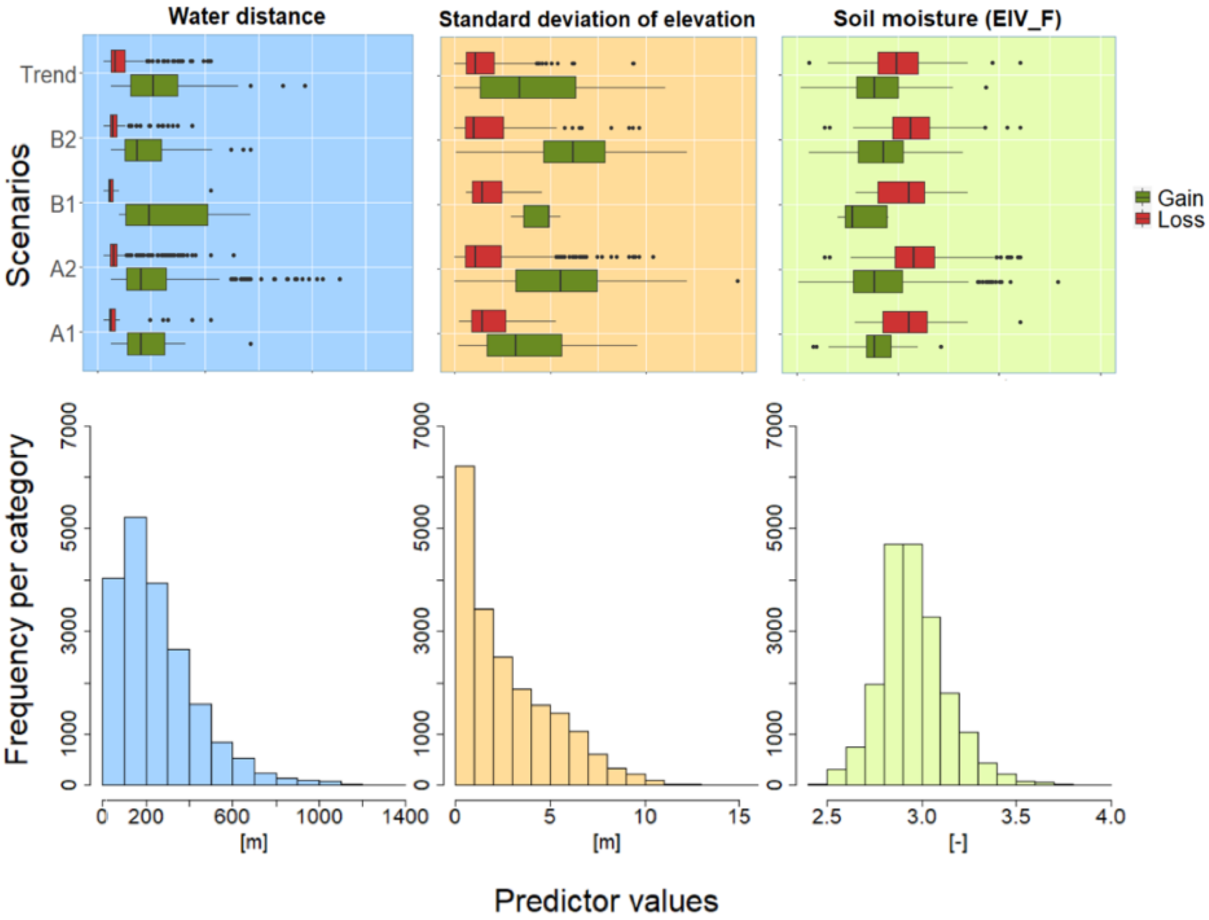


Figure 6: The boxplots (upper panels) show the values of the stable predictors of future urban areas that were predicted to have biodiversity hotspot gains or losses. Gains usually occurred in areas with a higher distance to water, a higher standard deviation, and lower soil moisture than loss areas. The histograms (lower panels) show the distribution of the stable predictors on all future urban areas. Similar predictor values are observed for the predicted biodiversity hotspot loss areas as for the most frequent future urban areas.

3.3. Effects of future land-use scenarios on individual species

Different habitat requirements of the species (Table 1) require adaptive conservation management strategies (e.g. Cushman (2006)). Therefore, Hamer and McDonnell (2008) suggest including considerations on the level community diversity as well as species-specific requirements.

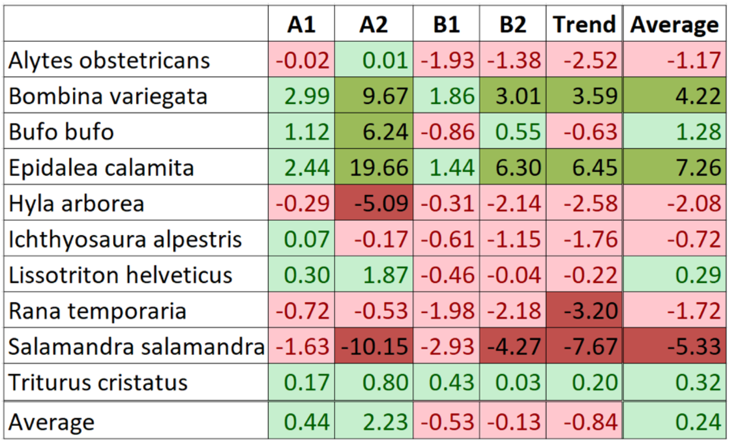
3.3.1. Composition of the species on modelled biodiversity hotspots

From the more threatened species (classified as "EN", Table 1), *Alytes obstetricans* (∼ 22 km^2) followed by *Hyla arborea* (∼ 20 km^2) covered the largest modelled biodiversity hotspot areas. The five least threatened species had the largest areas (each ∼ 26 km^2). The differences in the areas between the scenarios are low, but scenario A2 usually had the highest reductions in projected biodiversity hotspots per species compared to the reference scenario (Figure A.10).

3.3.2. Effect of future land change on individual species

The species range change (SRC, Table 4) is calculated as the difference between the percentage of gained and lost area in the future scenario compared to the reference scenario (see Figure A.1 for gain and loss values). Therefore, it indicates if gains (positive values) or losses (negative values) are higher, or if gains and losses are about in the same order of magnitude (neutral values).
A2 showed the most extreme changes followed by the Trend and B2 scenario. The lowest average changes were observed for scenarios A1 and B1. Three major patterns of SRC-responses were identified among all species: i) *Epidalea calamita* and *Bombina variegata* both showed positive values in all scenarios. Therefore, they were classified as the "high gain" group. ii) In contrast, *Salamandra salamandra* showed negative values in all scenarios and was hence classified as "high loss". iii) The SRC of all other species ranged between ± 3% in the majority of the scenarios, as gains and losses were nearly the same ("neutral group").

Table 4: Species range change (SRC, percentage of gains minus percentage of losses, Table A.1) for each species and scenario. Three response groups were distinguished: "High gain" (*Epidalea calamita* and *Bombina variegata*), "high loss" (*Salamandra salamandra*) and "neutral" (gains and losses in the same order of magnitude, all other species).



	A1	A2	B1	B2	Trend	Average
Alytes obstetricans	-0.02	0.01	-1.93	-1.38	-2.52	-1.17
Bombina variegata	2.99	9.67	1.86	3.01	3.59	4.22
Bufo bufo	1.12	6.24	-0.86	0.55	-0.63	1.28
Epidalea calamita	2.44	19.66	1.44	6.30	6.45	7.26
Hyla arborea	-0.29	-5.09	-0.31	-2.14	-2.58	-2.08
Ichthyosaura alpestris	0.07	-0.17	-0.61	-1.15	-1.76	-0.72
Lissotriton helveticus	0.30	1.87	-0.46	-0.04	-0.22	0.29
Rana temporaria	-0.72	-0.53	-1.98	-2.18	-3.20	-1.72
Salamandra salamandra	-1.63	-10.15	-2.93	-4.27	-7.67	-5.33
Triturus cristatus	0.17	0.80	0.43	0.03	0.20	0.32
Average	0.44	2.23	-0.53	-0.13	-0.84	0.24

For the further analysis, the two species with the most extreme SRC were analyzed: *Epidalea calamita* ("high gain") and *Salamandra salamandra* ("high loss"). To capture the clearest trends of possible changes, only the most extreme scenario A2 was included.
At one extreme, *Epidalea calamita* (representing the group of "high gains") showed almost no increase of urban percentage in loss areas (+ 0.5 %), but a high increase of this category in gain areas (+ 42 %, Figure A.11). This indicates that the species gained habitats in future urban areas while no habitats were lost in urbanizing areas. On loss areas, the percentage of intensive agriculture (+ 14 %) increased at the expense of pasture agriculture (- 16 %). Both categories representing agricultural land use decreased on the gain areas (- 20 %). *Epidalea calamita* was the only species that showed a slight increase in occurrence probability with increasing urban coverage in the focal window of 300 x 300 m (Figure A.12). Forest, pasture, and intensive agriculture all showed a slight decrease with increasing coverage (Figure 7).
At the other extreme, the urban percentage of *Salamandra salamandra* ("high loss") showed a higher increase on loss areas (+ 14 %) than its increase on gain areas (+ 10 %). On gain areas, the species showed a small increase in forest areas (+ 2 %). It had an increase in occurrence probability with increasing forest coverage (Figure 7).

