Evaluating the landscape connectivity of five amphibian species using circuit theory

Master Thesis

Supervisor / Referee: Janine Bolliger
Co-Referee: Felix Kienast

Location: WSL Landscape Dynamics - Landscape Ecology Research Group

Greg Churko
Master of Biology ETH
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Abstract

With their relatively restricted movement capabilities and diverse yet specific habitat requirements, amphibians are one of the most vulnerable groups of species to the threats of habitat loss, degradation, and fragmentation. The preservation and improvement of landscape connectivity are important conservation goals in fragmented landscapes as connectivity ensures the possibility of the dispersal of individuals and gene flow among habitats, promoting the resilience and persistence of populations over time. I used Circuitscape to generate continuous, high-resolution, and large-scale single- and multispecies current maps describing the functional and structural connectivity of five amphibian species in the Swiss canton Aargau. In the absence of empirical data relating movement patterns to the landscape, I used expert-opinion to develop resistance maps for each species, and performed a sensitivity analysis of the effect of resistance value selection on the connectivity maps under five possible scenarios of resistance. The resulting functional connectivity current maps highlight regions where connectivity is high or low on a landscape scale. Focusing in on specific areas elucidates the importance of fine-scale features that can inform decisions in development and land use change, suggest locations along highways where amphibian tunnels may be needed, or identify sensitive movement corridors that could benefit from reinforcing protective measures. The structural connectivity maps can guide restoration efforts, highlighting suitable locations for the creation of stepping stone ponds between isolated clusters of breeding populations. The sensitivity analysis indicated that the current maps were generally robust in the identification of high current corridors and regions. However, the relative current values of specific cells were highly sensitive to the selection of resistance scenario across species. Future research should prioritize the generation of resistance maps based off of field-collected data relating movement patterns to the landscape in order to improve the reliability of the current maps.

Key Words

Introduction

Habitat loss, degradation, and fragmentation are among the largest threats to biodiversity worldwide (Fahrig, 2003; Baguette, 2013). With their relatively restricted movement capabilities and diverse yet specific habitat requirements, amphibians are one of the most vulnerable groups of species to these threats (Cushman, 2006). Through a multitude of compounding factors, land conversion as a result of anthropogenic activities plays a major role in the reduction of the abundance and distributions of many amphibians (Cayuela *et al*, 2015). Although these population-level effects are the aggregate result of complex local interactions between individuals and their environment, habitat loss and degradation predominantly lead to the decline of local populations through the loss of available resources in a given area (Joly, 2001; Baguette *et al*, 2013). Consequently, these smaller populations have reduced genetic variability and are more vulnerable to demographic and environmental stochasticity (Baguette *et al* 2013; Eterovick *et al*, 2015). Habitat fragmentation then serves to exacerbate these threats by increasing the isolation of breeding populations, the likelihood of movement through inhospitable matrix, and the proportion of edge habitat, reducing the likelihood of successful dispersal between suitable habitat patches and increasing the risk of mortality (Bowne and Bowers, 2004; Fahrig, 2002; Chalfoun, 2002).

Landscape connectivity, defined as the degree to which the landscape hinders or promotes the movement of a species between habitat patches, is an important conservation concern in fragmented landscapes as it ensures the possibility of the dispersal of individuals and gene flow among habitats, promoting the resilience and persistence of populations over time (Taylor *et al.*, 1993). As landscape connectivity is determined by the interactions between landscape structure and species-specific responses to said structure, two aspects of landscape connectivity are commonly considered: structural and functional. Structural connectivity is the portion of connectivity determined exclusively by the configuration and composition of the landscape, independent from any biological information of the species of interest (Collinge and Forman, 1998). Alternatively, functional connectivity describes the realized connectivity of a species within the landscape, determined by the distribution, dispersal abilities, and behavioural response of the species (Tischendorf and Fahrig, 2000).

While most connectivity analyses focus on a single species, conservation planners with limited resources could benefit greatly from models that predict the movement patterns of multiple species. Several studies in the past have taken a multispecies approach to predicting landscape connectivity. Early attempts prioritized the selection of a single 'umbrella species' in their connectivity analyses, with the assumption that measures taken to preserve or restore connectivity for this species would benefit a number of other species (Lambeck, 1997; Beier *et al*, 2008). Naturally, the disadvantage of this approach is the difficulty in determining a suitable umbrella species in a community, if one exists at all (Beier *et al*, 2009). Alternatively, Koen *et al* (2014) produced a regional map of potential functional connectivity for a generalized suite of forest-dwelling species that successfully predicted the movement corridors of a bird and several amphibian species. However, this approach is limited to groups of species that share a similar behavioural response to the landscape. When the permeability of the landscape differs substantially among the focal species of a study, it would seem necessary to include separate resistant surfaces tailored to each species within the analysis. In a multi-species least-cost path analysis of connectivity, Beier *et al* (2009) achieved this by overlaying the movement corridors predicted by individual models derived from species-specific resistance maps.

Circuitscape is an open-source program based off of linkages between circuit and random walk theories that models the connectivity of a species in its surrounding landscape by relating plant and animal dispersal to electricity moving along a circuit board (McRae, 2006; McRae *et al*, 2008). Since its release in 2008, Circuitscape has steadily grown favor with landscape ecologists for its powerful ability to generate

predictions of movement patterns, gene flow, and genetic differentiation for a wide range of species at both small and large scales (Braaker *et al* 2014; Koen and Bowman, 2014; Novakowski *et ale*, 2015). The landscape is described as a resistance map, a grid of raster cells which represent the varying qualities of habitat or movement barriers tailored to a given species in the study landscape. Source and ground nodes representing start- and end-points for movements are then connected with electrical current, producing a current map that illustrates the probability of species movement through each cell of the landscape. As an advantage over least-cost analyses (see: Bunn *et al*, 2000), all possible movement routes are simultaneously considered, generating a continuous map of probabilities over the entire study region (McRae *et al*, 2008).

Circuitscape has been commonly used to model functional connectivity following one of two approaches that both produce valid yet different results. The first approach relies on species distribution data to place the source and ground nodes through which current is connected in order to predict movement patterns between occupied habitat patches (McRae *et al*, 2008; Dickson *et al*, 2013; Novakowski *et al*, 2015). By weighting current according to population size or habitat quality, abundance data can also be fit into the model. Likewise, node pair exclusions allow the introduction of species dispersal limitations. The resulting current maps estimate the realized functional connectivity occurring within the species' distribution as it exists today. Alternatively, a number of recent studies forego the inclusion of independently collected species data (which can be cost- and time-consuming to generate), instead placing nodes along the perimeter of a buffered study landscape (Walpole *et al*, 2012; Pelletier *et al*, 2014; Koen *et al*, 2014). The result is a continuous current map that is unbiased by the placement of nodes or sensitive to variation in empirical data. These maps describe the potential functional connectivity of the landscape, or species-specific structural connectivity, highlighting movement paths across the entire region, even in areas where the species is absent.

In this study, I used both approaches to create functional and species-specific structural connectivity maps of five endangered amphibian species in the Swiss canton Aargau and combined the results in order to produce multispecies connectivity maps that account for each species' unique movement ecology. With the inclusion of both functional and species-specific analyses of connectivity, the goal of the study was to offer conservation managers a large-scale and comprehensive evaluation of landscape connectivity in the form of continuous and high resolution current maps which highlight both the present and potential movement corridors for these species across the entire study region. Through consultation with two amphibian experts, I first created five different resistance maps for each species parameterized under a unique resistance scenario. Taking advantage of available distribution and demographic data for each species, I generated cumulative current maps under each resistance scenario for each species, which predict the functional connectivity occurring between breeding populations as they are presently situated in the canton. Then, I created a second set of models which assess species-specific structural connectivity across the entire canton. Based entirely off of each species' resistance map, these maps describe the landscape's potential for connectivity for a given species, ignoring their present distribution and dispersal limitations. I then combined the results for each species into functional and structural multi-species connectivity maps which highlight important regions shared by all species. Lastly, I performed a sensitivity analysis of the effect of resistance scenario selection on the functional connectivity maps of each species.

Methods

Study Species and Region

I elected to focus my analysis on five amphibian species: the common midwife toad (*Alytes obstetricans*), the yellow-belied toad (*Bombina variegata*), the natterjack toad (*Epidalea calamita*), the European tree frog (*Hyla arborea*), and the northern crested newt (*Triturus cristatus*). While the IUCN Red List of Threated Species designates each species' conservation status as 'Least Concern', all of these species are considered endangered under the most recent edition of Switzerland's own Red List (Schmidt and Zumbach, 2005) and have been designated as priority species in need of special conservation measures by the Canton Aargau's Department of Environment (Artenschutzkonzept). These assessments are the result of widespread population declines and regional disappearances, attributed predominantly to the loss of habitat due to anthropogenic modification of the environment and changes in land use patterns.

