From occurrence to eco-evolutionary dynamics

Assessing connectivity in a changing world through modelling and landscape genetics

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CHAPTER 5

Coupling satellite data with species distribution and connectivity models as a tool for environmental management and planning in matrix-sensitive species

"We cannot solve our problems with the same thinking we used when we created them."

— ALBERT EINSTEIN

Introduction

Climate change and continuing habitat loss through human land-use are currently considered as major threats for global biodiversity (BELLARD et al. 2012; DEVICTOR et al. 2012). Although not fully understood, some authors (e.g., HOF et al. 2011) assume synergistic effects between both processes could lead to an even more dramatic loss of biodiversity than predicted by studies, focusing on the effects of climate change alone (PARMESAN & YOHE 2003; THOMAS et al. 2004). Habitat loss and fragmentation might have serious consequences on demographic dynamics (FAHRING 2003), metapopulation structure (HANSKI 1998) and the genetic setup of populations (TEMPLETON et al. 1990; KEYGHOBADI 2007) by hampering the exchange of individuals between populations. This may lead to a loss of genetic variation (e.g., HABEL & SCHMITT 2012), potentially resulting in an increase of inbreeding depression (e.g., ANDERSEN et al. 2004; ZACHOS et al. 2007) and can ultimately threaten isolated populations with extinction (e.g., PETTERSON 1985). Therefore, detailed information on how populations are connected in the landscape is pivotal in guiding more effective and sustainable conservation measures.

Even though the importance of habitat connectivity has been recognized by both, researchers and nature conservationists (HALE et al. 2001; GILBERT-NORTON et al. 2010), habitat loss is still accelerating as a consequence of human activities across different spatial scales and is a major threat for biodiversity (FISCHER & LINDENMAYER 2007). Paying special attention to habitat connectivity during the planning process can help safeguard the ecological coherence (*sensu* Habitat Directive; COUNCIL OF THE EUROPEAN COMMISSION 1992) of an entire region and assist to avoid negative cumulative effects that might derive from different planning efforts in the same region (MANDELIK et al. 2005; THERIVEL & ROSS 2007; CANTER & ROSS 2010; DUINKER et al. 2013). Even though Environmental Impact Assessments (EIAs) aim to assess such negative environmental effects from infrastructure and other developments, an evaluation of connective elements is often neglected (GENELETTI 2006). While high standards regarding the legal basis for EIAs are already realized in many countries, their application and implementation pose significant challenges. These are due to time and financial constraints during EIA preparation, which are often accompanied by controversial political and public debates (CALDWELL 1991; DICKERSON & MONTGOMERY 1993; DE SMEDT 2010). As a consequence, it is hardly ever possible to

provide enough resources for surveys that sufficiently expand the target region beyond the finite area implemented in an EIA, which allows for an assessment of potential connectivity between populations of species of special conservation concern. In most cases, planned developments might affect smaller fragments of a previously larger, interconnected population (hereafter called the local population) or even just connective elements between permanently colonized habitat patches. For planning offices who normally conduct EIAs for specific developments, identifying or bounding the local population during the evaluation process of the affected habitat fragments therefore remains a great challenge.

Over the past decades, we have witnessed a tremendous increase in tools and environmental datasets that can support EIA procedures. These include geographic information systems (GIS) which have become increasingly important as a useful tool in environmental and urban planning for more than three decades now (SCHALLER 1990; MAGUIRE 1991; BURROUGH & MCDONNELL 1998; MORRIS & THERIVEL 2001). Today, GIS techniques have become crucial to visualize mapping results of EIAs and the underlying structural measures and allows for the integration of metapopulation theory (HANSKI 1994; 1998) into applications useful for conservation and environmental planning (NICHOLSON & OVASKAINEN 2009). A further consequence to the spread of GIS techniques is that the decision-making process for many more aspects in conservation is becoming more and more spatially explicit, such as the design of reserve networks (WILSON et al. 2009) or species-specific conservation management (e.g., RHODES et al. 2006; RÖDDER et al. 2010). Species distribution models (SDMs) have emerged as one of these new spatially explicit tools. Originally developed to work on biogeography-related questions on a macro-ecological scale, they have since been applied in a wide range of ecological disciplines (FRANKLIN 2009; PETERSON et al. 2011). Despite this frequent use in many disciplines, including conservation biology, there are few academic studies that give special emphasis to the conservation decision process (GUISAN et al. 2013) and for EIAs in particular (GONTIER 2006). Due to this lack of scientific guidance on how novel GIS-based techniques (including SDMs) could contribute to applied biological conservation, while considering their limits and methodological challenges (POSSINGHAM et al. 2001; ADDISON et al. 2013; GUISAN et al. 2013), confident use by non-experts is hard to realize (ADDISON et al. 2013, but see GUILLERA-ARROITA et al. 2015). Taking this into account, we aim here to provide guidance for the use of SDM techniques, in

combination with fine-grained remote sensing data and connectivity models, to assess the potential connectivity of habitat fragments in highly specialized species with a strong dependence on habitat structure.