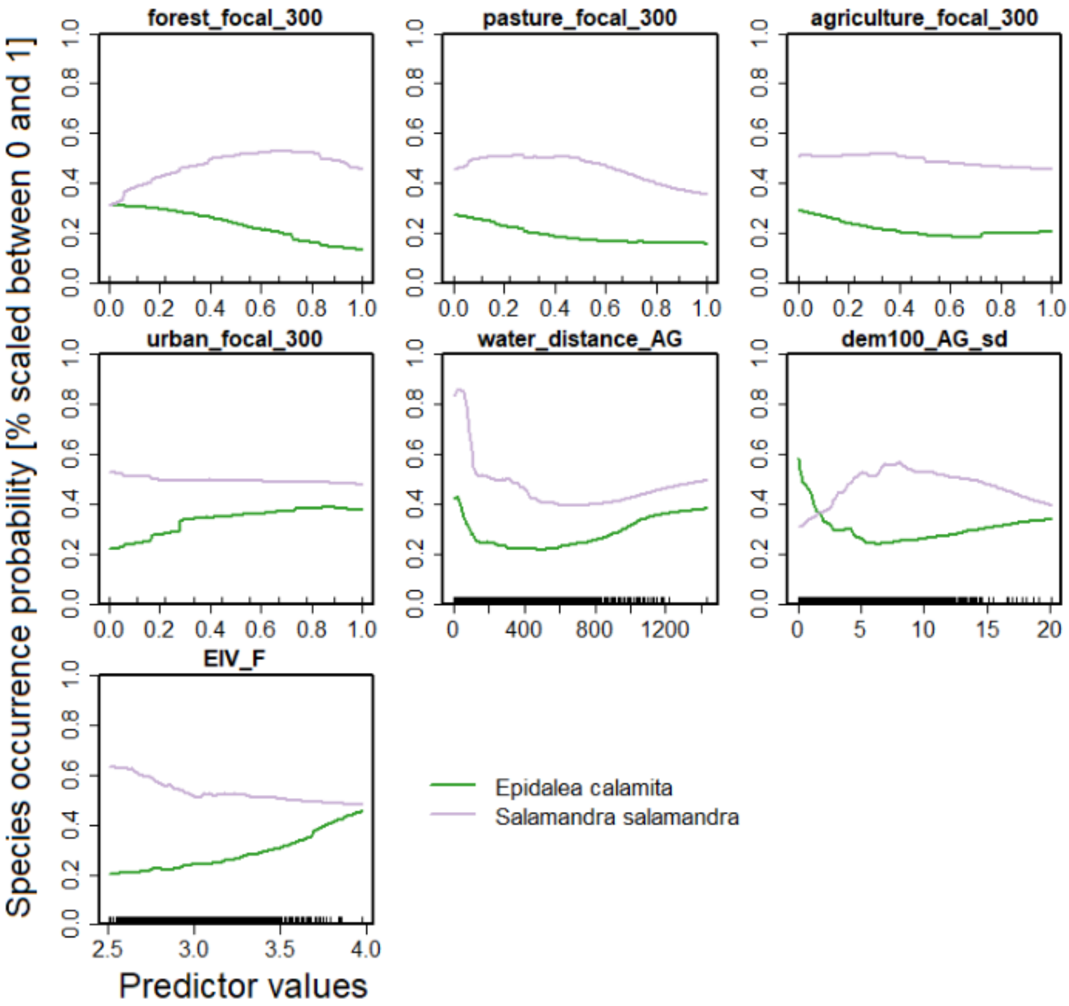


Figure 7: This are the response curves of the ensemble models from the two species with most extreme SRC changes *Epidalea calamita* (representing the group of "high gain") and *Salamandra salamandra* ("high loss"). The response curves of all species are found in Figure A.12.

3.4. Landscape inventories as a starting point for BGI to support amphibian biodiversity hotspots

To identify regions with existing or lacking coverage of BGI, the modelled biodiversity hotspot areas of the reference scenario (270 km^2) were overlapped with two landscape inventories: BLN and the "wetland" network of the REN (section 2.2). Overlaps between the modelled reference biodiversity hotspots and the BLN encompassed 48 km^2 (18 %), while 47 km^2 (17 %) covered the amphibian hotspots and REN. 19 km^2 (7 %) were covered by both inventories, while 195 km^2 (72 %) were not covered by any of the two inventories. Prominent modelled amphibian biodiversity hotspots areas that are covered by both inventories included e.g. the Reuss valley (Southeast of the canton, arrow 1 in Figure 8), or the Lake Hallwil (South, arrow 2 in Figure 8). A contiguous modelled amphibian biodiversity hotspot can be found along the Aare river (West, arrow 3). It is covered by the "wetland" REN network, but not by a BLN. In the Southwest of the Canton (arrow 4), modelled biodiversity hotspots are partly encompassed by REN areas, but no major BLN is found. This region of biodiversity hotspots in the reference scenario overlaps with areas, where at least two future land-use scenarios agreed on predicting biodiversity hotspot losses (Figure 5).

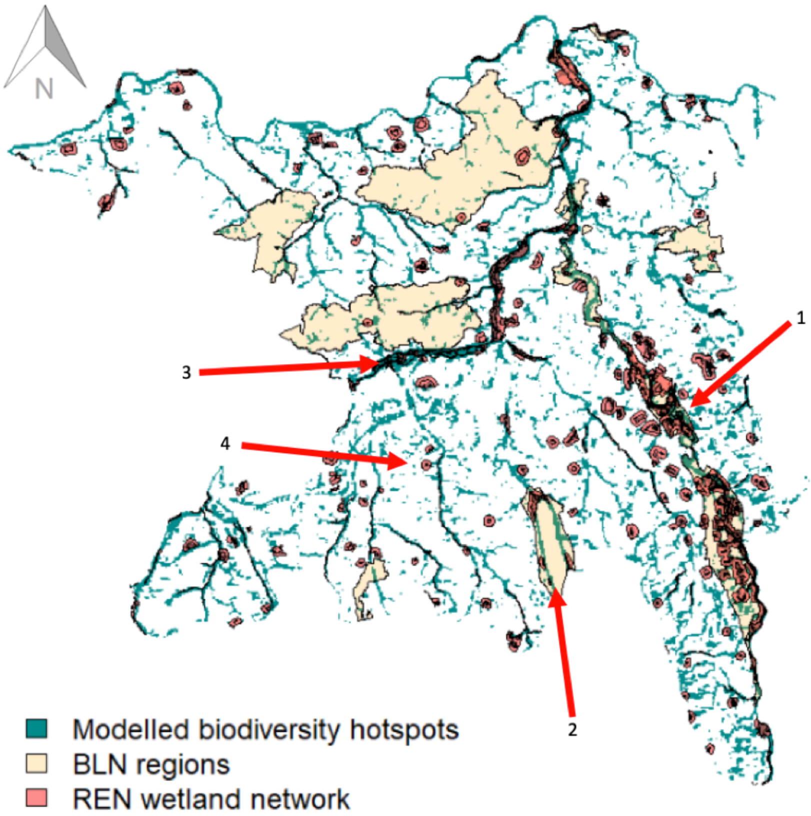


Figure 8: Modelled biodiversity hotspot areas (overlaps of at least seven predicted amphibian occurrences) of the reference scenario and their overlap with existing landscape inventories (BLN and the "wetland" network of the REN). The arrows highlight the following areas: 1) in the Reuss valley and 2) the Lake Hallwil there is an overlap between high biodiversity areas and the landscape inventories. 3) Along the Aare river, a large contiguous modelled biodiversity hotspot can be found that is covered by the REN but not by a BLN. 4) In the Southwest of the Canton (regions of Zofingen, Aarau, and Unterkulm), biodiversity hotspots and REN can be found, but no BLN. *Map sources: BLN (BAFU 2017c) and REN (BAFU 2011)*

4. Discussion

4.1. Model Assessment

All evaluation values indicated a better model performance than random ones and high spatial agreement between the real and predicted presences. Based on this, the models were assumed to be robust enough to predict species presence in the study area.

4.2. Effects of future land-use scenarios on amphibian biodiversity hotspots

The three scenarios that showed strongest urbanization on the expense of agricultural land (A2, B2 and Trend, Figures 2 and A.6) were also characterized by the highest losses in biodiversity hotspot areas (Figure 5). Areas with biodiversity hotspot loss had a higher increase of surrounding urban percentage than gain areas (Table 3). Urbanization could be confirmed as an important driver of amphibian biodiversity loss, which was also observed by e.g. Scheffers and Paszkowski (2012). Therefore, my initial hypothesis that scenarios predicting on the one hand high growth of population and economy and on the other hand have low support of governmental interventions could only be partly confirmed: urbanization associated with population growth was affirmed as an important driver, while the degree of intervention seemed to be less important, as A2 was modelled with "less intervention" and B2 with "more intervention" (Figure 2a). The degree of intervention mainly influences conservation and agricultural subsidies. For the two agricultural land uses, no clear trends could be derived (Table 3). This might have resulted from the missing response of modelled occurrence probabilities on changing values of surrounding agricultural coverage of most species (Figure A.12). Agricultural land uses can have both positive and negative influences on amphibians (Table 2), which could be a possible explanation for the observed unclear trend. Knutson et al. (2004) describes agricultural ponds as important secondary habitats. However, this benefit might be outweighed by the adverse effects of high levels of nutrients and pesticides (Brühl et al. 2013).

I did not expect that biodiversity hotspot gains and losses contributed nearly equally to the total predicted change (Figure 5). The analysis of the future urban areas that additionally showed changes in biodiversity hotspots provided possible starting points for explanations. According to the results in section 3.2.2, gains in species distributions on future urbanized areas can occur, provided that the surrounding coverage of forests is high (median was > 20 %) and the urban coverage low (median < 70 %, see Figure A.9). These values could serve as coarse thresholds for the planning of BGI regions. Forested areas provide important summer and hibernation habitats for many species (Table 1). An increasing percentage of forest in the surrounding of a breeding pond was shown to support a higher larval amphibian species richness (Rubbo and Kiesecker 2005). A high degree of urban areas usually indicates a high fragmentation and a low probability of suitable habitats (Parris (2006), Scheffers and Paszkowski (2012)). Additional insight on the biodiversity gain areas was provided through the analysis where urbanization occurred (Figures 6 and A.6). On average, urbanization occurred mostly along the river valleys, with a low standard deviation of elevation, and moderate soil moisture values. Consequently, the species gained in biodiversity hotspot areas mostly in areas with a larger distance to water, a higher standard deviation of elevation, and lower soil moisture. However, the response curves (Figure A.12) indicate lower suitability of these areas. Therefore, urbanization seems to reinforce a trend stated by Flory (1999): Primary, well-suited habitats of the amphibians in the river plains of the Canton are destroyed which forces amphibians to colonize less suited, secondary habitats on steeper slopes further away from the river plains. However, the maintenance of these secondary habitats requires large efforts. For the long-term conservation of the amphibians, the renaturation of primary habitats is of uttermost importance (Flory 1999).