Like most amphibians, all species occupy both aquatic and terrestrial habitat alternatively over two separate life-history stages. However, each species has its own unique ecology and, specifically important to this study, preference of habitat and mobility. Resultantly, the distributions and range of habitats occupied by each species both overlap and diverge from each other in a multitude of ways. For example, some of the species are generalists concerning their selection of breeding sites. However, *E. calamita*'s preference of shallow, ephemeral pools is in clear contrast with the deep, cool and permanent bodies of water where *A. obstetricans* larvae are typically found. Alternatively, while *T. cristatus* and *E. variegata* are often observed in deep forest cover, *H. arborea* and *E. calamita* normally avoid such terrain. Furthermore, *H. arborea* and *E. calamita* are highly mobile species with maximum dispersal ranges of five km or greater, while the three other species rarely move more than a few hundred meters from their natal ponds and have maximum recorded dispersal ranges of one to two km (Smith and Green, 2005; Ryser *et al*, 2003;). Consequently, any multi-species analysis that attempts to generalize the movement patterns of these species together must acknowledge these crucial differences.

The study region was the canton of Aargau situated in the central north of Switzerland (Fig. 1). Bordered by the Jura mountain range to the west and the Rhine to the North, the canton has an area of 1404 km^2 and is one of Switzerland's least mountainous regions, with elevations ranging between 261 – 903 m above sea level. As the third most populous canton in Switzerland despite the absence of any large cities, Aargau's natural landscape is one of the most highly fragmented of Switzerland. Roads and settlements occupy approximately 17% of the canton while another 44% is devoted to agriculture, split roughly equally between active arable land and pasture. The majority of the remaining landscape is covered by forest, at 36%, while wetlands make up around 3%.

Species Data

All breeding population data was derived from the volunteer-based Amphibian Monitoring Program of Canton Aargau (Fig.1; Table 1). The database contains detailed information for each species within the canton, including the coordinates and estimates of population size for all observed breeding sites dating back to 1992 (Schmidt *et al*, 2005). While population size estimates are reported by year in the database, sites are not uniformly visited each year. Consequently, year-by-year data gaps do exist for several breeding sites. For this reason, I included all breeding pond locations which had been occupied at least once in the last 10 years in the analysis. For those ponds with multiple recorded observations within the past 10 years, I used the geometric mean of each year's population size estimate.
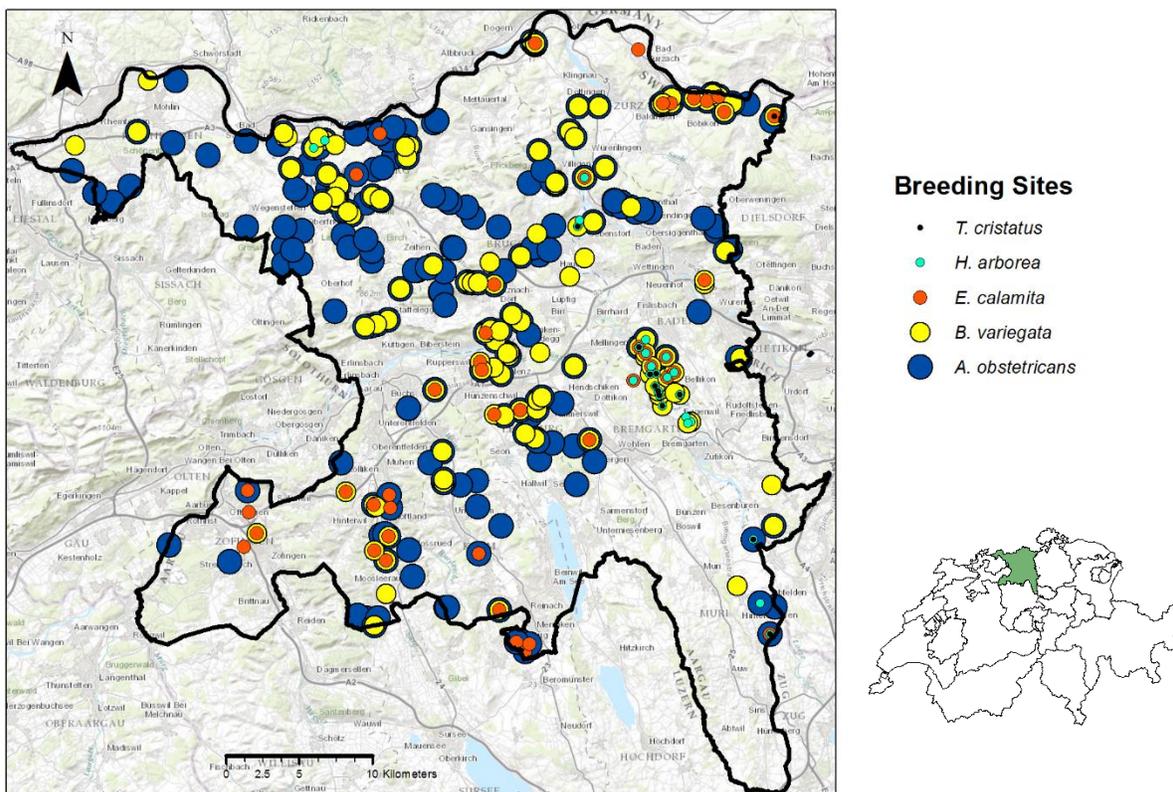
Figure 1: Locations of observed breeding sites from within the last 10 years for each species. In total, there are 12 *T. cristatus*, 26 *H. arborea*, 45 *E. calamita*, 126 *B. variegata*, and 211 *A. obstetricans* breeding populations. The figure in the lower right shows the position of AG within Switzerland.

Basemap source: Esri, HERE, DeLorme, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, © OpenStreetMap contributors, and the GIS User Community
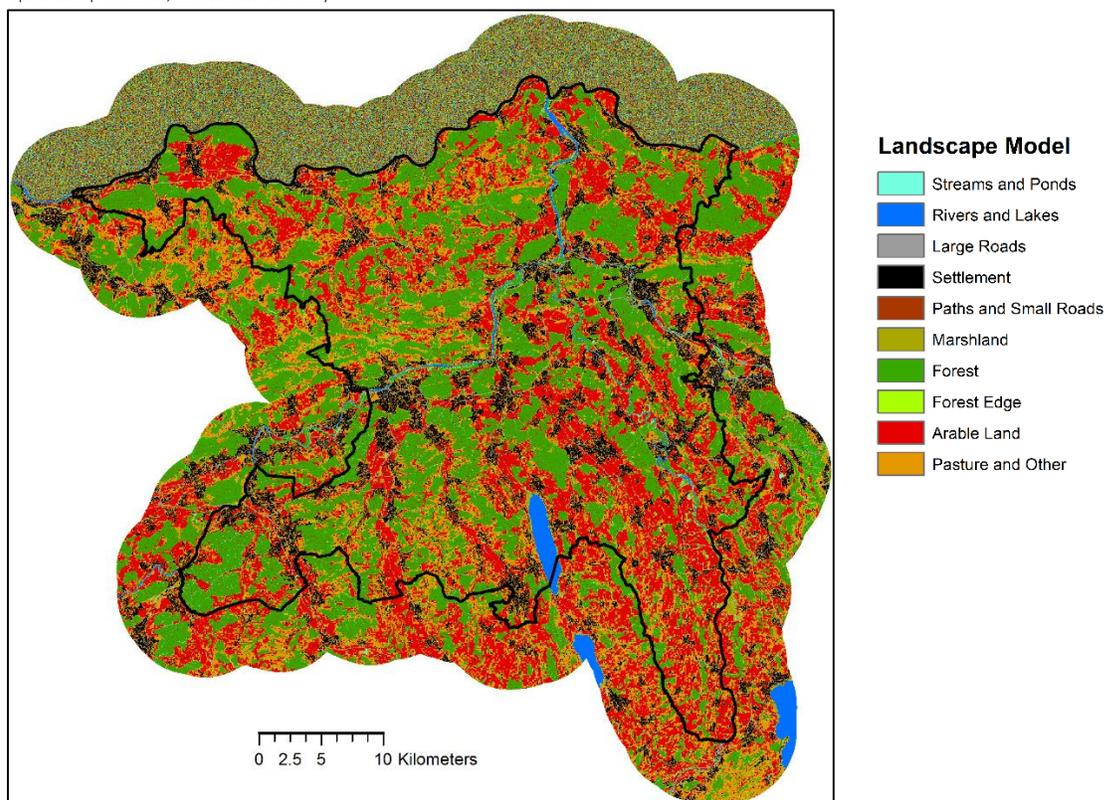
Figure 2: Land cover and land use data of Aargau and buffer region in raster format with a cell size of 10 m². Cells in the northern buffer region situated in Germany were randomly assigned to a category due to lack of equivalent available data.

Table 1: Summary of species data used in the analysis, including both the number of breeding ponds for each species and the maximum dispersal distances used in each analysis. Breeding pond numbers have been classified into four different size categories based off of the geometric mean of the estimated number of adult individuals at each site over the last ten years.