Connectivity models are another set of tools that have emerged from, or with the help of, GIS applications and benefit from the same developments in theory, data availability, and computer power over the past decades (e.g., HANSKI 1994; MOILANEN & NIEMINEN 2002; MCRAE 2008; VOGT et al. 2009; LAITA et al. 2011; MIMET et al. 2013). Connectivity is generally seen as species-specific as it depends on the behavior, habitat preference, and dispersal propensity of the focal species (JOHNSON & GAINES 1985). A useful metric of connectivity for manager guidance thus needs to make a very accurate estimation of the species-environment relationships under consideration of the afore mentioned species traits (FAGAN & CALABRESE 2006). Connectivity can be hereby broadly categorized into two main categories: structural and functional connectivity (CROOKS & SANJAYAN 2006). The former strictly focus on the spatial arrangement of landscape elements in the landscape matrix, while the latter incorporates some additional information on the species' movement either in direct (actual connectivity) or indirect (potential connectivity) form (FAGAN & CALABRESE 2006). It is really important to make these distinctions as data requirements differ and by this, the informational content a connectivity model can provide to a manager as well.

The combination of species distribution models, connectivity models and the underlying fine-scaled environmental datasets into a single framework has several advantages in the spatially-explicit assessment of population connectivity in matrix-sensitive species (i.e., species' movement responses functionally depend on the structure of the habitat matrix, cf. IMS 1995). Aside from a high applicability of the single approaches due to already available and easy to handle programs, the main advantage is that species-specific information on landscape-related habitat suitability can be combined with an objective parameterization of resistance values—two key aspects that typically lack in the construction of resistance surfaces (i.e. a GIS-raster of a hypothesized relationship of certain landscape parameters to species-specific connectivity; see SPEAR et al. 2010 for a discussion). Therefore, we recommend the use of SDMs as the first step of a two-step framework together with connectivity models and refer to this framework in the following as a potential connectivity model (Fig. 5.1; PCM). The PCM framework offers the possibility to quantify potential

dispersal corridors in matrix-sensitive species, where structural connectivity is highly similar to its respective functional (potential) connectivity (CROOKS & SANJAYAN 2006). Such a framework provides a valuable tool for environmental and planning agencies, as well as for non-governmental planning offices. To our knowledge, there is no hands-on guidance available on how to use the different approaches and data together in a PCM that allows us to quantify the importance of a specific site as connectivity habitat for a species of interest using remote sensing data (for a discussion on habitat models in EIAs in general, see GONTIER et al. 2010).
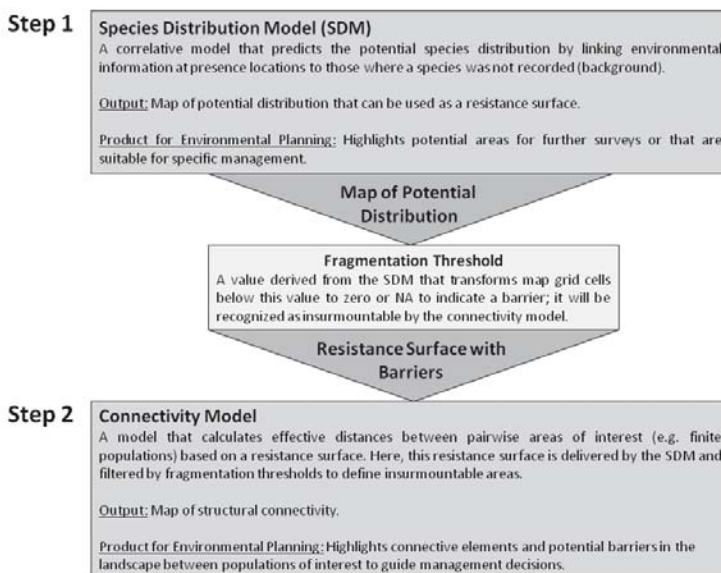

Figure 5.1: Two-step conceptual framework for performing potential connectivity models (PCM). The resistance surface generated within the SDM part of the PCM (Step 1) can also be used as a map of potential occurrence of the focal taxon for future assessments. Finally, within the connectivity model part of the PCM (Step 2), the resistance surface (transformed by the fragmentation threshold) is used to generate maps of structural connectivity for the focal taxon within a specific region. The use of different fragmentation thresholds is recommended to assess the reliability of potential corridors and the strength of barriers of isolated populations

In this study, we illustrate the application of fine-scale PCMs as a possible environmental planning tool using the sand lizard (*Lacerta agilis* Linnaeus, 1758), which is of high conservation concern, as a case study. The sand lizard is a rather common species in central Europe (AGASYAN et al. 2010) but suffers from population decline—particularly caused by increased habitat loss and fragmentation (BERGLIND

2000; ELLWANGER 2004). Consequently, it has become recognized as a threatened species and is protected under the EU Habitats Directive (92/43/EEC; ELLWANGER 2004), being listed in Annex IV as a species of community interest. Sand lizards are sensitive to fine-scale habitat features and often occupy ecotones or secondary habitats such as railway or road embankments (GLANDT & BISCHOFF 1988) and can often be considered having a classical metapopulation structure comprising interlinked habitat patches of different size and quality (BERGLIND 2004). It has been highlighted, that railways can act as an ideal corridor between suitable habitat patches (BLANKE 1999), whereas highways mirrored by noise walls may act as an insurmountable barrier for successful inter-population connectivity in this species (BLANKE 2010). These characteristics make the sand lizard a highly matrix-sensitive species. Increasing habitat loss of remnant populations—as a result of anthropogenic development of the landscape (particularly in rural areas) —make this species an ideal candidate organism for connectivity assessments. We evaluate the landscape connectivity amongst different sand lizard populations inhabiting a strongly urbanized region in Western Germany and are subject to varying fragmentation intensities and thus metapopulation dynamics. In particular, we conducted standardized surveys and sample high resolution occurrence records to generate a map of potential distribution which could be used (1) as prior information for future mapping efforts of sand lizard populations, and (2) for the evaluation of potential corridors, highlighting the importance of spatially explicit linkages of connective habitats between well-known populations.