The finding that losses and gains in biodiversity hotspot areas in all scenarios - even the ones with the highest risk of urbanization - are almost equally high, is desirable for the future conservation of amphibian species in the study area as no drastic decrease in the total occurrence area was predicted. However, it is questionable if the predicted biodiversity hotspot gain areas could indeed be successfully colonized in time. On the one hand, successful colonization would depend on the presence or creation of suitable habitats as well as their quality. For instance, the habitat suitability of newly created ponds or restored wetlands was shown to depend on chemical properties of the water like electrical conductivity (Stumpel and Voet 1998), or the presence of fish (Porej and Hetherington 2005). These important small-scale drivers of species occurrence could not be included in this study, as no data-set covering the whole study area is available and the model resolution of 100 x 100 m would be too coarse for this purpose. On the other hand, the additional areas of potential habitats need to be within a reachable distance from the loss areas. As the maximum migration distances, which were regarded as an indicator of dispersal ability (Dawideit et al. 2009), vary considerably (Table 1), species with a high distance might profit more from the establishment of new areas as observed by Lehtinen and Galatowitsch (2001). Della Rocca and Milanesi (2020) investigated the influence of dispersal ability on future distribution predictions for beetles under both climate and land-use change. They found that expansion of species distributions under climate change was predicted under the unrealistic assumption of unlimited dispersal, but not if accounting for the limited dispersal abilities of the endangered species.

4.3. Effects of future land-use scenarios on individual species

An important issue to consider for the establishment of additional protected areas is which species could be supported with it. While the occurrence number of the most and the least frequent species differ by a factor of 10 (Table 1), the differences between species were by far not that extreme when comparing the modelled biodiversity areas (Figure A.10), as the biodiversity hotspots seemed to encompass suited habitats for a wide selection of amphibian species. Therefore, it seems probable that also the most threatened species, such as *Triturus cristatus*, could benefit from additional protection of these areas.

The species were classified into three groups according to their SRC. The balance between the gain and loss areas of biodiversity hotspots in the future (Figure 5) was also visible in the SRC: most species were classified in the "neutral group" with only minor predicted changes. The two species with the most extreme changes were further analyzed: *Epidalea calamita* (SRC of up to + 20 % in A2) represented the "high gain" group and *Salamandra salamandra* (SRC of - 10 % in A2) the "high loss" group (Table 4).

The high gains of *Epidalea calamita* in all scenarios with high urbanization (A2, B2, and Trend) matches the response curve of the species (Figure 7). It is the only species that showed a slight increase of probability occurrence with an increasing percentage of urban areas in the surrounding 300 m (Figure A.12). As a result, it showed the highest increase of surrounding urban coverage on gain areas, while urban areas did not contribute to loss areas (Figure A.11). Its evaluation metrics of the ensemble model in the reference scenario scored among the highest of all species (Figure 4). Nevertheless, it is questionable if the modelling results for *Epidalea calamita* are realistic. The species needs specific habitats (Table 1, Mermod, Zumbach, Aebischer, et al. (2010)). Rubbo and Kiesecker (2005) hypothesized that species with general habitat requirements are more resilient to urban development and therefore found more frequently in urban or suburban habitats. Typical secondary dynamic habitats of *Epidalea calamita* like quarries are not found within cities. Private gardens have - if any - mostly static ponds and thus do not provide suitable habitats either (Mermod, Zumbach, Aebischer, et al. 2010). Therefore, occurrence data that was gathered on construction sites or quarries that might coincidentally be near cities, could have misinformed the models. However, *Epidalea calamita* is additionally classified as "Pioneer" (Mermod, Zumbach, Aebischer, et al. 2010). According to Aubry (2012), the reproductive success of the species mainly depends on the absence of predators, while it is surprisingly resilient regarding various environmental factors like pH. This resilience might indicate that the species could potentially profit from urban BGI, provided that pioneering conditions with the absence of aquatic predators like fish are maintained with an appropriate management strategy.

Contrary to *Epidalea calamita*, *Salamandra salamandra* showed high losses in all future scenarios with urbanization. The specialization on forest areas as described by Küry (2003) is reflected in the response curves. It showed the highest increase of probability with an increasing share of surrounding forest (Figure A.12). Additionally, the species shows the highest increase of forest percentage on gain areas (Figure A.11). Its preference for pristine and undisturbed habitats (Flory 1999) might explain why urban areas are not suitable for the species. Therefore, the conservation of the species might be better supported by the continuation of the FOEN (2013) strategy which does not allow net losses of forest areas than with BGI implementation in urban areas.

4.4. Landscape inventories as a starting point for BGI to support amphibian biodiversity hotspots

Two landscape inventories were included as a starting point to establish BGI for long-term amphibian conservation. Generally, BLN and REN of the Canton of Aargau were located in areas where also high modelled amphibian biodiversity was predicted by the models in the reference scenario. Each BLN and REN covered around 18 % of modelled biodiversity hotspot areas and 7 % were covered by both inventories. However, 72 % were not covered by any of the two included landscape inventories. The coverage of the BLN differed by region. Some regions like the Reuss valley (BAFU 2017b) are well covered and can be considered to already have an intact network of BGI with legally binding protection laws. Other regions, like the Southwest of the Canton, encompassed parts of the REN "wetland" network, but no BLN. As several models agreed in predicting losses of amphibian biodiversity hotspots in this region (Figure 5), this finding could support decisions to establish additional areas with legally binding protection laws.
The selection of BLN regions and the "wetland" REN network as a base for a BGI network was meant to serve as a first overview for the identification of well and poorly-covered regions. However, the selection is not conclusive. For a more detailed analysis, additional frameworks like groundwater protection zones could be included. Amphibians might profit from these, as agricultural activities like soil drainage are restricted and the potential pollution of the soil and water must be prevented in these areas (BUWAL 2004).

4.5. Limitations

The present study allowed to assess the influence of future land-use scenarios on the scales of both amphibian biodiversity and individual species. However, there are various limitations.

A major caveat of this study is the modelling resolution of 100 x 100 m. The coarse resolution was predetermined by the resolution of the future land-use scenarios and allowed to investigate broad trends. However, the habitat suitability for amphibians is probably determined on a smaller scale by the presence of suitable aquatic spawning grounds and summer as well as hibernation habitats in the vicinity. This can not be adequately represented in hectare-sized pixels. An additional important characteristic is the connectedness of the landscapes which was not addressed in this study. Suitable structures like hedgerows allow the exchange between populations while major roads act as isolation barriers (Hels and Buchwald 2001).

The occurrence data gathered by the cantonal volunteer-based Amphibian Monitoring is a standardized and long-term data source. As it is gathered with expert knowledge rather than random citizen-science observations, the quality of the data is expected to be high. Nevertheless, some limitations have to be taken into account. As only spawning grounds are sampled, no information on the habitats that the animals need throughout the rest of the year is available. Furthermore, most sampling sites are in agricultural land, which results in undersampling of forests and urban areas. Even though each selected breeding site is visited three times during the breeding season, species are expected to be detected

imperfectly (Schmidt 2005). As two of the three visits are nocturnal, species with no (newts and salamanders) or less conspicuous mating calls might be overseen.
The definition of the biodiversity hotspot areas only included the species richness, which is a widespread measure to assess influences of habitat change on amphibians (Gardner, Barlow, and Peres 2007). As discussed by e.g. Devictor et al. (2010) and Hillebrand et al. (2018), more aspects like genetic or functional diversity have to be included to adequately represent the multi-faceted nature of biodiversity.

Concerning the land-use predictors, it is questionable if such a highly fragmented and complex landscape like the study area can be depicted in only four different land-use classes. Out of the four land-use predictors, the two agricultural categories are expected to be the most problematic, as according to Esch et al. (2014) a combination of observations with different sensors at multiple scales in multiple seasons is needed to realize a robust classification system. The model responses regarding agricultural land use were the least unambiguous (see e.g. Figure A.9 c and d). Probably more than two categories would be needed to adequately represent the complexity of agricultural land uses. The intensity of the agriculture, as well as the presence of suitable aquatic habitats and connecting landscape elements like hedges, varies decisively between individual farms and regions. Additionally, in contrast to the stable land uses of forest and urban areas, pasture and intensive agriculture are expected to vary most between the years. Furthermore, within a hectare of agricultural land, it is expected that both pasture and intensive agriculture could occur. A further source of uncertainty lies in the processing of the aerial photographs. Although the interpretation is conducted with a standardized procedure, there is a classification error. As described by the SFSO (n.d.), the error in estimation increases with decreasing frequency and decreasing size of contiguous areas. While the relative sampling error of the categories Closed Forest, Pasture and Intensive agriculture as well as of Urban/settlement areas is below 1.4 %, there is a considerable error of the categories Open Forest and Overgrown of 19 and 31 %. The problem of the high sampling error of the least frequent categories was avoided by merging the categories with other classes (Table 2). Although they were merged with the most similar categories, this procedure nevertheless increased the heterogeneity within the four land-use categories.
The future land-use scenarios of Price et al. (2015) were developed to identify likely risk areas of land abandonment and urbanization. Spatially exact modelling of future land use is not possible. Unforeseen future developments might change future developments completely. Furthermore, the scenarios were developed and validated on a national scale. On the one hand, this can be considered as an advantage, as the Canton of Aargau is unlikely to develop independently from the national framework. On the other hand, Switzerland includes highly different regions (Camenzind et al. 2011). Although this has been taken into account in the modelling process, the predicted changes might still be not specific enough for the study area. Additionally, it was not possible to explicitly include all legal frameworks. For instance, the cantons are obliged to define water areas ("Gewässerraum") since 2011 (BPUK et al. 2019). In these areas, no new installations are allowed to be built and only extensive agriculture is possible. This might alleviate urbanization pressure in the lower river valleys (Figure 6), which would mitigate the trend described by Flory (1999) that amphibians are forced to colonize secondary habitats which are less suited for the species.

Some decisions during the modelling process introduced additional uncertainties. The transition of the probability to binary (presence/absence) maps included the definition of a threshold. If a too low threshold is used, the presence of species is overestimated (Freeman and Moisen 2008). The thresholds were calculated in order to maximize the TSS and ranged between 24 and 48 %. About one fifth of the total study area was predicted to contain amphibian biodiversity hotspot areas (Figure 8). This might indicate an overestimation of the species distributions.