	Breeding Pond Population Sizes				
# of Individuals	*A. obstetricans*	*B. variegata*	*B. calamita*	*H. arborea*	*T. cristatus*
1 to 5	146	58	30	6	12
6 to 20	58	38	9	8	0
20 to 50	7	19	5	9	0
50+	0	11	1	3	0
Total	211	126	45	26	12
Maximum Dispersal Distance	2 km	1.5 km	5 km	12 km	1.5 km

I consulted the literature to find the maximum recorded dispersal distances for each species seen in Table 1 (Baker *et al*, 2011; Primus, 2013; Ryser *et al*, 2003; Smith and Green, 2005). Due to variations in context and availability of dispersal data, determining a consensus distance proved challenging for most species. Additionally, citing the strong correlation between dispersal records and study area size, Smith and Green's (2005) suggest that most dispersal data is likely underestimated as a consequence of mark-recapture study design. As such, with the aim of ensuring the inclusion all possible migration paths in the functional connectivity analyses, I used the maximum values found in the literature for each species and rounded up to the nearest 500 m.

Landscape Resistance Maps

In the absence of empirical data concerning habitat resistance values for all included species, I developed the resistance maps used in the study through consultation with two amphibian experts and performed a sensitivity analysis on the selection of habitat resistance values. To account for each species' unique habitat preferences, I created separate landscape resistance maps for each species in the analysis. I first met with each expert separately to introduce them to my study and discuss the most important landscape attributes to include in a landscape resistance model for each species. Both experts regarded the inclusion of any factors other than land cover and land use as unnecessary for reasons of parsimony and uncertainty. Outside of elevation and its derivatives (i.e. aspect, slope), which they deemed unimportant in the relatively flat canton of Aargau, both experts were of the opinion that any other factor would either be highly correlated with land cover and land use categories, or require the introduction of too many assumptions. Following the initial interviews, I decided upon a final set of 10 land cover and land use categories to include in the resistance maps (Fig. 2).

With the land cover and land use categories chosen, I generated a raster dataset of the canton using ArcGIS version 10.2.2 Desktop (Fig. 2). Land cover data derived from Swisstopo's Topological Landscape Model (swissTLM; geometric accuracy within one to three meters) was used to generate the first eight categories seen in Fig. 1 (Sullivan *et al*, 2008). Through combination with the 100 m^2 resolution GEOSTAT's Arealstatistik model (Bundesamt für Statistik, 2014), I was able to add more detail to open land by distinguishing between arable land and pasture, resulting in a regional landscape model consisting of 10 x 10 m pixels. This resolution was chosen as a suitable compromise between the fine-scale perception and movement capabilities of amphibians and the computer processing intensity of the connectivity analyses (see Appendix A for detailed information on the construction of the landscape model). To allow the possibility of cross border current flow and avoid the introduction of any other

unnecessary border effects in the connectivity analysis, I also included a 5 km buffer around the study region (Koen *et al*, 2014). Due to the lack of equivalent available data in the northern buffer region that occurs in Germany, I randomly allocated each cell to a category.

To generate cost surfaces for each species, I then asked the experts to rank each land category according to its permeability to movement with respect to each species. From the resulting lists of rankings, I concatenated a final master ranking of land cover and land use categories for each species (Table 2), simplified into four tiers of resistance (habitat, favourable matrix, less favourable matrix, and strong barriers) in order to reconcile any differences of opinion between the two experts.

Using these rankings, I created five cost surface maps for each species based off of a suite of resistance value transformations: null, exponential, sigmoidal, logarithmic, and linear (Table 3; Figure 3). Each set of values scaled from 1-1000, with categories representing habitat assigned a resistance of 1 and those representing strong barriers set to 1000. With reasonable success, exponential power of 10 sequences have been commonly used in the literature to assign increasing resistance values to gradients of poorer habitat when empirical movement data is unavailable (Koen *et al*, 2014 and Clauzel *et al*, 2013). Alternatively, Rayfield and Fortin (2010) show that least-cost analysis results are most sensitive to the location of high contrast transitions between the values of resistance categories. In order to maximize the effect of this phenomenon in the sensitivity analysis, I chose to complement the exponential resistance scale with the sigmoidal, logarithmic, and linear scenarios (dotted lines in Table 3). For the remaining scenario, I chose a null model which only penalized movement through strong barriers, considering all other land cover and land use categories equally permeable.

Table 2: Land cover and land use categories ranked into four tiers according to their resistance to movement for each species, increasing from low (habitat) to high (strong barrier).

Landscape Category
1. Streams and Ponds
2. Rivers and Lakes
3. Large Roads
4. Settlements
5. Paths and small roads
6. Marshland
7. Forest
8. Forest edge
9. Arable land
10. Pasture

Resistance Tier	A. obstetricans	B. variegata	B. calamita	H. arborea	T. cristatus
Habitat	1	1, 7	5, 9	1, 6	1, 6
Favourable Matrix	5, 7, 8	5, 6, 8	1, 6, 8, 10	8, 10	7, 8
Less Favourable Matrix	6, 9, 10	9, 10	7	5, 7, 9	5, 9, 10
Strong Barrier	2, 3, 4	2, 3, 4	2, 3, 4	2, 3, 4	2, 3, 4

Table 3: The resistance values from each transformation for each landscape resistance tier. Habitat and strong barriers were always valued at 1 and 1000, respectively. The dotted lines indicate the locations of high contrast transitions between resistance tiers.

Resistance Tier	Null	Exponential	Sigmoidal	Logarithmic	Linear
Habitat	1	1	1	1	1
Favourable Matrix	1	10	100	900	333
Less Favourable Matrix	1	100	900	990	666
Strong Barrier	1000	1000	1000	1000	1000
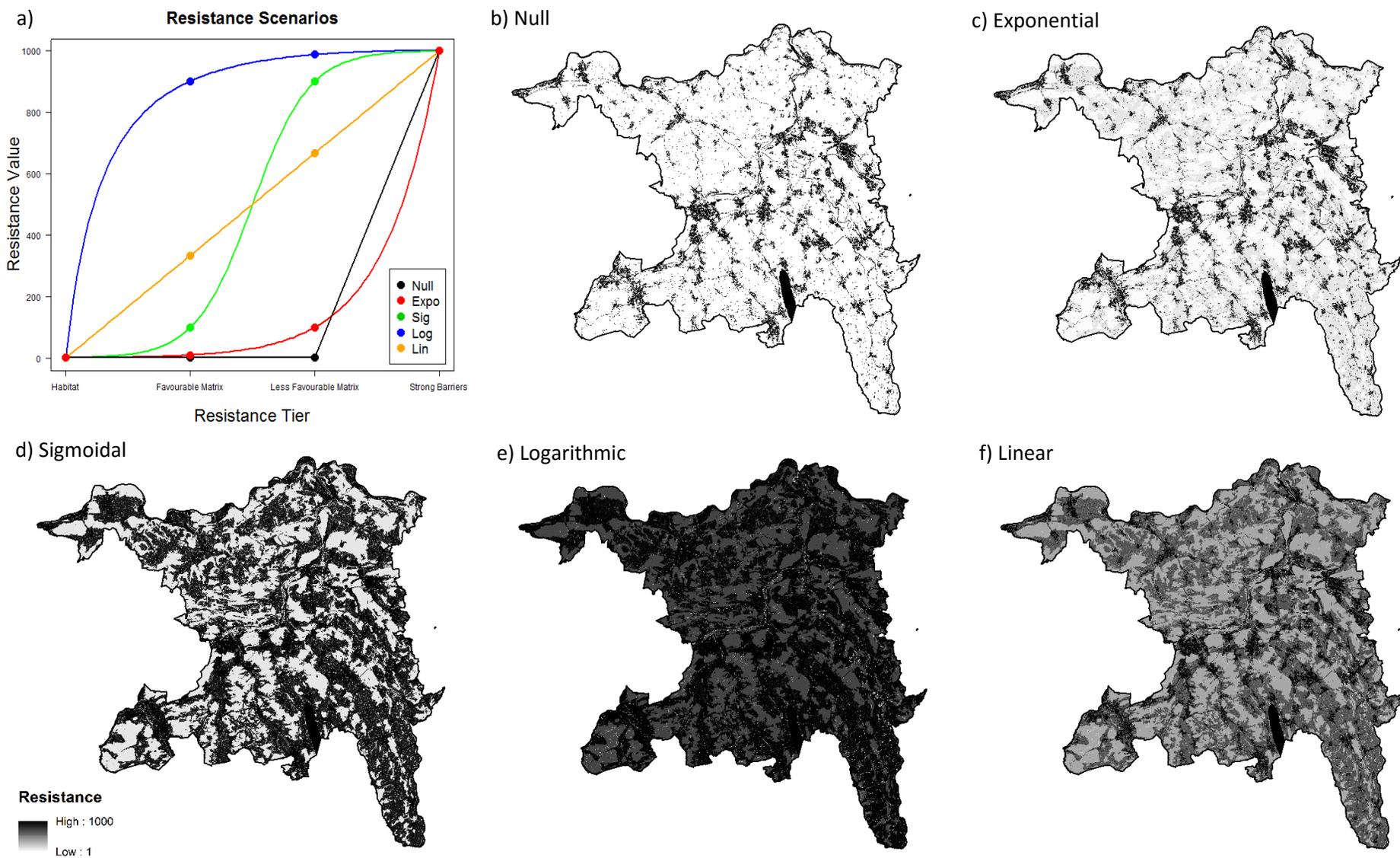
Figure 3: Panel (a) depicts the five theoretical resistance scenario transformations used to create the resistance maps. Panels (b-f) show examples of the five resistance maps used in Circuitscape analyses for each species (seen here for *A. obstetricans)*. Cells are shaded from white to black with increasing resistance. Each resistance map is derived by assigning one of the five resistance scenarios from panel (a) to the habitat resistance rankings for each species in Table 1.