Material and methods

Study area and data sampling

The study area comprises over 400 km², covering the city of Cologne and immediate surroundings, located in Western Germany (50.9°N, 7.0°E). Cologne is Germany's fourth-largest city and is located within the Rhine-Ruhr Metropolitan Area. Geographically, the study region can be described as a lowland area, with an altitudinal range between 35 and 118 m a.s.l.. The area is surrounded by more mountainous areas (Rhenish Uplands in the south, the High Fens and Eifel in the west, and the Bergisches Land in the east) while it is connected to other lowland areas in the north. The Rhine River divides the study region into a western and eastern part. The area has a long tradition of human land use and has been used for

settlements and agriculture for several thousands of years. This has led to a patchy landscape structure of settlements, arable lands, meadows, shrubs and forests in its surroundings, as well as densely populated areas intersected by fallows, parks and gardens within the city of Cologne.

Building on the results of a preliminary survey with the objective of spotting sand lizard populations and identifying suitable habitat patches, we selected 30 study sites within the area, covering all known local populations within the city of Cologne, and further sites of high structural suitability where existence was so far unconfirmed. Between May and September 2011, each site was surveyed for 60 minutes on five different dates, under favorable weather conditions, along standardized transects with a length of approximately 250 m, following the guidelines of ELLWANGER (2004). The location of each sand lizard sighting was accurately measured using a GPS device (Garmin Etrex Vista HCx), resulting in a total of 1,204 occurrence locations of 22 populations (no sand lizard populations were detected at eight of the sites). Condition status of each population was evaluated following a standardized ABC evaluation scheme for monitoring species after Art. 11 and 17 of the Habitat Directive in Germany (ELLWANGER 2004; SCHNITTER et al. 2006; LANUV NRW 2010). This allows for an easy, transparent and comparable evaluation of the species' condition status by allocating classes A (excellent), B (good) or C (poor) for different aspects, such as population status, habitat quality and threats, as well as a summary classification for the whole population. For example, an excellent population (class A) is characterized by the sighting of > 20 individuals per hour of all ages and sexes found during the visits along a 250 m transect (ELLWANGER 2004), a habitat of superior quality with a fine-scale structuring and a close connection to neighboring populations within a 500 m range as well as less risk for threats such as presence of feral cats, no (or few) streets or paths as well as > 1,000 m to the next urban areas. In contrast, a poor population (class C) is characterized by less than 10 individuals per hour without any young or subadult individuals, a habitat of low structural quality without adequate places for reproduction, neighboring populations >1 kilometer apart and severe threats such as cats, many paths or streets and a close distance to urbanized areas. Class B would be located in between A and C in its respective conditions.

Satellite data

Fine-scale satellite data was obtained from the NASA Landsat 5-TM satellite archive via the USGS Global Visualization Viewer (http://glovis.usgs.gov/; accessed on September 10th, 2011). We obtained three nearly cloud-free Landsat 5 scenes acquired on August 4th, 2009, June 4th, 2010, and October, 10th 2010, with a grain size of 30 m x 30 m. The scenes were selected based to cover several months during the main activity stages of the sand lizard, which ranges from April to October including the main season of dispersal of the offspring (August – October). This allows us to account for phenological changes in vegetation throughout the activity season which are important to characterize the sand lizard's habitat (GLANDT & BISCHOFF 1988). To minimize possible confounding effects and artifacts of the scenes due to past developments, we focus on images that were captured not more than two years prior our sampling. The scenes covered the southern part of Northrhine-Westphalia, including southerly adjacent parts of Rhineland-Palatinate. All datasets were radiometrically corrected using the Empirical Line Correction method (ROBERTS et al. 1985) as implemented in ENVI version 4.5 (ITT 2008), based on bright (urban) and dark (water) reference spectra, extracted from the respective images. Each scene comprised of seven raw spectral bands, each representing a special part of the electromagnetic spectrum. From the spectral bands 1-5 and 7, we calculated a several spectral indices, namely the Normalized Difference Vegetation Index (NDVI) as well as greenness, brightness, and moisture according to the Tasseled Cap Transformation (CRIST & CICONE 1984). Furthermore, effective at-satellite temperature was obtained from spectral radiance values of band 6 using the Landsat 5-TM Thermal Band Calibration Constants (NASA, 2002). Since multi-collinearity among the predictors hampers the interpretability of species-environment relationships (HEIKKINEN et al. 2006; DORMANN et al. 2013), we estimated the pairwise cross-correlation among the 33 remotely-sensed environmental layers (including 6 bands and 5 indices for 3 time steps). We retained 18 low intercorrelated ($R^2 < 0.75$) predictors entering the SDM, which we assumed to be best suited for characterizing the micro habitats of sand lizards in terms of vegetation structure, density and water stress, as well as temperature (see also GLANDT & BISCHOFF 1988). We thus did not give a priori favor to calculated indices over raw bands as raw bands might include important variation that might get lost in the tasseled cap transformation. Table 5.1 shows the used bands and gives an ecological explanation of their meaning.