5. Conclusion

Land-use change, especially urbanization, are important drivers of worldwide biodiversity decrease (Foley et al. (2005), Liu, He, and Wu (2016)). This threatens the provision of ecosystem services for future generations. The concept of BGI can help to alleviate conflicts between natural and human ecosystems in both urban and rural landscapes (Kowarik, Fischer, and Kendal 2020).
This thesis allowed to assess the influence of different land-use scenarios on biodiversity hotspots, derive coarse thresholds on how gains of biodiversity hotspot areas might be possible on future urban areas, detect differences in the influence of the land-use scenarios on individual species, and identify regions with existing and missing coverage by landscape inventories as starting points for BGI.

As expected, scenarios with a high degree of urbanization showed the highest losses in future biodiversity hotspots. Therefore, urbanization could be confirmed as an important driver of amphibian biodiversity change, as described by e.g. Scheffers and Paszkowski (2012). However, it was not expected that gains in the modelled biodiversity hotspots were nearly equally as high as the losses. According to the models, gains in biodiversity hotspots on urbanizing areas are possible, provided that the surrounding coverage of urban land use is below a threshold of 70 % and the percentage of forest cover is higher than 20 %. These values could serve as coarse thresholds for how BGI could be planned in urbanizing areas. The effect of agricultural land-use coverage could not be determined in this study.
Comparing the stable predictors of changing biodiversity hotspot areas on future urban areas, gains mostly occurred within a higher distance to water, a higher standard deviation of elevation, and lower soil moisture, despite decreasing habitat suitability of these areas. This is a consequence of urbanization, which in the included scenarios occurs mainly in the low elevation areas of Canton along the major river valleys. In these flat areas with high proximity to water and high soil moisture, primary habitats of amphibians can be found. Therefore, the future scenarios predict a continuation of the trend that amphibians are displaced from their primary habitats and forced to colonize less suitable, secondary habitats (Flory 1999). As the maintenance of secondary habitats requires large efforts, the renaturation of primary habitats should be prioritized.

The model results indicated that a wide range of species could profit from the protection of the modelled biodiversity hotspots, as the most endangered species (e.g. *Triturus cristatus* or *Hyla arborea*) were also represented to a large extent on biodiversity hotspot areas. However, the comparison of the two species with the most extreme SRC changes is an example of the need for additional species-specific conservation strategies. While the implementation of urban BGI might be suitable for the pioneering species *Epidalea calamita*, *Salamandra salamandra* might profit more from consistent protection of forest areas.

While some modelled amphibian biodiversity hotspots like the Reuss valley are already well protected by existing BLNs and can be considered to already have coverage of BGI, other regions like the Southwest of the Canton (regions of Zofingen, Unterkulm, and Aarau) lack legally binding protection areas. As several models agreed to predict losses of amphibian biodiversity hotspots in these regions, this finding might support decisions to improve BGI for amphibian conservation in this area. To ensure connectivity, the REN "wetland" network could serve as a starting point of where these areas with legally binding protection goals could be placed.

5.1. Outlook

In order to gain more precise and further insights on amphibian conservation, the effect of land-use change, and the planning of BGI, I propose several further investigations.

Firstly, the applied methods of this thesis could be improved to gain more precise results. To further decrease the uncertainties, the number of different models, evaluation runs, and pseudo-absence data-sets could be increased. Furthermore, the application of different methods to derive the binarization thresholds could indicate how reliable the resulting occurrence distributions were.

The modelling in the resolution of 100 x 100 m of this study, which allowed the application of the future land-use scenarios derived by Price et al. (2015), could be complemented with high-resolution models to derive more specific recommendations for BGI that support amphibian biodiversity or meet species-specific requirements.

Provided that suitable occurrence data-sets are available, the study could be repeated for a larger study area in Switzerland. This could for instance include the whole Central Plateau. This could allow the development of adequate conservation strategies in areas with a high risk of amphibian biodiversity loss across cantonal borders.

Additional standardized and long-term monitoring data would allow more generalised findings. On the one hand, monitoring programs could include other threatened species like insects, aiming to maximize the benefits of BGI for multiple species groups (Pinho et al. 2016). On the other hand, monitoring programs could focus more on urban areas. As urbanization is predicted to continue in the next decades, its adverse effects should be met with adequate strategies to mitigate adverse effects on biodiversity (Kowarik, Fischer, and Kendal 2020). However, amphibians are reported to be understudied in urban and suburban areas (McDonnell and Hahs (2008), Scheffers and Paszkowski (2012)). Additional to species richness, genetic data could capture another aspect of biodiversity. As recently described by Yannic et al. (2021) in a study investigating *Salamandra salamandra* in the Canton of Lucerne, genetic data could contribute to better understand what land use poses barriers for amphibian movement.

As a practical application, the overlay of the landscape inventories with modelled amphibian biodiversity hotspots could serve as a map of where the potential of the restoration of wetlands on the nowadays drained agricultural areas is highest. According to Weber et al. (2019), many drainage works in Switzerland require reconstruction. Therefore, the time for rewetting of areas that can support amphibian biodiversity and connect habitats is favourable. A special focus could be put on areas that are predicted to show high future biodiversity losses.

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A. Appendix

A.1. Methods

A.1.1. Species data

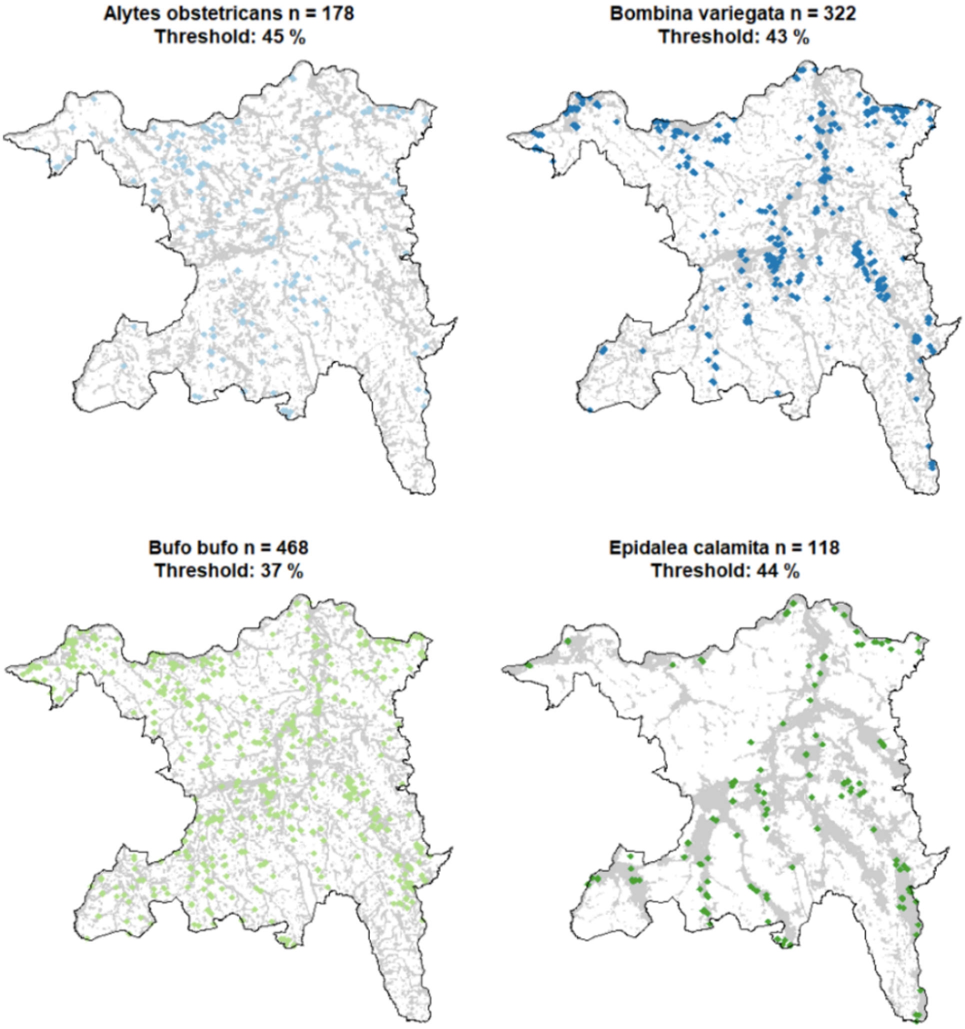


Figure A.1: Occurrences, binarization thresholds, and modelled presence in the reference scenario (grey) for each focal species.