Circuitscape Analysis.

I used Circuitscape version 4.0.5 to model two different interpretations of landscape connectivity for each amphibian species in Aargau. The first set of models made use of available population data from the Amphibian Monitoring Program to estimate the functional connectivity that exists between the distributions of each species as they exist today. These maps indicate the relative likelihood of movement occurring across all cells in the landscape for each species under the five different resistance scenarios (Fig. 3). I ran Circuitscape in pairwise mode, using the breeding ponds seen in Fig. 1 as the source and ground nodes for current, iteratively connecting all possible pairings. If the distance between ponds exceeded the maximum dispersal distance of a given species (Table 1), that pairing was excluded from the analysis. To reduce processing times, I also masked out all regions of the resistance maps that were outside of the maximum dispersal range of any breeding pond. Following the hypothesis that the number of emigrants from a subpopulation scales with population size, I varied the current leaving each breeding pond according to its geometric mean population size over the last 10 years. As the option to vary source node strength in pairwise mode does not yet exist in the Circuitscape program, each pairwise map was multiplied by the geometric means of the included populations. By summing each weighted pairwise map together, I created a cumulative current density map for each species and resistance scenario, highlighting the relative likelihood of movement occurring between subpopulations as they are presently situated in the region.

Alternatively, I created a second set of Circuitscape models independent from population data, which connected current between randomly placed nodes along the perimeter of the study region. As these analyses are based entirely on the configuration of each species' resistance map, they serve to describe the hypothetical structural connectivity for each species across the entire region, including areas where subpopulations are absent. To avoid the introduction of current density bias surrounding source nodes within the study region, I randomly placed the nodes along the perimeter of the 5 km buffer region outside the canton as suggested by Koen *et al*, 2014. This buffer, which represents $10 - 20\%$ of the width of the study region, allows current emitted from the source nodes along the perimeter of the map to sufficiently disperse before entering the study region. All source nodes were set equally to 1A current. Since I was uncertain of the minimum number of nodes required to create a fully saturated current density map of the study region, I first ran two separate Circuitscape analyses for *A. obstetricans*, with 25 (300 node pairings) and 40 nodes (780 node pairings), respectively. As the analysis with 40 nodes required six days to complete and the Pearson correlation coefficient comparing 10,000 randomly selected cells in each map was 0.98, the remaining analyses were performed with 25 nodes. Despite this concession, I was forced to limit all analyses to the exponential resistance scenario due to time and computational limitations.

From the resulting individual species current maps, I created a final multi-species cumulative-current map for both sets of Circuitscape models. Absolute current values in the functional connectivity maps scaled differently among species due to large differences in the number and size of subpopulations. Therefore, I first transformed the current maps into quantiles of 20 before summing them together in order to ensure equal representation of all species in the multi-species functional current maps. To generate the multi-species structural connectivity maps, each species current map was transformed into a binary representation of high current flow, with the highest 25% of cells coded as one. By summing each binary current map together, the value of each cell in the multi-species structural connectivity map describes the number of species for which it is likely to have a high connective value.

Sensitivity Analysis

To examine the degree to which the selection of resistance values impacts the resulting current maps, I measured the percent overlap of the locations of high current regions and calculated Spearman's rank correlations between each resistance scenario. To calculate the percent overlap among resistance sets, I compared the locations of cells with the highest 20% current values after omitting all cells with a current of zero. Since it was expected that each current map would have a current density bias in the cells immediately surrounding each breeding site, I dropped the top 5% of cells in order to focus on overlap occurring away from the source and ground nodes. Alternatively, correlation was calculated using Spearman's rank coefficient as the absolute current values in each cell scaled differently depending on the transformation of resistance values. I randomly selected 5% of the cells from the masked study regions used in the Circuitscape analyses, and compared current values between each resistance set. From the results of both metrics, I then calculated the mean and standard deviation for each pairwise comparison across species.

Results

Circuitscape analysis

Each species' cumulative current map generated using population data displays a cantonal overview of areas where functional connectivity among breeding populations remains high (Fig. 4a; see Appendix B for the other four species). High current regions signify areas with an increased relative likelihood of movement occurring in each cell as a function of population size, the density of interconnected breeding sites, and the degree to which the landscape restricts and concentrates movement. In *A. obstetricans*' current map (Fig. 4a), we see a number of breeding pond clusters exhibiting strong functional connectivity within the canton: the northwest region around the town of Frick is obviously exceptionally well connected relative to other parts of the canton, but regions around Baden, Zurzach, and centrally along the river Aare also show a high flow of current. Alternatively, areas showing marginal current flow indicate areas where, despite the presence of connected populations, functional connectivity is low relative to other regions due to small population sizes and/or low numbers of breeding sites.

Additionally, each functional connectivity map can be focused on particular regions to highlight the importance of specific landscape features to dispersal between breeding sites. Fig. 4b highlights how these regional current maps can elucidate explicit locations where movement is most likely to occur as a consequence of the configuration of the landscape. For instance, the forest stand south of Frick (1) appears crucial to the connectivity between the seven breeding populations in its vicinity. Alternatively, the current map highlights likely corridors through the city (2) that dispersers would likely take between the northern and southern population clusters. Furthermore, high current regions on adjacent sides of the highway east of the city (3) indicate a possible common crossing point for midwife toads in the area.