Table 5.1: Details of the spectral bands covered by Landsat and indices calculated based upon them. Variables finally included into the SDM after accounting for multi-collinearity are marked with an *x*.

Band	Wavelengths	Ecological meaning and application	Date of scene		
			Aug 4th 2009	Jun 4th 2010	Oct 10th 2010
1 - blue	450-520 nm	Characterization of vegetation types and water	x	x	x
2 - green	530-610 nm	Reflectance of photosynthetic active vegetation			
3 - red	630-690 nm	Characterization of plant species and soil types			
4 - NIR$_a$	700-1,300 nm	Suitable for determining vegetation age and health	x	x	x
5 - MIR-1$_b$	1,570-1,780 nm	Detection of snow, clouds, bare ground and vegetation under water stress	x	x	x
7 - MIR-2	2,100-2,350 nm	Characterization of geology and water bodies	x	x	x
6 - TIR$_c$	10,400-12,500 nm	Temperature measurements	x	x	x
Index	calculation				
NDVI	(NIR-red)/(NIR+red)	Landuse and vegetation density	x	x	x
greenness brightness wetness	Tasseled Cap Transformation, involving bands 1-5 & 7	comparable to a principal component analysis to transform correlated bands into orthogonal axes			

$_a$ NIR = Near Infrared; $_b$ MIR = Middle Infrared; $_c$ TIR = Thermal Infrared

Potential Connectivity Model

We accomplished the PCM in a two-step procedure, where we first predicted potential habitat suitability of sand lizards using an SDM approach. In the second step, the habitat suitability layer was transformed by two different fragmentation thresholds and used as resistance surfaces afterwards to compute the PCM. The conceptual design of this PCM framework is illustrated in Fig. 5.1, including the outcome of the analysis used for planning purposes.

Species distribution model

The basic concept behind the SDM is the prediction of environmental suitability by fitting spatially explicit information on species occurrence with the environmental conditions of a certain study area by using a predictive model (FRANKLIN 2009). A range of methods can be used to fit those models, even if the demands on input data and the weighting of environmental predictors differ among the approaches

(FRANKLIN 2009; PETERSON et al. 2011). For SDM development, we used the open source software, MAXENT 3.3.3e (PHILLIPS et al. 2006; PHILLIPS & DUDÍK 2008; ELITH et al. 2011), which has frequently outperformed other approaches, even under difficult circumstances (e.g., ELITH et al. 2006; HERNANDEZ et al. 2006; WISZ et al. 2008). MAXENT is a method focused on presence-only data and contrasts the environmental conditions at the presence records to a set of background locations where presence is unknown (i.e., background points; a detailed explanation of this method relevant for users is given in ELITH et al. 2011 and MEROW et al. 2013). Given our highly standardized sampling scheme including a high coverage of the majority of populations within the study area we used the entire set of records (n = 1,204) to account for different population sizes at the certain patches, which was mentioned to be an ideal prerequisite in presence-only models (FITHIAN & HASTIE 2013; MEROW et al. 2013). We randomly selected 10,000 background records from a rectangular area surrounding the city of Cologne, as the species potentially inhabits the whole region. We applied the standard settings of Maxent with a logistic output format, randomly splitting the entire set of species records in a bootstrap approach into 70% used for SDM training, and 30% for testing. This procedure was repeated 100 times and the average prediction per grid cell was used for further processing. The resulting map of potential distribution can be used as a resistance surface, were high values along the logistic distribution indicate low resistance after accounting for barriers (i.e. applying fragmentation thresholds, see Fig. 5.1 and next section), to calculate effective resistances between the investigated populations.

Fragmentation thresholds

To assess the sensitivity of the PCM, we modified the resistance surface based on two different fragmentation thresholds. Values of the resistance surface below the specific fragmentation threshold were set as absolute barriers for the connectivity model (see next section), whereas the other values remain as they are (i.e., bounded between the applied fragmentation threshold and 1). This is a crucial step in evaluating the sensitivity of the potential corridors, as a continuous surface without absolute barriers will lead to unrealistic potential movement paths in the landscape (e.g., the connectivity model might mistakenly connect patches across constructed areas or large water surfaces with very low suitability values). By comparing a more sensitive threshold against a more conservative one, regions of stable connective

predictions could be classified with a higher priority for planning issues, rather than regions where connective predictions are fluctuating. In turn, areas of high fluctuation in corridor predictability could be used for targeted compensation or restoration actions. In the selection of the two fragmentation thresholds we choose two different criteria, one focusing on the underlying occurrence records used to compute the SDM, and another based on the fitted logistic function of the SDM, to tackle different sources of uncertainty. In the former, we assume that 5% of the records used to build the SDM were situated at the edge of the species' source habitat (i.e., located close to the edge of the habitat patch, where the environmental information of the respective grid cell might be strongly influenced by surrounding unsuitable habitat) or even outside of it. This threshold (in the following referred to as 5th percentile occurrence threshold) highlights only those regions with strong structural connectivity between populations and can be seen rather sensitive. We defined the second threshold as the relative probability of habitat suitability at an occurrence record that had the next largest resistance value, compared to the one-sided 95% confidence limit of the logistic distribution (i.e., a value > 0.05 of the logistic distribution; in the following referred to as 5% logistic threshold). In our case, the latter threshold matches the logistic model output at bridges crossing the Rhine River, a major natural barrier in our study area. In consequence, the 5% logistic threshold gives a stronger emphasis to areas with a weaker structural connectivity and can be seen as conservative in comparison to the 5th percentile occurrence threshold. Although habitat suitability might be low, these habitat patches can still serve as stepping stones, providing a connection to other potential populations not discovered in this assessment.