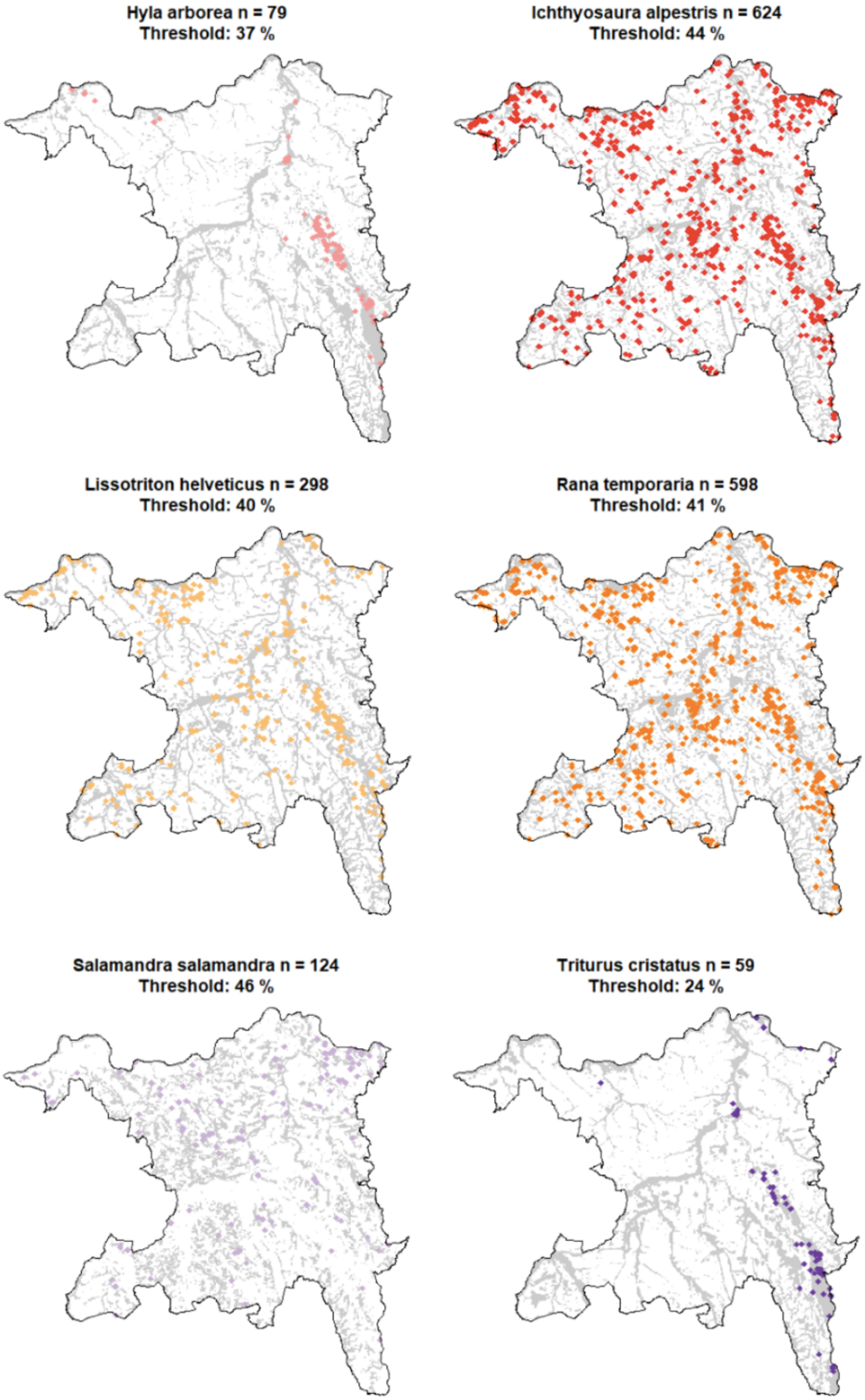


Figure A.2: Occurrences, binarization thresholds, and modelled presence in the reference scenario (grey) for each focal species.

A.1.2. Predictor rasters

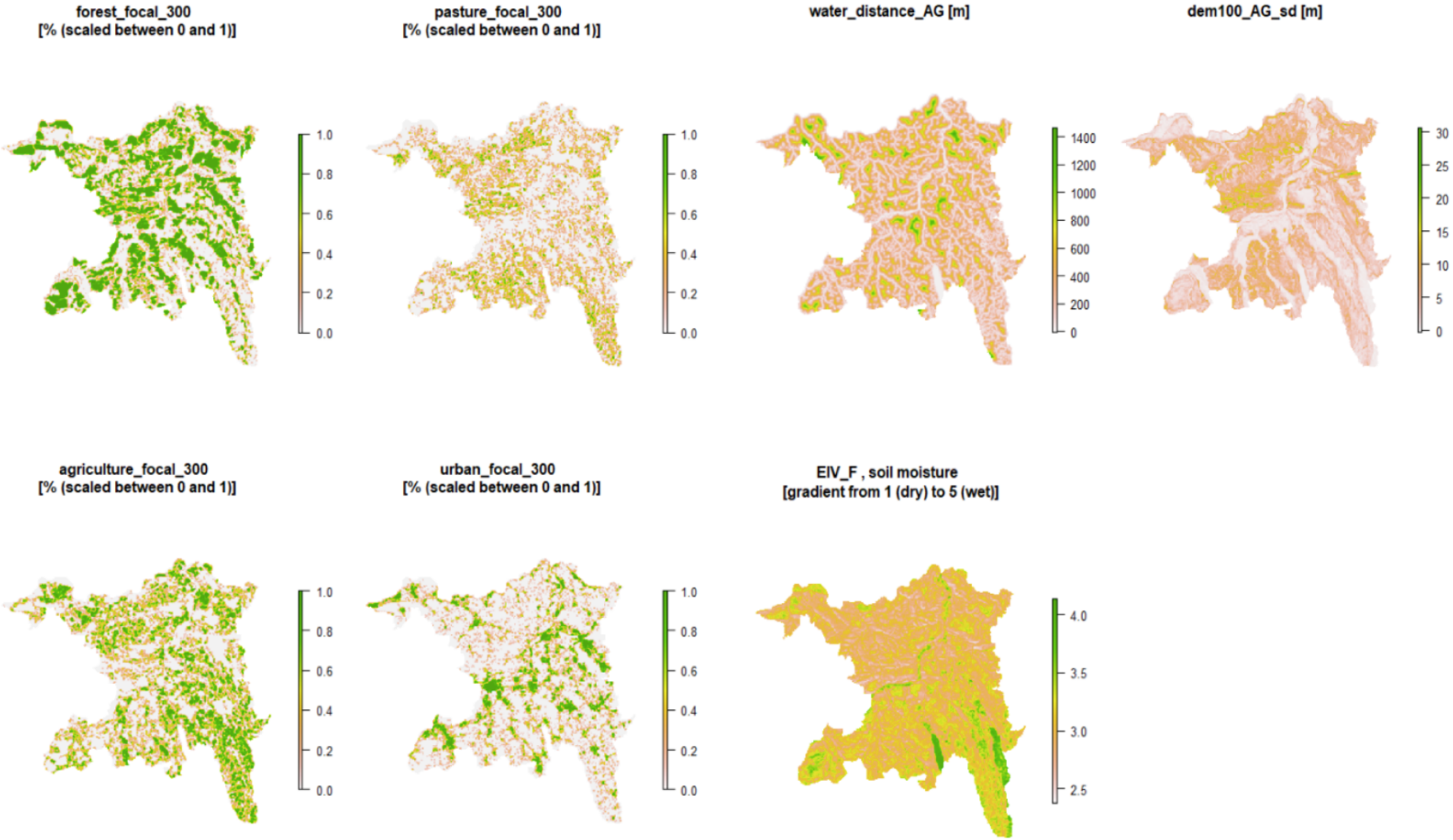
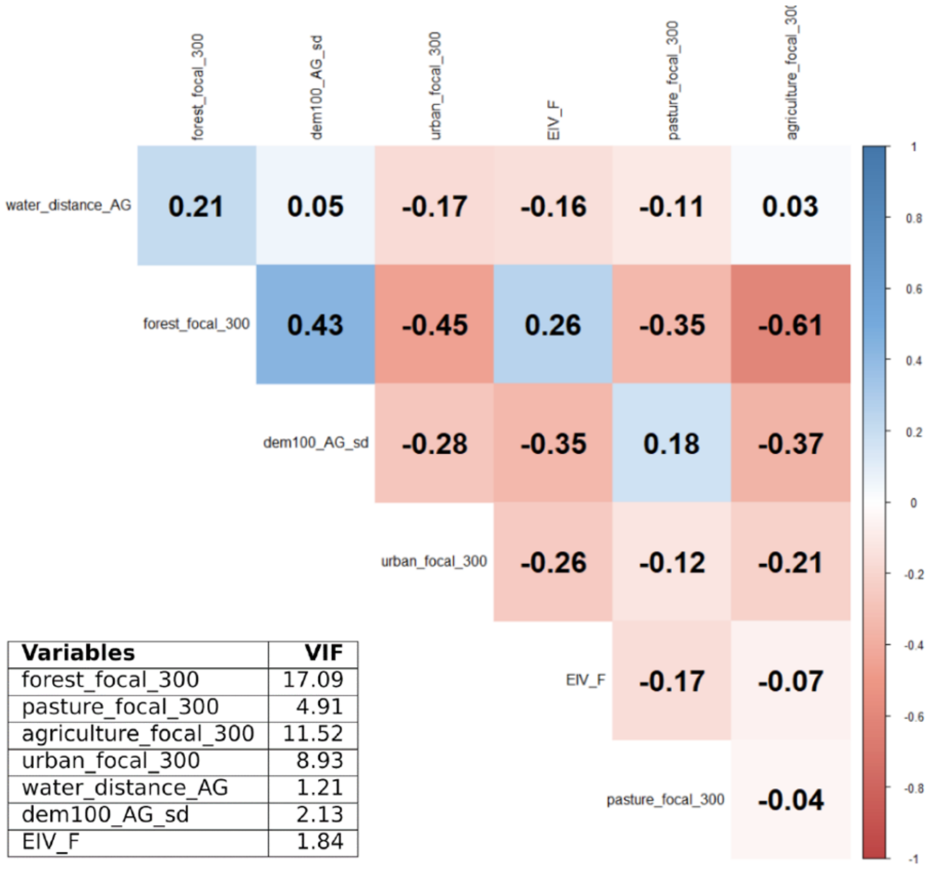


Figure A.3: Predictors of the reference scenario (areal statistics 2004/09 produced by the SFSO) and their units.

A.1.3. Correlation and variance inflation of the predictors

The Variance inflation factor and the Pearson correlation among the predictors of the reference scenarios were calculated (Figure A.4). Predictors are recommended to show lower correlations than a threshold of 0.7 (Green 1979) or 0.8 (Menard 2002). The highest absolute correlation of 0.61 among “Forest” and “Intensive agriculture” does not exceed these thresholds. Concerning the VIF, Guisan, Thuiller, and Zimmermann (2017) recommend excluding variables with a higher value than 10. However, values of VIF of 10, 20, 40, or even higher do not by themselves discount the results of regression analyses according to O’Brien (2007). The VIF of the predictors "Forest" and "Intensive agriculture" exceeded the threshold of 10. Nevertheless, both predictors were kept, as the loss of information would have been too severe if one predictor would have been excluded. The correlation was calculated with the package “stats” (R Core Team 2019b). The VIF was computed with the package “usdm” (Naimi et al. 2014).



	forest_focal_300	dem100_AG_sd	urban_focal_300	EIV_F	pasture_focal_300	agriculture_focal_30
water_distance_AG	0.21	0.05	-0.17	-0.16	-0.11	0.03
forest_focal_300		0.43	-0.45	0.26	-0.35	-0.61
dem100_AG_sd			-0.28	-0.35	0.18	-0.37
urban_focal_300				-0.26	-0.12	-0.21
EIV_F					-0.17	-0.07
pasture_focal_300						-0.04

Variables	VIF
forest_focal_300	17.09
pasture_focal_300	4.91
agriculture_focal_300	11.52
urban_focal_300	8.93
water_distance_AG	1.21
dem100_AG_sd	2.13
EIV_F	1.84

a) **b)**

Figure A.4: a) Variance inflation factors (VIF) and **b)** Pearson correlations of the predictor values of the reference scenario.