a) Functional connectivity current map for *A. obstetricans*
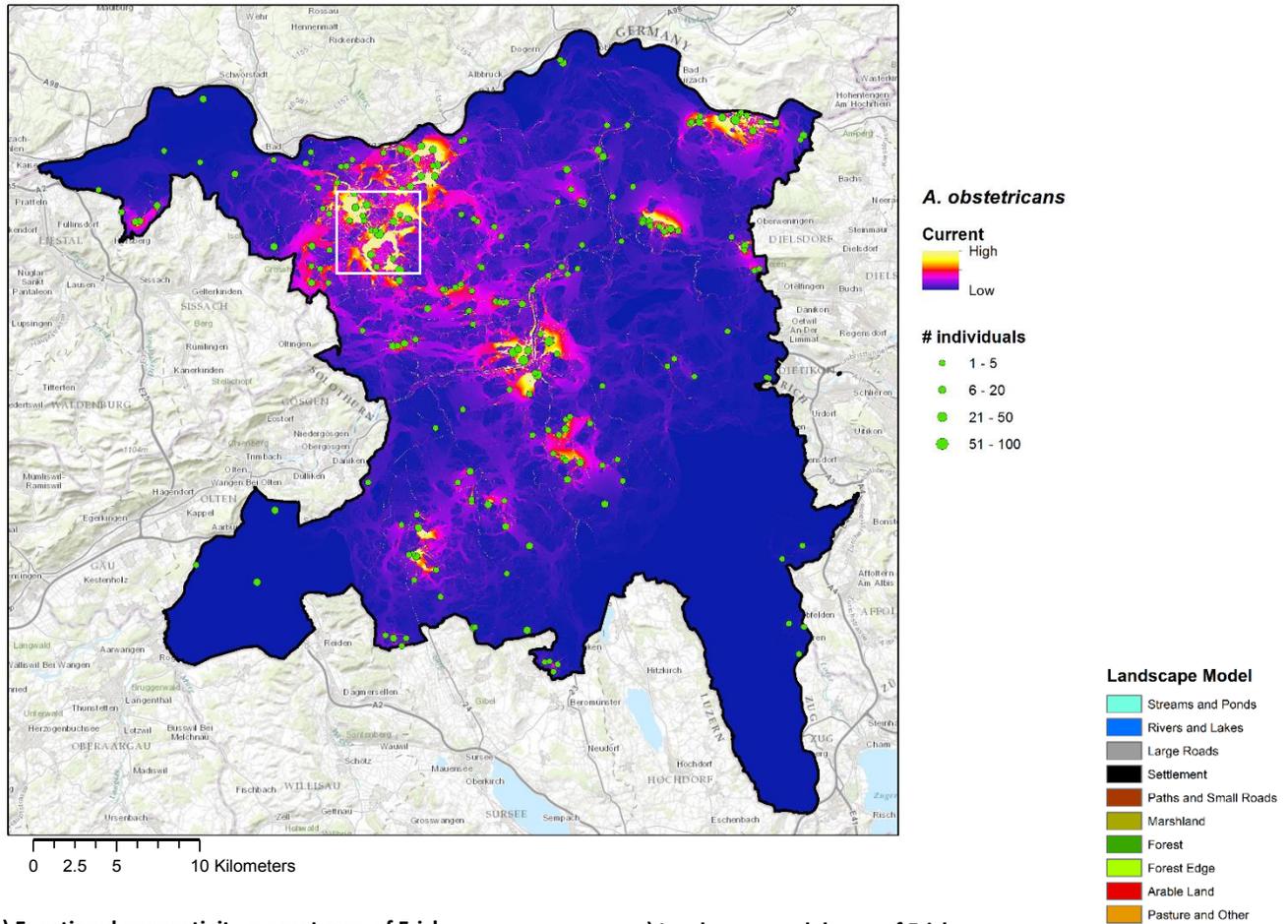
b) Functional connectivity current map of Frick
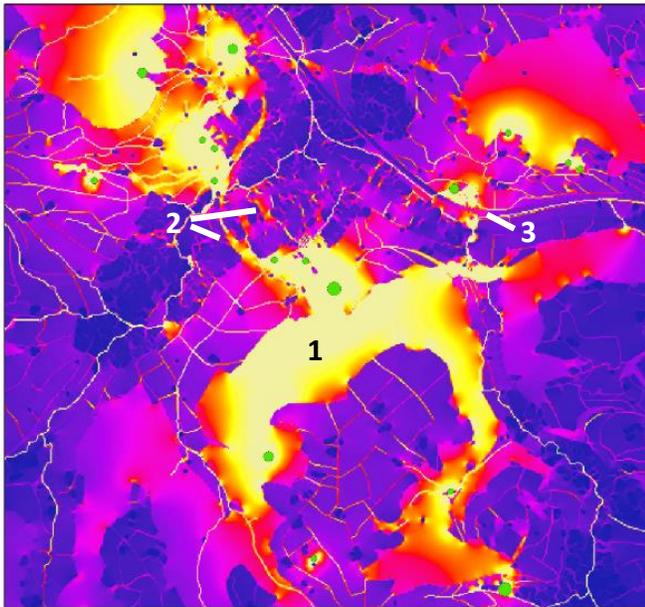
c) Landscape model map of Frick
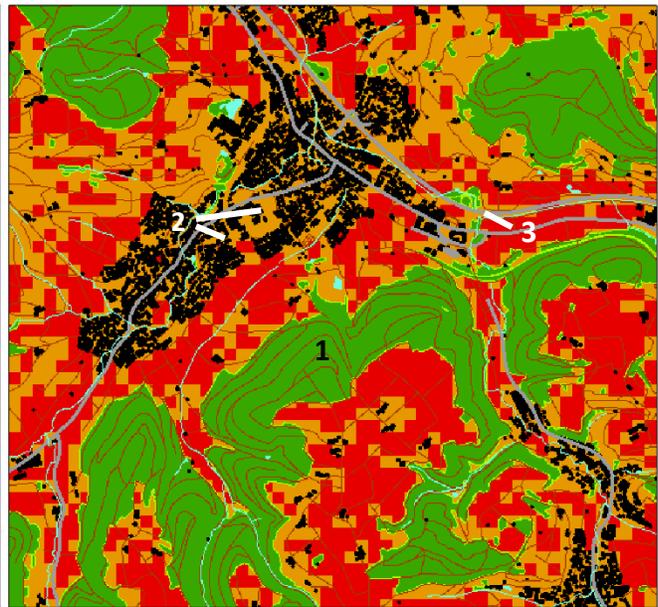
Figure 4: Panel (a) shows the functional connectivity current map for *A. obstetricans* under the exponential resistance scenario. Yellow cells indicate high flow of current. Breeding populations are indicated by green circles, sized according to the population sizes in Table 1. The white square indicates the enlarged region around the town of Frick shown in panels (b and c). High current regions in the functional connectivity map (b) show the importance of specific structures seen in the landscape model (c) to local connectivity. Of note, (1) the forest stand south of the town, (2) possible corridors through the town, or (3) a section of the highway that may have frequent crossing attempts.

a) Structural connectivity current map for *A. obstetricans*

Structural Connectivity

Current

High

Low

b) Functional Connectivity

◇ Cluster 1

● Cluster 2

c) Structural connectivity

0 0.5 1   2 Kilometers
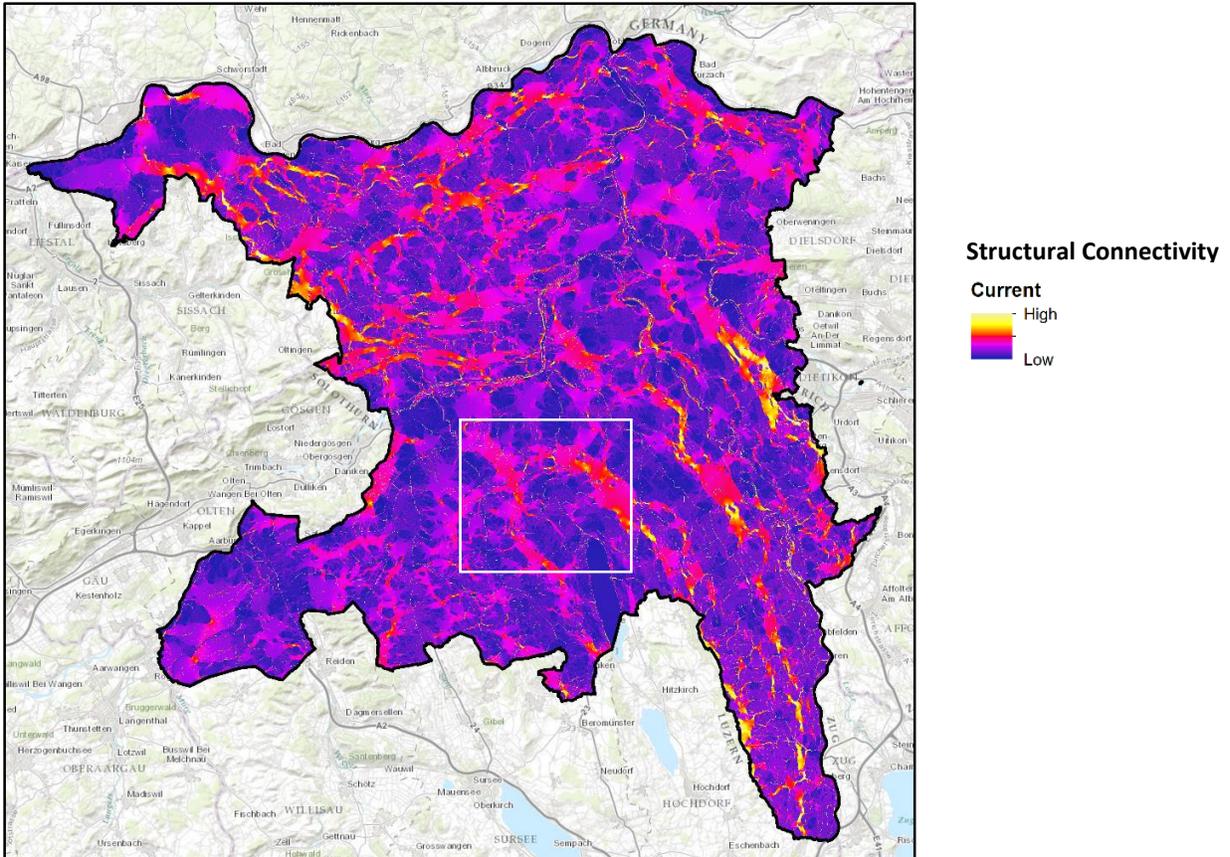
Figure 5: Panel (a) shows the structural connectivity current map for *A. obstetricans*, after removal of the 5 km buffer region. The white square indicates the enlarged region around the town of Seon shown in panels (b and c). The functional connectivity map of the Seon region (b) depicts two distinct breeding pond clusters separated by roughly 4 km. High current cells within the circled region in the structural connectivity map (c) indicate structurally, but not functionally, well-connected land between the clusters

a) Multi-species functional connectivity current map
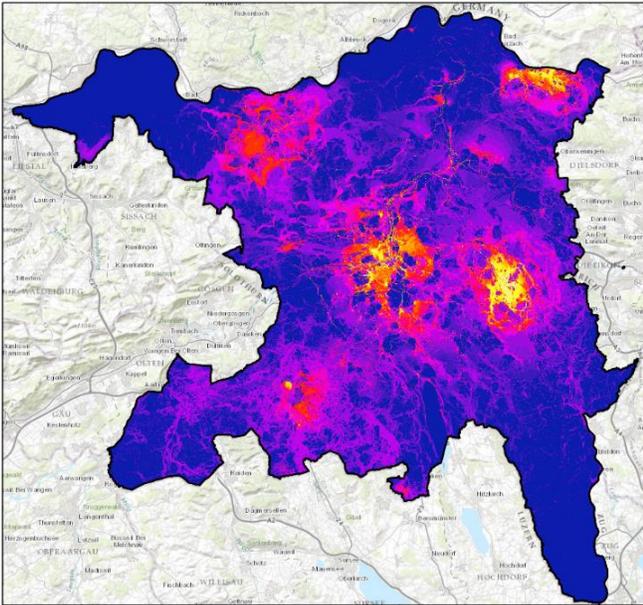
b) Multi-species structural connectivity current map
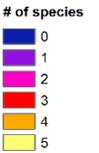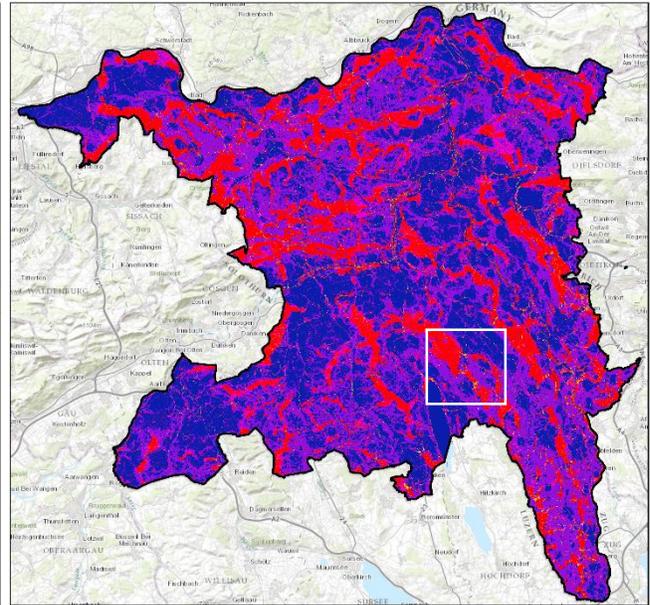
# of species
- 0
- 1
- 2
- 3
- 4
- 5