Connectivity model

Connectivity models allow the assessment of ecological coherence among locations of a given resistance surface by identifying barriers or corridors of functional exchange (e.g. in terms of individuals or genotypes). These tools become increasingly available and are of high relevance for conservation decision-making and environmental planning (CROOKS & SANJAYAN 2006). Approaches that consider multiple paths across the whole landscape add great value to our understanding of habitat connectivity compared to the more classical approaches such as least-cost path models, which focus on a single habitat corridor that minimizes the costs

between two sites (DRIEZEN et al. 2007; MCRAE & BEIER 2007; SAWYER et al. 2011). Among those approaches, connectivity measures based on electrical circuit theory are gaining much attraction in situations where random walk can be assumed (DOYLE & SNELL 1984; CHANDRA et al. 1997; MCRAE et al. 2008). This concept has been successfully shown to outperform other connectivity measures in a landscape-genetic framework (MCRAE & BEIER 2007). A detailed ecological description of connectivity measures underlying the circuit theoretic framework can be found in MCRAE et al. (2008). Briefly, following Ohm's law, circuit theory predicts the current flow from a set of nodes (i.e., grid cells of a two-dimensional GIS raster) along resistors (i.e., functional connections between the nodes that conduct current). The higher the resistance at the resistors, the lower the current flow is between the nodes. Additionally, both number and spatial configuration of the resistors influence current flow. The effective resistance (measured in ohm) can thus be seen as a measure of isolation between pairs of cells (for instance the isolation between populations or individuals) in a raster grid representing the landscape of interest. From this, this concept is similar to the ecological concept of effective distances, but in this case, measured by incorporating alternative pathways rather than a single least cost path.

For this purpose, CIRCUITSCAPE 3.5.4 (MCRAE & BEIER 2007; MCRAE et al. 2008) was used. In the Circuitscape analyses, a pairwise connection scheme was applied based on focal regions defined by the 22 surveyed sand lizard populations within the study area. Focal regions represent a lumped set of nodes where the species was found and that is not intersected by the surrounding habitat matrix. Grid cell connections were allowed in eight directions (i.e., including adjacent nodes in horizontal or vertical directions, as well as diagonal neighbor nodes; Queen's case). These settings were applied to the analysis of both resistance surfaces modified by the respective fragmentation thresholds.

Results

Estimated condition status of Colognes' sand lizard populations based on field observations

Following the recommendations of SCHNITTER et al. (2006) for ascertaining the condition status of sand lizard populations based on the count frequency of individuals observed along a transect, five of the 22 investigated populations were considered to be residing in excellent conditions (i.e., > 20 individuals found). Furthermore, nine populations were estimated to be in good conditions (i.e., 10 – 20 individuals found), while the remaining eight populations need to be considered as residing in poor or bad conditions (i.e., < 10 individuals found; Table 5.2). Also taking into account the general habitat conditions and recent threat factors (LANUV NRW 2010), the same five investigated lizard populations were assessed as status A (excellent preservation status), whereas eleven populations were assigned to status B (good preservation status). The remaining six populations were considered to reside in status C (poor to bad preservation status; Table 5.2).

Distribution of potential habitats

The performance of the SDM was excellent, with mean AUC_{test} of 0.899 (sd ± 0.006). Temperature-related variables of the satellite data acquired in August 2009 and June 2010 had, on average, the highest variable contribution (20.7 % and 18.3 %, respectively) followed by the middle-infrared-1 layer of June 2010 (15.0 %; Table 5.3). These predictors highlighted typically dry and hot sites as key habitats for this species, which is known to be of high importance for this species (GLANDT & BISCHOFF 1988). This finding is further supported by our field data that highlight the amount of dead wood, open-land vegetation, railway sidings, as well as diverse materials of anthropogenic origin (i.e., garden waste or demolition materials), as typical habitat features of adult sand lizards at the study plots. As derived from the SDM, the potential distribution of sand lizards in Cologne is increasingly patchy in the more central und urbanized parts of the city (Fig. 5.2a). Protected heath- and shrubland, as well as industrial wastelands, may therefore serve as the best potential habitats for sand lizards in this area. Nevertheless, habitats exposed to a strong anthropogenic influence such as the border areas of surface mining regions, railways and their

peripheries, as well as the widespread garden plots in suburban zones of Cologne, were predicted to provide suitable habitats for sand lizards. According to our modeling results, the highly urbanized area on the western side of the Rhine River, including the city centre, does not provide any potential habitats. In contrast, the eastern parts of the city and the more suburban western parts may provide potential habitats of high quality, which was also noted during the field surveys in 2011 (Nekum pers. obs.).