A.1.4. Spatial representation of the land-use changes in the future scenarios

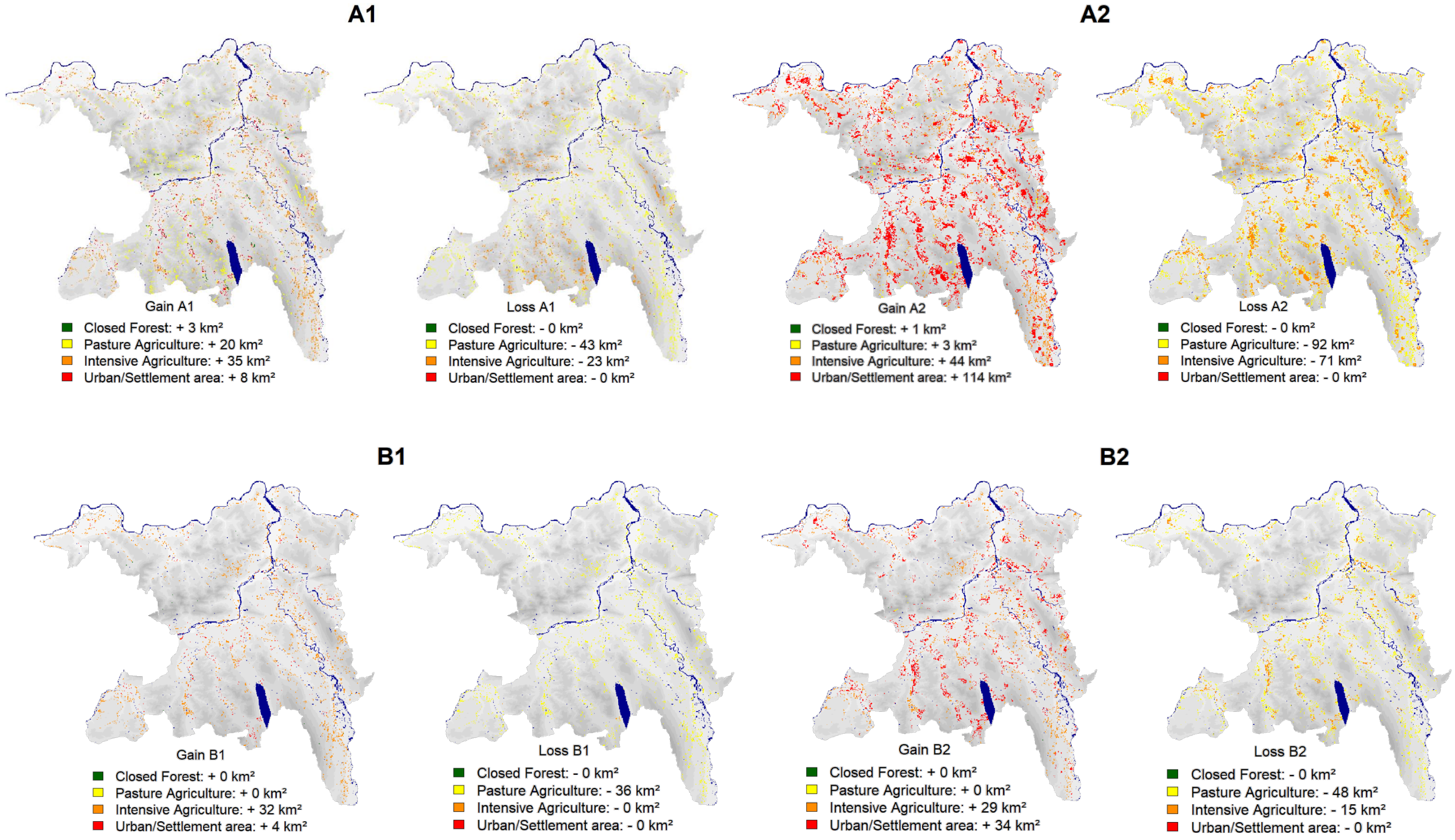


Figure A.5: Spatial representation of areas with changing land uses between the reference scenario (areal statistics 2004/09) and each future scenario developed by Price et al. (2015). Scenario A2 shows the most extreme changes.

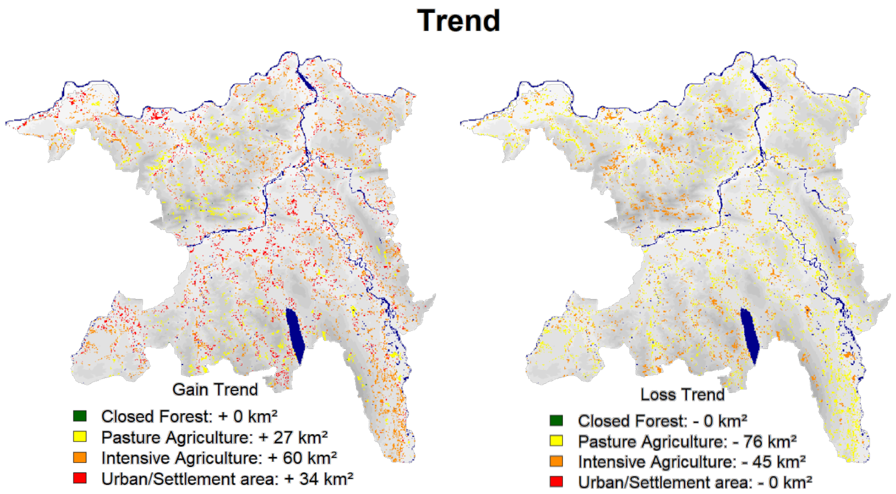


Figure A.6: Spatial representation of areas with changing land uses between the reference scenario (areal statistics 2004/09) and each future scenario developed by Price et al. (2015). The changes of the Trend scenario are more scattered than the other four scenarios.

A.2. Results

A.2.1. Model evaluation

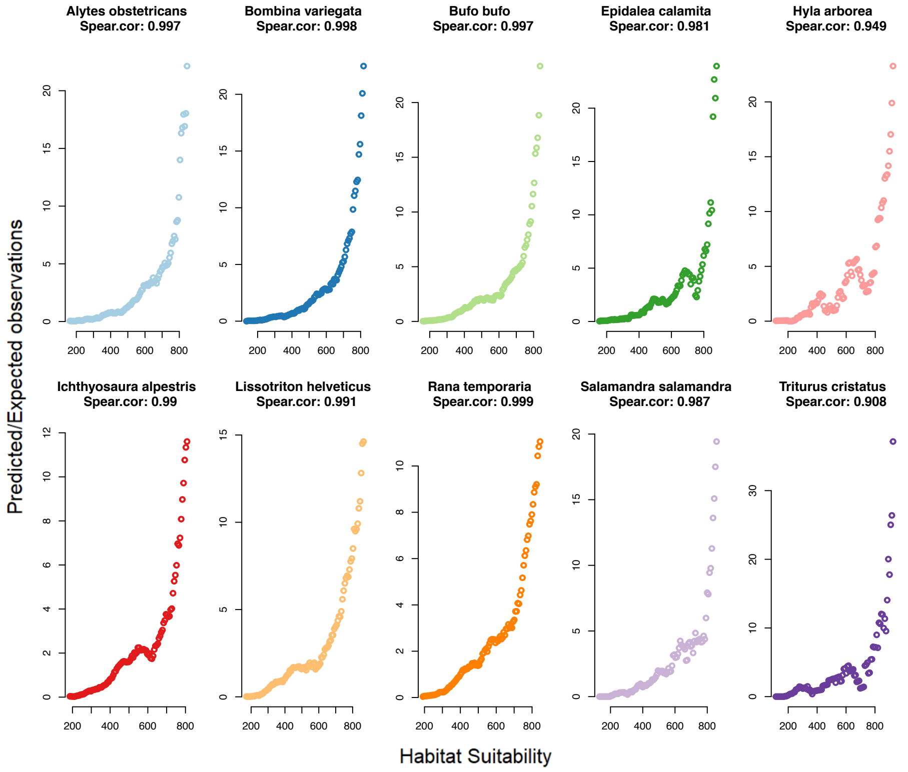


Figure A.7: Boyce index (Spearman correlation in the title) for each species of the ensemble models. The high values indicated that there is no systematic deviation of predicted and observed observations.

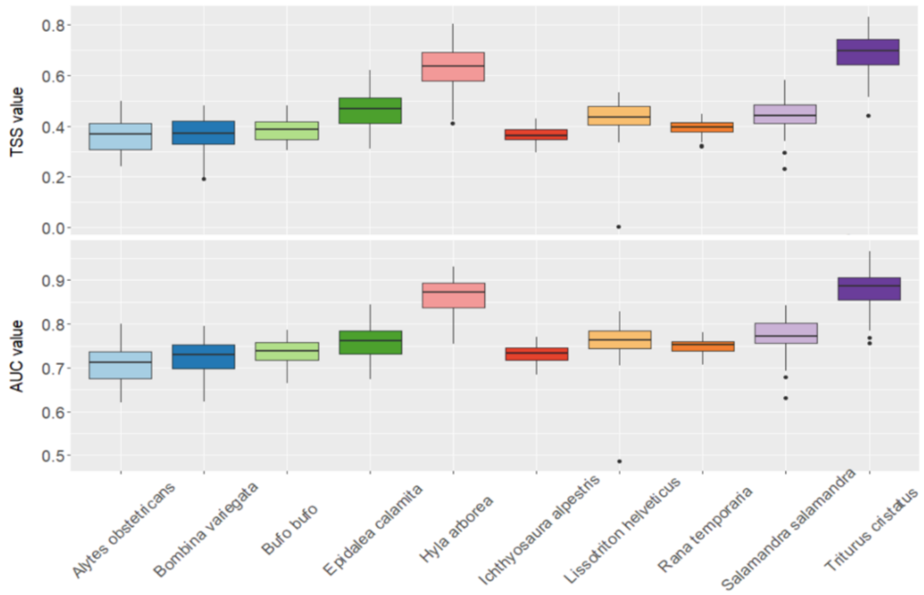


Figure A.8: The TSS (upper panel) and AUC (lower panel) values of the 80 individual models per species.