Figure 6: Multi-species (a) functional and (b) structural connectivity current maps. Structural connectivity map shown after removal of 5 km buffer region. Discrete color scale, from dark blue (0) to yellow (5), indicates the number of species for which each cell has a high structural connectivity current value. The white square indicates enlarged region shown in panel (c), south of the town of Wohlen.

c) Multi-species structural connectivity current map (Wohlen)

0   0.25 0.5   1 Kilometers
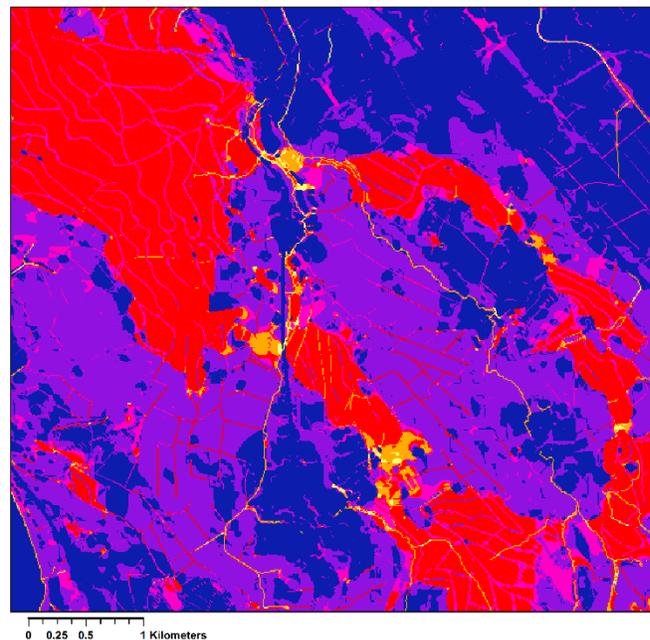
The structural connectivity maps (Fig. 5; see Appendix C for the other four species) highlight the likely corridors across the entire canton that each species would take if freed from the limitations of their current distributions and dispersal abilities. In Figure 5a, we see how the configuration of the landscape channels *A. obstetricans* across the canton into distinct routes, with blocks of low current land where the arrangement of settlements, highways, and major rivers has reduced the probabilities of dispersal in regions beyond their own restricted footprints. The movement corridors depicted in these maps present a valuable tool to restoration efforts with the intention of improving the functional connectivity between breeding sites. Figures 5b and 5c show an example of how the structural connectivity map can inform the improvement of connectivity between two breeding population clusters on either side of the town of Seon, isolated by approximately four km. While Fig. 5b shows that there is little to no functional connectivity between these two population clusters, the structural connectivity map (Fig. 5c) indicates that the forest stand north of the town would be a suitable corridor for dispersers in the vicinity. As such, this forest may represent a good location to concentrate restoration efforts, either by the construction of replacement ponds at high current cell locations, or through improving the suitability of any existing ponds to the midwife toad.

Table 4: Sensitivity analysis results comparing the functional connectivity current maps generated under each resistance scenario (Fig. 3). Each table shows across species mean and standard deviation for the pairwise comparisons of (a) the percentage of overlapping high current cells and (b) the Spearman's rank correlation coefficient between cells of each current map. Percent overlap was calculated by comparing the locations of cells with the highest 20% current, after excluding the highest 5%. Spearman's rank correlation coefficients were calculated by randomly selecting 5% of the cells in the masked study region of each species.

a)

	Null		Exponential		Sigmodial		Logarithmic		Linear	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Null	100	0	50	8	41	10	42	14	44	14
Exponential	-		100	0	77	5	60	9	68	7
Sigmoidal	-		-		100	0	74	12	82	8
Logarithmic	-		-		-		100	0	90	4
Linear	-		-		-		-		100	0

b)

	Null		Exponential		Sigmodial		Logarithmic		Linear	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Null	1.00	0.00	0.27	0.23	0.23	0.13	0.15	0.13	0.17	0.15
Exponential	-		1.00	0.00	0.56	0.33	0.34	0.29	0.41	0.26
Sigmoidal	-		-		1.00	0.00	0.43	0.35	0.46	0.36
Logarithmic	-		-		-		1.00	0.00	0.46	0.31
Linear	-		-		-		-		1.00	0.00

Finally, the multi-species current maps (Fig. 6) highlight locations where connectivity is collectively high among most amphibian species considered. Both connectivity current maps can be used in much the same way as the midwife toad-specific examples exhibited previously (Fig. 4 and 5), with the distinction that any inferences made would impact multiple species. The functional connectivity current map (Fig. 6a) highlights regions with overlapping species distributions, most notably the only region where all five amphibian species are present, along the river Reuss in the east of the canton. Additional high current locations include the northeastern region near Zurzach and central region along the Aare, where the midwife, yellow-bellied, and natterjack toads all exhibit relatively high functional connectivity. The structural connectivity current map (Fig. 6b) explicitly shows the number of species for which a landscape feature has a high connectivity value. From a landscape perspective, it is evident that there are no large swaths of land which all species are likely to find permeable. At most, the large forest stands appearing red across the canton suggest their high connective value to three species: the northern crested newt, and midwife and yellow-belied toads. However, at a regional scale (Fig. 6c), highly connective portions of land favored by all species can be identified. While the majority of these cells are streams and ponds, there also exists small tracts of land where the movements of all species are concentrated into important corridors.

Sensitivity Analysis

The percentage of overlap in the locations of high current cells among pairwise comparisons of resistance scenarios ranged from 41 − 90 % (Table 4a). Spearman's rank correlation coefficients were distinctly lower, varying from 0.15 − 0.56 (Table 4b). For both metrics, there was far less agreement in all comparisons that included the null resistance scenario (41 − 50 % with null vs 60 − 90 % all other comparisons; 0.15 − 0.27 vs 0.34 − 0.56). As the null resistance scenario only penalized movement through landscape elements within the strong barrier category, treating all other terrain as habitat, we can see how the inclusion of separate matrix landscape categories in the other scenarios has a strong effect on

the current maps. Excluding the null scenario, the exponential resistance scenario was predictably in lowest agreement with its inverse, the logarithmic, and, to a lesser degree, the linear model for both metrics. The logarithmic and linear scenarios both assign very high resistance values to the matrix categories compared to the exponential as can be seen in Fig. 3. However, it is interesting that despite this strong contrast, comparisons between these scenarios are still favoured over the null scenario. Even a slight structuring of the landscape into habitat/matrix classes evidently leads to a reasonably similar configuration of high current regions in the map, robust to parameter selection. Alternatively, across species standard deviations are notably different between the calculations of percent overlap and Spearman's rank correlation. While quite low in the overlap analysis, among species standard deviation in the correlation analysis was uniformly high. Species differences could be due to a multitude of factors, many of which would be derived by the interactive effects between species-specific resistance rankings and the differences in the landscape included in each species' own masked study region (configuration, fragmentation, and composition). However, fundamentally this variation shows the high sensitivity each species' current map exhibits to the choice of resistance scenario at a finer scale, where relative current values among cells are considered. These results suggest that while the model is generally robust in the identification of high current corridors and regions, it cannot be reliably used in applications that require the selection of a single best corridor from a number of possible options.

Discussion

To my knowledge, this is the first large-scale multispecies analysis of connectivity that simultaneously considers both functional and structural connectivity while also accounting for the unique behavioural responses of each study species to the landscape. There are a number of advantages to this approach. The complementary aspects of the functional and structural connectivity current maps provide a holistic understanding of the current state of connectivity within the study region, as well as the landscape's potential for connectivity with respect to these species, offering the insight required to both preserve and mitigate threats to connectivity, or improve and restore it. Through the use of Circuitscape, these insights are not limited to a few specific habitat patches or corridors, but are available in continuous, high-resolution, and large-scale maps over the expanse of the study region indicating all possible movement routes. Moreover, the species-specific approach used to generate the multispecies current maps offers the flexibility to include species with diverse movement ecologies and ensures that no species is potentially mismatched to the requirements of a single 'umbrella' species. While the multispecies current maps provide insights that can be used for the betterment of landscape connectivity for some or all of these species, each individual species current map can also be used independently to prioritize regions of focus in conservation efforts and in the identification of integral landscape features to connectivity for a single target species.