Table 5.2: Condition status of the investigated sand lizard populations in Cologne in 2011, following SCHNITTER et al. (2006). Site numbers correspond to those highlighted in Fig. 5.2. Classes: A = excellent, B = good, C = poor.

Site	Maximum abundance per day	Quality Class			
		Population	Habitat	Threats	Overall
1 - Bayer	7	C	B	B	B
2 - Knobw	21	A	A	B	A
3 - Horn	9	C	C	C	C
4 - Duenn	13	B	B	B	B
5 - Dellh	27	A	A	B	A
6 - Scha	7	C	B	B	B
7 - Poho	5	C	C	C	C
8 - Rad	4	C	C	C	C
9 - Joli	16	B	B	B	B
10 - Grem	12	B	B	B	B
11 - Imlue	2	C	C	C	C
12 - Leih	11	B	B	C	B
13 - WH08	29	A	A	A	A
14 - WH06	17	B	A	B	B
15 - WH05	11	B	B	B	B
16 - WH04	21	A	A	A	A
17 - WH01	28	A	A	B	A
18 - WH07	15	B	A	B	B
19 - WH02	12	B	B	B	B
20 - WH03	13	B	A	B	B
21 - Boeck	3	C	C	C	C
22 - S-Aue	2	C	B	C	C

Predicted connectivity between populations

The fragmentation thresholds of our models were 0.131 for the more sensitive 5th percentile occurrence threshold and 0.071 for the more conservative 5% logistic threshold. Depending on the fragmentation threshold applied, two notably different scenarios of the sand lizards' inter-population connectivity could be postulated for

predicting different proportions of the study area as suitable habitat (Fig. 5.2a). Figures 5.2b and 5.2c show the differences between the investigated populations for a detailed area located in the northeastern part of the city when applying the two different fragmentation thresholds. Direct comparisons highlight: (1) a conservative connectivity network between populations one, two and four; (2) a very sensitive connectivity network towards populations three and five; and (3) a strong isolation under both thresholds for population six.

Discussion

Today's practice in urban and environmental planning and management often lacks quantitative assessments of potential corridors that connect populations of species with a high conservation concern. Herein, we introduced a PCM based on fine-scale multispectral satellite data to assess the potential connectivity using sand lizards as a case study.

Applicability of the approach

By using different fragmentation thresholds as reliability measures of the potential corridors (ANDRÉN 1994; see also METZGER & DÉCAMPS 1997), we were able to highlight areas of strong connectivity, persistent isolation or of unstable connective networks (Fig. 5.2 b,c) with different implications for planning purposes and metapopulation dynamics. In particular, populations one, two and four appear to be located within a reasonably stable landscape matrix with structural elements connecting the populations into a viable metapopulation network, irrespective of the fragmentation threshold used. This conservative connectivity matrix should be preserved and considered when planning projects in this area become acute (i.e., by safeguarding connective elements). Due to the spatial configuration of available habitat patches, along with the (effective) distance among them, stochastic extinction events at certain patches can be balanced by migration events within a larger interconnected metapopulation (HANSKI 1994; MOILANEN & HANSKI 1998) which might be also beneficial under expected climate change (NICHOLSON & OVASKAINEN 2009). In contrast, population six showed a strong and consistent isolation from all other populations in this area for both threshold scenarios. Here, a closer look at the viability and genetic setup of the population would be beneficial to finally evaluate its

degree of threat. It is likely that, due to the strong isolation, the population might face a high extinction risk in the upcoming generations that are not yet apparent, due to 'nonequilibrium metapopulation dynamics' (*sensu* HANSKI et al. 1996) that reflect a situation where past habitat destructions will lead to future population extinctions (TILMAN et al. 1994). If necessary, efforts such as translocations from nearby populations or the establishment of novel connective elements could enhance the viability of this population, or its recolonization after local extinction. Finally, a sensitive connective network could be quantified between population three and five, with the stable connection network involving populations one, two and four, as mentioned earlier. Since the geographic distance exceeds the known dispersal distance of the sand lizard by several hundreds of meters, it should be unlikely that a direct exchange is realized between those patches. In addition, as the area is well-known and strongly urbanized, further connective populations that could act as stepping stones are very unlikely. Consequently, there is a low risk for further fragmentation of those populations when developments become realized in those areas. In turn, these potential linkage areas could be used for forced compensatory measures to restore habitat quality (e.g., along railway embankments), leading to a better ecological coherence through the establishment of new populations, or an increase in the size of already existing populations.