A.2.2. Dynamic predictors of changing biodiversity hotspot areas on future urban areas

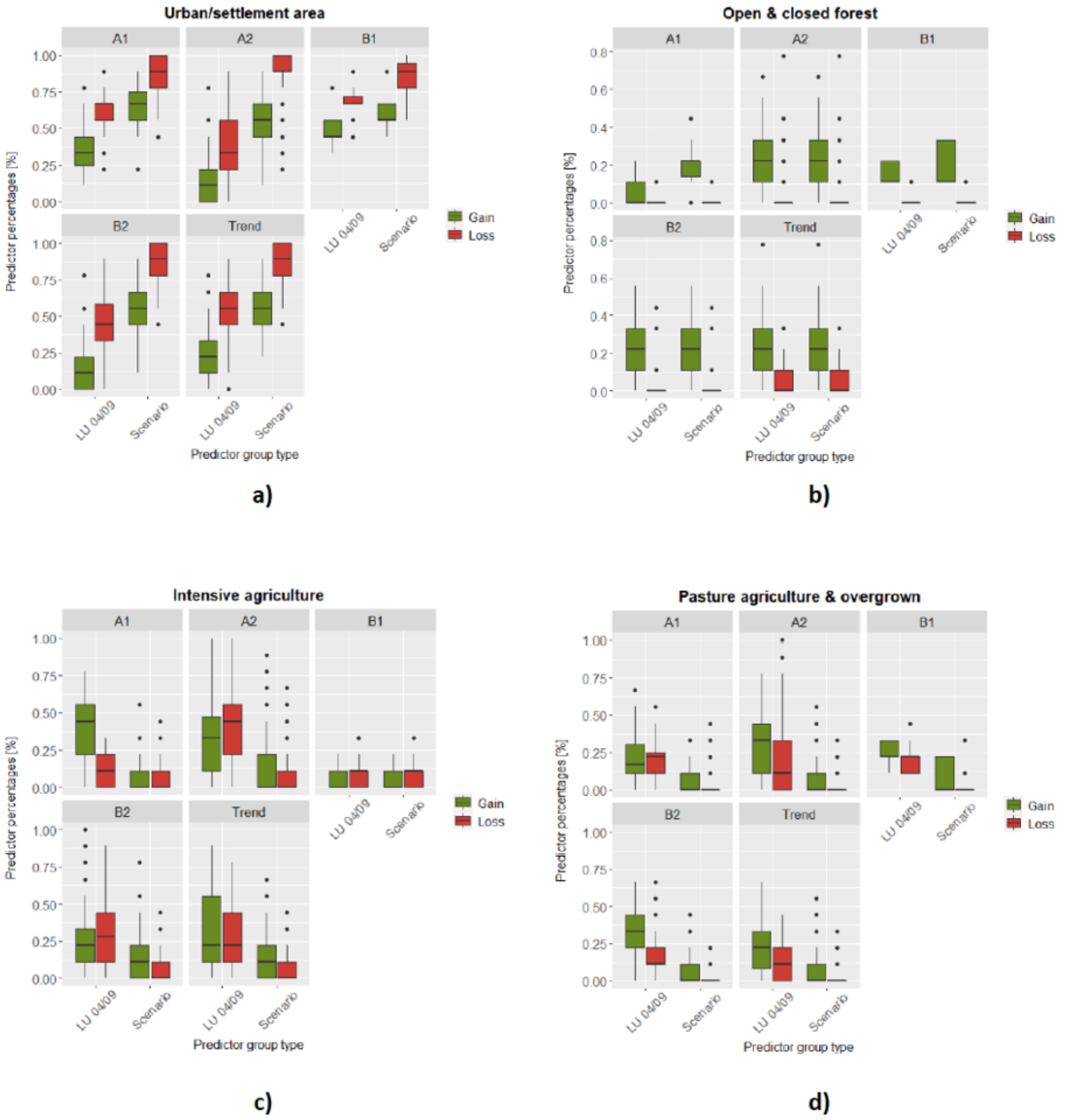


Figure A.9: Predictor analysis of biodiversity hotspot changes on areas that are predicted to be urbanized in the future scenarios. The four dynamic land-use predictors **a)** Urban/settlement area, **b)** Open & closed forest, **c)** Intensive agriculture and **d)** Pasture agriculture & Overgrown can be seen.

A.2.3. Effect of future land-use scenarios on individual species

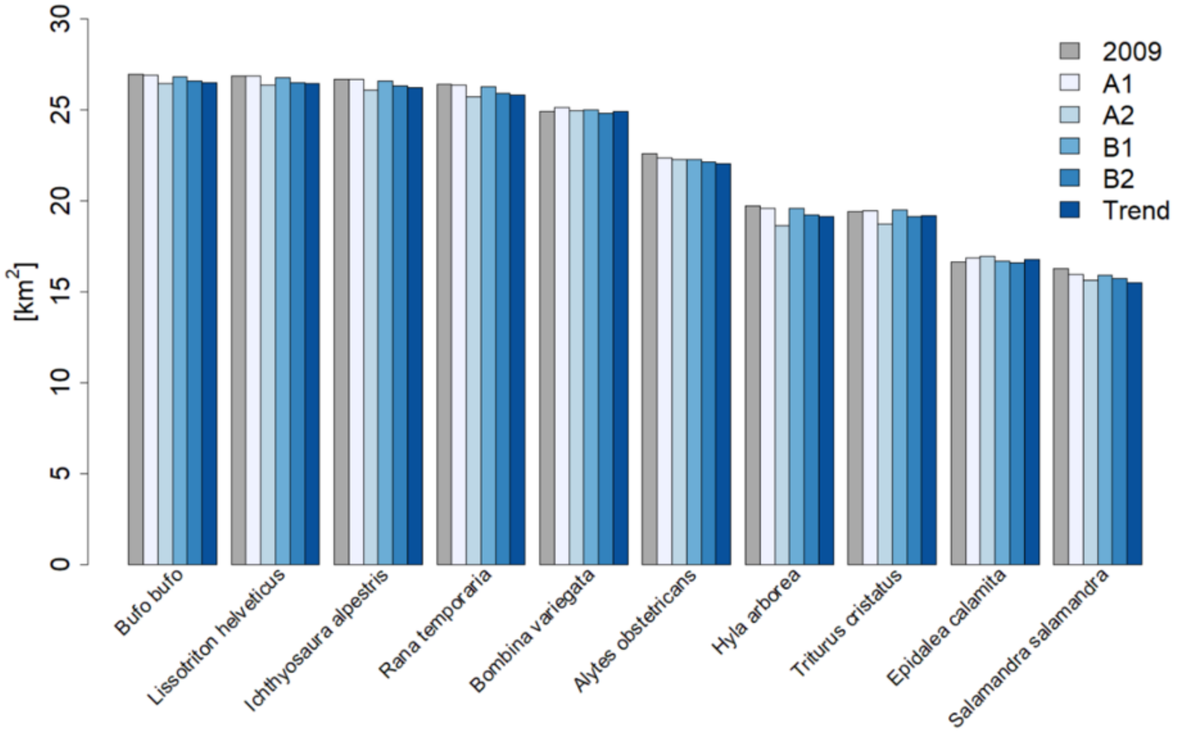


Figure A.10: Modelled biodiversity hotspot area per species and scenario. As the presence of seven species was set as a threshold for biodiversity hotspot areas, at least two of the more threatened species occur on every hotspot. The five least threatened species had the largest hotspot areas. *Alytes obstetricans* and *Hyla arborea* were the most frequent among the more threatened species.

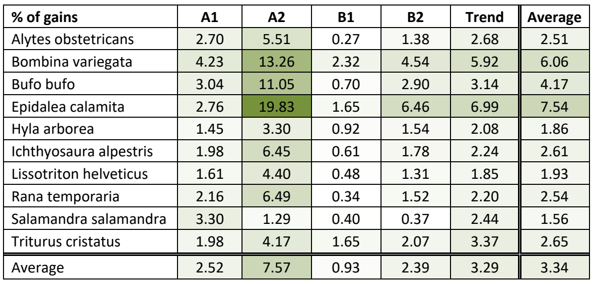
Gain and loss of predicted occurrence area per species and scenario

The percentages of gains and losses in predicted occurrence area were used to calculate the species range change (SRC, Table 4). The highest values for gains (Table A.1a) were observed in scenario A2, followed by the Trend scenario. A1 and B2 showed similar ranges of gains, while the values were lowest in the B1 scenario. In A2, *Epidalea calamita* showed the highest value for a gain (+ 19.8 %), followed by *Bombina variegata* (+ 13.2 %) and *Bufo bufo* (+ 11 %). Lowest gains in scenario A2 were observed for *Hyla arborea* (+ 3.3 %) and *Salamandra salamandra* (+ 1.3 %).

Similar as for the gains, the values for the losses (Table A.1b) were most extreme in scenarios A2 and Trend, followed by scenarios A1 and B2. The highest loss was observed in scenario A2 for *Salamandra salamandra* (- 11.4 %), followed by *Hyla arborea* (- 8.4 %), *Rana temporaria* (- 7 %) and *Ichthyosaura alpestris* (- 6.6 %). The lowest average values for losses among all scenarios were observed for *Epidalea calamita* (- 0.3 %) and *Lissotriton helveticus* (- 1.6 %).