Model Limitations

With the lack of independent movement data with which to validate the connectivity models and the resistance maps they are derived from, it is difficult to assess just how accurate these maps are. Despite reasonably high overlap of high current regions in the sensitivity analysis, the breadth of landscape resistance scenarios captured by the analysis is by no means all-inclusive. Nor is it likely that landscape categories can be cleanly divided into four categories of resistance rankings, or that the number

of categories would be equal across species. Only one landscape factor was considered: land cover / land use. The amphibian experts stressed the importance of parsimony in the landscape model, citing a general lack of fundamental knowledge on the intricacies of species-environment relationships in the literature for these species and amphibians in general (Cushman, 2006). Other factors, such as topographic position, watershed fidelity, road traffic, and microhabitats could possibly all have some effect on the movement patterns of amphibians (Peterman *et al*, 2014; Mullen *et al*, 2010; Cosentino *et al*, 2014; Lee-Jaw *et al*, 2015).

Furthermore, there are a number of assumptions involved in the modelling of functional connectivity based off of the distribution and demographic data of a species, and limitations to its applicability to other organisms. Using population data derived from large-scale monitoring programs introduces a high amount of uncertainty to the model due to imperfect detection probabilities, which can render abundance data biased and highly variable between years (Schmidt, 2005). Additionally, the scaling of current values emitted from nodes with population size to reflect an increased number of emigrants from larger populations heavily simplifies the complex process of dispersal. While this may be a general trend, dispersal triggers are poorly understood in many amphibian species and are likely to vary from year to year, individual to individual, and species to species (Baguette, 2013). Moreover, the quality and detail of data available to me through canton Aargau's Amphibian Monitoring Program is rare in most regions and for most species. Such large-scale and long-term monitoring programs require a large investment of time and resources, limiting the applicability of my method of modelling functional connectivity to other species.

It is also important to note that the current maps only indirectly describe the actual quality of the landscape with respect to supporting connectivity. High current regions within the functional connectivity maps are predominantly determined by the size and number of connected breeding populations within a maximum threshold of Euclidean dispersal distance, while landscape resistance simply *shapes* the flow of current. Generally, current that flows across regions of poor permeability to movement will be highly concentrated through the few landscape features that promote movement, like streams, while in more favourable areas current flows in wider swaths. However, such observations require a keen eye and are difficult to qualify. Furthermore, if no such features exist through poor terrain, the density of current will be indistinguishable from that of a uniformly high quality region of connectivity. Sinsch's (2014) review of the literature suggests this may actually be an accurate portrayal of the effect of landscape resistance on amphibian movements, with several studies finding a negligible effect of resistance on dispersal distances. However, it is also likely that the high cost of dispersal over poorer matrix habitat has a negative effect on the likelihood of an immigrant's reproduction success, which should be factored into predictions of functional connectivity (Baguette, 2013). An alternative approach may have been to determine likely node pairings using a maximum threshold of cost-distance rather than Euclidean distance (Bunn *et al*, 2000). However, without any data available to determine a suitable threshold value, I opted to refrain from the addition of more uncertainty to the model. Alternatively, Circuitscape does calculate an 'effective resistance' metric between each node pair in an analysis that is calculated as a function of the cumulative cost-distance and redundancy of paths between nodes (McRae *et al*, 2008). Perhaps further weighting of the amount of current flow between nodes according to this metric would allow a better representation of functional connectivity within the region that takes into account landscape quality.

Applications and Future Directions

Regardless of the limitations of the models within this study, I believe the methods outlined here to generate functional and species-specific structural connectivity maps will be very valuable to conservation efforts for these species within the canton Aargau and, if scaled up accordingly, for even more species and regions. Both sets of current maps generated within this study provide a great deal of information concerning the landscape connectivity of the study species in the region and could seemingly be used in a multitude of applications. The functional connectivity current maps act as excellent visual aids that are easily accessible and intuitively allow a user to locate areas within each species' distribution where connectivity is high or low on a cantonal scale. Focusing in on specific areas elucidates the importance of fine-scale features that can inform decisions in development and land use change, suggest locations along highways where amphibian tunnels may be needed, or identify sensitive movement corridors that could benefit from reinforcing protective measures. The structural connectivity maps can guide restoration efforts, highlighting suitable locations for the creation of stepping stone ponds between isolated clusters of breeding populations. Furthermore, they are particularly relevant to the design of green infrastructure, an increasingly popular concept in spatial planning policy that involves the strategic planning of development and land use to ensure the long-term persistence of biodiversity and ecosystem services (Naumann *et al*, 2011). Multispecies structural connectivity maps could provide decision-makers with the insight needed to mitigate the impact of development on biodiversity and identify regions where landscape connectivity can be improved.

Both the functional and structural connectivity models would undoubtedly be improved by the inclusion of empirically derived field-data that accurately relates the movement of dispersers to the landscape. There are a number of methods available to landscape ecologists for this purpose. Mark-recapture and telemetry studies can quantify the movement rates, distances, and paths of individuals in order to identify the behavioural responses of a species to its environment (Cushman, 2006). Besides being quite resource-intensive, the challenge with these methods is capturing the movements of an actual disperser. Many amphibians have a high fidelity to their natal ponds, and dispersal rates between breeding populations can be very low (Smith and Green, 2005). Movement patterns of an amphibian within its terrestrial home range to that of a dispersing individual exposed to various qualities of matrix habitat over much greater distances (Peterman *et al*, 2014). As such, the quality of such data importantly hinges on shrewd experimental design. Alternatively, the use of genetic tools to assess gene flow among populations represents a powerful means of relating dispersal patterns to the landscape. Through the comparison of the genetic characteristics between breeding ponds, it is possible generate estimates of gene flow that can then be used to estimate the resistance values of landscape features that separate them after accounting for the multigenerational processes the determine genetic structure (Baguette, 2013).

As the cost of a genetic analysis continues to lower, data relating species movement to the landscape will become more readily available (Wetterstrand, 2016). Additionally, while the structural connectivity current maps were particularly computer-intensive at the resolution used in this study, Anderson *et al* (2012) devised a method for large-scale Circuitscape analysis that handles the landscape using a tiling approach. Using such a method, entire maps of Switzerland could be created while retaining the high resolution necessary to locate important landscape features at a fine enough scale relevant to amphibians and other species with similar dispersal characteristics. Following these advancements, I envision the future availability of extensive databases of large-scale species-specific and multi-species connectivity maps capable of informing and guiding the needs of conservation efforts.

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Appendix A: Generating the landscape model

Table A: Protocol table indicating all data sources and specific layers within each data source (Objektart) selected to generate each category in the landscape model. The drawing order signifies priority layers in case of overlaps, with lower numbers having highest priority. Most layers were buffered by 10 m (one cell width) except for fine-scale linear features like streams and paths (5m), or the low drawing order / low resolution land use categories (none). Major roads were buffered by 15 m to ensure that they were always drawn at least two cells wide and acted as strong barriers (current jumps easily across the curves of linear single cell barriers in raster datasets because barrier cells are only connected at the corners instead of their sides). Any cell within the map lacking classification after filling the model with all other categories was assigned to 'Pasture'. This was done under the assumption that most of these cells would be marginal, undeveloped, open vegetated land, such as the areas around highway approaches, which would have similar characteristics to pastures.

Drawing Order	Land cover / Land use	Source	Selection	Type	Buffer	Notes
1	Streams	TLM_FLIESSGEWAESSER_2015	Objektart = Fliessgewaesser (4) and Verlauf = Oberirdisch (100)	Polyline	5m full	* overlap between the two data sources for streams and rivers => all stream data polylines that intersected river polygons were considered rivers
	Ponds	TLM_BODENBEDECKUNG_2015	Objektart = Stehende Gewaesser (10) and ShapeArea < 600,000	Polygon	10m full	
	Edges of rivers and lakes	TLM_BODENBEDECKUNG_2015	Objektart = Fliessgewaesser (5) and ShapeArea / ShapeLength > 10; Objektart = Stehende Gewaesser (10) and ShapeArea > 600,000	Polygon	-10m outside_only	
2	Rivers and lakes	TLM_BODENBEDECKUNG_2015	Objektart = Fliessgewaesser (5) and ShapeArea / ShapeLength > 10; Objektart = Stehende Gewaesser (10) and ShapeArea > 600,000	Polygon	none (see edges of rivers and lakes)	* marshland and lakes overlap in some locations => erased intersection of the two
3	Large roads	TLM_STRASSE_2015	Objektart = Autobahn, Autostrassen, 6m, 8m, 10m Strasse (2, 21, 9, 20, 8)	Polyline	15m full	
4	Settlements	TLM_GEBAUDE_FOOTPRINT_2015	Objektart = Gebaude, etc. (1-5)	Polygon	10m full	* overlapping features aggregated with dissolve function
5	Paths and small roads	TLM_STRASSE_2015	Objektart = 3m Strasse, 2m Weg (11, 15)	Polyline	5m full	
6	Marshland	TLM_BODENBEDECKUNG_2015	Objecktart = Feuchtgebiet (11)	Polygon	10m full	
7	Forest	TLM_BODENBEDECKUNG_2015	Objecktart = Wald, Wald offen (12, 13)	Polygon	none (see Forest edge)	
8	Forest edge	TLM_BODENBEDECKUNG_2015	Objecktart = Wald, Wald offen (12, 13)	Polygon	-10m outside_only	
9	Arable land	Areal Statistik 2004/2009	Objektart = Ackerland (41)	Point Raster (100 m resolution)	none	* 100m raster resampled down to 10m cell size to match other categories
10	Pasture and other	Areal Statistik 2004/2009	Objektart = Naturwiesen (42) and Heimwieden (43); + No Data	Point Raster (100 m resolution)	none	* 100m raster resampled down to 10m cell size to match other categories