Comparing the findings obtained from the PCM with the estimated condition status based on a standardized and transparent mapping scheme for the sand lizard illustrates the additional information that can be extracted from PCMs. Based on this, it is not necessary that well connected populations are also characterized by the highest overall condition status, as seen in population one and four, which are embedded in a stable connective network but achieved an overall condition status of 'B'. That is because the extent of the sites where individuals were found are rather small and consequently their carrying capacities are low. However, the strong connections between these sites with site two indicate a local population of a much better condition status that can facilitate local extinction events by migration from neighboring patches (see above). In turn, the strongly isolated population six also showed a condition status of intermediate level 'B'. As before, the condition status mainly focuses on habitat conditions at the site. In combination with the PCM, it becomes obvious that the condition status alone is insufficient to describe the situation adequately or is even misleading, as the high isolation could be problematic

for the persistence of this population in the future. The examples presented here highlight the benefits of additional information for a focal species that may complement EIAs and other conservation-relevant decision-making, and extend its scope to a broader perspective. We therefore strongly recommend the application of different fragmentation thresholds for PCMs to achieve a more dynamic perspective of structural elements in the landscape.
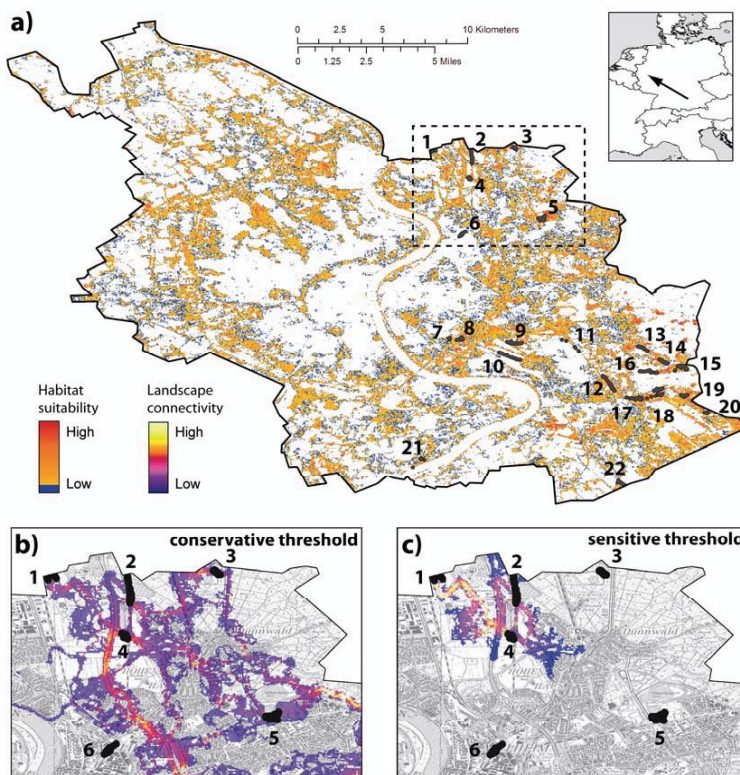

Figure 5.2: Potential distribution (a) and connectivity (b & c) of the sand lizard (*Lacerta agilis*) in the city of Cologne. The upper panel shows the predicted habitat suitability, where blue color highlights the value range between the two fragmentation thresholds used in this study. Non-colored regions were below the conservative 5% logistic threshold. The lower panel shows the structural connectivity for a snapshot area among focal populations (plotted as dark grey areas; indexed as in Table 2) in the northeast of the city (b) for the conservative 5% logistic threshold (0.071) and (c) for the sensitive 5th percentile occurrence threshold (0.131). The use of different fragmentation thresholds helps identify either conservative (populations one, two, four) as well as sensitive (populations three, five) corridor networks and highlights populations remaining in complete isolation (population six).

The successful exchange of individuals between populations, however, also depends on the existence of additional populations that may be highlighted by the

habitat suitability map. Due to the restricted dispersal propensity of our focal species, structural connective elements may become irrelevant when existing stepping stones (i.e., additional populations) are missing, which would ensure the ecological coherence in the metapopulation. Therefore, the first step is to assess the occurrence of potential additional populations identified by the habitat suitability map. Depending on the large distance among the different populations, we consider the potential corridors important for inter-population exchange in the sand lizard example.

Table 5.3: Variable importance as measured with three different procedures in Maxent. For each measure, the mean and the respective sd is shown. Values of the most important variables in either measure are highlighted in bold. Variable names are coded as follows for *month_year_spectral band/index* as denoted in Table 5.1.

	Variable contribution		permutation importance		Jackknife tests of variable importance			
					AUC_{test} without ...		AUC_{test} with only ...	
10_10_blue	0.55	0.320	1.05	0.446	0.898	0.006	0.634	0.013
10_10_MIR-1	5.17	1.264	6.87	1.387	0.897	0.006	0.679	0.013
10_10_MIR-2	0.77	0.303	3.37	1.179	0.897	0.006	0.611	0.013
10_10_NDVI	0.96	0.646	0.98	0.637	0.899	0.006	0.688	0.013
10_10_NIR	2.12	1.035	2.49	0.951	0.899	0.006	0.693	0.012
10_10_TIR	5.85	0.936	7.15	1.629	0.896	0.006	0.682	0.012
6_10_blue	1.03	0.520	2.11	0.937	0.899	0.006	0.659	0.012
6_10_MIR-1	**14.98**	**2.106**	**17.56**	**3.634**	0.896	0.006	0.696	0.012
6_10_MIR-2	2.22	1.658	3.66	1.464	0.898	0.006	0.655	0.013
6_10_NDVI	6.29	2.078	4.18	1.531	0.898	0.006	0.709	0.012
6_10_NIR	5.88	1.442	6.97	1.821	0.897	0.006	0.699	0.012
6_10_TIR	**18.29**	**2.945**	**15.01**	**2.572**	0.893	0.006	**0.757**	**0.011**
8_09_blue	4.60	1.294	5.09	1.287	0.897	0.006	0.685	0.011
8_09_MIR-1	2.50	0.667	2.58	0.946	0.898	0.006	0.682	0.012
8_09_MIR-2	2.70	1.099	2.25	0.786	0.898	0.006	0.664	0.011
8_09_NDVI	3.30	1.561	1.56	0.704	0.899	0.006	0.709	0.012
8_09_NIR	2.09	0.791	1.71	0.699	0.899	0.006	0.686	0.011
8_09_TIR	**20.70**	**2.696**	**15.40**	**3.460**	0.896	0.006	**0.761**	**0.011**