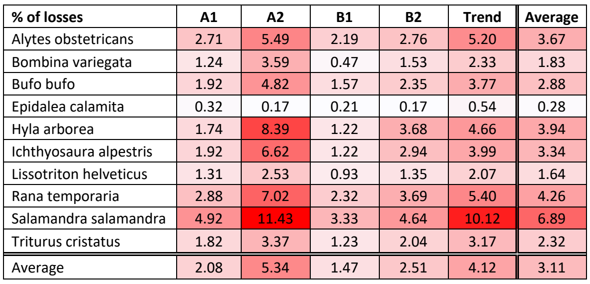
Table A.1: a) Percentage of area gains and **b)** losses per scenario and focal species. These values were used to compute the species range change (Table 4).

a)



% of gains	A1	A2	B1	B2	Trend	Average
Alytes obstetricans	2.70	5.51	0.27	1.38	2.68	2.51
Bombina variegata	4.23	13.26	2.32	4.54	5.92	6.06
Bufo bufo	3.04	11.05	0.70	2.90	3.14	4.17
Epidalea calamita	2.76	19.83	1.65	6.46	6.99	7.54
Hyla arborea	1.45	3.30	0.92	1.54	2.08	1.86
Ichthyosaura alpestris	1.98	6.45	0.61	1.78	2.24	2.61
Lissotriton helveticus	1.61	4.40	0.48	1.31	1.85	1.93
Rana temporaria	2.16	6.49	0.34	1.52	2.20	2.54
Salamandra salamandra	3.30	1.29	0.40	0.37	2.44	1.56
Triturus cristatus	1.98	4.17	1.65	2.07	3.37	2.65
Average	2.52	7.57	0.93	2.39	3.29	3.34

b)



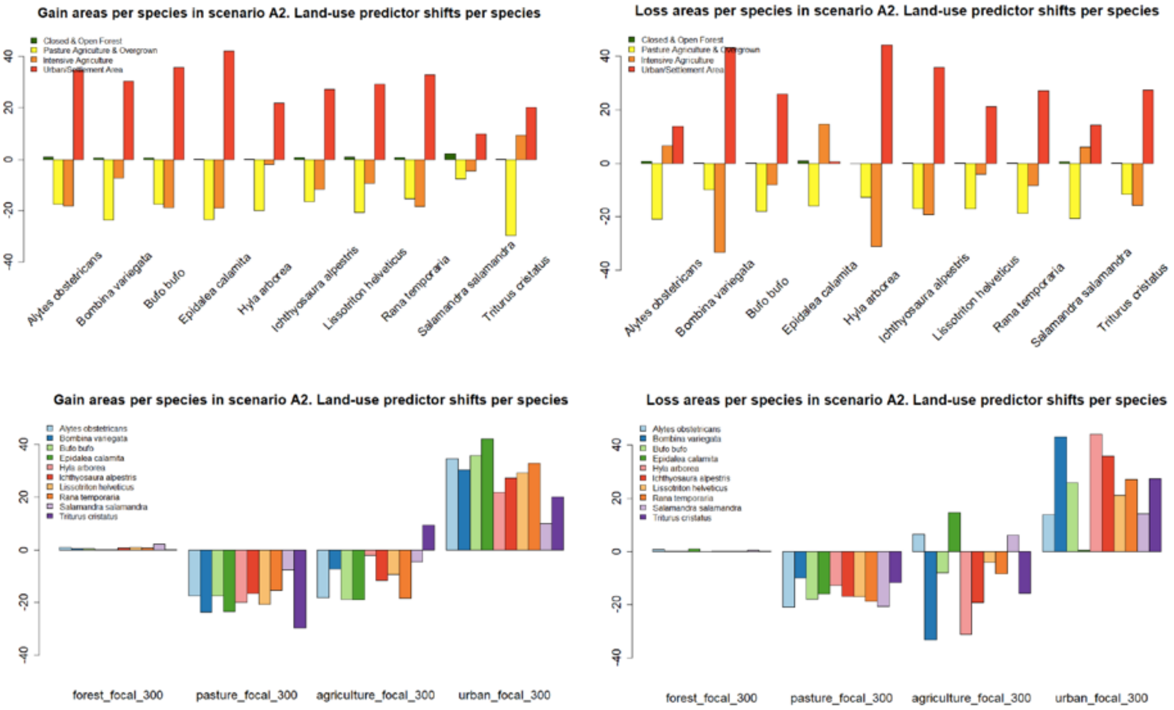
% of losses	A1	A2	B1	B2	Trend	Average
Alytes obstetricans	2.71	5.49	2.19	2.76	5.20	3.67
Bombina variegata	1.24	3.59	0.47	1.53	2.33	1.83
Bufo bufo	1.92	4.82	1.57	2.35	3.77	2.88
Epidalea calamita	0.32	0.17	0.21	0.17	0.54	0.28
Hyla arborea	1.74	8.39	1.22	3.68	4.66	3.94
Ichthyosaura alpestris	1.92	6.62	1.22	2.94	3.99	3.34
Lissotriton helveticus	1.31	2.53	0.93	1.35	2.07	1.64
Rana temporaria	2.88	7.02	2.32	3.69	5.40	4.26
Salamandra salamandra	4.92	11.43	3.33	4.64	10.12	6.89
Triturus cristatus	1.82	3.37	1.23	2.04	3.17	2.32
Average	2.08	5.34	1.47	2.51	4.12	3.11

Predictor changes on areas with predicted gains and losses

The change of the predictor values of areas where each species gained or lost can be seen in Figure A.11. Only scenario A2 was included, as it showed the most extreme changes (see section 3.2).

On gain areas, the percentage of urban land use increased for all species, but to varying degrees. Strongest increases were observed for *Epidalea calamita*, *Bufo bufo* and *Alytes obstetricans*. *Salamandra salamandra*, *Triturus cristatus* and *Hyla arborea* showed lowest increases. The percentage of both agricultural land-uses on gain areas decreased for all species, except for *Triturus cristatus*, which showed a slight increase of intensive agriculture.

On loss areas, the percentage of pasture agriculture decreased, but generally to a lower extent than on gain areas. No clear trend is visible regarding the change of percentage of intensive agriculture: for three species (*Alytes obstetricans*, *Epidalea calamita* and *Salamandra salamandra*) the percentage increased. *Bombina variegata* and *Hyla arborea* showed a strong (more than - 30 %) decrease in intensive agriculture, while the other species showed a decrease of less than - 20 %. Nearly no changes for both gains and losses occurred regarding the percentage of forest coverage.



Gain areas per species in scenario A2. Land-use predictor shifts per species

Loss areas per species in scenario A2. Land-use predictor shifts per species

Gain areas per species in scenario A2. Land-use predictor shifts per species

Loss areas per species in scenario A2. Land-use predictor shifts per species

Figure A.11: Change of the dynamic land-use predictors between the reference and scenario A2 for each species. The left panels show gains while the right panels show loss areas. The changes are either grouped by species (upper panels) or by land-use predictor (lower panels).

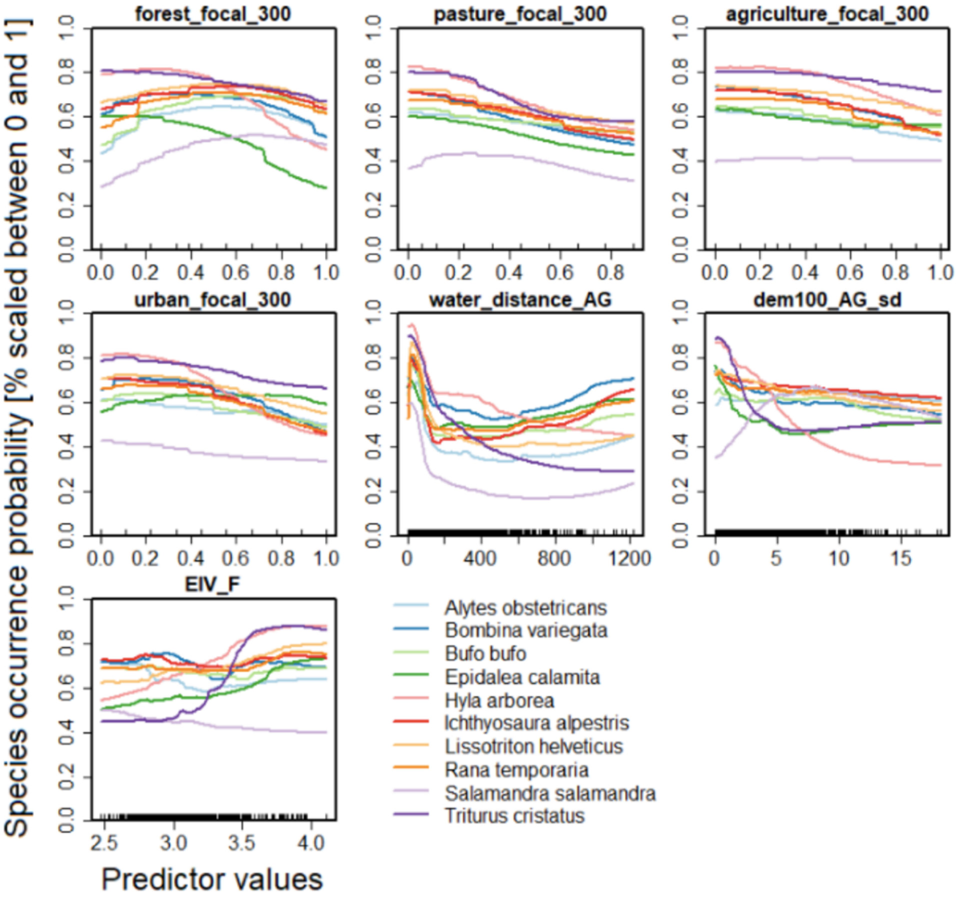


Figure A.12: Response curves of the ensemble models per study species. For most species, the occurrence probability increased with increasing forest coverage and slightly decreased with increasing pasture. The share of intensive agriculture did nearly not change the occurrence probability, while increasing urban percentage generally decreased the occurrence probability. For most species, occurrence probability increased with lower distance to water, lower standard deviation and higher soil moisture. The response curves of the two species with the most extreme SRC (*Epidalea calamita* and *Salamandra salamandra*) are additionally shown in Figure 7.

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