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Appendix B: Functional connectivity maps for all other species
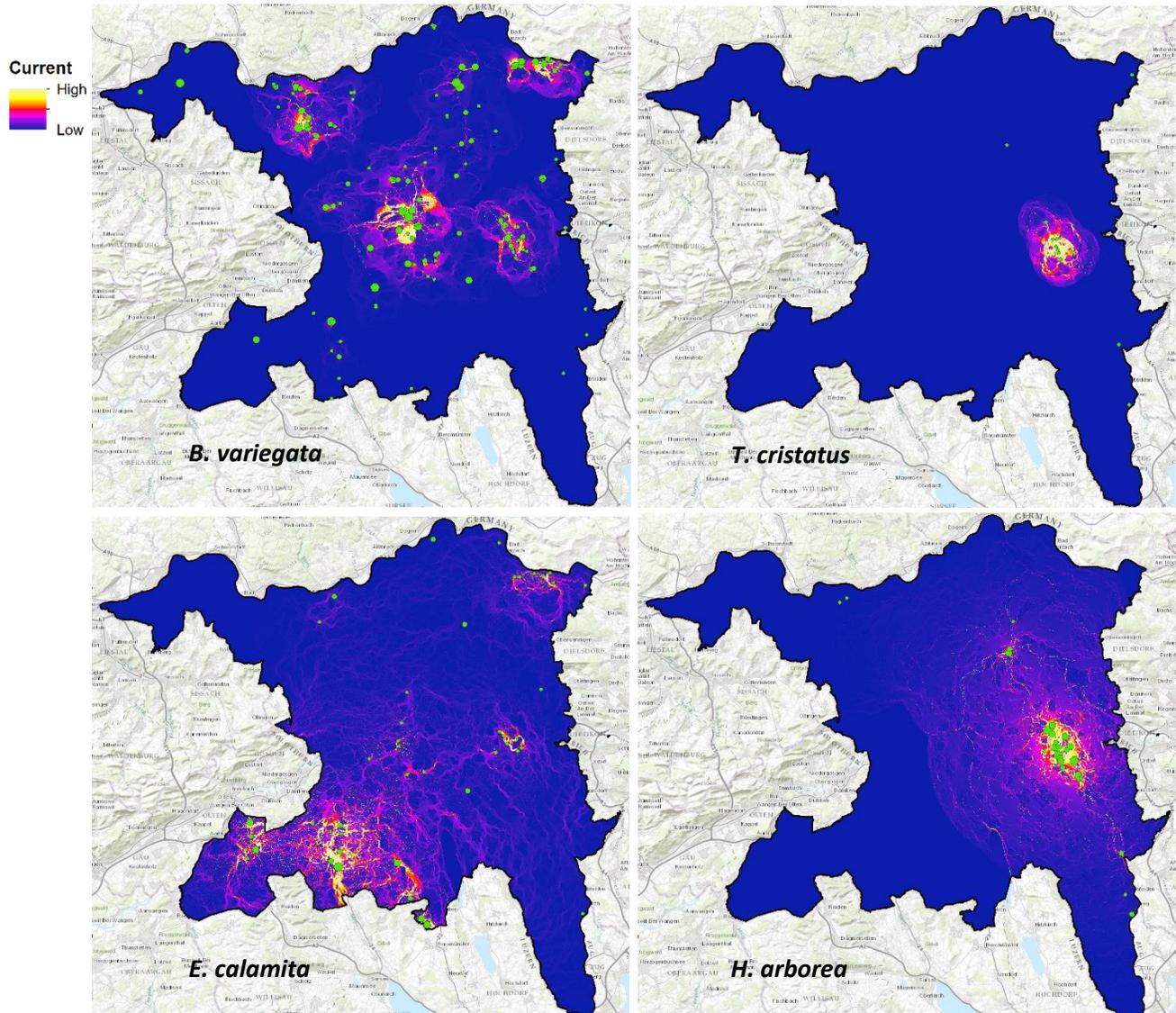
Figure B: Functional connectivity cumulative current maps for the European tree frog, northern crested newt, yellow-belied and natterjack toad.

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Appendix C: Structural connectivity maps for all other species
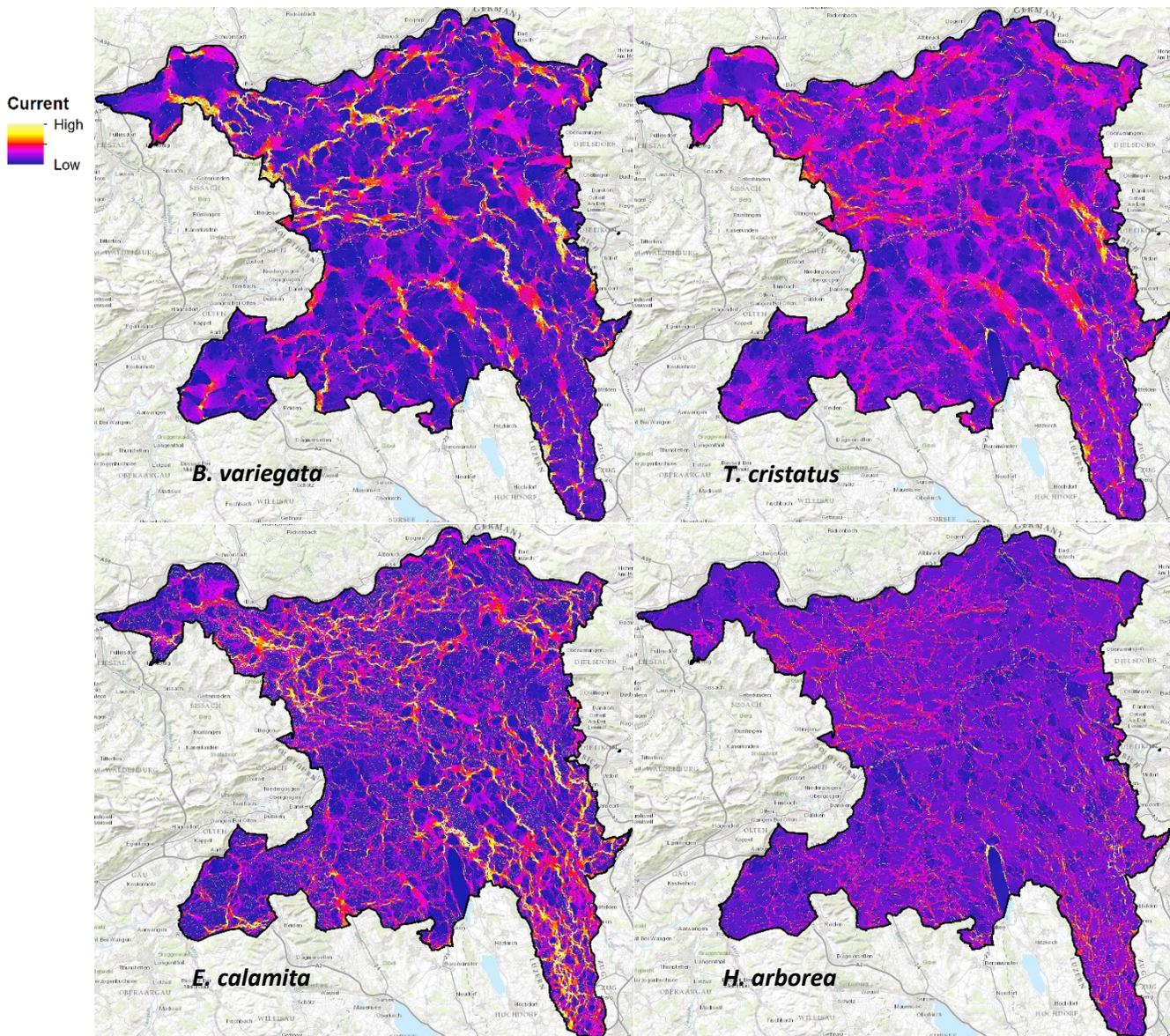
Figure C: Structural connectivity cumulative current maps for the European tree frog, northern crested newt, yellow-belied and natterjack toad.

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