A final aspect concerns the vulnerability of the populations due to climate change. Temperature is expected to increase by 1.6-3.8°C in Germany by 2080 (ZEBISCH et al. 2005). As temperature is an inherent factor for sand lizard's distribution, an increase of this magnitude could lead to local extinctions of populations and, consequently, a shift of current local distribution patterns. Reachable neighboring populations are therefore mandatory for a successful persistence of the metapopulation under climate

change. However, this would raise the need for more flexibility in reserve designs and conservation planning as shown for other lizard species (RÖDDER & SCHULTE 2010).

Data requirements and limitations for further applications

The applicability of the approach strongly depends on the species of interest. As mentioned throughout the manuscript, matrix-sensitive species are required for this approach as in these species functional connectivity closely matches structural connectivity and allows a direct link between habitat suitability and landscape connectivity. For instance, birds normally strongly diverge between functional und structural connectivity due to their high mobility and are therefore not suitable to this approach. However, matrix-sensitive species might be ideal surrogates for connectivity (so called umbrella or focal species; LAMBECK 1997; ROBERGE & ANGELSTAM 2004), as management implications based upon such species should also beneficial for other co-occurring species that share similar ecological demands (e.g., VOS et al. 2001) or who are functionally less bounded by the habitat structure, so further habitat will be preserved. Another approach might be to select different suitable species and independently conduct PCMs for each of them and overlay output maps of potential connectivity for a cumulative assessment of connectivity for an entire community of matrix-sensitive species in a specific region that can be used to guide site prioritization for further management. This can be advantageous when EIA studies need to assess a wider range of species in the same area that diverge in habitat demands.

Once a species or a set of species for a connectivity assessment has been chosen, the next step is the selection of appropriate environmental predictors and the compilation of species records. The number and spatial distribution of occurrence records is very important, as the SDM algorithms demand a specific minimum number of locations for model training. The MAXENT algorithm used here has been proven to provide good results, even though the number of occurrence records is low (HERNANDEZ et al. 2006; PEARSON et al. 2007; WISZ et al. 2008). However, the minimum number of species records also depends on the diversity of occupied habitats of the species. SDMs trained with few species records might already provide reasonable results if the target species occupies a narrow ecological niche and thus has very specific habitat demands. The development of an SDM for a generalist

species, however, would require a higher number of species records to cover the full variability of its occupied habitat types.

The selection of suitable predictor variables is a crucial step in SDM development. It has been shown that SDMs perform best based on predictors with a high biological relevance for the target species (RÖDDER et al. 2009; RÖDDER & LÖTTERS 2010). In the sand lizard example, we focused on variables capturing habitat features during the summer months, when the species is reproducing and dispersal is most likely. Here, temperature variables of the summer months June and August contributed most to the model, followed by middle infrared reflectance (MIR-1) in June (Table 5.3), which highlights dry areas and bare grounds (Table 5.1). However, the biological importance of predictors may vary among different taxa and geographic areas.

Our example of the sand lizards in Cologne highlights another issue: the extent to which the interpretation of output maps is ecologically meaningful. In this study, we focused on the assessment of connectivity among populations that occur on the eastern side of the Rhine River, which serves as a natural barrier. As only very few occurrences from the western part of the city were recorded in the field and information about existing populations is therefore largely lacking, assessments of habitat connectivity in this area are highly speculative. PCMs are hence most informative in areas where the majority of existing populations is known and thus available to train the connectivity model. In addition, connectivity assessments ignore populations that are located just outside this area of interest. Consequently, either the outer margins of a particular study site have to be excluded from a quantitative evaluation or additional populations located outside the area of interest have to be included in the analysis.

Conclusion

Despite some limitations, the application of PCMs for matrix-sensitive species of high conservation concern may be a helpful tool to quantify potential connectivity areas that can act as an additional source of information for urban and environmental planning. Adaptations of this method should be easily attainable, depending on the increasing availability of fine-scale environmental data for any matrix-sensitive species (e.g., provided by the RapidEye mission and the prospective launch of the Sentinel series, which will allow assessments on even finer spatial scales) and could

also support metapopulation models (MOILANEN & HANSKI 1998) suitable for conservation planning (NICHOLSON & OVASKAINEN 2009) by including the effective distances among habitat patches as measured by the PCM instead of Euclidean distances (MOILANEN & HANSKI 2006; NICHOLSON & OVASKAINEN 2009). Therefore, we strongly recommend the careful use of this tool in conjunction with conservation-related decision-making procedures such as EIAs. This tool will be a step towards to overcome recent shortcomings in the planning process that mainly emphasize the value of reproduction sites and attach less importance to inter-population connectivity for maintaining healthy and viable local populations.